# IDEAS AND PERSPECTIVES

# Fire and the Miocene expansion of C$_4$ grasslands

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## Abstract

C$_4$ photosynthesis had a mid-Tertiary origin that was tied to declining atmospheric CO$_2$, but C$_4$-dominated grasslands did not appear until late Tertiary. According to the 'CO$_2$-threshold' model, these C$_4$ grasslands owe their origin to a further late Miocene decline in CO$_2$ that gave C$_4$ grasses a photosynthetic advantage. This model is most appropriate for explaining replacement of C$_3$ grasslands by C$_4$ grasslands, however, fossil evidence shows C$_4$ grasslands replaced woodlands. An additional weakness in the threshold model is that recent estimates do not support a late Miocene drop in $p$CO$_2$. We hypothesize that late Miocene climate changes created a fire climate capable of replacing woodlands with C$_4$ grasslands. Critical elements were seasonality that sustained high biomass production part of year, followed by a dry season that greatly reduced fuel moisture, coupled with a monsoon climate that generated abundant lightning-igniting fires. As woodlands became more open from burning, the high light conditions favoured C$_4$ grasses over C$_3$ grasses, and in a feedback process, the elevated productivity of C$_4$ grasses increased highly combustible fuel loads that further increased fire activity. This hypothesis is supported by paleosol data that indicate the late Miocene expansion of C$_4$ grasslands was the result of grassland expansion into more mesic environments and by charcoal sediment profiles that parallel the late Miocene expansion of C$_4$ grasslands. Many contemporary C$_4$ grasslands are fire dependent and are invaded by woodlands upon cessation of burning. Thus, we maintain that the factors driving the late Miocene expansion of C$_4$ were the same as those responsible for maintenance of C$_4$ grasslands today.

## Keywords

Grasslands, Miocene, paleosols, photosynthesis, savannas, woodlands.

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## INTRODUCTION

C$_4$ photosynthesis is a variation on the typical C$_3$ pathway that leads to competitive advantages in environments where light and temperature are not highly limiting to carbon uptake (Ehleringer & Monson 1993). Since high light and high temperature environments give C$_4$ species a selective advantage over C$_3$, this pathway is best represented in grasslands with a warm growing season, in other words in summer-rain climates. Throughout the world today, tropical and subtropical savannas and grasslands are dominated by C$_4$ grasses, often comprising 90% or more of the grass flora (Tieszen *et al.* 1979; Rundel 1980; Keeley & Rundel 2003).

Models of photosynthetic efficiency predict C$_4$ is unlikely to evolve except under CO$_2$-limiting conditions (Fig. 1).

Atmospheric conditions throughout the early Tertiary would have been unsuitable for C$_4$ photosynthesis (Ehleringer *et al.* 1997). However, by early Oligocene, CO$_2$ levels (Fig. 2) were sufficiently limiting to spur their origin, but the C$_4$ pathway did not approach its current dominance of warm growing season grasslands until the late Miocene. Based on isotopic signatures of $\delta^{13}$C from carbonate paleosols (Fig. 2) and other sources, it appears that between 4 and 7 Ma there was a substantial increase in C$_4$ grasslands in widely separate parts of the globe (Cerling *et al.* 1993; Morgan *et al.* 1994; Stern *et al.* 1994; Latorre *et al.* 1997; Barry *et al.* 2002). It has been hypothesized that a late Miocene $p$CO$_2$ decline caused atmospheric levels to reach a critical CO$_2$-threshold where C$_3$ grasses were at a decided competitive disadvantage to C$_4$ grasses (Cerling *et al.* 1997; Ehleringer *et al.* 1997). Here we
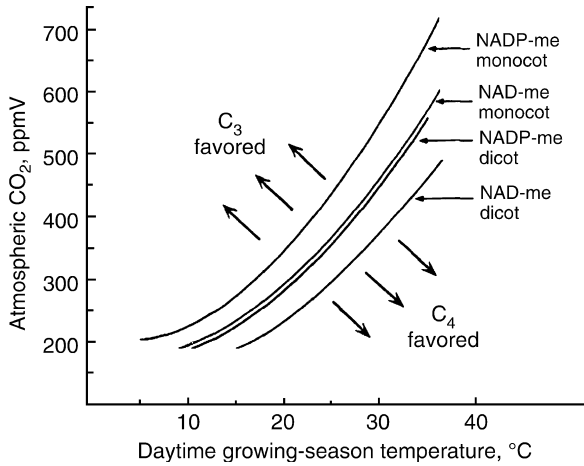
**Figure 1** A model of the threshold temperature and $CO_2$ levels favouring $C_3$ vs. $C_4$ grasses. Photosynthetic efficiency of $C_4$ grasses surpass that of $C_3$ grasses as temperatures increase and $CO_2$ levels decrease, and vice versa for C3 grasses. From Ehleringer *et al.* (1997) with permission from Springer Verlag.

argue that this $CO_2$-threshold model is insufficient to explain the late Miocene expansion in $C_4$ grasslands, and propose an alternative model that is unrelated to changes in $p CO_2$.

## ORIGIN OF $C_4$

It is critical to keep separate the question of $C_4$ evolution from $C_4$ expansion leading to dominance of tropical grasslands (Cerling *et al.* 1994). Direct fossil evidence of a

$C_4$ grass indicates a relatively late origin as the oldest fossils date to 12.5 Ma (Jacobs *et al.* 1999), or perhaps slightly earlier (Dugas & Retallack 1993), and the mid-Miocene is also the time when the first soil carbonate $\delta^{13}C$ signal of $C_4$ is recorded (Morgan *et al.* 1994). These lines of evidence would place the origin and the expansion of $C_4$ relatively close in time.

However, there are good reasons to believe these events were more widely separated. This evidence for a mid-Miocene origin is an unreliable means of pinpointing the timing of $C_4$ evolution. The fossil record is highly biased against recording macrofossils from the types of arid habitats where $C_4$ grass evolution is thought to have begun (Cerling 1999). Additionally, the soil carbonate $\delta^{13}C$ reflects the point where $C_4$ biomass was sufficient to override the $C_3$ $\delta^{13}C$ signal, and we estimate that as much as a quarter or more of the biomass could be $C_4$ and still generate a paleosol $\delta^{13}C$ value within the $C_3$ range. On the other hand, several lines of evidence are consistent with an earlier origin. For example, molecular clock estimates indicate the origin of one $C_4$ clade, the grass tribe Andropogoneae, dates back at least to the late Oligocene 25 Ma (Kellogg 1999) and other groups may push this date back even further (Sage 2004). In addition, the global distribution of many very large and strictly $C_4$ grass genera suggests an early origin for this pathway (Keeley & Rundel 2003). Thus, there is good reason to believe that by mid-Miocene, $C_4$ grasses had radiated widely and were poised to take advantage of any environmental changes that would favour $C_4$ grasses.
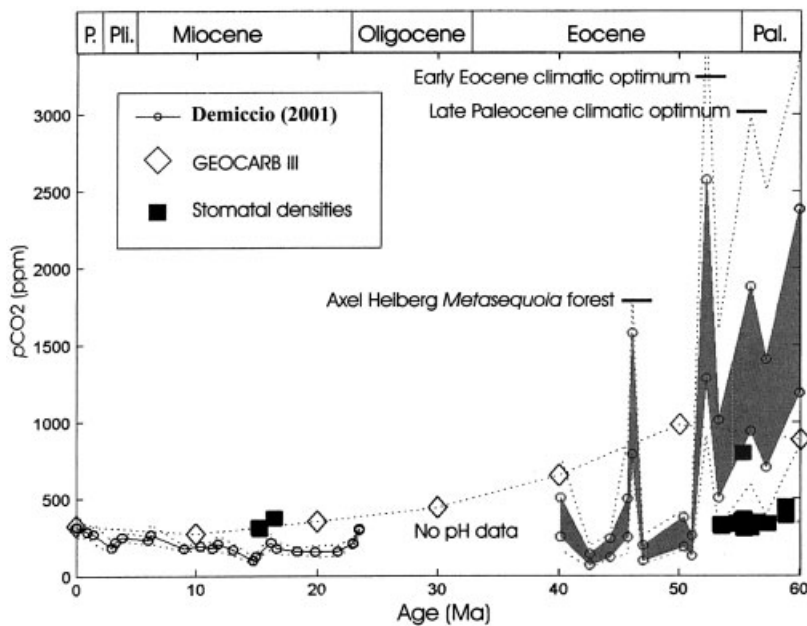


**Figure 2** Atmospheric $p CO_2$ since early Tertiary. Stomatal density data from Royer *et al.* (2001), diamonds from GEOCARB III model of Berner & Kothavala (2001) and open circles from Demicco *et al.* (2003); modified from Demicco *et al.* (2003) with permission from the Geological Society of America.

## CO$_2$ AS A DRIVER OF C$_4$ EXPANSION

The CO$_2$-threshold model (Fig. 1) is the most widely accepted explanation for the rapid expansion of C$_4$ grasslands during the late Miocene (Ehleringer *et al.* 1997; Cerling *et al.* 1998; Sage 1999). There are two reasons why we consider this model insufficient to account for the expansion of C$_4$ grasslands: (i) the threshold model is based on quantum efficiency differences between C$_3$ and C$_4$ that are best applied to predictions of competitive outcomes between similar growth forms; and (ii) there is little evidence of a late Miocene decline in palaeoatmospheric *p*CO$_2$.

The CO$_2$-threshold model is based on a quantum efficiency difference that predicts a photosynthetic advantage of C$_4$ over C$_3$ under certain conditions of temperature and CO$_2$ (Fig. 1). It is most appropriately applied to predicting the competitive outcome of similar growth forms, and applying this model more broadly is problematical because photosynthetic advantage is only one of many factors in the competition between different growth forms (Osmond 1987; Field *et al.* 1992; Henderson *et al.* 1995). For example, C$_3$ trees commonly outcompete C$_4$ grasses under atmospheric and temperature conditions estimated for the late Miocene, and once a C$_3$ tree has overtopped a C$_4$ grass, light levels and temperature both decrease (Belsky *et al.* 1989), diminishing the photosynthetic superiority of C$_4$.

This is an important limitation to the CO$_2$-threshold model because of a preponderance of evidence that the C$_4$ expansion in the late Miocene (Fig. 3) coincided with a change from woodland dominated landscapes to grasslands, and this appears to have been the case with African, South American, and North American C$_4$ grassland expansions (Morgan *et al.*
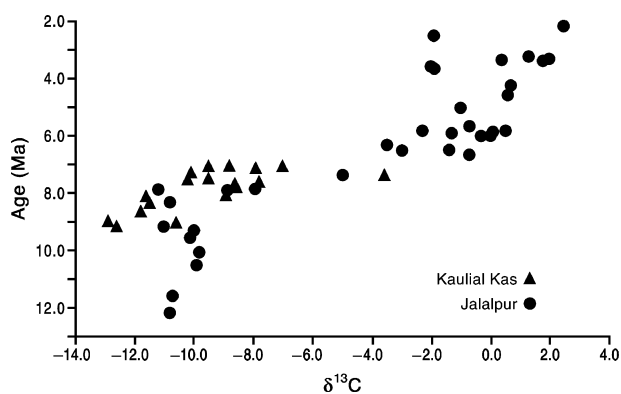


**Figure 3** Stable carbon isotope ratios (δ $^{13}$C) for paleosol carbonates during the late Miocene from two sites in northern Pakistan. These reflect the average δ $^{13}$C signal from plants growing at the time and are calibrated so that signatures less than −8 reflect C$_3$ dominated landscapes and greater than −2 are C$_4$ dominated. From Barry *et al.* (2002) with permission of the Paleontological Society.

1994; Janis *et al.* 2000; Retallack 2001; Fox & Koch 2003, 2004). Other evidence of grasslands replacing woodlands is a positive correlation between the δ $^{13}$C and δ $^{18}$O value of carbonate in many paleosols, which have been interpreted as indicative of a reduction in forest cover (Cerling *et al.* 1993). Shifts in the rate of fossil leaf and log deposition also suggest such changes in vegetation type (Quade *et al.* 1995). In addition, the palaeoecology of Neogene mammalian faunas supports the idea that the C$_4$ grassland expansion was at the expense of woodlands (Gunnell *et al.* 1995). Lastly, patterns of soil development in Pakistan, East Africa, and the central US all support a late Miocene formation of grasslands from woodlands (Retallack 2001).

Critical to the threshold model is the prediction of a marked decrease in CO$_2$ in the late Miocene (Fig. 2). However, Pearson and Palmer (2000) reported very slight changes in CO$_2$ over the last 20 Ma (between 200 and 300 ppmv) and Pagani *et al.* (1999a,b) reported a slight rise in CO$_2$ through the late Miocene (from 220 to 320 ppmv), as did Zachos *et al.* (2001) and Demicco *et al.* (2003). This lack of a late Miocene decline in *p*CO$_2$ does not in and of itself refute the model proposed by Cerling *et al.* (1997), since the quantum efficiency model (Fig. 1) is driven by a combination of temperature and CO$_2$. However, temperatures were declining in the late Miocene (Zachos *et al.* 2001), which is opposite of what would be needed for the quantum efficiency model to provide an explanation for the late Miocene C$_4$ grassland expansion.

Recently, it has been argued that in addition to declining CO$_2$, one of the important factors driving the expansion of C$_4$ grasses was increased aridity brought on by the Asian monsoon (Sage 2004). While aridity may have played an important role in the origin and radiation of C$_4$ grasses, by itself it is an insufficient explanation for the late Miocene expansion of C$_4$ grasslands. Paleosol data reveal an early origin for arid-adapted short grass prairies and these were well developed by early Miocene and were likely prime sites for the evolution of C$_4$ species. However, the late Miocene expansion of C$_4$ grasslands coincided with an expansion of grasslands into mesic sites, and the evolution from short-grass prairies to tall-grass grasslands (Retallack 2001).

Fire has occasionally been evoked as part of the explanation for the Tertiary expansion of C$_4$ grasslands, but always as a secondary factor following changes in aridity and CO$_2$ (Sage 2001; Bond *et al.* 2003a).

## FIRE AS AN ALTERNATIVE EXPLANATION FOR THE LATE MIOCENE EXPANSION OF C$_4$ GRASSLANDS

We hypothesize that the late Miocene conversion of woodlands to C$_4$-dominated grasslands was not because of atmospheric changes in *p*CO$_2$, nor to aridity *per se*, but rather the result of climate changes that created a novel fire climate

more pervasive than previously experienced in earth's history. One of the key features was a marked seasonality, with a warm moist growing season capable of sustaining high biomass production, followed by a dry season severe enough to convert this primary productivity into highly combustible fuels that would readily carry fire. This describes a monsoon climate, and like such climates today, would have been accompanied by abundant lighting at the end of the dry season (Keeley & Bond 2001). These monsoon climates typically produce a warm growing season immediately following the fire season, and within months the pre-fire biomass is restored (Sarmiento 1984). Such warm growing season conditions would have favoured $C_4$ grasses over $C_3$ grasses, and $C_4$ metabolism would have had an added benefit under such conditions that selected for rapid post-fire regrowth.

Climatically, the late Miocene was characterized by increasing seasonality in both temperate (Utescher *et al.* 2000) and tropical regions (Retallack 1991; Pagani *et al.* 1999a). These climate changes included a strong intensification of the Asian monsoon beginning *c.* 11 Ma (Quade *et al.* 1989). Such changes in climate were evident globally in alterations of oceanic sedimentation rates, which peaked between 5 and 12 Ma, and likely reflect greater continental weathering due to reduced global precipitation (Davies *et al.* 1977). The demonstrated rise of the Asian monsoon in the late Miocene would have increased convective storms with associated lightning at the end of a long dry season. Middle Miocene paleoclimatic data from New Zealand also suggest an abrupt change from humid Nothogagus forests to open stands of palms and eucalyptus, accompanied by abundant charcoal (Pole 2003).

Evidence of a late Miocene increase in fire incidence is the two to three orders of magnitude increase in charcoal deposition in marine sediments of the western Pacific Ocean (Fig. 4). These deep sea cores contain charcoal and particles with morphologies similar to modern trees and shrubs; it is presumed the charcoal arose from burning plant matter on land, which was subsequently moved by aeolian transport to these deposition sites. These cores show rapid increases in charcoal that parallel the late Miocene expansion of $C_4$ grasslands evident from South Asia (Fig. 3). Accompanying some of these cores were particles similar in morphology to modern grasses (Herring 1985), and other marine cores do in fact record the late Miocene $C_4$ grassland expansion (France-Lanord & Derry 1994; Freeman & Colarusso 2001).

The role of fire in driving the late Miocene expansion of $C_4$ grasslands has been noted before in the context of the quantum efficiency model (Bond & Midgley 2000; Bond *et al.* 2003). These authors have argued that low $CO_2$ levels would have slowed the rate of $C_3$ tree recovery after fire, relative to $C_4$ grasses, and modelling studies confirm this. While these studies may indeed support Pleistocene changes
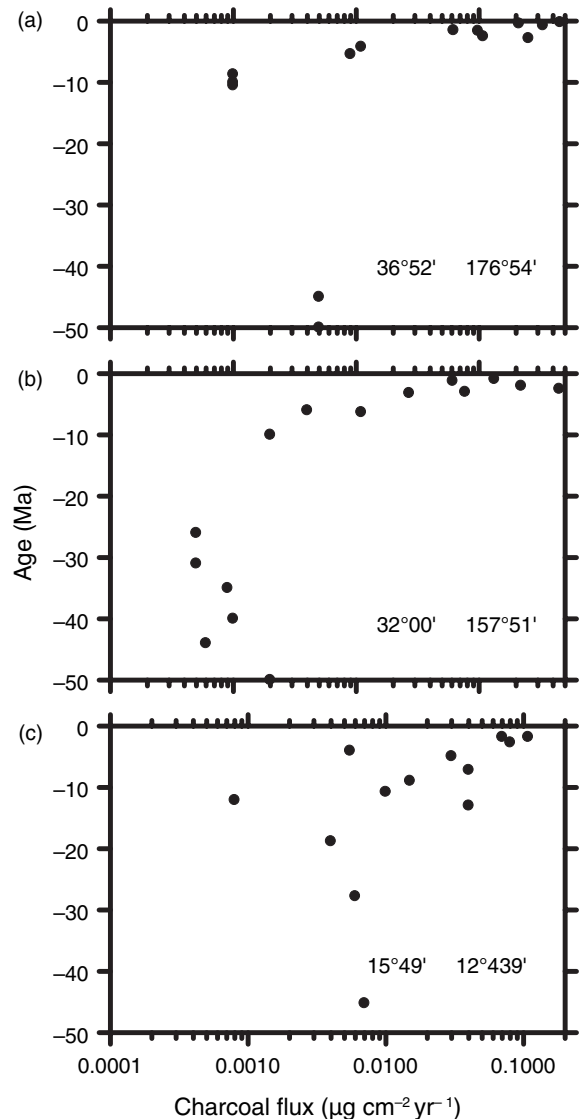


**Figure 4** Estimated charcoal flux from presumably aeolian transport to sites between 15° and 36° in the western Pacific Ocean from deep sea drilling cores. Sites (a) and (b) were east of southeast Asia and in the path of the Westerly Winds and charcoal would largely be the result of Aeolian transport. Site (c) was within 250 km of the Philippine Islands and sedimentation may have been an important contributor of charcoal. Data from Herring (1985).

in forest and grassland distribution (with documented changes in $p\text{CO}_2$) they are less applicable to Tertiary changes in $C_4$ since there is no evidence for $CO_2$ decline during the period of Miocene $C_4$ grassland expansion (Fig. 2). We suggest changes leading to a fire climate are sufficient drivers for the Miocene expansion of $C_4$ grasslands, and there is little reason to invoke a role for $p\text{CO}_2$. Indeed, in various parts of the world today we are seeing fire-driven expansion of $C_4$ grasslands and forest
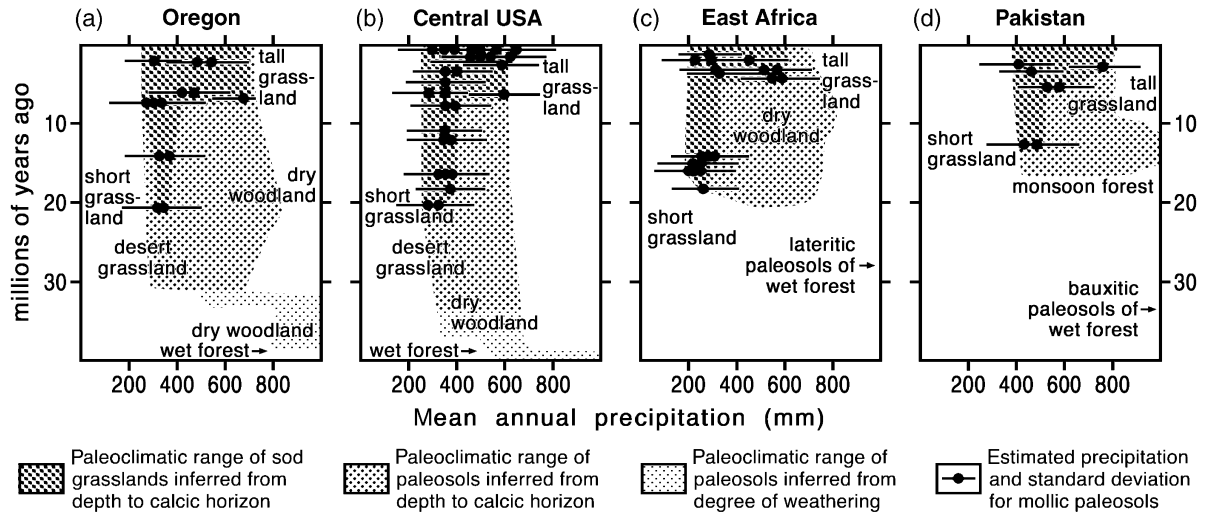
**Figure 5** Climatic expansion of grasslands through the Miocene in (a, b) North America; (c) East Africa, and (d) Pakistan. In all cases early Miocene grasslands are either desert grasslands or short grass prairies. Late Miocene grasslands were tall grass grasslands that replaced woodlands. From Retallack (2001) with permission of the University of Chicago.

decline (D'Antonio & Vitousek 1992; Rossiter *et al.* 2003), during a period of increasing global CO$_2$.

Also supportive of our hypothesis are the changes in grassland structure during the mid- and late Miocene uncovered by studies of paleosols (Retallack 2001), shown in Figure 5. These paleosols reflect an early origin for arid-adapted short grass prairies and a late Miocene expansion of mesic tall-grass grasslands. This is consistent with a model of C$_4$ grassland expansion because of increasing disturbance,
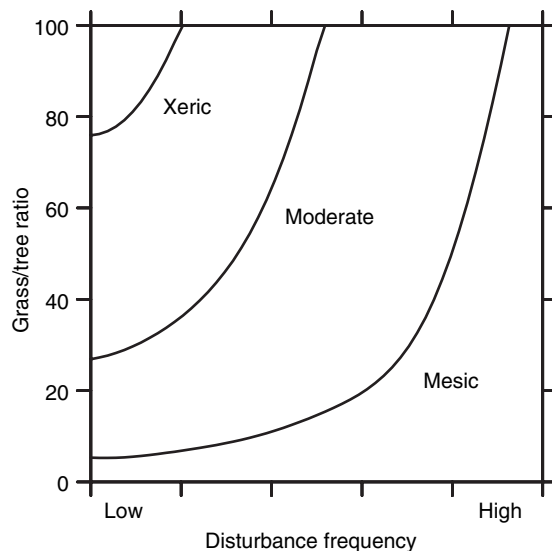


**Figure 6** Schematic model of the interaction between aridity and disturbance frequency on the ratio of herbaceous to woody vegetation; redrawn from Keeley (2002) with permission of Blackwell Science Ltd.

since disturbance is commonly required for grassland displacement of woody vegetation at the more mesic end of the moisture gradient (Fig. 6). There is empirical support for this in tropical settings, where, at the xeric end of the moisture gradient grasslands readily displace forests (Borchert 1998; Sankaran *et al.* 2004), but at the mesic end the primary determinant of whether or not woodlands and savannas move towards complete grassland is fire frequency (Jeltsch *et al.* 2000).

It is still unclear what role the very diverse Miocene grazing and browsing fauna would have played in this process (Janis *et al.* 2000, 2004). It seems unlikely that the global expansion of C$_4$ grasslands in the late Miocene would have been primarily a result of faunal disturbance, but in some regions browsers could have played an important preliminary role in opening up the forest (Fox & Koch 2004). This would have had cascading effects because it contributes to the drying of surface fuels (van Langevelde *et al.* 2003), and the trampling and destruction of trees increases the quantity of dried woody fuels, which further increases fire intensities. This is a feedback process and once moist forest canopies are opened the increasing probability of burning maintains these systems even in the absence of the initial disturbance factor (Cavelier *et al.* 1998).

## EXPANSION VS. MAINTENANCE OF C$_4$ GRASSLANDS

We argue that expansion and maintenance of C$_4$ grasslands are the same process. In other words, creation of a predictable and frequent fire regime not only drove the late Miocene expansion of C$_4$ grasslands, but is the same factor

currently responsible for maintaining $C_4$ grasslands. Modelling studies show that contemporary semi-tropical and tropical grasslands and savannas have the climate potential to form forests if fire were somehow removed from those ecosystems (Bond *et al.* 2005).

These models have a plethora of empirical support. It has long been known under a seasonal rainfall regime, fire plays a critical role in controlling the structure and composition of tropical savannas and grasslands (Sarmiento 1984; Ripley 1988; Soares 1990; Furley *et al.* 1992; Fensham *et al.* 2003; Hoffmann *et al.* 2003). These ecosystems extend broadly over large areas of the subtropical and tropical areas of the world and are typically dominated by a groundcover matrix of $C_4$ grasses. Savanna fires characteristically burn during the dry season or at the beginning of the wet season when convective storms produce lightning ignitions at intervals of anywhere from 1 to 5 years (Gillon 1983; Coutinho 1990). Extensive studies of the dynamics of savanna-forest boundaries carried out in many parts of the world have consistently demonstrated how the frequency of fires controls tree establishment.

Today the savanna-forest boundaries are strongly controlled by human activities that increase or decrease fire frequency, but most of these subtropical regions have sufficient lightning ignitions to replace human ignitions under natural conditions (Keeley & Bond 2001). Frequent fires characterize both wet and dry savannas in northwestern Australia, while dry forests are typically restricted to fire-protected habitats (Bowman 1992). Active protection from fire over a period of 15 years in this region allowed the rapid establishment of a microphyll shrub layer in the savanna-forest ecotone, and this layer facilitated the survival of tree seedlings (Bowman & Fensham 1991). Very similar findings have been made in West Africa where fire protection has rapidly led to tree seedling establishment in savanna habitats (Brookman-Amissah *et al.* 1980), and in Venezuela where 25 years of cattle grazing, which removes herbaceous fuels, and fire protection increased the density of tree seedlings 20-fold (San José & Fariñas 1991). Similar patterns to these have been documented for the cerrado savannas of central Brazil (Coutinho 1990; Hoffman 1999; Moreira 2000).

## CONCLUSIONS

A path model relating the important Miocene drivers of $C_4$ grassland expansion is illustrated in Figure 7. Significant portions of the landscape in tropical and subtropical latitudes were experiencing increasing seasonality, in the form of warm moist growing seasons alternating with a marked dry season. High biomass production during the growing season was critical in order to generate the potential fuel load capable of carrying fire. The dry season reduced
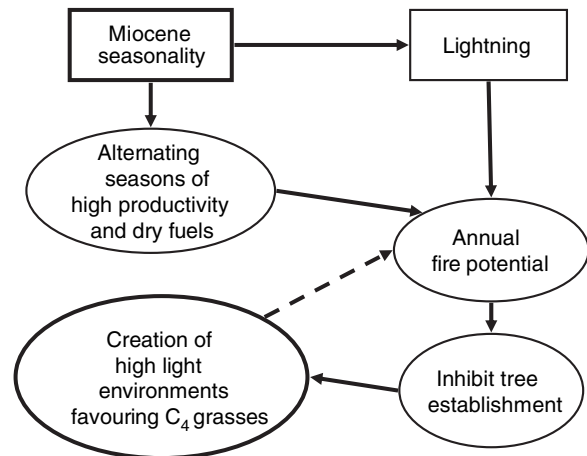


**Figure 7** Model of Miocene climate drivers (squares) and their impact on ecosystem processes (circles) leading to the expansion of $C_4$ grasslands.

fuel moisture sufficient for combustion and the developing monsoon climate produced an annual pattern of lightning ignitions at the end of the dry season when fuels were at their driest. Thus, the potential conditions for wildfire developed annually. Fires at high frequency of several times per decade crossed over the disturbance threshold of woodland elements. High light conditions favoured faster growing herbaceous elements and the basal meristem of grasses, coupled with their aggressive rhizomatous spread, favoured grassland development. At these latitudes the warm Miocene temperatures, coupled with the high light conditions were ideal for the rapid expansion of $C_4$ grasses. Rapid growth of these grasses further enhanced the potential for annual fires by production of heavy loads of fine fuels.

This scenario does not apply to all parts of the late Miocene landscape. Where seasonality developed, but was not tied to warm season precipitation, $C_4$ grasses lost out to $C_3$ grasses. At the more arid end of the moisture gradient where primary productivity was limited, there were insufficient fuels to carry fire. At the very mesic end of the gradient with a shorter dry season, high fuel moisture failed to carry fires and woodlands and forests were retained, except where regular disturbance by large herbivores opened the canopy sufficient to dry surface fuels.

Future work that could provide a closer link to changes in $C_4$ biomass and fires would be to demonstrate late Miocene increases of both from the same sediment samples. One area that would be worth exploring are the core samples taken from the Bengal Fan Deep Sea Drilling Project (http://www-odp.tamu.edu/public/pressrel_html/leg116b. html). A series of cores taken from the Bay of Bengal in the northeast Indian Ocean provides one of the largest and oldest sedimentation records and stretches more than

2500 km across the equator. One core has been found to reproduce the late Miocene C$_4$ expansion observed from terrestrial paleosols (Freeman & Colarusso 2001). However, to date, apparently no work has been done on charcoal deposition patterns from these marine sediments.

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