Contrasting simulated past and future responses of the Amazonian forest to atmospheric change

Sharon A. Cowling^{1*}, Richard A. Betts², Peter M. Cox², Virginia J. Ettwein¹,
Chris D. Jones², Mark A. Maslin¹ and Steven A. Spall²

¹Department of Geography, University College London, 26 Bedford Way, London WC1H 0AP, UK

²Meteorological Office, Fitzroy Road, Exeter, Devon EX1 3PB, UK

Modelling simulations of palaeoclimate and past vegetation form and function can contribute to global change research by constraining predictions of potential earth system responses to future warming, and by providing useful insights into the ecophysiological tolerances and threshold responses of plants to varying degrees of atmospheric change. We contrasted HadCM3LC simulations of Amazonian forest at the last glacial maximum (LGM; 21 kyr ago) and a Younger Dryas-like period (13–12 kyr ago) with predicted responses of future warming to provide estimates of the climatic limits under which the Amazon forest remains relatively stable. Our simulations indicate that despite lower atmospheric CO₂ concentrations and increased aridity during the LGM, Amazonia remains mostly forested, and that the cooling climate of the Younger Dryas-like period in fact causes a trend toward *increased* above-ground carbon balance relative to today. The vegetation feedbacks responsible for maintaining forest integrity in past climates (i.e. decreased evapotranspiration and reduced plant respiration) cannot be maintained into the future. Although elevated atmospheric CO₂ contributes to a positive enhancement of plant carbon and water balance, decreased stomatal conductance and increased plant and soil respiration cause a positive feedback that amplifies localized drying and climate warming. We speculate that the Amazonian forest is currently near its critical resiliency threshold, and that even minor climate warming may be sufficient to promote deleterious feedbacks on forest integrity.

Keywords: Amazon Basin; last glacial maximum; Younger Dryas; palaeovegetation modelling; rainforest resiliency; carbon balance

1. INTRODUCTION

The maximum extent to which the Amazonian forest can be developed for human industry without compromise of rainforest form and function is an issue of much importance and controversy (Nobre *et al.* 1991; Fearnside 2000; Laurance *et al.* 2001; Malhi 2002). Not only does the Amazon forest harbour a great proportion of the world's biological diversity, but perturbations to forest cover can have far-reaching regional and global climate consequences (Cox *et al.* 1999; Douville *et al.* 2000; Pielke *et al.* 2002). The role of vegetation in mediating the exchange of water and carbon between the biosphere and atmosphere is accentuated in the Amazon Basin, primarily owing to its size and high productivity (Richards 1996). Being able to predict the potential fate of the Amazonian rainforest with continued deforestation and potential future warming requires a deepened understanding of the ecophysiological and biophysical responses of tropical rainforests to both natural and anthropogenically induced environmental change.

Predictions of the range of possible responses of tropical rainforest to future scenarios of rising atmospheric CO₂ and global warming can be made using GCMs (Costa & Foley 2000; Cox *et al.* 2000; Levis *et al.* 2000; Zhang *et al.* 2001). Additionally, GCM simulations of past climates and palaeoplant distributions have much to offer (Prentice *et al.* 1998, 2000; de Noblet-Ducoudri *et al.* 2000; Harrison & Prentice 2003). Palaeomodelling research provides opportunities for model validations, for constraining our predictions of potential earth system responses to future warming, and for offering unique insights into the ecophysiological tolerances and threshold responses of tropical forests to varying degrees of atmospheric change.

Vegetation–climate interactions occur over a broad range of spatio-temporal scales, with first principal mechanisms centred on plant carbon and water balance. How vegetation is affected by environmental stimuli can be viewed as a continuum from smaller-scale responses in plant structure such as leaf-area production, to larger-scale modifications of vegetation composition such as species replacements. Being able to identify when a particular climatic catalyst, or combination of catalysts, is likely to cause a shift in vegetation response from simple effects on plant carbon balance to vegetation dieback is of the utmost concern to ecologists and other interested researchers.

*Author and permanent address for correspondence: Department of Geography, University of Toronto, 100 St George Street, Toronto, Ontario, M5S 3G3, Canada (cowling@geog.utoronto.ca).

One contribution of 17 to a Theme Issue 'Tropical forests and global atmospheric change'.

Our objectives in conducting vegetation–climate simulations using the fully coupled earth system model, HadCM3LC, were threefold. (i) To simulate the response of Amazonian forest to past changes in climate such as for long-term cooling during the LGM (21 kyr ago) and for short-term (abrupt) cooling during the YD (12.7–11.6 kyr ago). (ii) To provide an estimate of the climatic limits under which the Amazon Basin has remained predominantly forested. (iii) To investigate under what climatic and biophysical conditions the Amazonian forest becomes destabilized.

Since the HadCM3LC model does not distinguish between evergreen and deciduous (broadleaf) trees, ‘forest’ will be used loosely to refer to both tropical seasonal (dry) and rainforest types. Simulations of the Mid-Holocene climatic optimum are currently being conducted and interpreted by another Hadley-associated laboratory (P. Valdes, personal communication). Therefore, we chose to simulate a YD-like climate to contrast the effects of *long-term* versus *abrupt* climate change on forest processes in the Amazon basin. Because the climatic processes responsible for producing the YD-climate anomaly are still under investigation, we recognize that our simulations are intended to investigate responses of a ‘YD-like’ climate anomaly. This terminology will be used throughout the paper to distinguish sustained LGM climate effects from abrupt climatic changes.

2. METHODS

(a) *HadCM3LC model*

HadCM3LC couples the latest version of the Hadley ocean–atmosphere GCM (HadCM3; Gordon *et al.* 2000) to an ocean (HadOCC; Palmer & Totterdell 2001) and a terrestrial (TRIFFID; Cox 2001) carbon cycle model. It uses a horizontal resolution of 2.5° latitude by 3.75° longitude, and requires the use of flux adjustments (Johns *et al.* 1997). Increasing the sophistication of representation of biological processes within GCMs is the focal point of much recent climate modelling research (Cox *et al.* 2000; Friedlingstein *et al.* 2001; Joos *et al.* 2001). The latest version of the Hadley ocean carbon cycle model, for example, now contains a four-component (nutrient–phytoplankton–zooplankton–detritus) ocean ecosystem model that simulates the effects of light penetration, alkalinity and nutrient availability on biological carbon uptake (Palmer & Totterdell 2001).

TRIFFID, the dynamic global vegetation component of the land surface scheme, MOSES (Cox *et al.* 1999), simulates growth and replacement of vegetation of five functional types: broadleaf tree, needle-leaf tree, C₃ grass, C₄ grass and shrubs. Each modelled grid cell is predicted to contain a combination of functional groups, depending on: (i) climatic impacts on photosynthesis, plant respiration and leaf mortality; (ii) competition for light (i.e. taller trees outcompete shorter grasslands); (iii) competition for water (i.e. according to differences in rooting depth); and (iv) competition for carbon (i.e. shrubs outcompete trees in resource-depleted environments).

An allocation scheme determines the distribution of carbon resources into woody stem, root and leaf components, and is based on empirical allometric relationships (Cox 2001). A hydrological budget distributes precipitation between canopy interception, throughfall, water percolation through four soil layers, and runoff. The most important terrestrial variables in modifying regional climate processes are leaf surface area (i.e. LAI;

m² m⁻²) and stomatal conductance. LAI is estimated from a percentage of whole-plant carbon balance that is allocated to leaf production. Stomatal conductance and photosynthesis are calculated via a coupled leaf-level model (Cox *et al.* 1998).

(b) *Climate scenarios and simulations*

The *control* state of the climate system is derived from an experiment with pre-1850 boundary conditions, thus representing a climate–vegetation system defined by non-anthropogenic influence on atmospheric CO₂ (i.e. ‘potential vegetation’). Atmospheric CO₂ concentration was prescribed at 286 p.p.m.v. for the pre-industrial simulation according to ice-core CO₂ records. Two experiments with HadCM3LC were conducted to examine vegetation interactions with significantly different climates. The first was a simulation of the LGM, and the second an approximate representation of the climate of the YD cold period.

For the LGM simulation, atmospheric CO₂ concentration was prescribed at 200 p.p.m.v. Boundary conditions such as orbital parameters, changes in land area owing to sea-level decrease, and the extent of the ice sheets were also prescribed to be consistent with the LGM period (Hewitt *et al.* 2003; Jones *et al.* 2004). Sea-surface temperature and salinity values from a previous LGM simulation using HadCM3 (Hewitt *et al.* 2003) were used to derive flux adjustments for the HadCM3LC experiment. Vegetation cover was initialized from Wilson & Henderson-Sellers (1985) and simulations were continued until vegetation reached equilibrium.

The YD is a brief cold-climate anomaly occurring mostly in the Northern Hemisphere during the last deglaciation. A pulse of fresh water (glacial melt water) into the North Atlantic is believed to have caused this anomaly via effects on the THC (Broecker *et al.* 1988; Bard *et al.* 1990; Hughen *et al.* 2000). The response and stability of the THC in HadCM3 to both fresh water and anthropogenic forcing have been explored in previous studies (Thorpe *et al.* 2001; Vellinga & Wood 2002; Vellinga *et al.* 2002). These studies show that a single pulse of fresh water in the North Atlantic causes a temporary shut down of the THC and a significant cooling, not just within the region of the North Atlantic, but across most of the Northern Hemisphere. Such climate anomalies are characteristic of reconstructed YD climatology.

For our second simulation, therefore, a single pulse of fresh water was applied to the North Atlantic. Climate and vegetation responded dynamically to this forcing (i.e. the simulation experiment followed a trajectory defined by a transient system response rather than permitted to reach equilibrium). It should be noted that both atmospheric CO₂ concentration and insolation values were kept the same as for our pre-industrial control simulation; thus, this should not be viewed as a fully representative YD simulation, but rather a ‘YD-like’ modelling experiment.

Future climate change simulations using HadCM3LC have been reported and published elsewhere (Cox *et al.* 2000), but have been included in this paper as a point of comparison and as a focus for discussion. Future simulations were conducted using an arbitrary trajectory of atmospheric CO₂–temperature change (IS92a). At the end of the future climate simulation (AD 2100) CO₂ concentration reaches 980 p.p.m.v. (including vegetation–climate feedbacks), with temperatures warmed by *ca.* 5.5 °C (global mean) or 8.5 °C (global mean over land) excluding localized vegetation–climate feedbacks.

Table 1. Key biophysical variables simulated for each of our climate scenarios, pre-1850 (control), the LGM, YD and future global warming (future).

(Variables are temperature (T , °C), precipitation (P , mm d⁻¹), sensible heat flux (H , W m⁻²) and latent heat flux (LE, W m⁻²). Numbers are means.)

variable	control	LGM	YD	future
T	27	25	26	38
P	4.8	4.0	5.0	1.6
H	29.7	28.9	25.4	69.2
LE	98.1	91.5	101.0	34.2

3. RESULTS AND DISCUSSION

(a) Palaeoclimate data-model comparisons

Wherever mean values are reported, averages were calculated on an area of the Amazon Basin defined by 1.25° N and 16.25° S and by 69.375° W and 50.625° W. Key parameters describing the climate and biophysical features of each simulated scenario are presented in table 1. For pre-1850, surface temperatures fall within the range 18–31 °C, with an average basin temperature of 27 °C. Precipitation values were simulated at 4.8 mm d⁻¹, with sensible and latent heat fluxes averaging around 28.9 and 91.5 W m⁻², respectively.

LGM surface temperatures in the Amazon Basin were simulated to decrease by an average of 2 °C, although some regions experienced temperature cooling in the order of 10 °C. YD climate forcing resulted in an average cooling of 1 °C relative to pre-1850. Precipitation averaged 4.0 and 5.0 mm d⁻¹ for LGM and YD scenarios, respectively, with YD simulations showing strong regional trends. Whereas northwest Amazonia is simulated to be drier during the YD relative to pre-1850, the southeast is wetter, rendering an overall basin average that is slightly wetter than today. LGM climate resulted in a greater proportion of solar radiation converted into sensible relative to latent heat compared with pre-1850 (Bowen ratio = 0.32 relative to 0.30, respectively). By contrast, YD palaeoclimate simulations indicate a greater proportion of solar radiation distributed into latent versus sensible heat production (Bowen ratio = 0.25 relative to 0.30).

Modelled YD and LGM climatology are not in stark disagreement with palaeoclimate reconstructions. Alkenone data (e.g. Bard *et al.* 1997; Wolff *et al.* 1998) suggest that LGM tropical sea-surface temperatures were 3 °C cooler than today, whereas CLIMAP (1976, 1981) and our GCM-generated palaeoclimate indicate somewhat less continental cooling in the tropics, in the region of 2 °C. The degree of tropical cooling is contrasted by a variety of different palaeodata sources. Coral-based (Guilderson *et al.* 1994) and foraminifera-based (Mix *et al.* 1999) tropical sea-surface temperature reconstructions and analyses of noble gas concentrations in Brazilian groundwater (Stute *et al.* 1995) show a maximum LGM tropical cooling of 5 °C. Brazilian palynological data suggest a cooling of between 3 and 7 °C (Behling & Negrelle 2001; Behling 2002). Kaolinite oxygen and hydrogen isotopes in palaeosols from the Colombian Bogotá basin suggest an LGM cooling of 5–7 °C (Mora & Pratt 2001). High-altitude ice-core records from the Andes indicate

temperatures up to 12 °C lower during the LGM (Thompson *et al.* 1995, 1998), although this interpretation has since been reassessed to be more in the region of 3 °C (for more details see Pierrehumbert 1999).

More comprehensive syntheses of LGM terrestrial palaeoclimate data by Farrera *et al.* (1999) and Harrison & Prentice (2003) conclude that tropical cooling was in fact far from spatially uniform, even in the lowlands, and therefore large-scale extrapolated interpretations based upon individual sites should be made with caution. In this case, there remain few palaeoclimate data that provide temperature information for the spatial majority of the LGM Amazon Basin.

At the present time, similar syntheses of palaeodata for the YD have yet to be compiled, although it is assumed that the spatial variability of past temperature within the tropics would be of at least a similar nature to the LGM.

Palaeodata-model comparisons aside, we recognize that most GCMs consistently underestimate LGM (and also probably YD) temperatures by at least a third (e.g. P. Valdes, personal communication). If the Hadley GCM has consistently underestimated cold-stage temperatures in the Amazon Basin, this may have implications for the interpretation of modelling results, as previous modelling studies (e.g. Cowling *et al.* 2001) have cited temperature as an important biophysiological control on vegetation. Results produced from this study, therefore, should be considered conservative estimates of environmental change.

Comparison between modelled and reconstructed precipitation is particularly difficult because of the inherent limitations in reconstructing highly spatial variables such as rainfall across such large and diverse watersheds such as the Amazon Basin. Palaeoreconstructions of Amazon River discharge and lake levels support a general reduction in total precipitation as modelled here for the LGM (V. J. Ettwein, unpublished data; Mayle *et al.* 2000; Sifeddine *et al.* 2001). Palaeoecological studies from within the Basin also imply more arid LGM conditions (e.g. Behling 2002; Behling *et al.* 2002; Sifeddine *et al.* 2003; Vélez *et al.* 2003). By contrast, records from northwest Amazonia (Bush *et al.* 2002) and the Peruvian/Bolivian Altiplano (Baker *et al.* 2001a,b) imply wetter conditions at the LGM.

For the YD, lake and ice-core evidence from northern and northwest Amazonia and the Peruvian/Bolivian Altiplano suggest a wetter climate (e.g. Thompson *et al.* 1998; Sylvestre *et al.* 1999; Baker *et al.* 2001a,b; Ledru *et al.* 2001; Bush *et al.* 2002; Sifeddine *et al.* 2003). However, pollen data from sites in southern and southeast Brazil (e.g. Ledru 1993; Behling & Lichte 1996; Behling 2002), as well as larger-scale palaeoreconstructions from the Amazon Fan (V. J. Ettwein, unpublished data; Maslin & Burns 2000) and the Cariaco Basin (Haug *et al.* 2001) suggest increased aridity, in opposition to model simulations. For a more comprehensive review of the palaeodata, see Mayle *et al.* (2004).

Although our Hadley GCM-generated YD-like palaeoclimate displays similar regional trends in precipitation to palaeodata reconstructions, this variability is in an opposing direction. The apparent contradiction between modelled and data-reconstructed YD palaeoprecipitation may demonstrate the importance of tropical insolation in driving convectional (i.e. the ITCZ) precipitation over the Amazon Basin. Our YD-like modelling simulation

Figure 1. Percentage of broadleaf vegetation simulated for (a) the LGM and (b) YD-like palaeoclimate.

incorporates pre-industrial insolation values that are relatively out-of-phase with the YD by approximately half a precessional cycle, and would therefore simulate a more southerly zone of ITCZ-driven precipitation over the Basin relative to that implied by the palaeodata.

(b) *Persistence of the Amazonian rainforest to past changes in climate*

Scarcity of Amazonian palaeovegetation proxy data spanning the last glacial is to blame for over three decades of controversy concerning the integrity of the Amazon rainforest during Pleistocene climate cycles (Colinvaux *et al.* 2000, 2001). In connection with early theories on the origin of high diversity and high endemism in the neotropics, it was once assumed that the Amazonian rainforest disintegrated into small, isolated patches of forest because of (arid-induced) replacement of forest with grassland (Haffer's Forest Refugia Hypothesis; Haffer 1969; Haffer & Prance 2001).

The presence of forest patches ('refugia') in the Amazon Basin during glacial-interglacial cycles is no longer an issue of contention (Colinvaux *et al.* 2000, 2001). A growing number of pollen data indicate the presence of forest across the majority of the lowland basin (Colinvaux *et al.* 1996; Haberle & Maslin 1999; Mayle *et al.* 2000; De Freitas *et al.* 2001; Bush *et al.* 2002). Earlier simulations using biophysical dynamic vegetation models, BIOME3 (Cowling *et al.* 2001) and BIOME4 (Harrison & Prentice 2003), provide further evidence of the likely persistence

Figure 2. Difference in the percentage of C_4 -grass simulated for (a) the LGM and (b) YD-like palaeoclimate. Positive numbers represent an increase in grass percentage in the LGM–YD relative to pre-1850.

of Amazonian forest over Pleistocene climate cycles. It is only in the marginal areas near the outer boundaries of rainforest (i.e. forest–grassland ecotones) that grassland is simulated to replace tree functional types.

Similarly, our simulations using HadCM3LC strongly support the claim that the Amazonian forest remained relatively intact during past cold and dry periods. Both LGM and YD-like climate simulations result in broadleaf tree types dominating much of Amazonia (figure 1). The Hadley earth system model does not distinguish between trees of evergreen and deciduous life histories, and therefore can only identify ecosystems dominated by either forest or grassland. Modelling results indicate an increase in grass dominance mostly in regions near tree–grass ecotones, but widespread proliferation of C_4 grassland within the interior of the basin is not observed (figure 2).

Understanding the degree to which palaeovegetation of the Amazon Basin responded to past changes in climate is relevant for modern-day ecological theory for several reasons. First, the Amazonian forest seems to be surprisingly resilient to relatively large changes in past climate, confirmed by our simulated LGM and YD-like climate scenarios, as well as other independent modelling (Cowling *et al.* 2001; Mayle *et al.* 2004) and palaeodata research (Harrison & Prentice 2003). Rainforest resiliency to environmental change may have a strong basis in principles of plant carbon allocation, in particular,

Figure 3. Simulations of (a) percentage broadleaf cover and (b) C₄ grass under an arbitrary scenario of future climate change (IS92a).

Table 2. Carbon-related variables simulated for each of our climate scenarios, pre-1850 (control), the LGM, YD and future global warming (future).

(Variables are GPP (kg C m⁻² yr⁻¹), NPP (kg C m⁻² yr⁻¹), vegetation carbon (C_v, kg C m⁻²), plant respiration (R_p, kg C m⁻² yr⁻¹), soil respiration (R_s, kg C m⁻² yr⁻¹), and LAI of broadleaf types (LAI_b, m² m⁻²). Numbers are means.)

variable	control	LGM	YD	future
GPP	2.06	1.62	2.13	0.88
NPP	0.84	0.73	0.91	0.20
C _v	13.00	8.00	13.5	2.50
R _p	1.22	0.89	1.22	0.68
R _s	0.87	0.69	0.92	0.31
LAI _b	6.50	5.20	6.70	3.50

strategies that promote carbon conservation in the face of carbon-depleting environmental stresses.

The resiliency of Amazonian forest to past changes in climate is relevant for a second reason, relating to the political framework of deforestation and tropical land-use change in the tropics. Many who seek to provide support for continued deforestation in the Amazon Basin cite the apparent ephemeral nature of the rainforest over geological time (see discussion, Bunyard 2002). Their rationale follows that the forest has fragmented substantially in the past and recovered; therefore it can do so again today and

into the future. Such disturbing myths must be dispelled before they begin.

(c) The role of temperature cooling in promoting tropical forest resiliency

The mechanism underlying tropical forest persistence in past cold periods is not intuitive, and probably lies in the combination of biophysical responses of tropical plants to decreasing temperature. Comparison of simulated carbon-based variables between the LGM and YD-like climate supports the role of cooling in maintaining Amazonian forest (table 2). LGM climate differed from pre-1850 in that it was colder, drier and under the influence of lower atmospheric CO₂ levels (200 p.p.m.v.). Although above-ground (vegetation) carbon balance decreases during the LGM, the decline is not sufficient to promote widespread forest deterioration. The YD-like climate scenario is slightly colder than pre-1850. Even though the latter scenario is simulated for only a brief period, YD-like climate actually results in an *enhanced* above-ground carbon budget relative to pre-1850 controls (table 2).

Because the YD-like climate occurs over a relatively short period (with respect to the lifespan of tropical trees), areas that were dominated by grassland during the LGM remain as grassland during the YD (consistent with Mayle *et al.* 2000). Those areas, however, that remained predominantly tree covered during the LGM experience an enhancement in above-ground carbon following a YD-like climate anomaly. GPP, NPP, vegetation carbon and LAI all indicate a trend toward greater carbon retention and growth of forest during the cooler YD-like period relative to pre-1850 (table 2). This positive enhancement of above-ground carbon balance in forest vegetation following climate cooling would also have occurred in the LGM and thus may also be partly responsible for the maintenance of forest cover during glacial climate cycles.

We suggest that the trend toward increasing above-ground plant carbon in tropical regions during the YD-like cold anomaly is, in part, due to the influence of cooling on biophysical processes such as plant respiration and evapotranspiration. Cooler temperatures cause rates of evapotranspiration to decrease, thus helping to conserve carbon and water resources for plant growth and acclimatory processes. A decrease in total plant respiration (R_p) can also lead to conservation of plant carbon resources.

Plant respiration involves the loss of carbon (energy) to processes necessary in the repair and maintenance of plant tissue (called dark, maintenance or mitochondrial respiration), as well as in the competition between O₂ and CO₂ for active binding sites on Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase), a process called photorespiration. The amount of respiratory carbon allocated to tissue maintenance is related to the total amount of plant tissue requiring maintenance (i.e. total vegetation carbon, C_v; Dewar *et al.* 1999). Rates of photorespiration depend on ambient atmospheric CO₂ concentrations and temperature (Brooks & Farquhar 1985). A decrease in atmospheric CO₂ increases photorespiration, whereas temperature cooling in tropical regions causes a decrease in the rate of photorespiration.

If we assume that the proportion of plant carbon expired during maintenance respiration is related to total

above-ground carbon (C_v) and that this relationship is the same across all climate scenarios, then we can estimate relative changes in the contribution of photorespiration to total plant respiration (R_v) between climate simulations. This is because photorespiration remains unaffected by changes in C_v , responding only to variations in CO_2 and temperature.

$$R_{v\text{-control}}/C_{v\text{-control}} = R_{v\text{-scenario}}/C_{v\text{-scenario}}$$

For the LGM:

$$1.22/13.0 = x/8.0,$$

$$x = 0.75.$$

R_v would equal 0.54 if the contribution of photorespiration to R_v remained the same as in control simulations. However, HadCM3LC simulates an R_v of 0.89, indicating that increased rates of photorespiration following a reduction in atmospheric CO_2 probably influenced total plant respiration.

For the YD-like climate experiment:

$$1.22/13.0 = x/13.5,$$

$$x = 1.27.$$

R_v would equal 1.27 if the contribution of photorespiration to R_v remained the same as in the control. However, HadCM3LC simulates an R_v of 1.22, indicating that reduced rates of photorespiration following tropical climate cooling probably played a part in modifying total plant respiration during YD-like cold-climate anomalies.

(d) *Future warming and forest dieback*

Our simulated responses of Amazon forest to past changes in climate indicate a strong stabilizing relationship between low atmospheric CO_2 , cooler temperatures, above-ground (vegetation) carbon balance and tropical forest integrity. What happens to this relationship when environmental catalysts are reversed, as atmospheric CO_2 levels continue to increase and surface temperatures rise?

Under an arbitrary climate warming scenario (IS92a), Amazonian forest becomes highly unstable (Cox *et al.* 2000); the interior of the Amazon Basin becomes essentially void of vegetation, with only a very small percentage of broadleaf cover and C_4 grass simulated at the outermost edges of the basin (figure 3). All carbon-related variables indicate symptoms of wide-scale forest dieback: NPP is less than 25% of its pre-1850 value and vegetation respiration is depressed because of dramatic reductions in above-ground biomass (2.5 relative to 13 kg C m^{-2} ; table 2).

A critical mechanism promoting destabilization of the Amazon Basin in the future involves vegetation feedbacks on regional climate (Sellers *et al.* 1996; Betts *et al.* 1997, 2000, 2004; Cox *et al.* 2000). With progressively decreasing forest cover as a consequence of greater respiration under warming climate (Amthor 1991), recycling of water in the Amazonian watershed begins to break down, contributing to lower basin-wide precipitation (1.58 relative to 4.8 mm d^{-1} ; table 1). Coupling between vegetation processes (mostly evapotranspiration) and watershed hydrology can be extremely tight, with some regions of the Amazon Basin returning as much as 74% of annual

rainfall to the atmosphere (Sommer *et al.* 2002). Owing to the significant increase in the partitioning of incoming radiation into sensible versus latent heat production under future climate scenarios, surface temperatures soar, reaching, on average, 38°C (table 1).

The contribution of vegetation feedbacks relative to CO_2 climate forcing can be evaluated by comparing predicted Amazonian climate under similar CO_2 -warming scenarios, with and without vegetation–climate feedbacks. Two competing processes involving transpiration can occur under scenarios of elevated atmospheric CO_2 . A decrease in stomatal conductance reduces transpiration; however, increased NPP leads to higher LAI that in turn results in larger surface areas available for transpiration. Comparison of factorial modelling experiments by Betts *et al.* (2004) indicates that the prominent effect on transpiration arises from stomatal responses (not LAI) to rising atmospheric CO_2 . The authors predict that the overall physiological effect of vegetation responses to increased CO_2 is to cause further localized drying. The likelihood that LAI effects are less important than stomatal effects under conditions of increased CO_2 is supported by a metadata analysis of the response of LAI to elevated CO_2 within a variety of tree, crop and herbaceous experimental species (Cowling & Field 2003).

Whereas stomatal functioning probably predominates over LAI-related processes under elevated CO_2 climates, the same cannot be said for past periods of lower CO_2 . Under LGM climate scenarios, LAI has more dominant control of vegetation–climate feedbacks than physiologically based variables (Levis *et al.* 1999). This contradiction serves to highlight the dynamic nature of biosphere–atmosphere feedbacks.

(e) *Tropical forest thresholds and atmospheric change*

In contrasting the modelled influence of past and future atmospheric change on features of the Amazonian forest, we establish the presence of an ecosystem-level resiliency threshold that must be exceeded under future global change. In other words, the combined strengths of positive versus negative feedbacks in past climate scenarios greatly differ from the future, in that future atmospheric change results in strong positive feedbacks promoting enhanced drying and forest dieback. It is critical that this threshold be identified and fully understood to improve our predictions of future forest integrity.

The effects of low atmospheric CO_2 on ecosystem carbon balance are partly compensated by the influence of decreases in temperature on tropical forests, such that a reasonably wide range of low CO_2 and global cooling scenarios can be experienced without the Amazonian forest becoming unstable. By contrast, despite increases in atmospheric CO_2 (which should improve vegetation carbon balance), global warming results in a progressive decline in forest productivity, which in turn leads to further warming and drying climate feedbacks. Of potential limiting environmental controls on tropical forest, precipitation (water balance) is often indicated as pre-eminent in defining rainforest structure and function. We speculate, however, that over the long term (i.e. temporal resolutions greater than 10^3 years) tropical forests such as

the Amazon Basin are equally sensitive to high-temperature anomalies.

Defining the point (threshold) at which tropical ecosystems exceed their capacity for internal/external feedbacks compensating for the deleterious effects of warming on tropical plants (i.e. increased carbon loss due to ecosystem respiration) becomes difficult. We suggest that this threshold exists very near to current climatic (temperature) conditions. A source of supporting evidence can be found in the bulk of eddy-flux data collected to determine whether modern-day tropical forests are sources or sinks of CO₂ to or from the atmosphere (Malhi & Grace 2000; Malhi 2002; Falge *et al.* 2002).

Tropical forests can switch from source to sink (and vice versa) very rapidly (i.e. less than 10 °C) and under relatively minor changes in climate (Tian *et al.* 1998; Prentice & Lloyd 1998). During years of El Niño warming, Amazonian rainforest releases a large flux of CO₂ into the atmosphere, between 0.2 and 0.7 Pg C (Tian *et al.* 1998) or 10–20% of average annual regional productivity (Potter *et al.* 2001). Heightened tree mortality during warmer, drought-prone El Niño years is suggested to contribute to intra-annual fluctuations in biospheric carbon release (Williamson *et al.* 2000; Laurance *et al.* 2001), along with enhanced respiration (Jones *et al.* 2001) and increased fire activity (Keeling *et al.* 1995; Langenfelds *et al.* 2003).

4. CONCLUSION

Our ability to make predictions about the potential fate of the Amazonian rainforest in the near and distant future is strengthened by our understanding of the processes responsible for modifying past tropical forest integrity. Although rising atmospheric CO₂ should enhance tropical ecosystem carbon balance, this gain is more than compensated for by future positive feedback interactions on carbon loss processes. Strategies for maintaining tropical forest stability in the past (i.e. low-temperature effects on evapotranspiration and plant respiration) will not be active in the future. Further research aimed at determining critical thresholds for tropical forest stability is strongly required, and could involve a combination of methods including process-based modelling and manipulation-type experiments (Körner 2004).

S.A.C. was funded by an NERC operating grant. The contributions of R.A.B., P.M.C., C.D.J. and S.A.S. were supported by the UK Department for the Environment, Food and Regional Affairs under contract PECD 7/12/37. The authors thank Colin Prentice, Francis Mayle and Yadvinder Malhi for comments made on earlier drafts of this paper.

REFERENCES

- Amthor, J. S. 1991 Respiration in a future, higher CO₂ world. *Pl. Cell Environ.* **14**, 13–20.
- Baker, P. A., Rigsby, C. A., Seltzer, G. O., Fritz, S. C., Lowenstein, T. K., Bacher, N. P. & Veliz, C. 2001a Tropical climate changes at millennial and orbital timescales on the Bolivian Altiplano. *Nature* **409**, 698–701.
- Baker, P. A., Seltzer, G. O., Fritz, S. C., Dunbar, R. B., Grove, M. J., Tapia, P. M., Cross, S. L., Rowe, H. D. & Broda, J. P. 2001b The history of South American tropical precipitation for the past 25 000 years. *Science* **291**, 640–643.
- Bard, E., Hamelin, B., Fairbanks, R. & Zindler, A. 1990 Calibration of the ¹⁴C timescale over the past 30,000 years using mass spectrometric U-Th ages from Barbados corals. *Nature* **345**, 405–409.
- Bard, E., Rostek, F. & Sonzogni, C. 1997 Interhemispheric synchrony of the last deglaciation inferred from alkenone palaeothermometry. *Nature* **385**, 707–710.
- Behling, H. 2002 South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **177**, 19–27.
- Behling, H. & Lichte, M. 1996 Evidence of dry and cold climatic conditions at glacial times in tropical southeastern Brazil. *Quatern. Res.* **48**, 348–358.
- Behling, H. & Negrelle, R. R. B. 2001 Tropical rain forest and climate dynamics of the Atlantic lowland, southern Brazil, during the Late Quaternary. *Quatern. Res.* **56**, 383–389. (DOI 10.1006/qres.2001.2264.)
- Behling, H., Arz, H. W., Pätzold, J. & Wefer, G. 2002 Late Quaternary vegetational and climate dynamics in southeastern Brazil, inferences from marine cores GeoB 3229-2 and GeoB 3202-1. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **179**, 227–243.
- Betts, R. A., Cox, P. M., Lee, S. E. & Woodward, F. I. 1997 Contrasting physiological and structural vegetation feedbacks in climate change simulations. *Nature* **387**, 796–799.
- Betts, R. A., Cox, P. M. & Woodward, F. I. 2000 Simulated responses of potential vegetation to doubled-CO₂ climate change and feedbacks on near-surface temperature. *Global Ecol. Biogeogr.* **9**, 171–180.
- Betts, R. A., Cox, P. M., Harris, P. P., Huntingford, C. & Jones, C. D. 2004 The role of ecosystem–atmosphere interactions in simulated Amazon forest dieback under global climate warming (In preparation.)
- Broecker, W., Andree, M., Wolffli, W., Oeschger, H., Bonani, G., Kennett, J. & Peteet, D. 1988 The chronology of the last deglaciation: implications to the cause of the Younger Dryas. *Paleoceanography* **3**, 1–19.
- Brooks, A. & Farquhar, G. D. 1985 Effects of temperature on the CO₂/O₂ specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. *Planta* **165**, 397–406.
- Bunyard, P. 2002 Climate and the Amazon: consequences for our planet. *Ecologist* October, 1–11.
- Bush, M. B., Miller, M. C., De Oliveira, P. E. & Colinvaux, P. A. 2002 Orbital-forcing signal in sediments of two Amazonian lakes. *J. Paleolimnol.* **27**, 341–352.
- CLIMAP Project Members 1976 The surface of the ice age earth. *Science* **191**, 1131–1137.
- CLIMAP Project Members 1981 Seasonal reconstruction of the Earth's surface at the last glacial maximum. In *Geological Society of America, chart and map series* 36.
- Colinvaux, P. A., De Oliveira, P. E., Moreno, J. E., Miller, M. C. & Bush, M. B. 1996 A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science* **274**, 85–88.
- Colinvaux, P. A., de Oliveira, P. E. & Bush, M. B. 2000 Amazonian and neotropical plant communities on glacial timescales: the failure of the aridity and refuge hypotheses. *Quatern. Sci. Rev.* **19**, 141–169.
- Colinvaux, P. A., Irion, G., Rasanen, M. E., Bush, M. B. & De Mello, J. A. S. N. 2001 A paradigm to be discarded: geological and paleoecological data falsify the Haffer & Prance refuge hypothesis of Amazonian speciation. *Amazoniana* **16**, 609–646.
- Costa, M. H. & Foley, J. A. 2000 Combined effects of deforestation and doubled atmospheric CO₂ concentrations on the climate of Amazonia. *J. Climate* **13**, 18–34.

- Cowling, S. A. & Field, C. B. 2003 Environmental controls on leaf area production: implications for vegetation and land surface modelling. *Global Biogeochem. Cyc.* **17**, 1007. (DOI 10.1029/2002GB001915.)
- Cowling, S. A., Maslin, M. A. & Sykes, M. T. 2001 Paleovegetation simulations of lowland Amazonia and implications for neotropical allopatry and speciation. *Quatern. Res.* **55**, 140–149.
- Cox, P. M. 2001 Description of the TRIFFID dynamic global vegetation model. Technical note 24, Hadley Centre, UK Meteorological Office.
- Cox, P. M., Huntingford, C. & Harding, R. J. 1998 A canopy conductance and photosynthesis model for use in a GCM land surface scheme. *J. Hydrol.* **213**, 79–94.
- Cox, P. M., Betts, R. A., Bunton, C. B., Essery, R. L. H., Rowntree, P. R. & Smith, J. 1999 The impact of new land surface physics on the GCM simulation of climate and climate sensitivity. *Climate Dynam.* **15**, 183–203.
- Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. & Totterdell, I. J. 2000 Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184–187.
- De Freitas, H. A., Pessenda, L. C. R., Aravena, R., Gouveia, S. E. M., De Souza Ribeiro, A. & Boulet, R. 2001 Late Quaternary vegetation dynamics in the southern Amazon basin inferred from carbon isotopes in soil organic matter. *Quatern. Res.* **55**, 39–46.
- de Noblet-Ducoudri, N., Claussen, M. & Prentice, I. C. 2000 Mid-Holocene greening of the Sahara: first results of the GAIM 6000 yr BP experiment with two asynchronously coupled atmosphere/biosphere models. *Climate Dynam.* **16**, 643–659.
- Dewar, R. C., Medlyn, B. E. & McMurtrie, R. 1999 Acclimation of the respiration-photosynthesis ratio to temperature: insights from a model. *Global Change Biol.* **5**, 615–622.
- Douville, H., Planton, S., Royer, J. F., Stephenson, D., Tyteca, L., Kergoat, L., Lafont, S. & Betts, R. A. 2000 Importance of vegetation feedbacks in doubled-CO₂ climate experiments. *J. Geophys. Res.* **105**, 14 841–14 861.
- Falge, E. (and 31 others) 2002 Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agric. Forest. Meteorol.* **113**, 53–74.
- Farrera, I. (and 18 others) 1999 Tropical climates at the Last Glacial Maximum: a new synthesis of terrestrial palaeoclimate data. I. Vegetation, lake-levels and geochemistry. *Climate Dynam.* **15**, 823–856.
- Fearnside, P. M. 2000 Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. *Climatic Change* **46**, 115–158.
- Friedlingstein, P., Bopp, L., Ciais, P., Dufresne, J., Fairhead, L., LeTreut, H., Monfray, P. & Orr, J. 2001 Positive feedback between future climate change and the carbon cycle. *Geophys. Res. Lett.* **28**, 1543–1546.
- Gordon, C., Cooper, C., Senior, C. A., Banks, H., Gregory, J. M., Johns, T. C., Mitchell, J. F. B. & Wood, R. A. 2000 The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Climate Dynam.* **16**, 147–168.
- Guilderson, T. P., Fairbanks, R. G. & Rubenstone, J. L. 1994 Tropical temperature variations since 20 000 years ago: modulating inter-hemispheric climate change. *Science* **263**, 663–665.
- Haberle, S. G. & Maslin, M. A. 1999 Late Quaternary vegetation and climate change in the Amazon basin based on a 50 000 year pollen record from the Amazon fan, PDP site 932. *Quatern. Res.* **51**, 27–38.
- Haffer, J. 1969 Speciation in Amazonian forest birds. *Science* **165**, 131–137.
- Haffer, J. & Prance, G. T. 2001 Climatic forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. *Amazoniana* **16**, 609–646.
- Harrison, S. P. & Prentice, I. C. 2003 Climate and CO₂ controls on global vegetation distribution at the last glacial maximum: analysis based on palaeovegetation data, biome modeling and palaeoclimate simulations. *Global Change Biol.* **9**, 983–1004.
- Haug, G. H., Hughen, K. A., Sigman, D. M., Peterson, L. C. & Röhl, U. 2001 Southward migration of the inter-tropical convergence zone through the Holocene. *Science* **293**, 1304–1308.
- Hewitt, C. D., Broccoli, A. J., Mitchell, J. F. B. & Stouffer, R. J. 2003 A coupled model study of the last glacial maximum: was part of the North Atlantic relatively warm? *Climate Dynam.* **20**, 203–218.
- Hughen, K. A., Southon, J. R., Lehman, S. J. & Overpeck, J. T. 2000 Synchronous radiocarbon and climate shifts during the last deglaciation. *Science* **290**, 1951–1954.
- Johns, T. C., Carnell, R. E., Crossley, J. F., Gregory, J. M., Mitchell, J. F. B., Senior, C. A., Tett, S. F. B. & Wood, R. A. 1997 The second Hadley Centre coupled ocean-atmosphere GCM: model description, spin-up and validation. *Climate Dynam.* **13**, 103–134.
- Jones, C. D., Collins, M., Cox, P. M. & Spall, S. A. 2001 The carbon cycle response to ENSO: a coupled climate-carbon cycle model study. *J. Climatol.* **14**, 4113–4129.
- Jones, C. D., Spall, S. A. & Cox, P. M. 2004 Simulation of the climate-carbon cycle system at the Last Glacial Maximum. (In preparation.)
- Joos, F., Prentice, I. C., Sitch, S., Meyer, R., Hooss, G., Plattner, G. K., Gerber, S. & Hasselmann, K. 2001 Global warming feedbacks on terrestrial carbon uptake under the Intergovernmental Panel on Climate Change (IPCC) emission scenarios. *Global Biogeochem. Cyc.* **15**, 891–907.
- Keeling, C. D., Whorf, T. P., Whalen, M. & Van der Plicht, J. 1995 Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* **375**, 666–670.
- Körner, C. 2004 Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Phil. Trans. R. Soc. Lond. B* **359**, 493–498. (DOI 10.1098/rstb.2003.1429.)
- Langenfelds, R. L., Francey, R. J., Pak, B. C., Steele, L. P., Lloyd, J., Trudinger, C. M. & Allison, C. E. 2003 Interannual growth rate variations of atmospheric CO₂ and its δ¹³C, H₂, CH₄ and CO between 1992 and 1999 linked to biomass burning. *Global Biogeochem. Cycles* **16**, 1408.
- Laurance, W. F., Cochrane, M. A., Bergen, S., Fearnside, P. M., Dolmônica, P., Barber, C., D'Angelo, S. & Fernandes, T. 2001 The future of the Brazilian Amazon. *Science* **291**, 438–439.
- Ledru, M.-P. 1993 Late Quaternary environmental and climatic changes in central Brazil. *Quatern. Res.* **39**, 90–98.
- Ledru, M.-P., Cordeiro, R. C., Landim Dominguez, J. M., Martin, L., Mourguiart, P., Sifeddine, A. & Turcq, B. 2001 Late-Glacial cooling in Amazonia inferred from pollen at Lagoa do Caçó, northern Brazil. *Quatern. Res.* **55**, 47–56.
- Levis, S., Foley, J. A. & Pollard, D. 1999 CO₂, climate and vegetation feedbacks at the Last Glacial Maximum. *J. Geophys. Res. Atmos.* **104**, 31 191–31 198.
- Levis, S., Foley, J. A. & Pollard, D. 2000 Large-scale vegetation feedbacks on a doubled CO₂ climate. *J. Climatol.* **13**, 1313–1325.
- Malhi, Y. 2002 Carbon in the atmosphere and terrestrial biosphere in the 21st century. *Phil. Trans. R. Soc. Lond. A* **360**, 2925–2945. (DOI 10.1098/rsta.2002.1020.)

- Malhi, Y. & Grace, J. 2000 Tropical forests and atmospheric carbon dioxide. *Trends Ecol. Evol.* **15**, 332–337.
- Maslin, M. A. & Burns, S. J. 2000 Reconstruction of the Amazon basin effective moisture availability over the past 14 000 years. *Science* **290**, 2285–2287.
- Mayle, F. E., Burbridge, R. & Killeen, T. J. 2000 Millennial-scale dynamics of southern Amazonian rainforests. *Science* **290**, 2291–2294.
- Mayle, F. E., Beerling, D. J., Gosling, W. D. & Bush, M. B. 2004 Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Phil. Trans. R. Soc. Lond. B* **359**, 499–514. (DOI 10.1098/rstb.2003.1434.)
- Mix, A. C., Morey, A. E., Pisias, N. G. & Hostetler, S. W. 1999 Foraminiferal faunal estimates of paleotemperature: circumventing the no-analog problem yields cool ice age tropics. *Paleoceanography* **14**, 350–359.
- Mora, G. & Pratt, L. M. 2001 Isotopic evidence for cooler and drier conditions in the tropical Andes during the last glacial stage. *Geology* **29**, 519–522.
- Nobre, C. A., Sellers, P. J. & Shukla, J. 1991 Amazonian deforestation and regional climate change. *J. Climate* **4**, 957–988.
- Palmer, J. R. & Totterdell, I. J. 2001 Production and export in a global ocean ecosystem model. *Deep-Sea Res.* **48**, 1169–1198.
- Pielke, R. A., Marland, G., Betts, R. A., Chase, T. N., Eastman, J. L., Niles, J. O., Niyogi, D. D. S. & Running, S. W. 2002 The influence of land-use change and landscape dynamics on the climate system: relevance to climate-change policy beyond the radiative effect of greenhouse gases. *Phil. Trans. R. Soc. Lond. A* **360**, 1705–1719. (DOI 10.1098/rsta.2002.1027.)
- Pierrehumbert, R. T. 1999 Huascarán $\delta^{18}\text{O}$ as an indicator of tropical climate during the Last Glacial Maximum. *Geol. Res. Lett.* **26**, 1345–1348.
- Potter, C., Klooster, S., de Carvalho, C. R., Genovese, V. B., Torregrosa, A., Dungan, J., Bobo, M. & Coughlan, J. 2001 Modeling seasonal and interannual variability in ecosystem carbon cycling for the Brazilian Amazon region. *J. Geophys. Res. Atmos.* **106**, 10 423–10 446.
- Prentice, I. C. & Lloyd, J. 1998 C-quest in the Amazon Basin. *Nature* **396**, 619–620.
- Prentice, I. C., Harrison, S. P., Jolly, D. & Guiot, J. 1998 The climate and biomes of Europe at 6000 yr BP: comparison of model simulations and pollen-based reconstructions. *Quatern. Sci. Rev.* **17**, 659–668.
- Prentice, I. C., Jolly, D. & BIOME6000 participants 2000 Mid-Holocene and glacial-maximum vegetation geography of the northern continents. *J. Biogeogr.* **27**, 507–519.
- Richards, P. W. 1996 *The tropical rain forest*, 2nd edn. Cambridge University Press.
- Sellers, P. J. (and 10 others) 1996 Comparison of radiation and physiological effects of doubled atmospheric CO_2 on climate. *Science* **271**, 1402–1406.
- Sifeddine, A., Martin, L., Turcq, B., Volkmer-Ribeiro, C., Soubies, F., Cordeiro, R. C. & Suguio, K. 2001 Variations of the Amazon rainforest environment: a sedimentological record covering 30 000 years. *Palaeoclimatol. Palaeoceanogr. Palaeoecol.* **168**, 221–235.
- Sifeddine, A. (and 12 others) 2003 A 21 000 cal years palaeoclimatic record from Caçó Lake, northern Brazil: evidence from sedimentary and pollen analyses. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **189**, 25–34.
- Sommer, R., Sa, T. D. D., Vielhauer, K., de Araujo, A. C., Folster, H. & Vlek, P. L. G. 2002 Transpiration and canopy conductance of secondary vegetation in the eastern Amazon. *Agric. Forest. Meteorol.* **112**, 103–121.
- Stute, M., Forster, M., Frischkorn, H., Serejo, A., Clark, J. F., Schlosser, P., Broecker, W. S. & Bonani, G. 1995 Cooling of tropical Brazil (5°C) during the last glacial maximum. *Science* **269**, 379–383.
- Sylvestre, F., Servant, M., Servant-Vildary, S., Causse, C., Fournier, M. & Ybert, J.-P. 1999 Lake-level chronology on the southern Bolivian Altiplano (18° – 23°S) during Late-Glacial time and the early Holocene. *Quatern. Res.* **51**, 54–66.
- Thompson, L. G., Mosley-Thompson, E., Davis, M. E., Lin, P.-N., Henderson, K. A., Cole-Dai, J., Bolsan, J. F. & Liu, K. G. 1995 Late glacial stage and Holocene tropical ice core records from Huascarán, Peru. *Science* **269**, 46–50.
- Thompson, L. G. (and 11 others) 1998 25 000 year tropical climate history from Bolivian ice cores. *Science* **282**, 1858–1864.
- Thorpe, R. B., Gregory, J. M., Johns, T. C., Wood, R. A. & Mitchell, J. F. B. 2001 Mechanisms determining the Atlantic thermohaline circulation response to greenhouse gas forcing in a non-flux adjusted coupled climate model. *J. Climatol.* **14**, 3102–3116.
- Tian, H. Q., Melillo, J. M., Kicklighter, J. M., McGuire, A. D., Helfrich, J. V. K., Moore, B. & Vorosmarty, C. J. 1998 Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* **396**, 664–667.
- Vélez, M. I., Hooghiemstra, H., Metcalfe, S., Martínez, I. & Mommersteeg, H. 2003 Pollen- and diatom based environmental history since the Last Glacial Maximum from the Andean core Fúquene-7, Colombia. *J. Quatern. Sci.* **18**, 17–30.
- Vellinga, M. & Wood, R. A. 2002 Global climatic impacts of a collapse of the Atlantic thermohaline circulation. *Climatic Change* **54**, 251–267.
- Vellinga, M., Wood, R. A. & Gregory, J. M. 2002 Processes governing the recovery of a perturbed thermohaline circulation in HadCM3. *J. Climate* **15**, 764–780.
- Williamson, G. B., Laurance, W. F., Oliveira, A. A., Delamonica, P., Gascon, C., Lovejoy, T. E. & Pohl, L. 2000 Amazonian tree mortality during the 1997 El Niño drought. *Conserv. Biol.* **14**, 1538–1542.
- Wilson, M. F. & Henderson-Sellers, A. 1985 A global archive of land cover and soils data for use in general circulation climate models. *J. Climatol.* **5**, 119–143.
- Wolff, T., Mulitza, S., Arz, H., Pätzold, J. & Wefer, G. 1998 Oxygen isotopes versus CLIMAP (18 ka) temperatures: a comparison from the tropical Atlantic. *Geology* **26**, 675–678.
- Zhang, H., Henderson-Sellers, A. & McGuffie, K. 2001 The compounding effects of tropical deforestation and greenhouse warming on climate. *Climate Change* **49**, 309–338.

GLOSSARY

- GCM: general circulation model
 GPP: gross primary production
 ITCZ: intertropical convergence zone
 LAI: leaf area index
 LGM: last glacial maximum
 NPP: net primary productivity
 THC: thermohaline circulation
 YD: Younger Dryas