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Recent advances in ecosystem–atmosphere interactions: an ecological perspective

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The atmosphere and terrestrial ecosystems are fundamentally coupled on a variety of time-scales. On short time-scales, this bi-directional interaction is dominated by the rapid exchange of CO_2, water and energy between the atmosphere and the land surface; on long time-scales, the interaction involves changes in ecosystem structure and composition in response to changes in climate that feed back through biophysical and biogeochemical mechanisms to influence climate over decades and centuries. After briefly describing some early pioneering work, I focus this review on recent advances in understanding long-term ecosystem–atmosphere interactions through a discussion of three case studies. I then examine how efforts to assess the stability and resilience of ecosystem–atmosphere interactions over these long time-scales using Dynamic Global Vegetation Models are hampered by the presence of important functional diversity and heterogeneity within plant communities. Recent work illustrates how this issue can be addressed through the use of Structured Ecosystem Models that more accurately scale between the short-term physiological responses of individual plants and the long-term, large-scale dynamics of heterogeneous, functionally diverse ecosystems.

Keywords: atmospheric models; terrestrial ecosystem models; vegetation dynamics; climate change; land–atmosphere interactions; structured population models

1. INTRODUCTION

The connection between the ecosystems and climate of different regions forms the cornerstone of plant biogeography (Köppen 1936; Holdridge 1947; Walter *et al.* 1975; Bailey 1976), and the relationship between climate and plant function is a central theme in plant ecophysiology (Mooney *et al.* 1987; Woodward 1987; Woodward & McKee 1991; Lambers *et al.* 1998). Traditionally, both disciplines have viewed vegetation as a passive respondent to spatial and temporal variation in climate. It is now recognized, however, that the climate–ecosystem relationship is, in fact, bi-directional.

Beginning with the pioneering work by Charney (1975; Charney *et al.* 1975), who showed how the Sahara's arid climate is reinforced by lack of vegetation in this region, studies have explored the terrestrial land surface's influence upon the state of the atmosphere in several different regions including Africa (Sud & Fennessy 1982; Sud & Smith 1985), the Boreal zone (Bonan *et al.* 1992; Foley *et al.* 1994; Bonan 1995; de Noblet *et al.* 1996; Gallimore & Kutzbach 1996; TEMPO 1996; Kutzbach *et al.* 1998; Levis *et al.* 1999, 2000), the Amazon basin (Henderson-Sellers & Gornitz 1984; Dickinson & Henderson-Sellers 1988; Lean & Warrilow 1989; Shukla *et al.* 1990; Nobre *et al.* 1991; Eltahir & Bras 1993; Henderson-Sellers *et al.* 1993; Lean & Rowntree 1993; Dirmeyer & Shukla 1994; Zeng *et al.* 1996; Costa & Foley 2000), Asia (Fennessy *et al.* 1994; Meehl 1994) and North America (Fennessy & Xue 1995; Betts *et al.* 1996; Hansen *et al.* 1998; Bonan 1999), as well as globally (Shukla & Mintz 1982; Dickinson 1983; Sud *et al.* 1988; Delworth & Manabe 1989; Sellers *et al.* 1996*a*; Betts *et al.* 1997; Cox *et al.* 2000, 2001). Ecosystem–atmosphere interactions have been the subject of several reviews (Garratt 1993; Betts *et al.* 1996; Pielke *et al.* 1998; Foley *et al.* 2000); however, since their publication, there have been significant improvements in our ability to investigate the long-term dynamics of these interactions. This new direction in land–atmosphere studies is likely to be of particular interest to ecologists, because the increasing focus on long-term dynamics necessarily involves the consideration of ecological processes such as succession, disturbance and changes in community composition, in addition to the conventional emphasis on short-term biophysical and physiological processes.

(a) *The potential for ecosystem–atmosphere feedbacks*

Early investigations of ecosystem–atmosphere interactions were unidirectional studies that examined how changing the lower boundary conditions of the atmosphere over the continents within Atmospheric General Circulation Models (AGCMs) affected patterns of atmospheric circulation and near-surface climate. As noted earlier, the first studies of this kind were by Charney (1975; Charney *et al.* 1975), who demonstrated how the high albedo (surface reflectance) caused by the lack of vegetation in the Sahara sustains and reinforces its aridity.

The precipitation that falls over a region derives from two sources: the recycling of water evapotranspired over the region, and water vapour drawn in from surrounding areas, quantities known in the atmospheric sciences as the *moisture flux convergence* and *surface moisture flux*, respectively. The specific feedback mechanism investigated by Charney was the influence of albedo on the moisture flux

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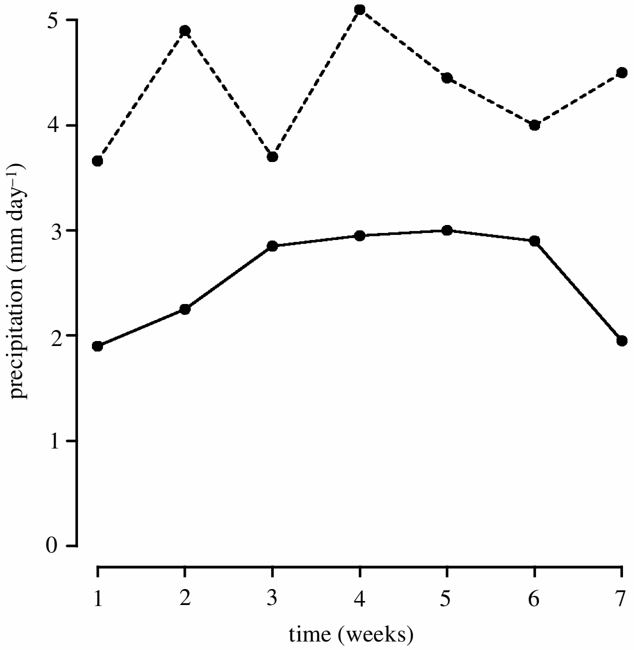

Figure 1. Albedo feedback on Saharan precipitation predicted by Charney (1975). The figure shows precipitation over Africa north of 18° N for albedo values of 14% (dashed line) and 35% (solid line), representing bare soil and vegetation, respectively. (Reproduced, with permission, from Charney (1975).)

convergence over the African continent. Changes in surface albedo affect the magnitude of this term by altering the strength of a thermally driven circulation pattern found in areas between the equator and subtropics known as Hadley cells. When surface albedo is high, a significant portion of the incoming solar radiation energy is reflected into space, cooling the troposphere above the Sahara. In response to this cooling, air is drawn in from neighbouring areas, forcing the air above the region to descend and, as it descends, it is compressed and becomes drier and warmer, thus inhibiting precipitation.

Charney showed that lowering the albedo of the desert surface from 35% to 15% as would occur, for example, by introducing vegetation cover, weakens this self-reinforcing mechanism, increasing the magnitude of the moisture flux convergence and thereby increasing precipitation over the Sahara (figure 1). Support for this land–atmosphere feedback has come from empirical studies, which have shown that inter-annual variation in the strength of drought in the Sahara–Sahel region is negatively associated with the strength of the Hadley circulation (Nicholson 1981, 1993; Lare & Nicholson 1994). Subsequent studies (Cadet & Nnoli 1987; Xue & Shukla 1993; Cook & Gnanadesikan 1991; Cook 1994; Dirmeyer 1994) have explored the influence of the land surface upon the second component of the moisture budget, the surface moisture flux. Since the magnitude of this term is determined by the rate of evapotranspiration from the land surface, vegetation exerts a direct influence on this other source of moisture for precipitation. For example, Dirmeyer (1994) showed that seasonal declines in evapotranspiration caused by the loss of vegetation cover during the Saharan dry season tend to exacerbate drought conditions during the spring and early summer. The results from these studies suggest that this additional feedback process is also important in determining the climate of the Sahara and Sahel (Cook & Gnanadesikan 1991).

Surface albedo is also implicated in maintaining the near-surface climate of northern latitudes. Palaeobotanical studies indicate that during the Holocene (from 9000 to 6000 years ago), boreal forests migrated northward in response to high-latitude warming caused by increased insolation due to changes in the Earth's orbit during this period. Atmospheric simulations by Bonan *et al.* (1992), Foley *et al.* (1994) and TEMPO (1996) showed that while the changes in solar forcing could account for a 1.8 °C warming in surface temperatures, the accompanying change from snow to forest cover and resulting reduction in surface reflectance almost doubles the temperature increase during this period from 1.8 °C to 3.4 °C. Subsequent studies by Gallimore & Kutzbach (1996) and de Noblet *et al.* (1996) have suggested that similar changes in the albedo of high-latitude regions may also have been involved in the initiation of the last ice age (115 000 years ago).

The Amazon Basin is another region that has been the subject of intense scrutiny for ecosystem–atmosphere feedbacks due to continuing deforestation in this region. While early atmospheric simulations found no significant effects of deforestation on the near-surface climate of Amazonia (Henderson-Sellers & Gornitz 1984; Dickinson & Henderson-Sellers 1988), subsequent results from higher resolution atmospheric models with more detailed land-surface biophysics have suggested that a pronounced regional ecosystem–atmosphere feedback exists in this region (Lean & Warrilow 1989; Shukla *et al.* 1990; Nobre *et al.* 1991; Henderson-Sellers *et al.* 1993). For example, in the study by Shukla *et al.* (1990), the net effects of deforestation on Amazonian climate included increases in surface temperatures of between 2 °C and 5 °C, and a 30% reduction in annual rainfall (figure 2). Significantly, the results of several of the studies (Lean & Warrilow 1989; Shukla *et al.* 1990; Nobre *et al.* 1991) suggest that the increases in temperature and reductions in precipitation over the basin are large enough to make the change in the state of the land surface irreversible, since deforestation produces near-surface conditions under which trees would be unable to regrow.

The influence of the land surface on the atmosphere in Amazonia is more complex than in the Sahara because it involves changes in the vegetation surface roughness, in addition to changes in surface reflectance and surface evapotranspiration. The simulations of Lean & Warrilow (1989) and subsequent analyses by Eltahir & Bras (1993), Dirmeyer & Shukla (1994) and Zeng *et al.* (1996) quantified the importance of these different ecosystem–atmosphere feedback processes. The increased albedo caused by the conversion from tropical forest to pasture reduces the upward transfer of latent energy, decreasing the moisture flux convergence over the continent and thus reducing precipitation. The decrease in surface roughness of the plant canopy caused by the forest-to-pasture transition reduces turbulent exchange in the boundary layer, decreasing evapotranspiration. This decreases the magnitude of the surface moisture flux, which further reduces precipitation. However, the overall response is complicated because the reduction in surface roughness increases

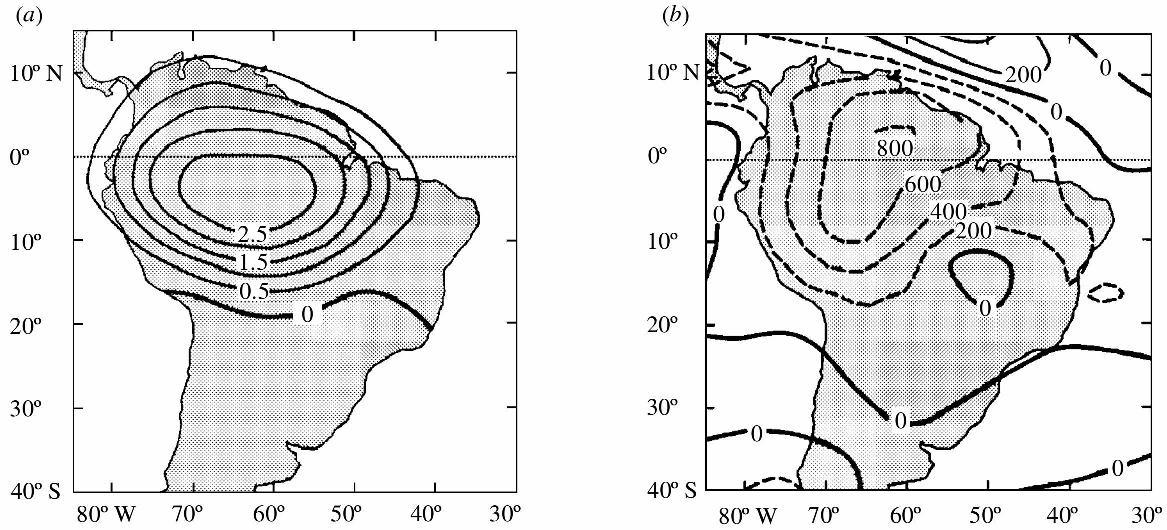

Figure 2. Effects of Amazonian deforestation predicted by Shukla *et al.* (1990). Differences between the annual mean of the deforestation and control cases (deforested − control) for the South American region: (*a*) surface temperature increase in degrees Celsius, and (*b*) total precipitation change (dashed lines indicate a decrease) in millimetres per year. (Reproduced, with permission, from Shukla *et al.* (1990).)

surface temperatures, which tends to increase the moisture flux convergence over the continent, counteracting the decrease in moisture flux convergence caused by the increase in surface albedo. This effect of surface roughness is relatively weak in the newer atmospheric models; however, this competing feedback process accounts for the results of the early studies that had found little effect of deforestation on Amazonian climate (Eltahir & Bras 1993).

(**b**) *Dynamic vegetation studies*

The above studies illustrated the potential for significant feedbacks between vegetation and climate, including the possibility of alternate states for the climate and ecosystems of a region. However, their findings have remained controversial owing to the prescribed nature of the land surface, which excludes a number of potentially important feedback mechanisms that may act to either maintain a climate in its new state or, alternatively, to restore the climate over longer time-scales. The known connections between the composition, structure and physiology of vegetation and the climate of different regions (Köppen 1936; Holdridge 1947; Walter *et al.* 1975; Bailey 1976; Mooney *et al.* 1987; Woodward 1987; Woodward & McKee 1991; Lambers *et al.* 1998) implies that ecosystems will respond to novel climatological regimes through a variety of mechanisms acting on different time-scales. Over short time-scales, the physiological responses of plants to ambient conditions (such as changes in diurnal patterns of stomatal opening and seasonal changes leaf phenology) can alter the fluxes of water, carbon and energy between the land surface and the atmosphere. Over longer time-scales, an additional suite of processes can change the composition and structure of the vegetation itself. Accordingly, subsequent investigations of ecosystem–atmosphere interactions have sought to incorporate aspects of the bi-directional coupling between ecosystems and climate.

Early studies focused on the fast time-scale responses of ecosystems to the atmosphere. Results from these studies showed how soil moisture, both directly and through its effect on plant stomatal resistance, becomes a source of short-term memory for near-surface climate variables, especially humidity, increasing temporal variability and shifting variability from higher to lower frequencies (Delworth & Manabe 1993; Betts *et al.* 1993; Xue *et al.* 1996). Recognition of the importance of the climatological memory that arises from these short-term ecosystem–atmosphere interactions led to improvements in the modelling of soil moisture and vegetation stomatal resistance within Numerical Weather Prediction models, which have improved weather forecasts for Europe, North Africa and the United States (Rowell & Blondin 1990; Betts *et al.* 1993; Xue *et al.* 1996). In seasonal environments, vegetation phenology also affects the surface energy budget. For example, Xue *et al.* (1996) showed that more accurate characterization of the seasonal patterns of foliar cover within an atmospheric model significantly improves predictions of summer temperatures over the continental United States. Empirical evidence for this phenology feedback mechanism has come from a study by Schwartz & Karl (1990), which showed that the leaf-out of deciduous trees in the eastern United States shifts the surface energy budget from sensible to latent heating, interrupting the increase in mean temperatures during the spring.

Following these successes at capturing short-term ecosystem–atmosphere feedbacks, researchers have begun to examine longer-term aspects of the vegetation–atmosphere interaction. The following three studies highlight some of the recent progress in this area.

(**c**) *Case study 1: vegetation as a source of climatalogical memory in the inter-decadal climate variability of the Sahel*

A nice illustration of the importance of longer-term vegetation–atmosphere interactions comes from a recent study by Zeng *et al.* (1999), which showed how vegetation dynamics influence inter-decadal variability in rainfall over the Sahel. While prescribed vegetation studies had shown the potential for vegetation feedbacks in this region, the long-term dynamics of this ecosystem–atmosphere

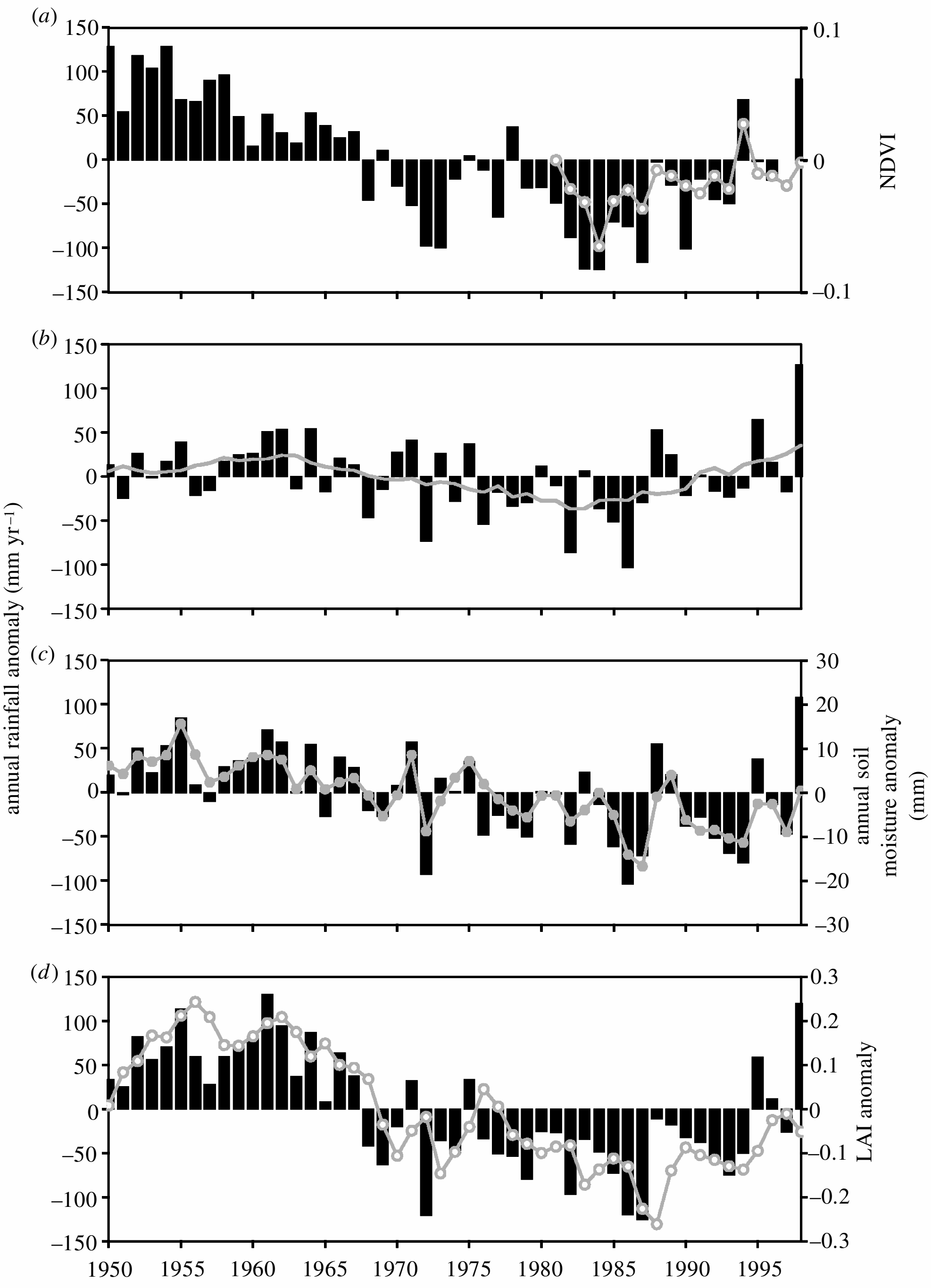

Figure 3. Annual rainfall anomaly (vertical bars) over the West African Sahel (13° N–20° N, 15° W–20° E) from 1950 to 1998. (*a*) Observations from Hulme (1994), (*b*)–(*d*) simulation results of Zeng *et al.* (1999). (*b*) Model with non-interactive land surface hydrology (fixed soil moisture) and non-interactive vegetation (sea-surface temperature influence only; AO). Smoothed line is a nine-year running mean showing the low-frequency variation. (*c*) Model with interactive soil moisture but non-interactive vegetation (AOL). (*d*) Model with interactive soil moisture and vegetation (AOLV). Also plotted (as connected circles labelled on the right) are (*a*) the normalized difference vegetation index (NDVI) (Tucker & Nicholson 1999), (*c*) the model-simulated annual soil moisture anomaly and (*d*) the model-simulated LAI anomaly. The soil moisture and LAI anomalies are computed relative to the 1950–1998 base period, while the NDVI data are relative to 1981. (Reproduced, with permission, from Zeng *et al.* (1999).)

interaction had not been explored. During the period 1950–1990, rainfall in this region exhibited a multi-decadal drying trend punctuated with marked inter-annual and inter-decadal variability (figure 3*a*). In particular, Zeng and colleagues were interested in how the land–atmosphere interaction may modulate the effect of changes in the surrounding ocean sea-surface temperatures that affect atmospheric conditions over the region.

They modelled vegetation cover with the following simple equation:

$$dV/dt = a\beta(w)(1 - e^{-kL}) - V/\tau, \qquad (2.1)$$

where V is the relative proportion of biomass cover within each climatological grid cell, t is time, a is the rate of carbon assimilation, L is the plant Leaf Area Index (LAI), k is the light extinction coefficient (taken as 0.75) and τ is the vegetation longevity (set to 1 year). LAI is proportional to V ($L = L_{\max} V$, where $L_{\max}$ is set to 8, the maximum observed LAI). Vegetation growth in this region is predominantly water limited; in the model this is captured by the function $\beta(w)$, which describes the effect of soil moisture on plant growth ($\beta = w^{1/4}$, where w is soil moisture measured in units of field capacity, such that w lies between 0 and 1). The value of a was adjusted so that equation (2.1) is zero when V and W are both equal to 1.

Vegetation cover (V) affects the atmosphere by modifying the albedo (A) and stomatal conductance (g_c) of the plant canopy. These two effects are captured through the following equations:

$$A = 0.38 - 0.3(1 - e^{-kL}), \tag{2.2}$$

$$g_c = g_{s_{\max}} \beta(w)(1 - e^{-kL})/k. \tag{2.3}$$

Equation (2.2) gives albedo values from 0.38 for desert ($V = 0$) to 0.08 for dense vegetation ($V = 1$). Equation (2.3) controls the amount of water lost through evapotranspiration, varying between zero in the absence of vegetation cover ($V = 0$) and $g_{s_{\max}}$ for dense vegetation cover ($V = 1$) in the absence of water limitation ($\beta = 1$).

Zeng *et al.* coupled equations (2.1)–(2.3) into a tropical atmospheric circulation model (Neelin & Zeng 2000; Zeng *et al.* 2000) and performed three runs of the coupled ecosystem–atmosphere model to quantify the importance of vegetation feedbacks in governing the pattern of inter-annual variability in rainfall seen in figure 3*a*. In all three simulations, the atmospheric model was forced with the observed pattern of sea-surface temperatures for the 1950–98 period. In the first (AOLV), vegetation and soil moisture were both interactive and thus the atmosphere, soil moisture and vegetation all contributed to the inter-annual pattern of variability. In the second (AOL), vegetation cover for each month was set to the average value for that month during the entire period, yielding vegetation that varied on a seasonal basis but with no year-to-year variability. In the third (AO), the soil moisture values for each month were similarly averaged, yielding a model with no year-to-year variability in either the vegetation or soil moisture.

When vegetation and soil moisture are non-interactive and only sea-surface temperatures vary inter-annually (AO), the ecosystem–atmosphere system exhibits weak inter-annual and inter-decadal variability in precipitation and a weak drying trend over the period compared with the observations (compare figure 3*a* and *b*). Allowing for interactive soil moisture (AOL) increases the drying trend over the interval and inter-annual variation in precipitation is increased slightly, but the amplitude of inter-decadal variability remains substantially less than observed (figure 3*c*). The inclusion of the vegetation feedback onto the atmosphere, however, results in substantial increases in the inter-decadal variability, closely matching the pattern of variability seen in the observations (figure 3*d*).

The vegetation–atmosphere interaction modifies precipitation patterns through a series of positive feedbacks. Decreases in rainfall reduce soil moisture availability and cause the vegetation to decline, decreasing evapotranspiration and increasing surface albedo. As discussed earlier, these biophysical changes reduce energy flux into the atmosphere, decreasing both the surface moisture flux and moisture flux convergence and thereby causing rainfall to decrease over the region. Through these long-term feedback processes, ecosystem–atmosphere interactions amplify and add decadal-scale memory to climate variability in the Sahel.

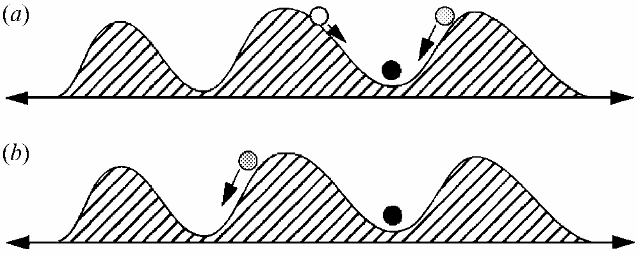

Figure 4. The movement of a ball on a landscape as an analogy of a climate system with multiple equilibria. The filled circle represents an equilibrium climate system, and the shaded circles mark the extent of the perturbations imposed on the system. The two cases represent the system's response to different perturbations: (*a*) small perturbations—a negative feedback leads to a full recovery; (*b*) larger perturbations—a positive feedback leads to a new equilibrium. (Reproduced, with permission, from Wang & Eltahir (2000*b*).)

(d) *Case study 2: multiple stable states. A green Sahara?*

When the positive feedbacks between the ecosystems and climate of a region are sufficiently strong and the dynamics of the interaction are coherent over large spatial and long temporal scales, they can give rise to alternative stable states for the biosphere–atmosphere system—an idea illustrated schematically in figure 4. Several recent studies of the long-term coupling between the atmosphere and vegetation of the Sahara support the idea of an alternate state for the climate and ecosystems of this region. The first study to suggest this was carried out by Claussen (1998), who, using a coupled climate–vegetation model, showed that the ecosystem–atmosphere system of North Africa yielded different solutions depending on the model's initial conditions. This finding may simply have been an artefact of the biogeographical model and asynchronous coupling procedure used in the study. (Biogeographical models assume that vegetation is in instantaneous equilibrium with climate and are coupled to AGCMs through an asynchronous updating procedure in which the output from the atmospheric model is periodically used to 'diagnose' the equilibrium vegetation distribution, which is then used to specify the characteristics of the land surface for the next time-step of the atmospheric model. In the case of Claussen (1998), the interval between updates was 6 years. The land–atmosphere interaction in asynchronously coupled models is not physically consistent due to the separate treatments of the surface energy balance by the atmospheric and vegetation models.) However, a subsequent investigation using a fully coupled, dynamic global vegetation model (Wang & Eltahir 2000*a*,*b*), strengthened the case for the existence of an alternative 'green' state for the Sahara region. When the coupled model was initialized with current vegetation patterns, the region formed a desert ecosystem and climate maintained by the self-reinforcing mechanisms described earlier (figure 5*a*,*c*). However, when initialized as forest, the coupled model yielded a mixture of grassland, woodland and forest ecosystems, maintained by a moister climate (figure 5*b*,*c*).

Empirical support for the existence of an alternate 'green' state for the Sahara has come from palaeobotanical studies. Fossil pollen records show that during the early to middle Holocene (from 12 000 to 5000 years ago), the Sahara region was covered by grasses and arid shrublands and had climate considerably warmer and wetter than today. Recent simulations using a coupled vegetation–atmosphere model (Claussen *et al.* 1999) have confirmed earlier work by Kutzbach *et al.* (1996), which suggested that a small decrease in incoming solar radiation caused by a change in the Earth's tilt during the Holocene triggered a shift between the moist and dry states. While this is not unequivocal evidence for true bi-stability because it involves a unidirectional change in environmental forcing, it suggests that, as illustrated schematically in figure 4, relatively mild changes in climatological forcing can shift the Sahara ecosystem–atmosphere system into a different basin of attraction.

(e) *Case study 3: role of ecosystem–atmosphere feedbacks in responses to global climate change*

Until recently, the models used to predict the consequences of continuing anthropogenic CO_2 emissions to the atmosphere have been coupled atmosphere–ocean models containing only crude representations of the land surface (Sellers *et al.* 1997). The recognition of the importance of ecosystem–atmosphere interactions for near-surface climate described earlier led to the development of coupled biosphere–atmosphere–ocean models. Initially, the terrestrial component of these models was similar to those introduced into Numerical Weather Prediction models, but incorporating the leaf-level response of plants to increasing atmospheric CO_2 in addition to their responses to changes in near-surface climate and soil moisture (e.g. Sellers *et al.* 1986, 1996*b*, 1997; Xue *et al.* 1991; Bonan *et al.* 1995; Randall *et al.* 1996).

Only very recently have longer-term ecosystem–atmosphere feedbacks been incorporated into coupled biosphere–atmosphere–ocean models, to form so-called 'Earth System Models'. A recent landmark study (Cox *et al.* 2000; Cox 2001) used an Earth System Model with fully interactive, dynamic vegetation to examine the role of ecosystem feedbacks in the climatological response to continuing anthropogenic CO_2 emissions. Transient simulations of the model were performed for the period 1860–2100 using a standard CO_2 emissions scenario. Initially, the response of the vegetation to increasing atmospheric CO_2 was consistent with the results from the earlier models, implying that terrestrial vegetation will take up carbon, thus slowing the rate of CO_2 build-up in the atmosphere (figure 6*a*). However, from 2010 onwards, the rate of terrestrial carbon accumulation slows and, by 2050, the land surface becomes a net source of CO_2 to the atmosphere (figure 6*a*). Two main effects are responsible for this carbon loss: collapse of the Amazon forests in response to atmospheric warming and rising CO_2 concentrations (figure 6*b*), and a global loss of soil carbon (figure 6*c*). The combined effect of these feedbacks

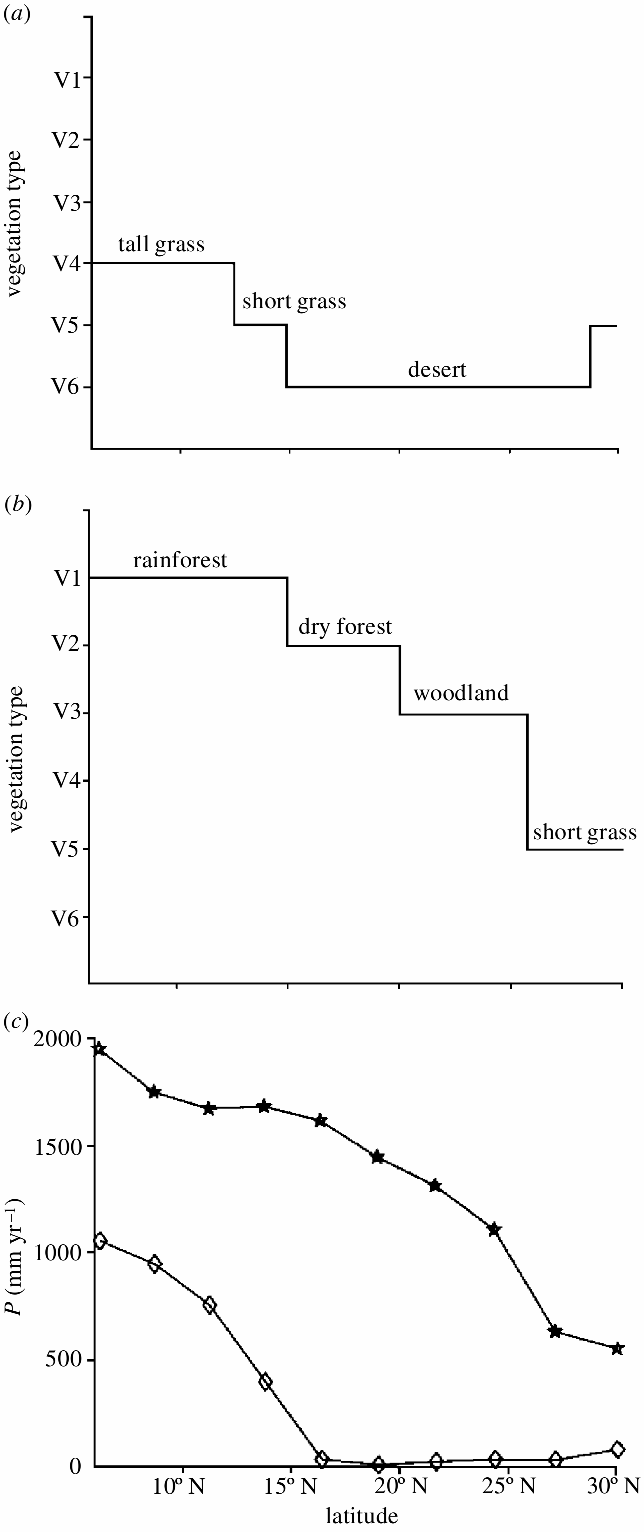

Figure 5. Results from Wang & Eltahir (2000*b*) showing multiple states for the African continent. (*a*,*b*) Equilibrium vegetation states that the coupled biosphere–atmosphere model develops when initiated from two initial conditions: (*a*) the model commences from a desert-covered West Africa (DIC); and (*b*) the model commences from a rainforest-covered West Africa (FIC). The vegetation types V1–V6 correspond to rainforest, dry forest, woodland, tall grass, short grass and desert, respectively. (*c*) The equilibrium annual precipitation that the biosphere–atmosphere model develops when starting from the two initial conditions. FIC: filled stars; DIC: open diamonds. (Reproduced, with permission, from Wang & Eltahir (2000*b*).)

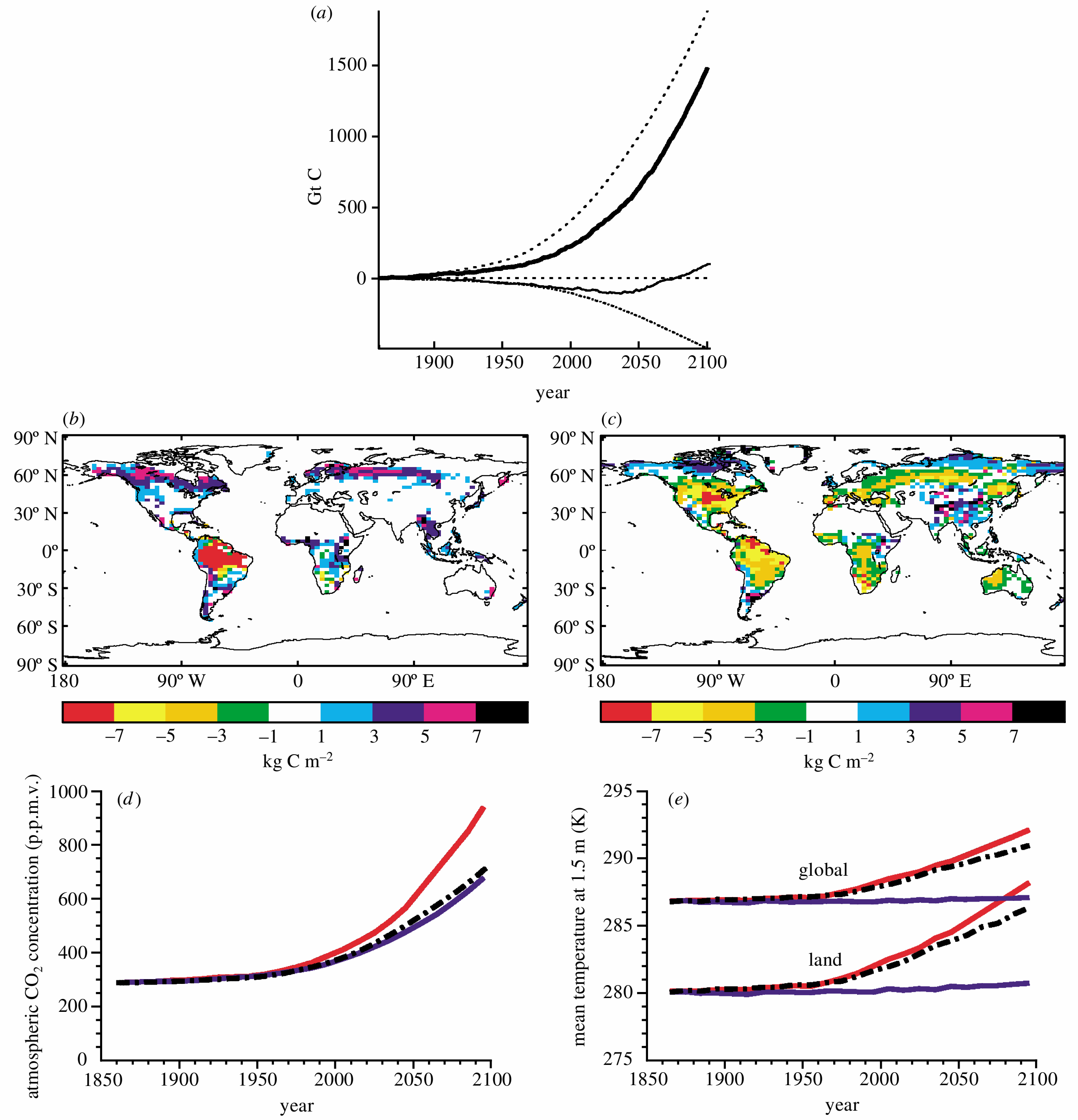

Figure 6. Ecosystem–atmosphere feedbacks in the climatological response to continuing global anthropogenic CO$_2$ emissions predicted by Cox *et al.* (2000) and Cox (2001). (*a*) Carbon budget during the fully coupled simulation. The thick line shows the simulated change in atmospheric CO$_2$; the dashed line shows the contribution of emissions. Land and ocean fluxes to the pattern atmospheric CO$_2$ increase are represented by a thin line and a dotted and dashed line, respectively, with negative values implying net uptake of CO$_2$. Note that the terrestrial biosphere takes up CO$_2$ at a decreasing rate from *ca.* 2010 onwards, becoming a net source at *ca.* 2050. By 2100 this source from the land almost balances the oceanic sink, so that atmospheric carbon content is increasing at approximately the same rate as the integrated emissions (that is, the airborne fraction is *ca.* 1). (*b*,*c*) Changes in vegetation carbon (*b*) and soil carbon (*c*) throughout the transient simulation. (*d*,*e*) Effect of climate–carbon-cycle feedbacks on atmospheric CO$_2$ concentrations and global warming. (*d*) Global mean CO$_2$ concentration and (*e*) global mean and land mean temperature versus year. Figures show comparisons between transient simulations with interactive CO$_2$ and dynamic vegetation (red lines) and a standard AGCM simulation with prescribed CO$_2$ and fixed vegetation (dotted and dashed lines) and a simulation that neglects CO$_2$-induced climate change (blue lines). (Reproduced, with permission, from Cox *et al.* (2000) and Cox (2001).)

between the terrestrial vegetation and the atmosphere is a substantial increase in the rate of CO$_2$ build-up in the atmosphere. By 2100, CO$_2$ concentrations are 33% higher and mean temperatures over the land surface 2 °C higher than in the absence of the vegetation–atmosphere interaction (figure 6*d*,*e*).

In addition to the above two effects identified by the authors, the findings of the Cox *et al.* study also imply that the high-latitude albedo feedback identified by Bonan *et al.* (1992) discussed earlier also arises in response to the CO_2-induced warming. As can be seen in figure 6*b*, there is a marked increase in above-ground carbon in the boreal zone, reflecting a change from snow-covered tundra to forest, which, as described earlier, lowers the albedo of the land surface and elevates surface temperatures. Further support for the emergence of the high-latitude albedo feedback mechanism in response to CO_2-induced global warming has come from two other recent studies (Betts *et al.* 1997; Levis *et al.* 1999), which found that the reduction in boreal albedo produces an additional 1–2.5 °C of warming over northern Canada and Eurasia, exceeding the cooling effect caused by the uptake of carbon caused by the tundra-to-forest transition.

2. LONG-TERM ECOSYSTEM DYNAMICS AT REGIONAL AND GLOBAL SCALES

The results from the above studies imply the existence of significant, long-term feedbacks between ecosystems and climate. However, the magnitude and even the direction of these feedbacks remain highly uncertain, in large part because our ability to accurately capture the long-term dynamics of ecosystem–atmosphere interactions is still in its infancy. In this section, I review the approaches to modelling long-term ecosystem dynamics used in the case studies, focusing in particular on the approaches used to scale between short-term responses of individual plants to changes in atmospheric forcing and long-term, large-scale changes in ecosystem structure and function. I then briefly discuss a new method for incorporating dynamic, sub-grid-scale ecosystem heterogeneity and its prospects for improving predictions of long-term ecosystem–atmosphere dynamics.

(a) *Long-term vegetation dynamics*

In some cases, the representation of an ecosystem's impact on the atmosphere can be extremely simple. For example, in case study (1) a single ordinary differential equation (equation (2.1)) was used to phenomenologically describe changes in the proportion of vegetation cover within each climatological grid cell as function changing moisture conditions in different years. Even with this extremely simple representation of the vegetation, and just two equations describing the effect of vegetation upon the biophysical properties of the land surface (equations (2.2) and (2.3)), Zeng and colleagues were able to capture the climatological memory provided by the vegetation and its impact on inter-annual and inter-decadal climate variability in the Sahel (figure 4). This approach is well suited to studies of land–atmosphere interactions over regions such as North Africa, where the vegetation dynamics and feedback processes involved are relatively simple and already well characterized.

The feedback mechanisms in the other two case studies were more complex, involving biophysical and, in the third case study, biogeochemical feedbacks resulting from changes in vegetation composition and physiological functioning and correlated changes in below-ground biogeochemistry. In both cases, these were investigated using Dynamic Global Vegetation Models (DGVMs)—models designed explicitly to simulate the long-term transient dynamics of ecosystems. A number of these models have been developed; however, most lack the features necessary to interact dynamically with atmospheric models (see Cramer *et al.* (2001) for a recent review). In a groundbreaking paper, Foley *et al.* (1998) coupled the IBIS DGVM (Foley *et al.* 1996) into a climate model by incorporating a biophysical land surface scheme (Pollard & Thompson 1995) to simulate the exchange of water, energy and momentum between the ecosystem and the atmosphere. Coupled versions of this model have been used in a number of ecosystem–atmosphere studies including those of Wang & Eltahir (2000*a*,*b*), discussed in case study (2). The TRIFFID DGVM used by Cox *et al.* 2000 (case study (3)) was coupled to the Hadley Centre climate model in a similar manner.

As in virtually all DGVMs, the influence of the atmosphere on long-term ecosystem dynamics in IBIS and TRIFFID are captured in the following way: a mechanistic model of photosynthesis that simulates the hourly-scale-coupled fluxes of carbon and water in and out of leaves as a function of radiation, temperature, humidity, soil moisture and atmospheric CO_2 concentrations (Farquhar & Sharkey 1982; Ball *et al.* 1986; Collatz *et al.* 1991, 1992; Leuning 1995) is coupled to a biogeochemical model that tracks the fate of carbon through a series of above-ground and below-ground pools. Through this formulation, the physiological responses of plants to changes in meteorological and soil moisture conditions within DGVMs propagate, altering the composition, structure and fluxes of ecosystems over decadal and century time-scales.

(i) *Approaches to scaling*

While the DGVMs used in the above coupled modelling studies contain detailed, mechanistic representations of leaf-level photosynthesis, their procedure for translating the leaf-level responses of individual plants into long-term, large-scale ecosystem-level responses is relatively simple. DGVMs represent the vast array of differences in plant structure and function by dividing Earth's vegetation into a few discrete plant functional types such as C_4 grasses, shrubs, broadleaf trees and evergreen conifers, which compete mechanistically above ground for light and below ground for soil moisture. However, the environment in which the plant functional types compete within each climatological grid cell of a DGVM is typically highly aggregated, with all plants experiencing similar, spatially averaged, resource conditions. In some models, such as IBIS, this averaging is done over the entire grid cell while in others such as TRIFFID, the plant functional types occupy separate portions of the grid cell and the averaging is done separately for each plant type. The net consequence of this spatial averaging is that the response of each plant functional type at the scale of the grid cell is essentially that of a single plant writ large.

The accuracy of this 'canopy as big leaf' scaling procedure is hampered by the presence of important fine-scale heterogeneity within ecosystems. Before proceeding further, it is useful to distinguish two qualitatively different sources of ecosystem heterogeneity. Exogenous or *abiotic* heterogeneity arises from static differences in the physical environment such as variation in topography, soil parent material or climatological forcing. Endogenous or *biotic* heterogeneity is a dynamic form of heterogeneity, which arises spontaneously even in a physically homogeneous environment. Two of the most important natural processes giving rise to biotic heterogeneity are the mortality of large adult trees and fire disturbances. These stochastic events, occurring at scales ranging from kilometres down to the scale of individual canopy tree-sized gaps, generate substantial, fine-scale spatial heterogeneity in resource availability that substantially alters the subsequent local dynamics of the plant canopy and below-ground ecosystem at scales well below the resolution of the climatological grid cells within DGVMs.

The absence of biotic heterogeneity that results from 'big leaf' scaling is a matter for concern in long-term ecosystem–atmosphere studies for two reasons. First, as would be expected from ecological theory (Grubb 1977; Pacala & Tilman 1994; Tilman 1994; Rees *et al.* 1996; Lehman & Tilman 1997; Bolker & Pacala 1997; Levin & Pacala 1997; Pacala & Levin 1997), by eliminating opportunities for resource partitioning, 'big leaf' scaling tends to yield mono-dominant plant communities—ecosystems comprised of single plant functional types. This absence of functional diversity that arises as a consequence of the spatial averaging of resource conditions within grid cells is a matter for concern because diversity is a fundamental factor affecting the stability and resilience of ecosystems to perturbation (May 1974; Schulze & Mooney 1993; Tilman *et al.* 1997; Grime *et al.* 2000; Kinzig *et al.* 2001; Loreau *et al.* 2001). Thus, while actual plant canopies are comprised of mixtures of plant types whose different physiological and life-history traits ensure a distributed response to perturbation, in traditional DGVMs that predict single vegetation types per grid cell, changes in ecosystem structure and function in response to changes in environmental forcing occur abruptly, uniformly and in concert.

Some newer DGVMs have incorporated schemes that maintain mixtures of functional types within grid cells despite the spatial averaging of resource conditions that accompanies 'big leaf' scaling. For example, TRIFFID abandons the conventional mechanistic description of competition used in IBIS and most other DGVMs and instead handles it phenomenologically, using a modified version of the classical Lotka–Volterra competition equations. This offers certain advantages over the mechanistic resource-based approach, not least the ease with which the model can be parameterized to yield coexistence of the different plant types, and thus predict functionally diverse ecosystems. However, using phenomenological approaches to model competition in functionally diverse plant communities is very challenging. While the number of parameters needed to describe interspecific competition mechanistically scales as n, where n is the number of plant functional types represented in the model, the number of parameters required to describe interspecific competition phenomenologically scales as n^2. Obtaining reasonable estimates for these n^2 competition coefficients that describe the impact of each plant type upon each of the other plant types, and then specifying how these vary with the environmental conditions found within different grid cells, substantially increases the number of model parameters. Even with the coarse representation of plant diversity in TRIFFID, which has just five plant functional types (compared with the 13 types in IBIS), this results in 25 coefficients per grid cell whose values are largely unknown and difficult to measure.

Second, in averaging over the scales at which fine-scale disturbances such as fire and canopy gap formation operate, 'big leaf' scaling eliminates the effects that these sub-grid-scale processes have upon the structure and biophysical properties of plant canopies. For example, in the Cox *et al.* study, the collapse of the Amazon forest occurs owing to a CO_2 and temperature-induced change in plant-level stomatal opening. However, the changes in temperature and moisture conditions that accompany rising CO_2 levels are also likely to significantly alter the occurrence and frequency of fires within Amazonia. Such climate-induced changes in the disturbance regimes acting upon ecosystems are likely to cause marked changes in ecosystem structure and composition, which could operate either alongside, counter to, or independent of, any changes in ecosystem composition caused by physiological responses of plants to altered environmental conditions.

(ii) *New approaches to scaling: Structured Ecosystem Models*

A new method for scaling plant level responses up to larger spatial and temporal scales, currently being implemented in the Geophysical Fluid Dynamics Laboratory coupled Earth System Model (AM3/OM3/LM3) (Anderson *et al.* 2003; S. W. Pacala and E. Shevliakova, personal communication), avoids the above problems that arise from 'big leaf' scaling, by drawing upon techniques developed in the ecological literature to account for dynamics of heterogeneous populations (Von Foerster 1959; Levin & Paine 1974; Kohyama 1993; Kohyama & Shigesada 1995; de Roos 1997). Ecologists have addressed the issue of fine-scale biotic heterogeneity within ecosystems for three decades using individual-based vegetation models, which mechanistically simulate the spatially localized and height-structured nature of competition between individual plants. These models naturally capture the fine-scale biotic heterogeneity in resource environments found within plant canopies caused by fine-scale disturbance processes such as fire and the stochastic death of canopy trees that are vital for the formation and maintenance of functionally diverse plant communities (Botkin *et al.* 1972; Shugart & West 1977; Shugart 1984; Huston *et al.* 1988; Urban 1990; Huston 1992; Bugmann 1996; Pacala *et al.* 1996; Smith & Urban 1988). Global versions of these models have been developed, for example the HYBRID model of Friend (Friend *et al.* 1997; Friend & White 2000); however, until recently, the only way to scale between the dynamics of individual plants and the long-term, large-scale dynamics of the heterogeneous plant canopy has been by performing repeated, stochastic simulations of large numbers of individual plants within each climatological grid cell. The computationally intensive and stochastic nature of these models has precluded their use in studies of ecosystem–atmosphere interactions.

Recent work has shown, however, that the dynamics of individual-based vegetation models such as HYBRID can be closely approximated using a system of size- and age-structured partial differential equations that track the dynamic sub-grid-scale biotic heterogeneity that results from fine-scale disturbance processes with plant canopies (Hurtt *et al.* 1998; Moorcroft *et al.* 2001). It was possible, using this approach, to construct a Structured Ecosystem Model (SEM), the Ecosystem Demography model (ED), which formally scales between the short-term, leaf-level responses of individual plants and the long-term, large-scale dynamics of a heterogeneous and functionally diverse ecosystem without the need for computationally intensive, individual-based simulations. The ability of SEMs such as ED to capture the effects of fire, windthrow and other sub-grid-scale disturbances upon canopy structure that maintain biotic heterogeneity and plant diversity within plant canopies (Moorcroft *et al.* 2001; Pacala *et al.* 2001; Hurtt *et al.* 2002) promises to substantially improve predictions of the long-term response of ecosystems to climatological perturbation in coupled modelling studies.

(iii) *The importance of sub-grid-scale ecosystem heterogeneity for land–atmosphere feedbacks*

Incorporating the dynamics of sub-grid-scale biotic heterogeneity into coupled modelling studies through the use of SDGVMs also promises to allow for a more comprehensive description of ecosystem–atmosphere interactions. In particular, sub-grid-scale fires generate additional land–atmosphere feedbacks resulting from the changes in atmospheric chemistry that accompany biomass burning (for reviews, see Crutzen & Goldhammer 1993; Andreae & Crutzen 1997). In addition, while a detailed discussion is beyond the scope of this review, results from mesoscale atmospheric modelling studies (which simulate atmospheric dynamics at high spatial resolution, with typical grid cell sizes of between 1 and 10 km^2 compared with 10 000–100 000 km^2 grid cells within AGCMs, enabling them to resolve important fine-scale atmospheric processes such as cloud formation), suggest that the kinds of sub-grid-scale ecosystem heterogeneity captured by SEMs exert a powerful influence on the dynamics of the atmosphere in some regions (Pielke *et al.* 1997; Pielke 2001). For example, work by Avissar and colleagues suggests that the contrasting biophysical properties of forest and agricultural areas being created by Amazonian deforestation is affecting convective cloud formation and altering the spatial distribution and reducing the total amount of precipitation that falls over the region (Avissar & Liu 1996; Baidya-Roy & Avissar 2002; Weaver & Avissar 2001). Such findings have come from short-term unidirectional studies, however, and their implications for the long-term climate and ecosystems of different regions have yet to be explored.

(b) ***Long-term soil dynamics***

The above discussion has focused exclusively on scaling between the short-term and long-term dynamics of the above-ground ecosystem. However, in the case of the Cox *et al.* study, a significant component of the global-scale ecosystem–atmosphere feedback arose from a temperature-driven release of soil carbon to the atmosphere. This result places new emphasis on improving our understanding of the long-term responses of below-ground ecosystems to climate change. Current parameterizations of the temperature and moisture dependencies of decomposition within ecosystem models reflect measurements of daily, weekly and monthly variability in below-ground respiration rates from empirical studies (Bowden *et al.* 1998; Davidson *et al.* 1998; Goulden *et al.* 1998; Savage & Davidson 2001; Randerson *et al.* 2002). The ability of these parameterizations to correctly characterize the response of below-ground ecosystems to more secular changes in environmental conditions over decadal and century time-scales is, however, largely unknown. Results from at least some soil warming and soil transplantation experiments suggest that, like the plant canopies that sit above them, below-ground communities are likely to adjust to longer-term environmental changes through a combination of physiological adaptation and longer-term compositional changes in the below-ground fauna (see Wardle (2002) for a recent review).

3. CONCLUSIONS

Building on early successes at capturing the fast time-scale dynamics of land–atmosphere interactions, recent investigations of ecosystem–atmosphere dynamics have offered compelling evidence that long-term changes in vegetation structure and composition significantly influence the behaviour of the atmosphere and climate at both regional and global scales. However, this new focus upon long-term aspects of the vegetation–atmosphere interaction places a new emphasis on the ability of DGVMs to accurately translate short-term physiological responses into long-term changes in ecosystem structure and function. SEMs offer a way to realistically capture the dynamics of functionally diverse, heterogeneous plant canopies over decades and centuries. When used in coupled modelling studies, these models promise to provide more accurate assessments of the stability and resilience of ecosystems to perturbation, thereby substantially improving predictions of long-term ecosystem–atmosphere dynamics.

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