

OPINION

The origin of the savanna biome

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Abstract

Savannas are a major terrestrial biome, comprising of grasses with the C₄ photosynthetic pathway and trees with the C₃ type. This mixed grass–tree biome rapidly appeared on the ecological stage 8 million years ago with the near-synchronous expansion of C₄ grasses around the world. We propose a new hypothesis for this global event based on a systems analysis that integrates recent advances in how fire influences cloud microphysics, climate and savanna ecology in a low carbon dioxide (CO₂) world. We show that fire accelerates forest loss and C₄ grassland expansion through multiple positive feedback loops that each promote drought and more fire. A low CO₂ atmosphere amplifies this cycle by limiting tree recruitment, allowing the ingress of C₄ grasses to greatly increase ecosystem flammability. Continued intensification of land use could enhance or moderate the network of feedbacks that have initiated, promoted and sustained savannas for millions of years. We suggest these alterations will overprint the effects of anthropogenic atmospheric change in coming decades.

Keywords: carbon dioxide, C₄ photosynthesis, cloud physics, feedbacks, fire, smoke, systems analysis

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Introduction

Savannas are one of the world's major terrestrial biomes, comprising of a dynamic mixture of trees and grasses that encompasses open woodland and grassland (Fig. 1, Sankaran *et al.*, 2005). At the global scale, they cover an area of some 33 million km² (Fig. 1, Ramankutty & Foley, 1999), are inhabited by one-fifth of the world's population and subject to intense human exploitation by conversion to agricultural and grazing land (Hoffmann *et al.*, 2002). The warm savanna grasses have evolved the C₄ photosynthetic pathway (Sage, 2004), greatly increasing photosynthetic efficiency in hot conditions or when atmospheric carbon dioxide (CO₂) is scarce (Ehleringer & Björkman, 1977), whereas trees utilize the ancestral C₃ type. The different photosynthetic pathways impart distinctive carbon isotope signatures on plants, soil carbonates and herbivore teeth that have been exploited to reveal a dramatic near-synchronous expansion of C₄ grasses around the world within about a million years (Ma) (Cerling *et al.*, 1997). This global event dates the origin of the modern savanna biome to the late Miocene, ~8 Ma (Fig. 2a–c) (Cerling *et al.*, 1997).

Explaining the geologically rapid appearance of C₄ savanna ecosystems onto the ecological stage remains a major scientific challenge. The leading hypothesis posits that atmospheric CO₂ fell below a critical threshold during the Miocene, where the photosynthetic efficiency of C₃ plants dropped below that of their C₄ counterparts (Ehleringer *et al.*, 1991; Cerling *et al.*, 1997). However, subsequent evaluation of this 'CO₂ starvation hypothesis' with multiple atmospheric CO₂ proxy records (Pagani *et al.*, 1999; Pearson & Palmer, 2000; Royer *et al.*, 2001) has consistently failed to show the anticipated decrease at any time during the entire 18 Ma duration of the Miocene (Fig. 2a) (Osborne & Beerling, 2006). In fact, declining CO₂ had already breached a critical threshold some 20 Ma earlier in the Oligocene, an event linked with the origin of the C₄ pathway (Pagani *et al.*, 2005; Tripathi *et al.*, 2005). Atmospheric CO₂ decline is, therefore, unlikely to be the sole driver of worldwide C₄ savanna expansion. Consequently, the well-documented rise of this extraordinarily successful terrestrial biome continues to demand explanation (Osborne & Beerling, 2006).

Here, we develop recent ideas about the origin of C₄ ecosystems by using systems analysis to integrate and synthesize the tremendous growth in knowledge of interactions between tropical savannas and the Earth system. The novel aspect of our work is its integration

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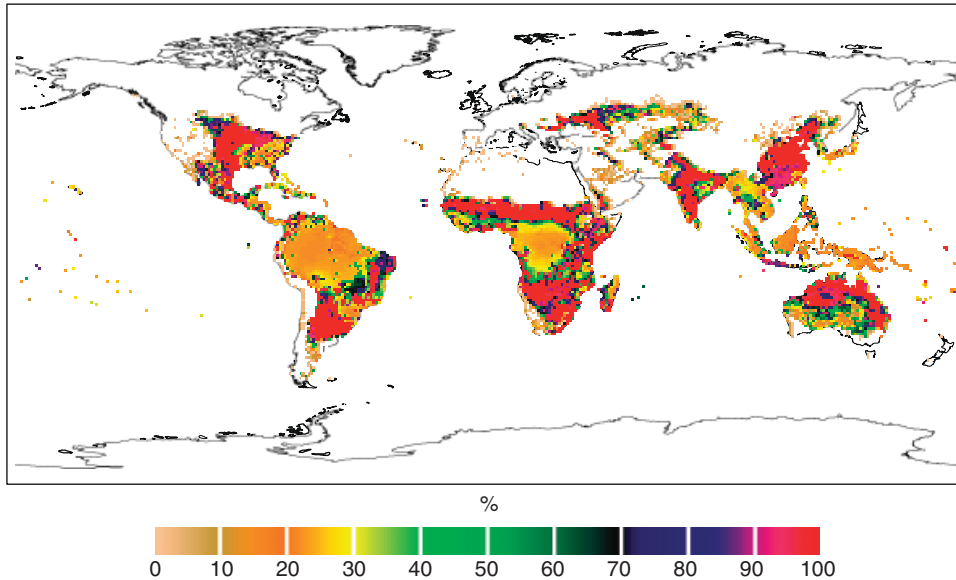


Fig. 1 Global distribution of modern C_4 savannas and grasslands (from Woodward *et al.*, 2004). Reproduced with permission of The Royal Society.

of recent advances in our understanding of how fire and smoke influence climate (Andreae *et al.*, 2004; Koren *et al.*, 2004), with previous work on savanna ecology in a low- CO_2 world (Bond & Midgley, 2000; Keeley & Rundel, 2003, 2005; van Langevelde *et al.*, 2003). The approach is extended to show why CO_2 starvation of the terrestrial biosphere is an essential primer of the Earth system for the origination of C_4 savanna ecosystems, and how the coevolution of herbivores (Janis *et al.*, 2000; MacFadden, 2000; Bond & Keeley, 2005) acts to disrupt or enhance the network. Continued anthropogenic global change and the intensification of land use will alter the future ecological success of savannas by acting in a predictable way on the feedback cycles.

Systems analysis is a concept borrowed from information theory (Forrester, 1971; Senge, 1990). It provides a powerful approach for analysing complex networks that has proved of great utility for discovering the existence and sign of potential feedback loops between and within biological and physical systems (Kump, 1988; Berner, 1999, 2004; Cochrane, 2003; Somerville *et al.*, 2004; Beerling & Berner, 2005). Our qualitative analyses are based on a synthesis of the literature focusing on three systems relevant to the origination of savannas, with fire, CO_2 and herbivores as the central nodes. The feedback diagrams that emerge are then interpreted to determine the number and nature of positive and negative feedback loops involved in the origination of savannas.

A network of fire–cloud–climate feedbacks

Our systems analysis begins with fire. C_4 savannas are the most frequently burned ecosystems in the world,

with fires typically every 2–3 years (Hoffmann *et al.*, 2002) and sometimes twice a year (Cochrane *et al.*, 1999). Fire initiates and sustains the savanna biome by removing and preventing the encroachment of forests (van Langevelde *et al.*, 2003; Bond *et al.*, 2005; Sankaran *et al.*, 2005) and becomes a feature of these ecosystems when C_4 grasses establish into forest gaps created by the death of trees during drought (Fig. 3, pathway *a–b–c–d*). As patches of C_4 grasses spread, the biomass they produce in the wet season increases fire frequency and severity by supplying abundant fuel in the dry season (Keeley & Rundel, 2005). In today's world, this feedback loop is estimated to maintain more than half of the land surface currently classified as C_4 savanna (Bond *et al.*, 2005).

Loss of forest cover entrains major changes in the hydrological cycle, slowing evapotranspiration and cloud formation, and reducing regional precipitation (Shukla & Mintz, 1984, Fig. 3, pathway *e–h*). Climate models indicate that the deforestation of Amazonia could decrease regional precipitation by 25% (Hayden, 1998). Tropical forests and grassland also recycle evapotranspiration with greatly differing efficiencies; Amazonian forests supply 88% of their own rainfall, whereas the short grasslands of the central Great Plains contribute only 15% (Hayden, 1998). Deforestation causes a longer dry season that enhances ecosystem susceptibility to fire (Fig. 3, pathway *e–h–o–i–a–b*) and causes further tree mortality, which accelerates the expansion of C_4 grasses (Fig. 3, pathway *e–h–o–j–b*).

Two major suites of positive feedbacks amplifying the central vegetation–fire and deforestation–fire pathways (*a–b–c–d* and *a–b–e–h–o–i*) are demonstrated by meteor-

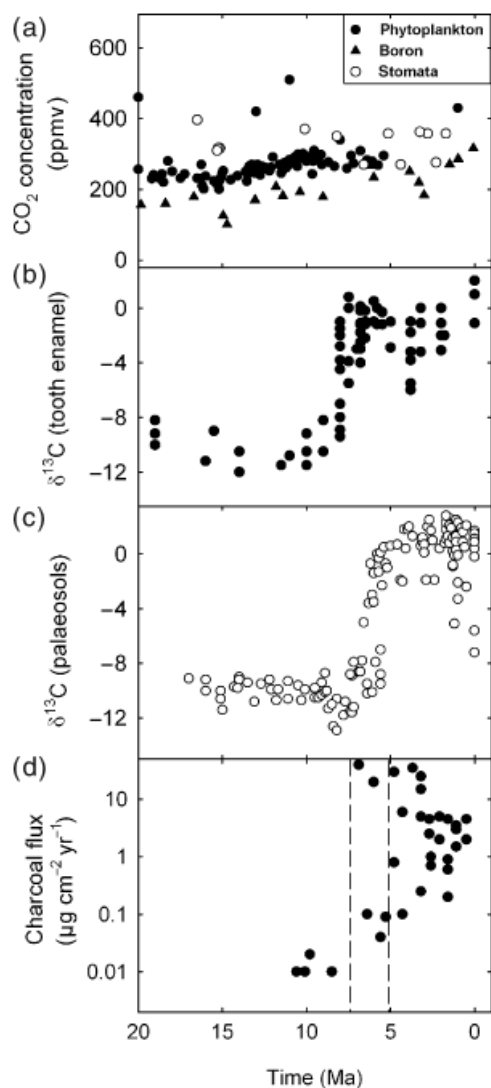


Fig. 2 Multiproxy records of vegetation and environmental change in the Tertiary. (a) Atmospheric CO₂ estimates from three independent proxies (Pagani *et al.*, 1999; Pearson & Palmer, 2000; Royer *et al.*, 2001). (b) Shifts in the carbon isotopic composition of the fossilized teeth of herbivores from East Africa (Cerling *et al.*, 1997). (c) Carbon isotope shifts in fossil soils (paleosols) from Pakistan (Cerling *et al.*, 1997), and (d) Changes in charcoal fluxes to western Pacific deep-ocean sediment cores from DSDP sites 302, 305 and 310 (Herring, 1985). Vertical dashed lines delineate the critical region of C₃ to C₄ transition.

ological observations in the troposphere above the savanna-forest boundary in Amazonia (Andreae *et al.*, 2004; Koren *et al.*, 2004; Cui *et al.*, 2006). The first operates via the effects of black smoke aerosols on the hydrological cycle. Black aerosols absorb solar radiation, heating the troposphere and reducing the net flux of energy to the Earth's surface (Menon *et al.*, 2002). This slows evaporation and cloud formation, and decreases

precipitation; although this effect may be exerted in a region at some distance from the fires themselves and is likely to occur mainly during the transition from dry to wet seasons. Tropospheric heating also indirectly diminishes precipitation at the regional scale via effects on atmospheric circulation (Graf, 2004; Lui, 2005). These pathways impact on fire (Fig. 3, pathway *f-g-h-o-i*) and tree mortality (Fig. 3, pathway *f-g-h-o-j-b-c-d*) by intensifying drought and leading to further positive feedbacks on C₄ grass expansion (Fig. 3 pathways *f-k-n-o-i* and *f-k-n-o-j-b-c-d*). Slowing of the hydrological cycle and reduced washing of aerosols from the atmosphere may increase the efficiency of these processes. Offsetting these effects may be an increase in soil moisture arising from reduced evapotranspiration.

In the second suite of feedbacks, smoke aerosols reduce the size of cloud droplets, strengthening convection to increase cloud longevity and make precipitation less frequent but more intense (Koren *et al.*, 2004). Extreme precipitation events in seasonally dry regions increase run-off, meaning that less water infiltrates into the soil. Sudden downpours from smoky clouds could, therefore, effectively reduce water availability, promote tree mortality and fire, and further reinforce the spread of C₄ savannas (Fig. 3, pathways *f-l-m-o-i* and *f-l-m-o-j-b-c-d*). Strong convection in smoky clouds also impacts on the transport of latent heat to the free troposphere, leading to significant shifts in tropical circulation patterns (Andreae *et al.*, 2004) and the potential for regional drying. A further direct result of fire is the formation of deep convective 'pyroclouds' above heavy smoke (Andreae *et al.*, 2004; Fromm *et al.*, 2005, 2006). As with smoky clouds, these cause intense thunderstorms, increasing lightning activity and igniting more fires (Fig. 3, pathway *p-q-r*).

The effects of trace gases released from savanna fires (Andreae & Merlet, 2001) could also entrain a further set of climatic feedbacks, which are not illustrated because the direction of change is highly uncertain without further model simulations. These can alter the oxidizing power of the troposphere, and the concentration and lifetime of greenhouse gases like CH₄ and O₃ (Lelieveld *et al.*, 2001; Hobbs *et al.*, 2003; Randerson *et al.*, 2005). Savanna fires are especially important sources of NO_x (NO + NO₂) contributing over half of that released by wildfire (Hobbs *et al.*, 2003), a source also augmented by increased lightning activity. NO_x is a necessary ingredient for tropospheric O₃ formation. Increased NO_x production therefore boosts the photochemical formation of tropospheric O₃, as observed in smoke plumes above savanna fires (Randerson *et al.*, 2005) and at the regional scale over southern Asia (Lelieveld *et al.*, 2001), with a potential feedback on climate.

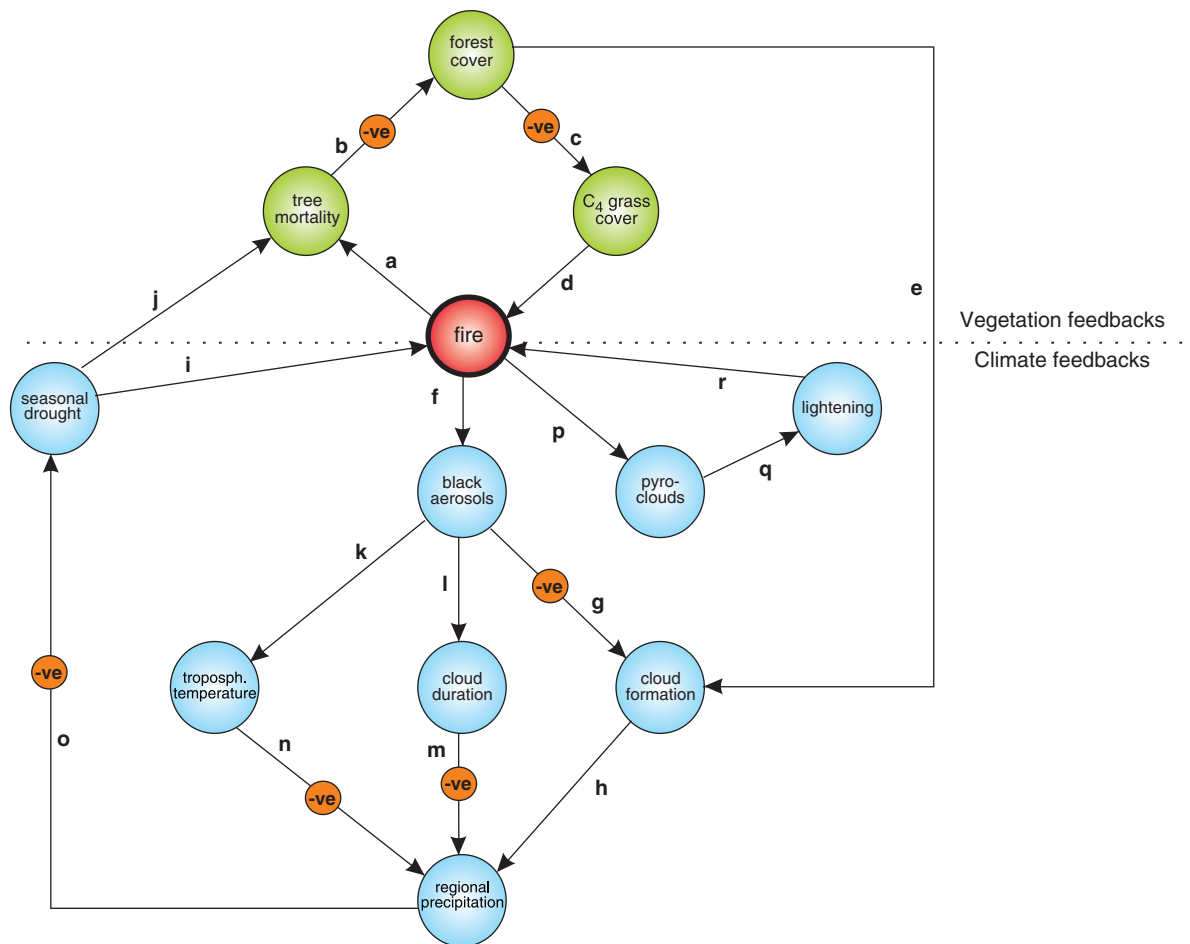


Fig. 3 A systems analysis of fire–climate feedbacks. Arrows originate with causes and end at effects. Plain arrows indicate direct responses, and arrows marked with $-ve$ symbol show inverse responses. Closed loops with an even number of $-ve$ labelled arrows or solely plain arrows are positive feedbacks, and those with an odd number of arrows with $-ve$ labels are negative feedbacks.

Positive feedback loops sustain the savanna biome

A remarkable emergent property of the network of interactions involving fire, smoke, climate and vegetation is that all of the feedback loops are positive (Fig. 3), creating a strongly self-reinforcing system that sensitizes vegetation to climate change. Accordingly, once initiated by external forcing, forest deterioration is accelerated inexorably towards the creation of the new C₄ savanna biome.

In southern Asia, forcing was likely provided during the Miocene by an increase in the severity of the dry season due to changes in monsoonal activity (Quade *et al.*, 1995), and ocean circulation (Mikolajewicz & Crowley, 1997; Gupta *et al.*, 2004; Diester-Hass *et al.*, 2005), and might even have involved the increased flux of interplanetary dust particles from an asteroid break-up (Farley *et al.*, 2006). Here, a manifestation of the newly proposed feedbacks might be the remarkable > 1000-fold increase in charcoal flux seen in deep-ocean

sediment cores of the western Pacific (Fig. 2d). The wind-blown charcoal originates in southern Asia (Herring, 1985; Keeley & Rundel, 2003, 2005), and contains charred fragments of grasses and wood (Herring, 1985). However, we note that well-documented increases in wind strength in the late Miocene (Rea & Janecek, 1982) could play a role in transporting the charcoal, and resolving its importance will hinge on documenting changes in the relative abundance of grasses and wood. Nevertheless, this issue notwithstanding, we note that the marked increase in charcoal flux apparently lags the conversion of forests to C₄ savannas in India and Pakistan by about a million years (Fig. 2b–d), as expected if the feedbacks operated in the sequence of climate change, vegetation response, and then fire.

Elsewhere in Central Africa, another key region of C₄ savannas, sharp increases in the abundance of charred grass cuticle from savanna fires have been reported in Atlantic Ocean sediments from the Niger Delta dating

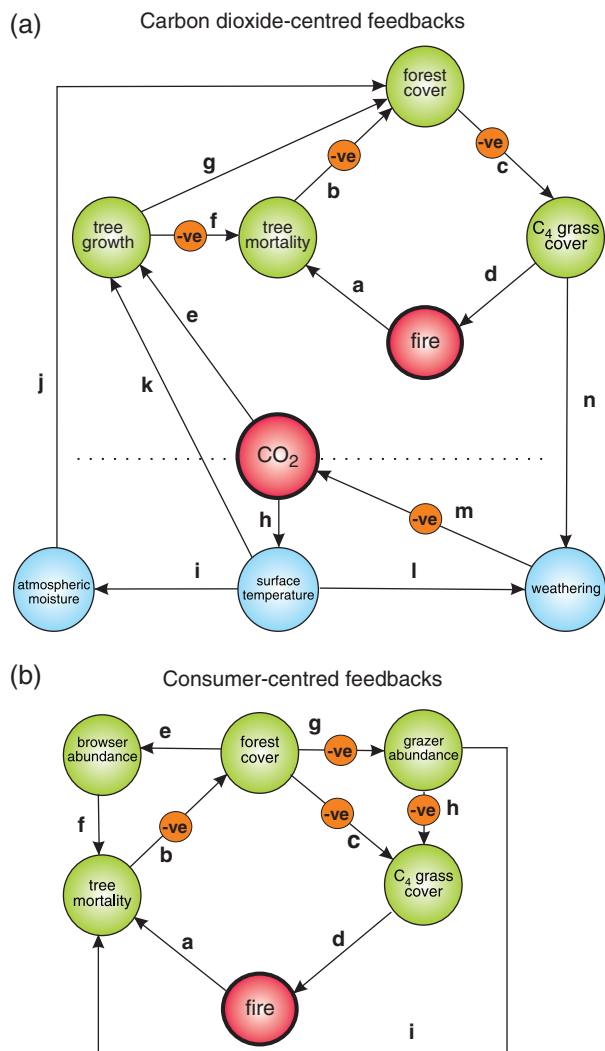


Fig. 4 Systems analyses of vegetation–fire feedbacks. (a) CO₂-centred mechanisms. (b) Consumer-centred processes. Key to interpreting diagram as in Fig. 3.

to 8 Ma ago (Morley & Richards, 1993; Retallack, 2001). Pollen evidence suggests these episodes of increased wildfire coincided with a drying of climate and the expansion of grasslands during the Miocene (Morley & Richards, 1993).

It is too early to say if sharp increases in the abundance of burned plant materials represent the ‘smoking gun’ for fire regime change in the sub-tropics; the data are simply too sparse in the critical region of transition. Certainly, it is not beyond the reach of modern geochemistry to bring the picture into sharper focus. In our view, this will entail high-resolution studies of the nature of the charcoal and its stable carbon isotope biomarker signature in marine sediments from the Indian Ocean as well as the Atlantic and Pacific. We suggest that the ‘fire–climate feedbacks hypothesis’ is

sufficient to explain the rapid transformation of forests to savanna across Old World continents in the Miocene, and contributes to the ecological success of savanna ecosystems in the present day.

Reprising the role of atmospheric CO₂ – priming the earth system

Even given their uncertainties, of the available proxy CO₂ records establish that the terrestrial biosphere experienced CO₂ starvation throughout the Miocene (Fig. 2a). In our view, this is not only an essential precondition for the fire–climate feedbacks hypothesis, but also entrains further important positive feedbacks within the long-term carbon cycle promoting the ecological success of C₄ savannas.

Preconditioning by low CO₂ operates by limiting the photosynthetic efficiency and growth rate of tree seedlings, preventing them from reaching the minimum height required to become fire-proof, and increasing the vulnerability of forest recruitment to fire (Bond & Midgley, 2000, Fig. 4a, pathway e–f). The Earth system is primed further by a global contraction in forest cover due to CO₂-limited growth (Beerling & Woodward, 2001, Fig. 4a, pathway e–g), and the cooler drier climate that results from a weakened atmospheric greenhouse effect (Pagani *et al.*, 2005; Tripathi *et al.*, 2005, Fig. 4a, pathway h–k–g). In contrast, savanna grasses with the C₄ pathway benefit from their CO₂-concentrating mechanism, which allows photosynthetic efficiency and productivity to be maintained even under conditions of CO₂ starvation (Ehleringer & Björkman, 1977; Ehleringer *et al.*, 1991). These physiological advantages could, in part, underlie savanna expansion in the Zaire and Amazon Basins during the last glacial maximum when CO₂ was 50% lower than today (Cerling *et al.*, 1998; Mayle *et al.*, 2004).

Together, these pathways (Fig. 4a, e–f, e–g and h–k–g) feed into and accelerate the closed positive feedback loop involving fire, tree mortality, forest cover and C₄ grass cover (Figs 3 and 4a, pathway a–b–c–d). Striking evidence for this effect is recorded in pollen and charcoal records from lake sediments in the Wonderkrater, South Africa, where savanna trees were absent during the last ice age. At this time, CO₂ concentrations were 50% lower than today’s value and fires more frequent (Scott, 2002). Trees only re-established at the site 10 kyr ago, after CO₂ had risen to its preindustrial level and the incidence of fire had declined (Scott, 2002).

Global shrinkage of forests in a CO₂-depleted atmosphere slows biotic weathering of magnesium–calcium silicate rocks, the major sink for atmospheric CO₂ on geological timescales (Berner, 1999, 2004; Beerling & Berner, 2005). However, the corresponding expansion

of C₄ savannas may partially offset this effect (Fig. 4a, pathways *e-g-c-n-m* and *h-k-g-c-n-m*) helping to ensure that atmosphere CO₂ remains low, although a cooler climate will slow rates of silicate rock weathering (Fig. 4a, pathway *h-l-m*). The strength of this feedback is also likely to depend on the extension of C₄ plants to high altitudes (Ehleringer *et al.*, 1997; Mora & Pratt, 2002), where rates of silicate weathering tend to be enhanced by high erosion rates and the uplift and exposure of fresh unweathered materials (Berner, 2004). Nevertheless, the C₄ savanna biome may act to maintain atmospheric CO₂ concentration close to the minimum so far observed (~180 ppm), allowing C₄ grasses to flourish at the expense of C₃ forests.

Coevolution of savannas and herbivores

The Miocene origin of the savanna biome saw the assembly of new communities of large ungulate herbivores (including horses, rhinos, antelope and elephants), which radiated dramatically to exploit the newly available food resources and open habitats (Stebbins, 1981; Janis *et al.*, 2000; MacFadden, 2000). The evolutionary diversification of these animals introduced a number of distinct feedbacks, two of which are the only negative examples in our analyses. Within the scope of this article, we highlight only the three that impact most directly on the central fire-forest-C₄ grassland loop (Fig. 4b, pathway *a-b-c-d*).

As large browsers diversified and increased in abundance in the new open landscape, consumption and physical damage of young and mature trees reduced closed forest cover in a manner similar to fire. This, in turn, may have regulated populations of obligate browsers like giraffes through a negative feedback loop (Fig. 4b, pathway *f-b-e*). However, according to our systems analysis, the feedback could have selected strongly for mixed feeders like elephants (which browse and graze) in southern Asia and Africa (Cerling *et al.*, 1998) by increasing the gain on pathway *a-b-c-d* (Fig. 4b).

The evolution of grazing herbivores in the late Miocene (Stebbins, 1981; Janis *et al.*, 2000; MacFadden, 2000) acted in the opposite manner, through a negative feedback loop, to reduce the gain on the same pathway. By selectively feeding on grasses, obligate grazers reduce the flammability of the ecosystem by lowering fuel load and indirectly allowing greater tree survivorship (Fig. 4b, pathway *h-d-a-b*), although the feedback may be less critical in tall mesic grasslands comprised of unpalatable species (Bond *et al.*, 2003). Furthermore, contraction of forest cover and grassland expansion would have reinforced this negative feedback loop by supporting larger grazer populations (Fig. 4b, pathway *g-h-d-a-b*). However, grazers may alternatively have engen-

dered a positive feedback loop because many species also consume and trample tree seedlings, reinforcing further savanna expansion (Fig. 4b, pathway *i-b-g*). The effects of herbivore evolution are therefore complex, entraining both positive and negative feedbacks, and will require quantitative modelling to elucidate their net direction and strength.

If negative, the feedbacks linked with herbivore evolution may act as a 'biotic brake' on savanna expansion, applied on the timescale of speciation that counteracts the physical feedbacks already uncovered. Today, these consumer feedbacks are presumably weakened considerably by the extinction of 65% of large mammal species that took place during the late Pleistocene (50–10 ka) (Barnosky *et al.*, 2004).

The future of the savanna biome

Anthropogenic forcing of the climate system and the human intensification of land use are the major determinants of the ecological future of savannas. Continued accumulation of greenhouse gases in the atmosphere is expected to raise global temperatures and atmospheric moisture content, as occurred during the Paleocene–Eocene thermal maximum, 55 Ma ago (Bowen *et al.*, 2004). Together with rising CO₂, these are likely to stimulate tree growth and forest cover (Beerling & Woodward, 2001) (Fig. 4a, pathways *e-g*, *h-k-g* and *h-i-j*), decelerating the positive feedback loop *a-b-c-d* (Fig. 4a). If future global change acts through these pathways over the coming decades, it will shift the dynamic balance of savanna tree-grass mixtures to favour the spread of woody plants (Bond & Keeley, 2005), unless prevented by land management practices.

The foremost land-use changes in Amazonia are the conversion of forest to pasture and the partial logging of forests, which increase the accidental ignition and severity of forest fires. These feed into the positive feedback loop *a-b-c-d* (Fig. 3) and threaten the integrity of large areas of tropical forest by accelerating its rapid conversion towards C₄ savannas (Cochrane *et al.*, 1999). In contrast, the effects of land use in savannas depend crucially on whether the exploitation of ecosystem resources centres on trees or grasses. Shrub and tree clearance for firewood, croplands and pastures causes a warming and drying of climate distinct from the radiative effects of smoke (Fig. 3, pathway *f-g-h-o-i*), but nevertheless promotes fire, doubling the loss of woody vegetation (Hoffmann *et al.*, 2002). Complete removal of trees from tropical savannas may increase fire frequency by up to 50% through this mechanism. Elsewhere, grazing by domestic animals breaks the fire cycle through pathways already described (Fig. 4b) restoring savanna by allowing encroachment of woody

plants (Briggs *et al.*, 2005). Given the chronic population pressures on the savanna biome, we suggest that land-use practices are likely to overprint any influence exerted by CO₂ and climate change in the coming decades.

Conclusions

Research over the past decade has revealed considerable evidence for a network of feedbacks that may explain the origin of savannas in the late Miocene. However, it will only be possible to place the smoke-climate pathways on a quantitative basis by using a nested hierarchy of model simulations; from local convective cloud models adapted for biomass burning (Trentmann *et al.*, 2003) through to larger self-organizing convection models (Nober & Graf, 2004) and dynamic global models of vegetation (Beerling & Woodward, 2001).

The role of feedbacks in the origination of C₄-dominated ecosystems in the New World remains to be satisfactorily explained (Osborne & Beerling, 2006). In North and South America, C₃ rather than C₄ grasslands replaced forests in the early Miocene, only to be succeeded by C₄ savannas at around the same time as those elsewhere in the Old World (Fox & Koch, 2003; Strömberg, 2004). Regional climate change is a likely candidate mechanism for this sequence because C₃ steppe grasslands require less precipitation than mesic C₄ savanna grasses (Retallack, 1997), but this possibility requires further investigation. Without the proposed fall in atmospheric CO₂ during the Miocene it is also now necessary to explain why northern hemisphere savannas originated in a latitudinal wave from the hot equator to the cooler climes of North America. The CO₂ starvation hypothesis had offered an elegant explanation because falling CO₂ lowers the temperature at which C₄ plants gain a photosynthetic advantage (Cerling *et al.*, 1997). We suggest that explaining the striking spread of savannas across the world will require attention to shift towards records of biomass burning in marine sediments as well as new detailed paleoclimatic records of regional climatic change.

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References

Andreae MO, Merlet P (2001) Emission of trace gases and aerosols from biomass burning. *Global Biogeochemical Cycles*, **15**, 955–966.

- Andreae MO, Rosenfield D, Artaxo P *et al.* (2004) Smoking rain clouds over the Amazon. *Science*, **303**, 1337–1342.
- Barnosky AD, Koch PL, Feranec RS *et al.* (2004) Assessing the causes of late Pleistocene extinctions on the continents. *Science*, **306**, 70–75.
- Beerling DJ, Berner RA (2005) Feedbacks and the coevolution of plants and atmospheric CO₂. *Proceedings of the National Academy of Sciences*, **102**, 1302–1305.
- Beerling DJ, Woodward FI. (2001) *Vegetation and the Terrestrial Carbon Cycle. Modelling the First 400 Million Years*. Cambridge University Press, Cambridge.
- Berner RA (1999) A new look at the long-term carbon cycle. *GSA Today*, **9**, 1–6.
- Berner RA (2004) *The Phanerozoic Carbon Cycle: CO₂ and O₂*. Oxford University Press, New York.
- Bond WJ, Keeley JE (2005) Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, **2**, 387–394.
- Bond WJ, Midgley GF (2000) A proposed CO₂-controlled mechanisms of woody plant invasion in grasslands and savannas. *Global Change Biology*, **6**, 865–869.
- Bond WJ, Midgley GF, Woodward FI (2003) What controls South African vegetation – climate or fire? *South African Journal of Botany*, **69**, 79–91.
- Bond WJ, Woodward FI, Midgley GF (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, **165**, 525–538.
- Bowen GJ, Beerling DJ, Koch PL *et al.* (2004) A humid climate state during the Palaeocene/Eocene thermal maximum. *Nature*, **432**, 495–499.
- Briggs JM, Knapp AK, Blair JM *et al.* (2005) An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *Bioscience*, **55**, 243–254.
- Cerling TE, Ehleringer JR, Harris JM (1998) Carbon dioxide starvation, the development of C₄ ecosystems, and mammalian evolution. *Philosophical Transactions of the Royal Society*, **B353**, 159–171.
- Cerling TE, Harris JM, MacFadden BJ *et al.* (1997) Global vegetation change through the Miocene/Pliocene boundary. *Nature*, **389**, 153–158.
- Cochrane MA (2003) Fire science for rainforests. *Nature*, **421**, 913–919.
- Cochrane MA, Alencar A, Schulze MD *et al.* (1999) Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science*, **284**, 1832–1835.
- Cui Z, Carlslaw KS, Yin Y *et al.* (2006) A numerical study of aerosol effects on the dynamics and microphysics of a deep convective cloud in a continental environment. *Journal of Geophysical Research*, **111**, D05201, doi: 10.1029/2005JD005981.
- Diester-Hass L, Billups K, Emeis KC (2005) In search of the late Miocene–early Pliocene “biogenic bloom” in the Atlantic Ocean (Ocean Drilling Program Sites 982, 925, and 1088). *Paleoceanography*, **20**, PA4001, doi: 10.1029/2005PA001139.
- Ehleringer J, Björkman O (1977) Quantum yields for CO₂ uptake in C₃ and C₄ plants: dependence on temperature, CO₂ and O₂ concentrations. *Plant Physiology*, **59**, 86–90.
- Ehleringer JR, Cerling TE, Helliker BR (1997) C₄ photosynthesis, atmospheric CO₂, and climate. *Oecologia*, **112**, 285–299.

- Ehleringer JR, Sage RF, Flanagan LB *et al.* (1991) Climate change the evolution of C₄ photosynthesis. *Trends in Ecology and Evolution*, **6**, 95–99.
- Farley KA, Vokrouhlicky D, Bottke WF *et al.* (2006) A late Miocene dust shower from the break-up of an asteroid main belt. *Nature*, **439**, 295–297.
- Forrester JW (1971) *Principles of Systems*. Wright-Allen Press, Massachusetts.
- Fox DL, Koch PL (2003) Tertiary history of C₄ biomass in the Great Plains, USA. *Geology*, **31**, 809–812.
- Fromm M, Bevilacqua R, Servranckx R *et al.* (2005) Pyro-cumulonimbus injection of smoke to the stratosphere: observations and impact of a super blowup in northwestern Canada on 3–4 August 1998. *Journal of Geophysical Research*, **110**, D08205, doi: 10.1029/2004JD005350.
- Fromm M, Tupper A, Rosenfeld D *et al.* (2006) Violent pyroconvective storm devastates Australia's capital and pollutes the stratosphere. *Geophysical Research Letters*, **33**, L05815, doi: 10.1029/2005GL025161.
- Graf HF (2004) The complex interaction of aerosols and clouds. *Science*, **303**, 1309–1311.
- Gupta AK, Singh RK, Joseph S *et al.* (2004) Indian Ocean high-productivity event (10–8Ma): linked to global cooling or to the initiation of the Indian monsoons. *Geology*, **32**, 753–756.
- Hayden BP (1998) Ecosystem feedbacks on climate at the landscape scale. *Philosophical Transactions of the Royal Society*, **B353**, 5–18.
- Herring JR (1985) Charcoal fluxes into sediments of the North Pacific Ocean: the Cenozoic record of burning. In: *The Carbon Cycle and Atmospheric CO₂: Natural Variations Archean to Present* (eds Sundquist ET, Broecker WS), pp. 419–442. American Geophysical Union, Washington, DC.
- Hobbs PV, Sinha P, Yokelson RJ *et al.* (2003) Evolution of gases and particles from a savanna fire in South Africa. *Journal of Geophysical Research*, **108**, 8485, doi: 10.1029/2002JD002352.
- Hoffmann WA, Schroeder W, Jackson RB (2002) Positive feedbacks of fire, climate, and vegetation and the conversion of tropical savanna. *Geophysical Research Letters*, **29**, 2052, doi: 10.1029/2002GL015424.
- Janis CM, Damuth J, Theodor JM (2000) Miocene ungulates and terrestrial primary productivity: where have all the browsers gone. *Proceedings of the National Academy of Sciences*, **97**, 7899–7904.
- Keeley JE, Rundel PW (2003) Evolution of CAM and C₄ carbon-concentrating mechanisms. *International Journal of Plant Sciences*, **164** (Suppl.), S55–S77.
- Keeley JE, Rundel PW (2005) Fire and the Miocene expansion of C₄ grasslands. *Ecology Letters*, **8**, 683–690.
- Koren I, Kaufman YJ, Remer LA *et al.* (2004) Measurement of the effect of Amazon smoke on inhibition of cloud formation. *Science*, **303**, 1342–1345.
- Kump LR (1988) Terrestrial feedback in atmospheric oxygen regulation by fire and phosphorus. *Nature*, **335**, 152–154.
- Lelieveld J, Crutzen PJ, Ramanathan V *et al.* (2001) The Indian Ocean experiment: widespread air pollution from south and Southeast Asia. *Science*, **291**, 1031–1036.
- Liu Y (2005) Enhancement of the 1988 northern U.S. drought due to wildfires. *Geophysical Research Letters*, **32**, L10806, doi: 10.1029/2005GL022411.
- MacFadden BJ (2000) Cenozoic mammalian herbivores from the Americas: reconstructing ancient diets and terrestrial communities. *Annual Review of Ecology and Systematics*, **31**, 31–59.
- Mayle FE, Beerling DJ, Gosling WD *et al.* (2004) Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Philosophical Transactions of the Royal Society*, **B359**, 499–514.
- Menon S, Hansen J, Nazarenko L *et al.* (2002) Climate effects of black carbon aerosols in China and India. *Science*, **297**, 2250–2253.
- Mikolajewicz U, Crowley TJ (1997) Response of a coupled ocean/energy balance model to restricted flow through the central American isthms. *Paleoceanography*, **12**, 429–441.
- Mora G, Pratt LM (2002) Carbon isotopic evidence from paleosols for mixed C₃/C₄ vegetation in the Bogota Basin, Colombia. *Quaternary Science Reviews*, **21**, 985–995.
- Morley RJ, Richards K (1993) Gramineae cuticle: a key indicator of late Cenozoic climatic change in the Niger Delta. *Review of Palaeobotany and Palynology*, **77**, 119–127.
- Nober E, Graf HF (2004) A new convective cloud field model based on principles of self-organization. *Atmospheric Chemistry and Physics Discussion*, **4**, 3669–3698.
- Osborne CP, Beerling DJ (2006) Nature's green revolution: the remarkable evolutionary rise of C₄ plants. *Philosophical Transactions of the Royal Society*, **B361**, 173–194.
- Pagani M, Freeman KH, Arthur MA (1999) Late Miocene atmospheric CO₂ concentrations and the expansion of C₄ grasses. *Science*, **285**, 876–879.
- Pagani M, Zachos JC, Freeman KH *et al.* (2005) Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. *Science*, **309**, 600–603.
- Pearson PN, Palmer MR (2000) Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature*, **406**, 695–699.
- Quade J, Cater JML, Ojha TP *et al.* (1995) Late Miocene environmental change in Nepal and the northern Indian subcontinent: stable isotopic evidence from paleosols. *Geological Society of America Bulletin*, **107**, 1381–1397.
- Ramankutty N, Foley JA (1999) Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochemical Cycles*, **13**, 997–1027.
- Randerson JT, van der Werf GR, Collatz GJ *et al.* (2005) Fire emissions from C₃ and C₄ vegetation and their influence on interannual variability of atmospheric CO₂ and δ¹³CO₂. *Global Biogeochemical Cycles*, **19**, GB2019, doi: 10.1029/2004GB002366.
- Rea DK, Janecek TR (1982) Late Cenozoic changes in atmospheric circulation decoded from North Pacific eolian sediments. *Marine Geology*, **49**, 149–167.
- Retallack GJ (1997) Neogene expansion of the North American prairie. *Palaeos*, **12**, 380–390.
- Retallack GJ (2001) Cenozoic expansion of grasslands and climatic cooling. *Journal of Geology*, **109**, 407–426.
- Royer DL, Wing SL, Beerling DJ *et al.* (2001) Paleobotanical evidence for near present-day levels of atmospheric CO₂ during part of the Tertiary. *Science*, **292**, 2310–2313.
- Sage RF (2004) The evolution of C₄ photosynthesis. *New Phytologist*, **161**, 341–370.
- Sankaran M, Hanan NP, Scholes RJ *et al.* (2005) Determinants of woody cover in African Savannas. *Nature*, **438**, 846–849.

- Scott LS (2002) Microscopic charcoal in sediments: quaternary fire history of the grassland and savanna regions in South Africa. *Journal of Quaternary Science*, **17**, 77–86.
- Senge PM (1990) *The Fifth Discipline*. Doubleday, New York.
- Shukla J, Mintz Y (1984) Influence of land-surface evapotranspiration on the earth's climate. *Science*, **215**, 1498–1501.
- Somerville C, Bauer S, Brininstall G *et al.* (2004) Toward a systems approach to understanding plant cell walls. *Science*, **306**, 2206–2211.
- Stebbins GL (1981) Coevolution of grasses and herbivores. *Annals of Missouri Botanical Gardens*, **68**, 75–86.
- Strömberg CAE (2004) Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the Great Plains of North America during the late Eocene to early Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **207**, 239–275.
- Trentmann J, Yokelson RJ, Hobbs PV *et al.* (2003) An analysis of the chemical processes in the smoke plume from a savanna fire. *Journal of Geophysical Research*, **108**, 4705, doi: 10.1029/2003JD003732, 2003.
- Tripati A, Backman J, Elderfield H *et al.* (2005) Eocene bipolar glaciation associated with global carbon cycle changes. *Nature*, **436**, 341–346.
- van Langevelde F, van de Vijver CADM, Kumar L *et al.* (2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, **84**, 337–350.
- Woodward FI, Lomas MR, Kelly CK (2004) Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society*, **B359**, 1465–1476.