

Commentary

The remarkable congruence of New and Old World savanna origins

Savanna occupies half the global tropical zone (Lehmann *et al.*, 2014) and is home to hundreds of millions of people. Usually comprising a mix of C_4 grasses and scattered trees, it can be as rich in plant species as tropical rain forests (Forzza *et al.*, 2010) and accounts for *c.* 30% of global terrestrial net primary productivity (Lehmann *et al.*, 2014). Despite its high biodiversity and importance to humanity, the scientific study of savanna and – perhaps more alarmingly – its conservation have been neglected relative to its better-known cousin, the tropical rain forest. In this issue of *New Phytologist*, Maurin *et al.* (pp. 201–214) present important new data that shed light on the evolutionary origin of savannas in Africa. For the first time for African savanna systems, they use evidence from time-calibrated phylogenetic trees to infer biome history, in particular the appearance of plants with adaptations to savanna fires that burn when the high fuel load of C_4 grasses ignites during the long dry season associated with the highly seasonal savanna climate. Understanding the role of fire in the origin and maintenance of savannas is critical at a time when global climate change and other human influences are combining to change the frequency of fire in tropical vegetation. As Maurin *et al.* point out, the terrestrial fossil record for charcoal is poor in deeply weathered savanna landscapes, but dated molecular phylogenies, such as those used by Maurin *et al.*, provide an alternative tool for investigating biogeographic history.

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The method used by Maurin *et al.* is to estimate the timing of the appearance of fire-adapted lineages, specifically the geoxylic suffrutex growth form – strange plants with massive underground woody axes or lignotubers that are hidden from surface fires, and with aerial shoots that are short in height and duration (Figs 1, 2). Frank White, one of the most influential 20th Century workers on African vegetation and plant taxonomy, called such plants, very

appropriately, ‘underground trees’ (White, 1976). White’s (1976: 59) observation that, ‘suffrutices not only are closely related to large trees and have presumably evolved from large trees or lianes, but occur in genera which except for their suffruticose members consist exclusively of large woody plants’ was highly prescient in foreseeing the results found by Maurin *et al.* using modern phylogenetics, nearly 40 yr later. White was inferring that these suffrutices were trees that had gone underground in an evolutionary sense, which is confirmed by Maurin *et al.*

Previously, savanna woody plant evolution has only been considered in South America (Simon *et al.*, 2009; Simon & Pennington, 2012), where phylogenetic studies revealed recent evolution of the geoxylic suffrutex growth form and of other woody species with adaptations to fires, such as thick corky bark, from lineages in surrounding biomes (Simon *et al.*, 2009). These recent origins in the past 4 million yr (Myr) are consistent with the fossil record of C_4 grasses that suggests a savanna expansion driven by the invasion of flammable grasses (Edwards *et al.*, 2010). Maurin *et al.* use a comprehensive dataset, sampling 1400 woody species including more than a quarter of the estimated 200 geoxylic suffrutices in the Zambesian region of southern Africa. They demonstrate multiple independent origins of the geoxylic growth form, mostly starting in the Pliocene (5–2.5 Myr ago), with the majority of divergences occurring within the past 2 Myr. This abrupt, rapid and phylogenetically scattered evolution of plants with fire adaptations is consistent with a savanna biome origin and expansion in African that is startlingly congruent in time with that in the Americas, adding important new evidence supporting the late Miocene/Pliocene origin of the savanna biome worldwide (Beerling & Osborne, 2006; Edwards *et al.*, 2010). Such trans-continental synchronicity of the frequent evolution of the geoxyle habit in the Pliocene strongly suggests a common global explanation. In this regard, a complex set of shared climate–fire–vegetation feedback mechanisms seems especially relevant. Several studies have suggested a key role for fire, whereby increased climatic seasonality contributed to enhanced and intensified fire activity, which triggered the global expansion of C_4 grasslands and the establishment of the world’s savannas (Beerling & Osborne, 2006; Edwards *et al.*, 2010; Scheiter *et al.*, 2012; Hoetzel *et al.*, 2013), as well as widespread evolution of the geoxyle and other fire-adapted growth forms that are one of the hallmarks of the tropical savanna biome today.

The Maurin *et al.* study supports conclusions that the evolution of adaptations to fire in woody plants may be a relatively simple process in developmental (Simon *et al.*, 2009) and genetic (Simon & Pennington, 2012) terms. This ease of adaptation to fire is what underlies the numerous evolutionary transitions into the savanna biome documented in Africa (Maurin *et al.*) and South America (Simon *et al.*, 2009), and it may reflect that fire adaptations such as thick, corky bark and the ability to root sprout may only require

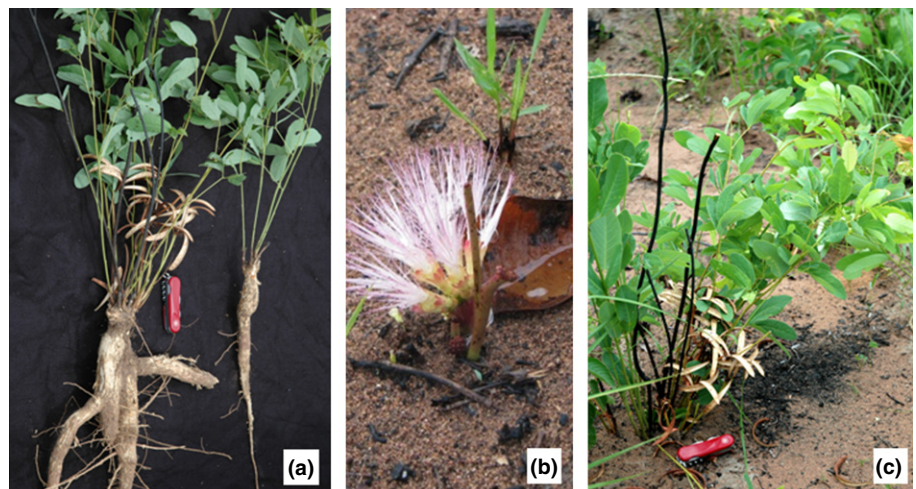


Fig. 1 *Euilea crispa* (Tunb.) Gürke (Ebenaceae), a typical geoxylic suffrutex of the African savannas showing the enlarged underground lignotuber and charred remains of last year's stems. Drawing courtesy of Rosemary Wise, from White's (1976) *Underground forests of Africa*, with permission.

changes in gene regulation rather than structural mutation (Simon & Pennington, 2012). What seems to be especially striking here is the ease with which plants can reallocate their biomass underground, something that chimes with the apparent evolutionary lability of plant growth forms more generally, such as shifts between annual and perennial habit, or the evolution of climbing habit. In the case of the underground trees, Maurin *et al.* suggest that they are an example of heterochrony – a change in timing of development – as the trees flower when they have a dwarf stature; however, this does not explain the key change of the massive transfer of woody biomass underground and there appear to be rather few data to show conclusively that geoxyles flower at a younger age than their arborescent congeneric counterparts.

Savannas appear to be an example where adaptive shifts from other biomes have played a key role in the generation of high tropical species diversity. The savanna biome boundary appears to have been permeable over evolutionary timescales to the ingress of woody lineages, or their *in situ* adaptation across a shifting biome boundary, because fire does not pose a significant adaptive barrier (Simon & Pennington, 2012). In both the Neotropical cerrado and African savanna, there is no need to invoke dispersal of pre-adapted lineages from other geographically distant fire-prone environments, but rather *in situ* adaptation of locally available lineages to fire. In the Neotropics, this contrasts with phylogenetic patterns seen in dry tropical forests – closed canopy forests that grow in similar seasonal climates to savannas, but on richer, often calcareous, rocky soils which may retain less water (Oliveira-Filho *et al.*, 2013). The available, though limited, phylogenetic evidence suggests that these dry forests are characterised by lineages that are often entirely confined to this biome across large geographical disjunctions (Schrire *et al.*, 2005), suggesting less frequent shifts to the dry forest biome – a pattern often characterised as phylogenetic niche (Donoghue, 2008) or biome (Crisp *et al.*, 2009) conservatism. Perhaps counterintuitively, it seems that fire may have been less of an adaptive barrier to woody plants in the tropics than switching between major soil types. Future research might focus on the nature of the morphological, physiological (Edwards & Donoghue, 2013; Donoghue & Edwards, 2014) and genetic

Fig. 2 *Calliandra longipes* Benth. (Leguminosae), a typical geoxylic suffrutex from the Cerrado of South America. Flowers emerge at ground level before the leafy shoots and shortly after burning, the fruits ripening and shedding seeds onto bare ground several weeks or months before competition from the fast-growing C₄ grass layer sets in and later completely conceals the suffrutices. (a) Enlarged underground lignotuber, short-lived functionally herbaceous shoots and ripe dehiscent fruits close to ground level; (b) flowers emerging before the leafy shoots resprout, on bare ground soon after fire; (c) leafy shoots, ripe dehiscent fruits and old charred shoots from the previous year. Photos courtesy of Colin Hughes (a, c) and Marcelo Simon (b).



(Simon & Pennington, 2012) transitions required to make an evolutionary switch from one major biome and to survive in another (Edwards & Donoghue, 2013; Donoghue & Edwards, 2014).

While the congruent recency of origin and phylogenetic lability of geoxyle evolution in the New and Old Worlds revealed by this study are striking, much remains to be explained, such as why so many species of plants have accumulated in the main area of South American savanna, the cerrado of central Brazil and Bolivia, which occupies a much smaller total area than the tropical savannas of Africa. The cerrado region has as many angiosperm species (c. 11 000) as the Brazilian Amazon (Forzza *et al.*, 2010), and the Sudanian and Zambesian savannas have a similar combined total (White, 1983). The species richness of the cerrado appears to be a result of many examples of *in situ* radiation of up to 50 or more species per clade (Simon *et al.*, 2009), which display various fire adaptations, including the geoxyle growth form. We suspect that such *in situ* radiations are less frequent in African savannas, and future work clearly needs to prioritise densely sampled, species-level phylogenies across numerous clades if we are to fully understand the evolution of savanna plants (Hughes *et al.*, 2013; Donoghue & Edwards, 2014). A strength of the Maurin *et al.* study is its taxonomic breadth, covering the entire woody flora of African savannas, but its weakness is a lack of dense species sampling of related species in other biomes. This lack of species sampling precludes identifying in many cases the exact phylogenetic point, and timing, of shifts between biomes. In comparison, the study of Simon *et al.* (2009) of South American savannas included dense species sampling, but focused on only four clades, three of which were legumes, so its generality was limited. Combining both approaches – phylogenetic breadth and dense sampling of species – for clades including savanna species in the Americas, Africa, Asia and Australia, may hold the key to further understanding the origin and expansion of the global tropical savanna biome.

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