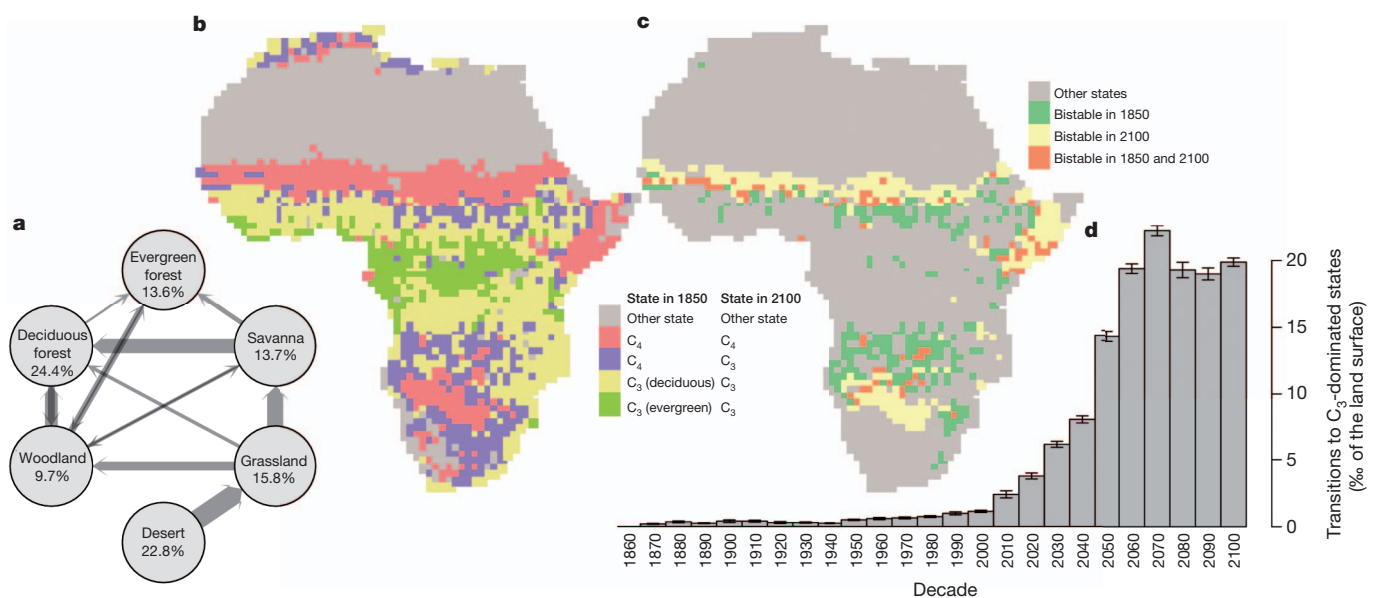


# Atmospheric CO<sub>2</sub> forces abrupt vegetation shifts locally, but not globally

Steven I. Higgins<sup>1</sup> & Simon Scheiter<sup>2</sup>

It is possible that anthropogenic climate change will drive the Earth system into a qualitatively different state<sup>1</sup>. Although different types of uncertainty limit our capacity to assess this risk<sup>2</sup>, Earth system scientists are particularly concerned about tipping elements, large-scale components of the Earth system that can be switched into qualitatively different states by small perturbations. Despite growing evidence that tipping elements exist in the climate system<sup>1,3</sup>, whether large-scale vegetation systems can tip into alternative states is poorly understood<sup>4</sup>. Here we show that tropical grassland, savanna and forest ecosystems, areas large enough to have powerful impacts on the Earth system, are likely to shift to alternative states. Specifically, we show that increasing atmospheric CO<sub>2</sub> concentration will force transitions to vegetation states characterized by higher biomass and/or woody-plant dominance. The timing of these critical transitions varies as a result of between-site variance in the rate of temperature increase, as well as a dependence on stochastic variation in fire severity and rainfall. We further show that the locations of bistable vegetation zones (zones where alternative vegetation states can exist) will shift as climate changes. We conclude that even though large-scale directional regime shifts in terrestrial ecosystems are likely, asynchrony in the timing of these shifts may serve to dampen, but not nullify, the shock that these changes may represent to the Earth system.

Assessing the consequences of climate change for life on Earth is one of the major challenges facing science and society. There is growing evidence that tipping elements, large-scale components of the Earth system that can be switched into qualitatively different states by small perturbations, exist in the climate system<sup>1,3</sup>. There is also evidence that ecosystems may be subject to analogous tipping phenomena. Such regime shifts have been observed locally<sup>5</sup>, but whether such shifts occur at regional scales remains speculative. The terrestrial ecosystem where regime shifts are most likely to have powerful repercussions on the Earth system is the vast savanna complex, a term we use to refer to grassland, savanna and forest ecosystems of tropical and subtropical regions. Regime shifts of relevance to the Earth system are likely in the savanna complex because of the large area it covers and because savannas are known to shift into alternative states such as forest or grassland<sup>6–10</sup>. Indeed, the stability of savannas has long been questioned by biogeographers, who noticed that they do not seem to be in equilibrium with their climate in the same way that forests seem to be<sup>11</sup>. The Amazon basin is prominent example of a region in the savanna complex where shifts to alternative vegetation states are predicted. Several studies have shown that decreased rainfall over the Amazon would induce forest dieback, a process that would be reinforced and accelerated by feedbacks with the climate system<sup>1,3,12,13</sup>. Despite the fact that large proportions of the savanna complex seem to



**Figure 1 | Transitions between vegetation states projected for the period 1850–2100. a**, The projected changes in vegetation states. The percentages indicate the proportion of the African surface that will be in different vegetation states in 2100. The width of the arrows shows the relative frequency of the vegetation transitions projected to occur between 1850 and 2100. **b**, The distribution of the most common state transitions between C<sub>3</sub>-dominated

states (woodland, deciduous forest and evergreen forest) and C<sub>4</sub>-dominated states (C<sub>4</sub> grassland and savanna). **c**, The distribution of bistable zones in 1850 and 2100. Bistable zones are savannas and C<sub>4</sub> grasslands that would undergo a transition to C<sub>3</sub>-dominated states if fire were suppressed. **d**, Frequency distribution of the timing of transitions from C<sub>4</sub>-dominated to C<sub>3</sub>-dominated vegetation states. Error bars indicate s.e.m. for replicate simulations ( $n = 9$ ).

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be predisposed to regime shifts<sup>9,10</sup>, uncertainty in how climate and land use will change in these regions, coupled with uncertainty in the mechanisms driving change, hampers our ability to predict change<sup>14</sup>.

Addressing change in the savanna complex requires consideration of the physiological and demographic mechanisms that have been invoked to explain savanna dynamics. A mechanistic perspective needs to consider how the fundamentally different architectures of grasses and trees influence both their capacity to capture and use resources and their responses to fire<sup>15</sup>. A key physiological difference is that trees use the C<sub>3</sub> photosynthetic pathway, whereas most tropical grasses use the C<sub>4</sub> photosynthetic pathway. These differences yield robust predictions<sup>16</sup>: high temperatures and low CO<sub>2</sub> concentrations select for the C<sub>4</sub> photosynthetic pathway, whereas low temperatures and high CO<sub>2</sub> concentrations select for the C<sub>3</sub> photosynthetic pathway. According to leaf-level physiological models based on this mechanism<sup>16</sup>, a doubling of the CO<sub>2</sub> concentration from 350 to 700 p.p.m. and a 2–5 °C increase in temperature will favour C<sub>3</sub> over C<sub>4</sub> photosynthetic types. The implication is that, at the leaf level, the impacts of predicted CO<sub>2</sub> changes overwhelm the impacts of predicted temperature changes. In addition to carbon uptake, differences in carbon demand and carbon allocation need to be considered<sup>17</sup>. Trees in savannas have a higher carbon demand than grasses because, being trees, they require more carbon to deploy a unit of leaf area than grasses do and they need to allocate large amounts of carbon to ensure that they rapidly attain sizes that prevent serious injury in grass fires<sup>17,18</sup>. In summary, the carbon budget of trees in savannas stands to benefit from increased atmospheric CO<sub>2</sub> concentration because of increased carbon uptake capacity fuelled by a high carbon demand. These carbon benefits setup a positive feedback loop: more tree biomass serves to suppress grass production and hence the severity of fires, which further increases the likelihood of the system tipping from a C<sub>4</sub>-dominated state to a C<sub>3</sub>-dominated state<sup>9,19</sup>.

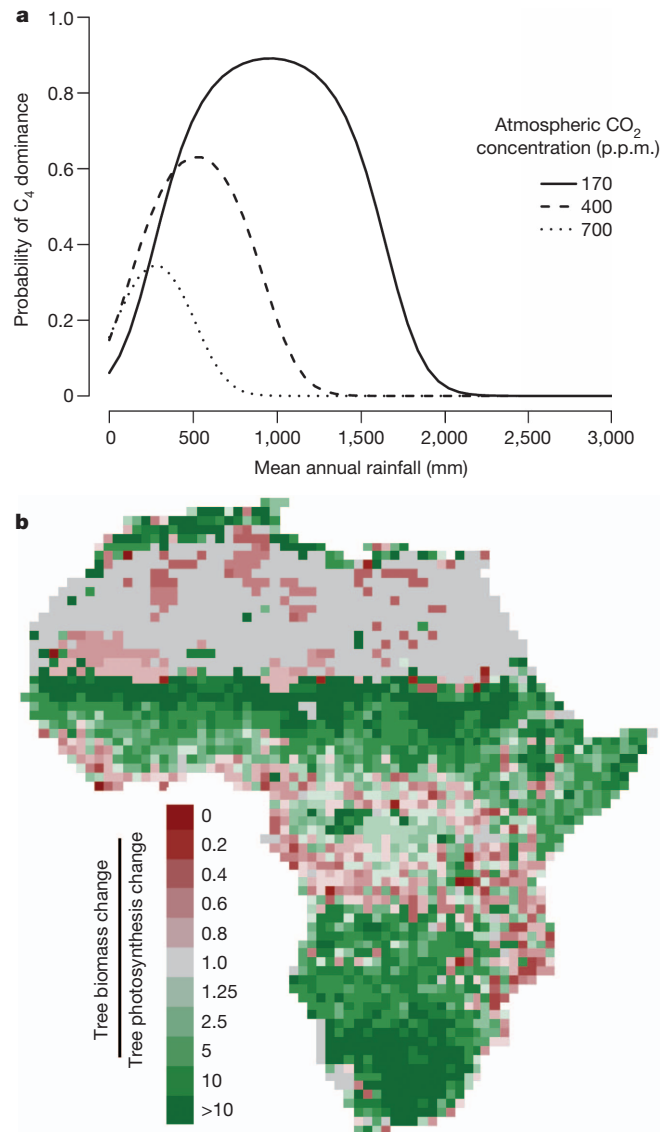
In this study we used a dynamic vegetation model<sup>20</sup> (see Supplementary Information) to assess vegetation shifts in grassland, savanna and forest formations that constitute the savanna complex. The model allows the assessment of shifts in the state of grassland, savanna and forest formations by explicitly considering how carbon assimilation may respond to atmospheric changes and how growth and resource competition interact with plant responses to injuries caused by fire (see Supplementary Information).

Our simulations of potential vegetation project marked shifts in vegetation state between 1850 and 2100 (Fig. 1a). There was a strong directionality in the shifts: deserts were replaced by grasslands, grasslands by savannas and woodlands, and savannas by forests (Fig. 1a). Collectively, the area occupied by C<sub>3</sub>-dominated (woodland, deciduous forest and evergreen forest) states increased from 31% to 47%. The area covered by savannas decreased from 23% to 14%, grasslands decreased from 18% to 16% and deserts from 28% to 23%. There was a clear geographical pattern to where these transitions occurred (Fig. 1b). In areas associated with and bounding on what are referred to as hot semi-arid climates in the Köppen–Geiger climate classification system<sup>21</sup>, the model projects that C<sub>4</sub>-dominated states (savanna and C<sub>4</sub> grassland) will undergo a transition to C<sub>3</sub>-dominated states (woodland, deciduous forest and evergreen forest). Further, the positions of bistable areas (areas that could be C<sub>3</sub>-dominated in the absence of fire, but are C<sub>4</sub>-dominated if fires occur) are projected to shift in location (Fig. 1c). Only a small overlap in the past and future distributions of bistable areas is projected. Moreover, most sites that are projected to remain C<sub>4</sub>-dominated (Fig. 1b, red pixels) are projected to switch to bistable states in 2100 (Fig. 1c, yellow pixels).

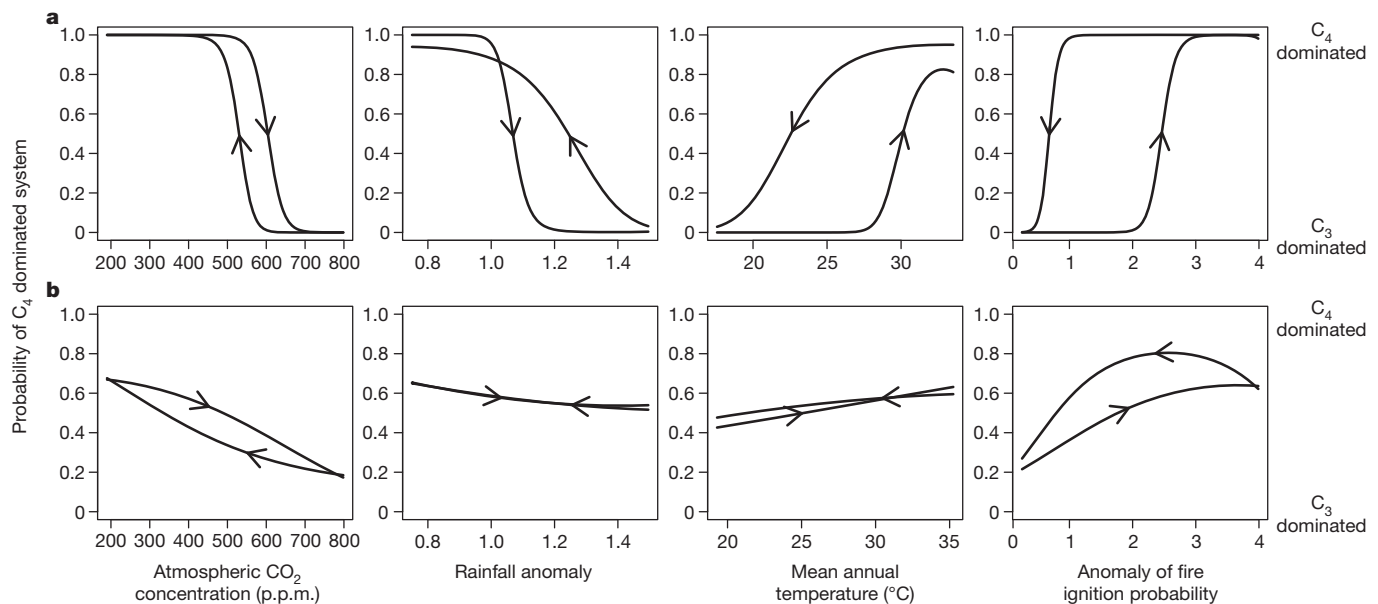
These marked shifts to woodland and forest have, according to the model, been occurring at low rates since 1850, but the rate of transition accelerates from 1.9‰ of the African land surface between 1990 and 2010 to 4.5‰ between 2010 and 2030, and to 11.2‰ between 2030 and 2050 (Fig. 1d). Although stochastic variation in the intensity of rainfall and fire events ensured that the confidence interval of a site's year of

transition spanned 48 years, the mean year when a site underwent a transition to a C<sub>3</sub> state was largely determined by the rate of temperature change at that site ( $F_{2,215} = 218.5$ ,  $P < 0.001$ ,  $R^2 = 0.67$ ). That is, those sites currently dominated by C<sub>4</sub> plants in which temperatures are projected to increase more rapidly shifted to C<sub>3</sub> dominance later. This is because the relatively rapid increase in temperature allows the C<sub>4</sub> plants to remain competitive for longer in the face of rising atmospheric CO<sub>2</sub> concentrations, which favour C<sub>3</sub> plants<sup>16</sup>.

To understand how moisture and atmospheric CO<sub>2</sub> interact to influence these changes (Fig. 1) we plot how the probability of vegetation being in a C<sub>4</sub>-dominated state changes with CO<sub>2</sub> concentration and rainfall (Fig. 2a). This plot reveals that at high CO<sub>2</sub> concentrations, C<sub>4</sub>-dominated states become more likely at sites with low rainfall (less than 250 mm), which explains why the model predicts that grasslands replace deserts (Fig. 1a). This interpretation is consistent with the



**Figure 2 | Sensitivity to rainfall and atmospheric CO<sub>2</sub> concentration.** **a**, The probability that a site will be C<sub>4</sub> dominated (C<sub>4</sub> grassland or savanna) as a function of rainfall for different atmospheric CO<sub>2</sub> concentrations. The data are from simulation runs for all sites in Africa. The low probability of C<sub>4</sub>-dominated ecosystems at low rainfall is because deserts are more likely at low rainfall, whereas at high rainfall C<sub>3</sub>-dominated ecosystems are more likely. **b**, The sensitivity of tree biomass change (the ratio of tree biomass in 2100 to that in 1850) to tree photosynthesis change (the ratio of tree photosynthesis in 2100 to that in 1850).



**Figure 3 | Hysteresis in vegetation state.** The probability that a site will be  $C_4$ -dominated ( $C_4$  grassland or savanna) as opposed to  $C_3$ -dominated (evergreen forest, deciduous forest or woodland) when forced by atmospheric  $CO_2$ , rainfall, mean annual temperature and fire ignitions. The arrows indicate whether the simulations were initiated with a low level of the forcing variable,

followed by an increase in the forcing variable or the converse (high initiation level, followed by a decrease). **a**, Local scale: responses estimated from 100 replicate simulations performed at a single site. **b**, Continental scale: estimates based on simulations replicated across Africa (excluding deserts and  $C_3$  grasslands).

theory that the water use efficiency of vegetation increases with atmospheric  $CO_2$  concentrations<sup>22</sup>. At the high end of the rainfall gradient (Fig. 2a), the shift to  $C_3$ -dominated states is both forced and catalysed by atmospheric  $CO_2$ . At pre-industrial  $CO_2$  concentrations,  $C_4$  dominance extends to regions with high rainfall (more than 1,500 mm), whereas at the  $CO_2$  concentrations expected in 2100,  $C_4$ -dominated states are restricted to regions with lower rainfall (less than 750 mm; Fig. 2a).

The trend towards increased woody biomass (Fig. 1a) is not a simple function of  $CO_2$  concentration; it is a function of the conditions under which  $CO_2$  fertilization shifts the competitive balance in favour of trees, setting up a positive feedback cycle involving light competition and fire suppression that further suppresses grasses and promotes trees<sup>8,9,17</sup>. This is illustrated by the large between-site differences in the sensitivity of change in tree biomass to changes in tree photosynthetic rate (Fig. 2b). That is, although small changes in photosynthetic rates can translate into large changes in woody biomass, this sensitivity is highly dependent on context.

Hysteresis, the dependence of a system's response to changes in forcing factors on its history, is an indicator of systems characterized by catastrophic regime shifts<sup>6</sup>. There was clear evidence of a hysteresis effect in the transition between  $C_3$ -dominated and  $C_4$ -dominated vegetation states at local scales (Fig. 3a). That is, the critical level of the environmental factor (be it  $CO_2$  concentration, rainfall, temperature or fire ignitions) required to force a transition to an alternative state was dependent on the system's historical states. When the results of the hysteresis simulations are averaged over the African continent, the hysteresis signal is removed or considerably weakened (Fig. 3b). This is simply because each site has its own critical threshold that is determined by site-specific environmental covariates; averaging over these covariates removes the hysteresis signal. The implication is that although abrupt regime shifts may be observed at local sites (Fig. 3a), these shifts will, when averaged over a continent, seem to occur smoothly (Fig. 3b). The consequence of this averaging effect is that any impulse to the atmosphere arising from the terrestrial land surface of the savanna complex may be smoothed.

Our findings that shifts from  $C_4$ -dominated to  $C_3$ -dominated ecosystems are to be expected in the savanna complex are consistent

with empirical observations<sup>23–25</sup>, with chamber experiments on the response of savanna trees and  $C_4$  grasses to atmospheric  $CO_2$  concentration<sup>26</sup>, and with leaf physiological models<sup>16</sup>. Although these projections of increasing tree dominance seem to contradict studies that project forest dieback in the Amazon<sup>12</sup>, this may simply be because our analysis assumes that rainfall remains constant, whereas projections of Amazon forest dieback are based on climate simulations that project decreased rainfall<sup>14</sup>. The high uncertainty in precipitation change over Africa led us to assume that rainfall remained at ambient levels (see Supplementary Information), but future studies should consider changes in rainfall as well as feedbacks between vegetation and rainfall<sup>13</sup>.

Here we have shown that although abrupt shifts in vegetation states are possible at the local scale, the timing of these shifts will not be coincident at the continental scale. The implication is that although a considerable proportion of the African continent will—land use allowing—shift to more woody vegetation states, these continental changes will be spread over a longer period than local scale analyses suggest. This study, together with palaeoecological evidence<sup>27</sup>, suggest that atmospheric  $CO_2$  has been and will be a major factor shaping vegetation change.

## METHODS SUMMARY

We used the aDGVM (adaptive Dynamic Global Vegetation Model), a dynamic global vegetation model<sup>20</sup> (see Supplementary Information). The aDGVM integrates plant physiological processes generally used in dynamic global vegetation models (DGVMs<sup>28</sup>) with novel submodels that allow plants to dynamically adjust carbon allocation and leaf phenology to environmental conditions. The model considers four basic functional types: a savanna tree, a forest tree, a  $C_4$  grass and a  $C_3$  grass. We used a simplified dichotomous scheme to classify model output into seven vegetation types. We identified areas of vegetation change by running forward simulations for Africa at a  $1^\circ$  grid resolution for the period between 1850 and 2100 under Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios (SRES) A1B projection provided by ECHAM5 (ref. 29). The large uncertainty in precipitation projections for Africa led us to assume that rainfall remained at ambient levels<sup>30</sup> (see Supplementary Information). The simulations focus on potential vegetation; in other words, land-use impacts are ignored. Testing whether the model system exhibited hysteresis effects was achieved by first increasing an environmental factor linearly from a low level to a high level and by decreasing the environmental factor linearly from a high level to a low level.

**Full Methods** and any associated references are available in the online version of the paper.

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## METHODS

**Basic model structure.** We used the aDGVM (adaptive Dynamic Global Vegetation Model), a dynamic global vegetation model<sup>20</sup>. A complete description is provided in ref. 20; we provide only a summary here. The aDGVM integrates plant physiological processes generally used in dynamic global vegetation models (DGVMs<sup>28</sup>) with novel submodels that allow plants to dynamically adjust carbon allocation and leaf phenology to environmental conditions. The aDGVM is individual-based, which means that it keeps track of state variables such as above-ground and below-ground biomass, height, leaf area index and leaf phenological status for individual plants. The model considers four basic functional types: a savanna tree, a forest tree, a C<sub>4</sub> grass and a C<sub>3</sub> grass (see Supplementary Information). For this study we used a simplified dichotomous scheme to classify model output into seven vegetation types (Supplementary Fig. 1).

**Simulation experiments.** We simulated the potential vegetation of Africa at a 1° grid resolution for the period between 1850 and 2100 under Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios (SRES) A1B projection provided by ECHAM5 (ref. 29). The use of other scenarios does not qualitatively change our results. Because of the large uncertainty in the precipitation projections of the IPCC SRES simulations we assume that precipitation remains as defined by the Climate Research Unit's empirical climate data<sup>30</sup>. For all simulations, the model was initialized with 100-year spin-up using the environmental conditions of 1850.

**Forward simulations.** We ran forward simulations from 1850 to 2100. Nine replicate simulations with and without fire were performed. Each simulated grid cell was classified into one of the seven vegetation types (Supplementary Fig. 1). There was high spatial agreement between the maps produced by replicate simulations ( $\kappa > 0.75$ ). We calculated the transition rates between the different vegetation types observed between 1850 and 2100 (Fig. 1a) in the presence of fire. We plotted, for the most frequent transition categories, where these transitions occur in Africa (Fig. 1b). We plotted the distribution of bistable sites (C<sub>4</sub> grasslands and savannas that could be C<sub>3</sub>-dominated (woodland, deciduous forest or evergreen forest) if fire were suppressed) for 1850 and 2100 (Fig. 1c).

We ran 100 replicate simulations for each grid cell and estimated the year in which transitions from C<sub>4</sub>-dominated systems (C<sub>4</sub> grassland and savanna) to C<sub>3</sub>-dominated systems (woodland, deciduous forest and evergreen forest) occurred (Fig. 1d). Stable estimates of the mean time of transition for grid cells were obtained for sample sizes of 50 replicate simulations. The 95% confidence interval of the year in which a transition was observed in an individual grid cell spanned 48 years. Linear regression models were used to identify which factors influenced the mean time at which a transition occurred.

**Sensitivity to CO<sub>2</sub> and rainfall.** Simulations were run for constant CO<sub>2</sub> concentrations (170, 400 and 700 p.p.m.) and ambient climatic conditions for all Africa. These simulations were summarized by using a logistic regression to estimate how rainfall influenced the probability of vegetation being in a C<sub>4</sub>-dominated state (C<sub>4</sub> grassland and savanna; Fig. 2a).

The forward simulations were used to calculate the sensitivity of tree biomass change to changes in the photosynthetic rates of trees (Fig. 2b). This sensitivity was defined as (tree biomass at 2100/tree biomass at 1850)/(tree photosynthesis at 2100/tree photosynthesis at 1850); high sensitivity would imply that a small change in the photosynthetic rate of trees produces a large change in tree biomass. The photosynthetic rates are the potential photosynthetic rates (assuming saturating moisture supply, but variation in CO<sub>2</sub>, incoming photosynthetically active radiation and temperature with site)<sup>30</sup>.

**Hysteresis effects.** Simulation experiments were conducted to explore whether the model showed hysteresis effects when vegetation underwent a transition between C<sub>4</sub>-dominated (C<sub>4</sub> grassland and savanna) and C<sub>3</sub>-dominated (woodland, deciduous forest and evergreen forest) states. We set all environmental conditions to ambient<sup>30</sup> conditions. For selected environmental factors (atmospheric CO<sub>2</sub> concentration, mean annual temperature anomaly, mean annual precipitation anomaly and fire ignition anomaly) we first increased the environmental factor linearly from a low level to a high level and then decreased the environmental factor linearly from a high level to a low level. The low and high levels for CO<sub>2</sub> were 190 p.p.m. and 800 p.p.m., respectively. The temperature anomaly was -8 °C to +8 °C relative to ambient. The mean annual precipitation anomaly was 0.75–1.5 of ambient. The fire ignition anomaly was 0–4 of the standard ignition probability. The period over which we increased and decreased the forcing variable was 350 years. Spin-up for these simulations involved running the model for 100 years at the high or low level of the forcing variable, with other parameters being set to ambient.

In a first hysteresis experiment we ran 100 replicate simulations for a single site (25° S, 31° 35' E; 570 mm mean annual precipitation). For these simulations CO<sub>2</sub> was set to 550 p.p.m. because this was, for this site, the CO<sub>2</sub> concentration required for shifts from savanna to woodland and/or forest. At the continental scale, we simulated vegetation of Africa at a 2° grid resolution. In each simulation year we recorded whether each replicate simulation was in a C<sub>4</sub>-dominated or a C<sub>3</sub>-dominated state. For the local scale simulations these replicates were 100 repeat simulations at a single site. For the continental scale simulations the replicates were each pixel in the 2° grid of Africa. These data were then summarized using a logistic regression, with C<sub>4</sub>-dominated or C<sub>3</sub>-dominated as the binary response variable, and the forcing factor (atmospheric CO<sub>2</sub> concentration, mean annual temperature anomaly, mean annual precipitation anomaly or fire ignition anomaly) as the independent variable (Fig. 3).