UNIVERSIDADE FEDERAL DE SÃO CARLOS
CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

CARACTERIZAÇÃO DOS GRUPOS FUNCIONAIS DE ESPÉCIES ARBÓREAS DO CERRADO.

Orientador: Prof. Dr. Carlos Henrique Britto de Assis Prado

São Carlos-SP
2016

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CARACTERIZAÇÃO DOS GRUPOS FUNCIONAIS DE ESPÉCIES ARBÓREAS DO CERRADO.

Mariana Prado Borges

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais do Centro de Ciências Biológicas e da Saúde da Universidade Federal de São Carlos, como parte dos requisitos necessários para a obtenção do título de Doutor em Ciências, área de concentração: Ecologia e Recursos Naturais.

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RESUMO

O Cerrado é um complexo vegetacional marcado pela sazonalidade climática, onde a presença de uma estação seca impõe às espécies arbóreas um estresse hídrico periódico. As espécies arbóreas são frequentemente agrupadas segundo o grau de deciduidade foliar em decíduas, sempre verdes e semidecíduas. A associação da deciduidade foliar com grupos funcionais é debatida na literatura. Assim, o objetivo central dessa tese foi testar hipóteses sobre a existência, a estrutura e o funcionamento de grupos funcionais de espécies arbóreas do cerrado, bem como sua coincidência com o grau de deciduidade foliar. A caracterização dos grupos funcionais teve por objetivo mostrar as relações de interdependências entre as características da copa e como cada grupo responde ao estresse ambiental. Para tal, utilizamos: (1) metadados sobre período de floração referente a 92 espécies em diferentes localidades; (2) metadados sobre 15 espécies da reserva de cerrado da UFSCar (São Carlos-SP) combinados com dados coletados em campo na mesma área; e (3) dados experimentais sobre alterações climáticas no cerrado, coletados em campo, sob condições naturais, nos anos de 2013 e 2014 na reserva da UFSCar. As características de órgãos da copa distribuídos no tempo e no espaço foram analisados sob diferentes métodos estatísticos (ANOVA, qui-quadrado, estatística circular, Kruskal-Wallis, Permanova, distribuição em scatter plot, e análise de conectância de redes). Os resultados nos permitiram concluir: (1) A existência de ao menos três grupos funcionais de espécies arbóreas de cerrado; (2) Os grupos funcionais estão em um gradiente funcional que coincide com a fenologia foliar; (3) A deciduidade foliar é apenas um atributo de uma série de características da copa (duração de floração, pico de floração, relações ramo-folhagem, arquitetura da copa, inclinação do ramo, partição de biomassa entre os órgãos da copa) que caracterizam os diferentes grupos; (4) As inter-relações entre as diversas características de copa constituem a síndrome, que resulta em diferentes estratégias adaptativas para superar o estresse hídrico em cada um dos grupos funcionais; (5) As espécies semidecíduas apresentam respostas adaptativas exclusivas que permitem classificá-las como um grupo à parte de decíduas e sempre verdes.

ABSTRACT

The Cerrado is a vegetation complex characterized by climate seasonality that imposes to tree species a water stress during the dry season. Cerrado tree species are frequently classified according to the leaf deciduousness degree as deciduous, evergreen and semideciduous. The association of leaf deciduousness with functional groups is discussed in the literature. Thus, the main aim of this thesis was to test hypotheses about the existence, structure and behavior of functional groups of cerrado tree species and its coincidence with the leaf deciduousness. The characterization of the functional groups aimed to show the relationships of inter-dependencies among the crown characters and how each group responds to environmental stress. For this, we used: (1) metadata of flowering period of 92 species in different localities; (2) metadata of 15 species in the UFSCar cerrado reserve (São Carlos-SP) combined with data collected in field in the same reserve area; and (3) experimental data about climatic alterations in the cerrado, collected in filed, under natural conditions, for the years of 2013 and 2014 in UFSCar reserve. The crown traits distributed in time and space were analyzed at different statistical methods. (ANOVA, chi-square, circular statistic, Kruskal-Wallis, Permanova, scatter plot distribution, and network connectance analyses). According to our results, we concluded: (1) The existence of at least three functional groups of cerrado tree species; (2) The functional groups are in a functional that agree with the leaf phenology; (3) The leaf deciduousness is only one attribute in a list of crown traits (flowering duration, flowering peak, shoot-foliage relationships, crown architecture, shoot inclination, biomass partitioning among crown organs) distinctive of the different groups; (4) The interrelationships among the several crown traits constitutes a syndrome resulting in a distinct plant strategy to overcome the water stress in every functional group; (5) The semideciduous species present exclusive adaptive responses that allow their classification in a separate group of deciduous and evergreen.

INTRODUÇÃO

As florestas e savanas são os ecossistemas que cobrem a maioria das áreas naturais nos trópicos (Lüttge 1997). Um número considerável de ecossistemas tropicais é considerado *hotspots* ou são áreas que apresentam uma concentração excepcional de espécies endêmicas e passam por processos de perda de habitats (Myers et al. 2000). Dezesseis dos 25 *hotspots* identificados até o momento estão nos trópicos, incluindo o Cerrado no Brasil (Myers et al. 2000).

O Cerrado é um complexo vegetacional que incorpora fitofisionomias desde campos abertos (campo limpo) até formações florestais (cerradão). Dentre as formações vegetacionais do Cerrado, há aquelas que são classificadas como formações savânicas, como o campo sujo, campo cerrado e cerrado *sensu stricto* (Coutinho 2002). O Cerrado é marcado pela sazonalidade climática com uma estação chuvosa seguida de uma estação seca (Franco et al. 2014). Essa sazonalidade climática também é encontrada nas formações savânicas em outros continentes como na África e Austrália (Eamus et al. 1999). No Cerrado a estação chuvosa ocorre de outubro a março e a estação seca de abril a setembro (Prado et al. 2004; Damascos et al. 2005; Monteiro & Prado 2006).

A sazonalidade climática impõe às plantas de Cerrado um estresse hídrico periódico, marcado pela diminuição da disponibilidade de água nas camadas superficiais do solo e um aumento significativo da demanda evaporativa do ar (Prado et al. 2004; Franco et al. 2014). O estresse hídrico durante a estação seca impõe alterações fisiológicas e morfológicas que evitam a perda excessiva de água, como a diminuição da condutância estomática e um sistema radicular profundo (Franco et al. 2014). Outra característica das espécies arbóreas de savanas, que frequentemente é associada às adaptações para superar os efeitos da seca, é a deciduidade foliar. No Cerrado, as espécies apresentam deferentes padrões de deciduidade e produção foliar. As espécies classificadas como decíduas são aquelas que perdem todas as folhas no ápice da seca, ficando por um período de 30 dias ou mais sem folhas, e que recompõem a folhagem de forma rápida e sincrônica na transição da estação seca para a chuvosa. Já nas espécies consideradas sempre verdes a abscisão e produção foliar ocorrem de forma contínua durante todo o ano. Por fim, as espécies

classificadas como semidecíduas são aquelas cuja abscisão foliar ocorre do início ao fim da estação seca, prossegue durante o período de produção rápida e sincrônica de novas folhas, e termina no início da estação chuvosa. Dessa forma, as semidecíduas não apresentam um período com a copa livre de folhas, como as decíduas, e nem abscisão e produção foliar contínua, como as sempre verdes.

A deciduidade foliar é frequentemente utilizada na literatura como modo de agrupamento das espécies arbóreas de Cerrado (Lenza & Klink 2006; Goldstein et al. 2008; Pirani 2009; Rossato et al. 2009; Silvério & Lenza 2010). Diversos estudos buscaram encontrar características comuns entre espécies pertencentes a cada grupo fenológico foliar, corroborando (Damascos et al. 2005; Souza et al. 2009a, b, 2011; Borges & Prado 2014), ou negando (Goldstein et al. 2008; Cianciaruso et al. 2013) a hipótese de que DE, SD e SV constituem grupos funcionais de espécies arbóreas no Cerrado.

O termo 'grupo funcional' é entendido como um grupo de organismos que respondem de modo similar a um conjunto de fatores ambientais (Gitay & Noble 1997). Portanto, um grupo funcional não é composto por organismos que apenas apresentam características em comum, mas pelo fato de apresentarem respostas similares às pressões do ambiente. As características (traços) apresentados pelas espécies vegetais podem estar correlacionados de modo a estabelecerem "síndromes" (Reich et al. 2003). Conjuntos diferentes de características irão compor síndromes distintas, que por sua vez determinam distintas estratégias adaptativas para obter sucesso no ambiente. Assim, não basta apenas elencar uma série de características comuns entre as espécies de cada grupo (DE, SD e SV), essas características necessitam estar inter-relacionadas formando síndromes. O conjunto de inter-relações que potencializa a planta a superar as pressões ambientais (síndrome) forma um acervo de diversas competências (estratégias adaptativas). Ou seja, um fato é o conjunto das inter-relações dos atributos da planta resultando em uma síndrome o outro fato são as competências que emergem dessas inter-relações resultando em estratégias adaptativas. As mesmas estratégias adaptativas podem estar presentes em um grupo de plantas sem relações

taxonômicas, formando um grupo funcional. No entanto, é necessário identificar onde estão e quais são as características morfológicas e/ou fisiológicas e suas inter-relações capazes de definir os grupos funcionais.

Dessa forma, uma questão fundamental para a caracterização dos grupos funcionais é o nível de organização da planta onde opera as variações das características de um grupo de espécies em resposta às pressões ambientais. Em outras palavras, é importante definir em qual nível organizacional da planta as características são sensíveis às respostas ambientais de modo a mostrarem não só as variações dos atributos, mas também suas inter-relações. Os níveis de organização de um organismo segue uma sobreposição hierárquica, que vai de moléculas, células, tecidos, órgãos, conjunto de órgãos (população de órgãos) até o organismo como um todo (Gomes & Prado 2007). Tentativas em identificar grupos funcionais em espécies arbóreas de Cerrado falharam quando analisaram os níveis organizacionais inferiores ao conjunto de órgãos (populações de órgãos), como quantidade de nitrogênio por massa de folhas, área foliar específica, tempo de vida das folhas (Cianciaruso et al. 2013), condutividade hidráulica dos tecidos foliares, variação no potencial hídrico da folha (Goldstein et al. 2008). De fato, existe um número limitado de soluções para uma dada pressão ambiental (Meinzer 2003) fazendo com que os grupos funcionais invés de diferirem apresentem a mesma solução em um determinado nível de organização da planta.

Os níveis de organização inferiores (*e.g.* de molécula a tecido) interagem de forma hierárquica e apresentam caraterísticas emergentes que se apresentam somente nos níveis imediatamente superiores (*e.g.* órgãos). Essas características emergentes são irredutíveis, ou seja, não podem ser capturadas em níveis de organização menores, mesmo com metodologias e equipamentos sofisticados, pois simplesmente não estão lá. São as características emergentes e irredutíveis em um determinado nível de organização que podem ser capturas a fim de caracterizar uma síndrome (as inter-relações dessas características) e, por sua vez, as estratégias de adaptação da planta. O desafio é encontrar o nível de organização correto onde características emergentes podem ser capturadas (medidas), listadas (várias dessas características), testadas em suas inter-relações

(correlacionadas estatisticamente) identificando a síndrome e significadas em bases ecofisiológicas a fim de definir o grupo funcional.

Assim, a existência dos grupos funcionais de lenhosas do Cerrado fundamenta-se em três hipóteses principais: 1- as inter-relações entre diferentes características na copa resultam em uma síndrome e em uma estratégia adaptativa específica em cada grupo funcional; 2- as características da copa responsáveis pela composição das síndromes são aqueles que estão acima do nível de organização de órgão, como populações de ramos, flores ou folhas, ou seja, populações de órgãos; 3- os eixos que sustentam direta e simultaneamente, de maneira mecânica e fisiológica, as populações de folhas e flores também devem apresentar características intrínsecas (como o ângulo e o comprimento) capazes de compor a lista de atributos, manter inter-relações consistentes com populações de órgãos e promover dessa forma a caracterização das síndromes em cada grupo funcional.

As relações estabelecidas entre as populações de órgãos e seus eixos de sustentação determinam o funcionamento da copa como um todo em cada grupo funcional. Nesse sentido, as características emergentes das relações ramo-folhagem, arquitetura da copa e partição de biomassa nos compartimentos da copa determinam as respostas fenológicas da parte aérea da planta, como produção e deciduidade de folhas e a floração. Além disso, o desdobramento e a persistência do meristema apical nos ramos é específico em cada grupo funcional (Damascos et al. 2005) desempenhando papel significativo na forma de crescimento e ocupação do espaço aéreo.

Cada grupo funcional apresenta uma forma de aquisição de recursos como água e carboidratos, bem como uma forma de uso desses recursos, ou seja, como são estocados e mobilizados sazonalmente no Cerrado. A mobilização de recursos reservados em estruturas vegetativas é necessária para suprir a demanda durante a estação seca, principalmente nas espécies DE que perdem toda a área fotossintética no pico da estiagem de inverno no Cerrado (Prado et al. 2004; Borges & Prado 2014). Apesar da redução da fotossíntese líquida imposta pela alta demanda

evaporativa do ar (Prado et al. 2004), a manutenção de toda ou parte da folhagem pelas espécies SV e SD, respectivamente, permite a manutenção de uma fonte de carbono contínua.

Os ramos ortotrópicos (Sousa et al. 2009b) associados com uma constante fonte de carboidratos oriundos da fotossíntese corrente promovem uma maior persistência da flor e aumentam a duração de floração nas SV (Borges & Prado 2014). Em contrapartida, a dependência das espécies DE da mobilização das reservas como fonte de carboidratos resulta em menor período de floração, como forma de poupar as reservas para o final da estação seca quando as folhas e as flores estarão em formação. Adicionalmente, a maior exposição da flor nos ramos plagiotrópicos aos estresses ambientais (Souza et al. 2009b) não favorece uma prolongada permanência da florada no ramo. As características das espécies SD, intermediárias entre DE e SV, resultam em um período de floração também intermediário ente dos dois grupos. O fato de manterem parcialmente a folhagem permite as SD usarem tanto recursos correntes quanto estocados. Adicionalmente, a combinação de características de DE e SV propicia às SD uma distribuição da floração ao longo do ano diferenciada, com dois picos (Borges & Prado 2014).

DE, SD e SV do Cerrado se diferenciam por meio das relações ramo-folhagem (Sousa et al. 2009a, b), da arquitetura de copa (Sousa et al. 2011), e dos padrões de floração (Borges e Prado, 2014). Isso implica necessariamente em estratégias adaptativas diferenciadas para superar o estresse hídrico durante a estação seca. A arquitetura pouco ramificada das DE (Sousa et al. 2011) propiciam uma reduzida resistência à ascensão da seiva via xilema facilitando o desdobramento sincrônico de folhas no final da estação seca. Por outro lado, o elevado potencial de perda de água por transpiração devido à extensa área foliar (Sousa et al. 2009a) e aos ramos plagiotrópicos (Sousa et al. 2009b) requerem que as espécies DE derrubem suas folhas no auge da estação seca (Capítulo 2). Com uma copa sem folhas, os recursos necessários para produção de nova folhagem são oriundos de reservas de carboidratos nas DE. As espécies DE necessitam, ainda, recompor rapidamente a capacidade fotossintética da copa logo no início da estação chuvosa para garantirem melhor assimilação de carbono para o crescimento e reprodução no ano corrente e para o próximo

período de seca, por meio de reservas (Capítulo 2). Assim, a produção de órgãos pré-formados em gemas garante uma rápida recomposição da folhagem em menos de 30 dias nas DE (Damascos et al, 2005). De forma contrastante, as SV apresentam copa com mais ramificações (Sousa et al. 2011) que impõem maior resistência à ascensão da seiva via xilema, uma menor área foliar por ramo e por folha (Sousa et al. 2009a) que implica em uma transpiração potencialmente menor, e ramos ortotrópicos que protegem a folhagem da excessiva perda de água devido ao auto sombreamento (Sousa et al. 2009b). Desse modo, as SV mantêm sua folhagem durante a seca e a utilizam para garantir os recursos necessários por meio da fotossíntese corrente para o crescimento e reprodução (Capítulo 2), pois novas folhas ocorrem de forma contínua durante todo ano (Damasco et al. 2005). As SD compartilham características com DE e SV, apresentando valores médios intermediários para vários atributos. Ademais, a combinação de características faz das SD um grupo único, com elevado grau de conectância entre os componentes da copa, coordenando a permanência da folhagem em função da intensidade da estiagem de inverno no Cerrado (Capítulo 2).

Em um cenário de reduzida precipitação anual e mensal e, consequentemente, aumento da demanda evaporativa do ar, os grupos funcionais respondem de maneira diferente seguindo as suas competências promovidas pelas estratégias adaptativas correspondentes. Isso foi testado no ano de 2014 (Capítulo 3). A reduzida conectância entre os componentes da copa das SD contribuiu para uma maior plasticidade, refletindo em uma modulação mais ampla da distribuição da biomassa entre os compartimentos da copa (Capítulo 3). Essa modulação favoreceu tecidos foliares garantindo a aquisição de recursos por meio da fotossíntese, posteriormente ao distúrbio ambiental (seca intensa em 2014). Tal plasticidade confere ao grupo maior estabilidade e, consequentemente, maior resiliência (Hütt & Lüttge 2005). DE e SV, apesar de apresentarem estratégias distintas para a obtenção de recursos e superação do estresse hídrico sazonal, enfrentam os mesmos desafios quando a precipitação é significativamente reduzida (Capítulo 3). Um intenso decréscimo na precipitação durante a formação das reservas afetou o crescimento e a reprodução das DE crescendo em condições naturais em 2014 (Capítulo 3). Da mesma forma, a reduzida disponibilidade de água

impactou o crescimento contínuo das SV e influi na sua reprodução, seja na redução de biomassa alocada, ou atraso e redução do período de floração em 2014 (Capítulo 3).

O objetivo central dessa Tese é testar hipóteses sobre a existência, a estrutura e o funcionamento de grupos funcionais de lenhosas do Cerrado, bem como sua coincidência com os grupos fenológicos foliares. Utilizamos características distribuídas no tempo e no espaço de órgãos da copa para caracterizar cada grupo funcional. Essa caracterização teve por objetivo estabelecer as relações entre as características da copa e mostrar suas interdependências. Por meio e após a caracterização de cada grupo funcional tentamos capturar como esses grupos respondem diante de fatores de estresse ambiental natural como a intensa estiagem de 2014.

Por outro lado, é necessário identificar objetivos específicos que podem melhor apresentar esse trabalho. Para cada grupo funcional das espécies arbóreas do Cerrado buscou-se:

1- Verificar as relações entre duração de floração e distribuição da mesma ao longo do ano caracterizando cada grupo.
2- Identificar as características da copa que são responsáveis por definir os grupos funcionais e, principalmente, destacar a interdependência e o significado dessas características para a vegetação do Cerrado.
3- Identificar detalhes das estratégias de adaptação ao estresse hídrico sazonal de cada grupo com base na inter-relação de características ao nível da copa.
4- Identificar os efeitos da diminuição da precipitação e aumento da demanda evaporativa do ar do ano de 2014 na alocação de biomassa entre os componentes da copa (ramo, folha e flor) e nos padrões de floração relacionando-os com as estratégias adaptativas de cada grupo.
5- Projetar, com base na resposta dos grupos sob a intensa estiagem de 2014, a resposta desses grupos funcionais em um cenário de alteração climáticas recorrentes e/ou permanentes.

Para testar as hipóteses apresentadas nessa Tese utilizou diferentes conjuntos de dados, a saber:

- Metadados sobre período de floração referente a 92 espécies, disponíveis em seis trabalhos publicados na literatura (Borges & Prado 2014 - capítulo 1);
- Combinação de dados publicados com dados coletados em campo, para a mesma área de estudo (capítulo 2);
- Dados oriundos de experimentação em campo, sob condições naturais, testando a respostas das espécies às mudanças climáticas (capítulo 3).

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CAPÍTULO 1: RELAÇÕES ENTRE DECIDUIDADE FOLIAR E CARACTERÍSTICAS DA FLORAÇÃO DE ESPÉCIES ARBÓREAS DE CERRADO *

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RELATIONSHIPS BETWEEN LEAF DECIDUOUSNESS AND FLOWERING TRAITS OF WOODY SPECIES IN THE BRAZILIAN NEOTROPICAL SAVANNA

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Abstract: The relationships between foliage permanence and flowering throughout the year were analyzed in 92 woody species of Cerrado vegetation categorized as either deciduous (DE), semideciduous (SD) or evergreen (EV). Flowering of DE, SD and EV species was investigated via three variables, measured over the course of the year: flowering duration (FLD), calculated as the number of months in flower in each species; flowering distribution (FDI), calculated as the number of species in flower per month; and flowering peak (FPE), defined as the four consecutive months yielding the highest number of species in flower. The months with the highest numbers of species in flower were October (52 species), September (50) and August (49). These months correspond to the period of transition from the dry season to the wet season. In the majority of species studied, seasonal climatic factors were strong enough to induce fruit formation in the dry season and seed dispersal in the following wet season, when sufficient water was available to support germination and plantlet growth. However, significant differences in FLD, FDI and FPE were found among the leaf phenological groups. High FLD in EV species is likely favored by the continuous input of resources from the year-round foliage. In contrast, DE species employ reserves of carbon, water and nutrients to form new leaves and flowers on a crown free of foliage at the end of the dry season. In DE species, their low FLD may reduce the impact of flowering on reserve consumption. SD species showed an intermediate level of foliage persistence, resulting in intermediate FLD values. In addition, SD species exhibited a different pattern of flowering distribution from those of DE and EV species. Many SD species have two flowering periods per year. The first period occurs when the crowns are full of leaves, in the middle of the dry season in June, similar to EV species. The second occurs when only half of the original foliage area is present, near the peak of the dry season in September, similar to DE species. Therefore, despite the strong influence of seasonal climatic conditions on the flowering

behavior of DE, SD and EV woody species of Cerrado vegetation, these leaf phenological groups differ significantly in FLD, FDI and FPE.

Key-words: deciduous, evergreen, flowering behavior, foliage persistence, phenology, semideciduous

Short title: Leaf deciduousness and flowering in Cerrado woody species

Introduction

Tropical savannas are a widespread biome throughout the world and consist of a discontinuous stratum of trees over a largely continuous layer of grasses (Huntley and Walker 1985; Williams et al., 1997). The climate of tropical savanna regions is marked by seasonality, with a wet season followed by a dry season; during the latter, little to no rain falls (Huntley and Walker 1985; Tothill and Mott 1985). The Brazilian Cerrado is a neotropical savanna with multiple physiognomies and is found primarily in the central region of Brazil. In the Cerrado, the wet season occurs between October and March and the dry season between April and September (Prado et al., 2004; Damascos et al., 2005; Monteiro and Prado, 2006). The main factors that affect plant growth and development in Cerrado vegetation are the availability of water and nutrients in the soil, irradiance and the corresponding evaporative demand in the atmosphere, herbivory and fire (Medina and Silva, 1990; Prado et al., 2004; Santos et al., 2012).

The woody species of tropical savannas show varying levels of leaf deciduousness that allow them to cope with water stress in both the soil and atmosphere during the dry season (Willians et al., 1997; Oliveira, 2008; Prado et al.; 2004: Santos et al., 2012). Deciduous (DE) woody species in Cerrado vegetation shed their leaves at the end of the dry season, remaining leafless for nearly 30 days. They undergo leaf production during a short period at the end of the dry season (Damascos et al., 2005). Semideciduous (SD) woody species in Cerrado

vegetation shed approximately half of their leaves during the dry season and can rapidly regain their original foliage area during the same season (Lenza and Klink, 2006). In contrast, evergreen (EV) woody species of the Cerrado retain a near-constant foliage area throughout the year and have continuous leaf production (Damascos et al., 2005; Lenza and Klink, 2006). The three different deciduousness groups (DE, SD and EV) also differ significantly in the patterns of leaf and branch growth (Damascos et al., 2005), crown structure (Souza et al., 2009b; Souza et al., 2011) and in the mass or surface area relationships between shoots and foliage (Souza et al., 2009a).

Foliage maintenance in DE, SD and EV Cerrado woody species is expected to influence the relationships between photosynthetic production in autotrophic tissues and the consumption of photosynthates in heterotrophic tissues. At the end of the dry season, Cerrado DE species likely mobilize their reserves of carbohydrates, water and nutrients from the roots, stems and branches for flushing the new foliage on a crown free of leaves, as do temperate DE species (Luxmoore, 1991; Kozlowski and Pallardy, 1996; Larcher, 2003). As EV Cerrado woody species have a permanent foliage area, they may use the ongoing net photosynthesis as a source of carbohydrates and the xylem mass flow as source of water and nutrients throughout the year. In addition, Cerrado EV species can mobilize reserves stored in heterotrophic tissues, as do EV species in temperate climates (Kozlowski and Pallardy, 1996; Larcher, 2003). In contrast, SD Cerrado species may function similarly to either DE or EV species with respect to carbohydrate, nutrient and water use, as they retain a large photosynthetically active area throughout the year but only half of their full foliage area at the peak of the dry season. Despite these large behavioral differences among DE, SV and EV species, the relationships between heterotrophic and autotrophic phenological events, such as flowering and foliage persistence, have not yet been studied in Cerrado woody species.

Flowering in Cerrado woody species is concentrated during the transition from the dry season to the wet season, indicating that flower production is not strictly limited by soil water availability (Batalha and Mantovani, 2000; Franco et al., 2005; Lenza and Klink, 2006). However, there is a significant reduction in net photosynthesis in DE, SD and EV species during the dry season (Prado et al., 2004). At least some reserves stored in vegetative structures are expected to be mobilized to meet the carbon demand of reproductive structures produced during the dry season. Therefore, leaf deciduousness should be strongly correlated with the onset and duration of flowering in DE, SD and EV woody species in Cerrado vegetation. Adequate amounts of maintained foliage area and carbohydrate reserves are needed to meet the demand of reproductive structures during the dry season in woody species of Cerrado vegetation.

EV species of the Cerrado have more vertical (orthotropic) branches than the other two types of woody species, which promotes foliage self-shading from the apex to the base of the branch (Souza et al., 2009b). Therefore, the flowers of EV species may be less exposed to ambient stress factors, such as irradiance and evaporative air demand, than those of other types of woody species. The orthotropic branches associated with the constant source of carbohydrates yielded from ongoing net photosynthesis can promote flower persistence and increase flowering duration. In contrast, DE species strongly depend on reserve mobilization to meet the demands of reproductive structures in a crown free of foliage or with newly developing leaves, as is present in the transition from the dry to the wet season (Damascos et al., 2005). The high exposure of flowers on plagiotropic branches (Souza et al., 2009b; Santos et al., 2012) and the intense consumption of reserves for leaf and flower formation during the dry season may result in a shorter period of flower persistence in DE species than in EV species. SD species show a level of branch inclination intermediate between those of EV and

DE species and retain half of their foliage during the dry season. Thus, SD species may exhibit an intermediate level of flower persistence.

We aimed to identify the months of flowering in the DE, SD and EV woody species of the Cerrado and to test for temporal correspondence over the course of the year between the amount of foliage maintained and floral characteristics such as flower persistence, the period of flowering and the period during which the most species are in flower in each leaf phenological group. Therefore, we seek to identify associations in Cerrado woody species beyond those already established between foliage maintenance and both canopy structure (Damascos et al., 2005; Souza et al., 2011) and shoot-foliage relationships (Souza et al., 2009a, b). The relationships between foliage maintenance and flowering behavior will reveal other interdependent relationships in DE, SD and EV species and will more clearly define functional groups in Cerrado woody species.

Materials and Methods

Literature data

We consulted the literature to classify the woody species of the Cerrado into three leaf phenological groups: deciduous, semideciduous and evergreen. Published papers were found using Web of Science and Google Scholar using the keywords “phenology”, “Cerrado”, “woody species” and “tree species”. For Google Scholar, the same keywords in both English and Portuguese were used. We selected all papers containing data on the flowering period or foliar deciduousness of Cerrado woody species, including those species from different Cerrado vegetation physiognomies, such as in *campo cerrado*, *cerrado sensu stricto* or in *cerradão* (cerrado woodland). Nine published works were considered (Table 1). A total of 92 species were represented, of which 37 were DE, 21 were SD, and 34 were EV.

Insert Table 1

The groups "continuous evergreen species" and "seasonal evergreen species" described in Silvério and Lenza (2010), Pirani et al. (2009) and Lenza and Klink (2006) were considered here as one group of "evergreen species" (EV). According to these authors, continuous evergreen species replace their leaves continuously throughout the year, whereas seasonal evergreen species produce young leaves either before or simultaneously with foliage abscission at the end of the dry season. Because there is no period of significant loss of foliage area in either group of species, we pooled them together as evergreen species (EV). Where deciduousness classifications differed among published works, we used the classification of the most recent paper. In cases of disagreement over flowering period, we considered all months during which flowers were reported in all works. Additional information on the pollinator guilds of each species were obtained from published works other than those nine consulted for the relationships between flowering and leaf phenology.

Variables of flowering traits

Among the leaf phenological groups (DE, SD and EV), three variables were used to compare flower persistence and the number of species in flower during the year. The "Flowering Duration" (FLD) was calculated as the number of months of the year that each species had flowers. Using the FLD value, it was possible to compare the number of months in flower among leaf phenological groups. The "Flowering Distribution" (FDI) was calculated as the number of species in flower per month. The "Flowering Peak" (FPE) was defined as the four consecutive months with the highest number of species in flower. Using the FPE value, it was possible to compare those periods with the highest number of species in flower among DE, SD and EV groups. The duration of four months was chosen for the calculation of FPE based on the data from the nine published works listed in Table 1. These published studies identify the period from August through November as that during which the majority of DE, SD and EV Cerrado woody species have flowers during the year.

Data analysis

We conducted three independent data analyses of pairs of leaf phenological groups: EV and DE, DE and SD, EV and SD. Because normality of the FLD values was identified by the Shapiro-Wilk test, the FLD data were subject to an ANOVA and a subsequent Bonferroni test to detect significant differences among the mean FLD values. The Chi-Square test (x^2) was used to analyze the FDI values, taking into account the percentage of species in flower in each group per month throughout the year. The FPE values were analyzed using a circular statistic (Watson-Williams test) for two independent samples. For this analysis, the four consecutive months with the highest number of species flowering were converted into degrees, increasing by 30º increments per month, such that January corresponded to 30º and December corresponded to 360º (Zar, 1984). Differences in pollinator guilds among leaf phenological groups were tested using the Chi-Square test (x^2). Significance was evaluated as $p<0.05$ for all analyses. The statistical tests were carried out using the programs Biostat 5.0 (Belém, Brazil, 2007) and Mystat 12 (Washington, USA, 2007).

Results

The months in flower during the year and the leaf deciduousness category of each of the 92 species are shown in Table 2. The annual phenogram of flowering for all 92 woody species and the period of the wet and dry seasons throughout the year are presented in Figure 1. The months with the highest number of species in flower were August (49 species), September (50), October (52) and November (40), corresponding to the transition period from the dry to the wet season. In contrast, the months with the lowest numbers of species in flower were March (22) and April (25), corresponding to the transition from the wet to the dry season (Figure 1). Figure 2 shows the number of months in flower for each leaf phenological group. DE and EV had the lowest number of species in flower during March and April,

respectively, and both groups had the highest number of species in flower in October (Figure 2). Unlike DE and EV, SD had two periods with a high number of species in flower: June, during the dry season; and September, during the transition from the dry to the wet season (Figure 2). SD species also had two distinct periods with a low proportion of species in flower: November, shortly after the second peak in the number of species in flower, and April, during the transition from the wet to the dry season (Figure 2).

Figure 1

Table 2

The ANOVA showed significant differences ($F = 5.522$; $p = 0.005$) in mean FLD among leaf phenological groups (Figure 3). There was a gradual increase in FLD from 3.9 in DE to 5.1 in SD and 5.7 months in EV (Figure 3). However, the Bonferroni test (Table 3) revealed significant differences in mean FLD only between DE and EV (Table 3). The results presented in Figure 3 and Table 3 support the hypotheses that EV species maintain flowers over a longer time period than DE species during the year and that SD species exhibit an intermediate flowering duration.

Table 3

The anticipation of flowering in June (Figure 2) differentiated significantly the FDI and the FPE values of SD species in relation to DE and EV species (Table 3). DE and EV species had similar periods of both the lowest and highest percentage of species in flower (Figure 2), resulting in no significant differences in FDI and FPE (Table 3).

Despite the similar values of FDI and FPE in DE and EV species throughout the year, some variation is evident. In DE species, there is a rapid increase in the percent of species in flower from July onwards (Figure 2), a time during which winter drought typically intensifies. In contrast, in EV species, the percent of species in flower increased gradually throughout the entire dry season from May to October, peaking together with DE species at the start of rainfall in October (Figure 2). This difference between DE and EV in the pattern of increase in the number of species in flower culminates in the middle of the dry season (July), with 28% and 50% of DE and EV species in flower, respectively (Figure 2). No significant differences

Figure 2

Figure 3

Figure 2	Figure 3

were found among DE, SD and EV species in the composition of the pollinator guilds, indicating that the type of leaf deciduousness does not significantly influence the relationship between pollinator and flowering behavior.

Discussion

The community of Cerrado woody species has flowers throughout the year, but the highest number of species in flower occurs during the transition from the dry to the wet season (Batalha and Mantovani, 2000; Silva et al., 2011). Similar behavior was found in an Australian savanna woody community (Williams et al. 1997; Williams, 1999). This general behavior of savanna woody communities can be interpreted as an adaptation to climatic seasonality. Peaks in flowering or fruiting from the late dry season to the early wet season have also been described for seasonal tropical forests in India (Selwyn and Parthasarathy, 2006) and Mexico (Cortés-Flores et al., 2013). Periods of flowering and subsequent fruiting are adjusted to the seasonal climate, allowing seed dispersion and germination during the onset of the following wet season, facilitating seedling establishment and maximizing the first growing period (Oliveira, 2008, Cortés-Flores et al., 2013). If flowering were to occur earlier, for example, at the end of wet season between March and April, it could result in excessive water stress for establishing seedlings, whose roots penetrate only the upper soil layer until after September. Therefore, there are few species in flower at the end of the wet season (March-April), Figure 1 illustrates the significant influence of water stress on the reproductive phenology and seedling establishment of woody species (Franco, 2002; Oliveira, 2008; Silva et al., 2011; Cortés-Flores et al., 2013). In addition to water stress in the upper soil layer, the decreasing photoperiod, the decrease in mean maximum and minimum monthly temperatures, and the increasing daily evaporative demand of the air should induce the onset of flowering in

woody species of Cerrado at the end of the dry season. These climatic factors may signal the beginning of the drought period or may directly intensify water stress.

However, the presence of flowers in Cerrado woody vegetation throughout the year indicates that seasonality does not solely determine floral phenology (Sarmiento and Monasterio, 1983; Oliveira, 2008). Indeed, only the superficial layer of the soil loses a significant amount of capillary water at the peak of the dry season. The layers below 0.85 cm retain a water potential greater than -1.5 MPa throughout the year, allowing the continued activity of adult woody species (Oliveira, 2008; Oliveira et al., 2005; Franco, 2002). In fact, in a cerrado woodland physiognomy with 70% of the area covered with arboreal species, 82% of the water used during the dry season was extracted from soil deeper than 1.0 m (Oliveira et al., 2005). Moreover, the occurrence of flowers just before the onset of the dry season indicates some woody species may be able to produce seeds that remain viable until the subsequent wet season or produce seedlings that can rapidly reach the wet soil layer, 0.85 cm beneath the soil surface, after germination.

In DE and EV species, the patterns of flowering throughout the year were similar to those generally observed in Cerrado woody species. However, SD species exhibited a different pattern, with a unique flowering distribution. This behavior of SD species and the variation in FLD among groups may be correlated with the distinct source-sink relationships inherent to the different patterns of foliage persistence among leaf phenological groups. EV species maintain a permanent area of foliage and therefore the same amount of leaf area for photosynthetic gas exchange and transpiration. In theory, this should permit the same capacity for net photosynthesis and distribution of water and mineral nutrients throughout the year along the branches. In actuality, net photosynthesis decreases in EV species during the dry season, although it does not stop completely as in DE species free of leaves (Prado et al., 2004). Therefore, the maintenance of a constant area of transpiration and photosynthesis

throughout the year likely enables EV species to meet the demand of high FLD (Table 3) and contributes to the gradual increase in the number of species in flower during the dry season (Figure 2). The ability of EV species to meet the demands of flowering using currently available resources (water, nutrients and carbohydrates) does not preclude their use of stored reserves during the dry season.

In contrast, DE species exclusively use their reserves of carbon, water and nutrients to form new leaves and flowers at the end of the dry season, when their crowns are free of foliage or have leaves in an advanced stage of senescence. These reserves are formed during the preceding growing season and are likely stored in stems, branches and roots, as in temperate deciduous species (Larcher, 2003). An intense mobilization of reserves is needed to support the flush of foliage and flowers in a crown free of leaves, as occurs in DE species between the middle and end of the dry season (Damascos et al., 2005; Prado et al., 2004; Souza et al., 2009a, b). Indeed, the rapid increase in the percentage of DE species in flower during the dry season (Figure 2) indicates a high capacity of reserve mobilization during a period of minimal and largely ineffective foliage area. One potential way of reducing the demand for reserves and improve reserve restoration is via a low FLD, as observed in DE species (Table 3).

SD species maintain a photosynthetically active leaf area throughout the year, as at least half of their foliage area is retained throughout the dry season. The flowering peak observed in June may be possible by using the current resources from the foliage, as in EV species. Thus, flowering in several SD woody species into the middle of the dry season in June (Figure 2) may offset some of the costs of flower production by the use of existing foliage area and the presence of weak environmental stresses, before the peak of the dry season in September. In contrast, SD species likely have the reserves needed to meet the demands of flower production in a crown partially free of leaves at the end of the dry season,

similar to DE species. The mobilization of reserves in a crown with half of its peak foliage area allows another flowering peak in SD species, as observed in September at the end of the dry season. The distinct patterns of FDI and FPE in SD species over the year (Table 3) do not corroborate the hypothesis of a flowering behavior of SD species intermediate to those of EV and DE species. The combination of features characteristic of the other two groups (DE and EV) in SD species produced a unique flowering pattern in the latter, with two periods with a high percentage of species in flower, one in the middle of the dry season and another at the end. This flowering behavior allows a more homogeneous distribution in the percent of SD species in flower throughout the year (Figure 2), resulting in significant differences in FDI and FPE between SD species and both DE and EV species (Table 3).

However, the intermediate FLD of SD species, relative to DE and EV species, corresponds with the intermediate values they exhibit in several vegetative morphological traits, including individual leaf area, shoot length, density of leaf number, leaf/shoot mass ratio (Souza et al., 2009a), distance in links between different types of nodes (Souza et al., 2011) and branch inclination (Souza et al., 2009a, b). The intermediate position of SD species demonstrated in previous studies and apparent in their FLD in the present study corroborates the distinctiveness of functional groups of Cerrado woody species based on the maintenance of foliage during the year (Damascos et al., 2005; Souza et al., 2011).

In addition to being influenced by distinct source-sink relationships, flowering duration may be correlated with branch inclination. In EV species, the self-shading of foliage promoted by orthotropic branches and the persistence of foliage throughout the year may affect the reproductive structures. Flowers may be more protected from direct solar irradiance and excessive water loss by the shade provided by permanent foliage, similar to the self-shading of leaves in EV species (Souza et al., 2009b; Santos et al., 2012); this may contribute to their greater FLD. In contrast, plagiotropic branches increase the exposure of flowers to

climatic stress factors, particularly during the dry season, which may contribute to the low FLD observed in DE species. In SD species, the branch inclination and persistence of the foliage area is intermediate to those of DE and EV species (Souza et al., 2009a, b) and may contribute to the intermediate value of FLD observed in SD species.

The absence of differences among leaf phenological groups in the composition of their pollinator guilds suggests that the extent of foliage persistence and other crown attributes of each phenological group (shoot angle, the number of links and nodes in crown) do not affect the complex interactions between floral characteristics and pollinator groups. The pollination process involves direct mutual adaptations between flower and pollinator. In addition, many of the variables associated with pollination are unrelated to either flower permanence on branches or the distribution of flowering throughout the year. Several other floral attributes can influence the composition of the pollinator guild, such as floral display size, the number of open flowers per plant, flower position on branches, visual and olfactory cues and the presence of nectaries.

Variation in FLD, FDI and FPE patterns among the leaf phenological groups of Cerrado woody species supports their classification as distinct functional groups. The strong relationships observed between flowering behavior and leaf deciduousness adds to our knowledge of interdependent relationships in DE, SD and EV woody species of the Cerrado, such as those previously established between foliage maintenance and both crown structure (Damascos et al., 2005; Souza et al., 2011) and shoot-foliage (Souza et al., 2009a, b). Additionally, these relationships between flowering behavior and leaf phenology reveal structural and functional interdependences between the vegetative and reproductive structures and sheds light on the distinctiveness of functional groups of Cerrado woody species based on phenology.

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Table 1. Published works surveyed in the present study containing data on the floral or foliar phenology of deciduous, semideciduous and evergreen woody species in three Cerrado vegetation physiognomies: *campo sujo* [1], *cerrado sensu stricto* [2] and *cerradão* [3].

Phenology data	Work	Cerrado physiognomy
Floral + foliar	Silvério and Lenza, 2010	1, 2, 3
Floral + foliar	Pirani et al., 2009	2
Floral + foliar	Lenza and Klink, 2006	2
Floral	Tannus et al., 2006	1
Floral	Weiser and Godoy, 2001	2
Floral	Batalha and Mantovani, 2000	1, 2, 3
Foliar	Souza et al., 2011	2
Foliar	Rossatto et al., 2009	1, 2, 3
Foliar	Goldstein et al., 2008	1, 2, 3

Table 2. Months of the year with the occurrence of flowering in Cerrado woody species with different levels of leaf deciduousness: deciduous (DE), semideciduous (SD), and evergreen (EV). Black bars indicate the months during which each species exhibited flowers, according to Silvério and Lenza (2010) [1], Pirani et al. (2009) [2], Lenza and Klink (2006) [3], Tannus et al. (2006) [4], Weiser and Godoy (2001) [5], Batalha and Mantovani (2000) [6], Souza et al. (2011) [7], Rossatto et al. (2009) [7] and Goldstein et al. (2008) [9]. The pollinator guilds of each species are shown in the last column: bat (ba); bee (be); beetle (bt); butterfly (bu); fly (fl); hummingbird (hb); moth (mo); small insects (si); wasp (wa); wind (wi).

Family/specie	Leaf deciduousness	Months in flower												Source	Pollinator guilds
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Anacardiaceae															
Astronium fraxinifolium Schott ex Spreng.	DE					■	■	■	■	■				2	wi [h]
Annonaceae															
Annona coriacea Mart.	DE	■										■	■	2,4	bt [a, e]
Annona crassiflora Mart.	DE										■	■	■	2, 4, 5, 6	bt [a, e]
Duguetia maregraviana Mart.	EV							■	■	■	■	■	■	2, 6	bt [e]
Xylopia aromatica (Lam.) Mart.	EV	■	■	■	■	■	■	■	■	■	■	■	■	2 ,5, 6	bt [g]
Apocynaceae															
Aspidosperma macrocarpon Mart.	DE								■					2	mo [a, b, h]
Aspidosperma tomentosum Mart.	DE						■	■	■	■	■			2, 4, 7, 9	mo [a, b, h]
Hancornia speciosa Gomez	DE				■	■	■	■	■	■	■			2, 4, 6	mo [a, b, h]
Himatanthus obovatus (Müll. Arg.) Woodson	SD	■	■	■	■	■	■						■	2, 4, 6	mo [a, b, h]
Araliaceae															
Schefflera macrocarpa (Cham. & Schltdl.) Frodin	EV					■	■				■	■		2, 9	be, fl [h]
Asteraceae															
Piptocarpha rotundifolia (Less.) Baker	EV	■	■	■	■	■	■	■	■				■	2, 4, 6, 7	si, bu [a, d]
Bignoniaceae															
Tabebuia aurea (Silva Manso) Benth. & Hook. f. ex S.Moore	DE						■	■		■	■			2, 6	be [a]
Tabebuia ochracea (Cham.) Standl.	DE								■	■				2, 4,5, 6	be [a, d]
Burseraceae															
Protium heptaphyllum (Aubl.) Marchand	DE						■	■	■	■				2, 6	si [g]
Caryocaraceae															
Caryocar brasiliense Cambess.	DE				■	■			■	■	■	■	■	2,4,5,6,7,9	bt, mo [a, d, h]
Celastraceae															
Salacia crassifolia (Mart. ex Schult.) G. Don	DE										■	■		2	be, fl [h]
Chrysobalanaceae															
Couepia grandiflora (Mart. & Zucc.) Benth. ex Hook. f.	DE								■	■	■	■	■	2, 4, 5, 6	be, mo [d, h]
Licania humilis Cham. & Schltdl.	EV					■	■	■	■	■	■			2, 4, 5, 6	fl, wa, bu [h]
Clusiaceae															

Kielmeyera coriacea Mart. & Zucc	DE	2, 3 ,4 ,9	be [a]
Kielmeyera rubriflora Cambess.	DE	1, 2, 6	be [a, d]
Kielmeyera variabilis Mart.	DE	6, 10	be [d]
Combretaceae			
Buchenavia tomentosa Eichler	DE	2	si [a]
Connaraceae			
Connarus suberosus Planch.	EV	2, 3, 7	si [a]
Rourea induta Planch.	EV	2, 3, 5, 6	be [a]
Dilleniaceae			
Curatella americana L.	SD	2	be [f]
Davilla elliptica A. St.-Hil.	SD	1,2,3,4,6	be [a, d]
Ebenaceae			
Diospyros hispida A. DC.	DE	2, 4, 7	mo [d, h]
Erythroxylaceae			
Erythroxylum suberosum Mart	DE	3,4,6,9	wa, be [d]
Fabaceae			
Anadenanthera falcata (Benth.) Speg.	DE	5,7	be [d, h]
Andira cujabensis Benth.	DE	2	be [a, h]
Andira paniculata Benth.	DE	2	be [h]
Acosmium dasycarpum (Vog.) Yakovl.	DE	3	be, bt [h]
Copaifera langsdorffii Desf.	EV	2	be [a, g]
Dimorphandra mollis Benth.	SD	2,3	si [a]
Enterolobium gummiferum (Mart.) Macbr.	DE	2,6	-
Hymenaea stigonocarpa Mart. ex Hayne	SD	2	ba [d, h]
Machaerium acutifolium Vogel	EV	2,4,6	be [a, d]
Bowdichia virgilioides Kunth	SD	2,6	be [a]
Dalbergia miscolobium Benth.	SD	2,3,6,9	be [a]
Dipteryx alata Vogel	EV	2	be [f]
Diptychandra aurantiaca Tul	DE	2	-
Pterodon pubescens (Benth.) Benth.	DE	2,6,9	be [h]
Sclerolobium paniculatum var. rubiginosum (Mart. ex Tul.) Benth.	EV	2	si [a]
Sclerolobium paniculatum var. subvelutinum Benth.	EV	2	si [a]
Stryphnodendron adstringens (Mart.) Cov	SD	3,4	be, fl [d, h]
Stryphnodendron polyphyllum Benth.	SD	6,7	-
Vatairea macrocarpa (Benth.) Ducke	DE	2	si [a]
Icacinaceae			
Emmotum nitens (Benth.) Miers	EV	2	be, fl [h]

Lauraceae				
Mezilaurus crassiramea (Meisn.) Taub. ex Mez	SD		2	-
Lecythidaceae				
Eschweilera nana (O. Berg) Miers	SD		2	-
Loganiaceae				
Strychnos pseudoquina A. St.-Hil.	EV		2	mo [a, b, h]
Lythraceae				
Lafoensia pacari A. St.-Hil.	DE		2,6	ba, mo [a, d, h]
Malpighiaceae				
Byrsonima basiloba A. Juss.	EV		2	be [a]
Byrsonima coccolobifolia Kunth	DE		1,2,4	be [a, d]
Byrsonima crassa Nied.	SD		4,5,8,9	be [a]
Byrsonima pachyphylla A. Juss.	EV		1,2	be [h]
Byrsonima verbascifolia (L.) DC.	EV		2,3,4,5	be [d]
Maregraviaceae				
Norantea guianensis Aubl.	DE		2	-
Malvaceae				
Eriotheca gracilipes (K. Schum.) A. Robyns	SD		2,4,7	be [a, d, h]
Eriotheca pubescens (Mart. & Zucc.) Schott & Endl.	EV		2	be [h]
Melastomataceae				
Miconia albicans (Sw.) Triana	EV		2,3,4,7	be [a, d]
Miconia fallax DC.	EV		3,4	be [a]
Miconia ligustroides Naudin	EV		6,10	be [a, d]
Mouriri elliptica Mart.	EV		2	be [a]
Myrsinaceae				
Myrsine guianensis (Aubl.) Kuntze	EV		3,4,9	be, wi [h]
Tibouchina stenocarpa (DC.) Cogn.	SD		4,6,7	be [d]
Myrtaceae				
Blepharocalyx salicifolius (Kunth) O.Berg.	SD		3,9	be [c, d, h]
Eugenia aurata O. Berg	SD		1,2,5,6	be [a, h]
Eugenia dysenterica DC.	DE		2	be [c, h]
Myrcia camapuanensis N. Silveira	EV		2	be [a, h]
Myrcia lanuginosa O. Berg	EV		1,2	be [h]
Myrcia multiflora (Lam.) DC	DE		2	be [c, h]
Myrcia pallens DC.	EV		2	be [h]
Myrcia tomentosa (Aubl.) DC.	SD		6,8	be [c, h]
Myrcia variabilis DC	SD		2	be [h]

Psidium myrsinoides O. Berg	DE		2	be [h]
Nyctaginaceae				
Guapira noxia (Netto) Lundell	DE		4,6,8	si [a]
Ochnaceae				
Ouratea hexasperma (A. St.-Hil.) Baill.	EV		1,2,3	be [h]
Ouratea spectabilis (Mart. ex Engl.) Engl.	EV		1,2,6	be [a, d]
Proteaceae				
Roupala montana Aubl.	EV		1,2,3,6,7,9	mo [a, b]
Rubiaceae				
Palicourea rigida Kunth	EV		2,5,6	hb, be [a, d]
Tocoyena formosa (Cham. & Schltdl.) K. Schum.	DE		2,4,5,6	mo [a, s, d, h]
Salicaceae				
Casearia sylvestris Sw.	SD		2,3,6	be, fl [g, h]
Sapotaceae				
Pouteria ramiflora (Mart.) Radlk.	SD		2,5,6	mo [a]
Styracaceae				
Styrax camporum Pohl	EV		4,10	be [g]
Styrax ferrugineus Nees & Mart.	SD		3,5,6,8,9	be [a]
Urticaceae				
Cecropia pachystachya Trécul	EV		2	si [g]
Vochysiaceae				
Qualea grandiflora Mart.	DE		1,2,3,4,6,9	mo [a, s, h]
Qualea multiflora Mart.	DE		1,6	be [a]
Qualea parviflora Mart.	DE		1,2,4,6,9	be [a]
Salvertia convallariodora A. St.-Hil.	EV		2	mo [f, h]
Vochysia tucanorum Mart.	EV		5,6,8	be, mo [a, d]

[a] Martins and Batalha, 2006
[b] Oliveira et al., 2004
[c] Gressler et al., 2006
[d] Ishara and Maimoni-Rodella, 2011
[e] Gottsberger, 1999
[f] Ribeiro and Tabareli, 2006
[g] Borges, 2011
[h] Gottsberger and Gottsberger, 2006

Table 3. Pairwise comparisons of flowering duration (FLD), flowering distribution (FDI) and flowering peak (FPE) of deciduous (DE), semideciduous (SD) and evergreen Cerrado woody species. B = Bonferroni statistical value, df = degree of freedom, F = Circular statistical value. Values in bold indicate significant difference ($p<0.05$) between leaf phenological groups.

Phenological groups	FLD (Bonferroni)			FDI (Chi-Squared)		FPE (Circular statistical)	
compared	Diference	B	p	x^2	p	F	p
DE and EV	1.81	0.92	**0.002**	12.38	0.335	1.16	0.324
DE and SD	1.20	1.06	0.052	33.79	**<0.01**	6.04	**0.042**
EV and SD	0.61	1.08	0.342	40.91	**<0.01**	11.44	**0.012**

Figure 1

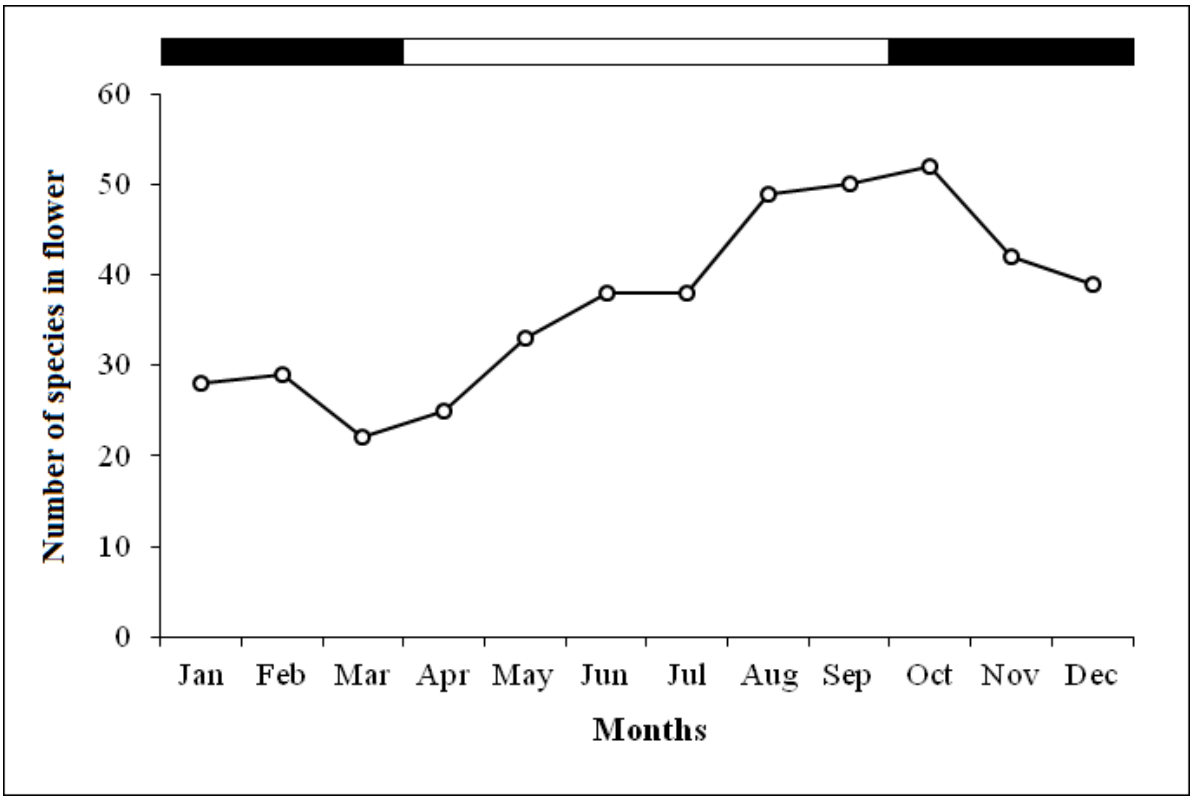
Number of species in flower
60
50
40
30
20
10
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Months

Figure 2

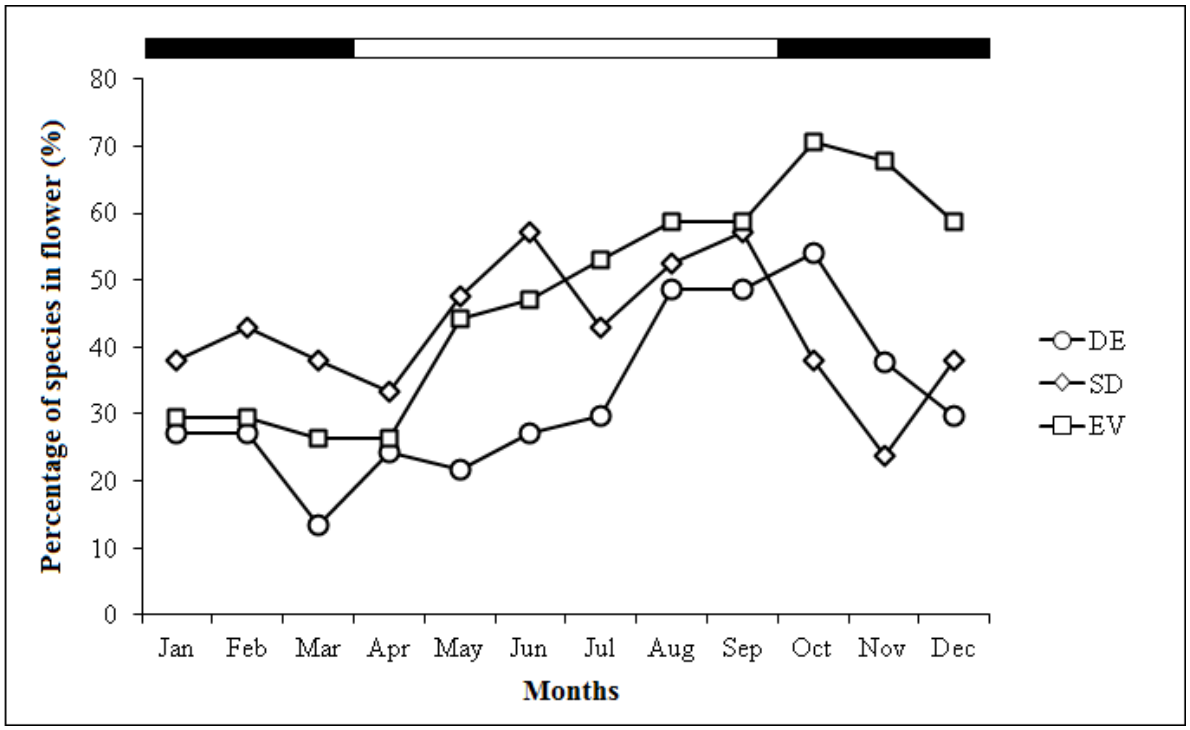
Percentage of species in flower (%)
80
70
60
50
40
30
20
10
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Months
DE
SD
EV

Figure 3

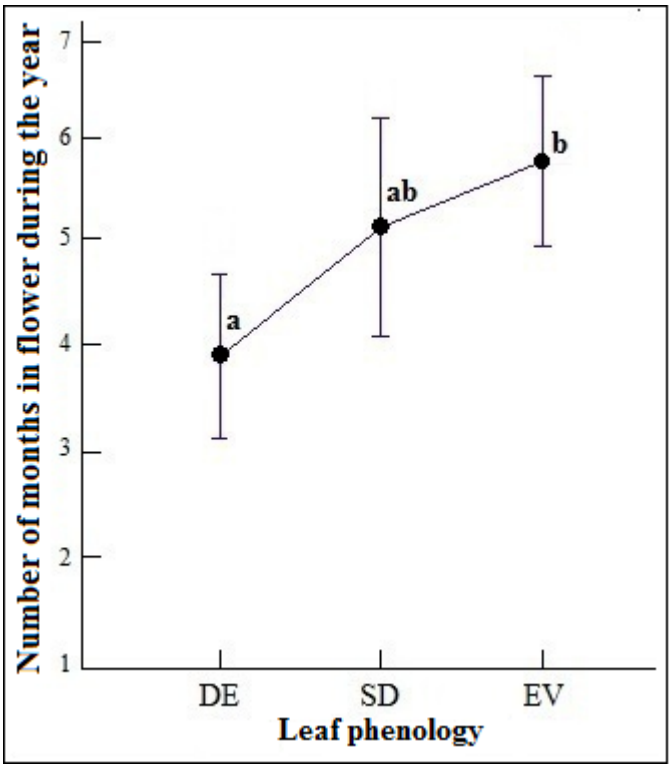
Number of months in flower during the year
7
6
5
4
3
2
1
a
ab
b
DE
SD
EV
Leaf phenology

Figure 1. Number of species in flower over the course of the year in deciduous, semideciduous, and evergreen groups (as classified according to phenological data from the literature listed in Tables 1 and 2), considering all 92 Cerrado woody species studied. The white bar at the top of the figure represents the period of the dry season, and black bars indicate the periods of the wet season, over the course of the year.

Figure 2. Percentage of Cerrado woody species in flower per month throughout the year. The number of deciduous (DE), semideciduous (SD) and evergreen (EV) species considered, based on the literature listed in Tables 1 and 2, were 37, 21 and 34, respectively. The white bar at the top of the figure represents the period of the dry season, and black bars indicate the periods of the wet season, over the course of the year.

Figure 3. Number of months in flower present over the year in Cerrado woody species with distinct leaf deciduousness: DE = Deciduous, SD = Semideciduous, and EV = Evergreen. Solid circles indicate main values, and bars indicate the confidence interval (95%). Different letters above the circles indicate significant differences ($p<0.05$) in mean values among groups.

CAPÍTULO 2: O SIGNIFICADO DAS CARACTERÍSTICAS DE COPA NA DEFINIÇÃO DOS GRUPOS FUNCIONAIS DAS ESPÉCIES ARBÓREAS DE CERRADO *

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The meaning of crown traits in functional groups of cerrado tree species

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Abstract

Questions: What are the relationships among crown traits of tree species? How is the intensity of connections among crown traits in a network perspective? Do crown traits represent variations along a continuum of functional groups? How the crown traits and their trade-offs define the plant strategies?

Location: Cerrado vegetation in Southeast Brazil

Methods: We sampled five adults per species growing under natural conditions in a cerrado *sensu stricto* physiognomy. We analyzed 20 attributes concerning the crown architecture, shoot-foliage relationships, and biomass partitioning in shoots of 18 tree species classified as deciduous (DE), semideciduous (SD) and evergreen (EV). Geometrical, topological and decomposition datasets compounded the crown architecture. The shoots-foliage relationships were determined on mass, on area, or on length basis. The biomass partitioning was the proportion of dry mass among flowers, foliage, and stalks.

Results: Relationships between crown architecture and shoot-foliage traits separate DE, SD, and EV into distinct functional groups. DE showed more biomass allocated to leaves, large leaf area indexes and more exposed foliage in plagiotropic shoots, resulting in greater potential of leaf transpiration. So, DE drops their leaves as a strategy to avoid water losses during the dry season. The low resistance to water flow in less furcate crown supports the reestablishment of full foliage in a flush in DE. Contrastingly, the more furcate crown of EV requires permanent foliage for moving the water column during the year. To avoid excessive water loss, EV presented reduced leaf transpiration area (smaller leaf area indexes and lower biomass allocated into leaves) and self-shaded foliage on orthotropic shoots. SD showed

intermediate values of crown traits between DE and EV. In SD, the highest global connectance among crown traits allows the coordination of foliage deciduousness according to the drought intensity.

Conclusions: The reliance among crown organs is appropriate to captures the emergent features that define the strategy of each functional group of Cerrado trees. Leaf deciduousness is only one of several crown traits. DE and EV presented opposite plant strategies to overcome the stresses imposed by the dry season. The transitional position represented by average values of crown traits in SD resulted in a specific functional group.

Keywords: biomass partitioning, climate seasonality, crown architecture, leaf deciduousness, plant strategy, shoot compartments, traits reliance, water scarcity.

Nomenclature

Abbreviations:

DE = Deciduous

SD = Semideciduous

EV = Evergreen

LAS = leaf area per shoot (cm^2)

LN = leaf number per shoot

LDI = leaf display index on shoot (cm^2 cm^{-1})

DLN = density of leaf number on shoots (cm-1)

ILA = individual leaf area (cm^2)

LSR = leaf/shoot ratio (g g^{-1})

SL = length of shoot (cm)

SI = angle of shoot inclination

FN = number of final nodes

EN = number of emission nodes

RN = number of regular nodes

NO = number of total nodes

LI = number of links

DN = distance between nodes on link basis (number of links between different nodes and neighboring final nodes)

FSR = flower/shoot ratio (g g^{-1})

FLR = flower/leaf ratio (g g^{-1})
RVR = reproductive/vegetative ratio (g g^{-1})
AHR = autotrophic/heterotrophic ratio (g g^{-1})
FBP = flower biomass proportion
LBP = leaf biomass proportion

Introduction

Ecologists have placed emphasis on the use of non-phylogenetic organisms' classifications for describing the ecosystems structure and functioning (Gitay & Noble 1997). The term 'functional group' defines a group of organisms that respond in a similar way to a set of environmental factors (Gitay & Noble 1997). Specific traits from a plant functional group are useful to understand how a set of species overcome natural stresses (Tecco et al. 2013). Indeed, a limited number of functional groups can capture significant ecosystem dynamics (Gitay & Noble 1997; Pérez-Harguindeguy et al. 2013).

The Brazilian Cerrado is a vegetation complex with the predominance of neotropical savannas. Cerrado has been threatened by farming activities, especially in the last 35 years, since lost a half of its original area according to the official data of Brazilian government (2011). Human transformations in a vast area, like Brazilian Cerrado, have caused changes in land use and land cover that may alter the climate pattern (Hirota et al. 2011). Functional groups could be used to maximize the recuperation of Cerrado woody strata, since they explore natural resources avoiding excessive competition under- and aboveground. Therefore, functional groups of woody plants are an important concept to guide the recuperation of degraded areas.

Cerrado woody species show different leaf deciduousness patterns. Deciduous species (DE) shed all their leaves at the peak of the dry season, remaining leafless for 3–6 weeks, and produce new leaves in a flush in the transition of dry to wet season (Damascos et al. 2005; Souza et al 2011). Evergreen species (EV) retain a near-constant foliage area and have continuous leaf abscission and production all year round (Damascos et al. 2005; Oliveira & Marquis 2002). In semideciduous species (SD) leaves are steadily abscised beginning at the dry season, throughout leaf flush, and on into at the start of wet season (Oliveira & Marquis 2002). The deciduousness in SD species varies according to the drought intensity during a year in Cerrado vegetation (Borchert 1998). DE, SD, and EV species are functional groups

because they exhibit particular characteristics in Cerrado. Deciduous species show leaves preformed in buds, determining the number of leaves on shoots previously. These preformed leaves expand synchronously in a leaf flush during less than 30 days at the end of the dry season (Damascos et al. 2005). In contrast, EV species produce new leaves by neoformation throughout the year. In EV species, the total number of leaves on a shoot is undefined during the shoot expansion (Damascos et al. 2005). As a result, leaf-shoot relations are different on mass or area basis comparing DE and EV species of Cerrado vegetation (Souza et al. 2009a). Furthermore, in these groups, there are distinct characteristics of crown architecture (Souza et al. 2011), apical meristem on shoots (Damascos et al. 2005), shoot inclination (Souza et al. 2009b), and shoot-foliage relationships (Souza et al. 2009a).

DE, SD, and EV species frequently co-occur in seasonal savannas of Americas, Africa, India and Australia (Eamus 1999). EV savanna trees have greater leaf mass fraction and growth rates than DE species and only DE show trade-offs between investment in carbohydrate reserves and growth (Tomlinson et al. 2014). DE species in Australian savanna have leaves with high nitrogen content to support a high-carbon assimilation rate during the wet season. Consequently, their short-lived leaves fix large amounts of carbon for a short period. On the contrary, EV species present longer leaf-life-span and assimilate carbon for 12 months per year with lower nitrogen allocation in leaves (Eamus 1999).

Nonetheless, certain morphological and physiological leaf traits cannot predict functional groups in Cerrado woody species (Cianciaruso et al. 2013). These authors found leaf-life-span, leaf nitrogen by mass leaf unit, specific leaf area, and maximum net photosynthesis did not differ among woody species with different leaf habit. Goldstein et al. (2008) stated grouping Cerrado woody species into functional categories is somewhat arbitrary. In fact, in six Cerrado woody species with different leaf habit, the diurnal variation of leaf water potential as a function of leaf-specific hydraulic conductivity showed a functional convergence instead functional groups. Similar merging of species occurred when considered the stomatal conductance as a function of the leaf area per unit sapwood area (Goldstein et al. 2008), and the leaf gas exchange and the morning leaf water potential under natural drought (Prado et al. 2004)

Despite the constraints depicted by Cianciaruso et al. (2013), Goldstein et al. (2008), and Prado et al. (2004), we perceive functional groups of Cerrado woody species at levels of plant organization higher than leaf morphology or physiology (Damascos et al. 2005; Souza et al. 2009a, b, 2011; Borges & Prado 2014). Indeed, there are a limited number of physiological

solutions to a given problem of plant adaptation (Meinzer 2003). The identification of what plant organization level assuredly operates the variation of traits in a group of plant species as a response to environmental pressures is a challenge.

Plant trait variation typically involves correlated traits that arise because of inevitable trade-offs among attributes either in the same or across levels of plant organization (Reich et al. 2003). It defines the successfulness of syndromes, which in turn determines the plant strategies to adapt to environmental gradients (Reich et al. 2003). We hypothesize it is much harder to identify functional groups of Cerrado woody species considering leaf morphology or physiology. Instead, functional groups can be captured by the traits and their reliance at a higher level of plant organization, because of the inevitable trade-offs among leaf morphological, physiological and phenological attributes. Therefore, the crown traits could capture the emergent traits of foliage attributes through the behavior of shoot growth and its space acquisition. The trade-offs among several crown traits constitute a syndrome resulting in a distinct plant strategy in every functional group of Cerrado woody species.

Some questions are relevant to understand the formation and clarify the meaning of functional groups of Cerrado woody species. How are the relationships among crown characteristics? How is the intensity of connections among crown traits in a network perspective? Do the crown traits of Cerrado woody species represent variations along a continuum of functional groups? How the crown features and their trade-offs define the plant strategies in Cerrado environment? Is it possible to find the same strategies in woody species of savannas worldwide? In this article we [1] described variation in plant crown traits, [2] identified and discuss the level of commitment among crown traits in a whole-plant perspective leading into different plant syndromes and plant strategies, and [3] verified whether the evidences support a model of plant strategies that result in functional groups in Cerrado woody species.

Methods

Study area and climate

We collected all datasets within a Cerrado *sensu stricto* area of 86 ha located at 850 m a.s.l. in São Carlos county, São Paulo State, Brazil (22º 00'–22º 30' S and 47º 30' – 48º00' W). The Cerrado *sensu stricto* physiognomy shows a woody stratum formed by trees and shrubs over a herbaceous layer, giving more than 30% of crown cover as described by

Oliveira-Filho & Ratter (2002). In the study area, the climate is tropical Cwa according to the Köppen's climate classification, with a dry winter and wet/hot summer (Alvares et al. 2014). The rainy season occurs between October-March and the dry season between April-September (Prado et al. 2004). The mean annual precipitation and air temperature were 1420 ± 168 mm and 22 ± 0.4 ºC, respectively (Souza et al. 2009a). The water table is between 10-15 m deep below a dystrophic oxisol, a typical soil category found in the core area underneath the Brazilian Cerrado (Oliveira et al. 2005).

Plant species

The woody species studied was classified according to leaf deciduousness and were well represented in the study area. DE: *Anadenanthera peregrina var. falcata* (Benth.) Altschul, *Aspidosperma tomentosum* Mart., *Caryocar brasiliense* Cambess, *Diospyros hispida* A. DC., *Kielmeyera variabilis* Mart. & Zucc., *Guapira graciliflora* Mart. ex J. A. Schmidt; SD: *Casearia sylvestris* Sw., *Eriotheca gracilipes* (K.Schum) A. Robyns, *Stryphnodendron adstringens* (Mart.) Coville, *Stryphnodendron polyphyllum* Mart. *Tibouchina stenocarpa* (DC.) Cogn.; EV: *Miconia albicans* (Sw.) Steud., *Miconia ligustroides* (DC.) Naudin, *Piptocarpha rotundifolia* (Less.) Baker, *Styrax camporum* Pohl, *Connarus suberosus* Planch., *Shefflera macrocarpa* (Cham. & Schltdl.) Frodin, *Myrcia bella* Cambess. We intended to collect the biomass partitioning data with the same 15 species used by Souza et al. (2009a, 2011). However, the EV species *Connarus suberosus* and *Styrax camporum*, and the DE species *Aspidosperma tomentosum* did not show enough individuals flowering at the time of data collection. Thus, we replaced the two EV species by *Shefflera macrocarpa* and *Myrcia bella*, and the DE species by *Guapira graciliflora*.

Sampling design

We used three categories of crown characteristics: shoot-foliage traits, crown architecture, and biomass partitioning. The datasets of shoot-foliage traits were obtained from Souza et al. (2009a). Geometrical, topological and decomposition datasets, derived from Sousa et al. (2009a; 2011), compounding the crown architecture category. We obtained the biomass partitioning among flowers, leaves, and the axis of shoots (stalks) during 2012-2013.

In our analyses, we used only those variables that showed mean values significantly different ($p<0.05$) between DE and EV species. SD species usually present intermediate characteristics with mean values comparable to DE or EV species (Souza et al. 2009a, 2011; Borges & Prado 2014). Therefore, we did not consider the available datasets with significant

mean value only between SD and DE species or only between SD and EV species resulting in 20 out of 27 records of crown characteristics.

We used eight variables per shoot from Souza et al. (2009a): leaf area per shoot (LAS, cm^2), number of leaves (LN), shoot length (SL, cm), shoot inclination (SI, degrees), leaf display index (LDI, $cm^2\ cm^{-1}$), density of leaf number (DLN), individual leaf area (ILA, cm^2), and leaf by shoot axis (stalk) dry mass (leaf/stalk ratio, LSR, $g\ g^{-1}$). Therefore, in Souza *et al.* (2009a), six variables (LAS, LN, LDI, DLN, ILA, and LSR) were the shoot-foliage traits and two (SL and SI) were the geometrical attributes of crown architecture used here.

The decomposition characteristics of the crown structure were the number and kinds of nodes (NO) and the number of links (LI) obtained from Souza et al. (2011). Links are the stem, limbs, and shoots connecting the nodes and nodes are the regions of junctions among stem, limbs or shoots. We used the three kinds of nodes stated by Souza et al. (2011) in our analyses. Final nodes (FN) are very often situated at the edge of a crown network, connecting the last shoots with their corresponding apical meristem (Souza et al. 2011). Each node receives only one link and, usually, emits two links during crown growth resulting in a regular node (RN), which are the majority of crown nodes. The third kind of nodes is the emission node (EN) that emits three or more links and is rare in the crown (Souza et al. 2011). We also added the dataset "total number of nodes" (NO). It was calculated by the summation of all kinds of nodes per species (regular, final and emission nodes) as shown by Souza et al. (2011).

The topological attribute of the crown architecture was the average value of the distance between different nodes (DN). DN was counted by the number of links between the various kinds of nodes or connecting the neighboring final nodes (Souza et al. 2011). The mean value of DN was obtained per species by the summation of all distances between the kinds of nodes or between the neighboring final nodes (Souza et al. 2011).

We collected the six variables about biomass partitioning at the end of the dry season in 2012 until the next dry season in 2013. We used five adult individuals per species, randomly chosen, growing in a cerrado *sensu stricto* fragment, for determining the dry mass of flower, leaf and the axis of a shoot (stalk). All biomass data were collected per shoot. In each, we monitored the development of five marked buds three times a week. In every species, we collected the flowers as soon as the flower buds bloom, and the stalk of each shoot with their corresponding leaves after the whole growth season. The flowers, stalk, and

the leaves of shoots were dried separately in a stove under 60ºC. We weighed the dry mass of collected material with an analytical balance (Mettler AE260 DeltaRange, Switzerland).

The dry biomass values from flowers, leaves, and stalks allowed us to calculate per shoot, on the dry mass basis: flowers per stalk (FSR), flowers per foliage (FLR) and flowers per foliage plus stalk (reproductive/vegetative ratio, RVR). The dry mass of leaves divided by the dry mass of flowers and stalks resulted in the autotrophic/heterotrophic ratio of a shoot (AHR). The dry mass of flowers or dry mass of leaves divided by the summation of the dry mass of all shoot parts (flowers + leaves + stalk) produced the flower biomass proportion (FBP) and the leaf biomass proportion (LBP), respectively.

Data analysis

The surveyed studies (Souza et al. 2009, 2011) provided the datasets and the differences among DE, SD, and EV species for the variable LAS, LN, LDI, DLN, ILA, LSR, SL, SI, FN, EN, RN, and LI. We have to test the differences among DE, SD and EV for unpublished data (biomass partitioning datasets, NO, and DN). All unpublished variables did not show a normal distribution, requiring the non-parametric analysis of variance Kruskal-Wallis test (Zar 1999). The statistical tests were carried out by software Biostat 5.0 (Belém, Brazil, 2007) and Mystat 12 (Washington, USA, 2007).

We used the multivariate analysis Non-Parametric MANOVA (Permanova) to identify which of the crown traits datasets (shoot-foliage traits, crown architecture, and biomass partitioning) most affect the separation of functional groups. Permanova is a non-parametric test of the significant difference between two or more groups, based on any distance measure, in which the permutation of group membership computes the significance (Anderson 2001). We used the Bray-Curtis distances measure and the permutation of group membership with 10,000 replicates. We did one Permanova test for each of three crown traits datasets (crown architecture, shoot-foliage relationships, and biomass partitioning) and one test considering all datasets. We did not remove the correlated variables once the correlations among variables play no role in Permanova analysis (Anderson 2001). According to Anderson (2001), by using permutations, the test requires no specific assumption concerning the number of variables or the nature of their individual distributions or correlations. All multivariate analyses were carried out with PAST software 2.17c (Oslo, Norway, 2013).

We used a scatter plot to analyze the level of correlation between two traits, the number of total nodes (NO) and the leaf area per shoot (LAS), which represent crown

architecture extension and shoot-foliage patterns, respectively. We chose one variable of each of these two categories (crown architecture and shoot-foliage) since they showed a significant difference in Permanova tests. Besides, LAS and NO were collected independently, and there was no autocorrelation among them. Also, we chose the logarithmic regression trend line since it showed the best fit curve for the dataset on scatter plot. In the graph, the regression trend line and its respective equation were carried out with Microsoft Office Excel 2010.

To assess the level of commitment among the crown attributes in DE, SD, and EV species, we evaluated the differences in modulation of crown traits in a network for every functional group. We considered modulation as the change in the mean strength of connections among a network of elements, which was measured through the connectance according to Amzallag (2001) and Souza et al. (2009c). To calculate connectance, we specified a collection of paired variables without autocorrelation in a network (Fig. 1). We divided the network of crown traits into two sub-networks, the shoot-foliage network, and the architecture network. No pairing was made with biomass variables since they are highly autocorrelated and unable to separate DE, SD and EV species in multivariate analyses Permanova. Seven relationships compose the shoot-foliage sub-network: LAS-LN, LAS-DNL, LAS-LSR, DNL-LSR, LN-LDI, LSR-LDI, and LSR-ILA. Twelve relationships integrate the architecture sub-network: NO-DN, NO-LI, NO-SI, NO-SL, DN-LI, SI-LI, SL-SI, DN-FN, DN-EN, FN-EN, LI-EN, and SI-EN. The relationship LAS-NO made the connection of the sub-networks. The Pearson correlation coefficient (r) obtained for each paired variable in the network was used to determine the strength of connections between variables. Subsequently, r-values were normalized by z-transformation, becoming z-values, as defined by Amzallag (2001): $z = 0.5 \ln[(1+|r|) / (1-|r|)]$. We calculated the global network connectance (Cg) as the average of z-values (Amzallag 2001). We considered one Cg for each sub-network (Souza et al. 2009c). The values of Cg in shoot-foliage sub-network (Cg_{sf}) and architecture sub-network (Cg_{ar}) were obtained using the z-values of corresponding paired variables of each group. The total connectance of each functional group (Cg_{total}) was calculated considering the z-values of all paired variables in both sub-networks and the z-values of LAS-NO, the relationship that connects both sub-networks.

Results

The variables about the size of foliage showed significantly higher average values in DE than in SD or EV species (Table 1). These traits were leaf area per shoot (LAS), leaf display index (LDI), the density of leaf number (DLN), individual leaf area (ILA), and leaf/shoot ratio (LSR). Indeed, about foliage traits, only the leaf number per shoot (LN) was significantly lower in DE than in EV species (Table 1). Besides, the autotrophic/heterotrophic ratio (AHR) and the leaf biomass proportion (LBP) were significantly greater in DE than in SD or in EV species (Table 2). Therefore, DE showed virtually the highest average values at $p<0.05$ in all datasets regarding the foliage dimension on shoots.

On the other hand, the geometrical features, as shoot length (SL) and shoot inclination (SI), showed average values higher in EV than in SD or in DE species (Table 1). Besides, the topological and the decomposition attributes of crown presented higher values in EV than in DE species. Therefore, the number of nodes (FN, EN, RN and NO), the distance between nodes and the number of links were significantly greater in EV than in DE species (Table 1). Since the links and nodes are made, respectively, of shoots and shoot junctions, EV allocated more resources than DE species in shoot axis (stalks) for supporting leaves and flowers. The same occurred in SD species since there were no significant differences between SD and EV species regarding FN, EN, RN, and NO.

The biomass ratios flower/stalk (FSR), flower/leaf (FLR), reproductive/vegetative (RVR), and the flower proportion (FBP) presented the higher average values in SD and EV species (Table 2). Therefore, the biomass allocation in reproductive structures is more limited in DE species (Table 2). Summarizing the results, by comparison on shoot basis, DE species allocate relatively more resources in foliage and EV and SD in flowers and shoot axis (stalks). In other words, DE species allocate relatively more biomass in autotrophic parts, and EV and SD species into heterotrophic structures in shoots (flowers and stalks).

As expected, SD species showed intermediate mean values in all of those 20 variables studied (Tables 1 and 2). SD showed significant differences ($p<0.05$) about DE and EV species in only seven out of 20 features studied. Five of these characteristics were shoot-foliage traits (LAS, LDI, DLN, ILA, and LSR) and two were geometrical traits of crown architecture (SL and SI). Therefore, considering DE and EV collectively, SD species were not different regarding the decomposition (FN, EN, RN, NO, LI) and the topological (DN) crown traits (Table 1). The same goes for shoot biomass distribution outcomes (Table 2). Besides,

the Permanova showed the crown traits datasets were not able to separate SD from DE or EV (Table 3).

The Permanova indicated the shoot-foliage and the crown architecture qualities separated DE and EV into two distinct groups (Table 3). On the other hand, by biomass partitioning, it was not possible to separate any group (Table 3). The absence of distinct groups using biomass partitioning probably is due to the high standard deviation values presented in every group (Table 2). Despite the high standard deviation and coefficient of variation values for all groups, the Kruskal-Wallis test could capture significant differences between DE and EV species associated with biomass partitioning in shoots (Table 2).

The scatter plot showed a moderate correlation between NO and LAS (r^2= 0.54). The graph showed NO decreases with the LAS increasing in exponential decay manner (Fig. 2). Despite the apparent continuum, most of the EV species were grouped at the left top, showing small LAS and high NO. Contrastingly, DE species was grouped at middle down on Fig. 2, presenting values of LAS from intermediate to high and low values of NO. Contrastingly, the SD species showed up dispersed among EV and DE species. The Fig. 2 corroborates EV species have an extended crown structure and a small investment in foliage while DE species have simple crown architecture and relatively high investment in foliage. The dispersion of SD species (Fig. 2) completes their particular dataset of traits and an intermediate position found by the analysis of variance and the multivariate analysis (Tables 2 and 3, respectively).

The connectance analyses showed SD with the major value of global connectance in all networks (Table 4). Besides, the difference among SD and other groups (DE and EV) was usually high. The Cg_{total} of SD was 67.8 and 83.3% higher than DE and EV species, respectively. The Cg_{sf} presents the major discrepancy (4.2 and 2.3 times higher in SD than in DE and EV, respectively) and Cg_{ar} showed the minor difference (16.3 and 37% higher in SD than DE and EV, respectively). DE and EV presented similar Cg_{total}, with little difference between them and DE being slightly higher (9.2%) than EV. Although, when analyzed the sub-networks (shoot-foliage and architecture networks) DE and EV were more dissimilar (Table 4). The Cg_{ar} was 17,8% superior in DE about EV. Contranstly, Cg_{sf} was 58.8 % higher in EV compared to DE (Table 4). These differences in Cg_{total}, Cg_{sf}, and Cg_{ar} values for DE, SD, and EV corroborate the existence of three different functional groups among Cerrado tree species, and the values from SD species provide unique properties to this group.

Discussion

The mean values of crown traits on Tables 1 and 2 showed significant differences among DE, SD, and EV Cerrado tree species. However, the examination of a single trait cannot predict any emergent property at a higher level of plant organization (Bertolli et al. 2014). A simple list of significant differences between groups of species is not relevant to a whole-plant perspective (Reich et al. 2003). Only the commitment among crown traits presented in Tables 1 and 2 could capture the emergent properties and showed the constitution of each functional group of Cerrado tree species. On the other hand, the significant differences in average values (Tables 1 and 2) straightforwardly depict the same attribute fluctuating significantly in each group of species. This variation was not isolated but connected to the other crown traits and their corresponding alterations (*e.g.* Fig. 2). Indeed, the results of Permanova (Table 3) considered the variation of three groups of crown datasets with shoot-foliage and architecture traits, separating DE and EV species.

The changed interdependence among distinct parts of crown (Table 3 and Fig. 2), the different strength among crown traits in a network (Table 4), and even the dissimilar foliage deciduousness result in a particular behavior of crown space filling, different resource use and particular responses of natural stresses among groups of Cerrado tree species. When crown development is quite dissimilar among groups (Tables 1-3) it is unlikely to find comparable crown structure, equivalent response to water stress and analogous use of resources as light. Thus, the functional groups of tree species are products of the competencies to overcome, simultaneously, the environmental stresses and the limitations to acquire natural resources in Cerrado area. The process of evolution in these functional groups is the continuous acquisition of competencies by a plant strategy that is not necessarily the same over the life cycle.

The EV strategy involves the interdependence among permanent foliage, neoformation of shoots and leaves, orthotropic shoots, and extended topology of crown architecture. The neoformation of foliage demands one permanent meristematic tissue able to produce some orders of shoots throughout the seasons, as detected in EV species by Damascos et al. (2005). Furthermore, the continuous shoot growth and leaf production sustain the evergreen habits and the higher number of nodes and links in an extended crown (Table 1). One extensive shoot network increases the resistance of mass flow during the ascending sap via xylem (Cruiziat et al. 2002). Consequently, the crown of EV species requires a permanent foliage

area as a driven force of suction for moving the water column during the whole year into a xylem with more regular nodes, additional kind of nodes and extra links.

On the other hand, the foliage maintenance during the dry season implies in increased potential for water loss by foliage transpiration. Notwithstanding, EV species present reduced leaf transpiration area as a consequence of smaller leaf area indexes (Table 1) and lower biomass allocated in leaves (Table 2) than DE species. Besides, the leaf transpiration area in EV is self-shaded on orthotropic shoots (Table 1), moderating the foliage exposition to solar irradiance. These leaf and shoots characteristics permit to keep moving the mass flow into the xylem without losing an excessive amount of water in the dry season. The full leaf area and the continuous foliage development of EV species expose their green shoots permanently to atmospheric conditions over the year (Damascos et al. 2005). It means that the aboveground environment could strongly shape the shoot features decreasing the variation of shoot-foliage traits among EV species. Indeed, EV species virtually showed the lower coefficient of variation for all crucial crown traits (Table 1) and they appeared closely related each other in a scattered plot NO-LAS (Fig. 2).

Contrastingly, DE strategy involves the interdependence among higher leaf area on plagiotropic shoots, preformation of shoots and leaves in buds, reduced crown structure, and synchronous foliage formation in a flush on shoots free of leaves at the end of dry season. DE presented larger leaf area indexes (Table 1) and more investment in photosynthetic leaf tissues (Tables 1 and 2, Franco et al. 2005) that results in excessive foliage exhibition and high transpiration potential. Also, DE species have a simpler crown network, fewer links and nodes with shorter distance between nodes than EV species, which decreases the maximum resistance of mass flow via xylem in ascending-sap. Subsequently, the flush of foliage in DE is possible on simple crow architecture by unfolding preformed leaves in buds. On the other hand, the dropping of exposed large leaves is required at the peak of the dry season.

The foliage preformation in buds (Damascos et al. 2005) and a root system reaching deep soil layer (Jackson et al. 1999) allow DE species to support the flush of leaves and flowers at the peak of the dry season. The Cerrado soil shows water potential greater than -1.5 MPa below 0.85 cm since only the superficial layer loses capillary water during the dry season (Oliveira et al. 2005). Admittedly, a significant root pressure, as indicated by Kramer (1983), could be involved in the initial unfold of leaves, flowers, and shoots. Furthermore, the simple crown structure of DE and higher Cg_{ar} among different kinds of nodes and links than EV (Table 4) implies in a prompt response to endogenous sings. In other words, a signal from

the roots or crown for opening the buds at the end of the dry season could be rapidly propagated in DE crown network. In short, the quick restoration of full foliage in a flush in DE, even before the heavy rains (Damascos et al. 2005), is facilitated by deep roots and preformed leaves in buds on a reduced crown topology with components strongly connected.

The production of flowers and leaves in a short time at the end of the dry season also depends on the size of reserves and the corresponding mobilization capacity in DE. Therefore, leaf, flower, and the stalk of shoot growing at the end of the dry season are competitive processes for reserves. DE species could cover the high demand of foliage flush diminishing the investments in flowering (Table 2, FSR, FLR, FBP, RVR, and FBP) and shortening the flowering duration (Prado & Borges 2014). Alternatively, EV species maintain a constant photosynthetic area throughout the year, enabling them to use current resources (water, nutrients and carbohydrates) in flower production (Borges & Prado 2014). Therefore, the use of affordable resources during the whole year allows high biomass allocation in flowers (Table 2) and greater flowering duration in EV than in DE species (Prado & Borges 2014). The dependency of reserves availability at every year and the smallest value of shoot-foliage connectance result in a major variation of autotrophic/heterotrophic ratio and leaf biomass proportion values in DE (Table 2). Furthermore, ambient factors cannot shape the preformed shoots intensely in DE during only one month of shoot flush contrasting to EV species with continuous shoot growth over the year. Then, co-occurring DE species virtually presented the greater coefficient of variation of shoot-foliage and crown architecture attributes than EV species (Table 1).

SD group shares characteristics with DE and EV species follow-on in between foliage persistence with intermediate mean values in all features analyzed (Tables 1 and 2). Also, SD could not be separated from DE and EV groups in multivariate analysis (Table 3). The scattered pattern of distribution of SD species (Fig. 2) and their highest connected crown structures (Table 4) confirms the existence of three instead two discrete functional groups of tree species in Cerrado (DE, SD, and EV). Therefore, SD encloses characteristics from DE and EV (Tables 1-3) resulting in a particular functional group. As described by Borges & Prado (2014), the shared characteristics of SD species of Cerrado vegetation result in unique reproductive behavior, with two flowering peaks during the year.

Semideciduous habit demands greater connectance among their crown components to coordinate the foliage deciduousness according to the drought intensity at every dry season. Therefore, high connectance implies in a rapid propagation of signs among crown

components for changing the deciduousness each year. Briefly, SD group includes selected crown traits from DE and EV species with a strong connection of these features constituting a singular functional group of tree species in Cerrado. Moreover, the highest values of Cg, C_{sf}, and C_{ar} place SD as a discrete functional group with particular crown structure and behavior.

The adaptive strategies identified in Cerrado tree species can be associate to Grime's competitor, stress-tolerator, ruderal (CSR) theory (Grime 1977). Following the assumptions of CSR theory, the EV strategy can be defined as 'competitive', once they present continuous leaf production, keep the photosynthetic area around all the year, show more branched crown, and more resources allocated, relatively, on reproduction tissues. The DE drop their leaves during the dry season, produce shoots and leaves in a flush from preformed buds, storage carbohydrate e water, and allocate lesser resources on reproductive tissues, which are, as a whole, typical adaptive responses of 'stress-tolerate' strategy. Lastly, SD present diversity in traits (shared with DE and/or EV) and high modulation capacity (high Cg) that define a unique plant strategy that are the combines 'competitive' and 'stress-tolerate'.

Seasonality is the significant driving force that selects plant strategies in tree species of Cerrado. In savannas with similar seasonality, it is possible to find tree species with comparable interdependence among crown traits and analogous strategies to overcome water shortage. Furthermore, the presence of same patterns of leaf deciduousness in trees of other savannas in Africa and Australia (Eamus 1999) indicates that similar plant strategies at the crown level may be involved in space filling, resource use, and in response to seasonal water stresses.

The criterion of biological diversity indicated for the sustainable management of tropical tree vegetation is based on the ecosystem, species and genetic diversity (ITTO 2005). Survival rate, herbivory frequency, frost susceptibility and seed dispersal could be attributes to select species in Cerrado restoration (Pilon & Durigan 2013). However, including functional groups of tree species of Cerrado vegetation is unconsidered until now, despite the functional group criterion be crucial for recovering ecosystems (Palmer et al. 1997; Schulze & Mooney 2012). Management and conservation strategies need to maintain the diversity of functional groups as a way to keep the community proprieties. The Cerrado management and conservation designs require including deciduous, semideciduous and evergreen species once these have been identified as distinct functional groups. The different adaptive strategies of these three groups of tree species contribute to maximize the community functioning and increase its resilience.

Conclusions

Our results showed functional groups of Cerrado tree species are not arbitrary. Notwithstanding, just the permanence of foliage does not determine the functional groups, but it is a consequence of intertwined crown traits that constitute different syndromes. No value exists in a list of characteristics of a tree species for determining a functional group. Instead, the commitment among crown traits captures the emergent features in a whole-plant strategy that define the functional groups in Cerrado tree species. The mobilization of storage reserves at the end of the dry season in a simple topology and highly connected components of the crown, and the preformed organs in buds determines the success of aerial space filling in a flush in DE species. Contrastingly, the growth of the crown in EV species is firmly connected to environmental conditions over the year producing continuously an extended crown with orthotropic shoots. This growth depends on the activity of the meristematic tissues at shoot apex and the going-on of permanent foliage over the year in pace with ambient conditions. SD combines traits from DE and EV species to form unique group provided with fine-tuned response to environment variations. SD confirms the DE and EV as discrete groups and connects them in a gradient of crown attributes. These three distinct functional groups give resistance and resilience to Cerrado vegetation by exploring ambient resources in different scales of time and space avoiding the excessive competition.

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Table 1. Mean values of shoot-foliage traits and crown architecture data of 15 Cerrado woody species classified as deciduous, semideciduous and evergreen. Shoot-foliage traits: LAS = leaf area per shoot (cm^2), LN = leaf number per shoot, LDI = leaf display index on shoots (cm^2 cm^{-1}), DLN = density of leaf number on shoot (cm^{-1}), ILA = individual leaf area (cm^2), LSR = leaf/shoot ratio (g g^{-1}). Crown architecture traits: SL = length of shoots (cm), SI = angle of shoot inclination, FN = number of final nodes, EN = number of emission nodes, RN = number of regular nodes, NO = total number of nodes, LI = number of links (number of shoots), and DN = distance between nodes (number of links between different nodes). Different letters after mean values indicate significant differences ($p < 0.05$, Kruskal-Wallis) among leaf phenological groups. SD = standard deviation. CV = coefficient of variation. Data obtained from [1]Souza *et al.* (2009a) and [2]Souza *et al.* (2011)

Group	Data	LAS[1]	LN[1]	LDI[1]	DLN[1]	ILA[1]	LSR[1]	SL[1]	SI[1]	FN[2]	EN[2]	RN[2]	NO[2]	LI[2]	DN[2]
DE	Mean	419a	6.8b	106.4a	1.6a	77.5a	11.0a	8.4c	42.0c	12.0b	6.0b	37.0b	55.0b	83.0b	4.7b
	± SD	±125	±3.3	±95.0	±1.6	±46.0	±6.6	±5.3	±2.5	±2.0	±1.0	±5.0	±22.0	±33.0	±0.9
	CV%	29.8	48.5	89.2	93.8	59.4	60.0	63.1	5.6	16.6	42.9	13.5	40.0	39.8	19.3
SD	Mean	372b	7.2b	68.5b	0.8b	74.2b	7.7b	11.1b	54.0b	21.0a	12.0ab	72.0a	105a	163a	5.9a
	± SD	±331	±3.9	±122	±0.4	±77.0	±2.7	±5.4	±5.8	±3.0	±2.0	±10.0	±52.0	±79.0	±0.6
	CV%	88.9	54.1	178.1	43.3	103.7	35.1	48.6	10.7	14.3	16.6	13.9	49.5	48.5	10.1
EV	Mean	152c	7.8a	9.7c	0.55c	20.1c	5.7c	16.3a	62.0a	24.0a	14.0a	107a	146a	236a	7.6a
	± SD	±40.0	±1.6	±2.0	±0.1	±6.8	±0.9	±1.9	±2.6	±2.0	±2.0	±12.0	±50	±81.0	±2.2
	CV%	26.3	20.5	20.6	8.0	33.8	15.8	11.7	4.1	8.3	14.3	11.2	34.2	34.3	29.1

Table 2. Dry biomass partitioning and dry biomass proportions in shoots of 15 Cerrado woody species distributed in deciduous, semideciduous and evergreen. FSR = flower/shoot ratio (g g^{-1}), FLR = flower/leaf ratio (g g^{-1}), RVR = reproductive/vegetative ratio (g g^{-1}), AHR = autotrophic/heterotrophic ratio (g g^{-1}), FBP = flower biomass proportion and LBP = leaf biomass proportion. Average values ± standard deviation values in every leaf phenological group are in bold. Different letters after average values indicate significant differences ($p < 0.05$, Kruskal-Wallis) among leaf phenological groups. CV = coefficient of variation

Group	Species	FSR	FLR	RVR	AHR	FBP	LBP
DE	*A. falcata*	0.84	0.09	0.08	5.37	0.07	0.83
	C. brasiliense	2.02	0.68	0.48	1.82	0.28	0.57
	D. hispida	0.48	0.05	0.05	6.18	0.04	0.85
	K. variabilis	1.74	0.36	0.29	2.34	0.20	0.67
	G. graciliflora	1.69	0.35	0.28	2.59	0.19	0.67
	Group mean	**1.35b**	**0.31b**	**0.24b**	**3.66a**	**0.16b**	**0.72a**
	± SD	**±0.68**	**±0.23**	**±0.16**	**±1.72**	**±0.08**	**±0.11**
	CV%	50.4	74.2	66.7	47.0	50.0	15.3
SD	*C. sylvestris*	1.56	0.31	0.26	2.07	0.20	0.67
	E. gracilipes	2.96	0.48	0.41	1.98	0.26	0.63
	S. adstringens	1.40	0.20	0.17	3.29	0.14	0.74
	S. polyphyllum	2.85	0.41	0.35	1.94	0.26	0.65
	T. stenocarpa	1.72	0.78	0.53	0.97	0.33	0.47
	Group mean	**2.01a**	**0.41a**	**0.34 a**	**2.05b**	**0.24a**	**0.63b**
	± SD	**±0.81**	**±0.16**	**±0.13**	**±0.71**	**±0.07**	**±0.08**
	CV%	40.3	39.0	38.2	34.6	29.2	12.7
EV	*M. albicans*	1.68	0.33	0.28	2.16	0.21	0.66
	M. ligustroides	1.71	0.43	0.33	1.73	0.23	0.60
	P. rotundifolia	0.67	0.23	0.17	1.07	0.14	0.63
	S. macrocarpa	4.80	0.68	0.59	1.80	0.35	0.58
	M. bella	3.04	0.97	0.72	1.58	0.37	0.49
	Group mean	**2.38a**	**0.53a**	**0.42a**	**1.67b**	**0.26a**	**0.59b**
	± SD	**±1.32**	**±0.27**	**±0.21**	**±0.52**	**±0.09**	**±0.07**
	CV%	55.5	50.9	50.0	31.1	34.6	11.9

Table 3. Non-Parametric Multivariate Analyzes of Variances (NPMANOVA) for three groups of crown traits of 15 Cerrado woody species classified as deciduous (DE), semideciduous (SD) and evergreen (EV). Values in bold indicate significant difference ($p<0.05$) between functional groups

Functional groups compared	Shoot-foliage traits		Crown architecture		Biomass partitioning		All variables	
	F	p	F	p	F	p	F	p
DE and EV	22.79	**< 0.01**	12.97	**< 0.01**	1.80	0.17	16.78	**<0.01**
DE and SD	1.32	0.36	2.37	0.11	0.94	0.38	1.94	0.20
EV and SD	2.53	0.15	1.89	0.22	0.79	0.52	2.29	0.19

Table 4. Global connectance of crown traits (Cg_{total}), shoot-foliage (Cg_{SF}), and architecture (Cg_{Ar}) networks.

Global connectance	DE	SD	EV
Cg_{total}	0.59	0.99	0.54
Cg_{sf}	0.17	0.88	0.27
Cg_{ar}	0.86	1.00	0.73

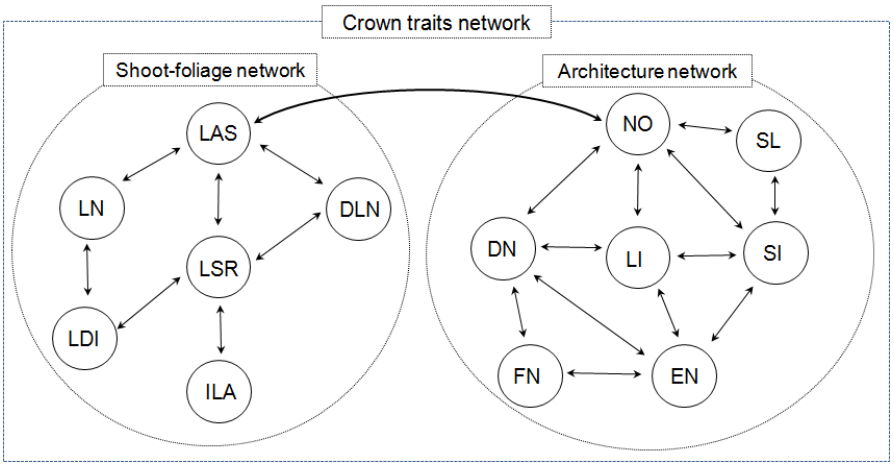

Fig. 1. Schematic representation of crown traits network composed by shoot-foliage and architecture networks. Arrows represent connection among variables. LAS = leaf area per shoot (cm^2), LN = leaf number per shoot, LDI = leaf display index on shoot (cm^2 cm^{-1}), DLN = density of leaf number on shoots (cm^{-1}), ILA = individual leaf area (cm^2), LSR = leaf/shoot ratio (g g^{-1}), NO = number of total nodes, LI = number of links, DN = distance between nodes on link basis (number of links between different nodes and neighboring final nodes), SL = length of shoot (cm), SI = angle of shoot inclination, FN = number of final nodes, EN = number of emission nodes.

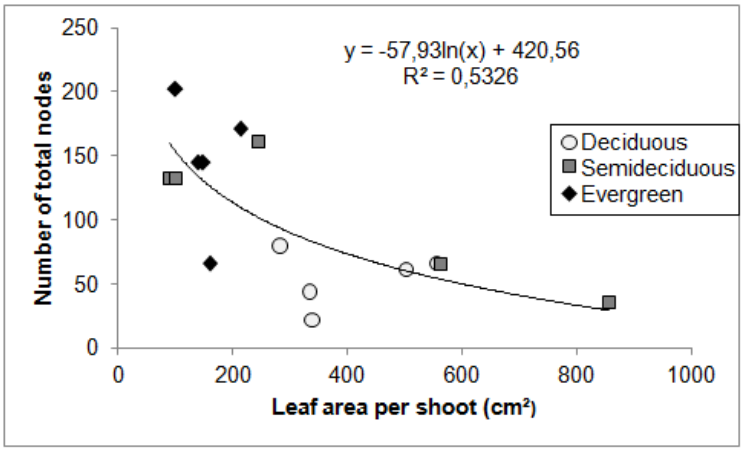

Fig. 2. Logarithmic regression of the number of total nodes in a crown as a function of leaf area per shoot in deciduous, semideciduous and evergreen woody species of Cerrado vegetation.

CAPÍTULO 3: RELAÇÕES ENTRE AS ALTERAÇÕES CLIMÁTICAS E OS GRUPOS FUNCIONAIS DAS ARBÓREAS DE CERRADO *

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Relationships between climatic alterations and functional groups of Cerrado tree species

Running read: Climatic alterations and cerrado tree species

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Abstract: This study identifies the effects of climate alterations in growing and flowering of deciduous (DE), semideciduous (SD) and evergreen (EV) cerrado tree species under natural conditions in a Cerrado reservoir of São Carlos County (SP, Brazil). We compared the flowering period and the biomass allocation among flowers, leaves, and stalks between two consecutive years (2013-2014) in nine tree species classified as DE, SD or EV. We evaluate the annual and monthly rainfall, monthly mean air relative humidity and air temperature in 2013 and 2014 using as reference the historical period of climate data (1961-2015). 2013 was considered similar to the period of historical data. Nonetheless, 2014 showed an intense drought, with total annual rainfall decreased (27%) and the mean air temperature was 1.2 °C upper than the historical data. Despite the dissimilar growth patterns, DE and EV decreased biomass allocation in all shoot compartments in 2014 keeping the ratio of autotrophic/heterotrophic tissues. In contrast, SD changed the biomass investment from heterotrophic (flowers) to autotrophic (leaves) tissues and maintained the total biomass allocated in shoots in 2014. The combination of low global connectance (Cg) among shoots compartments and the decreasing Cg under severe drought in 2014 makes SD the most stable group keeping same biomass allocation in shoots. This study confirms SD as a distinct functional group with the great ability to self-adjust under climate alterations. Despite the size of plant reserve and its mobilization capacity, the shoot growth is affected in the current year under climate alterations.

Key-words: Biomass partitioning in shoots, drought, leaf deciduousness, plasticity, stability.

Introduction

Tropical savannas are widespread around the world, found in Americas, Africa, Australia, India and South East Asia (Eamus 1999, Archibold 2012). The vegetation of savannas is characterized by a stratum of trees over a largely layer of grasses (Collinson 2012, Borges and

Prado 2014). The Cerrado shows various physiognomies with a core area in the central region of Brazil, from open grasslands to dense woodlands (Oliveira-Filho and Ratter 2002, Ribeiro and Walter 2008). The Cerrado´s domain is marked by the climate seasonality, with well-defined wet and dry seasons (Eiten 1982, Oliveira-Filho and Ratter 2002). Water shortage in the upper layer and high air evaporative demand impose a water stress, constituting significant drive forces that select and modulate morphologies and physiologies of plant species in Cerrado vegetation Franco 2002, Prado et al. 2004, Chapter 2).

Deciduous (DE), semideciduous (SD), and evergreen (EV) tree species institute distinct functional groups with different strategies to overcome the scarcity of water during the dry season (Chapter 2). DE showed high transpiration potential due to large leaf area (Souza et al.2009a), plagiotropic shoots (Souza et al. 2009b), and low resistance to ascending-sap via xylem in a simple crown architecture (Souza et al. 2011). Therefore, DE drops their leaves in the dry season to avoid excessive water loss and too many negative values of leaf water potential (Chapter 2). With a crown free of leaves, DE species mobilize water and photosynthates from the reserves enabling a rapid growing of leaves and flowering at the end of the dry season before significant rainfall (Chapter 2).

Contrastingly, EV species keeps same foliage area over the year (Damascos et al. 2005). It is possible since EV showed self-shading leaves and small foliage area in orthotropic shoots (Souza et al. 2009a, b). EV species show reduced stomatal conductance during the dry season avoiding an elevated transpiration rate (Prado et al. 2004). The extended crown structure in EV (Souza et al. 2011) demands foliage persistence to surpass the high resistance of ascending-sap via xylem (Chapter 2). Additionally, the maintenance of foliage by EV allows them to use ongoing resources of water and photosynthates (Chapter 2). Although low values of monthly rainfall during dry season entails in water shortage, soil layers deeper than 0.85 cm retain water potential greater than -1.5 MPa throughout the year in Cerrado (Oliveira et al. 2005). As EV does not have a high transpiration

demand (Chapter 2), they can explore water in deep soil layers without threatened their water balance during the dry season.

Cerrado has been vulnerable by farming activities in the last 35 years, once lost a half of its original area according to the official government data (MMA/IBAMA 2011). Human transformations in a vast area, like Brazilian Cerrado, have caused changes in land use and land cover that may alter the climate pattern (Hirota et al. 2010). Changes in climate patterns, like temperature and rainfall, have affected plants around the world in distinctive ways. Plant phenologies, such as flowering, leafing, and fruiting, can be altered by changes in air temperature (Fitter and Fitter 2002, Menzel et al. 2006). The plant sexual reproduction might be particularly susceptible to effects of climate changes, especially in flower production, quantity and quality of pollen, seed and fruit characteristics and germination rates (Hedhly et al. 2008). Climate changes also can modify the pattern of distribution of plant species in different biomes (Gottfried et al. 1999, Lenoir 2009, Wu 2010), including the Brazilian Cerrado (Simon et al. 2013).

In a scenario of decrease of annual and monthly precipitation and, consequently, an increase in air evaporative demand the functional groups of cerrado tree species can show different patterns of response affecting their growing and reproduction. The synchronous growing of shoot, leaf, and flower in a flush during about 30 days of DE species are strongly dependent on reserve mobilization since this fast growing occurs at the end of the dry season (Damascos et al. 2005, Borges and Prado 2014). If a rainfall decreasing takes place during the wet season, the reserves formation can be affected, threatening the flush of the new cohort of leaves in the next growing season. On the other hand, EV species show a continuous growing during the year by maintaining constant the photosynthetic area (Damascos et al. 2005). Due to the dependency of EV of ongoing resources, a reduction in rainfall at any time could affect the current shoot and leaf formation. Besides, the scarcity of water before and during the flowering period may affect the flower production of EV.

SD present intermediate features between DE and EV species (Souza et al. 2009a, b, 2011, Borges and Prado 2014, Chapter 2). As a result, SD may show a unique response, different from DE and EV, as occurred for flowering distribution (Borges and Prado 2014). The combination of features from DE and EV may result in a unique adaptive response. The SD species also present a high crown traits connectance that implies in a rapidly sings propagation inside the crown to modulate deciduousness according to the environment (Chapter 2). These characteristics of SD may support high stability under environmental disturbance.

We hypothesized the occurrence of climate alterations (markedly low rainfall, high air evaporative demand and high air temperature) will affect biomass allocation among crown compartments of Cerrado trees. As DE, EV and SD present different traits, syndromes and plant strategies at the crown level of organization (Chapter 2), each group will be affected differently by the driest event. We supposed drought would affect the reserves formation of DE species. Consequently, the biomass investment in stalks, leaves and flowers in the next growing season of a shoot will be lesser compared to a year with normal rainfall and air temperature. Concerning to EV, significant decreasing in rainfall will probably affect the continuous growing by neoformation, implying in smaller biomass investment in vegetative structures. As a consequence, the photosynthetic area of EV will be reduced, also affecting the biomass investment in flowers and delaying flowering time. We hypothesized SD will be less affected by climate alteration than DE and EV since they will, probably, modulate the biomass allocation among shoot organs, favoring leaves, as a way to guarantee resource acquisition in next grow season. The plasticity in modulate biomass allocation probably gives to SD more stability and, consequently, ability to survive in the Cerrado area affected by climatic alterations.

This study identified the effects of low rainfall, high temperature, and high air evaporative demand in vegetative growing and flowering in Cerrado tree species under natural conditions. We evaluated the changes in growing by quantifying the biomass allocated in flowers, leaves and stalks

in a year with normal rainfall and air temperature, 2013, and in the next year with low rainfall and high air temperature. We also predicted the potential impacts of these ecophysiological alterations in the cerrado tree species in a scenario of future climatic changes that alter the annual rainfall regime.

Material and Methods

Study area and climate

This study was carried out in a reservoir of natural vegetation with 86 ha of Cerrado *sensu stricto* physiognomy in Federal University of São Carlos (UFSCar), São Carlos county, State of São Paulo, Southeast of Brazil. The reservoir is located at 850 m a.s.l. on 22º 00'–22º 30' S and 47º 30' – 48º 00' W. The Cerrado *sensu stricto* physiognomy shows a woody *stratum* giving 30-50% of crown cover over an herbaceous layer (Eiten 1982). The climate of the area is Cwa according to the Köppen's climate classification, with a dry winter and wet/hot summer (Alvares et al. 2014). The rainy season occurs between October-March and the dry season between April-September (Prado et al. 2004, Monteiro and Prado 2006). The historical mean annual rainfall and air temperature on the reservoir area were 1500 ± 319 mm and 20.5 ± 0.6 ºC, respectively (Figure 1). The water table is between 10-15 m deep below a dystrophic oxisol, a typical soil category found in the core area underneath the Brazilian Cerrado vegetation (Oliveira et al. 2005).

Climate data analyzes

We obtained the climatic data from National Institute of Meteorology (INMET) from remote access via the site www.inmet.org.br. The climatic data are referred to the weather station of São Carlos, located 750 m far from the study area (21º 96'S; 47º 86' W; 856 m a.s.l.). We collected monthly data concerning mean air temperature (°C), relative air humidity (%) and the total rainfall (mm) from 1961 to 2015. The climate data in INMET database was available per month. Monthly

data was given by mean values of daily measures for air temperature and relative air humidity. The monthly value for rainfall was the summation of daily rainfall measures. We calculated the annual value of the mean air temperature and the total rainfall for each year from 1961 to 2015 giving the annual historical mean. We calculated monthly rainfall, mean air temperature, and relativity air humidity to the same period (1961 to 2015). We used the data about temperature and rainfall to plot three climatic diagram of Walter and Lieth (1967), one for historical data and the others for 2013 and 2014. As a rule, in the climatic diagram of Walter and Lieth, the hottest months occupied the central position. Although, to attempt our study aim of compare two discrete years (2013 and 2014), we adapted the climatic diagrams following the chronological sequence of months of the year.

Biomass allocation variables

We choose three tree species from each functional group, DE, SD and EV (Table 1). We selected these nine species since they presented two flowering events, 2013 and 2014, with a suitable number of individuals. We collected data of dry mass of flower, leaf and shoot axe (stalk) during two years, 2013 and 2014 (Table 1). For every year, we sampled five adult individuals per species, randomly chosen among individuals with flower buds. We sampled five shoots per individual and monitored their development three times a week. We collected flowers as soon as the flower buds bloom and the corresponding leaves and stalks after the whole growth season on each individual. Flowers, stalks, and leaves were dried in a stove under 60ºC until constant weight and the dry mass measured with an analytical balance (Mettler AE260 DeltaRange, Switzerland).

We compared the biomass allocation in flowers, leaves, and stalk using the absolute and proportional values per species and phenological group (DE, SD, and EV). Thereby, we calculated six variables per shoot. We calculated flower (FB), leaf (LB) and stalk (SB) biomass by their corresponding dry mass on every sampled shoot. We calculated the flower (FBP), leaf (LBP) and stalk (SBP) biomass proportion by the corresponding dry mass compartment divided by the total

marked shoot dry mass. Therefore, the total dry mass used for calculating FBP, LBP and SBP was the summation of dry masses of the stalk, leaves and flowers in each corresponding shoot sampled.

Statistical analyzes

Once data of most variables did not show normal distribution, we carried out the non-parametric analyzes of variance Kruskal-Wallis test (Zar 1999) to test significant differences at $p<0.10$ in biomass allocation in shoot compartments in both flowering periods. The statistical tests were carried out by software Mystat 12 (Washington, USA, 2007).

We evaluated differences in modulation of biomass allocation by analyzing the changes in global network connectance (Cg) among shoot compartments between the years 2013-2014. The network connectance analyses (Amzallag 2010) are largely applied in vegetative ecophysiological researches (Prado et al. 2004, Souza et al. 2005, Camargo Bortolin et al. 2008, Souza et al. 2009c). To define connectance, we specified a collection of paired variables of interest in the network. The following relationships compose the biomass allocation network: SB-LB, SB-FB, LB-SF. The Pearson correlation coefficient (r) obtained for each paired variable in biomass allocation network was used to determine the strength of connections between variables. Afterward, r-values were normalized by z-transformation, becoming z-values, and Cg obtained as the average of z-values (Amzallag 2010): $z = 0.5 \ln[(1+|r|) / (1-|r|)]$. We considered modulation as the change in the mean strength of connections among network elements, which was measured by Cg values (Amzallag 2010).

Results

The historical period of 54 years showed 1500±319 mm and 20.5±0.6 °C as mean values of rainfall and air temperature, respectively (Figure 1). These values were similar to those found in an area with equivalent altitude (912 m a.s.l.) in a core region of Cerrado domain, in Formosa County,

Goiás state, Brasil (15º 54' S and 47º 33' W). In Formosa, the mean historical data of rainfall and temperature, respectively, are 1719 mm and 20.9 °C (Gottsberger and Silberbauer-Gottaberger 2006). On the other hand, considering the historical data, the coefficient of variance of rainfall was significant (21%). In fact, there was high annual variation of total rainfall with a peak in 1983 (2437 mm) and lowest value in 1979 (788 mm), Figure 1. Therefore, the Cerrado community in São Carlos County was naturally exposed to water shortage in a historical data series. It was brought about in 1963, 1979, 1988, 2008 and 2014 when the total rainfall decreased more than 21% about the average and was bellow the confidence interval, showing 883, 788, 937, 1074 and 1097 mm, in that order (Figure 1).

Comparing rainfall by season, all months in summer of 2014 showed lower rainfall values than the historical or 2013 datasets (Figure 2). Only three months (September, November and December) presented greater values of total rainfall. Two months in Spring 2014, November and December, concentrated 44% of total annual rainfall. The total annual rainfall in 2013 and 2015 (1540 and 1369 mm, respectively) did not differ from historical data being within the confidence interval (Figure 1). Besides, the 2013 rainfall was well distributed along the year usually following the monthly rainfall historical data (Figure 2). Only two months (May and Octuber) in 2013 presented higher values of rainfall, and one month (December) showed lower rainfall rate. This last data indicated that the driest of 2014 began in December of 2013.

Concerning mean air temperature, all months in 2014, except July, presented high values compared to the historical. In 2013, three months (May, June, and November) presented greater and three months (April, August, and October) presented lower values of mean air temperature than historical data (Figure 3). The mean air temperature in 2013 and 2014 were 20.7 and 21.7 °C, respectively, 0.2 °C and 1.2 °C above the corresponding temperature historical data, in that order. The mean air temperature in 2014 was upper the confidence interval of historical data (Figure 1).

Instead of rainfall, the mean value of air temperature in 2015 (21.6 °C) did not return toward to temperature historical data (Figures 1).

The mean air relativity humidity in 2014 stayed below the historical data during all months of Summer, one in winter (August) and one in spring (October) (Figure 3). In the other months, the values were similar the historical data. The historical and 2013 data were similar; the greater discrepancy occurred in June and July 2013, which were upper the historical, and in December, which was lower (Figure 3).

The Walter-Lieth climatic diagram for São Carlos county for the period of 1961-2015 (Figure 4A) showed the typical precipitation pattern described for Cerrado region, with the wet season taking place during spring and summer (October-March) (Prado et al. 2004, Monteiro and Prado 2006). Comparing the illustrative figure about rainy distribution in 2013 and 2014 (Figure 4B), the wet season of October 2013 to March 2014 was anomaly, with low rainfall from December 2013 to February 2014. Additionally, during February 2014 the region experimented an untypical driest period. Another anomaly perceived during the study period was a increase in driest period in the winter 2014 (Figure 4B). Two months, June and August 2014, showed lower rainfall rate than expected for these months.

The flowering period showed differences in four of nine studied species in 2014 due to climate alterations. *Caryocar brasiliense* (DE), *Miconia albicans* (EV) and *Myrcia bella* (EV) delayed by 1-2 months the beginning of the flowering period (Table 1). *C. brasiliense* and *M. bella* reduced the period of flowering duration (Table 1). On the other hand, *Eriotheca gracilipes* presented an increased in flowering duration in 2014 (Table 1).

With the exception of *Miconia ligustroides* (EV), all studied species showed significant changes in biomass of shoot compartments in 2014 (Table 2). Three species - *C. brasiliensis* (DE), *M. albicans* (EV) and *M. bella* (EV) - reduced the allocation of biomass in flowers, leaves, and stalks. Two species – *Anadenathera falcata* (DE) and *Tibouchina stenocarpa* (SD) – allocated less

biomass in flowers and stalks. The other three species, *Guaripa graciliflora* (DE) reduced biomass in stalks and *Casearia sylvestris* (SD) in flowers. Contranstly, *E. gracilipes* (SD) increased biomass allocated in leaves (Table 2).

All DE species showed reduction stalk biomass proportion in 2014 (Table 2). *A. falcata* showed an increase in the biomass proportion in leaves and flowers. *C. brasiliensis* kept the same proportion of biomass allocated in flowers and leaves (Table 2). About SD species, *C. sylvestris* and *T. stenocarpa* present lower biomass proportion in flowers and higher in leaves in 2014 than in 2013 (Table 2). Conversely, about biomass in stalks, these two species had opposite behavior, *C. sylvestris* increased stalks biomass proportion, while *T. stenocarpa* decreased (Table 2). *E. gracilipes* just showed a raise in biomass proportion allocated in leaves (Table 2). Lastly, among EV species, *M. albicans* and *M. bella* presented stalk biomass proportion smaller in 2013 than in 2014 (Table 2). *M. bella* showed a decrease in biomass proportion in leaves and an increase in flowers (Table 2). *M. ligustroides* not differed between the both years.

The three functional groups showed statistical differences in biomass allocation in 2014 when compared to 2013 (Figure 5-7). From 2013 to 2014 DE and EV species showed significant reduction of total shoot biomass (Figure 5) without alteration in the ratio of autotrophic per heterotrophic shoot biomass (Figure 6). Contrastingly, SD species did not change the total shoot biomass (Figure 5) and increased significantly the biomass allocated in autotrophic tissues from 2013 to 2014 (Figure 6).

In DE, SD and EV species the mean value of flower biomass on shoot reduced significantly from 2013 to 2014 by 32, 24 and 29%, respectively (Figure 7). SD species presented the lowest decreasing of flower biomass and contrasting shoot biomass partitioning from 2013 to 2014. While the leaf biomass diminished by around 25% in DE and EV species in 2014 the SD species increased foliage biomass by 17% (Figure 7). The mean value of stalk biomass in shoots was significantly lower in 2014 only in DE and EV species. In 2014, while the FBP decreased and LBP enhanced in

SD, there were no significant differences in DE and EV species (Figure 7). The absence of significant difference in SBP in only one group confirmed the contrasting behavior of biomass partitioning in shoots of SD species (Figure 7). The strength of connection (Cg) considering the biomass partitioning among shoot compartments was lower in SD species in 2013 and 2014, and similar in DE and EV (Table 3). Moreover, only SD species decreased the mean value of Cg from 2013 to 2014 (Table 3).

Discussion

The tendency of increasing annual mean air temperature from 2005-2015 and the intense drought during summer and winter 2014 in São Carlos (Figure 1) agrees with the prediction of warming temperatures caused by rising of greenhouse gases. The rising of the concentration of greenhouse gases, like CO_2, may induce a scenario of warming temperatures, increasing the incidence of fires events and extreme droughts in the Cerrado region (Franco et al. 2014) The simulation of rising air temperature and decreasing rainfall in Cerrado and forest ecosystems showed a reduction in tree cover and increasing frequency of fire events (Hirota et al. 2011). Indeed, the Cerrado of São Carlos experienced both high mean air temperature and an intense drought in 2014 (Figures 1-4). Despite no fire event had been observed in the study area during 2014, the low rainfall and air relative humidity leads to an accumulation of dry biomass, which associates to high temperatures makes the area more vulnerable to fires events (Hirota et al. 2011).

On the other hand, the climatic alterations experienced in Brazilian Cerrado during 2014 could be a consequence of a natural cycle of the Pacific Ocean temperature, called Pacific Decadal Oscillation (PDO). PDO occurs in the Pacific Ocean during cyclic periods spending 20-30 years (Mantua et al. 1997). During the ‘cold’ or ‘negative’ phase the east Pacific becomes cooler and part of western Pacific Ocean warms. The opposite occurs during the ‘warm’ or ‘positive’ phase (Mantua et al. 1997). The last cold phase occurred in the period of 1947-1976, and the last warm

phase in 1977-1998 (Molion 2005). The PDO entered in a new cold phase in 1999, in which it must remain until about 2025 (Molion 2005). The PDO cold phase correlates with an increase in the frequency of La Niña events and intensity and decrease of El Niño frequency events (Andreolli and Kayano 2005). In the last PDO cold phase (1947-1976), the peak of cooling occurred around the beginning of the 60s when low rainfall took place during summer in Brazilian center-south region in 1963 (Figure 1). After that, annual rainfall values returned to normal in the following years (Figure 1). As PDO entered into a cold phase in 1999, 2014 match with the peak of PDO (Molion 2005). Therefore, the low precipitation observed during 2014 may be a consequence of a periodic oscillation in Ocean Pacific temperatures. The 2015 rainfall returned to normal conditions in São Carlos (1369 mm, Figure 1). Independently of climatic causes behind 2014 drought, the changes in shoot biomass allocation corroborate the hypothesis that the occurrence of climate alterations affects the ongoing biomass allocation in cerrado trees (Table 2).

The decreasing of biomass investment in flowers may be a way to avoid overspending with reproduction during the current stress period (summer and winter in 2014) and in the next growing season (spring 2014). Reproductive tissues as flowers demand right away high investment and commit reserves to seeds and future fruits. Decreasing sexual reproduction was a strategy to overcome the 2014 climate perturbation in studied functional groups. Indeed, in plants with sexual reproduction, there is a trade-off at physiological level for allocating resources into vegetative or reproduction growth (Williams 1966, Obeso 2002). The reduction in sexual reproduction could be crucial for surviving under continuous or recurrent climate alterations.

Even with similar behavior about biomass allocation in flowers, the biomass partitioning in shoot compartments and the total biomass allocated per shoot were not equivalent among DE, SD and EV species in 2014. These differences were a consequence of various plant strategies in each functional group (Chapter 2), resulting in different shoot response to climate alterations. Although the contrasting plant strategies of DE and EV to overcome the winter water shortage (Chapter 2),

both groups showed comparable shoot response facing climatic alterations in 2014. DE and EV diminished the biomass allocation in all shoot compartments (Figures 5 and 7) keeping proportionally the same biomass allocation into flowers and leaves between studied years at the expenses of low investment into stalks in 2014 (Figure 7). Regardless of the similar response in DE and EV, the mechanism behind it is fundamentally different.

DE species present flowers, leaves and stalks preformed in buds that expand synchronously in a leaf flush at the end of the dry season, around August and September (Souza et al. 2009a, Table 1). As new shoot compartments expand before the heavy rains, DE needs to employ their reserves (Luxmoore 1991, Koslowski and Pallardy 1996, Larcher 2003). Therefore, the growing of shoot compartments is competitive processes for reserves (Chapter 2). The reserves formation in cerrado DE species takes place during the rainy season, between October and March (Prado et al. 2004). December 2013, January and February 2014 presented low values of rainfall (Figures 2) compromising the formation of water and carbohydrates reserves for unfolding shoots at the end of next winter. Accordingly, even the rainfall above the mean value during September of 2014 (Figure 2), the DE decreased biomass investment in shoot compartments, since was not possible to use the ongoing resources for buds already formed and expanded.

On the other hand, EV species use current resources for stalks, leaves and flowers formation in a new production of shoots. It occurs in a continuous growing along the year with intense activity during the rainy season (Prado et al. 2004). The period of low rainfall, especially in summer 2013-2014 and in winter 2014 included the growing season or flowering period for EV studied species (Figure 2 and Table 1). As predicted by our hypothesis, the low water availability in 2014 affected the ongoing assimilated carbon for allocating in shoot organs decreasing the total biomass allocated in shoots in EV species (Figures 5 and 7). However, for maintaining the same proportion of biomass in leaves and flowers DE and EV species invested less in stalks (Figure 7). Prioritizing foliage and flowers EV species assure photosynthetic capacity and sexual reproduction in the next growing

season, constituting their resilience under the 2014 water stress (Souza and Lüttge 2015). The plasticity in the proportion of allocated biomass in shoot compartments gave to DE and EV a certain degree of stability (Souza and Lüttge 2015). However, comparing to SD species, DE and EV presented a discreet modulation of the proportion of biomass allocated among shoot organs in response to environmental disturbance.

The behavior of SD shoots under climate alterations in 2014 (Tables 2-3, Figures 5-7) showed unique characteristics as found previously by Borges and Prado (2014) and in Chapter 2. SD presented plasticity in modulating the biomass allocation from heterotrophic to autotrophic tissues (Figure 6) and specifically from flowers to leaves (Figure 7). Also, SD species showed high stability in total biomass (Figure 5). The low Cg in the network of shoots biomass compartments (Table 3) gave more freedom and autonomy to SD to modulate the biomass allocation among shoots compartments. It corroborates the hypothesis that SD will be the group more plastic and stable under environment perturbations.

Under changing environmental conditions, the system can assume a new state of organization to return to the previous state after the cessation of external disturbance (Souza and Lüttge 2015). Therefore, under environmental perturbation, suppress or decreasing reproduction capacity is a way to redirect resources to growth, in particular to tissues that will increase the survival capacity in future after disturbance. As depicted before, the biomass allocation in flowers dropped in all functional groups (Figures 7). On the other hand, increasing investment in foliage under water stress demands a high degree of autonomy for assuring the photosynthetic capacity in the next growing season. Indeed, SD species was the unique group that increased foliage biomass under 2014 water shortage (Figure 7).

Furthermore, the absence of significant variation in biomass allocated in stalks (Table 2 and Figure 7) reinforced the high stability in SD under environmental perturbation. Stalks are the axis that sustains all crown appendages such as leaves, flowers, fruits, buds, and the apical meristem.

Maintain the investment in stalks proportionally ensure at least in part the aerial space filling. Stalks guarantee the support of the development of vital organs of the shoot and keep crown growing. Therefore, the maintenance of stalk biomass proportion between years indicated that SD species were able to keep the potential of crown structures for growing, reproduction, resource acquisition as light and aerial space filling.

There is a close correlation between the stability of a system and the plasticity of its responses as we found in SD species (Souza and Lüttge 2015). These authors proposed a quadruped-scheme of plasticity, diversity, complexity and stability. According to this scheme, complexity is close related to diversity, and both support the plasticity. Stability, in turn, is a consequence of complexity, diversity and plasticity (Souza and Lüttge 2015). In fact, SD species presented a diversity of traits, which are the combination of features of DE and EV (Souza et al. 2009a, b, 2011, Borges and Prado 2014) given to the group an intermediate distribution between DE and EV (Chapter 2). The complexity of SD species was demonstrated in high global connectance (Cg) of crown traits network (Chapter 2) and low Cg among biomass allocation in shoot compartments (Table 3). The diversity of characteristics and complexity in Cg support the present results of plasticity in SD. This group was especially able to modulate biomass distribution among crown compartments (Figures 5-7) and decreased Cg under 2014 water stress to do that (Table 3). On the other hand, the presence of two flowering peaks in SD species (Borges and Prado 2014) demonstrates their high plasticity in phenology of reproductive parts. The combination of diversity of traits, high Cg of crown traits networks and high plasticity is responsible for high stability in SD species. High stability was demonstrated here by the maintenance of following events in 2014: 1 - total biomass allocation between years (Figure 5), 2 – stalk biomass proportion (Figure 7), and 3 - unchanged flowering beginning and duration (Table 1).

The present study showed DE, SD and EV species exhibited plastic features that allow resilient response to environmental stress caused by a deficit in rainfall. Though, as previously

assumed in our hypotheses, SD appears as a more stable group and, consequently, the group of species probably more able to survive and remain in a Cerrado scenario affected by climatic changes. The response of DE and EV provides enough resilience to these species if the climatic alteration happens punctually. Thus, after the stress period, DE and EV species may recover to the previous state. In a scenario of more recurrent climatic alteration, DE and EV could not be viable, since the total biomass allocated in shoots will be significantly affected. By another side, the SD strategies seem to allow the persistence of the species in a scenario of recurrent climatic alterations, since they presented a high plasticity and stability in shoot biomass allocation. This plasticity can favor the biomass allocation in crown organs that are essential to individual survival, as leaves. Therefore, all groups have the ability to overcome a climatic change if it was sporadic and punctual, like as a PDO event. Nonetheless, in a scenario of continuous and permanent climatic alterations, SD appears to be the group with more chances to respond successfully to environmental alteration and remaining in Cerrado area.

Conclusion

Our study indicated seasonal climate alterations affected flowering, and production and partitioning of biomass in shoots of Cerrado trees. Shoots of DE and EV species kept the same biomass investment in flowers and leaves at the expense of lower investment in stalks. On the other hand, SD demonstrated plasticity changing the biomass allocation from heterotrophic (flowers) to autotrophic (leaves). SD species displayed stability in maintaining the biomass allocated into stalks and the total biomass in shoots. Considering the biomass partitioning among shoot compartments, low values of global connectance (Cg) gave plasticity to SD species under the water stress in 2014. The combination of low Cg with two sources of carbon and nutrients (ongoing and stored reserves) provided stability in total biomass of shoots in SD species. High shoot plasticity and stability make SD the group most able to adapt flowering and biomass partitioning under climate change. Our

study confirms SD species as a particular functional group with an important role in plant communities of Cerrado.

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Table 3. Flowering periods of nine Cerrado tree species presented in this work. DE = deciduous, SD = semideciduous, EV = evergreen. Black bars indicate flowering periods of tree species.

Species	**Leaf deciduouness**	**Flowering periods**
		2012	2013	2014
		N D	J F M A M J J A S O N D	J F M A M J J A S O N D
Anadenanthera falcata (Benth.) Speg.	DE			
Guaripa graciliflora	DE			
Caryocar brasiliense Cambess..	DE			
Casearia sylvestris Sw.	SD			
Eriotheca gracilipes (K. Schum) A. Robyns	SD			
Tibouchina stenocarpa (DC.) Cogn.	SD			
Miconia albicans (Sw.) Triana	EV			
Miconia ligustroides (DC.) Naudin	EV			
Myrcia bella Cambess.	EV			

Table 4. Average values ± standard deviation of biomass (g) allocated in flowers (FB), leaves (LB) and stalk (SB) of shoots in 2013 and 2014 in nine woody species of Cerrado vegetation. FBP = flower biomass proportion; LBP = leaf biomass proportion; SBP = stalk biomass proportion. DE = deciduous; SD = semideciduous; EV = evergreen. In same species, different letters after standard deviation indicate significant difference ($P < 0.1$, Kruskal-Wallis) and the absence of letter indicates no difference between years.

Species	Leaf deciduousness	FB		FBP		LB		LBP		SB		SBP	
		2013	2014	2013	2014	2013	2014	2013	2014	2013	2014	2013	2014
A. falcata	DE	0.48 ±0.21a	0.30 ±0.18b	0.07 ±0.04a	0.05 ±0.04b	5.84 ±2.02	5.76 ±3.40	0.83 ±0.05a	0.85 ±0.12b	0.69 ±0.37a	0.43 ±0.34b	0.10 ±0.04a	0.06 ±0.02b
G. graciliflora	DE	0.54 ±0.46	0.38 ±0.25	0.19 ±0.13	0.19 ±0.11	2.11 ±1.45	1.62 ±0.97	0.67 ±0.14	0.72 ±0.13	0.40 ±0.23a	0.17 ±0.07b	0.14 ±0.06a	0.09 ±0.05b
C. brasiliense	DE	6.40 ±2.10a	4.26 ±1.35b	0.27 ±0.08	0.29 ±0.07	15.3 ±8.93a	9.21 ±3.89b	0.58 ±0.09	0.59 ±0.08	4.05 ±2.24a	1.79 ±0.68b	0.16 ±0.05a	0.12 ±0.03b
C. sylvestris	SD	0.40 ±0.03a	0.25 ±0.01b	0.20 ±0.06a	0.13 ±0.06b	1.48 ±0.51	1.53 ±0.77	0.67 ±0.05a	0.71 ±0.08b	0.30 ±0.12	0.35 ±0.16	0.13 ±0.02a	0.17 ±0.03b
E. gracilipes	SD	1.36 ±0.63	1.16 ±0.56	0.26 ±0.13	0.19 ±0.09	3.63 ±1.72a	4.72 ±1.96b	0.63 ±0.12a	0.70 ±0.09b	0.67 ±0.44	0.90 ±0.82	0.11 ±0.04	0.12 ±0.06
T. stenocarpa	SD	2.40±0.90a	1.78 ±0.63b	0.33 ±0.09a	0.28 ±0.09b	3.58 ±1.73	3.80 ±1.17	0.47 ±0.10a	0.58 ±0.08b	1.44 ±0.56a	0.88 ±0.17b	0.20 ±0.03a	0.13 ±0.04b
M. albicans	EV	1.12 ±0.60a	0.71 ±0.17b	0.21±0.09	0.19 ±0.07	3.66 ±1.62a	2.77 ±0.95b	0.66 ±0.09	0.71 ±0.07	0.76 ±0.40a	0.41 ±0.20b	0.13 ±0.04a	0.10 ±0.03b
M. ligustroides	EV	0.56 ±0.43	0.51 ±0.16	0.23 ±0.12	0.24 ±0.09	1.39 ±0.65	1.41 ±0.64	0.60 ±0.12	0.61 ±0.09	0.42 ±0.27	0.33 ±0.15	0.17 ±0.02	0.15 ±0.03
M. bella	EV	0.28 ±0.18a	0.19 ±0.09b	0.29 ±0.12a	0.43 ±0.13b	0.51 ±0.19a	0.23 ±0.13b	0.57 ±0.11a	0.46 ±0.13b	0.13 ±0.07a	0.05 ±0.03b	0.14 ±0.04a	0.12 ±0.04b

Table 5. Normalized values of Pearson's correlation coefficient (z-values) for paired traits of biomass allocated in shoots compartments used to calculate the global connectance in 2013 and 2014 in deciduous (DE), semideciduous (SD) and evergreen (EV) species. Cg = Global connectance according to Amzallag (2001). SB = stalk biomass (g), LB = leaf biomass (g), FB = flower biomass (g).

	2013			2014		
	DE	SD	EV	DE	SD	EV
SB-LB	1.16	0.95	1.29	1.16	1.02	1.38
SB-FB	1.19	0.97	0.83	1.29	0.41	0.97
LB-FB	0.83	0.51	0.93	0.76	0.50	1.00
Cg	1.06	0.81	1.02	1.07	0.64	1.11

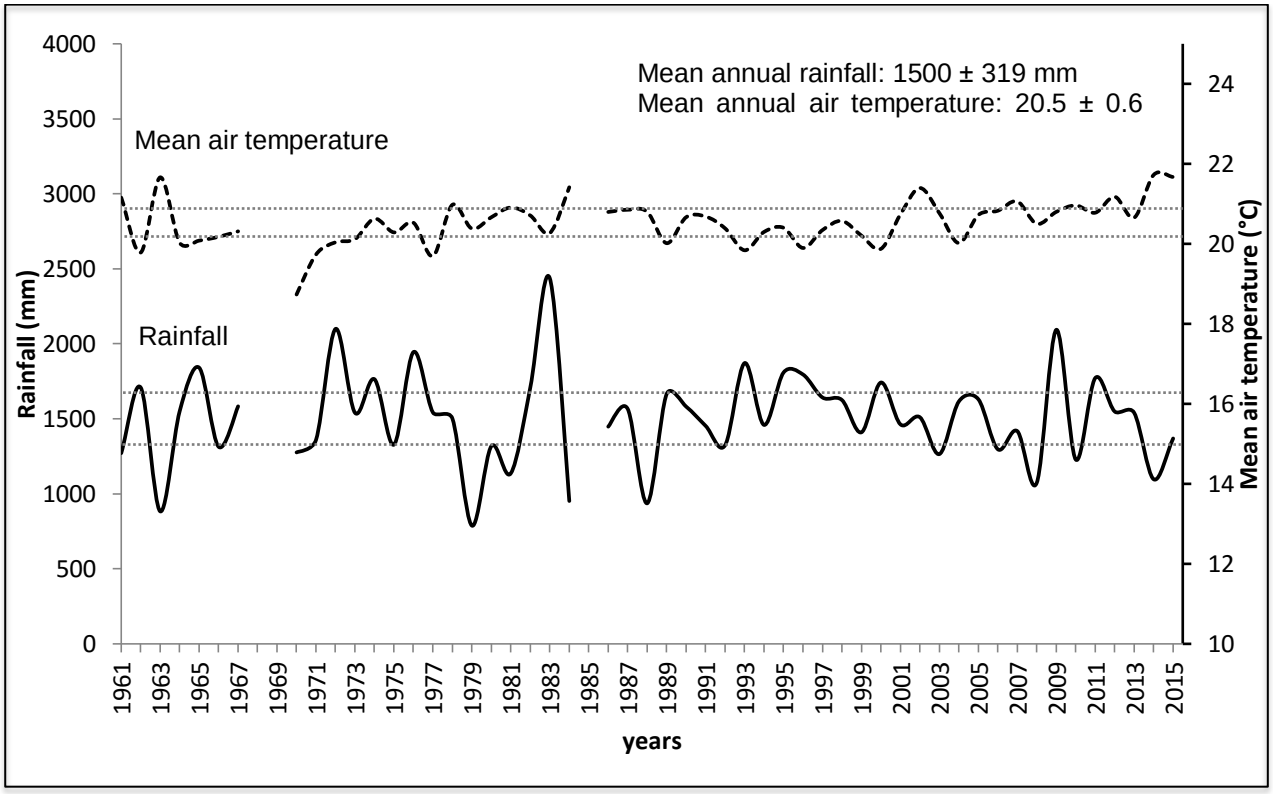

Figure 4. Mean annual rainfall and air temperature from 1961 to 2015 of São Carlos County, State of São Paulo, Brazil. Data recorded in the weather station of São Carlos (21º 96'S; 47º 86' W; 856 m a.s.l.) 750m far from the study area. Data obtained from Brazilian National Institute of Meteorology (INMET). The missing data are those for 1968, 1969 and 1985. Continuous line: rainfall (mm); Dashed line: mean air temperature (°C). Dotted lines delimit the confidence intervals of rainfall (1500 ± 144 mm) and mean air temperature (20.5 ± 0.26 ºC).

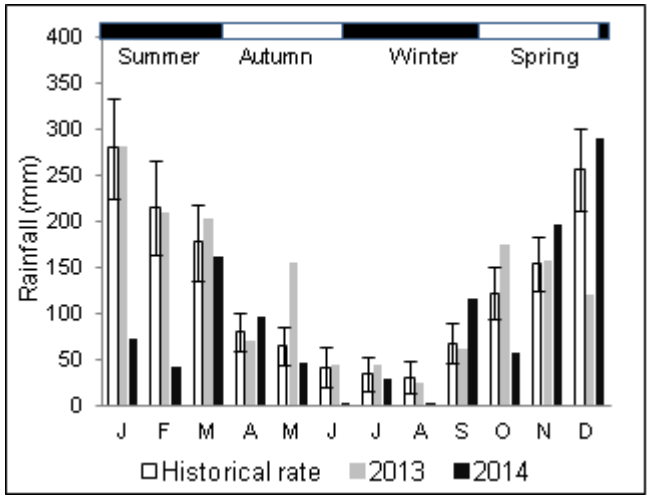

Figure 2. Total monthly rainfall from 1961 to 2015 - historical mean data with confidence intervals – (white bars), 2013 (gray bars), and 2014 (black bars).

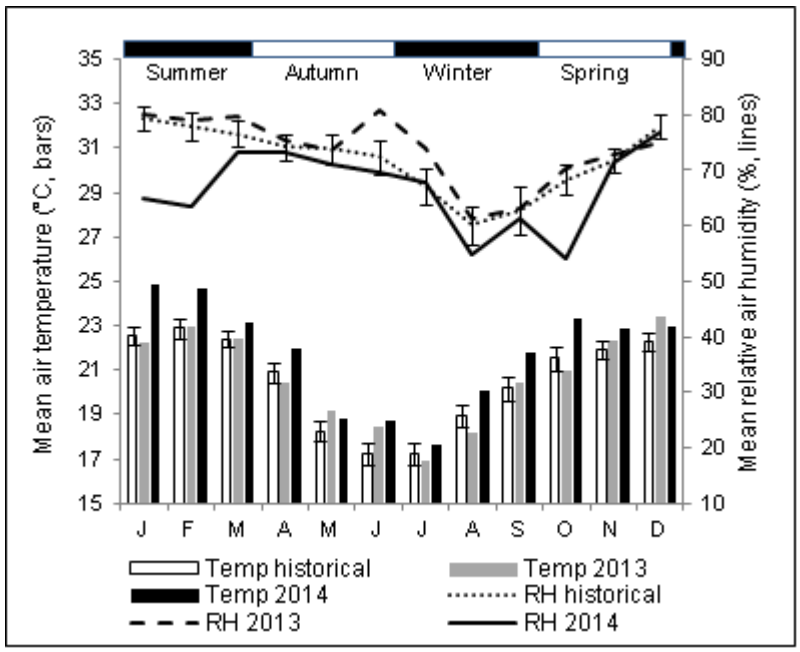

Figure 3. Average monthly air temperature and air relative humidity in 2013 and 2014. White bars and dotted line (with confidence intervals) = 1961-2015; gray bars and dashed line = 2013; Black bars and continuous line = 2014.

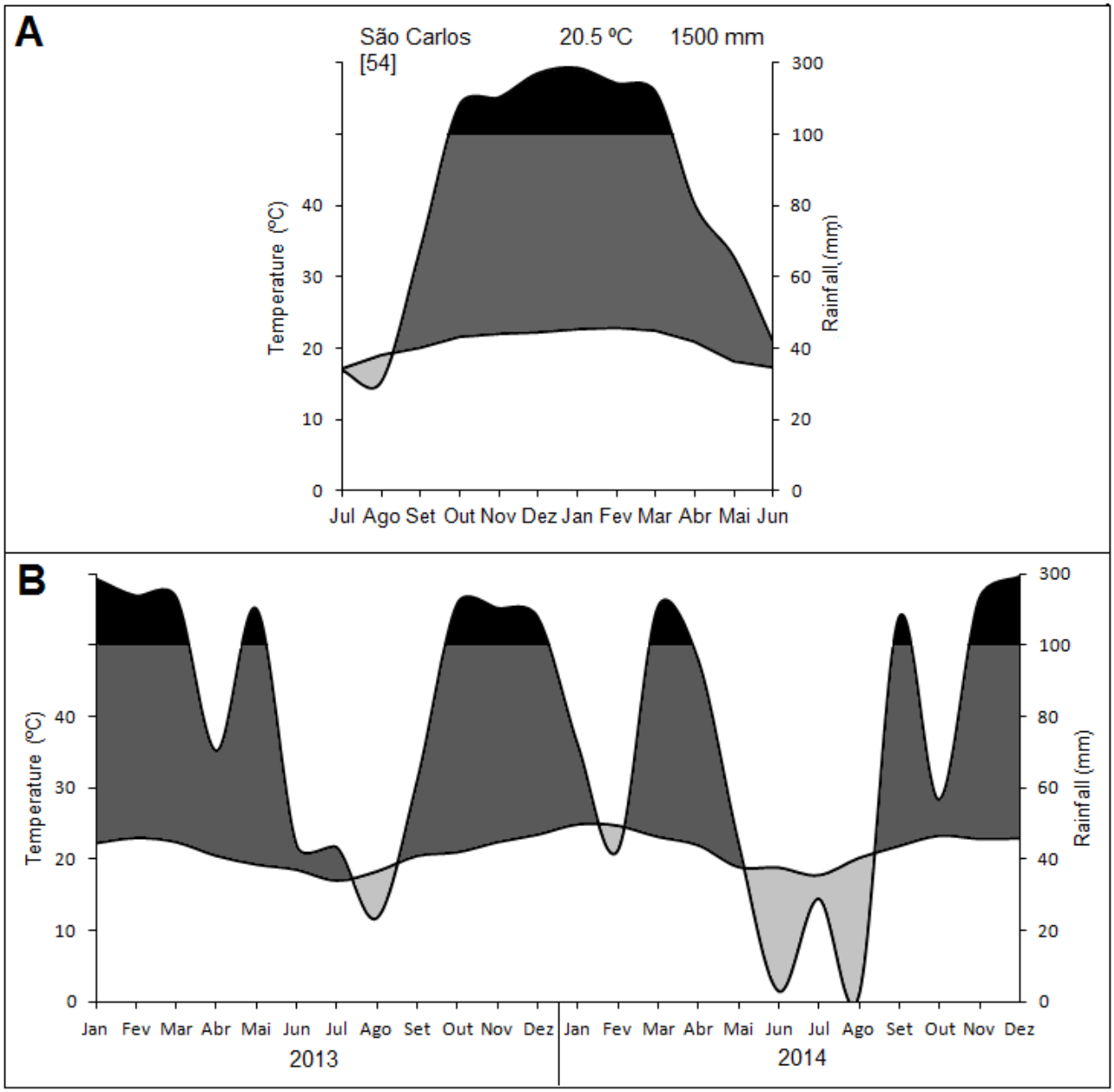

Figure 4. Diagram of Walter and Lieth of São Carlos county (856 m a.s.l.) from 1961 to 2015 (A), and illustrative figure of 2013 - 2014 period (B). Black area indicates wet periods, dark gray area indicates humid periods, and pale grey area indicates dry periods.

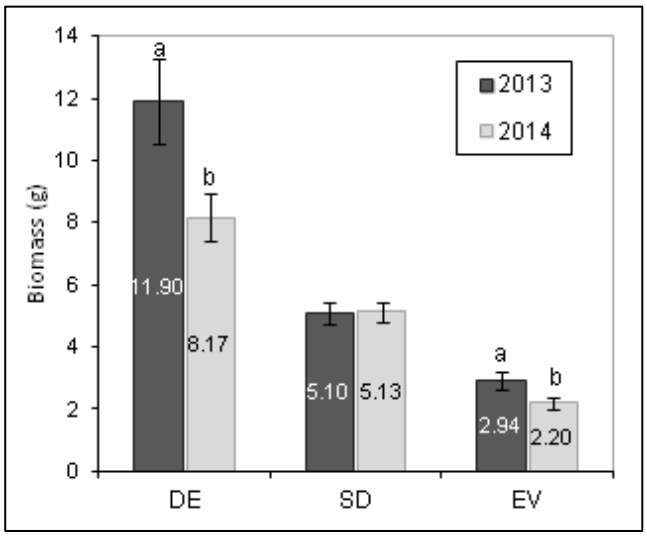

Figure 5. Total biomass (g) allocated in shoots in 2013 and 2014 in deciduous (DE), semideciduous (SD) and evergreen (EV) tree species. Different letters above columns indicate significant differences ($p < 0.1$, Kruskal-Wallis) between years.

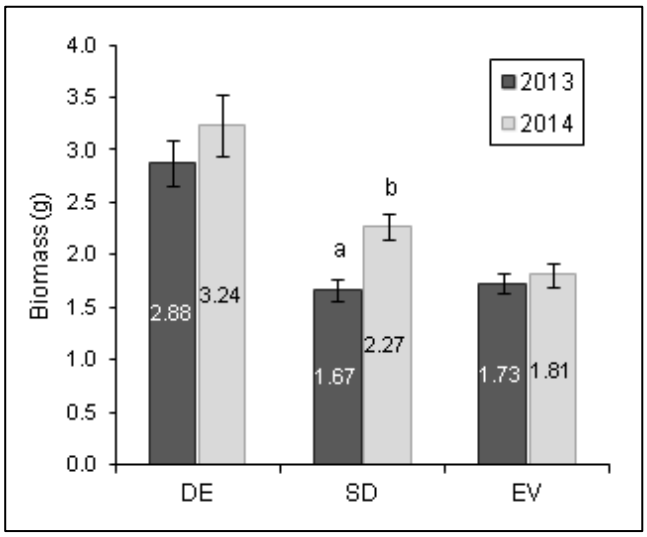

Figure 6. Biomass ratio (g) allocated in autotrophic (leaves) per heterotrophic (flowers + stalk) shoot structures in 2013 and 2014 in deciduous (DE), semideciduous (SD) and evergreen (EV) tree species. Different letters above columns indicate significant differences ($p < 0.1$, Kruskal-Wallis) between years.

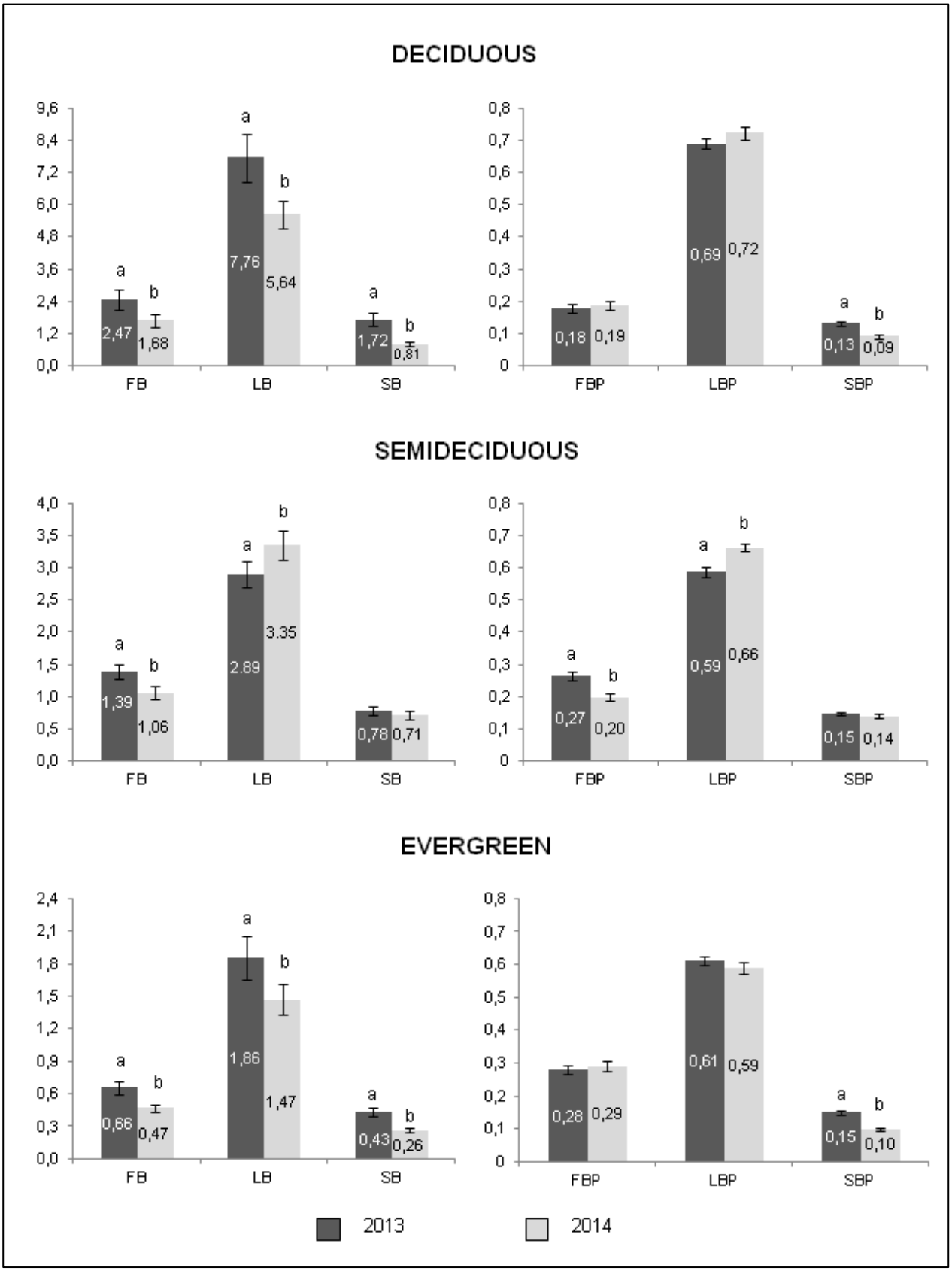

Figure 7. Biomass (g) allocated in flowers, leaves and stalk in shoots in functional groups of deciduous, semideciduous and evergreen tree species in Cerrado in 2013 and 2014. FB = flower biomass; LB = leaf biomass; SB = stalk biomass; FBP = flower biomass proportion; LBP = leaf biomass proportion; SBP = stalk biomass proportion. Different letters above columns indicate significant differences ($p < 0.1$, Kruskal-Wallis) between years in same compartment or in same biomass proportion.

CONSIDERAÇÕES FINAIS

Os estudos conduzidos nos três capítulos dessa Tese, na forma de manuscritos, nos permitiram caracterizar os grupos funcionais de árvores do Cerrado por meio de suas estruturas e funcionamentos em nível de organização da copa. Essas características mostraram inter-relações que definiram síndromes específicas em cada grupo. As características emergentes dessas inter-relações atribuem competências específicas em cada grupo funcional que permitem a superação das limitações naturais ao longo do ano. Essas competências formam conjuntos de estratégias adaptativas que caracterizam cada um dos grupos funcionais de árvores do Cerrado. A permanência da folhagem é apenas uma característica da população de folhas. Essa permanência específica em cada grupo se relaciona com vários outros atributos de porções autotróficas e heterotróficas da copa. Portanto, decíduas, semidecíduas e sempre verdes arbóreas do Cerrado apresentam várias outras características associadas à deciduidade foliar, como, por exemplo, o período de floração.

Nas espécies sempre verdes, os ramos ortotrópicos promovem o auto sombreamento de uma folhagem com menor área individual de folha e menor área transpiracional por ramo. Tanto a posição do ramo como a morfologia da folhagem evita a perda excessiva de água. A persistência da folhagem ao longo de todo o ano mantém constante a transpiração, o fluxo da seiva no xilema e a fonte de carboidratos por meio da fotossíntese corrente. O sombreamento ao longo dos ramos em combinação com o permanente fluxo de recursos via xilema e floema propiciam uma maior permanência da florada e constante produção de folhas e ramos ao longo do ano nas arbóreas sempre verdes do Cerrado. Por outro lado, a copa das espécies sempre verdes apresenta mais ramificações impondo maior resistência à ascensão da seiva via xilema por meio da inerente perda de carga em cada nó da ramificação. A manutenção da folhagem nas sempre verdes garante o movimento do fluxo no xilema e floema em uma copa mais ramificada, com maior número de ramos e nós. A dependência de carboidratos oriundos da fotossíntese corrente nas sempre verdes impactou de forma significativa o crescimento vegetativo e reprodutivo no ano com estresse hídrico

mais acentuado (2014). Apesar de reduzirem a biomassa total nos ramos sob estresse hídrico mais severo, as sempre verdes alocaram, proporcionalmente, mais biomassa em flores e folhas. Esse comportamento provavelmente tentou garantir a capacidade reprodutiva e fotossintética em período subsequente à estiagem de 2014.

As espécies decíduas necessariamente mobilizam as reservas para produção da nova folhagem no pico da estação seca quando apresentam a copa livre de folhas. Em plena estação seca, as folhas, ramos e flores crescem de maneira acelerada a partir de gemas com estruturas pré-formadas nas árvores decíduas do Cerrado. É intensa a competição entre os compartimentos do ramo por recursos estocados anteriormente na estação de crescimento. Essas estruturas do ramo são drenos que crescem de forma sincrônica (em pulso). Os ramos plagiotrópicos das decíduas expõem fortemente à atmosfera esses drenos, que competem por recursos estocados. A forte exposição nos ramos às condições atmosféricas e a intensa competição por recursos limitam o período de floração nas decíduas. O elevado potencial de transpiração, devido à exposição nos ramos plagiotrópicos da área foliar comparativamente maior, impõe a perda total da folhagem no auge da estação seca. As decíduas necessitam, ainda, recompor rapidamente a capacidade fotossintética da copa logo no início da estação chuvosa para reporem as reservas. A arquitetura de copa pouco ramificada, com poucos nós e ramos, propicia reduzida resistência à ascensão da seiva xilemática por perda de carga. Uma copa com menos nós e ramos e uma folhagem pré-formada em gemas facilita o desdobramento sincrônico de folhas no final da estação seca nas árvores decíduas do Cerrado. Para essas espécies, a recomposição das reservas de carboidratos depende, principalmente, da disponibilidade de água na estação de crescimento. O intenso decréscimo na precipitação durante a formação das reservas (verão de 2014) afetou o crescimento e a reprodução nos ramos das espécies decíduas. Como as sempre verdes, as decíduas investiram biomassa em maior proporção em flores e folhas durante o estresse hídrico de 2014 como estratégia de garantir a capacidade reprodutiva e fotossintética futura.

As espécies semidecíduas compartilham características com as decíduas e as sempre verdes, apresentando valores médios intermediários para vários atributos da copa. A combinação de características de decíduas e sempre verdes faz das semidecíduas um grupo único, com elevado grau de conectância entre os componentes da copa como um todo, possibilitando a coordenação do grau de permanência da folhagem em função da intensidade da estiagem de inverno no Cerrado. Por outro lado, as semidecíduas são as que apresentam o menor valor de conectância global para a alocação de biomassa entre os compartimentos do ramo alterando fortemente as proporções de alocação entre esses compartimentos em função da intensidade da estiagem. Ademais, as semidecíduas foi o único grupo que reduziu a conectância global para a alocação de biomassa com a intensificação do estresse hídrico em 2014. Os atributos intermediários das semidecíduas permitem tanto a obtenção de recursos correntes via fotossíntese, mantendo parcialmente a folhagem, quanto a utilização de recursos estocados nas reservas para a recomposição da folhagem. Essa combinação de características também resulta em uma distribuição da floração diferenciada ao longo do ano. Somente as semidecíduas apresentaram dois momentos com grande quantidade de espécies com flores (dois picos de floração) ao longo do ano. A combinação da diversidade de características fortemente conectados ao nível da copa, e da plasticidade em modular a alocação de biomassa entre os compartimentos do ramo são responsáveis por fazer das semidecíduas o grupo mais estável perante distúrbios ambientais, como as mudanças climáticas.

As diferentes estratégias adaptativas encontradas para as espécies arbóreas de cerrado nos permitem concluir a existência de ao menos três grupos funcionais. Isso porque as espécies semidecíduas apresentam respostas adaptativas exclusivas que permitem classificá-las como um grupo à parte de decíduas e sempre verdes. Porém, esses grupos funcionais estão em um gradiente funcional que coincide com o gradiente fenológico apresentado pelas espécies de cerrado. Portanto, a deciduidade foliar esta associada aos grupos funcionais, uma vez que, ela é um atributo de uma série de características de copa que caracterizam os diferentes grupos.