



Evidence of the effects of fire on branching and leaf development in cerrado trees

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ABSTRACT

We discuss evidence of effects of an accidental fire on shoot growth and leaf development in six cerrado tree species with distinct leaf phenologies. Buds of all six species were marked before shoot and leaf emergence in the dry season. After fire, leaf and shoot growth were monitored weekly and specific leaf area (SLA) was determined. Shoot order was determined in the growing season. Evergreens and semideciduous woody species had rapid leaf and shoot growth and decreased leaf life span (LLS) after fire compared with published data for evergreens in cerrado areas without fire. On the other hand, *Kielmeyera variabilis*, a deciduous species, showed intense branching and produced two orders of shoots in one growing season. Fires promote rapid leaf and shoot growth in evergreens owing to reserve accumulations that allow survivorship after disturbances. However, the leaves produced by evergreens after fire had high SLAs and were discarded before the next rainy season (short LLS). This leaf cohort was produced with less carbon per leaf, and the decreased LLS prevented herbivory and water loss during the dry season. Fire is an important factor of cerrado environments, influencing leaf production and shoot architecture in cerrado trees.

Keywords: disturbance, leaf life span, shoot growth, specific leaf area, shoot order

Introduction

Plant architecture is the compromise between environmental constraints and plant body functionality (Sussex & Kerk 2001; Reinhardt & Kuhlemeier 2002; Meinzer 2003; Barthélémy & Caraglio 2007). Crown branching patterns balance the need to expose leaves to light to perform photosynthesis and the need to ensure that light exposure does not damage the photosynthetic apparatus (Souza *et al.* 2009b). Thus, plant architecture is important for exploiting the horizontal light gradient and refers to the whole plant shape and its spatial arrangement (Poorter *et al.* 2006).

In the cerrado, there are few studies regarding plant architecture, and most of them concern shoot growth (Rossato & Franco 2008; Souza *et al.* 2009a; b; Rossato 2009; Rossato *et al.* 2009). Only four studies deal with whole crown architecture (Souza *et al.* 2011; Santos *et al.* 2012) or modular growth (Damascos *et al.* 2005; Damascos 2008) of woody cerrado species. In general, cerrado species with perennial foliage adjust shoot growth to the rainy period, while those with deciduous foliage produces leaves and shoots before the first rains (Damascos *et al.* 2005; Lenza & Klink 2006; Damascos 2008). According to Lenza & Klink (2006) and Silvério & Lenza (2010), evergreens that show intense leaf production only in the rainy period

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were classified as evergreens with seasonal growth. Woody cerrado species have distinct branching patterns according to their leaf phenology. Evergreen species produce up to three shoot orders in one growing season, while deciduous species produce just one order (Damascos *et al.* 2005; Damascos 2008). In addition, there are other architectural differences between deciduous and evergreen species in cerrado vegetation. Deciduous species have plagiotropic shoots, where leaves receive a similar amount of light along the shoot (Souza *et al.* 2009a; b). On the other hand, evergreens have orthotropic shoots, where distal shoot leaves receive greater irradiance than basal shoot leaves. These differences result in a complex crown in evergreens that has more shoots and nodes than in deciduous trees (Souza *et al.* 2011), which affects light utilization during the day (Santos *et al.* 2012). However, the crown architecture in cerrado habitats can be modified by environmental characteristics such as periodic fires.

Fire has long shaped vegetation in cerrado regions (Miranda *et al.* 2002) and occurs in the rainy season primarily from lightning and in the dry period from human actions (Miranda *et al.* 1993). Woody plants are adapted to this environmental condition and show several morphological traits associated with fire (Simon & Pennington 2012). The bark tissue of woody species is thick to protect internal tissues from fire damage (Hoffmann *et al.* 2003; Simon & Pennington 2012). Fire may stimulate and synchronize flowering and seed production in cerrado species, primarily shrub and herbaceous (Coutinho 1982; Cirne & Miranda 2008). Fire events can change the balance between sexual and vegetative reproduction to favor the latter (Hoffmann 1999). Owing to reserve structures, such as a xylopodium, cerrado species can resprout more intensely and increase stem radial growth after fire (Hoffmann 2002; Medeiros & Miranda 2008; Diniz & Franceschinelli 2014). Even though fire events have direct effects on plant growth, there is no information about fire effects on post-shoot growth and branching in cerrado woody species.

Here we investigated the effect of an accidental fire on shoot growth and branching pattern on six woody cerrado species with distinct leaf phenologies. Fire events can change plant growth, so we expected adjustments in their leaf and shoot growth. In evergreens, fire may change the continuous pattern of leaf production and cause a flush of leaves in a short period to compensate for the lost biomass. In deciduous species, with the whole crown affected by fire, the intense shoot growth with more shoot orders produced in a same growing season is expected. Also, owing to lost biomass on tree crown due to fire event, it is expected an increase in dependence of climate variables, such as precipitation and air temperature, for leaf production and branching, regardless of leaf deciduousness. The study of fire effects on branching patterns in woody cerrado species can improve understanding of fire as a factor shaping cerrado vegetation.

Materials and methods

Study area, climate, and fire event

The study was carried out in a cerrado *sensu stricto* area located within an 86-ha natural reserve in the Federal University of São Carlos, São Paulo state, Brazil (21°58'–22°00'S 47°51'–47°52'W). According to the Köppen climatic classification, the region is between Aw and Cwa. The regional climate is tropical with a wet summer between October and March and a dry season between April and September (Damascos *et al.* 2005). The monthly precipitation and air temperatures during the study period are shown in Figure 1. The soil was classified as a dystrophic Oxisol. The cerrado *sensu stricto* area studied presents a two-layered system (Ribeiro & Walter 1998) with herbaceous plants and trees.

There was an intense natural burn on August 2006. The fire affected about 80 % of the Cerrado reserve in Federal University of São Carlos (personal observation). Only *K. variabilis* plants had their whole aerial part killed by fire event. The others five cerrado species were the crown burned, in general from 50 % to 75 % of the whole aerial part.

Plant species and meteorological conditions in the period of study

The species chosen for this study were two deciduous trees, *Diospyros hispida* A. DC. (Ebenaceae) and *Kielmeyera variabilis* Mart. & Zucc. (Calophyllaceae); two semideciduous trees, *Casearia sylvestris* Sw. (Salicaceae) and *Eriotheca gracilipes* (K. Schum.) A. Robyns (Malvaceae); and two evergreens, *Miconia ligustroides* (DC.) Naudin (Melastomataceae) and *Piptocarpha rotundifolia* (Less.) Baker (Asteraceae). The morphological traits for these species are described in Souza *et al.* (2009a; b).

The pattern of precipitation and air temperature was very marked in both 2006 and 2007 (Fig. 1). Between April and August of 2006 and 2007, low precipitation (except July 2007) and temperatures characterized the dry season. However, between September and March, high precipitation and temperature marked the rainy season (Fig. 1).

Shoot and leaf growth

Five buds were marked prior to opening on each of five individuals per species ($n = 5$ per species, 30 total) after an accidental fire on August 2006. The marked buds were from apical resprout in shoots damaged by fire. The cohort of buds was followed from September 2006 to August 2007. Budbreak was recorded when small leaves were seen emerging from the bud, following Damascos *et al.* (2005). Marked buds and the organs derived from them were observed at 7-d intervals during the wet and dry seasons.



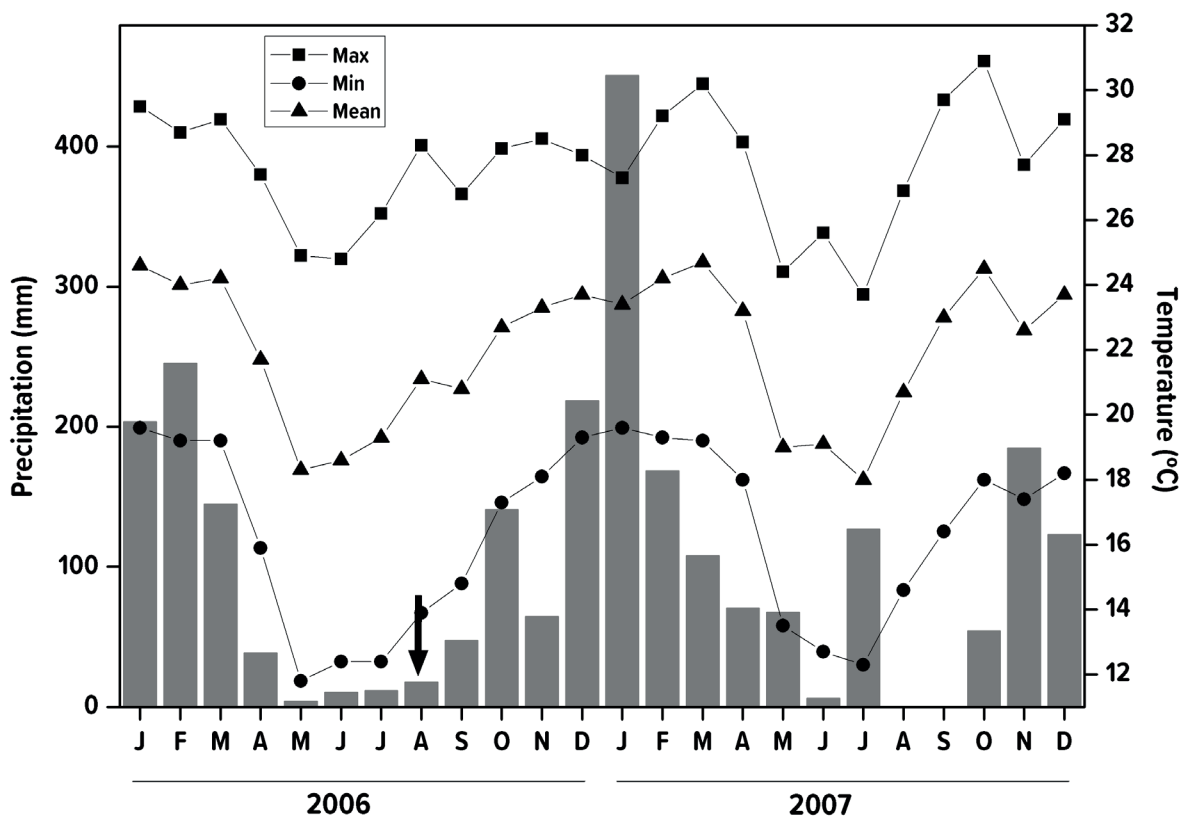


Figure 1. Precipitation and temperature (mean, maximum, and minimum) during 2006 and 2007. The data were recorded at station 83726 of the Brazilian national meteorological service, located 1 km from the study area. The black arrow indicates the month when the fire occurred.

The number of leaves was monitored on shoots during the whole growing season.

To evaluate leaf and shoot development in six woody cerrado species, the leaf expansion interval (LEI, days to full expansion), leaf expansion rate (LER, mature leaf area divided by LEI, $\text{cm}^2 \text{days}^{-1}$), shoot expansion interval (SEI, days to full expansion), shoot expansion rate (SER, mature shoot length by SEI, cm days^{-1}) and leaf life span (LLS, days) were determined. The SEI and SER were determined only on A1 shoots of all species. The shoot length and the length and width of each leaf or leaflet were recorded weekly until growth stopped, at which time the SER and LER were calculated. The maximum length and width of each leaf and shoot were measured at each sampling date, using a ruler. The LLS was noted weekly, and leaves were considered finished when about 90% of the total leaf area was yellowish or when they dropped from the stem.

Branching pattern

During the growing season (2006–2007), the shoots that emerged from axillary buds on parental shoots were classified as first-order axis (A1) shoots (Barthélémy *et al.*

1991; Damascos *et al.* 2005), those produced from axillary buds on A1 shoots were second-order (A2) shoots, and those developed from axillary buds on A2 shoots were third-order (A3) shoots. The final shoot length was determined when shoots stopped growing.

The fate of the apical meristem (flowering, persistence, or abscission) of all shoots (A1, A2, and A3) was determined at the end of the growing season.

Specific leaf area

In each species, 50 shoots previously marked (current-year shoots) were utilized for leaf collection. The leaf area was determined for all leaves on these 50 shoots in each of the six species studied. The leaves were digitized with a scanner and the area was determined using the software Image-Pro, version 5.0 (Media Cybernetics, USA). Afterward, leaves were dried in a stove at 60°C to constant weight (Pérez-Harguindeguy *et al.* 2013), and then the mass was measured with an analytical balance (Mettler AE 260 DeltaRange, US). Specific leaf area was obtained by dividing leaf area by leaf dry mass (SLA, $\text{cm}^2 \text{g}^{-1}$).

Statistical Analysis

A one-way analysis of variance (ANOVA) and *a posteriori* Tukey's test were used to check for differences ($P < 0.05$) among species and species merged into phenological groups in relation to LEI, SEI, LER, SER, LLS, and SLA. Pearson's correlation was used to analyze the relationship between mean monthly number of leaves on A1, A2, and A3 shoots and monthly precipitation and temperature. All statistical analyses were performed with the program R (R Core Team 2014).

Results

Shoot and leaf growth

All species had begun A1 shoot extension at the end of September (09/26/2006), with the exception of *K. variabilis* (deciduous), which only experienced budbreak in early October (10/10/2006).

Miconia ligustroides, an evergreen species, showed the highest LEI (35 days) and SEI (47 days; both $P < 0.05$), and *Eriotheca gracilipes* (semideciduous) had the lowest LEI (20 days) and SEI (16 days, Tab. 1), respectively (both $P < 0.05$). However, *E. gracilipes* showed the highest LER (3.6 cm² days⁻¹) and SER (0.7 cm² days⁻¹; both $P < 0.05$), and *M. ligustroides* and *Casearia sylvestris* had the lowest LER (0.3 cm² days⁻¹) and *M. ligustroides* the lower SER (0.3 cm² days⁻¹; both $P < 0.05$; Tab. 1). The LLS was higher ($P < 0.05$) in *C. sylvestris* (semideciduous, 260 days) and *Diospyros hispida* (deciduous, 256 days) and lower in *Kielmeyera variabilis* (deciduous, 183 days). When the data set was merged into phenological groups, deciduous species showed the highest LEI (28 days; $P < 0.05$), evergreens had the highest SEI (38 days; $P < 0.05$), and semideciduous trees had the highest values of LER (1.9 cm² days⁻¹) and SER (0.6 cm² days⁻¹, Table 1). There was no difference ($P > 0.05$) in LLS among species merged into phenological groups (Tab. 1).

The SLA value was highest in semideciduous *C. sylvestris* (85 cm² g⁻¹) and lowest in deciduous *D. hispida* (57 cm² g⁻¹). The SLA was lower in deciduous group than in semideciduous and evergreen group when species were merged into phenological groups (Tab. 1).

All six species presented a leaf flush on A1 shoots at the end of dry season, in September 2006, with the exception of *K. variabilis*, which produced a new leaf cohort only in October 2006. The period of leaf flushing on A1 shoots corresponded to the beginning of rains and rising air temperatures (Fig. 1). However, leaf production on A2 shoots began at the end of October 2006 in *Casearia sylvestris* and *K. variabilis* and at the end of February 2007 in *M. ligustroides*. Only *M. ligustroides* produced A3 shoot leaves at the end of April 2007.

In deciduous species, there was a positive correlation (Tab. 2, $P < 0.05$) between monthly precipitation and leaf

production on A1 and A2 shoots (Tab. 2, Fig. 2), and in *K. variabilis* (deciduous) the leaf production on A1 shoots was positively correlated ($P < 0.05$) with mean monthly air temperature (Tab. 2, Fig. 2). In semideciduous species *E. gracilipes* and *C. sylvestris*, only A1 leaf production was positively correlated (Table 2, $P < 0.05$) with precipitation and only *E. gracilipes* with air temperature (Tab. 2, Fig. 2). The leaf production of A1 shoots in evergreens (*Piptocarpha rotundifolia* and *M. ligustroides*) was positively correlated (Table 2, $P < 0.05$) with precipitation and temperature, but A2 and A3 leaf production was negatively correlated (Table 2, $P < 0.05$) with precipitation and temperature in *M. ligustroides* (Fig. 3).

Branching pattern

The species *P. rotundifolia* (evergreen), *E. gracilipes* (semideciduous), and *D. hispida* (deciduous) produced only A1 shoots over the whole growing season (dry and wet periods, Fig. 3). However, *K. variabilis* (deciduous) and *C. sylvestris* (semideciduous) produced two orders of branching (A1 and A2) in the same season (Fig. 3). Only *M. ligustroides* produced A3 shoots in the same growing season.

Only deciduous species experienced shoot apex death, and *K. variabilis* had persistent and flowering shoots too. All evergreens and semideciduous species had persistent shoot apices and/or shoot flowering (Fig. 3).

Discussion

In general, evergreen and semideciduous species produce buds, shoots, and leaves throughout the whole year (Damascos *et al.* 2005) and are more dependent on short-term assimilation than deciduous species (Damascos 2008). Organ neo-formation in evergreen and semideciduous cerrado species result in leaf and shoot production along several months in dry and rainy season, expending resources during a longer period. In this way, just a minimum accumulation could be possible owing to continuous nutrient and energy costs, so these species become more dependent of short-term carbon assimilation (Damascos 2008). On the other hand, deciduous species with buds with organ preformation probably spent reserves accumulated in the previous rainy season, since this kind of bud represents an additional cost to the plant, mainly in dry period (Damascos 2008). However, in our study, evergreen species produced leaves and A1 shoots as rapidly as did deciduous species (in approximately 30 days). According to Damascos *et al.* (2005), evergreen (*Miconia albicans* (Sw.) Triana) and semideciduous (*Leandra lacunosa* Cogn.) species in cerrado areas without burning event, typically take 58 and 61 days to expand their leaves, respectively. In addition, fire negatively affected evergreen and semideciduous species' LLS (247 and 241 days, respectively) in our study; the normal LLS of evergreen and semideciduous species in cerrado range



Table 1. Leaf and shoot growth parameters in six woody cerrado species growing from 2006 to 2007 after a fire. LEI (days) = leaf expansion interval, SEI (days) = shoot expansion interval, LER (cm² days⁻¹) = leaf expansion rate, SER (cm days⁻¹) = shoot expansion rate, LLS (days) = leaf life span, and SLA (cm² g⁻¹) = specific leaf area. Lowercase letters compare parameters among six species in columns and capital letters compare phenological groups (ANOVA, $P < 0.05$).

Species	LEI	SEI	LER	SER	LLS	SLA
Deciduous						
<i>Diospyros hispida</i>	37 ± 13 a	26 ± 7 bc	1.7 ± 0.6 b	0.4 ± 0.2 cd	256 ± 6 a	57 ± 1.8 c
<i>Kielmeyera variabilis</i>	25 ± 8 b	33 ± 17 b	1.1 ± 0.5 c	0.5 ± 0.3 bcd	183 ± 3 c	61 ± 1.0 c
Mean ± SE	28 ± 8 A	29 ± 9 B	1.4 ± 0.4 B	0.4 ± 0.2 B	220 ± 37 A	59 ± 1.0 B
Semideciduous						
<i>Casearia sylvestris</i>	23 ± 8 c	33 ± 9 b	0.3 ± 0.1 d	0.5 ± 0.1 bc	260 ± 4 a	85 ± 1.5 a
<i>Eriotheca gracilipes</i>	20 ± 10 de	16 ± 10 c	3.6 ± 2.0 a	0.7 ± 0.5 a	220 ± 4 b	71 ± 1.7 b
Mean ± SE	22 ± 6 C	24 ± 8 B	1.9 ± 1.0 A	0.6 ± 0.3 A	241 ± 19 A	78 ± 1.2 A
Evergreens						
<i>Miconia ligustroides</i>	35 ± 13 a	47 ± 24 a	0.3 ± 0.1 d	0.3 ± 0.1 d	248 ± 8 ab	78 ± 2.6 ab
<i>Piptocarpha rotundifolia</i>	19 ± 8 e	29 ± 10 b	1.3 ± 0.6 bc	0.6 ± 0.4 ab	245 ± 8 ab	77 ± 2.0 ab
Mean ± SE	26 ± 9 B	38 ± 13 A	0.8 ± 0.3 C	0.5 ± 0.2 B	247 ± 2 A	78 ± 1.7 A

Table 2. Pearson's correlation coefficient among the leaf production on A1, A2 and A3 shoots and precipitation and air temperature in six woody cerrado species. T=air temperature; P=precipitation. Bold values indicate $P < 0.05$.

Species	R ² values					
	A1 x T	A1 x P	A2 x T	A2 x P	A3 x T	A3 x P
<i>M. ligustroides</i>	0.6	0.7	-0.6	-0.5	-0.6	-0.6
<i>P. rotundifolia</i>	0.6	0.7	-	-	-	-
<i>C. sylvestris</i>	0.7	0.7	-0.2	0.2	-	-
<i>E. gracilipes</i>	0.2	0.7	-	-	-	-
<i>K. variabilis</i>	0.7	0.8	0.4	0.6	-	-
<i>D. hispida</i>	0.3	0.7	-	-	-	-

from approximately 364 to 780 days for evergreens (Lenza 2005; Damascos *et al.* 2005; Franco *et al.* 2005) and from 247 to 371 for semideciduous (Damascos *et al.* 2005). Even with the lack of LLS data from cerrado species published in the literature, the LLS from our species seem to have been adversely affected by fire. Also, fire increased the speed of shoot expansion of evergreens. Rossato & Franco (2008), studying five evergreens from cerrado found shoot mean growth ranging from 0.23 to 1.38 cm per month. In our study, *M. ligustroides* and *P. rotundifolia* showed mean shoot growth range from 9 to 18 cm for month. Therefore, the fire could increase the speed of leaf and shoot expansion in evergreens and semideciduous woody cerrado species but decreased LLS. Another morphological adjustment of evergreens and semideciduous trees was a decreased SLA (Tab. 1). In a study with 125 woody species, Cianciaruso *et al.* (2013) found no evidence of differences in SLA among distinct phenological groups in cerrado vegetation, but in our study, leaves of evergreens and semideciduous species had more area than mass per leaf. Therefore, less carbon was allocated per leaf and with a thinner structure; there was a decrease in LLS. This low LLS associated with high SLA could result in similar values of net photosynthesis between evergreens and deciduous species, as found by Souza *et al.* (2009b), who studied the same species in the cerrado area. The low LLS in evergreens and semideciduous species

could be linked with high SLA values and together higher air temperatures and lower soil moisture in the burned area induces plants to drop their leaves to reduce water loss in the dry season. Therefore, decreased LLS allowed evergreen leaves to translocate resources from old to new leaves and not lose resources. In cerrado, woody species showed nutrient translocation, primarily K, Mg, P and N, from old to new leaves (Medeiros & Haridasan 1985; Leitão & Silva 2004), hence, the young leaves could maintain the level of nutrients in the plant (Leitão & Silva 2004).

According to Simon & Pennington (2012), fire-resistant traits such as thick bark and a xylopodium have evolved together with the rise to dominance of flammable C₄ grasses, which are common in the cerrado. Cerrado species are adapted to frequent fires so the quick shoot growth in all six species could be the result of reserve accumulations that allow plants to survive fire disturbance (Braz *et al.* 2000). This is primarily when species are top killed by fire, as *Kielmeyera variabilis* was in our study, that they exhibit intense resprouting. *Kielmeyera variabilis* showed high leaf and shoot expansion together with the lowest LLS. In addition, *K. variabilis* produced two orders of shoots in the same growing season. Deciduous species produce only one order of shoots per growing season (Damascos *et al.* 2005; Damascos 2008), originating from buds with preformed organs. Owing to the death of the whole crown in



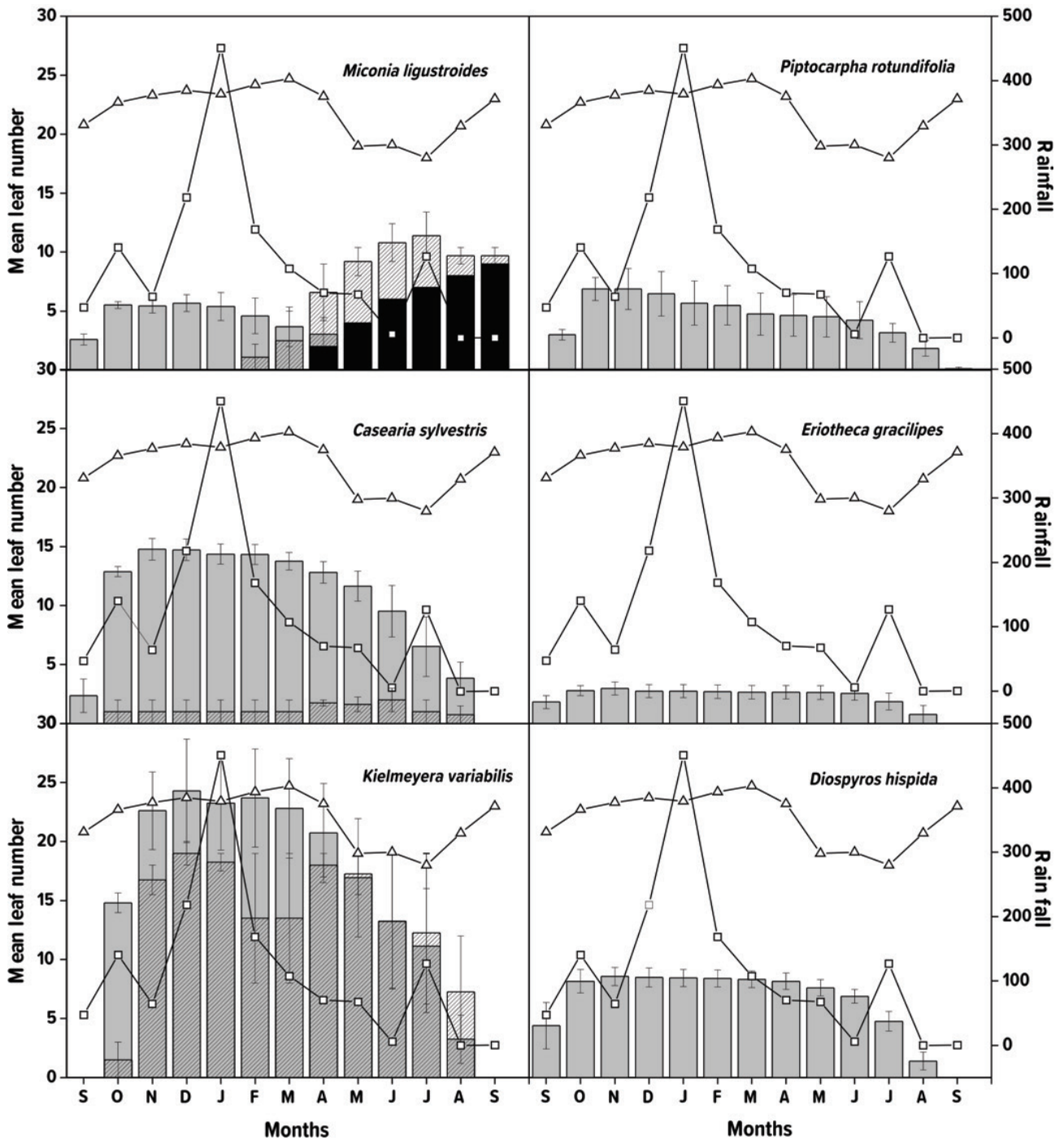


Figure 2. Leaf number produced during dry and wet seasons in 2006 and 2007 on shoots of A1 (gray columns), A2 (inclined lines), and A3 (black columns) in the six cerrado species studied. The line with triangles indicates the mean air temperature and the line with squares indicates the mean monthly precipitation.

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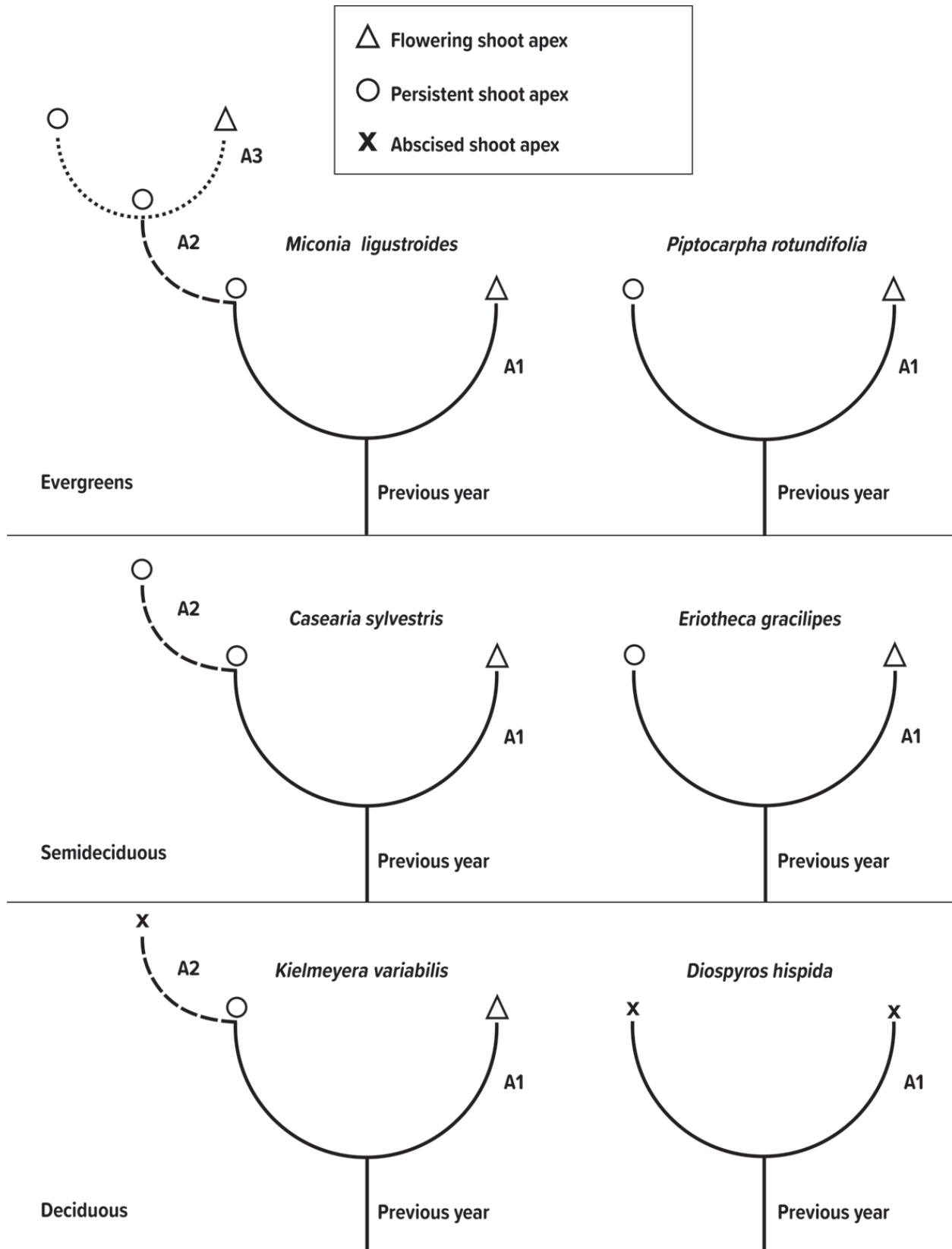


Figure 3. Branching diagrammatic representation of the six woody cerrado species studied, during the dry and wet seasons in 2006. A1, first order axis (continuous line) emerged at the beginning of the wet season; A2, second-order axis (dashed lines) emerged from axillary buds of A1 shoots; A3, third-order axis (dotted lines) emerged from axillary buds of A2 shoots. Previous-year shoots are shown as thick lines at the base. Based on Damascos *et al.* (2005).



K. variabilis, the subsequent aboveground growth involved a massive, rapid flush from root buds to replace the entire aerial structure lost in the fire. Also, the fast shoot growth showed by the cerrado species studied may be the result of ash deposition after fire in the soil surface (Silva & Batalha 2008; Pivello *et al.* 2010). Ashes release soluble compounds fertilizing the soil and providing higher nutrient content, mainly N, K and Mg, for quick use by plant species.

Another phenological adjustment due to the fire was the positive relationship of leaf production on A1 shoots with precipitation and temperature in evergreen species. *Miconia albicans*, an evergreen species, did not present a correlation between leaf production on A1 shoots and precipitation and temperature (Damascos *et al.* 2005). However, following fire, evergreens (*M. ligustroides* and *P. rotundifolia*) adjust and produce a flush of leaves to replace the photosynthetic area in a short period.

Fires promoted leaf and shoot growth in the six cerrado trees. Cerrado trees are adapted to fire events and even with high damage on the crown, they showed intense and accelerated shoot and leaf development after fire, especially in the evergreens and semideciduous species. On the other hand, if the fire damage involves the whole crown, the branching pattern can be altered and more shoot orders can be produced in the same growing season, even in deciduous species. It is important to study the relationship between fire and shoot and leaf development to understanding how fire modulates leaf production and whole-plant architecture in cerrado vegetation. Further studies on the relationship between fire and aerial growth of trees will help understanding how fire shape modular growth of cerrado trees.

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Evidence of the effects of fire on branching and leaf development in cerrado trees

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