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Reviewed work(s):

Source: *International Journal of Plant Sciences*, Vol. 173, No. 6 (July/August 2012), pp. 711-723

Published by: [The University of Chicago Press](#)

Stable URL: <http://www.jstor.org/stable/10.1086/665973>

Accessed: 17/09/2012 06:38

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EVIDENCE FOR ADAPTATION TO FIRE REGIMES IN THE TROPICAL SAVANNAS OF THE BRAZILIAN CERRADO

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A recent controversy concerns whether plant traits that are assumed to be adaptations to fire originally evolved in response to selective factors other than fire. We contribute to this debate by investigating the evolution of the endemic woody flora of the fire-prone Cerrado of central Brazil, the most species-rich savanna in the world. We review evidence from dated phylogenies and show that Cerrado lineages started to diversify less than 10 million years ago. These Cerrado lineages are characterized by fire-resistant traits such as thick, corky bark and root sprouting, which have been considered to have evolved as adaptations to drought or nutrient-deficient soils. However, the fact that the lineages carrying these features arose coincident with the rise to dominance of flammable C₄ grasses and expansion of the savanna biome worldwide, and postdating the earlier origin of seasonal climates and the nutrient-poor, acid Cerrado soils suggests that such traits should be considered as adaptations to fire regimes. The nature of these features as adaptations to fire is further suggested by their absence or poor development in related lineages found in fire-free environments with similar edaphic conditions to the Cerrado and by their repeated independent origin in diverse lineages. We present evidence to demonstrate that the evolutionary barrier to entry to the Cerrado is a weak one, presumably because of the ease of evolution of the necessary adaptations to fire regimes for lineages inhabiting neighboring fire-free biomes.

Keywords: adaptive radiation, exaptation, Neotropics, phylogenetic niche conservatism, plant evolution.

Introduction

This article addresses a recent controversy concerning whether plant traits that are commonly assumed to be fire adaptations in habitats prone to fires originally evolved in response to selective factors other than fire (Bradshaw et al. 2011a, 2011b; Keeley et al. 2011). The debate has largely focused on vegetation in Mediterranean climate regions, concentrating on traits such as resprouting, serotiny, and germination induced by heat and smoke. Bradshaw et al. (2011a) contended that traits considered as fire adaptations have complex origins and that factors other than frequent fire have driven their evolution. Hence, they consider these traits to be exaptations rather than adaptations. Keeley et al. (2011) responded by pointing out that while some features may have arisen, perhaps in prototypic form, before the establishment of a fire regime (and therefore could be considered as exaptations), they can be subsequently shaped by a fire regime and therefore should be considered as adaptations. We revisit this debate in a novel setting not considered by Bradshaw et al. (2011a, 2011b), the fire-prone tropical savannas (the “Cerrado”) of central Brazil. We also consider data from time-calibrated phylogenetic trees, which Bradshaw et al. (2011a, 2011b) did not use to investigate the origin of potential adaptations to fire.

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The Brazilian Cerrado

This article focuses on the largest and most species-rich area of savanna in the Neotropics, the Cerrado of central Brazil. In this article we examine the evolutionary transitions to the Cerrado, so it is important to place savannas in the context of other major biomes of lowland tropical South America because these may be the source biomes for the diversity found in the Cerrado. From an ecological perspective, these biomes are defined on the basis of variation in climate, edaphic factors, and fire regime. In tropical South America, we distinguish rain forest, seasonally dry tropical forest (SDTF), and savanna (Pennington et al. 2006a; Särkinen et al. 2011; fig. 1). Rain forest is found in areas with humid climates on a variety of soil types (Fine et al. 2005), but in areas with significant dry seasons, it gives way to savanna and SDTF (Malhi et al. 2009). Within these drier regions, SDTF grows on soils of relatively high pH and nutrient status, while savanna is found on acid, dystrophic soils (Pennington et al. 2006a; Lloyd et al. 2009). Fire is not an important ecological factor in SDTF, whereas the abundance of C₄ grasses makes savannas flammable in the dry season (Pennington et al. 2006a).

The Cerrado of central Brazil, covering 2 million km², represents the largest area of savanna in the Neotropics. Compared to other savannas in the New World, the Cerrado is by far the most important in terms of species richness and levels of endemism, with 80% of the woody species not shared with any other savanna region (Lenthall et al. 1999). If species from nonsavanna vegetation types such as gallery forests that

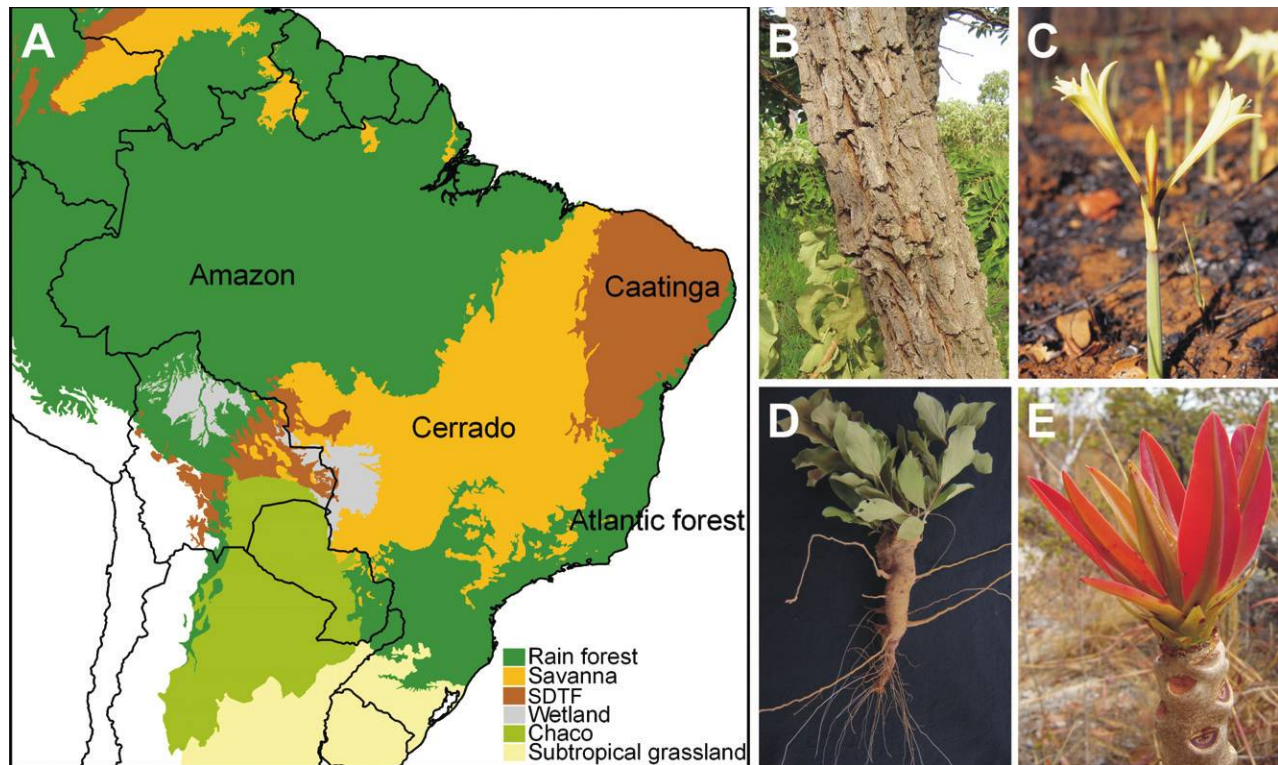


Fig. 1 A, Map of major vegetation types in South America showing the location of the Cerrado and surrounding biomes. Photographs illustrating fire adaptations found in the Cerrado: B, thick corky bark of *Machaerium opacum* (Leguminosae) protects internal tissues from fire; C, *Hippeastrum goianum* (Amaryllidaceae) takes advantage of the absence of competitors to reproduce after fire; D, underground organ (xylopodium) of *Anemopaegma* sp. (Bignoniaceae) enables the plant to resprout after aboveground parts are killed by fire; E, thick terminal branch of the treelet *Kielmeyera coriacea* (Clusiaceae) is more fire resistant than thin branches.

occur in the Cerrado region are included, it houses more than 10,000 vascular plant species (Mendonça et al. 2008; Ratter et al. 2011; Forzza et al. 2012), as many as are found in the Brazilian Amazon (Forzza et al. 2012). Comparable diversity levels between Amazonia and the Cerrado are also found at smaller spatial scales: 1500 species were found in a 1300-ha Cerrado reserve near Brasília (IBGE 2004), whereas 2200 species were recorded in a larger 10,000-ha reserve in central Amazonia (Ribeiro et al. 1999). Locally within the Cerrado, plant diversity can reach more than 300 species ha⁻¹ (Gottsberger and Silberbauer-Gottsberger 2006). Isolated areas of savanna also occur within the Amazon rain forest. These disjunct Amazonian savannas are found on poor, sandy soils (Solbrig 1993), and with two exceptions (Alter do Chão in the State of Pará and Humaitá in the State of Amazonas) contain few woody species in comparison with the Cerrados of central Brazil (Ratter et al. 2003). An additional relatively species-rich area of savanna vegetation with strong floristic affinities with the Cerrado is found in the Bolivian Chiquitano (Killeen and Nee 1991; Navarro and Ferreira 2004).

The Cerrado region of central Brazil contains several vegetation types, including patches of SDTF and mesic gallery forests along rivers. In this article we concentrate on the dominant savanna vegetation type known as “cerrado sensu lato.” Cerrado sensu lato varies in its openness, from an almost closed woodland known as cerradão to open grasslands

with sparsely scattered shrubs and small trees. Fire frequency is thought to be a major factor determining the openness of Cerrado vegetation (Durigan 2006), although soil properties may also play a role (Goodland and Pollard 1973).

Fire has been a prevalent force shaping terrestrial ecosystems since early geological ages (Bond and Midgley 2012, p. 569). Accumulation of biomass mostly from C₄ grasses during the dry season is the main source of fuel for surface fires in modern savannas. However, although C₄ grasses originated and started to diversify during the Oligocene (Edwards et al. 2010; GPWG II 2012), the record of carbon isotope ratios in fossil teeth and palaeosoils, charcoal particles, and pollen suggests that C₄ grasslands were not widespread globally until 6–8 on ago (Cerling et al. 1997; Beerling and Osborne 2006; Stromberg 2011). This has led to suggestions that Neotropical C₄ savannas including the Cerrado are geologically young (Pennington et al. 2006b; Gottsberger and Silberbauer-Gottsberger 2006), postdating the origin of Neotropical rain forests that are well documented in the early Cenozoic by fossils (Burnham and Johnson 2004). It is also likely that Neotropical savannas postdate the establishment of SDTF, which is estimated as ~30–40 Myr ago by the onset of diversification in dated phylogenies of biome-specific clades (Becerra 2005; Pennington et al. 2006a).

There is no fossil record for the wider Cerrado flora, but if the origin of the biome is tied to the recent expansion of C₄

grasses and their promotion of a novel fire regime, the implication is that the features of Cerrado plants that confer resistance to fire might have a similarly recent origin. There is, however, a long history of attributing some features of woody Cerrado plants that confer resistance to fire to the seasonal climate and poor soils of the Cerrado (Rawitscher et al. 1943; Rawitscher and Rachid 1946; Arens 1963; Goodland and Pollard 1973; reviewed by Gottsberger and Silberbauer-Gottsberger 2006). Given that the oxisols that cover much of the Cerrado are ancient, probably of Tertiary origin (Motta et al. 2002), and that global climates became increasingly arid from the middle Eocene (reviewed by Willis and McElwain 2002), the hypothesis of evolution in response to climate and soil would imply an earlier origin of elements of the Cerrado flora.

In this review article, we first examine the features of plants that enable them to survive the seasonal climate, frequent fires, and nutrient poverty of the Cerrado. We then examine the evidence from phylogenies that include taxa restricted to the Cerrado to investigate (1) the number of times lineages have entered the Cerrado, (2) the timing of the origin of the Cerrado-confined lineages, (3) influence of neighboring biomes in the assembly of the Cerrado flora, and (4) whether some fire-related traits evolved as a response to a new fire regime.

What Features Enable Woody Plants to Survive in Neotropical Savannas?

Coping with Fire

The fire regime in savannas poses major challenges to perennial plants, which have to tolerate a highly destructive and frequent disturbance. A diverse set of morphological features are found in Cerrado plants that enable them to cope with fire, including the allocation of biomass to underground organs coupled with ability to resprout, thick corky bark (insulation that protects internal tissues), thick terminal branches (more resistant to fire), densely packed leaf bases, stipules that protect shoot apices from fire, and specialized phenological and reproductive strategies, including early maturity and fire-induced flowering (Eiten 1972; Sarmiento and Monasterio 1983; Coutinho 1990; Miranda et al. 2002; Hoffmann et al. 2003; Gottsberger and Silberbauer-Gottsberger 2006; fig. 1). In this article we focus particularly on the occurrence of corky bark and extensive underground organs, which attracted the attention of early naturalists such as Warming (1908), whose pioneer work on the ecology of the Cerrado flora in the nineteenth century highlighted the occurrence of fire adaptations in a large number of species belonging to different plant families. A key reason for this focus is the debate of exaptation versus adaptation, because corky bark and extensive underground organs are features that have been suggested to have evolved in response to seasonal climates or poor soils of the Cerrado (Rawitscher et al. 1943; Rawitscher and Rachid 1946; Arens 1963; Goodland and Pollard 1973; reviewed by Gottsberger and Silberbauer-Gottsberger 2006) rather than as adaptations to fire (Rizzini and Heringer 1962; Coutinho 1982).

Developing a habit classification for Cerrado plants is difficult. As several authors have pointed out, there is intergradation of growth forms between trees, shrubs, and perennial

plants that appear herbaceous but sprout each year from woody rootstocks (Eiten 1972; Gottsberger and Silberbauer-Gottsberger 2006; Ratter et al. 2006). The vast majority of Cerrado plants are perennial, even among those in the ground layer, and true annual plants are very rare (Eiten 1972). Frequent fire favors species with perennial, woody, underground organs—some of them massive and many times larger than the aerial parts—that enable plants to resprout effectively after fire. These underground systems are diverse and differ in their anatomy, origin, structure, and the way they originate new buds. A typical belowground organ present in a number of Cerrado plants is the xylopodium (fig. 1D), a lignified belowground organ that can exhibit both shoot and root anatomical structure and has high capacity to form new shoot buds (Apezato-da-Glória et al. 2008). Although surface fires in the Cerrado can reach temperatures as high as 500°C aboveground, the increase in soil temperature during burning is negligible (Miranda et al. 2009) and therefore causes little or no damage to underground plant organs. Not surprisingly, underground biomass can represent up to 70% of all plant biomass in Cerrado communities (Castro and Kauffman 1998).

The terminology used to describe the growth form of perennial, woody plants with xylopodia is confusing. Such plants have been given various names, including xylohemicyptophyte (Gottsberger and Silberbauer-Gottsberger 2006), geoxyle and hemixyle (Sarmiento and Monasterio 1983; Ratter et al. 2006), or geoxylic suffrutex (White 1976). In this article, we will use the simplest term, “geoxyle” to describe these plants that have woody xylopodia underground but only limited and often short-lived aerial shoots. In extreme cases, species have massive (>8 cm diameter) belowground systems that can radiate for several meters, with some individuals forming patches up to 10 m in diameter (e.g., in *Andira humilis*; Pennington 2003). The term “underground trees” for these plants (White 1976) seems very appropriate.

Coping with Drought and Nutrient-Poor Soils

Neotropical savannas occur in areas where the climate is too seasonal to support rain forest. The Cerrado has an average precipitation for more than 90% of its area of 800–2000 mm and a very strong dry season during the southern winter (~May–September; Dias 1992). In addition to this climatic challenge, savanna plants have to cope with nutrient-poor, acid soils that are low in nitrogen and phosphorus and, in many areas of the Brazilian Cerrado, with levels of aluminium that are toxic to many plants not adapted to this soil type.

The dry season represents a physiological challenge to savanna plants and is overcome in diverse manners by the Cerrado flora. Cerrado trees are generally evergreen, though many drop a proportion of their leaves in the dry season (Gottsberger and Silberbauer-Gottsberger 2006; Franco 2008), and it is well known that they have profound root systems (Franco 2002). It seems that these deep roots are able to tap groundwater even at the height of the dry season, which, coupled with stomatal control of transpiration and decrease in total leaf area, allows Cerrado trees to maintain water balance (Franco 2008). For example, Brodribb et al. (2002) showed that *Curatella americana*, a dominant species in the Cerrado, was able to maintain stem-specific conductivity at a basically constant level through

dry and wet seasons in the Santa Rosa National Park, Costa Rica.

It has been widely suggested that woody xylopodia and thick bark that confer resistance to fire in woody Cerrado plants may be exaptations that evolved in response to the special soils and seasonal climate of the Cerrado. For example, xylopodia were considered by some workers to act as a water reservoir, which is supported by studies of some species that show high water, starch, and soluble sugar content (Carvalho and Dietrich 1993). However, in other cases, water content has been shown to be low (Coutinho 1982) but mineral content high, leading to suggestions that xylopodia originated as a response to nutrient-poor soils. Scholz et al. (2007) examined the role in water storage of the “living bark,” the outer parenchyma, situated between the vascular cambium and the dead bark tissue of the periderm. This layer is often thick in Cerrado trees, representing a substantial part of the stem tissues in cross section (Coradin 2000; Gottsberger and Silberbauer-Gottsberger 2006). They found that while the outer parenchyma did contribute to total stem water capacitance, its contribution was relatively low compared to that of the sapwood, and they suggested that its primary role might be to store soluble carbohydrates or to act as a thermal insulator, protecting the cambium and phloem from fire.

Phylogenetic Studies and What They Tell Us about Evolution of Features Conferring Fire Resistance in the Cerrado

Molecular phylogenies can provide essential information for ancestral area inference and the study of ecological transitions (biome changes) within lineages (Crisp et al. 2009). When dated, they can also give an estimate of the time of origin of lineages carrying features conferring fire resistance. A recent study used dated phylogenies of four plant groups (*Mimosa*, *Andira*, *Lupinus*, and *Microlicieae*) comprising 3%–4% of the Cerrado flora to shed light on the origin of this fire-prone biome (Simon et al. 2009). Here we have been able to examine a number of studies that included a representative sample of Cerrado species. A list of relevant phylogenies containing Cerrado species and the evidence provided by these groups on the evolution of the Cerrado flora is summarized in table 1. Importantly, these expand the taxonomic sampling of Cerrado lineages into seven new families; Simon et al.’s sampling was concentrated in Leguminosae.

It is clear, however, that densely sampled phylogenies of plants with sufficient Cerrado species sampled are still rare. A search on the Phylota Browser database (Sanderson et al. 2008; release 1.5, May 2011) for sequences/phylogenies of the Cerrado’s 34 most common woody genera as listed by Ratter et al. (2003) showed that most genera (47%) have insufficient data to reconstruct phylogenies (phylogenetic clusters with four or more species not available). The remaining genera for which phylogenies are available are either not densely sampled and/or do not include Cerrado species. Among these woody groups, only the genera *Andira* (Leguminosae) and *Eriotheca* (Malvaceae) are well sampled in that they include all Cerrado species.

Evolutionary “Entry” of Lineages into the Cerrado and Origin of Biome-Specific Morphologies

The fact that many woody plants of the Cerrado have congeners in surrounding forest biomes led Prance (1992) and Hoffman and Franco (2003) to suggest that entering the Cerrado biome is a simple switch to make in evolutionary terms, a point that has been reaffirmed by subsequent authors. For example, Pennington et al. (2006b) pointed out that of the 121 woody species in 90 genera listed by Bridgewater et al. (2004) as dominating the Brazilian Cerrado, 99 species belong to 72 genera that also have species found in rain forests. At a broad phylogenetic scale, the scattered distribution of some features characteristic of Cerrado plants is striking. For example, xylopodia have originated in parallel numerous times. Figure 2A maps the phylogenetic distribution at ordinal level across angiosperms of 94 species with xylopodia found in 1 ha of Cerrado at Botucatu, São Paulo State (of 301 species total; data from Gottsberger and Silberbauer-Gottsberger 2006). Species with xylopodia in this Cerrado community have originated in 19 orders, almost certainly independently because if this feature is mapped on a single family (Leguminosae, 13 species bearing xylopodia in eight genera), it is also phylogenetically dispersed (fig. 2B).

At a finer phylogenetic scale, the vast majority of Cerrado genera lack a phylogenetic framework that would allow a reconstruction of the evolutionary history of biome-specific traits. Reduction in life forms from large forest trees and investment in underground organs have been hypothesized to have occurred in different plant groups such as *Annona*, *Jacaranda*, and *Andira* (Warming 1908; Gottsberger and Silberbauer-Gottsberger 2006), although in most cases phylogenies are not available to verify these hypotheses. One Cerrado genus for which an adequate species-level phylogeny is available is *Mimosa* (Simon et al. 2009). This study documented 11 lineages that have entered the Cerrado independently, with multiple origins of xylopodia in several clades. A single clade within *Mimosa* that is rich in Cerrado endemics contains 50 species and includes a great diversity morphological features and life forms (fig. 3), reflecting the diverse ways that plants evolved to withstand fire: (1) trees with leaves crowded at the top of the branches, thick terminal branches, and persistent stipules to protect the trunk from fire (pachycaul rosette trees); (2) shrubs with perennial aerial parts growing from xylopodia (persistent geoxyles); and (3) prostrate functionally herbaceous and wand-like subshrubs with aerial parts growing annually from xylopodia (recurrent geoxyles). Another example is *Manihot*, for which the Cerrado is the main centre of diversity with 38 species, most of them endemics. Character and ancestral area reconstructions suggest that the diversification of *Manihot* in the Cerrado involved crucial changes related to growth habit and development of tuberous roots that allowed species adapt to the Cerrado environment (Duputié et al. 2011).

The display of diversification of a range of life forms in the Cerrado typified by *Mimosa* is a signature of adaptive radiations associated with fulfillment of new ecological opportunities, as documented in other plant groups that undergone fast evolution when ecological opportunities are available (Baldwin and Sanderson 1998; Hughes and Eastwood 2006). In these cases, despite such extreme morphological variation, there is

Table 1
Phylogenetic Studies Containing Cerrado Taxa Showing Taxon Sampling, Evidences for Derived/Multiple Origins, Crown/Stem Age Estimates, and Evolution of Fire Adaptations in Cerrado Lineages

Study group	Taxon sampling ^a	Cerrado lineages are derived	Multiple origins (lineages)	Age (Myr)	Ancestral area (lineages)	Evolution of fire adaptation	Reference
<i>Andira</i> (Leguminosae)	4/4	Yes	Yes (2)	.7–1.8/2.9–3.7	Rain forest (2)	Xylopodium, thick corky bark	Simon et al. 2009
<i>Eriotheca</i> (Malvaceae)	3/3	Yes	Yes (2)	...	Rain forest (2)	Thick corky bark	Duarte et al. 2011
Hyptidinae (Lamiaceae)	112/190	Yes	Yes (6)	...	SDTF (6)	Xylopodium	Pastore et al. 2011
<i>Lupinus</i> (Leguminosae)	5/11	Yes	No (1)	1.9/2.6	Subtropical grasslands (1)	...	Simon et al. 2009
<i>Manihot</i> (Euphorbiaceae)	17/47	Yes	Yes (5)	<6.6	Rain forest (4), SDTF (1)	Xylopodium	Chacón et al. 2008; Duputié et al. 2011
Microlicieae (Melastomataceae)	25/200	Yes	No (1)	9.8/17.1	Wetland (1)	Xylopodium	Simon et al. 2009
<i>Mimosa</i> (Leguminosae)	100/200	Yes	Yes (11)	.4–8.4/1.9–11.3	SDTF (4) (most lineages equivocal reconstruction)	Xylopodium, pachycaul tree	Simon et al. 2009
<i>Ruellia</i> (Acanthaceae)	15/52	Yes	Yes (?)	...	?	Xylopodium	Tripp 2007
<i>Schefflera</i> (Araliaceae)	4/13	Yes	Yes (2)	...	Rain forest (2)	Thick corky bark	Fiaschi and Plunkert 2011
<i>Styrax</i> (Styracaceae)	4/16	Yes	Yes (2)	...	?	Thick corky bark	Fritsch 2001
<i>Viguiera</i> (Asteraceae)	9/22	Yes	?	<3.0	?	Xylopodium	Schilling et al. 2000

^a Cerrado species sampled in the phylogeny/total Cerrado species according to Mendonça et al. (2008). SDTF = seasonally dry tropical forest.

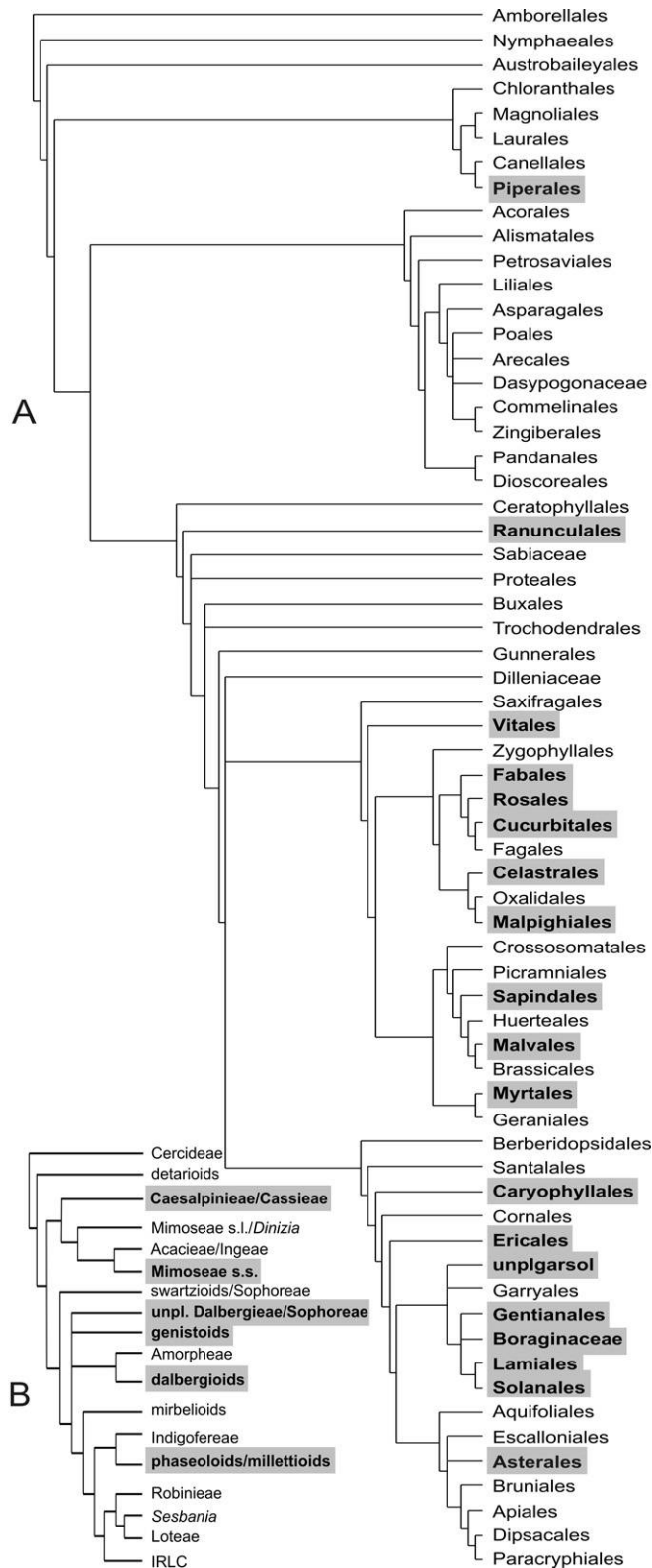


Fig. 2 Phylogenetic distribution of 94 species with xylopodia found in 1 ha of Cerrado at Botucatu, São Paulo State (Gottsberger and Silberbauer-Gottsberger 2006), showing that xylopodia are dispersed phylogenetically and have originated in 19 angiosperm orders (A) and also in six Leguminosae major clades (B).

little genetic diversity among these species, which may be a signature of rapid and recent evolution. The geological recency of species radiations in the Cerrado is confirmed by dated phylogenies, as discussed in the following section.

Analyses of the phylogenetic structure of biological communities have generally been used to investigate contemporary ecological forces that assemble local biotas (Vamosi et al. 2009) but also offer an alternative to single-taxon phylogenetic approaches for investigating the historical construction of biomes (Pennington et al. 2006b). Cerrado plant communities show phylogenetic overdispersion, which implies that more phylogenetic diversity is present in Cerrado plots than expected by chance alone (Silva and Batalha 2009). This contrasts with vegetation types that exhibit phylogenetic clustering, including some SDTF plant communities in Brazil (Silva and Batalha 2010). These findings, based on the entire flora, corroborate the evidence of multiple transitions of plant lineages into the Cerrado as shown by individual phylogenies.

Timing of Entry of Lineages into the Cerrado

All Cerrado clades for which dated phylogenies are available are dated younger than 10 Ma, with most lineages diversifying at 5 Ma or less. The additional examples surveyed here (table 1) confirm the conclusions presented by Simon et al. (2009) that Cerrado clades are recent and coincide in age with fossil evidence for the expansion of ecosystems dominated by C_4 grasses. For many phylogenies, absolute age estimates are not available (e.g., several examples in table 1). However, even in these cases, the derived position of Cerrado lineages, often placed toward the tips of phylogenies, suggests recent origin of savanna clades.

Source Biomes

Previous ancestral area reconstructions of 15 Cerrado lineages found that fire-adapted groups evolved from a diverse range of biomes that includes SDTF, rain forests, subtropical grasslands, and wetlands (Simon et al. 2009). Although most area reconstructions in *Mimosa* were equivocal, three lineages were inferred to be derived from SDTF. Two *Andira* lineages originated from rain forest, while *Lupinus* and Microlicieae Cerrado clades evolved from subtropical grassland and wetland, respectively.

Another example of biome shift into the Cerrado comes from a recent study focused on the Neotropical tree genus *Eriotheca* (Malvaceae; Duarte et al. 2011). *Eriotheca* occurs mostly in rain forests but is also present in SDTF and in the Cerrado. A phylogeny comprising two-thirds of all known species of *Eriotheca* and including all three Cerrado taxa shows that savanna lineages evolved multiple times from a predominantly rain forest preference (fig. 4). An ancestral area optimization onto a topology derived from a three-gene data set from Duarte et al. (2011) was performed here under a parsimony criterion using the software Mesquite (Maddison and Maddison 2010). This analysis suggests that all three fire-adapted *Eriotheca* species (*E. pubescens*, *E. gracilipes*, and *E. parvifolia*) evolved from a rain forest ancestor and that each of these represent independent lineages that undergone biome shifts (fig. 4). Similarly, a phylogeny of *Schefflera* (Fiaschi and Plunkett

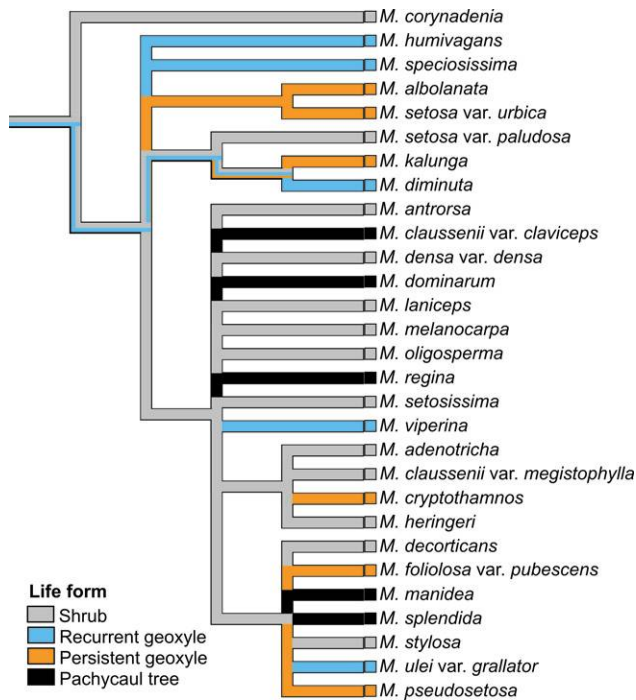


Fig. 3 Evolution of fire-adapted life forms in a clade of *Mimosa* rich in Cerrado endemics, reflecting the diverse ways that plants evolved to withstand fire: pachycaul trees (trees with leaves crowded at the top of thick terminal branches); persistent geoxyles (shrubs with perennial aerial parts growing from xylopodia); and recurrent geoxyles (functionally herbaceous and wand-like subshrubs with aerial parts growing annually from xylopodia). Modified from Simon et al. (2009).

2011) shows evolution of Cerrado species from rain forest ancestors, while a study of the species-rich subtribe Hyptidinae (Lamiaceae) suggests a general pattern of primary distribution within SDTF followed by secondary events of diversification into the Cerrado (Pastore et al. 2011).

Overall the source biomes of the Cerrado are diverse, with ancestral lineages present in a range of different biomes. For those transitions that we were able to infer based on available molecular phylogenies (table 1), the ancestral biome was recorded as rain forest (10 lineages), SDTF (11), subtropical grassland (1), and wetland (1). The common pattern of fire-adapted woody species endemic to the savannas of the Cerrado derived from rain forest ancestry may be prevalent in many genera in which rain forest species predominate. Floristic affinities between the flora of the Cerrado and the Atlantic and Amazon rain forests have been pointed out by a number of authors (Heringer et al. 1977; Sarmiento 1983; Prance 1992; Oliveira-Filho and Fontes 2000), particularly in the woody species, given that most of the predominant Cerrado genera also contain species endemic to rain forests. Such affinities resulting from rain forest to Cerrado biome transitions as inferred for *Andira* and *Eriotheca* are expected to have occurred in many other ecologically important Cerrado woody genera such as *Aspidosperma*, *Annona*, *Caryocar*, *Dimorphandra*, *Palicourea*, *Qualea*, and *Vochysia* because all have congeneric species in rain forest. Densely sampled phylogenies of these genera are still needed to corroborate this hy-

pothesis, but the current data, albeit scarce, provide compelling evidence that geologically recent ecological transitions from other biomes have been an important force in shaping Cerrado plant diversity.

Discussion and Conclusions

The Age of the Cerrado, the Number of Woody Plant Lineages That Occupy It, and Where They Came From

We found no evidence to support the hypothesis (Cole 1960; Ratter et al. 1997; Oliveira-Filho and Ratter 2002) that the Cerrado is a vegetation type of great antiquity (Cretaceous) or that its woody elements are possible precursors of the adjacent Amazonian and Atlantic rain forests. On the contrary, the data available so far suggest that endemic Cerrado lineages arose from the late Miocene onward, derived from numerous ancestral lineages from diverse surrounding biomes. Phylogenetic and floristic evidence suggests that the woody Cerrado flora is composed of multiple independent lineages from disparate plant families. The Cerrado therefore appears to be an example where shifts between major biomes can play an important role in the generation of species diversity, contrasting with the prevalence of phylogenetic niche conservatism suggested by other authors (Donoghue 2008; Crisp et al. 2009). Intriguingly, phylogenetic niche conservatism may be

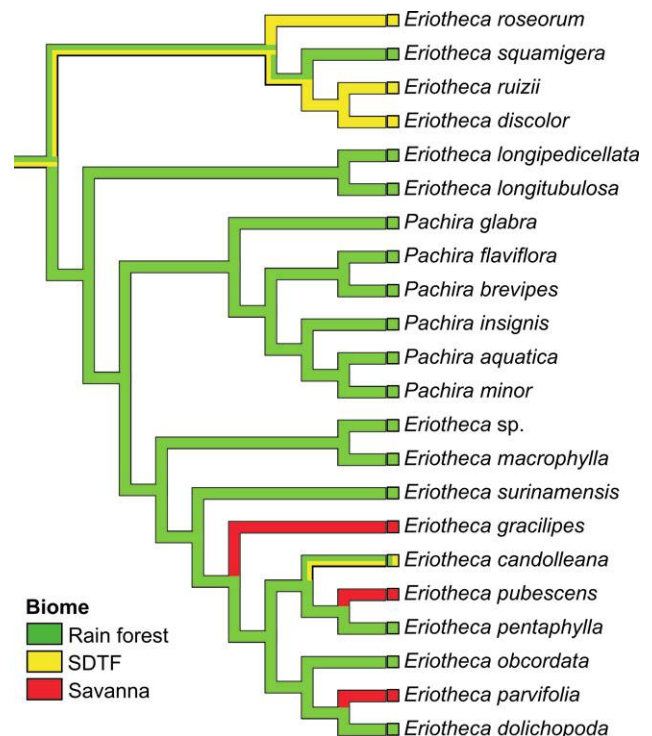


Fig. 4 Ancestral biome optimization onto a phylogeny of the genus *Eriotheca* (Malvaceae) derived from a three-gene data set from Duarte et al. (2011) showing that savanna fire-adapted lineages evolved from rain forest ancestors.

much more prevalent in other fire-prone biomes, including the southern hemisphere Mediterranean climate sclerophyll biomes (Crisp et al. 2009). For example, the fynbos vegetation of the Cape Floristic Region (CFR) is characterized by a few highly species-rich species radiations (e.g., *Erica*, *Protea*, *Phyllis*). These most likely originated and radiated within the CFR (Linder and Hardy 2004), and their diversification started at different times between the late Oligocene and late Miocene, unlike the more even-aged, recent diversification in the Cerrado. Overall, Crisp et al. (2009) demonstrated significantly more phylogenetic shifts from fire-prone Southern Hemisphere sclerophyll biomes into other surrounding biomes—the opposite pattern of the Cerrado.

Therefore, the historical assembly of the Cerrado appears to be entirely different compared to that of the Southern Hemisphere flammable shrublands. This may relate to the shrublands being crown, low-fire-frequency systems, lacking a large grass element, where woody plants use different traits (e.g., serotiny) to tolerate fire. Such fire-adaptive traits seem to have an ancient origin in Mediterranean vegetation systems, with fire-adapted lineages dating back to the early Paleocene (Crisp et al. 2011; He et al. 2011). The evidence from dated phylogenies that Cerrado-confined lineages arose only from the late Miocene onward is coincident with the rise to dominance of C₄ grasses. Given the importance of fire as part of the ecology of the Cerrado, this is strong evidence that in central Brazil, the Neogene spread of grassy biomes, possibly at the expense of closed forests, was driven by novel fire regimes (see topic below). This is a contrasting scenario to that for North American grasslands where paleontological evidence suggests that already established C₃ grasslands were replaced by C₄ grasslands in the late Miocene (Stromberg and McInerney 2011).

Adaptation versus Exaptation in the Woody Cerrado Flora

The multiple, independently derived woody plant lineages endemic to the Cerrado are characterized by traits such as thick, corky bark and root sprouting, which are absent or less marked in related lineages found in forests that do not burn. We believe that the weight of the evidence suggests that these traits, characteristic of the most abundant and ecologically dominant woody species of the Cerrado, should be considered as adaptations to fire regimes, a conclusion that contrasts with that of Bradshaw et al. (2011a), who judged features of fire-tolerant plants in Mediterranean biomes as exaptations. Three lines of evidence support our conclusion:

1. Lineages possessing these traits are confined to the fire-prone Cerrado and the traits are absent or less marked in related species in other biomes. For example, corky bark is absent in most *Andira* species, which predominate in rain forest biomes (Amazonia and the Atlantic coastal forests of Brazil). However, shift into the fire-prone Cerrado biome coincided with the evolution of corky bark in all Cerrado species of *Andira* (fig. 5), except in *A. humilis*, which evolved a modified geoxylic growth form, with an extensive network of underground woody shoots that resembles an underground tree. Endemic Cerrado species have thicker insulating bark compared to congeneric species found only in closed rain forest or SDTF (Hoffmann et al. 2009) and allocate more biomass to roots (Hoffmann and Franco 2003), and this

tendency exists at the seedling stage (Hoffmann et al. 2004). Hoffman and coauthors also suggest that investment in underground biomass allows the Cerrado species to access a greater pool of nonstructural carbohydrates for postfire recovery.

2. There is no phylogenetic evidence suggesting origins of features such as corky bark or xylopodia before the rise to dominance of flammable C₄ grasses as predicted in the case of exaptation. In most cases, Cerrado lineages are apically nested in phylogenies, with young stem ages. If the fire-resistant features that characterize these lineages had arisen earlier in older lineages that subsequently diversified in a new fire-prone Cerrado environment, in some cases one would expect to find a species-rich Cerrado radiation on a long, basally divergent phylogenetic branch, with a crown node age that predated the late Miocene (fig. 6). However, in all cases, crown node ages are dated younger than 10 Ma, with most younger than 5 Ma (table 1).

3. Hypotheses of exaptation for corky bark and xylopodia center on their supposed utility in nutrient-poor soils and to a lesser extent, seasonal climates. Amazonian rain forests that border the Cerrado are found on soils that are equally nutrient poor (Ratter 1992), but the Amazonian forest flora is not characterized by xylopodia or corky bark. Indeed the rapid current spread of rain forest tree species into savanna areas at the Amazon-Cerrado transition (Ratter et al. 1973) strongly argues against edaphic control of the savanna-forest ecotone. The same argument applies to the network of gallery wet forests that grow side by side with savannas in central Brazil, frequently on similar soils. Adaptive explanations for these features based on climatic seasonality and water balance also seem unlikely. Cerrado and SDTF are interdigitated in many regions of central Brazil, with SDTF growing on richer soils derived from base-rich bedrock but experiencing identical climates. SDTF trees do not have thick, corky bark comparable to Cerrado species. Furthermore, as outlined above, Scholz et al. (2007) found that the outer “living bark” of Cerrado trees contributed relatively little to total stem water capacitance compared to that of the sapwood and that its primary role might be fire protection.

Ease of Evolution of Adaptations and Genetic Reasons for It

The Cerrado appears to be an example where adaptive shifts between major biomes can play an important role in the generation of species diversity, contrasting with the prevalence of phylogenetic niche conservatism suggested by other authors (Donoghue 2008; Crisp et al. 2009) for biomes such as those found in the high Andes (Donoghue 2008). Our results suggest that the Cerrado flora is composed of multiple independent lineages in disparate plant families and that the key adaptive shift has been to cope with fire. The frequent adaptive shifts and phylogenetic overdispersion in Cerrado plant communities suggest that fire does not pose a significant adaptive barrier. In the case of the Cerrado, biome boundaries appear to have been permeable to the ingress and recruitment of lineages from a range of fire-free vegetation types, suggesting lack of phylogenetic niche conservatism.

Natural fires in tropical rain forests, a major source biome for the Cerrado, are rare events and are likely to produce high levels of tree mortality (Uhl and Kauffman 1990; Cochrane

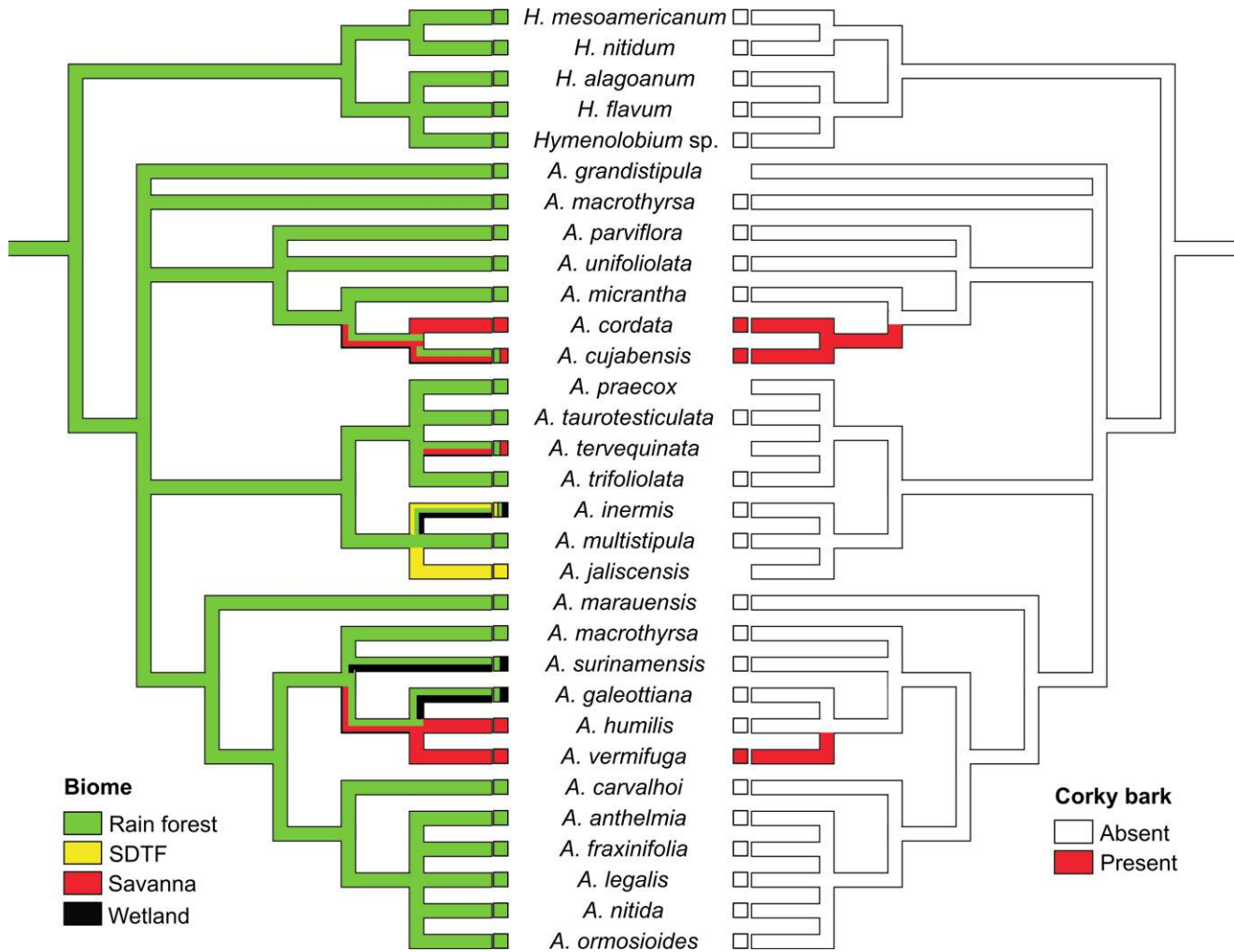


Fig. 5 Association between biome shift and evolution of fire adaptation in *Andira* (Leguminosae). *Left*, ancestral biome optimization. *Right*, evolution of corky bark, which coincides with biome change from rain forest to Cerrado. Shorter branches on the right represent missing data.

and Schulze 1999). On the other hand, Cerrado plants are well suited to survive frequent fires. The independent origin of fire adaptations across many plant families and genera suggests that adaptations to the fire regime of tropical savannas may be easily acquired. The changes required to thicken bark, redistribute leaves toward the tips of fewer stouter branches or shift woody biomass to underground structures all represent morphological/architectural modifications that seem to be easy to generate given the morphological plasticity found within some species (e.g., *Caryocar brasiliense*, which can be a low geoxyle or large tree). The potential genetic developmental simplicity of such shifts compared to more complex plant physiological adaptations (e.g., frost) are likely to account for this ease and evolutionary lability of fire adaptation. Genetic evidence from population level studies indicates low levels of genetic divergence between rain forest and Cerrado species congeners, therefore suggesting that the acquisition of the genetic toolkit required for fire adaptation cannot be complex. For example, the Cerrado tree *Caryocar brasiliense* shares a number of haplotypes with its rain forest congeners *Caryocar microcarpum* and *Caryocar villosum*, implying high levels

of genetic similarity and possibly recent speciation (Collevatti et al. 2009). Another example of recent evolution of Cerrado species is provided by a population genetic study (Ramos et al. 2009) involving *Hymenaea courbaril* (wet/gallery forest, thin bark) and *Hymenaea stigonocarpa* (savanna, thick corky bark), which are often found in the same site in central Brazil. Although this pair of congeneric species is ecologically and morphologically distinct, the low levels of genetic divergence between them suggest recent biome transition and associated evolution of fire adaptation.

What Vegetation Existed in Central Brazil before the Cerrado?

Although there are a number of studies addressing the Quaternary palaeoflora of central Brazil (e.g., Ledru 2002), the time frame covered, restricted to only a few thousand years ago, provides no information on the origin of the current Cerrado flora or the Tertiary history of the vegetation of central Brazil. Tertiary fossil data from the Cerrado region is virtually nonexistent (Burnham and Graham 1999). There-

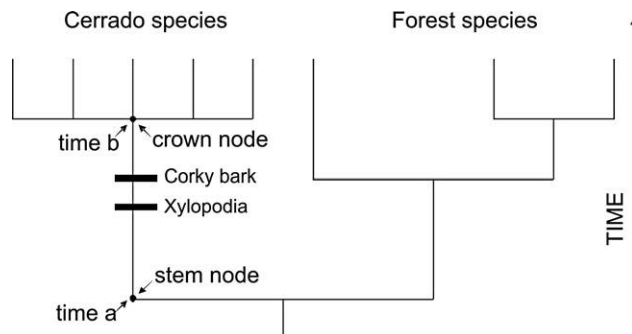


Fig. 6 Features used to tolerate fire (corky bark, xylopodia) could have originated at any time between the stem and crown node of a Cerrado clade (time a and time b). If the date of the crown node (time b) is predates the late Miocene, when C_4 grasses became dominant, this hypothetical dated phylogeny is potentially consistent with exaptation because it would indicate that corky bark and xylopodia most likely evolved before the origin of the C_4 grass fire regime.

fore, any speculation about what vegetation existed in central Brazil before the origin of a fire-prone, C_4 -grass-rich Cerrado is by necessity speculative.

We suggest that the predecessor of the savannas in central Brazil before the expansion of C_4 grasses and their accompanying fire regime was probably some type of closed canopy tropical forest with different levels of deciduousness depending on climate seasonality and edaphic factors. Fire exclusion experiments show that rain forest species are able to invade savanna and outcompete fire-adapted species in the absence of fire (Geiger et al. 2011), indicating that closed canopy forests might develop in the Cerrado's nutrient poor soils. On the other hand, typical SDTF species tend to grow on richer soils such as limestone outcrops. Considering that soil features changes very slowly in geological time and that the oxisols that predominate in central Brazil are rather ancient (Motta et al. 2002), it seems unlikely that SDTF trees specialized in high-fertility soils would have been able to occupy vast areas in central Brazil before the Cerrado.

It is likely that the process of adaptive switch and concomitant adaptation of woody lineages to a new fire regime occurred gradually. Lineages able to overcome this environmental filter were gradually flourishing in an expanding new fire-prone biome. The fact that many Cerrado lineages switched to a savanna within the last 2 Myr (table 1) suggests that ecological transitions from fire-free into fire-prone environments are an ongoing process.

Suggestions for Future Research Directions

Clearly, the understanding of the origins and evolution of the Brazilian Cerrado will greatly benefit from phylogenetic studies that sample intensively at species-level and that cover a more substantial number of endemic plant lineages. In particular, it would be valuable to study ecologically dominant groups. These include Leguminosae, for which the necessary well-sampled species-level tree would be challenging given the species richness of the family, and the phylogenetic dispersion of the numerous Cerrado elements (e.g., fig. 2B). A

more realistic target would be Vochysiaceae, which is ecologically dominant in the Cerrado, especially the genus *Qualea*, and rich in fire-adapted woody species.

Phylogenetic data suggest that the entry of plant lineages into fire-prone savanna ecosystems is an easy evolutionary step. This is perhaps because many of the required features are already possessed in prototypic form by many woody plants and may require only simple genetic changes including gene regulation rather than structural mutation. For example, corky bark merely reflects highly active cork cambium activity in the periderm, and the ability to root-sprout is already possessed in some form by many woody plants (Del Tredici 2001). An approach of comparative transcriptomics using next-generation DNA sequencing offers an exciting new route to investigate at the genetic level the basis of key evolutionary events (e.g., Tavares et al. 2010; Ness et al. 2011). Furthermore, work on model organisms may help to identify candidate genes. Relevant work includes investigation of the genetic architecture of root development in *Arabidopsis thaliana*, including lateral root length, which is considered an adaptation to drought (Loudet et al. 2005). A comparative transcriptomics approach could elucidate the evolution of fire-related morphologies by revealing which genes are differentially present and expressed in congeneric pairs of fire-resistant and fire-susceptible species. Cerrado and adjacent gallery forests in central Brazil provide an excellent opportunity for such work because of the presence of parapatric, congeneric species pairs that grow in each of these environments. Some morphological and physiological features of 22 savanna-gallery forest species pairs including bark thickness, resprouting ability have already been studied (Hoffmann et al. 2009). In addition, new opportunities for understanding the genetic causes associated with the evolution of phenotypic plasticity, which is a common feature in Cerrado plants, are being revealed in nonmodel organisms (Blackman et al. 2011).

Savannas are a ubiquitous component in the landscape of many continents. Although these areas may differ in their physical attributes such as total rainfall, soil fertility, and species composition (Lehmann et al. 2011), they share common features such as seasonal climate, predominant grass cover, and fire susceptibility. Not surprisingly, many of the fire adaptations present in the Cerrado are also frequently found in other savannas, such as in Africa (White 1976; Gignoux et al. 1997). It would be interesting to verify whether some of the features postulated for the evolution of the Cerrado flora hold for other savanna systems, such as the recent diversification of endemic lineages associated with expansion of savanna biome worldwide and the ease of adaptation to fire across plant groups from fire-free biomes. Data on Australian Myrtaceae suggest that fire-adapted monsoonal savanna lineages evolved multiple times and are derived from sclerophyll or rain forest biomes (Crisp et al. 2011). Although some of these transitions happened during the Miocene, other Myrtaceae fire-adapted lineages are significantly older than the postulated origin of the Cerrado flora and global expansion of C_4 -grass-dominated biomes. Future studies should focus on the evolutionary history of endemic/fire-adapted plant groups in African and Australian savannas, in order to verify whether congruent patterns with evolution of the Cerrado flora emerge and to provide evidence on the origin of fire-adapted traits.

Acknowledgments

We thank Missy Holbrook for discussions on tree physiology, Kirsten Bomblies for discussions on genetics of root development, José Floriano Pastore for discussions on the

evolution of Lamiaceae, and Peter Linder for information about the history of the Cape Flora. In particular, we thank Jim Ratter for sharing his deep knowledge based on five decades of research dedicated to understanding and conserving the Brazilian Cerrado.

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