OPINION

The origin of the savanna biome

DAVID J. BEERLING and COLIN P. OSBORNE
Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

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; Tripati 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.
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-CO₂ world (Bond & Midgley, 2000; Keeley & Rundel, 2003, 2005; van Langevelde et al., 2003). The
approach is extended to show why CO₂ starvation of
the terrestrial biosphere is an essential primer of the
Earth system for the origination of C₄ savanna ecosys-
tems, and how the coevolution of herbivores (Janis et al.,
2000; MacFadden, 2000; Bond & Keeley, 2005) acts to
disrupt or enhance the network. Continued anthropo-
genic 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 informa-
tion 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; Beer-
ling & 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, CO₂
and herbivores as the central nodes. The feedback dia-
grams 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. C₄ 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 remov-
ing 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
C₄ grasses establish into forest gaps created by the death
of trees during drought (Fig. 3, pathway a–b–c–d). As
patches of C₄ 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 C₄ 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 eva-
potranspiration with greatly differing efficiencies; Amazo-
nian forests supply 88% of their own rainfall, whereas
the short grasslands of the central Great Plains con-
tribute only 15% (Hayden, 1998). Deforestation causes a
longer dry season that enhances ecosystem susceptibil-
ity to fire (Fig. 3, pathway e–h–o–i–a–b) and causes
further tree mortality, which accelerates the expansion
of C₄ 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-
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 NOx (NO + NO2) contributing over half of that released by wildfire (Hobbs et al., 2003), a source also augmented by increased lightning activity. NOx is a necessary ingredient for tropospheric O3 formation. Increased NOx 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.
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
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 & Bjo¨ rkman, 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

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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 C₃ 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, 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 C₃ 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 counters 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


