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PADRÕES FENOLÓGICOS E ATRIBUTOS REPRODUTIVOS DE ESPÉCIES LENHOSAS NO CERRADO DO ESTADO DO MARANHÃO, BRASIL

Dinnie Michelle Assunção Lacerda

São Luís - MA
2017

DINNIE MICHELLE ASSUNÇÃO LACERDA

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Tese apresentada ao Curso de Doutorado do Programa de Pós-Graduação em Biodiversidade e Biotecnologia da Rede BIONORTE, na Universidade Federal do Maranhão, como requisito parcial para a obtenção do Título de Doutor em Biodiversidade e Biotecnologia.

Orientador: Prof. Dr. EDUARDO BEZERRA DE ALMEIRA JÚNIOR

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Dedico este trabalho a minha filha, Alice.

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RESUMO

Estudos fenológicos em nível de comunidade em áreas com escassas informações podem contribuir para o entendimento mais abrangente acerca da dinâmica das comunidades vegetais, possibilitando o foco em grupos de espécies que podem trazer importantes avanços para linhas mais específicas de conhecimento sobre fenologia. Assim, o presente estudo teve como objetivo geral determinar o padrão fenológico de comunidades vegetais lenhosas em duas áreas de cerrado no Estado do Maranhão. As áreas de coleta, inseridas no cerrado *stricto sensu*, estão localizadas no município de Barreirinhas e no Parque Estadual de Mirador (PEM), Maranhão. Os dados referentes à produção e queda de folhas, floração e frutificação foram estimados mensalmente durante 24 meses, em indivíduos com circunferência do tronco ao nível do solo 10 cm. Foram marcados 1418 indivíduos, sendo 706 indivíduos em Barreirinhas, correspondendo a 43 espécies, e 712 no PEM, representados por 65 espécies. Os testes estatísticos utilizadas incluem análises circulares de Rayleigh, de Watson Williams, testes de diferenças de medianas (Mann-Whitney) e de comparações de distribuições (Teste G). O capítulo I (a ser submetido à revista Brazilian Journal of Botany) trata da caracterização e comparação das duas comunidades, cujos resultados mostram uma maior concentração dos eventos foliares de queda e dos eventos de produção (de folhas e flores) durante o período de seca para as duas áreas, podendo se estender até o período chuvoso (produção de folhas novas e frutificação). As síndromes de dispersão mostram estreita relação com as respostas encontradas para a frutificação, predominando a zoocoria nas duas áreas. O capítulo II (pulicado na revista Flora) avaliou cinco populações com ampla ocorrência em áreas de cerrado e presentes nas duas áreas, buscando investigar se as respostas nas populações diferem entre as áreas e se apresentam comportamento semelhante ao das comunidades em que estão inseridas, excluindo, assim, possíveis efeitos ligados às diferenças na composição de espécies entre as áreas. As respostas encontradas nos dois capítulos são semelhantes, com comunidades ou populações conespecíficas mostrando ajustes às variáveis locais, ligadas principalmente à temperatura e ao fotoperíodo, associadas à diferenças no período de ocorrência da seca em cada área. As fenofases ocorrem ou se intensificam antecipadamente no PEM, evidenciando os ajustes às condições climáticas locais e contribuindo com informações sobre a plasticidade das espécies submetidas a diferentes condições abióticas. O capitulo III (submetido à revista Acta Botanica Brasilica) avalia a relação entre a fenologia reprodutiva de espécies sempre verdes (SV) e decíduas (DEC) no PEM. Foram encontradas diferenças em atributos reprodutivos entre os grupos (SV e DEC) em relação à floração, indicando a ocorrência antecipada e maior duração dos eventos fenológicos nas SV em relação às DEC. Para a frutificação, as principais diferenças entre DEC e SV foram relacionadas à distribuição diferente dos percentuais de atividade entre os grupos e sua maior intensidade nas SV. Essas respostas refletem diferentes estratégias de uso da água por esses grupos. Portanto, este estudo fornece dados ecológicos antes inexistentes nessa região e pouco abordadas em área de cerrado, contribuindo para o entendimento das respostas fenológicas e suas associações com o clima.

Palavras-chave: Fenologia, Populações conespecíficas, Sazonalidade, Savana, Variações climáticas.

ABSTRACT

Phenological studies at the community level in areas with scarce information may contribute to a more comprehensive understanding of the dynamics of plant communities. Such studies also allow the focus on groups of species that can bring important advances to lines more specifics of knowledge regarding phenology. Thus, with the overall objective to determine the phenological pattern of woody plant communities in two cerrado areas in the State of Maranhão, it was conducted the present study. The collection areas, in cerrado *stricto sensu*, are located in the Barreirinhas and at Mirador State Park (MSP), Maranhão State. It were estimated visually the percentage data regarding leaf production, leaf fall, flowering and fruiting during 24 months, monthly, in individuals with trunk circumference at the soil level $\geq$10 cm. It was marked 1418 individuals, being 706 in Barreirinhas, beloging to 43 species, and 712 at MSP, represented by 65 species. Statistical tests used included Rayleigh and Watson Williams analyses, median differences (Mann-Whitney) and distributions (G-tests). The Chapter I (to be submitted to the Brazilian Journal of Botany) deals with the characterization and comparison of the two communities, whose results show a higher concentration of leaf fall events and production events (leaf and flower) during the dry season for both areas. At the beginning of the rainy season, the production of new leaves and fruiting, which increase since the end of the dry period, remain intense. The dispersion syndromes show a close relationship with the responses found for fruiting, predominating the zoocoria in both areas. The chapter II (accepted by Flora Journal) evaluates five populations with wide occurrence in cerrado areas, present in both areas, seeking to investigate whether responses at the populations differ between areas and show similar behavior to the communities in which they are inserted, thus excluding possible effects related to differences in species composition between areas. The responses found in the two chapters are similar, with conspecific communities or populations showing adjustments to local variables, mainly related to temperature and photoperiod, associated to differences in occurrence in the period of drought in each area. Phenophases occur or intensify earlier in the MSP, showing the adjustments to the local climatic conditions and contributing with information on the plasticity of the species in different abiotic conditions. The third article (submitted to the Acta Botanica Brasilica) evaluates the relationship between reproductive phenology of evergreen (EG) and deciduous (DEC) species in MSP. Were found differences in reproductive attributes between the EG and DEC groups in relation to flowering, indicating the early occurrence and longer duration of phenological events in EG in relation to DEC. For fruiting, the main differences between DEC and EG were related to the different distribution of activity percentage between the groups and their greater intensity in the EG. These responses reflect different strategies of water use by these groups. Therefore, this study provides ecological information previously non-existent in this region and little addressed in the cerrado area, contributing to the understanding of phenological responses and their associations with climate.

Key words: Phenology, Conspecific populations, Seasonality, Savanna, Climatic variations.

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dry season (SDS), Maranhão State, Brazil. LF=leaf fall; LFl=leaf flushing; Flw=flowering; S=start; P=peak; na= not available. F = circular statistical value; *p=probability value.*

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SUMÁRIO

1. INTRODUÇÃO GERAL

O cerrado é o segundo mais extenso ecossistema da América do Sul, com alto nível de endemismo e alta diversidade da flora (> 7.000 espécies), sendo caracterizado pela forte sazonalidade de chuvas, alta irradiância e temperaturas, e pela presença de fogo (FRANCO et al., 2014). As queimadas frequentes assumem um papel importante em moldar a fisionamia e influenciar na composição das espécies nessas áreas (MOREIRIA, 2000; SIMON & PENNINGTON, 2012; SILVA et al. 2013).

Como as demais savanas, é atribuída à sazonalidade climática a insfluência sobre os padrões de crescimento e reprodução das plantas, sendo o regime hídrico, temperatura e radiação solar (comprimento do dia e insolação) apontados como fatores determinantes da fenologia foliar e reprodutiva (LENZA & KLINK, 2006; PIRANI et al., 2009).

O domínio Cerrado é caracterizado por apresentar fitofisionomias e composição florística muito diversificada ao longo de sua área de ocorrência (RATTER et al., 2003; FELFILI et al., 2004; FONSECA & SILVA-JÚNIOR, 2004; LEMOS et al., 2013), o que, associado à sua ampla distribuição, submete suas espécies às variações no regime climático, e implica na determinação das respostas fenológicas existentes. Essa condição direciona os padrões de crescimento e reprodução de suas espécies vegetais, originando estratégias adaptativas que respondem às variações impostas pelo clima e pelo regime hídrico (OLIVEIRA, 2008). Fatores bióticos, relativos à interação com animais para a polinização e dispersão de sementes, são também considerados importantes na determinação dos padrões de floração e frutificação das plantas. Assim, fatores abióticos e bióticos conferem diferentes pressões seletivas, podendo ser classificados, respectivamente, como fatores proximais (que funcionam como "gatilho") e finais (que são selecionados para um determinado período) conectados aos eventos fenológicos (VAN SCHAIK et al., 1993).

Esses fatores são normalmente abordados em estudos fenológicos, que procuram esclarecer a sazonalidade dos fenômenos biológicos, contribuindo para a compreensão de importantes questões ecológicas e evolucionárias (FORREST & MILLER-RUSHING, 2010), sendo um atributo adaptativo chave para moldar a distribuição das espécies (CHUINE, 2010).

Os estudos fenológicos em comunidades no cerrado incluem diferentes linhas de abordagem, como a caracterização geral das áreas de estudo (PIRANI et al., 2009), comparação entre comunidade pertencentes a diferentes formações vegetais (SILVA et al., 2011; NEVES et al., 2017), comparações envolvendo diferentes estratos e síndromes de dispersão (BATALHA & MARTINS, 2004), e grupos baseados na fenologia foliar (LENZA & KLINK, 2006). Esses estudos favorecem também abordagens envolvendo espécies ou grupos de espécies com caraterísticas relevantes a serem avaliadas, como por exemplo, a avaliação em uma família com maior número de representantes (BULHÃO & FIGUEIREDO, 2002), gêneros que ocorrem em outras formações (ROSSATTO et al., 2009), populações conespecíficas (LACERDA et al., 2017), e espécies com diferente fenologia foliar (DALMOLIN et al., 2015).

Padrões com crescimento periódico e marcadamente sazonal têm sido verificados nas diferentes abordagens fenológicas em áreas de cerrado, determinando diretamente as estratégias reprodutivas e vegetativas das espécies (PIRANI et al., 2009; DALMOLIN et al., 2015; NEVES et al., 2017), influenciadas pelo regime hídrico, temperatura e fotoperíodo (SILVÉRIO & LENZA, 2010; SILVA et al., 2011; ROSSATTO, 2013; DALMOLIN et al., 2015). Assim, diferenças climáticas entre áreas são determinantes para definição dos padrões fenológicos predominantes (CAMARGO et al., 2011).

Dentre as variáveis que condicionam as respostas das espécies, a presença de um longo período seco no cerrado (de 4 a 7 meses) (INMET, 2017), impõem respostas adaptativas relacionadas à tolerância da seca (FRANCO et al., 2005; GOLDSTEIN et al., 2008), que geralmente diferem entre espécies decíduas e sempre verdes (SOUZA et al., 2009; BORGES & PRADO, 2014). Assim, além do clima, características adaptativas das espécies podem ampliar as possibilidades de respostas encontradas. Nesse contexto, as decíduas diferem das sempre verdes por possuírem estratégias relacionadas a evitar os efeitos da seca, limitando a atividade fisiológica o que resulta, por exemplo, na perda das folhas durante este período. Já as sempre verdes toleram a seca, desenvolvendo adaptações fisiológicas que maximizam o estoque de água e a atividade fotossintética, e mantêm reservas de carbono suficientes para permitir a sobrevivência (VICO et al., 2014; SOUZA et al., 2015).

Com base nas amplas possibilidades de investigações relacionadas acima, e na expectativa de ampliar as áreas com estudos fenológicos no cerrado e investigar a relação entre as características fenológicas e o clima, esta tese buscou de modo geral caracterizar a fenologia de duas comunidades do cerrado. Essas áreas, submetidas à diferenças quanto ao regime climático, estão situadas no estado do Maranhão, no município de Barreirinhas e no Parque Estadual de Mirador, ocupando uma região entre o clima úmido amazônico e o clima semi-árido, predominante na região Nordeste. Este estudo possibilitou a caraterização geral e a comparação das respostas encontradas entre essas comunidades (Capítulo I), comparações entre as respostas de populações comuns às duas áreas (Capítulo II) e de grupos de espécies com fenologia foliar contrastante (sempre verdes e decíduas) em uma das áreas (Capítulo III), permitindo, portanto, a compreensão de importantes funções ecológicas que regem o comportamento de comunidades e espécies em áreas de cerrado.

2. REFERENCIAL TEÓRICO

2.1 Importância dos estudos fenológicos

As observações do período de ocorrência dos eventos vegetativos e reprodutivos das plantas são historicamente adotadas nas sociedades humanas como indicadores sazonais, existindo estudos científicos direcionados para a fenologia que datam do século XVIII (NORD & LINCH, 2009). O período em que os eventos fenológicos ocorrem é crucial para determinar a viabilidade das espécies e como alterações em seu ritmo estão afetando a abujndância e distribuição das espécies (CHUINE, 2010; MILLER-RUSHING et al., 2010; BUITENWERF et al., 2015).

Nos últimos anos, os estudos fenológicos vêm adquirindo crescente importância devido às respostas que fornecem frente às alterações climáticas, considerando a sensibilidade das plantas diante dos fatores abióticos (CLELAND et al., 2007; CRIMMINS et al., 2009; PRIMACK et al., 2009; MILLER-RUSHING et al., 2010; DIEZ et al., 2012; RICHARDSON et al., 2013). Vários estudos envolvendo espécies tropicais mostram que os eventos fenológicos são influenciados por fatores como pluviosidade, temperatura e fotoperíodo (RATHCKE & LACEY, 1985; VAN SCHAIK et al., 1993; SEGHIERI et al., 1995; MORELLATO et al., 2000; BATALHA & MARTINS, 2004; JONES et al., 2014).

As respostas das plantas a esses fatores podem ser avaliadas em níveis individuais até ecossistêmicos (CLELAND et al., 2007), compondo, assim, uma importante fonte de avaliação que permite compreender os processos referentes à partilha de recursos, à competição, e sobre os mecanismos que permitem a manutenção das comunidades (CHUINE, 2010). Em nível de comunidade, podem, por exemplo, fornecer dados sobre a vulnerabilidade ou resiliência de grupos de espécies em relação à mudanças no clima (MORELLATO et al., 2016). Em nível ecossistêmico, esclarecem aspectos ligados à regulação da fotossíntese, às amplas interações competitivas e trocas com o sistema climático, incluindo os fluxos de água, energia e CO2 (RICHARDSON et al., 2012; 2013).

A manutenção dessas relações ecológicas em diferentes níveis implica na prática de medidas ligadas à conservação, que podem ser subsidiadas pelos dados fenológicos e utilizadas nos protocolos de gerenciamento da conservação, provendo informações a serem usadas para conservação e manejo (MORELLATO et al., 2016).

2.2 Fenologia na região neotropical sazonalmente seca

As investigações com espécies tropicais ganham destaque a partir da década de 1960, em estudos de comunidades realizados principalmente na Costa Rica. Dentre eles, os estudos em ecossistemas sazonalmente secos, que incluem essencialmente savanas e florestas secas (VICO et al., 2014), trouxeram resultados importantes sobre as respostas fenológicas encontradas, indicando as relações climáticas determinantes nesses processos. Na América Central, estudos pioneiros associaram a relação da floração com a baixa precipitação e radiação solar (FOURNIER & SALLAS, 1966; JANZEN, 1967), ou a influência do estresse hídrico na fenodinâmica foliar em floresta tropical semidecídua (DAUBENMIRE, 1972). Comparações entre florestas secas e úmidas na mesma região indicaram repostas fenológicas diferenciadas para as duas formações (FRANKIE et al., 1974). Outras contribuições importantes relativas à comparações entre áreas e sobre a influência das chuvas na floração das espécies foram desenvolvidos nos anos seguintes (OPLER et al., 1976; 1980). A influência do estresse hídrico sobre a fenologia ganha destaque nas investigações que se seguem na América Central (BORCHERT, 1983; REICH & BORCHERT, 1984).

Tais estudos, até então pioneiros para o conhecimento da fenologia nessas regiões, apresentavam abordagens em diferentes níveis, e nortearam o desenvolvimento das novas linhas de pesquisa em fenologia em outras partes do mundo, esclarecendo questões, até então, inexploradas.

A ampliação das pesquisas na área possibilitou abordagens mais complexas, envolvendo estudos de revisão referentes às causas evolucionárias e consequências dos diferentes padrões fenológicos (RATHCKE & LACEY, 1985), sobre a fenologia em florestas tropicas e sua relação com consumidores primários (VAN SCHAIK et al., 1993), ambos adotando discussões que incluem, dentre outras, as regiões tropicais sazonalmente secas.

Na região Neotropical, a diversidade de padrões observada, na maioria das vezes, converge nessas áreas com sazonalidade hídrica marcada, onde os eventos vegetativos e reprodutivos das plantas são, em parte, um reflexo de ajustes às variações abióticas (JANZEN, 1967; FRANKIE et al., 1974; OPLER et al., 1980; MIRANDA, 1995; BULHÃO & FIGUEIREDO, 2002; LENZA & KLINK, 2006; SILVÉRIO & LENZA, 2010; SILVA et al., 2011; ROSSATTO, 2013). Nessas regiões sazonais, embora algumas espécies apresentem estratégias fenológicas distintas relacionadas à adaptação ao regime hídrico (FRANCO et al., 2005; ROSSATO, 2013), a maioria delas perde folhas durante o período seco (LEIGH & WINDSOR, 1982; BORCHERT et al., 2002; LENZA & KLINK, 2006; PIRANI et al., 2009; SILVÉRIO & LENZA, 2010; LIMA et al., 2012). A floração pode se concentrar nos meses mais secos (JANZEN, 1967; DAUBENMIRE, 1972; FRANKIE et al., 1974; LENZA & KLINK, 2006; PIRANI et al., 2009) ou no início do período chuvoso (MONASTERIO & SARMIENTO, 1976; BATALHA & MANTOVANI, 2000; SILVA et al. 2011). Ervas e arbustos florescem na estação chuvosa (MONASTERIO & SARMIENTO, 1976; BATALHA & MARTINS, 2004), demonstrando maior dependência da disponibilidade hídrica do meio para as fenofases de produção. Já a frutificação pode ocorrer em diferentes períodos do ano, demonstrando menor sazonalidade na sua distribuição (MONASTERIO & SARMIENTO, 1976; BATALHA & MARTINS, 2004; LENZA & KLINK, 2006; PIRANI et al., 2009; MORELLATO et al., 2013).

2.3 Fenologia em savanas

Os ecossistemas tropicais sazonalmente secos, que ocorrem nas Américas, África, Índia e Austrália (EAMUS, 1999), incluem longas faixas nas regiões tropicais em baixas ou médias latitudes, sujeitas à sazonalidade hídrica marcada, com extensos períodos de baixa pluviosidade (inferior a 60 mm mensais) ou ausência completa de chuvas (VICO et al., 2014). Dentre eles, as savanas são encontradas amplamente distribuídas na América do Sul, África e Austrália.

Na Austrália, estudos sobre fenologia vegetativa em comunidades de savanas são escassos e mostram um padrão semelhante ao encontrado no cerrado, com queda foliar na seca e produção de folhas durante período seco ou no começo do período chuvoso, diferindo entre os hábitos foliares (WILLIAMS et al., 1997) e entre áreas (MA et al., 2013). Quanto à fenologia reprodutiva, os picos são observados durante o final do período seco, favorecendo a germinação e desenvolvimento das plântulas durante o período chuvoso (WILLIAMS et al., 1999).

Nas savanas da África, queda e produção de folhas se concentram durante o período seco, sendo utilizado em muitos estudos o termo “green-up” para se referir ao “esverdeamento” da cobertura vegetal, oriundo da produção de folhas, que, para as lenhosas, ocorre predominantemente durante a seca, e levanta questões referentes às estratégias presentes nas plantas que permitem atividades de produção durante o período de escassez de água no ambiente (BIE et al., 1998; ARCHIBALD & SCHOLES, 2007; GUAN et al., 2014; RYAN et al., 2017), quando o fotoperíodo e a temperatura exibem associações frequentes com os fenômenos foliares (ARCHIBALD & SCHOLES, 2007; SEGHIERI et al., 2012) e reprodutivos (WHITE, 1994; SEGHIERI et al., 2012).

No Brasil, Eugen Warming, em sua publicação intitulada Lagoa Santa, de 1892, foi o pioneiro em estudos relacionados à periodicidade das plantas com o clima no cerrado

(KLEIN, 2000). Quase um século depois, na década de 1970, os estudos fenológicos em áreas de cerrado ganham mais notoriedade. Desde então, muitos deles abordaram o tema fenologia em diversas regiões do país, variando em nível de abordagem, em relação ao número de espécies consideradas e aos eventos fenológicos avaliados (BARRADAS, 1972; GOTTSBERGER & SILBERBAUER-GOTTSBERGER, 1983; MIRANDA, 1995; BATALHA & MANTOVANI, 2000; BULHÃO & FIGUEIREDO, 2002; LENZA & KLINK, 2006; MUNHOZ & FELFILI, 2007; PIRANI et al., 2009; ROSSATTO, 2013; DALMOLIN et al., 2015). Embora, nem sempre, os estudos sejam unânimes em mostrar um padrão bem definido na relação dos eventos fenológicos e climáticos, avaliações em comunidades mostram que a fenofase vegetativa de queda exibe picos no período seco, e renovação de folhas apresentam, na maioria dos casos, picos no período seco ou na transição deste para o chuvoso (SARMIENTO et al., 1985; MIRANDA, 1995; GOUVEIA & FELFILI, 1998; OLIVEIRA & GIBBS, 2000; BULHÃO & FIGUEIREDO, 2002; LENZA & KLINK, 2006; PIRANI et al., 2009; DALMOLIN et al., 2015). A floração também se concentra no período seco ou na transição deste para o período chuvoso (OLIVEIRA & GIBBS, 2000; BATALHA & MANTOVANI, 2000; BULHÃO & FIGUEIREDO, 2002; LENZA & KLINK, 2006; PIRANI et al., 2009). A amplitude de estratégias fenológicas existentes é resultado de forças seletivas, que incluem as variações ambientais e direcionam as estratégias de sobrevivência e reprodução das espécies (SARMIENTO et al., 1985).

Nos estudos que envolvem análises estatísticas entre fenologia e dados climáticos no cerrado, associações com precipitação, temperatura e fotoperíodo e/ou insolação, indicam que as variações da temperatura e radiação solar (diminuição ou aumento) durante a seca são importantes fatores preditores das fenologias vegetativa e reprodutiva em diversas áreas de distribuição do cerrado (LENZA & KLINK, 2006; PIRANI et al., 2009; SILVÉRIO & LENZA, 2010; SILVA et al., 2011; BARBOSA et al., 2012; DALMOLIN et al., 2015; LACERDA et al., 2017).

2.4 Abordagens comparativas no cerrado: comunidades e espécies

Diversos estudos com diferentes direcionamentos empregam abordagens envolvendo comparações de padrões fenológicos em áreas de cerrado, tanto para comunidades quanto populações, considerando, por exemplo, aspectos referentes à fenologia foliar (LENZA & KLINK, 2006; ROSSATTO, 2013); comparações entre estratos (BATALHA & MANTOVANI, 2000; BATALHA & MARTINS, 2004); em relação a outros tipos de formações (SILVA et al., 2011; NEVES et al., 2017); diferenças intraespecíficas (GOULART et al., 2005; CAMARGO et al., 2011) e interespecíficas (DALMOLIN et al., 2015).

Dentre os estudos mais recentes envolvendo a fenologia de comunidades, algumas respostas sobre eventos vegetativos e reprodutivos, em geral, assumem a existência de gatilhos (fatores proximais) semelhantes em diferentes áreas (NEVES et al., 2017), embora nem todos tenham exibido as mesmas respostas em relação à presença ou ausência de chuvas. As associações com os modos de dispersão (fator final) também são recorrentes nestas avaliações (BATALHA & MARTINS, 2004; PIRANI et al., 2009).

Em estudo envolvendo uma comunidade lenhosa no cerrado Central (Brasília), a classificação das espécies em diferentes grupos fenológicos vegetativos permitiu sua distinção mais detalhada, sendo empregados critérios claros para a definição de espécies sempre verdes (com crescimento contínuo ou sazonal, e percentual de cobertura da copa – PICP – na comunidade sempre superior a 50%), brevidecíduas (perda de folhas por curto período e redução do PICP entre 30 e 50%) e decíduas (perda de folhas por um período de 3 a 4 semanas e redução do PICP entre 0 e 10%) (LENZA & KLINK, 2006). Os autores também verificaram a predominância da floração na transição entre o período seco e chuvoso, e frutificação variando de acordo com as síndromes de dispersão, com as espécies anemocóricas e autocóricas mais intensas durante a seca, e zoocóricas no período chuvoso.

No cerrado de Mato Grosso, a classificação quanto à deciduidade mostrou a ocorrência da maioria das espécies decíduas (44%) ou brevidecíduas (16%). A queda foliar teve pico em agosto e correlação com precipitação e fotoperíodo (negativas). O brotamento aumentou no final do período seco, antes das chuvas, acompanhando o aumento na temperatura. A floração foi maior durante o período seco, correlacionada a diminuição da precipitação e fotoperíodo. A frutificação de espécies zoocóricas (maioria) ocorreu de forma contínua, exibindo correlação negativa com precipitação e positiva com temperatura. A frutificação das anemocóricas ocorreu nos meses mais secos (PIRANI et al., 2009).

Em São Paulo, um estudo sobre causas ambientais e filogenéticas na comparação da fenologia reprodutiva entre uma área de cerrado e uma de floresta ripária, não evidenciou importância da restrição filogenética para a ocorrência das fenofases e mostrou um comportamento diferente em relação aos estudos descritos anteriormente, com floração e frutificação nas duas áreas durante o período úmido e evidências de variáveis relacionadas à radiação solar (SILVA et al., 2011).

Fatores como fotoperíodo e insolação foram os mais associadas à floração em um gradiente incluindo cerrado, transição e floresta tropical seca na Chapada Diamantina (BA).

Esta fenofase se manifestou continuamente no cerrado, com um discreto aumento durante o início do período chuvoso, enquanto na área de transição e floresta seca a floração se restringiu ao período chuvoso (NEVES et al., 2017). Os resultados deste estudo revelam, adicionalmente, diferenças fenológicas relacionadas ao uso da água entre as comunidades avaliadas, principalmente associadas à densidade do lenho das espécies e características do solo, que implicam nas respostas anteriormente descritas.

Estudos envolvendo comparações intraespecíficas em áreas de cerrado indicam que as respostas dependem das espécies consideradas. Populações de *Plathymenia reticulata* Benth., por exemplo, não mostraram diferenças fenológicas vegetativas ou reprodutivas em populações inseridas em cerrado, floresta Atlântica e transição entre elas em áreas próximas no estado de Minas Gerais. Neste estudo, a sincronia entre populações foi elevada e as diferenças dentro de cada uma das três populações foram maiores (GOULART et al., 2005). Já em populações de *Xylopia aromatica* (Lam.) Mart. no Estado de São Paulo, dispostas em diferentes orientações cardinais (um grupo voltado para a face leste e outro para a face sul), houve maior percentual de indivíduos, maior sincronia e maior duração das fenofases na face leste, sob maior luz incidente, maiores temperaturas e copa mais aberta (CAMARGO et al., 2011). Esse resultado indica que dentro de uma espécie, mesmo em áreas geográficas próximas, há um ajuste de suas respostas em relação ao clima. As avaliações com populações da mesma espécie (conespecíficas), podem ajudar a compreender a extensão da variabilidade fenológica como estratégia de sobrevivência em diferentes ambientes, como os fatores abióticos influenciam os padrões fenológicos (GOULART et al., 2005; LACERDA et al., 2017), e a ocorrência das espécies (NOVAES et al., 2010).

No estudo da fenologia de 27 espécies arbóreas localizadas em cerrado marginal no nordeste do Maranhão, as espécies exibiram queda foliar seguida por brotamento e floração durante a seca, com os períodos de crescimento e dormência alternando-se de modo mais sincronizado com as variações no fotoperíodo, energia radiante e temperatura. A frutificação mostrou-se mais variável, com diferentes estratégias de dispersão na seca ou chuva, associadas, respectivamente, ao hábito decíduo (ou semidecíduo) e sempre verde das espécies (FIGUEIREDO, 2008).

2.5 Estresse hídrico e relações com o hábito foliar em savanas

Uma vasta região nos trópicos está exposta a uma seca anual prolongada (WORBES, 1995), resultando em uma situação períodica de estresse na vegetação natural. A tolerância à seca de espécies lenhosas é uma das características mais importantes para um estabelecimento bem sucedido. Devido à grande diversidade de espécies nos trópicos e às diferenças extremas dos tipos climáticos, existe uma ampla gama de estratégias de superação do estresse imposto pela seca.

As espécies de vegetação lenhosa podem iniciar o crescimento usando reservas de carbono armazenadas e adquiridas durante a fase de produção anterior (SCHEITER & HIGGINS, 2009). Também podem ter acesso a recursos hídricos do solo e estocados no tronco para sustentar a atividade vegetativa durante a estação seca (SCHOLZ et al., 2007) e desenvolver estruturas mais complexas de tolerância e resistência à dessecação através de raízes mais profundas e armazenamento de água no tronco (CHEN et al., 2009; HASSELQUIST et al., 2010; PINEDA-GARCIA et al., 2013).

As respostas das plantas relacionadas à disponibilidade de água podem envolver diferentes níveis de avaliação, como o estrutural (relacionado às propriedades hidráulicas do caule, às características foliares e radiculares), o fisiológico (relacionado às estratégias de uso da água e trocas gasosas) e fenológico (relacionado à periodicidade sazonal da atividade do meristema) (HOLBROOK, 1995). Assim, diferentes linhas de investigação podem ser levantadas para a compreensão das estratégias de uso da água pelas plantas. Dentre elas, aquelas referentes à deciduidade e as respostas fenológicas associadas.

Diferentes estratégias ligadas à manutenção e troca das folhas podem ser encontradas nessas áreas, com espécies de folhas perenes ou sempre verdes, decíduas e semi ou brevidecíduas, que frequentemente co-ocorrem (EAMUS, 1999). Estudos recentes avaliam em diferentes níveis as características comuns ou diferenças entre as espécies pertencentes a estes diversos grupos fenológicos. Alguns deles encontram convergência de traços (traits), usados para a definição dos grupos funcionais (LIMA et al., 2012; BORGES & PRADO, 2014), apoiando a hipótese de que as espécies podem ser agrupadas dependendo dos caracteres que definem a manutenção e troca de folhas.

Espécies sempre verdes, que mantêm alta cobertura da copa e da função foliar ao longo do ano (FU et al., 2012), são distinguíveis por suas estratégias de tolerância à seca (VICO et al., 2014; SOUZA et al., 2015), que incluem maior resistência à cavitação (FU et al., 2012), maior tempo de vida da folha e altas taxas de crescimento (ROSSATTO, 2013; TOMLINSON et al., 2014), menor área foliar específica e uso mais conservativo da água (EAMUS, 1999; FRANCO et al., 2005). Além disso, podem desenvolver rapidamente um sistema radicular e acessar a água em camadas mais pronfundas do solo (HASSELQUIST et al., 2010).

Por outro lado, as espécies decíduas permancem sem folhas durante parte do período seco, exibindo estratégias ligadas à redução da atividade fisiológica e evitação da seca, que incluem maior eficiência hidráulica do caule (FU et al., 2012), menor investimento na produção de tecidos não fotossintetizantes das folhas, folhas com maior área foliar específica e atividade fotossintética, associadas à maior eficiência no uso da água (FRANCO et al., 2005). Tais diferenças podem influenciar diretamente os padrões reprodutivos, evidenciando diferenças quanto às respostas reprodutivas entre esses grupos.

No Brasil, Borges e Prado (2014), compilaram dados de diversos estudos fenológicos em áreas de cerrado a fim de verificar a associação entre floração e deciduidade. Os autores verificaram diferenças na duração, distribuição e pico, em espécies sempre verdes, semidecíduas e decíduas. A diferença mais marcante ocorreu com relação à maior duração da floração nas espécies sempre verdes, porque a manutenção das folhas favorece a proteção das flores contra insolação direta e a produção de nutrientes para a manutenção da fenofase. Já nas espécies decíduas, a menor duração da floração pode reduzir a utilização das reservas de carbono, água e nutrientes no final da estação seca, quando a copa está sem folhas. O estudo, no entanto, não utilizou informações referentes à intensidade das fenofases, considerou as diferenças relacionadas às classificações quanto à deciduidade e também diferentes fitofisionomias do domínio Cerrado, adotadas nos estudos dos quais os dados foram obtidos (BATALHA & MANTOVANI, 2000; LENZA & KLINK, 2006; PIRANI, et al. 2009; ROSSATO, et al., 2009). Portanto, dados mais detalhados, que incluam, por exemplo, a mesma fitofisionomia, a intensidade das fenofases e espécies com fenologia foliar contrastante bem definida, podem fornecer respostas ainda mais esclarecedoras sobre a associação entre a fenologia foliar e reprodutiva.

3. OBJETIVOS

3.1 Geral

Determinar o padrão fenológico de comunidades vegetais lenhosas em duas áreas de cerrado no Estado do Maranhão.

3.2 Específicos

- Comparar os padrões fenológicos das comunidades lenhosas nas duas áreas de estudo.
- Relacionar a frutificação às síndromes de dispersão das espécies nas duas comunidades.
- Comparar a fenologia em populações conespecíficas nas duas áreas.
- Investigar a relação entre a fenologia foliar e características reprodutivas de espécies no Parque Estadual do Mirador.
- Avaliar a influência dos fatores abióticos de pluviosidade, temperatura e comprimento do dia nas fenofases de queda e produção de folhas, floração e frutificação em nível de comunidade e populacional, em espécies lenhosas nas duas áreas.

4. JUSTIFICATIVA

O levantamento de informações ecológicas básicas, como os estudos fenológicos, podem auxiliar na compreensão da variação dos padrões fenológicos entre diferentes áreas, subsidiar estudos ecofisiológicos e sobre mudanças climáticas, recebendo o status de ciência ambiental integrativa (MORELLATO *et al*., 2013). Os estudos fenológicos de comunidades vegetais em áreas de cerrado são escassos (MORELLATO *et al*., 2013). No Estado do Maranhão, existem somente quatro estudos publicados sobre a fenologia de espécies vegetais do cerrado: um para a comunidade (FIGUEIREDO, 2008), um envolvendo família (BULHÃO & FIGUEIREDO, 2002) e dois envolvendo espécies (MENDES *et al*., 2011; LACERDA *et al*., 2017). A localização geográfica do Estado inclui um dos extremos de ocorrência do cerrado, em condições únicas, na transição entre o clima úmido da Amazônia e semi-árido do Nordeste. Desse modo, estudos que investiguem os aspectos sazonais e reprodutivos das espécies de plantas nessas áreas podem contribuir para o entendimento mais abrangente acerca da dinâmica das comunidades vegetais em áreas de savana e para subsidiar estudos com abordagens mais específicas.

A elucidação de como as espécies respondem a diferentes condições climáticas, auxilia na compreensão dos seus mecanismos adaptativos, na previsão de alterações nos eventos fenológicos e na dinâmica das populações, o que inclui o acompanhamento e avaliações dos efeitos das mudanças climáticas sobre as espécies. A observação das respostas fenológicas entre comunidades ou populações vegetais submetidas a diferentes regimes climáticos, pode fornecer informações, mesmo em curto prazo, acerca da associação dos padrões fenológicos com eventos climáticos distintos, contribuindo para a compreensão da diversidade fenológica e da plasticidade de respostas encontradas.

Embora muitos estudos tenham sido realizados em diferentes regiões de savanas ao redor do mundo, existem algumas lacunas, seja pela escassez de estudos em algumas regiões ou, principalmente, pelo fato de que existe uma grande variedade de espécies, muitas delas sem registros fenológicos e cada uma com comportamentos biológicos e histórias evolutivas distintas.

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6. LISTA DE PUBLICAÇÕES

CAPÍTULO I: Respostas fenológicas diferem entre duas comunidades lenhosas de cerrado no nordeste do Brasil

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Resumo

Neste estudo, buscamos caracterizar a fenologia vegetativa e reprodutiva em comunidades vegetais presentes em duas áreas de cerrado na região nordeste do Brasil e comparar as respostas fenológicas entre essas comunidades, localizadas no município de Barreirinhas e no Parque Estadual de Mirador – PEM, Estado do Maranhão. Essas áreas apresentam diferenças relacionadas às temperaturas, ao fotoperíodo, e à quantidade e distribuição de chuvas, com predominância antecipada da duração do período seco e de maiores variações na temperatura e fotoperíodo na área do PEM. A fenologia de comunidades presentes nessas áreas foi avaliada mensalmente, entre abril de 2014 e março de 2016, sendo adotada uma escla semi-quantitativa para registro dos dados de queda foliar, folhas novas, floração e frutificação. A partir disso, determinamos as datas médias de início e pico das fenofases por meio da estatística circular, o percentual de atividade e de intensidade para cada fenofase, e efetuamos comparações entre as respostas de cada comunidade por meio do teste de Watson Williams. As relações das fenofases com os dados climáticos foram investigadas por meio de regressão linear múltipla. Adicionalmente, foram definidos os hábitos foliares, as síndromes de dispersão de cada espécie. As comunidades apresentaram sazonalidade em relação aos eventos fenológicos avaliados, com as fenofases se manifestando predominantemente na segunda metade do período seco, principalmente nos dois meses que antecedem o início das chuvas − agosto e setembro no PEM; outubro e novembro em Barreirinhas. No início do período chuvoso, a produção de folhas novas e frutificação continuaram intensas, assim como no fim do período seco. No PEM, houve uma forte associação das fenofases com a temperatura. Em Barreirinhas, além da temperatura, que se associou às fenofases de queda foliar e floração, o fotoperíodo mostrou relação com a produção de folhas e a frutificação. A ocorrência antecipada das fenofases no PEM em relação à Barreirinhas explica possíveis ajustes das espécies às condições climáticas locais.

Palavras-chave: Fenologia, Floração, Frutificação, Queda foliar, Savana.

1. Introdução

A periodicidade dos eventos fenológicos e suas relações com a sazonalidade climática têm sido amplamente avaliadas nos últimos anos, principalmente devido à influência que as alterações climáticas recentes têm exercido sobre o funcionamento dos ecossistemas (Walther 2010; Richardson *et al.* 2013; Visser 2016). Em regiões com sazonalidade hídrica marcada, a abordagem indissociada entre fenologia e clima tem demonstrado a possível influência de fatores como temperatura e fotoperíodo entre aqueles mais relacionados à periodicidade dos eventos fenológicos, mesmo em baixas latitudes, onde as variações desses fatores são menores (Silvério e Lenza 2010; Seghieri *et al.* 2012; Borchert *et al.* 2015; Lacerda *et al.* 2017).

Outra abordagem frequentemente empregada nesses estudos se refere à relação com a dispersão dos frutos e sementes, considerada como um fator final ligado ao comportamento fenológico das espécies, e intrinsicamente relacionado à sobrevivência e manutenção das populações (Van Schaik *et al.* 1993; Batalha e Martins 2004; Pirani *et al.* 2009; Athayde e Morellato 2014).

Estudos fenológicos realizados em comunidades vegetais fornecem respostas abrangentes referentes às suas relações com fatores bióticos e abióticos (Ma *et al.* 2013; Guan *et al.* 2014; Hawes e Peres 2016; Dahlin *et al.* 2017; Neves *et al.* 2017), levando à compreensão ampla sobre aspectos que influenciam o comportamento das espécies e aqueles relacionados ao fluxo de carbono, água e energia nos ecossistemas (Miranda *et al.* 1997; Eamus *et al.* 2016).

No Brasil, estudos desenvolvidos sobre comunidades em áreas de cerrado apontam claros padrões de crescimento periódico e marcada sazonalidade influenciando diretamente as estratégias vegetativas e reprodutivas das comunidades (Batalha e Martins 2004; Lenza e Klink 2006; Munhoz e Felfili 2007; Silvério e Lenza 2010; Neves *et al.* 2017). Diversos estudos nessas áreas mostram que, em geral, as fenofases se intensificam no período seco ou na transição entre o período seco e chuvoso (Barbosa *et al.* 2012; Borges e Prado 2014; Dalmolin *et al.* 2015). Muitos desses estudos empregam abordagens comparativas que incluem investigações das variações fenológicas entre anos (Pirani *et al.* 2009), entre espécie lenhosas e herbáceas (Batalha e Martins 2004), entre fisionomias distintas (Tannus *et al.* 2006), ou entre grupos de espécies com distintos hábitos foliares (Borges e Prado 2014). No entanto, comparação entre comunidades com semelhante fisionomia de cerrado, submetidas a diferenças climáticas, ainda não foram investigadas. Tais estudos podem responder a importantes questões ligadas aos fatores que influenciam as respostas dessas comunidades e suas adaptações ao clima.

No Estado do Maranhão, uma extensa área de cerrado se localiza entre a Amazônia e a Caatinga (floresta seca), favorecendo a ocorrência de condições climáticas diferentes quanto à distribuição e variações nas chuvas, temperaturas e radiação solar (Alvares *et al.* 2013). Considerando a importância dos estudos fenológicos para a compreensão das variações existentes e previsões no cenário de mudanças climáticas, a sua inclusão nessa ampla faixa de cerrado é necessária, apesar de incipiente (Bulhão e Figueiredo 2002; Figueiredo 2008; Lacerda *et al.* 2017). Assim, neste estudo, buscamos caracterizar a fenologia vegetativa e reprodutiva em comunidades vegetais presentes em duas áreas de cerrado no Estado e comparar as respostas fenológicas entre essas comunidades, que estão sujeitas a diferenças quanto ao regime climático. Nossa predição é de que as comunidades exibirão padrões diferenciados, acompanhando as variações climáticas locais.

2. Material e métodos

2.1 Área de estudo

O estudo foi realizado em duas áreas de cerrado *sensu stricto* no Estado do Maranhão: no município de Barreirinhas (03°01'17"S, 43°06'28"W) e no Parque Estadual de Mirador (06°37'55"S, 45°52'38"W), em um trecho inserido nos municípios de Formosa da Serra Negra e Mirador. A altura média dos indivíduos em Barreirinhas é de 4 m e a espécie com maior valor de importância é *Plathymenia reticulata* Benth. (Fabaceae). No Parque a altura média é de 3,9 m, e *Qualea parviflora* Mart. (Vochysiaceae) é a espécie com maior valor de importância (dados não publicados).

O clima nas duas áreas apresenta um período seco e outro úmido, diferindo quanto à distribuição das chuvas e temperaturas. Segundo a classificação de Koppen, o clima é do tipo As em Barreirinhas, e do tipo Aw no Parque Estadual do Mirador (Alvares *et al*., 2013). Para fins de simplificação, o Parque Estadual de Mirador será referido aqui como PEM, e Barreirinhas, nas tabalas e figuras, como Barr.

Dados históricos (1986 a 2016) evidenciam variações quanto à duração do período seco em cada área, no entanto, observa-se um maior volume de chuvas na região de Barreirinhas (1.700 mm) quando comparado ao PEM (1.200 mm). Durante o período de estudo, o período seco (pluviosidade abaixo de 60mm) foi mais longo para a região de Barreirinhas, com 6 meses (julho a dezembro), enquanto no PEM a duração do período seco foi de 4 a 5 meses (maio ou junho a setembro). A temperatura média, considerando os dados históricos, foi de 27 ºC nas duas áreas, no entanto a amplitude térmica mensal foi maior no PEM (18.4 ºC em agosto e 38.2 ºC em setembro) do que em Barreirinhas (21 ºC em agosto à 37.9 em novembro). Os dados foram obtidos do Instituto Nacional de Meteorologia – Estação Chapadinha (nº 82.382) e Balsas (nº 82.768), 2017) (Fig. 1) (INMET, 2016). O fotoperíodo varia gradualmente de 11h e 57min em Junho e 12h e 18min em Dezembro em Barreirinhas; e de 11h e 44min em Junho a 12h e 31min em Dezembro no PEM (Fonte: http://www.sci.fi/~benefon/sol.html) (Fig. 1). A altitude médaia em Barreirinhas está em torno de 90 m, com os solos do tipo latossolos amarelos, arenosos, contendo alto conteúdo de areia grossa e teor de argila entre 5 e 6%. No PEM, a altitude varia de 300 a 600 m, e os solos predominantes na região são neossolos litólicos e latossolos amarelos, do tipo franco arenosos, predominando areia fina, e teor de argila em torno de 10% (dados não publicados).

Foram obtidos os dados climáticos mensais de precipitação total, temperaturas médias, máximas e mínimas (Fonte: http://www.inmet.gov.br/portal/) e fotoperíodo (Fonte:

http://www.sci.fi/~benefon/sol.html), referentes aos meses de abril 2014 a março de 2016, usados para associação com os dados fenológicos (Fig. 1).

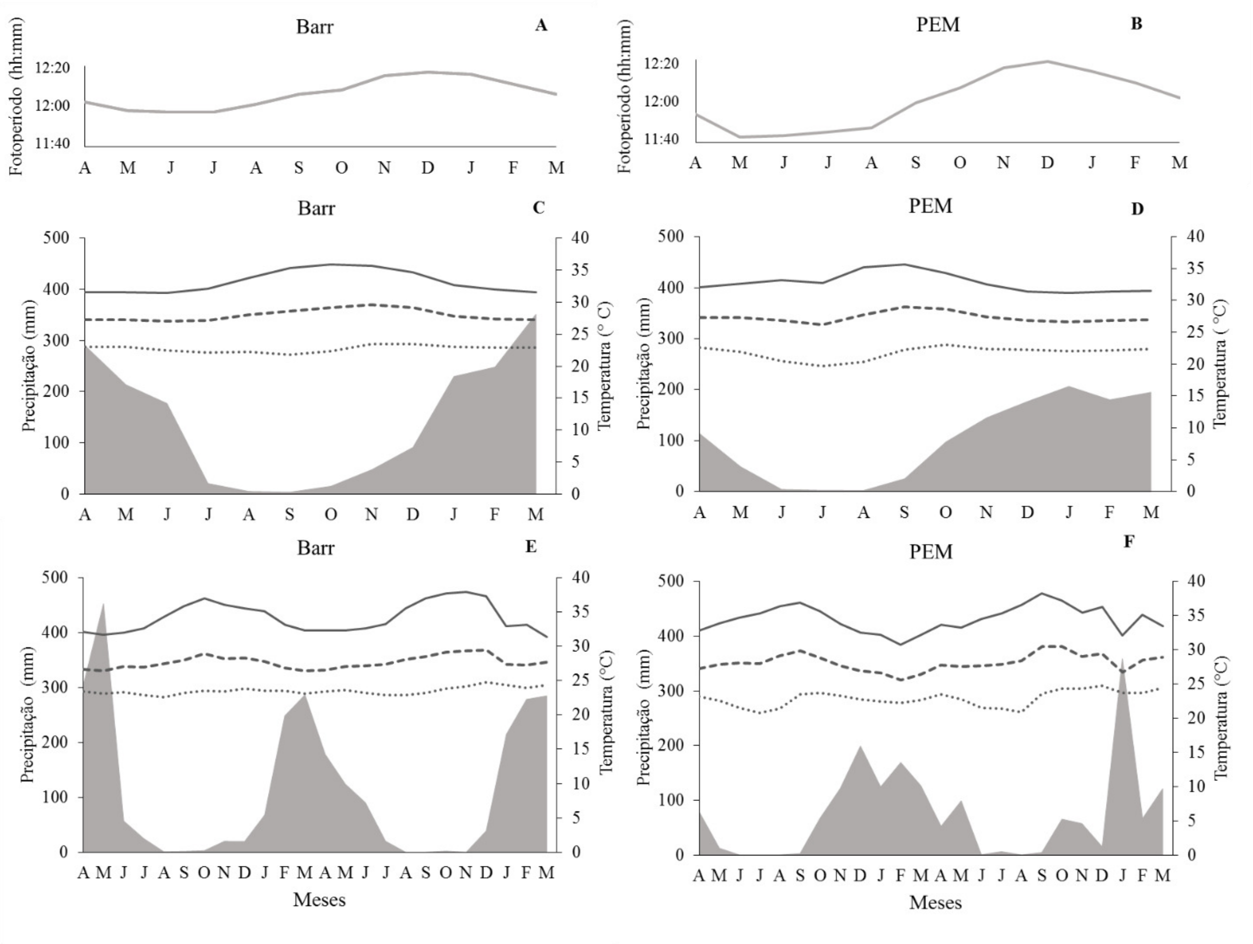

Figura 1: Fotoperíodo (A; B) e dados climáticos históricos mensais (entre 1986 e 2016) (C; D) e entre os anos de 2014 e 2016 (E; F): chuvas (área preenchida), temperaturas máximas (linhas contínuas), temperaturas médias (linhas tracejadas intermediárias) e mínimas (linhas tracejadas inferiores) em áreas de cerrado (Barreirinhas − Barr; Parque Estadual de Mirador − PEM), Maranhão, Brasil.

2.2 Dados fenológicos

Queda foliar, folhas novas, floração e frutificação foram acompanhados mensalmente, entre abril de 2014 e março de 2016, em todos os indivíduos lenhosos marcados nas duas áreas, que apresentaram circunferência mínima do tronco ≥10 cm ao nível do solo. Os indivíduos marcados estavam inseridos em 20 parcelas medindo 20 x 20 metros, distando 100 metros e foram identificados pelo sistema de classificação APG IV (2016). Durante o período de estudo não houve incidência de fogo nas áreas amostradas.

Nesses indivíduos foram feitas estimativas semi-quantitativas mensais das fenofases (categorias de 0 a 4, com 25% de intervalo entre elas), segundo o percentual de intensidade proposto por Fournier (1974). Cada fenofase foi definida como se segue: queda foliar, como proporção da copa com ausência de folhas; folhas novas se referindo às folhas recém formadas ou em expansão; floração incluindo flores em botão ou abertas; frutificação foi considerada pela presença de frutos imaturos e maduros. Determinamos também o percentual de atividade das fenofases – percentual de espécies manifestando as fenofases – em cada área, mensalmente.

Adicionalmente, foi definido para cada espécie seu respectivo hábito foliar, sendo as espécies classificadas em sempre-verdes, brevidecíduas e decíduas, de acordo com Lenza e Klink (2006), com adaptações. As sempre-verde apresentaram percentual de intensidade de cobertura da copa acima de 50%, podendo produzir folhas sazonalmente, ou por longos períodos do ano. As brevidecíduas substituíram a copa completamente durante o período seco, permanecendo sem folhas ou com poucas folhas senescentes por um período curto de poucas semanas. As decíduas, perderam completamente suas folhas por um período superior a um mês, podendo chegar a três meses de deciduidade completa.

2.3 Síndromes de dispersão

As síndromes de dispersão das espécies foram estabelecidas segundo a classificação de Van der Pijl (1982), por meio da análise morfológica dos diásporos e com o auxílio da literatura. As espécies foram agrupadas em três grupos de dispersão: 1) anemocóricas - dispersas pelo vento, 2) autocóricas - barocoria e dispersão explosiva e 3) zoocóricas - dispersão por animais.

2.4 Análise dos dados

A estatística circular foi utilizada para detectar a sazonalidade e para comparação entre as áreas. Inicialmente, as datas de observação foram convertidas em ângulos, sendo que um ano correspondente à 360º (cada dia corresponde a 0,9863º). Nós determinamos as datas de início (ângulo médio – ou data média – em que cada indivíduo manifestou a fenofase pela vez) e pico (ângulo médio – ou data média – em que cada indivíduo manifestou a maior intensidade da fenofase) de todos os indivíduos amostrados, utilizados para a obtenção das médias por espécie e, a partir destas, para cada comunidade, em todas as fenofases.

Para testar a ocorrência de sazonalidade foi utilizado o teste de Rayleigh e obtidos o ângulo médio e sua data correspondente, o vetor r e o desvio padrão angular. O vetor r fornece uma medida do grau de sazonalidade, variando de 0 (quando a fenofase é uniformemente distribuída durante o ano) a 1 (quando a fenofase se concentra em uma única data). Quando o ângulo médio foi estatisticamente significante, nós empregamos o teste de Watson-Williams (F) para verificar se as datas de início e pico para cada fenofase, entre as áreas, apresentaram diferenças (Zar 2010). Para a frutificação, foram também realizadas as análises circulares referentes à cada síndrome e, quando o ângulo foi significativo, as datas médias foram comparadas dentro de cada área (entre as síndromes) e entre as mesmas síndromes entre áreas. As análises circulares foram executadas por meio do software ORIANA 4.0 (Kovach 2011).

Para verificar possíveis relações entre as fenofases e os dados climáticos e de fotoperíodo (todos referidos como climáticos, para simplificação do texto), foram realizadas análises de regressão múltipla entre o percentual de intensidade de cada fenofase, em cada área, e o conjunto dos dados climáticos mensais de cada área (precipitação média, temperaturas máximas e mínimas médias e fotoperíodo).

3. Resultados

Foram acompanhados 1.418 indivíduos, distribuídos em 79 espécies nas duas áreas. Sendo um total de 43 espécies em Barreirinhas (706 indivíduos) e 65 espécies no PEM (712 indivíduos), com 30 espécies comuns às duas áreas (Tabela 1).

Tabela 1: Espécies agrupadas em famílias, suas síndromes de dispersão (SD) e hábito foliar registrados em duas áreas de cerrado, Maranhão, Brasil. Barr= Barreirinhas; PEM= Parque Estadual de Mirador; N=número de indivíduos Zoo=zoocoria; Ane= anemocoria; Au=autocoria; SV=sempre verde; DED=decíduo; BVD= brevidecíduo.

Famílias / Espécies	N (Barr)	N (PEM)	SD	Habito foliar (Barr/PEM)
Anacardiaceae				
Anacardium occidentale L.	6	15	Zoo	SV
Astronium fraxinifolium Schott	-	3	Ane	DEC
Tapirira guianensis Aubl.	7	4	Zoo	SV
Annonaceae				
Annona coriacea Mart.	1	6	Zoo	BVD
Xylopia aromatica (Lam.) Mart.	-	3	Zoo	SV
Apocynaceae				
Aspidosperma macrocarpon Mart. & Zucc.	-	4	Ane	BVD
Himatanthus drasticus (Mart.) Plumel	22	13	Ane	SV
Hancornia speciosa Gomes	14	5	Zoo	BVD/DEC
Araliaceae				
Schefflera burchellii (Seem.) Frodin & Fiaschi	-	8	Zoo	SV
Asteraceae				
Cyrtocymura scorpioides (Lam.) H. Rob.	-	1	Ane	DEC
Bignoniaceae				
Cybistax antisyphilitica (Mart.) Mart.	6	-	Ane	DEC
Tabebuia aurea (Silva Manso) Benth. & Hook. f. ex S.Moore	-	5	Ane	DEC
Zeyheria tuberculosa (Vell.) Bureau ex Verl.	4	1	Ane	DEC
Calophyllaceae				
Kielmeyera lathrophyton Saddi	-	21	Ane	BVD
Kielmeyera speciosa A.St.-Hil.	-	7	Ane	DEC
Caryocaraceae				
Caryocar coriaceum Wittm.	13	26	Zoo	SV
Chrysobalanaceae				
Hirtella ciliata Mart. & Zucc.	19	27	Zoo	SV
Hirtella racemosa Lam.	1	-	Zoo	SV
Licania sp.	-	1	Zoo	BVD

Famílias / Espécies	N (Barr)	N (PEM)	SD	Habito foliar (Barr/PEM)
Clusiaceae				
Platonia insignis Mart.	-	1	Zoo	SV
Combretaceae				
Combretum leprosum Mart.	2	1	Ane	DEC
Connaraceae				
Connarus suberosus Planch.	-	51	Zoo	SV
Rourea induta Planch.	4	-	Zoo	SV
Dilleniaceae				
Curatella americana L.	-	16	Zoo	BDV
Ebenaceae				
Diospyros hispida A.DC.	-	12	Zoo	DEC
Erythroxylaceae				
Erythroxylum suberosum A.St.-Hil.	5	16	Zoo	DEC
Euphorbiaceae				
Manihot violacea Pohl	32	-	Zoo	DEC
Maprounea guianensis Aubl.	-	1	Zoo	DEC
Fabaceae				
Andira cordata Arroyo ex R.T.Penn. & H.C.Lima	-	10	Zoo	SV
Bowdichia virgilioides Kunth	3	2	Ane	SV/BVD
Desmodium barbatum (L.) Benth.	1	-	Zoo	SV
Dimorphandra gardneriana Tul.	17	16	Zoo	BVD
Dipteryx alata Vogel	1	-	Zoo	SV
Hymenaea stigonocarpa Mart. ex Hayne	-	4	Zoo	BVD
Leptolobium dasycarpum Vogel	-	15	Ane	DEC
Parkia platycephala Benth.	31	2	Zoo	SV
Piptadenia sp.	2	-	Au	BDC
Plathymenia reticulata Benth.	169	13	Ane	DEC
Poecilanthe parviflora Benth.	-	5	Au	DEC
Pterodon emarginatus Vogel	-	9	Ane	BDC
Stryphnodendron coriaceum Benth.	44	11	Zoo	SV/BDC
Stryphnodendron rotundifolium Mart.	-	24	Zoo	DEC
Tachigali subvelutina (Benth.) Oliveira-Filho	-	10	Ane	SV
Vatairea macrocarpa (Benth.) Ducke	6	12	Ane	BVD
Hypericaceae				
Vismia guianensis (Aubl.) Choisy	-	1	Zoo	SV
Icacinaceae				
Emmotum nitens (Benth.) Miers	-	1	Zoo	SV
Lecythidaceae				
Lecythis lurida (Miers) S.A.Mori	26	-	Au	SV
Loganiaceae				
Antonia ovata Pohl	2	-	Ane	BVD
Lamiaceae				
Vitex cymosa Bertero ex Spreng.	-	1	Zoo	DEC
Hyptidendron canum (Pohl ex Benth.) Harley	-	1	Zoo	BDC
Lythraceae				

Famílias / Espécies	N (Barr)	N (PEM)	SD	Habito foliar (Barr/PEM)
Lafoensia pacari A.St.-Hil.	3	20	Ane	DEC
Malpighiaceae				
Byrsonima crassifolia (L.) Kunth	13	67	Zoo	SV/BVD
Byrsonima rotunda Griseb.	12	19	Zoo	BVD
Melastomataceae				
Miconia albicans (Sw.) Triana	-	1	Zoo	BVD
Mouriri elliptica Mart.	-	8	Zoo	SV
Moraceae				
Brosimum gaudichaudii Trécul	-	3	Zoo	BVD
Myrtaceae				
Eugenia dysenterica (Mart.) DC.	-	24	Zoo	DEC
Myrcia guianensis (Aubl.) DC.	10	-	Zoo	SV
Myrcia splendens (Sw.) DC.	4	5	Zoo	SV
Myrciaria floribunda (H.West ex Willd.) O.Berg	1	-	Zoo	SV
Psidium myrsinites DC.	34	13	Zoo	BVD/DEC
Nyctaginaceae				
Guapira cf. *graciliflora* (Mart. ex Schmidt) Lundell	1	2	Zoo	BVD
Ochnaceae				
Ouratea hexasperma (A.St.-Hil.) Baill.	8	11	Zoo	SV
Opiliaceae				
Agonandra brasiliensis Miers ex Benth. & Hook.f.	27	2	Zoo	BDC/DEC
Rubiaceae				
Cordiera rigida. (K.Schum.) Kuntze	1	1	Zoo	SV/BVD
Palicourea rigida Kunth	-	1	Zoo	SV
Tocoyena formosa (Cham. & Schltdl.) K. Schum.	-	16	Zoo	DEC
Salicaceae				
Casearia arborea (Rich.) Urb.	-	5	Zoo	SV
Casearia sylvestris Sw.	-	10	Zoo	BVD
Sapindaceae				
Magonia pubescens A.St.-Hil.	-	4	Ane	DEC
Matayba heterophylla (Mart.) Radlk.	1	-	Zoo	BVD
Sapotaceae				
Chrysophyllum arenarium Allemão	3	-	Zoo	BVD
Pouteria sp.	4	9	Zoo	SV
Siparunaceae				
Siparuna guianensis Aubl.	-	1	Zoo	SV
Vochysiaceae				
Qualea grandiflora Mart.	28	48	Ane	BVD/DEC
Qualea parviflora Mart.	70	41	Ane	BVD/DEC
Vochysia gardneri Warm.	-	4	Ane	BVD
Salvertia convallariodora A.St.-Hil.	46	12	Ane	SV

Todas as fenofases nas duas áreas exibiram comportamento sazonal nas suas datas de pico de queda foliar e de início e pico da produção de folhas, floração e frutificação, ocorrendo sempre antes no PEM, com exceção do início da produção de folhas, que não mostrou diferenças nas datas médias entre as áreas (Tabela 2).

As fenofases vegetativas apresentaram maiores valores do vetor r, indicando maior sazonalidade. Para queda foliar, não foi possível determinar as datas de início nas duas áreas, pois as espécies perderam folhas constantemente ao longo do ano, mesmo que em pequenas proporções. O pico da queda foliar, de folhas novas e floração ocorreram com datas médias correspondentes ao meses de setembro no PEM e em outubro em Barreirinhas. Para a produção de folhas, o início e pico da floração e frutificação correspondem todos ao mês de setembro no PEM e ao mês de Novembro em Barreirinhas (Tabela 2).

Tabela 2: Resultados da estatística circular para a sazonalidade e datas de pico (P), da queda da folha (QF), datas de início (I), pico das fenofases de folhas novas (FN), floração (Flr) e frutificação (Frt); Teste de Watson Williams (F) para comparação das datas médias das fenofases de espécies lenhosas em áreas do cerrado em Barreirinhas (Barr) e no Parque Estadual do Mirador (PEM), Maranhão, Brasil.

	Barr	PEM	Barr	PEM	Barr	PEM	Barr	PEM	Barr	PEM	Barr	PEM	Barr	PEM
Local	QF-P	QF-P	FN-I	FN- I	FN-P	FN-P	Flr-I	Flr-I	Flr-P	Flr-P	Frt-I	Frt-I	Frt-P	Frt-P
Ângulo médio	285.73	241.48	272.68	265.81	318.76	286.48	293.03	244.63	300.97	257.39	306.58	255.02	321.00	266.65
Data média	17 Out	02 Set	04 Out	27 Set	20 Nov	18 Out	25 Out	06 Set	02 Nov	18 Set	07 Nov	16 Set	22 Nov	28 Set
Comprimento do vetor (r)	0.54	0.68	0.51	0.67	0.61	0.70	0.37	0.32	0.37	0.32	0.36	0.23	0.31	0.25
Desvio angular	55.13	45.52	56.84	46.31	50.88	44.67	64.28	66.82	64.07	66.48	64.66	71.28	67.40	70.28
Rayleigh (R)	46.19	88.28	43.68	86.86	51.48	89.80	31.88	41.27	32.22	42.17	31.24	29.17	26.50	31.96
Rayleigh (p)	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
Watson-Williams (BARR/PEM)	QF	FN-I	FN-P	Flr-I	Flr-P	Frt-I	Frt-P							
F	29.17	0.66	18.29	14.40	12.57	13.57	14.47							
p-valor	< 0.01	0.5763	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01							

O percentual de atividade das espécies em cada comunidade, referente a todas as fenofases, atingiu em geral valores maiores antes no PEM. Para todas as espécies, a queda foliar, que era constante ao longo do ano, mesmo que em pequenas proporções ou em poucos indivíduos, exibiu percentual de 100% de atividade.

A atividade de folhas novas nas duas áreas aumentaram progressivamente a partir do mês de junho, com máximo de espécies em outubro no PEM (entre 78 e 80% das espécies), e nos meses de novembro, com 88 % (primeiro ano) e janeiro com 97.7% (segundo ano) em Barreirinhas (Fig. 2A).

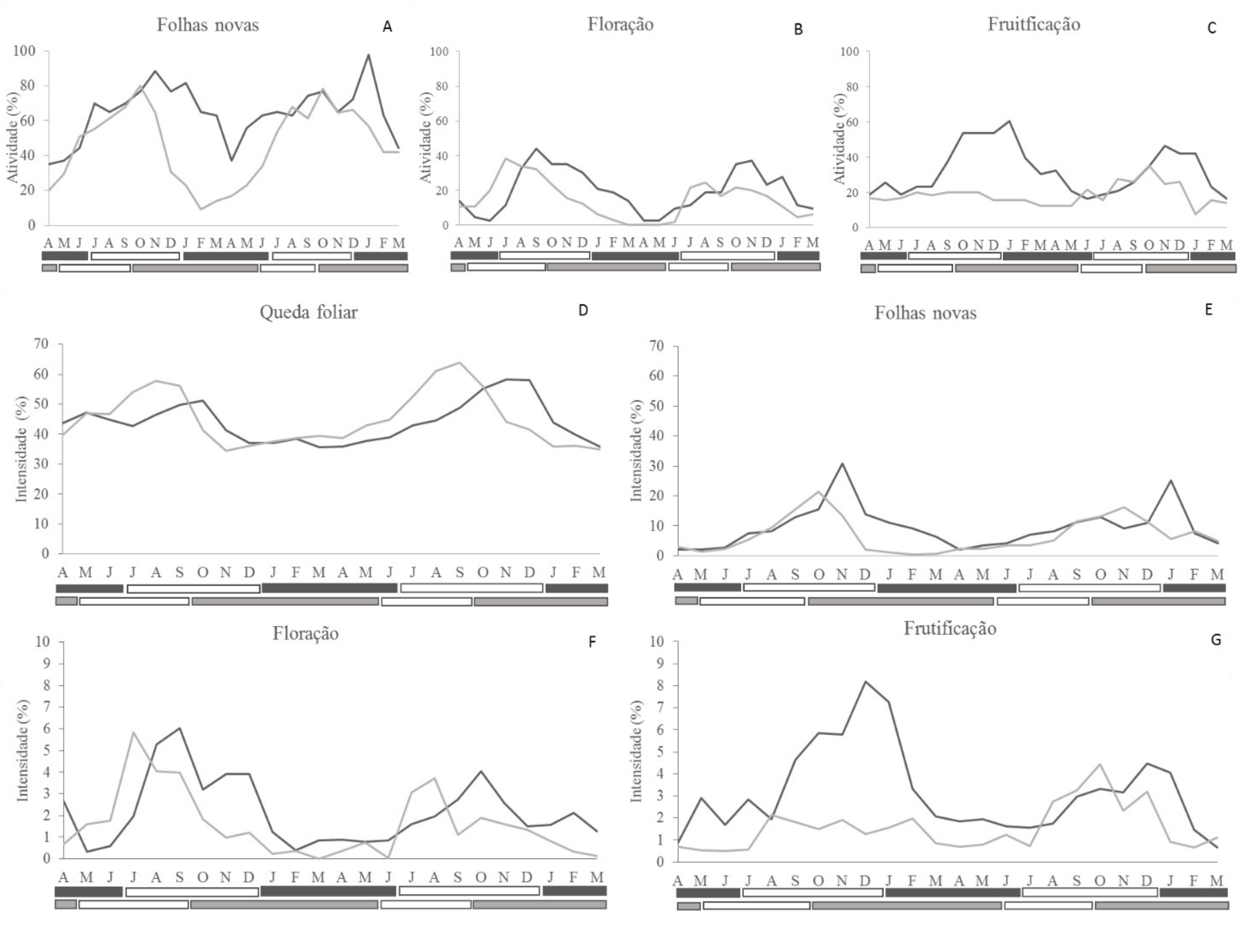

Figura 2: Distribuição mensal dos percentuais de atividade de folhas novas (A), floração (B) e frutificação (C); percentual de intensidade de queda foliar (D), folhas novas (E), floração (F) e frutificação (G) entre abril de 2014 e março de 2016, em áreas de cerrado em Barreirinhas (Barr – cinza escuro) e no Parque Estadual de Mirador (PEM - cinza claro), Maranhão, Brasil. Letras

representam as iniciais dos meses do ano. Barras preenchidas representam o período chuvoso, e barras não preenchidas representam o período seco.

O percentual de atividade para a floração aumentou rapidamente no primeiro ano nas duas áreas. No PEM, os meses de julho a setembro apresentaram percentuais maiores no primeiro ano, entre 32 e 40%, e nos meses de julho, agosto e outubro no segundo ano apresentaram percentuais entre 21.5 e 24.6%. Em Barreirinhas, de setembro a novembro, do primeiro ano, e de outubro a novembro do segundo, o percentual de espécies em floração foi de 34.8 a 44. 2% (Fig. 2B).

Quanto à frutificação, em Barreirinhas, os meses outubro a janeiro (primeiro ano), e de novembro a janeiro (segundo ano), exibiram maiores percentuais de atividade, variando de 41.8 à 60.5%. No PEM, os maiores percentuais foram observados somente no segundo ano, entre os meses de agosto (26.1%) e dezembro (35.4%) (Fig. 2C).

A intensidade das fenofases exibiu tendências semelhantes às datas de pico e percentuais de espécies, com aumento observado antes no PEM em relação a Barreirinhas (Fig. 2D-G). A queda foliar no PEM, teve maiores percentuais em agosto e setembro, variando de 56% a 63.9%. Em Barreirinhas, em outubro e novembro (primeiro ano), e em novembro e dezembro (segundo ano), a fenofase atingiu percentuais entre 41.4 e 58% (Fig. 2D).

O hábito foliar predominante diferiu entre as áreas. Em Barreirinhas, a maioria das espécies apresentou o hábito sempre verde (48.8%), seguida pelas brevidecíduas (32.5%) e decíduas (18.6%). No PEM, a maior proporção foi de espécies decíduas (35.4%), seguida por sempre verde (33.8%) e brevidecíduas (21.5%) (Tabela 1).

As folhas novas tiveram intensidade mais marcada no PEM nos meses de outubro (primeiro ano) e novembro (segundo ano), com 21 e 16%, respectivamente. Em Barreirinhas, os maiores percentuais foram em novembro (primeiro ano), com 30.7, e janeiro (segundo ano), com 25% (Fig. 2E).

A floração no PEM exibiu percentuais máximos de intensidade nos meses de julho (primeiro e segundo ano) e agosto (segundo ano), que variaram de 3 e 5.8%. Em Barreirinhas, a floração atingiu um máximo de 6% em setembro (primeiro ano), e de 4% em outubro (segundo ano) (Fig. 2F).

A frutificação mostrou um padrão definido em Barreirinhas, com maior intensidade em dezembro e janeiro nos dois anos, entre 4 e 8.2%. No PEM, houve um aumento não muito expressivo entre os meses de agosto e fevereiro do primeiro ano (entre 1.3 e 2.13%). No segundo ano, entre os meses de agosto e dezembro ocorreu um aumento que variou de 2.3 a 4.4% em (Fig. 2G).

Considerando a dispersão nas duas áreas, um total de 52 (66%) espécies apresentaram síndrome de dispersão zoocórica, 23 (29%) foram anemocóricas e 3 autocóricas (Tabela 1). Em Barreirinhas, 28 (65.1%) foram zoocóricas, 13 anemocóricas (30.2%) e 2 autocóricas (4.6%). No PEM, 43 (66.15%) espécies foram zoocóricas, 21 (32.31%) anemocóricas e 1 (1.54%) autocórica (Tabela 1). A autocoria, por apresentar somente uma espécie representante no PEM e duas em Barreirinhas, foi excluída das análises envolvendo a dispersão.

Quanto às síndromes, dentro de cada área, o pico médio da anemocoria em Barreirinhas ocorreu um pouco mais de dois meses antes da zoocoria, e no PEM com quase dois meses de diferença (Tabela 3). Entre as áreas, houve diferenças de aproximadamente dois meses entre as datas de início e pico de zoocoria, ocorrendo antes no PEM. Também diferiram as datas de pico para anemocoria, que ocorreu cerca de um mês e meio antes no PEM (Tabela 3). Os picos de zoocoria corresponderam ao início do período chuvoso no PEM e último mês seco em Barreirinhas, enquanto a anemocoria ocorreu durante a seca tardia.

Tabela 3: Testes de estatística circular para a sazonalidade e datas de início (I) e pico (P) médias por síndrome de dispersão de espécies lenhosas em frutificação em áreas de cerrado em Barreirinhas (Barr) e no Parque Estadual do Mirador (PEM), Maranhão, Brasil.

Dispersão	Zoocoria				Anemocoria			
	Início		Pico		Início		Pico	
Local	Barr	PEM	Barr	PEM	Barr	PEM	Barr	PEM
Ângulo médio	323.42	269.00	345.65	281.69	262.50	210.51	277.15	230.14
Data média	24/nov	30/set	17/dez	13/out	24/set	29/set	08/out	22/ago
Comprimento do vetor médio (r)	0.548	0.264	0.5436	0.278	0.413	0.248	0.416	0.298
Desvio angular	54.448	69.5306	54.7399	68.824	62.1029	70.25	61.9379	67.8549
Rayleigh (R)	22.486	37.176	22.2882	39.276	9.902	8.688	9.977	10.455
Rayleigh (p)	< 0.01	< 0.01	< 0.01	< 0.01	< 0.05	ns	< 0.05	< 0.05
	Intra área (zoocoria/anemocoria)				Entre áreas (Barr/PEM)			
	Barr - S	Barr - P	PEM - P		Zoo-S	Zoo-P	Ane-P	
F (Watson-Williams)	21.084	25.020	6.409		6.662	12.817	3.776	
p-valor	< 0.0001	< 0.0001	0.0122		0.0109	0.0008	0.049	

Quanto à relação com as variáveis climáticas, todas as fenofases no PEM apresentaram associação positiva significativa com temperatura máxima. Adicionalmente, queda foliar e floração também mostraram associação com temperatura mínima, negativa, e frutificação com fotoperíodo (Tabela 4). Em Barreirinhas, queda foliar e floração exibiram associação com temperatura máxima, ambas positivas (Tabela 4). Folhas novas e a frutificação mostraram relação positiva com o fotoperíodo (Tabela 4).

Tabela 4: Análise de regressão múltipla avaliando o efeito das variáveis climáticas sobre a fenologia de comunidades lenhosas de cerrado em Barreirinhas (Barr) e no Parque Estadual do Mirador (PEM), Maranhão, Brasil. R^2= coeficiente de determinação; *p=probabilidade*; ß= coeficiente de regressão. Variáveis: Tmin=temperatura mínima média do ar; Tmax= temperatura máxima média do ar; Foto=fotoperíodo.

Local	Queda foliar	Folhas novas	Floração	Frutificação
PEM	$R^2 = 0.83$ $p < 0.01$	$R^2 = 0.69$ $p < 0.05$	$R^2 = 0.60$ $p < 0.01$	$R^2 = 0.57$ $p < 0.01$
	Tmax $\beta = 4.4$	Tmax $\beta = 2.2$	Tmax $\beta = 0.61$	Tmax $\beta = 0.39$
	Tmin $\beta = -2.9$		Tmin $\beta = -0.85$	Foto $\beta = 3.30$
Barr	$R^2 = 0.73$ $p < 0.01$	$R^2 = 0.55$ $p < 0.01$	$R^2 = 0.43$ $p < 0.05$	$R^2 = 0.62$ $p < 0.01$
	Tmax $\beta = 4.1$	Foto $\beta = 85.27$	Tmax $\beta = 0.29$	Foto $\beta = 25.92$

4. Discussão

As comunidades exibiram significativa sazonalidade em relação aos eventos fenológicos avaliados, com ocorrência e/ou intensificação de todas as fenofases concentradas na segunda metade do período seco, principalmente nos últimos dois meses que antecedem o início das chuvas. No início do período chuvoso também pode ser verificada alta intensidade e ocorrência dos eventos de folhas novas e frutificação. As diferenças na temperatura ou fotoperíodo mostram-se importantes gatilhos associados à ocorrência ou intensificação das fenofases durante o período seco ou na transição deste para o chuvoso. A ocorrência antecipada das fenofases no PEM em relação à Barreirinhas justifica possíveis ajustes às condições climáticas locais e demonstra que comunidades do cerrado são sensíveis para responder às variações presentes em baixas latitudes.

Estudos realizados em savanas têm apontado para a ocorrência ou intensificação das fenofases durante o período seco ou na transição deste para o chuvoso (Williams *et al.* 1997, 1999; Pirani *et al.* 2009; Silvério e Lenza 2010; Seghieri *et al.* 2012). Tais respostas podem variar entre áreas quanto ao período de ocorrência, já que as chuvas, temperatura e disponibilidade de luz podem apresentar diferentes padrões de distribuição ao longo do ano em áreas com regimes climáticos distintos. Assim, alterações nesses fatores são, presumivelmente, determinantes para a previsão dos eventos fenológicos em áreas de savanas.

As duas comunidades apresentaram um aspecto semidecíduo, com espécies apresentando diferentes níveis de manutenção de folhas na copa ao longo do ano, condicionando do hábito sempre-verde até o completamente decíduo. A sazonalidade nas datas de pico e o maior percentual de intensidade de queda durante o período seco nas duas áreas refletem estratégias que permitem às plantas evitar que seus tecidos desidratem (Franco *et al.* 2005; Meinzer *et al.* 2008; Goldstein *et al.* 2008; Scholz *et al.* 2016), especialmente quando há um aumento da temperatura, o que está possivelmente associado ao aumento da demanda evaporativa (Dalmolin *et al.* 2015). Tal resposta, frequentemente associada a mecanismos fisiológicos, anatômicos e morfológicos – como ajuste do potencial osmótico dos tecidos, raízes profundas, baixa densidade do lenho, alterações na condutância estomática e no padrão de crescimento – cria condições que permitem às plantas aumentarem sua capacidade de absorção e/ou retenção de água na seca (Borchert 1994; Franco *et al.* 2005). Essas adaptações favorecem eventos de produção e crescimento, como a formação de folhas e flores, que necessitam de água e nutrientes para se desenvolverem (Borchert 1996).

A presença de folhas novas nas duas comunidades aumentando ainda durante o período seco e se estendendo até o início do período chuvoso é um fenômeno também evidenciado em outros estudos no cerrado (Rivera *et al.* 2002; Lenza e Klink 2006; Figueiredo 2008; Pirani *et al.* 2009; Dalmolin *et al.* 2015) e savanas da África (Archibald e Scholes 2007; Guan *et al.* 2014; Ryan *et al.* 2017). Esta fenofase tem sido associada à temperatura (Pirani *et al.* 2009; Silvério e Lenza 2010; Seghieri *et al.* 2012) e fatores relacionados à radiação solar, como fotoperíodo ou insolação (Rivera *et al.* 2002; Archibald e Scholes 2007; Ryan *et al.* 2017), mostrando neste estudo associação com o aumento da temperatura no PEM e do fotoperíodo em Barreirinhas.

A comunidade de Barreirinhas apresentou durante a maior parte do período de estudo, maiores percentuais de atividade e de intensidade para as folhas novas, assim como menores valores do vetor r para esta fenofase e para queda foliar em relação ao PEM. Esses resultados indicam uma menor sazonalidade dos eventos vegetativos em Barreirinhas. Tal fato associado à predominância de espécies sempre verde nessa área e de decíduas no PEM, apontam para a existência de diferenças quanto ao grau de deciduidade das duas comunidades, inclusive entre espécies comuns às áreas.

Diferenças quanto ao grau de deciduidade entre as áreas podem aparecer como resultado de restrições filogenéticas, em função da composição de espécies (Davies *et al.* 2013), como também das características climáticas locais (Singh e Kushwaha 2006). Considerando, inclusive, que algumas espécies comuns às duas áreas exibem diferenças quando à deciduidade, são factíveis as respostas orientadas pelas diferenças climáticas. Nesse caso, seria esperado que a comunidade do PEM experimentasse um menor estresse hídrico, por apresentar durante o período de estudo, um período seco mais curto do que em Barreirinhas, e, consequentemente, menor deciduidade. No entanto, um fato contrário ocorre, o que significa que outras variáveis podem influenciar esta resposta, como diferenças na profundidade do lençol freático (Oliveira *et al.* 2015) ou, mais provavelmente, o maior volume de chuvas em Barreirinhas, que pode favorecer a manutenção de maior umidade no solo nessa área e, consequentemente, as diferenças quanto à deciduidade.

Com relação à floração, o padrão anual, verificado na maioria das espécies desse estudo, converge com outros em áreas de savanas (Williams *et al.* 1999; Singh e Kushwaha 2006; Lenza e Klink 2006; Pirani *et al.* 2009; Silvério e Lenza 2010; Neves *et al.* 2017), bem como a sua sazonalidade durante o período seco (Williams *et al* 1999; Singh e Kushwaha 2006; Pirani *et al*. 2009; Silveira *et al*. 2015) ou na sua transição deste para o chuvoso (Lenza e Klink 2006; Selwyn e Parthasarathy 2006; Silvério e Lenza 2010). A associação com temperaturas mais elevadas, que ocorrem em diferentes períodos em cada área, pode sinalizar a proximidade com o período chuvoso seguinte, quando o desenvolvimento e/ou dispersão dos frutos pode ser vantajoso para muitas espécies (Williams *et al.* 1999).

Neste estudo, a floração predominou nos meses finais do período seco, o que possivelmente favorece a atração por polinizadores (Janzen 1967) e a sincronização do estabelecimento das sementes com o início da estação chuvosa (Silveira *et al*. 2015), indicando não existir limitação da reprodução por escassez de água no ambiente. Tal ocorrência está associada às conhecidas adaptações para reserva e alocação de água e nutrientes em espécies de savanas (Goldstein *et al*. 2008; February e Higgins 2016) também requeridas para a floração.

Quanto à frutificação, um padrão mais variável em sua distribuição temporal é esperado em estudos em cerrado (Batalha e Martins 2004; Lenza e Klink 2006; Tannus *et al.* 2006; Pirani *et al.* 2009; Morellato *et al.* 2013), indicando a presença de diferentes estratégias relacionadas à dispersão, germinação e estabelecimento das espécies em nível de comunidade. Neste estudo, foram encontradas espécies frutificando ao longo de todo o ano, com proporções ligeiramente maiores no final do período seco e início do período chuvoso. A sazonalidade menos marcante desse evento indica que as espécies apresentam estratégias e mecanismos fisiológicos diferentes, que permitem um número regular de espécies se dispersando ao longo do ano.

O aumento da frutificação verificado nos meses finais do período seco e iniciais do período chuvoso, que se associam às variações na temperatura ou fotoperíodo, permitem inferir que um maior número de espécies apresenta esse comportamento a fim de sincronizar a germinação ao período chuvoso (Van Schaik *et al.* 1993; Silveira *et al.* 2015). Assim, as plântulas poderiam desenvolver o sistema radicular durante a estação de chuvas, antes de serem submetidas ao estresse hídrico da estação seca subsequente (Fenner 2012). Em Barreirinhas, os maiores percentuais de espécies em frutificação e de intensidade da fenofase pode ser atribuído a diferentes fatores não avaliados aqui, como os relativos à abundância de polinizadores ou competição por eles entre as espécies, ou às condições de aquisição e manutenção de recursos que permitam o desenvolvimento de frutos. Assim, avaliações adicionais são recomendadas para elucidar pontos importantes acerca dessas diferenças.

Considerando as síndromes de dispersão, estudos realizados em ecossistemas tropicais têm apontado a ocorrência de diferentes proporções quanto aos principais modos de dispersão encontrados: zoocoria, anemocoria e autocoria (Bullock *et al.*1995; Griz and Machado 2001; Ishara e Maimoni-Rodella 2011; Jacobi e Carmo 2011; Kuhlmann e Ribeiro 2016).

No cerrado, tais diferenças são principalmente associadas ao regime hídrico, à formação vegetal predominante e às forma de vida (Silva *et al.* 2011; Kuhlmann e Ribeiro 2016), com a zoocoria sendo a estratégia mais representativa entre as espécies lenhosas, arbustivas e arbóreas (Batalha e Martins 2004; Lenza e Klink 2006; Tannus *et al.* 2006; Kuhlmann e Ribeiro 2016). Neste estudo, quando observadas suas distribuições e datas médias de início, é possível identificar diferenças dentro e entre áreas, quanto às dispersões anemocóricas e zoocóricas. O pico de anemocoria antes da zoocoria está associado ao favorecimento desses modos de dispersão nas estações seca e chuvosas, respectivamente.

A dispersão de espécies anemocóricas no período seco facilita tanto a abertura dos frutos como a dispersão das sementes, condições estas favorecidas pelo aumento nas velocidades dos ventos, pela baixa umidade do ar e redução das folhas na vegetação (Frankie *et al.* 1974). Já a zoocoria, que apresentou picos no final do período seco e início do chuvoso, é favorecida pelo aumento das chuvas, quando os frutos carnosos podem se manter atrativos para a fauna por um longo tempo (Kuhlmann e Ribeiro 2016). Entre áreas, os resultados reforçam que as diferenças climáticas encontradas exercem influência sobre o período de frutificação dos diferentes grupos de dispersão, com a ocorrência antecipada da frutificação das espécies anemocóricas e zoocóricas no PEM em relação à Barreirinhas.

Por fim, os resultados encontrados neste estudo indicam que as respostas manifestadas em nível de comunidade em áreas de cerrado podem sofrer ajustes em relação às variáveis climáticas, mesmo quando suas variações não são amplas. Assim, pequenas alterações no clima são suficientes para direcionar diferentes respostas nas comunidades de plantas. No caso de áreas de cerrado, as variações na temperatura ou comprimento do dia (possivelmente também um adicional aumento na disponibilidade de luz causado pela diminuição das nuvens) que ocorrem durante o período seco, têm se mostrado importantes sobre fenologia (Pirani, *et al.* 2009; Silvério e Lenza 2010; Barbosa *et al.* 2012; Vogado *et al.* 2016; Garcia *et al.* 2017; Neves *et al.* 2017), e apoiam os resultados deste estudo. As respostas encontradas ampliam o conhecimento de como populações e comunidades se comportam em diferentes regimes climáticos e fornece subsídios para a previsão de suas possíveis respostas frente às mudanças climáticas recentes.

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CAPÍTULO II: Do conspecific populations exhibit divergent phenological patterns? A study case with widespread savanna species

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Abstract

Widespread savanna tree species can grow and survive at sites that diverge in water availability and seasonality, thus these species may be able to adjust their phenology in response to site variations. Here we evaluated vegetative and reproductive phenology in five woody species whose populations grow at two savannas sites under divergent climatic regimes, inserted in a large transitional zone between the Amazon forest and the semi-arid region. Patterns of leaf fall, leaf flush and flowering were recorded monthly for five woody species growing under longer (LDS) and shorter (SDS) dry seasons. We evaluated the seasonality, the start and peak dates for phenological events and the associations between phenophases and climatic data. We found a close relationship between phenological events and site temperatures, with phenological peaks in the LDS occurring, in general, about one to three months later than at the SDS site. Leaf fall coincides with warmer and drier periods when the day length is shorter. Leaf production and flowering were associated with increased day length in some populations. Our results support the hypothesis that the conspecific populations have a high degree of association with climatic variables, especially temperature and day length, showing distinct phenological responses associated to the local climatic differences.

Keywords: Cerrado; Day length; Phenology; Seasonality; Temperature.

1 Introduction

Phenological events are associated with a wide variety of ecological processes (Forrest and Miller Rushing, 2010), and are therefore important to our understanding of species-level relationships (Goulart et al., 2005; Zalamea et al., 2011; Dalmolin et al., 2015) and adaptive mechanisms (Grogan and Schulze, 2012; Worbes et al., 2013; Guan et al., 2014). Phenology can also explain the temporal organization of plant communities (Stevenson et al., 2008; Kushwaha et al., 2011; Diez et al., 2012; Hawes and Peres, 2016; Ryan et al., 2017), because phenological events are linked to climatic and biotic factors (Pau et al., 2011; Tang et al., 2016), affecting the capacity of plants to acquire resources for growth and reproduction (Nord and Lynch, 2009; Nord et al., 2011).

Phenological responses of plant communities may diverge between sites, even if those sites are similar in species composition (Forrest et al., 2010). This suggests that climatic parameters are a stronger influence than species identity in determining phenological behavior (Pau et al., 2011). This may be especially evident for plant communities of the Brazilian savanna (Cerrado), where it is possible to find a great variety of phenological patterns following climatic variations along an extensive latitudinal and altitudinal gradient (Bulhão and Figueiredo, 2002; Batalha and Martins, 2004; Pirani et al., 2009; Silva et al., 2011; Rossatto 2013). The wide climatic variations in the Cerrado are due to its occurrence in disjunctive areas in the Amazon; in a continuous strip that runs from Brazil's Northeast to Center-South regions; and in the Southeast region of the country (Bridgewater et al., 2004). This continental occurrence subjects Cerrado plant communities to distinct regimes of dry season duration and annual rainfall amount (Alvares et al., 2013).

In tropical and sub-tropical regions, the amplitude in phenological events is often correlated with different climatic variables, including water availability (Dalmolin et al., 2015), photoperiod and light intensity (Yeang, 2007; Zimmerman et al., 2007) and temperature variations (Pau et al., 2013). For savannas in particular, water availability − especially its decrease during the end of the wet season − is cited as one of the main factors driving leaf fall patterns (Bulhão and Figueiredo, 2002; Lenza and Klink, 2006; Rossatto et al., 2009; Guan et al., 2014). Flowering and leaf renewal are concentrated during the dry period; but especially during the transition from the late dry to the rainy season, a time of the year when day length and temperatures increase and first rains begin to fall (Figueiredo, 2008; Lenza and Klink, 2006; Pirani et al., 2009; Borges and de Assis Prado, 2014; Dalmolin et al., 2015; Ryan et al., 2017). The production of leaves and flowers during this transitional period has some advantages for savanna plants: the canopy reaches full development and is ready for maximal carbon gain just as the first rains start (Franco et al., 2005); an early flowering allows sufficient time for the complete fruit production and seed dispersal, which increases the success of seed germination and establishment (Batalha and Martins 2004). However, if the rainy period was delayed, and plants were not plastic enough to adapt their strategies, they would suffer from prolonged drought.

Although a typical regime of alternation between dry and rainy periods prevails in the savannas, the duration of the dry season, distribution of precipitation, average air temperatures and day length duration are highly variable (Rivera et al., 2002; Silva et al., 2008; Alvares et al., 2013). Temperature and day length are considered important drivers for phenological events in savanna species (Rivera et al., 2002), especially for vegetative growth. Ascertaining how species respond to such differences enables the predictions of changes in phenological events and of population dynamics, and contributes importantly to the assessment of how climate change affects natural populations (Franco et al., 2014). The use of conspecific populations (represented by individuals of the same species, but growing at different sites) is an interesting approach to comprehend local adaptations to climatic aspects (Panchen and Gorelick, 2016).

In the present study, we evaluated vegetative and reproductive phenology in five species whose populations grow at two savannas sites (Cerrado), under distinct climatic regimes, in a large transitional zone between the Amazon forest and the semi-arid region. These sites exhibit differences in the duration of the dry season: one of them shows higher total rainfall, but a longer dry season, while the other have lower rainfall, but a shorter dry season. Additionally, short dry season site shows the highest temperature and longest day length variations earlier than the long dry season site. This study aimed to answer whether: 1) differences in the seasonal climatic patterns of these sites influence the period, start and peaks, of the phonological events, 2) phenological events are associated with temperature and day length independently of the dry season duration. We hypothesize that if phenological phenomena are intrinsically linked to climatic variables at these sites, the shorter dry season will promote phenological events to occur earlier in comparison to the longer dry season. These responses will occur because leaf events and flower production are supposedly related to temperature and day length, which increase from mid to late dry season on each site and are indicative of the following rainy period.

2 Material and methods

2.1 *Study sites and climate*

We conducted our study at two savanna sites (regionally known as Cerrado stricto sensu) in the northeastern region of Brazil: the first site is located at Barreirinhas municipality (03°01′17″S, 43°06′28″ W) and the second at the Mirador State Park (06°37′55″S, 45°52′38″W), both in Maranhão State, Brazil (Fig. 1). The climate is As in Barreirinhas, and Aw in Mirador State Park (Alvares et al., 2013), both of which are classified as tropical with two distinct seasons – dry and rainy – but differing in terms of totalrainfall and in the dry season length, as observed during the study period (Fig. 2). For the sake of simplification and to clearly associate each study site with its respective climate, the Barreirinhas region will be referred to as the longer dry season (LDS) region, and Mirador State Park, as shorter dry season (SDS) region (Fig. 2).

Fig. 1 Sites selected for phenological observations: Barreirinhas (longer dry season − LDS) and Mirador State Park (shorter dry season − SDS), Maranhão State, Brazil.

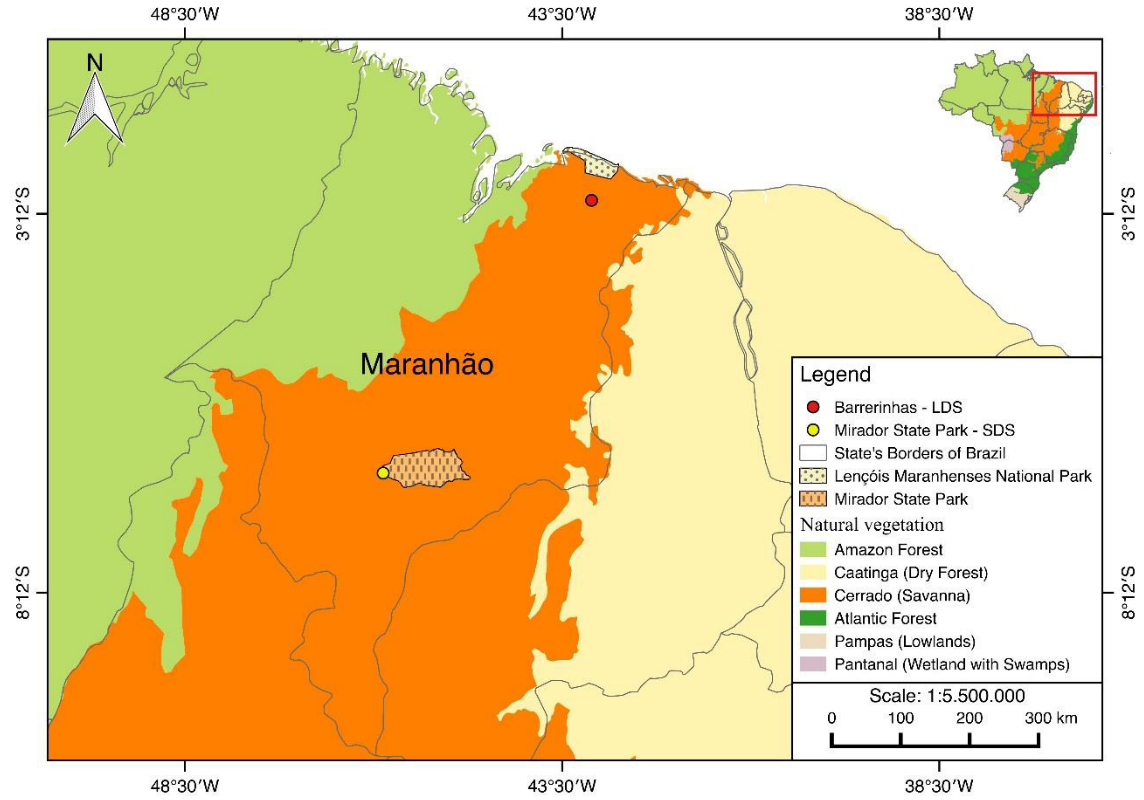
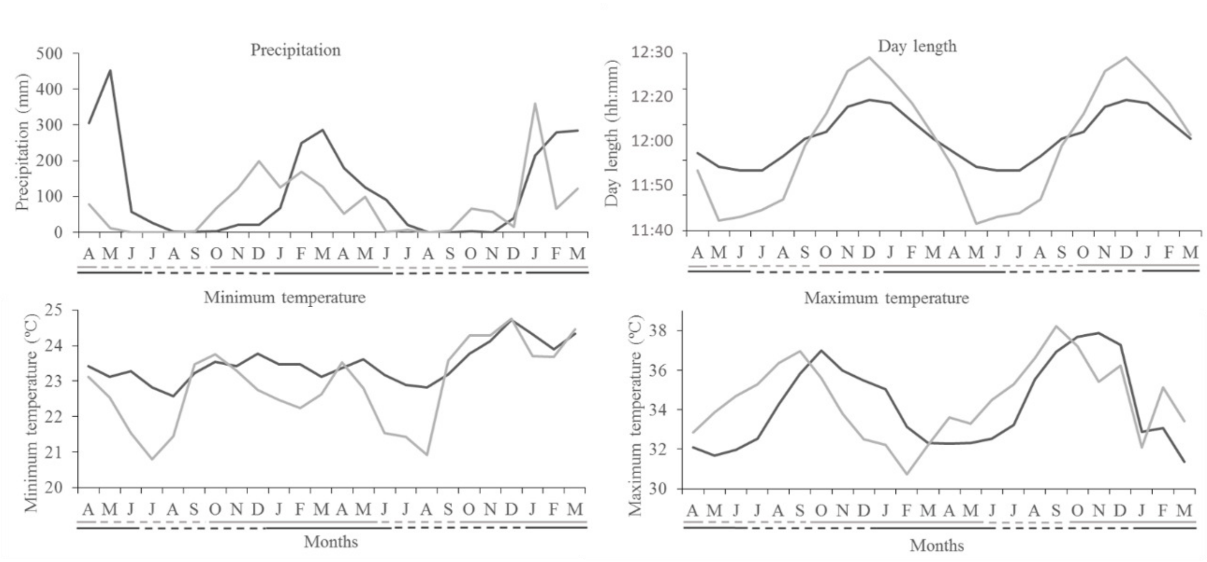


Fig. 2 Climatic data (April 2014 to March 2016) for LDS − longer dry season site (dark gray lines) and SDS − shorter dry season site (light gray lines), Maranhão State, Brazil. Rainy season indicated by continuous lines below the x axis; dry season indicated by dotteddashed lines below the x axis.



The annual historical rainfall average for a 30-year period in LDS (from 1986 to 2016) was 1,700 mm; average monthly air temperature is around 27 °C, with a mean maximum of 34 °C, mean monthly minimum of 23 °C, and a dry period between July and late December, when the first rains begin to fall. The thermal amplitude, considering mean monthly data, varies from 8 to 14 °C (INMET − Instituto Nacional de Meteorologia/Chapadinha Station (n° 82.382), 2017). The day length varies from 11 h and 57 min in June to 12 h and 18 min in December (Source: http://www.sci.fi/~benefon/sol.html). Altitudes around 90 m are predominant and the soils are sandy yellow latosols, with a high content of coarse sand and clay, being generally poorer than SDS soil (Appendix A, Supplementary material).

In SDS, the annual historical average rainfall was 1,200 mm; the monthly mean air temperature of 27 °C, monthly mean maximum of 33 °C and monthly mean minimum of 22 °C. Although SDS and LDS sites show similar ranges of mean temperature variation, mean monthly data show that the SDS region has a greater thermal amplitude − from 7 to 16 °C (INMET, Balsas Station (n° 82.768), 2017) −, and a dry period extending from May to September. Despite little variation, the day length also has greater amplitude earlier in SDS area, going from 11 h and 44 min in June, to 12 h and 31 min, in December (Source: http://www.sci.fi/~benefon/Sol.html). The altitude ranges from 300 to 600 m, and the predominant soils in the region are litholic and yellow latosols, of the sandy loam type, with a high content of fine sand, and about 10% clay (Appendix A, Supplementary material). The monthly climatic data of total precipitation, mean maximum and mean minimum air temperatures (Source: http://www.inmet.gov.br/portal/) and day length (Source: http://www.sci.fi/~benefon/sol.html), for the period from April 2014 to March 2016, were obtained for association with the phenological data.

2.2 *Phenological study*

The vegetative (leaf fall and flush) and reproductive (flowering) phenology were recorded monthly in populations of five woody species that are common to the study sites and widely distributed in typical savanna areas of the Brazilian territory: *Byrsonima crassifolia* (L.) Rich. (Malpighiaceae), *Caryocar coriaceum* Wittm. (Caryocaraceae), *Hirtela ciliata* Mart. & Zucc. (Chrysobalanaceae), *Qualea grandiflora* Mart. (Vochysiaceae) and *Plathymenia reticulata* Benth. (Fabaceae). We marked and monitored all individuals of these species in 20 plots (20 × 20 m), covering 1.6 ha at each site. We sampled individuals with a minimum of 10 cm of trunk circumference at the ground level. Conspecific populations presented different densities in each area, implying a different number of individuals sampled per species. The number of individuals in LDS and SDS were, respectively: 69 and 11 for *B. crassifolia*; 13 and 26 for *C. coriaceum*; 19 and 27 for *H. ciliata*; 28 and 48 for *Q. grandiflora* and 140 and 11 for *P. reticulata*. Vouchers for these species are deposited in the Universidade Federal do Maranhão herbarium (Herbarium MAR).

Over a period of two years (between April 2014 and March 2016), we made monthly visual estimates of the percentage of crown area in each individual that presented the following signs: losing brown leaves (for leaf fall); flushing new leaves (for leaf flush); flower buds and/or open flowers (for flowering). Estimates for leaf fall, leaf flush and flowering were made using a scale of five categories: 0, 1, 2, 3 and 4, at intervals of 25% (0: 0%; 1: 1–25%; 2: 26–50%; 3: 51–75% and 4: 76–100%), following the methodology described by Fournier (1974). We calculated monthly averages of the percentage for each studied population, using the sum of the intensity values obtained for all individuals and dividing by the maximum possible value (number of individuals multiplied by four). This value was converted into a percentage.

2.3 *Statistical analysis*

We applied circular statistics to detect seasonal trends at the start (the mean date in which each population manifested the phenophase for the first time) and peak dates (the mean date in which each population showed the highest value for intensity) for a given phenological event. We also compared phenological patterns between the conspecific populations at both sites. For this, the months were converted to angles at 30° intervals. The circular parameters were estimated for each conspecific population - mean start and peak dates and length of mean vector (r).

To test the occurrence of seasonality, the Rayleigh Z test was applied. If the probability value is significant, the concentration intensity around the mean angle, represented by the vector r, is considered as a measure of the degree of seasonality, ranging from zero to one. It was not possible to determine the mean date of leaf fall start, since the activity in this phenophase was continuous in all individuals of the evaluated species, though it differed in intensity of occurrence. We performed the Watson-Williams two-sample (F) test when the mean angle was significant, to determine whether conspecific populations exhibit a similar seasonal pattern across areas (Zar, 2010). The analyses related to circular statistics were performed in the software ORIANA 4.0 (Kovach, 2011).

The species *P. reticulata* had only one flowering record in SDS and was therefore excluded from the statistical evaluations of this phenophase. In addition, we used multiple regression analysis to evaluate the association between phenological events (dependent variables) and monthly climatic variables, such as total precipitation, mean maximum and minimum air temperatures, and day length (independent variables). For these analyses, we showed only the significant relationships and the respective beta values (the effect of the independent variable on the dependent variable) (Zar, 2010).

3 Results

All species exhibited seasonal behavior on their peak dates of leaf fall as well on the start and peak dates of leaf flushing and flowering (Fig. 3 Table 1). In LDS, these phenomena were concentrated between July and December, whereas in SDS, they occurred from August to October, predominantly in the driest months. Independently of the species, the phenological phenomena tended to occur about one to three months earlier in SDS than in LDS (Fig. 3 Table 1).

Fig. 3 Fournier intensity (percentage) for leaf fall, leaf flushing and flowering in the species *B. crassifolia*, *C. coriaceum*, *H. ciliata*, *Q. grandiflora* and *P. reticulata*, for LDS − longer dry season site (dark gray lines) and SDS − Sshorter dry season site (light gray lines), Maranhão State, Brazil. Rainy season indicated by continuous lines below the x axis; dry season indicated by dotted lines below the x axis.

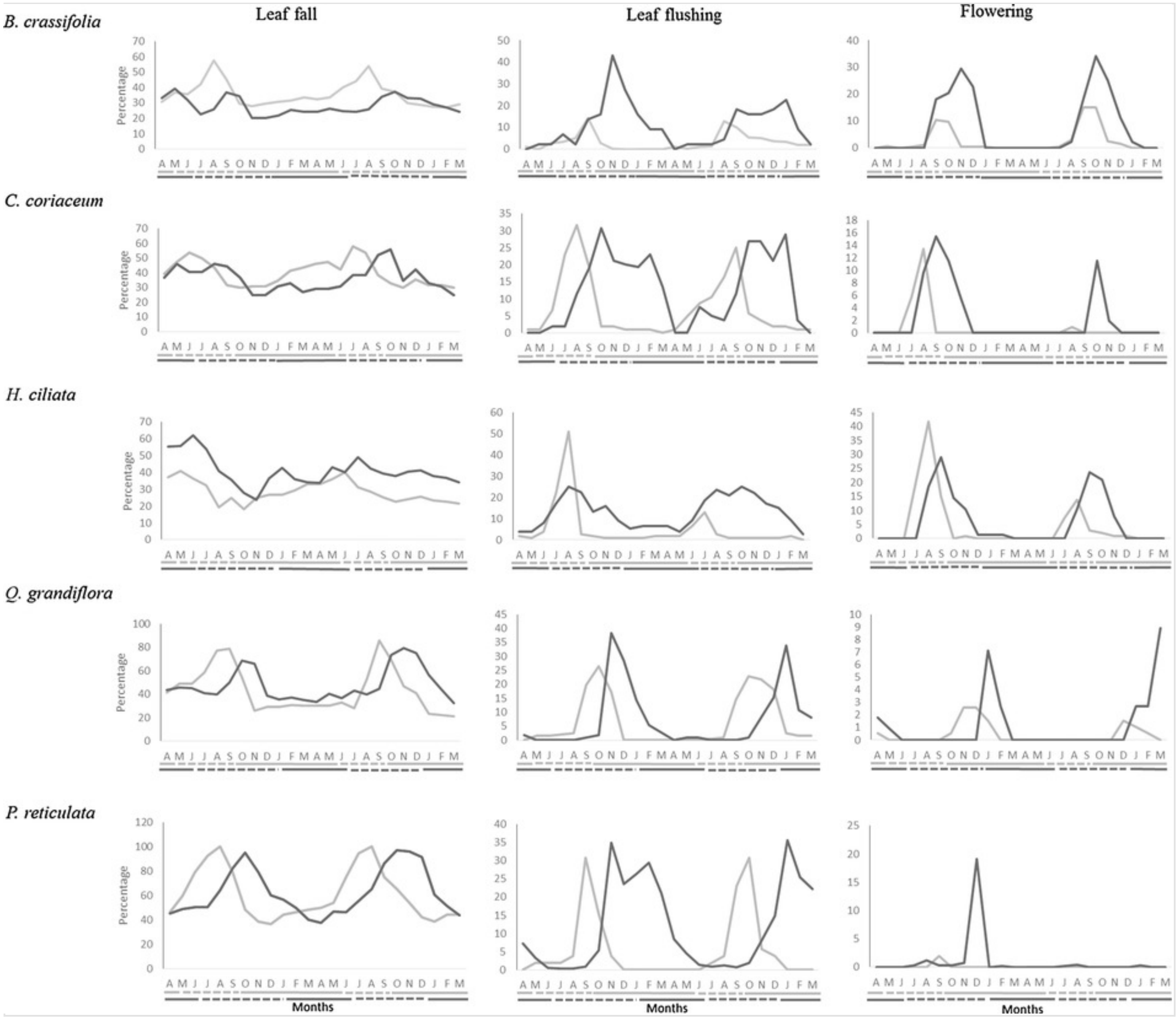


Table 1 Circular statistics for seasonality occurrence and mean dates for leaf fall peak and the start and peak for leaf flushing and flowering in savanna woody species subjected to longer dry season (LDS) and shoter dry season (SDS), Maranhão State, Brazil. LMV: length of the mean vector; LF = leaf fall; LFl = leaf flushing; Flw = flowering; P = peak; S = start; na = not available. Significance levels: * P < 0.001.

,Sites		LDS					SDS				
Species	Statistics	LF-P	LFl-S	LFL-P	Flw-S	Flw-P	LF-P	LFl-S	LFL-P	Flw-S	Flw-P
B. crassifolia	Mean Date	27 Oct (295.8°)	01 Oct (270.1º)	01 Dec (330.2º)	15 Oct (284º)	09 Nov (308.7º)	25 Aug (233.6º)	25 Sep (263.9º)	11 Oct (279.5º)	1 Oct (269.9º)	14 Oct (282.8º)
	LMV (r)	0.92	0.72	0.84	0.89	0.89	0.82	0.83	0.82	0.9	0.93
	Rayleigh Test (Z)	17.74^*	11.37^*	15.54^*	16.81^*	16.62^*	72.04^*	91.13^*	87.68^*	66.78^*	71.85^*
C. coriaceum	Mean Date	30 Sep (268.5°)	25 Sep (263.6°)	05 Nov (304.1°)	10 Oct (279°)	19 Oct (287.5°)	02 Aug (210.9°)	12 Aug (220.4°)	05 Sep (244.5°)	17 Aug (225.2°)	12 Aug (220.8°)
	LMV (r)	0.86	0.75	0.65	0.87	0.92	0.85	0.71	0.75	0.96	0.99
	Rayleigh Test (Z)	17.86^*	14.74^*	9.59^*	8.89^*	10.07^*	31.6^*	24.08^*	26.8^*	6.49^*	6.92^*

,Sites		LDS					SDS				
Species	Statistics	LF-P	LFl-S	LFL-P	Flw-S	Flw-P	LF-P	LFl-S	LFL-P	Flw-S	Flw-P
H. ciliata	Mean Date	22 Jul (199.6°)	20 Jul (197.6°)	14 Sep (252.6°)	11 Sep (249.7°)	06 Out (274.7°)	29 Jun (176.6°)	04 Aug (212.4°)	14 Aug (222.4°)	15 Aug (223.3°)	29 Aug (236.9°)
	LMV (r)	0.45	0.67	0.8	0.96	0.91	0.94	0.87	0.92	0.94	0.96
	Rayleigh Test (Z)	6.02*	17.86*	23.02*	29.51*	25.77*	7.95*	32.72*	35.66*	30*	32.36*
Q. grandiflora	Mean Date	19 Nov (317.9°)	20 Dec (348.9°)	09 Jan (8.1º)	24 Feb (53.7°)	25 Feb (55.12°)	23 Sep (261.5°)	01 Oct (269.9°)	13 Nov (312.3°)	17 Dec (345.8°)	11 Dec (339.7°)
	LMV (r)	0.89	0.81	0.86	0.91	0.9	0.88	0.72	0.79	0.93	0.52
	Rayleigh Test (Z)	34.6*	37.01*	38.93*	19.03*	18.86*	72.8*	50.26*	54.83*	12.05*	3.84*
P. reticulata	Mean Date	05 Nov (304.8º)	22 Dec (350.6º)	01 Jan (0.9º)	28 Dec (356.9º)	30 Dec (358.2º)	19 Ago (226.9º)	18 Set (257.4º)	08 Oct (276.7º)	na	na
	LMV (r)	0.95	0.86	0.85	0.93	0.98	0.94	0.84	0.91		
	Rayleigh Test (Z)	64.09*	52.98*	51.35*	62.51*	69.50*	23.43*	17.87*	21.72*		

For *B. crassifolia*, the mean start and peak dates occurred from October to December at LDS, and from August to October in SDS. The events showed significantly different start and peak dates (Table 2), with a delay of few days to two months at LDS (Table 1). The intensity of events exhibited the same trend, with uneven distribution between sites and higher proportions occurring earlier in SDS than in LDS. The duration of leaf flushing and flowering was longer in LDS than in SDS (Fig. 3).

Table 2 Watson Williams test results for comparisons among the mean start and peak dates for leaf fall, leaf flushing and flowering in savanna species subjected to longer (LDS) and shorter dry season (SDS), Maranhão State, Brazil. LF = leaf fall; LFl = leaf flushing; Flw = flowering; S = start; P = peak; na = not available. F = circular statistical value; p = probability value.

Species	Statistics	LF-P	LFl-S	LFl-P	Flw-S	Flw-P
B. crassifolia	F	61,219	0.45	36,856	3,528	20,243
	p	<0.001	0.503	<0.001	0.063	<0.001
C. coriaceum	F	47,601	14,405	22,015	16.67	16.096
	p	<0.001	<0.001	<0.001	<0.001	<0.001
H. ciliata	F	1,155	2,584	18,046	33,029	54,258
	p	0.289	0.112	<0.001	<0.001	<0.001
Q. grandiflora	F	115,156	116,974	78,434	65,327	20,071
	p	<0.001	<0.001	<0.001	<0.001	<0.001
P. reticulata	F	76.517	63.753	67.109	na	na
	p	<0.001	<0.001	<0.001		

For *C. coriaceum*, the mean dates of phenophases occurred from September to November in LDS, and from August to September in SDS (Table 1), with all phenophases showing significant differences between sites (Table 2). In LDS, start and peak events for this species occurred about one to two months later than in SDS (Table 1), and the duration of leaf flushing and flowering was longer. In SDS, higher intensity percentages of all phenophases occurred earlier than in LDS (Fig. 3).

For *H. ciliata*, the mean dates occurred from July to October in LDS, and from June to August in SDS. The events followed a pattern similar to those reported for the previous species, with a delay of one to two months in LDS (Table 1), except to leaf flushing start. As for the activity of the phenophases percentages, leaf fall had the most irregular pattern throughout the year. The highest proportions of leaf flushing and flowering intensities in SDS preceded those in LDS, where their duration was prolonged (Fig. 3).

Between *Q. grandiflora* populations, the mean dates of phenophases were concentrated between November and February in LDS, and between September and December in SDS. The delay for this species was about two to almost three months (Table 1), with different mean start and peak dates (Table 2). The highest proportions of all SDS phenophases preceded those of LDS (Fig. 3). The leaf flushing and flowering pattern in LDS, referring to the phenophases duration, was not verified for this species (Fig. 3).

Phenological events in *P. reticulata* differed between sites (Table 2), with start and peak dates distributed from November to January in LDS and from August to October in SDS, with a delay of three months for all phenophases in LDS (except to Flow-S and Flow-P) (Table 1). Considering the intensity of events, we observed the same pattern of earlier occurrence in SDS and a longer leaf flushing duration in LDS (Fig. 3).

We found that maximum (positive trend) or minimum air temperatures (mostly negative trend) and day length were significantly associated with the intensity of the phenophases (Table 3). For most species, leaf fall, increased as maximum temperature increase at both sites, but it was also associated with a decrease of minimum temperatures in SDS. Day length also had a negative association with leaf fall in *C. coriaceum* and *H. ciliata*, for both sites (Table 3).

For all species in SDS, except to *H. ciliata*, leaf flushing was related to the temperature (positive trend). In LDS, *B. crassifolia*, *Q. grandiflora* and *P. reticulata* showed association between leaf flushing and day length (positive trend), while for *C. coriaceum* and *H. ciliata*, maximum temperature (positive trend) and precipitation (negative trend) were, respectively, more associated with leaf flushing (Table 3). Flowering was not associated with climatic variables in *C. coriaceum* and *P. reticulata* (Table 3). For *B. crassifolia*, flowering was related to increases in maximum temperature at both sites. For *H. ciliata*, this event was associated with the decrease of the minimum temperature in SDS and an increase of the maximum temperature in LDS. *Q. grandiflora* exhibited significant relationship between flowering and day length in SDS (Table 3).

Table 3. Multiple regression analyses results assessing the effect of climatic variables on phenology in savanna species subjected to longer dry season (LDS) and shorter dry season (SDS), Maranhão State, Brazil. NA − not available, NS −not significant. R2 = coefficient of determination; p = probability value and β = standardized regression coefficients. Variables: MinT = mean minimum air temperature; MaxT = mean maximum air temperature; DL = day length; Ppt = precipitation.

	LDS			SDS		
Species	Leaf fall	Leaf flushing	Flowering	Leaf fall	Leaf flushing	Flowering
B. crassifolia	R^2 =0.70 $p < 0.01$ MaxT β = 4.3 MinT β =7.3	R^2=0.71 $p <0.01$ DL β=97.27	R^2=0.74 $p <0.01$ MaxT β =7.3	R^2 =0.77 $p < 0.01$ MaxT β =2.82 MinT β =- 43.5	R^2=0.63 $p <0.01$ MaxT β = 2.65	R^2=0.62 $p <0.01$ MaxT β = 2.69
C. coriaceum	R^2 =0.57 $p < 0.01$ MaxT β = 6.0 DL β = −13.2	R^2=0.75 $p <0.01$ MaxT β=4.4	NS	R^2 = 0.77 $p < 0.01$ MinT β = − 3.23 DL β = −26.61	R^2=0.72 $p <0.01$ MaxT β =4.7 MinT β= −4.6	NS
H. ciliata	R^2 =0.44 $p < 0.05$ DL β= −81.56	R^2=0.55 $p <0.01$ Ppt β= −0.01	R^2=0.61 $p <0.01$ MaxT β=4.12	R^2 = 0.62 $p < 0.01$ DL β = −31.64	NS	R^2=0.47 $p <0.05$ MinT β = −5.02
Q. grandiflora	R^2 =0.67 $p < 0.01$ MaxT β = 5.57	R^2=0.71 $p <0.01$ DL β=178.3	NS –	R^2 =0.67 $p < 0.01$ MaxT β =11.52	R^2=0.73 $p <0.01$ MaxT β=4.44	R^2=0.65 $p <0.01$ DL β =0.45
P. reticulata	R^2=0.92 $p <0.01$ MaxT β =11.32	R^2=0.91 $p <0.01$ DL β=0.55	NS	R^2=0.92 $p <0.01$ MaxT β =7.66 MinT β =- 10.9	R^2=0.59 $p <0.01$ MaxT β =4.64	NA

4 Discussion

Our results support the hypothesis that phenological phenomena are intrinsically linked to climatic variables, especially temperature and day length, independent of the site. We also confirm that a shorter dry season, in comparison to a longer dry season, promotes earlier occurrence of phenological patterns, because temperature and day length reaches a greater variation earlier at SDS site than at the LDS. The conspecific populations of the five evaluated species showed distinct behavior for all phenological events between the two sites, with differences in the start and peak dates. Peak dates generally occurred about one to three months later in LDS. This difference may represent levels of local adaptation and a high degree of phenotypic plasticity related to adjustments for the selective abiotic pressures driving leaf and flower production (Pellissier et al., 2014; Panchen and Gorelick, 2016; Silva Moraes et al., 2017).

The start and peak dates and the highest proportions of leaf fall intensity for the conspecific populations occurred at different times during drought in each area, accompanying the variations in temperature and/or decrease in day length at both sites. The association between temperature and leaf fall is presumably related to the increase in evaporative demand and water stress, with consequent loss of leaves, which was already reported for some savanna areas in Brazil (Bulhão and Figueiredo, 2002; Silvério and Lenza, 2010).

As for the relationship with day length, this variable decreases during the early dry period, and may also function as a factor associated with leaf fall (Garcia et al., 2017), signaling climatic changes. Day lengh is the only variable correlated with leaf fall in *H. ciliata* at both sites, and was included among the variables related to leaf fall in *C.coriaceum*. The species *B. crassifolia* shows different degrees of leaf deciduousness, with greater crown cover and smaller variations in the proportions of leaf fall in LDS. The *H. ciliata* species also showed lower seasonality for this event (shorter length of vector r) in this area. We can postulate that these differences in the degree of intraspecific deciduousness among Cerrado species are indicative of high levels of plasticity against climatic aspects (Kuster et al., 2017), which allows them to cope with very distinct climatic regions of the Brazilian territory.

Leaf flushing showed generally consistent differences in the start and peak dates with distinct distribution of the intensity percentage throughout the year for both sites. This confirms the occurrence of the pre-rain green-up phenomenon reported for some savanna species in Central Brazil (Rivera et al., 2002; Franco et al., 2005; Silvério and Lenza, 2010; Dalmolin et al., 2015). This phenomenon is characterized by the appearance of new leaves before the rainy season. This strategy is reported to avoid plant nutrient losses due to herbivory or leaching (Van Schaik et al., 1993); to maximize carbon gain by increasing CO2 assimilation (Rossatto et al, 2009; Dalmolin et al., 2015) and to make the best use of available nutrients in the soil as rainfall increases (Scholes and Walker, 2004; Nord and Lynch, 2009). During the pre-rain green-up, plants take advantage of the higher temperatures to quickly produce and expand their leaves. The influence of temperature on leaf flushing has been reported in tropical seasonally dry regions, such as savannas in Brazil (Pirani et al., 2009; Silvério and Lenza, 2010) and Africa (Seghieri et al., 2012) and may be a key variable for this process (Chambers et al., 2013). The delayed leaf production at LDS site (compared to plants in SDS) may be an adjustment to avoid overexposure of leaves produced during the dry season, which can decrease productivity in savanna plants.

The influence of day length has been reported as a trigger factor for leaf flush and flowering events in tropical regions, including savanna areas (Rivera et al., 2002; Yeang, 2007; Renner, 2007; Zimmerman et al., 2007; Pau et al., 2013; Borchert et al., 2015; Ryan et al., 2017). Although the results of the multiple regression did not show a clear relationship between the phenophases and day length, the leaf flush for all the species in LDS, except H. *ciliata*, increased considerably during the end of the dry period, when day length increases. In SDS, the increase in leaf flushing during the middle and end of the dry period occurs when there is a decrease in clouds and a higher incidence of solar radiation. Thus, as photosynthetic rates are higher in young leaves, the production of new leaves during the period of greater day length and/or irradiance favors photosynthesis and carbon gain (Wright and Van Schaik, 1994), since savanna plants has specific mechanisms to use and store water during the dry season (Goldstein et al., 2008). Therefore, the occurrence of production and growth phenophases during the period of low or no precipitation, indicates the existence of mechanisms that allow plants to rehydrate or maintain internal water levels (Worbes et al., 2013) and are favored by the transfer of assimilated products, which link directly to the growth organs and promote the production of leaves (Ryan et al., 2017) flowers and fruits (Pau et al., 2013; Zimmerman et al., 2007; Camargo et al., 2011; Borchert et al., 2015).

Flowering, which followed the trend of earlier occurrence in SDS, was less related to the climatic variables of each site. However, in *B. crassifolia* and *H. ciliata*, flowering was associated with variations in temperature during the dry period, and in *Q. grandiflora*, it was associated with the increased day length in SDS during the early rainy season. Although the populations of other species did not show significant results in relation to climatic variables, they showed a degree of seasonality compatible with different flowering strategies. Flowering occurred in *C. coriaceum* at both sites during the dry period, under higher irradiance and temperatures, and in *Q. grandiflora* in LDS, during early rainy season, with increased day length. *P. reticulata* in LDS had its flowering peak in the final days of the dry period. Thus, for both the evergreen species and the deciduous species, the water restriction in the environment does not limit flowering in general (Lenza and Klink, 2006; Tannus et al., 2006; Figueiredo, 2008; Pirani et al., 2009; Camargo et al., 2011; Silva et al., 2011; Barbosa et al., 2012). Regarding temperature, it is widely recognized as a variable that affects plant distribution and metabolism, and is an important requirement for flowering (Grace, 1987). Its influence on leaf production and flowering in savannas appears to be more important than the influence of water availability in dry and wet season (Seghieri et al., 2012).

In summary, we characterized the phenological responses in conspecific populations under distinct climates, showing that temperature and day length are the major drivers for phenological events, independent of the site. The duration of the dry season does not limit growth phenomena, but shorter dry seasons allows plants to produce leaves and flowers earlier than under longer dry seasons, because temperature and day length start to increase earlier in SDS site. This strategy indicates higher phenotypic plasticity in savanna woody plants, aligned with adjustments to maximize carbon gain and reproductive success.

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CAPÍTULO III: Reproductive phenology differ between evergreen and deciduous species in savannas from northeastern Brazil

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ABSTRACT

Evergreen (EG) and deciduous (DEC) species exhibit distinct strategies to overcome dry periods and achieve adequate water status, necessary for reproduction and growth. Such particularities may result in distinct reproductive strategies between these groups. Thus, we evaluated the phenology in EG and DEC groups, comparing and differentiating their reproductive phenophases in a Brazilian savanna area (*cerrado sensu stricto*), located in Mirador State Park, Maranhão State, associating such patterns with leaf fall and flushing. Leaf fall, leaf flushing, flowering and fruiting data were monitored between April 2014 and March 2016 in 12 EG and 13 DEC species. To check differences between EG and DEC in terms of flowering and fruiting patterns, we compared their phenological time, activity, intensity and duration of phenophases. We found earlier occurrence and longer duration of flowering in EG in relation to the DEC group; for fruiting, EG differs from DEC in relation to the activity along the year and the intensity, greater for EG group. These responses may reflect the distinct water-use strategies adopted by EG and DEC groups and confirm that differences in their ecophysiological strategies may exert influence on their reproductive phenology.

Keywords: *cerrado*, flowering, fruiting, leaf fall, leaf flushing, leaf habit.

Introduction

The classification of plant species in deciduous (DEC) and evergreens (EG) was developed as a manner to better understand ecophysiological strategies related to water acquisition, storage and transport to overcome the scarcity of this resource in ecosystems with a clear drought period (Eamus & Prior 2001). Many studies conducted in seasonal tropical ecosystems explored this functional classification to understand how marked seasonality have direct influence on vegetative and reproductive strategies (Franco *et al.* 2005; Ishida *et al.* 2006; Lenza & Klink 2006; Rossatto 2013; Vico *et al.* 2015; Méndez-Alonzo *et al.* 2013;Tomlinson *et al.* 2014; Álvarez-Yépiz *et al.* 2017).

According with such studies, evergreen species maintain high crown cover throughout the year (Fu *et al.* 2012), showing leaves with a high leaf life span and elevated shoot growth (Rossatto 2013). Physiological strategies include instantaneous lower photosynthetic capacity, but higher photosynthetic capacity in a long term, coupled with a more conservative water use (Eamus 1999; Franco *et al.* 2005). In contrast, deciduous species shed their leaves during the dry season, exhibiting strategies linked to the reduction of physiological activity and drought avoidance, which include higher stem hydraulic efficiency (Fu *et al.* 2012), elevated capacitance (Bucci *et al.* 2016) and the production of leaves with higher specific leaf area and elevated instantaneous photosynthetic capacity (Franco *et al.* 2005). Functional leaf differences between DEC and EG species have been well documented in the last decades (Takashima *et al.* 2004; Franco *et al.* 2005; Goldstein *et al.* 2008; Rossatto 2013; Vico *et al.* 2015; Tomlinson *et al.* 2014, Scalon *et al.* 2017), however, how distinct canopy maintenance strategies affects the occurrence and duration of reproductive aspects was not well explored.

Since evergreens maintain their canopy during drought periods, by presenting a series of strategies such as deep roots, decreases in leaf transpiration by stomatal control and low canopy cover, they are capable to assimilate carbon along the entire dry season, which in turn implies more available resources to flower and produce fruits during this adverse period (Jonasson 1989; Kloeppel *et al.* 2000). Deciduous, in contrast, do not retain their canopy during the dry period because they are not capable to maintain their leaves in an environment with high evaporative pressure during the dry season (Meinzer *et al.* 1999), even if being capable to achieve soil layers with elevated moisture (Jackson *et al.* 1999; Goldstein *et al.* 2008). They, however, rely in their lighter woods to store water in their trunks (Choat *et al.* 2005), a manner to slowly achieve adequate water balance and produce new leaves at the end of the dry period. Such differences between evergreen and deciduous plants may affect their reproductive strategies, since the deciduous achieve an adequate water status latter in the dry season, in comparison with evergreens (Hasselquist *et al.* 2010).

Phenological studies relies in investigations about the timing of recurrent life cycle events and its association with abiotic factors, such as precipitation, temperature and photoperiod, which acts as strong selective pressures of phenological responses (Morellato *et al.* 2016; Mendonza *et al.* 2017; Lacerda *et al.* 2017). A series of approaches have been adopted in phenological studies, especially the use of functional groups with similar vegetative phenology to understand how their life cycle events occur in time (Williams *et al.* 1999; Singh & Kushwaha 2006; Borges & Prado 2014). Studies using such method reported that in tropical dry forest, EG species exhibit longer flowering duration in comparison with DEC species, also reporting differences in the distribution and peaks occurrence for reproductive events. Additionally, it was reported that flowering periodicity might be associated with leaf loss and the required time for fruit development (Singh & Kushwaha 2006).

The Brazilian savannas are subjected to a strong climatic seasonality, which acts driving phenological events (Vilela *et al.* 2017), allowing the coexistence of species with different degrees of deciduousness. These species exhibit morphological traits and physiological mechanisms that allow their survival during the dry period (Franco *et al*. 2005; Souza *et al*. 2011; Scalon *et al*. 2017). Thus, considering the fact that evergreens and deciduous drastically differ in their way to conserve and use water resources during dry periods in savannas, we expect that reproductive phenological events may differ between these two functional groups. Here we examine reproductive phenology of EG and DEC in woody savanna species from Northeastern Brazil to answer whether flowering and fruiting behavior differ between DEC and EG in the following aspects: a) phenological times, b) activity and intensity of the phenophases and c) the phenophases duration. We hypothesize that different water-use strategies by EG and DEC would affect their time, activity, intensity and duration of flower and fruit production. Since EG species maintain its canopy during the drought period, they would be able to produce flowers and fruits for longer periods during the dry season. In contrast, DEC species should flower and produce fruits in the late dry season, for a short period, since their strategies imply a slow and gradual recovery of their water status during the entire dry season. These strategies would be also associated with annual cycles of leaf fall and leaf production.

Material and Methods

Study area

We conducted this study in a Brazilian savanna area (*cerrado sensu stricto*), located in Mirador State Park (06°37'55"S, 45°52'38"W), a protected area in the Maranhão State, northeast region of Brazil, covering 437,845 ha, between April 2014 and March 2016. The vegetation at Mirador State Park has an average height of 3.9 m, with a density of 898.75 ind.ha^{-1}. *Qualea parviflora* Mart. is the species with greater importance values, and the Fabaceae family is the most representative (data not published). The regional climate according the Köppen's classification is Aw (Alvares *et al*. 2013), being tropical with distinct dry and rainy periods. The historical average rainfall, for a 30-year period, was 1,200 mm; the monthly mean air temperature was 27 ºC, maximum monthly mean of 33 ºC and minimum of 22 ºC (INMET 2016, Balsas station, nº 82.768). Altitude varies from 300 to 600 m, and the predominant soils in region are litolic neosols and yellow latosols. Monthly data for the period of study was obtained from the National Institute of Meteorology (INMET 2016, Balsas station, nº 82.768).

Species selection

Data were collected in selected species sampled in 20 randomly distributed plots (20 x 20 m, apart 100 m from each other) in a typical savanna area of Mirador State Park. In each plot, we sampled all individuals that had ≥ 10 cm of trunk circumference at ground level. We selected 25 species belonging to 18 families, which were classified as evergreens (EG) or deciduous (DEC) (Table 1). The classification of species in EG or DEC was performed considering literature information (Franco *et al*. 2005; Lenza & Klink 2006; Pirani *et al*. 2009; Rossatto 2013). Evergreen (EG) species were characterized by a high proportion of crown cover (in general close to or greater than 70%) during the entire year; deciduous (DEC) species were those that completely loses leaves during the dry period, typically for a period higher than four weeks (Franco *et al*. 2015).

Samples of botanical material were taken to the Laboratory of Botanical Studies (LEB) in the Department of Biology of Universidade Federal do Maranhão (UFMA), where they were identified and classified using the classification system of APG IV (2016).

Table 1. Woody species and their families from distinct leaf phenology in Mirador State Park, Northeastern Brazil. N= number of sampled individuals, EG=evergreen, DEC=deciduous.

Family / Species	**N**	**Leaf Phenology**
Anacardiaceae		
Anacardium occidentale L.	15	EG

Apocynaceae		
Himatanthus drasticus (Mart.) Plumel	13	EG
Hancornia speciosa Gomes	5	DEC
Araliaceae		
Schefflera burchellii (Seem.) Frodin & Fiaschi	8	EG
Bignoniaceae		
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	5	DEC
Calophyllaceae		
Kielmeyera speciosa A.St.-Hil.	7	DEC
Caryocaraceae		
Caryocar coriaceum Wittm.	26	EG
Chrysobalanaceae		
Hirtella ciliata Mart. & Zucc.	27	EG
Connaraceae		
Connarus suberosus Planch.	51	EG
Ebenaceae		
Diospyros hispida A.DC.	12	DEC
Erythroxylaceae		
Erythroxylum suberosum A.St.-Hil.	16	DEC
Fabaceae		
Leptolobium dasycarpum Vogel	15	DEC
Plathymenia reticulata Benth.	13	DEC
Stryphnodendron rotundifolium Mart.	24	DEC
Tachigali subvelutina (Benth.) Oliveira-Filho	10	EG
Lythraceae		
Lafoensia pacari A.St.-Hil.	20	DEC
Melastomataceae		
Mouriri elliptica Mart.	9	EG
Myrtaceae		
Myrcia splendens (Sw.) DC.	5	EG
Psidium myrsinites DC.	13	DEC
Ochnaceae		
Ouratea hexasperma (A.St.-Hil.) Baill.	12	EG
Rubiaceae		
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	17	DEC
Salicaceae		
Casearia arborea (Rich.) Urb.	10	EG
Vochysiaceae		
Qualea grandiflora Mart.	48	DEC
Qualea parviflora Mart.	41	DEC
Salvertia convallariodora A.St.-Hil.	12	EG

We monitored phenological behavior in all individuals of each species (with a minimum of 5 individuals). Samples of botanical material were taken to the Laboratory of Botanical Studies (LEB) in the Department of Biology of Universidade Federal do Maranhão (UFMA), where they were identified and classified using the APG classification system IV (2016).

Phenology

We monitored phenological behavior in all individuals of each species (with a minimum of 5 individuals) and visually estimated the phenophases of leaf fall, leaf flushing, flowering and fruiting for each individual, between April 2014 and March 2016. The estimate was made according to the percentage intensity proposed by Fournier (1974), with the observed values distributed on a semi-qualitative scale comprising five categories: 0 to 4, in intervals of 25% (0: 0%; 1: 1–25%; 2: 26–50%; 3: 51–75% and 4: 76–100%). The plants were generally considered to be under leaf fall when the crown was losing leaves; in leaf flushing when producing new leaves; in flowering when showing flower buds and/or open flowers; and in fruiting when immature and mature fruits were present.

To check the phenological differences between EG and DEC groups in terms of flowering (FL) and fruiting (FR) patterns, we compared the following: start date (FLST; FRST) − mean angle in which each group manifested the phenophase for the first time, obtained by the estimates of the population means (from the individual estimates); peak dates (FLPK; FRPK) − mean angle in which each group showed the highest value for intensity, obtained in the same way as the start; activity (FLAC; FRAC) − monthly percentage of species manifesting the phenophases; intensity (FLIN; FRIN) − monthly percentage of intensity, obtained by the mean intensity of the populations in each group, following the methodology described by Fournier

(1974); phenophases duration (FLDR; FLDR) − estimated for each group by the population means, based on the average duration among individuals.

Statistical analysis

To test the occurrence of seasonal patterns in the flowering and fruiting phenophases for EG and DEC groups, we used circular statistics (Morellato *et al.* 2000; Morellato *et al*, 2010). Initially, the months were converted into angles, in intervals of 30° (0º corresponding to January, until 330º corresponding to December). We calculated for these phenophases in each group (EG and DEC) their mean angles, angular standard deviations and r vector lengths (considered as a measure of the degree of seasonality, ranging from zero to one), referring to start (FLST; FRST) and peak (FLPK; FRPK) dates.

To verify the occurrence of a seasonal pattern in the groups, the significance of the angle was determined through the Rayleigh z test for circular distribution (Morellato *et al.* 2000; Morellato *et al*, 2010). A Circular analysis was carried out in the software ORIANA 4.0 (Kovach 2011). When the mean angle was significant, we performed the Watson-Williams test (Zar 2010) to verify whether the mean angles of the reproductive events differed between the functional groups (EG and DEC), and if so, to determine whether they exhibited a similar seasonal pattern in FLST, FLPK, FRST, FRPK. The activity (FLAC; FRAC) of reproductive phenophases in each functional group was compared using the G test (McDonald 2014). The intensity (FLIN; FRIN) and duration (FLDR; FLDR) of the reproductive phenophases were compared between the functional groups using the Mann-Whitney U test, considering that not all the samples conformed to the assumption of normality and variance homogeneity (Zar 2010). All the tests considered a significance level lower than 0.05.

Results

Start and Peak Dates

The start and peak dates of flowering showed seasonality for EG and DEC groups (Tab. 2), with significant differences found between them (Tab. 3). In the EG and DEC, the mean angle for FLST corresponded to the month of August, and for FLPK, in both, to the month of October. Regarding fruiting, significant seasonality was observed only for FRST and FRPK in EG, thus in this phenophase, the groups were not compared by the Watson Williams test (Tab. 3).

Table 2. Comparison between Evergreen and Deciduous groups, located in Mirador State Park, Brazil, considering their flowering and fruiting traits: Watson-Williams for the start (FLST-Flowering; FRST-Fruiting) and peak dates (FLPK-Flowering; FRPK-Fruiting), G test for activity (FLAC-flowering; FRAC-fruiting) and Mann-Whitney for intensity (FLIN-flowering; FRIN-fruiting) and duration (FLDR-flowering; FLDR-fruiting). F= circular statistical value, G= G test value, U= Mann Whitney test value, nc= not calculated.

		Flowering	Fruiting
Watson Williams		FLST-Start	FRST- Start
	F	6.7	n.c.
	p	0.01	-
		FLPK-Peak	FRPK-Peak
	F	4.6	n.c.
	p	0.03	-
G test		FLAC-Activity (%)	FRAC-Activity (%)
	G	164.34	141.64
	p	<0.01	<0.01
Mann-Whitney		FLIN-Intensity (%)	FRIN-Intensity (%)
	U	230	164
	p	n.s.	0.01
		FLDR-Duration	FRDR-Duration
	U	27	47
	p	0.03	n.s

Table 3. Circular statistics tests of seasonality and average start and peak dates of the flowering and fruiting phenophases of woody species, per functional group, in Mirador State Park, northeastern Brazil. EG=evergreen leaf exchange, DEC=deciduous.

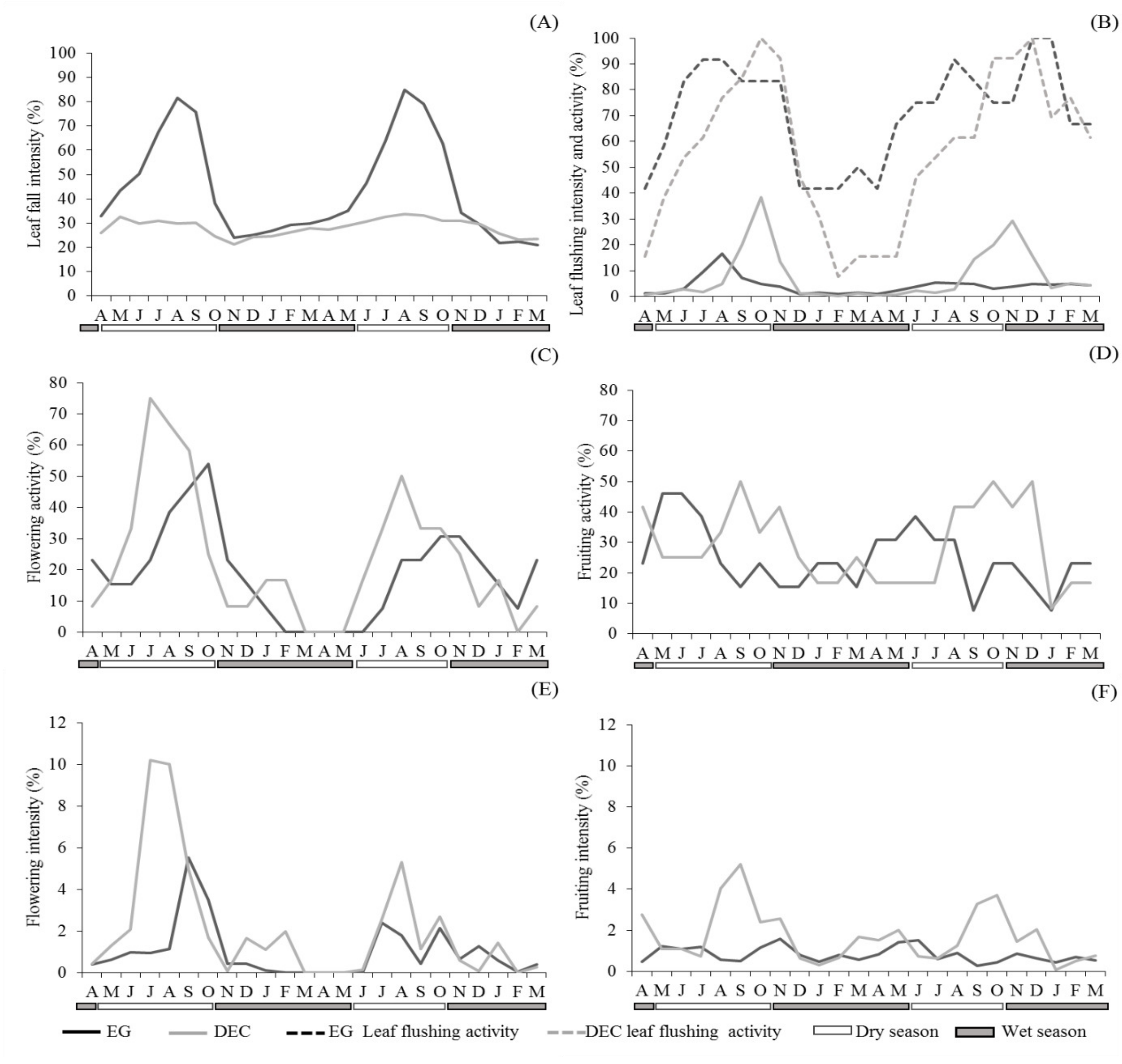
Phenophase	Flowering				Fruiting			
Variable	EG-Start	EG-Peak	DEC-Start	DEC-Peak	EG-Start	EG-Peak	DEC-Start	DEC-Peak
Mean Vector (μ)	225.52	234.77	292.55	292.38	250.77	279.61	201.39	177.04
Mean date	16 Ago	27 Ago	24 Oct	24 Oct	12 Sep	11 Oct	24 Jul	29 Jul
Length of Mean Vector (r)	0.50	0.52	0.59	0.63	0.51	0.52	0.31	0.27
Circular deviation	57.15	55.85	51.78	48.99	56.58	56.05	66.95	68.99
Rayleigh Test (Z)	6.06	6.34	3.49	4.02	6.04	6.25	1.10	0.83
Rayleigh Test (p)	< 0.01	< 0.01	< 0.05	< 0.05	< 0.01	< 0.01	ns	ns

Activity

The EG and DEC groups differed in terms of their flowering (FLAC) and fruiting (FRAC) activities along the year (Tab. 3, Fig. 1C-D). Both groups showed higher values in the FLAC between July and December, corresponding to part of the dry period and the early rainy season.

In general, the percentage curves for flowering show higher values earlier in EG, between July and August; in DEC, the month of August indicates an evident increase in the FLAC and higher percentages that can extend from October to December. Between February and June the decrease or absence of flowering species was observed, which shows a shorter interval in the EG in relation to DEC (Fig. 1C). In both groups, for most species, flowering occurs concomitant to the leaf flushing period or after this. Exceptions were found for deciduous *Lafoensia pacari*, *Hancornia speciosa* and *Tabebuia aurea*, whose flowering occurs during the period of leaf senescence, before the total deciduousness. We also found such pattern for the DEC *Qualea grandiflora* and EG *Schefflera burchellii*, whose flowering occurs with leaves already fully expanded.

Figure 1. Average monthly distribution in evergreen (EG) and deciduous (DEC) groups: (**A**) intensity percentage in leaf fall; (**B**) activity and intensity percentages of leaf flushing; (**C**, **D**) flowering and fruiting activities (FLAC; FRAC); (**E, F**) flowering and fruiting intensities (FLIN; FRIN). Mirador State Park, northeastern Brazil. Letters represent the initials of the months of the year, between April 2014 and March 2016. Bars below the x-axis represent the dry and wet months for the study period.



The FRAC was more irregularly distributed than the flowering in both groups and this was more evident in the DEC, although in this group it is possible to verify higher percentages between May and August, which is the end of the rainy period and part of the dry period, when leaf fall begins, but before the fully deciduousness (Fig. 1A-D). In the species *Diospyrus hispida* and *Erythroxylum suberosum* fruiting occurs during leaf flushing period, and in *Tocoyena formosa*, with fully expanded leaves, during rainy season in these species. In EG, FRAC presented higher percentages from September to December, which corresponds to the late dry season and part of the rainy season, after greater percentage of leaf flushing (Fig. 1D).

Intensity

Concerning flowering and fruiting intensity, we found significant differences between the groups just in fruiting (FRIN), although the EG presented, in general, greater percentages in FLIN in relation to the DEC (Tab. 3, Fig. 1E). FLIN was more variable than FLAC, due to the influence of percentage intensity variations at the species level (Fig. 1C-E). For example, among the DEC, between December and February there was a high flowering percentage in the *Casearia arborea* and *S. burchellii*. As for the DEC, in July, we observed the flowering of the species *T. aurea*.

The FRIN, greater in EG than in DEC, exhibit an additional peak different from FRAC in EG between the months of March and May, which corresponds to the high intensity in fruiting of the species *Mouriri elliptica* and *S. burchellii* (Fig. 1F). In DEC, the variation was greater and presents a distinct response in relation to FRAC. In this group, for example, between October and December (Fig. 1F), the high percentage of fruiting in *E. suberosum* (in the first year), increases the intensity in this month.

Phenophases duration

The flowering duration differed between the groups (Tab. 3), with a median, in months, of 1.6 in EG (minimum about 1 month; maximum 2.2 months) and 1.3 for the DEC (minimum less than 1 month; maximum 1.6 months). The fruiting period did not differ significantly between functional groups (Tab. 3), with a median duration of fruiting of 1,9 months in EG (mininum about 1 month; maximum 3,8 months) and 1.7 in DEC (minimum less than 1 month; maximum 3.3 months).

Discussion

Our predictions concerning differences in reproductive phenology between EG and DEC plants were confirmed. We found clear differences regarding the time, activity and duration for the flowering and also for the fruiting (activity and intensity) in the studied savanna species. In addition, we observed differences in the time of vegetative phenology associated with reproductive events. These results provide evidence that distinct ecophysiological strategies adopted by EG and DEC may exert significant influence on their reproductive phenological behavior.

For both functional groups, we found seasonality in flowering, which occurred from the middle to late dry period in the EG, and in the late dry season to early rainy season in the DEC. These results, found for the majority of studied species, were similar to that reported for environments with marked water seasonality, with flowering occurring in the dry season (Williams *et al*. 1999; Singh & Kushwaha 2006; Pirani *et al*. 2009), but especially during the transition between dry and rainy periods (Lenza & Klink 2006; Selwyn & Parthasarathy 2006; Silverio & Lenza 2010). In this study, the early occurrence in flowering start and peak dates, associated with flowering activity differences, converge in the same direction, indicating that flowering in EG occurs earlier. This discrepancy between the groups occurred in a clear association with the period of new leaves production, usually preceding or concomitant to it.

This fact is possibly intrinsically associated with the annual cycles of leaf senescence and production, indicating different strategies regarding the use of internal and available resources in the environment (Fu *et al*. 2012; Lima *et al*. 2012).

The significant increase in flowering activity in DEC species in late dry season and in early rainy season indicates that this event starts under severe seasonal water restriction in the environment, but not for the plant, which has mechanisms for rehydration of its tissues (Holbrook 1995; Goldstein *et al*. 1998; Scholz *et al*. 2007). During the leafless period, the gradual restoration of water levels is expected in DEC species, which is associated with efficient hydraulic characteristics (Fu *et al*. 2014) especially the use of water store in the trunk (Borchert 1994). This mechanism allows adequate conditions to DEC plants increase their capacity for retention of water gradually, until the late dry season (Borchert *et al*. 2004; Franco *et al*. 2005), when flowering increases. Thus, a consistent pattern is observed, similar to the scheduled species inserted in the drought-deciduous species group, which may respond to changes in temperature or photoperiod for leaf production (Vico *et al*. 2015). Another possibility is that flowering starts during the end of the dry season because DEC seeds need to promptly germinate when water and nutrients are available in the rainy season (Scholes & Walker 2004; Nord & Lynch 2009). In this way, the time required for fruiting and seed dispersal can determine the time of occurrence of this phenomenon (Singh & Kushwaha 2006). These events are interconnected in time to adjust plant fitness in seasonal hydric conditions (Kimball *et al*. 2012).

For most DEC species, flowering occurred partially or completely during the leaf flushing period, ranging from the late dry season to early rainy season. In the species *Lafoensia pacari*, *H. speciosa* and *T. aurea*, flowering manifested earlier in relation to the other species, during the first half of the dry period and concomitantly with senescence and leaf fall. While in

Q. grandiflora, the flowering occured after other species, in rainy season and with full crown. These responses, which diverges to general pattern, led to the lowest synchrony (lower vector length) in start and peak dates. Thus, although a general response is found for DEC species, alternative patterns can emerge and may reflect different strategies of water absorption, storage and resource allocation in this group (Lima *et al*. 2012; Wolfe & Kursar 2015).

In EG, both, the occurrence of start and peak dates during drought, as well as the differences in activity percentages, represented particularities clearly associated with foliar habit in this group. Flowering in the mid-dry period reinforces the presence of strategies related to drought tolerance, supported by known physiological mechanisms that minimize water loss, maintains photosynthetic activity and sufficient carbon gain, allowing the maintenance of its productivity activities during the dry season (Eamus & Prior 2001). In this group, leaf exchange and flowering occur simultaneously and earlier in relation to DEC, indicating the growth reestablishment, possible due to the mobilization of water and nutrients by the plant. Thus, internal alterations compensate water limitations of the environment, such as use of water storage, adjustment of tissue osmotic potential and reduction of leaf transpiration − by stomatal conductance − favors early flowering (Meinzer et al. 1999). Additionally, these conditions result in advantages to flowering such as: the reduction of damage caused to flowers by rainfall, herbivory and increased activity of pollinating agents, mainly represented by bees (Janzen 1980; van Schaik *et al*. 1993).

As for flowering duration, two situations may justify the differences found between the groups: although in both groups flowering occurs generally during the leaf flushing period, in deciduous it generally coincides with a short and intense period of leaf flushing. This relation may suppose a relationship with a high mobilization of reserves, to be used in the development of both leaves and flowers, which may decrease the flowering period in this group. In EG, the longer flowering duration associated with gradual leaf flushing may be related to drought tolerance strategies, which allow for a longer investment in production phenomena (*e.g*. leaves and flowers). Thus, we assume that flowering duration is linked to the differences in resources use in EG and DEC (Tomlinson *et al*. 2013). A similar response was found by Borges & Prado (2014) in Brazilian savannas, who associated it with the availability of resources from photosynthesis and the branch inclination, which may favors the protection of reproductive structures by the permanent leaves presence.

Regarding fruiting, their development phases for both groups extend into the dry and rainy periods. Although only EGs showed significant seasonality, differences related to fruiting activity between functional groups may indicate a possible association with the different fruit development requirements of each group, mesocarp type (fleshy and dry), dispersal and seed germination strategies. The fruiting activity in EG increased rapidly after flowering, in the late dry season and during the early rainy, indicating an efficient allocation of resources for fruit production. This is possibly connected to conditions that facilitate the maintenance of fleshy fruits and also to a larger number of dispersal agents during the period of greater humidity. Moreover, this behavior may allow seeds to germinate and establish during the wet season (Venable & Brown 1988; Fenner 2012). Three exceptions occur in this group: the species *Salvertia convallariaeodora* and *Himatanthus drasticus* (both species have dry fruits), whose fruiting was recorded exclusively during the dry period, and *S. burchellii*, whose fruiting occurred in the transition from the rainy to the dry season. In these species, features related to seed characteristics and germination requirements may present particularities that complement the explanations regarding these findings (Vieira *et al*. 2008; Bewley & Black 2012).

In DEC, the peak of fruiting activity in late rainy season and early dry season, possibly reflect the requirement of water supply for fruit development during almost the entire rainy season and dispersion facilitated by the conditions in the next dry season, when there is less crown coverage by leaves, facilitating the dispersion. It is common among the DEC the production of orthodox seeds with longer longevity, which may justify the fruiting during the early dry season (Figueiredo 2008). For other species in this group, which present fleshy fruits, fruiting during the rainy season is possibly associated with different tolerances to the seeds desiccation in the species of this group or to occurrence of dormancy, which can complement the interpretation of the data (Tweddle *et al*. 2003; Vieira *et al*. 2008). The greater intensity percentage of fruiting in EG species in relation to DEC is supposedly associated to the mechanisms that favors an efficient pollination in this group, however, investigations that address more specific aspects are necessary and may improve new insights in this way. Aspects referring to investments in fruit production after the maximum period of leaf production may contribute to additional understanding, since allocation of photosynthesis products, more efficient in the new leaves, can be harnessed for the production of a large number of fruits.

Differences in flowering and fruiting between evergreens and deciduous sustain the different functions related to this classification. We showed that being a deciduous or an evergreen implies certain specific characteristics related to the time of occurrence (start and peak dates), activity, duration and intensity of reproductive events, which are intrinsically coupled with leaf fall and flushing patterns.

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Table and Figure legends

Table 1. Woody species and their families from distinct leaf phenology in Mirador State Park, northeastern Brazil. N= number of sampled individuals, EG=evergreen, DEC=deciduous.

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7. CONSIDERAÇÕES FINAIS

As informações apresentadas neste trabalho contribuem para a ampliação do conhecimento sobre dinâmica do comportamento fenológico em nível de comunidade e de espécies, empregando uma abordagem até então não considerada para áreas de Cerrado: comparações de mesmo tipo de formação vegetal e mesma fitofisionomia, submetida a diferenças climáticas. Além disso, inclui uma região com caraterísticas únicas considerando sua área de ocupação, entre a floresta amazônica e a caatinga, e com escassez de informações quando comparada com outras áreas de cerrado.

As comparações de comunidade (capítulo I) e de populações conespecíficas (capítulo II) confirmam respostas similares: as fenofases mudam seu período de ocorrência se ajustando às variáveis climáticas locais, acompanhando as variações de temperatura e/ou fotoperíodo que ocorrem principalmente durante o período seco em cada área de estudo. Tais variáveis se associam à tendência geral de ocorrência antecipada das fenofases no Parque Estadual de Mirador (PEM).

Os resultados permitem acrescentar informações sobre os fatores que dirigem as respostas nessas áreas, cujas variações na temperatura e fotoperíodo não se apresentam tão amplas, como ocorre em latitudes maiores. Isso permite inferir que fatores considerados importantes em áreas do cerrado central e do sudeste também atuam em baixas latitudes, tornado possível a interpretação de repostas de um modo mais abrangente.

Adicionalmente, as respostas encontradas quando comparados grupos com fenologia foliar contrastante (espécies sempre verdes − SV e decíduas − DEC) (capítulo III), mostram que, dentro do padrão geral, ainda é possível encontrar respostas diferentes, indicando diferenças nas estratégias de superação das condições desfavoráveis associadas ao período seco, que permitem às SV manifestarem picos das fenofases reprodutivas antes das DEC, manterem uma floração mais longa e maior intensidade de frutificação. Essas diferenças mostram-se intrinsicamente relacionadas aos ciclos de queda e produção de folhas nos dois grupos e refletem diferentes estratégias de uso da água neles presentes, com as SV adotando estratégias mais conservativas em relação às DEC.

Os diferentes aspectos sobre fenologia aqui considerados revelam os mecanismos que regem as respostas em determinados níveis (comunidades, populações, grupos de espécies), aqui avaliados com abordagens fenológicas básicas, mas que apresentam-se úteis e fundamentais para a compreensão desses fenômenos e para futuros estudos que empreguem avaliações temporais ou espaciais da fenologia e suas relações com o clima.

ANEXOS

ANEXO 1

Fotos das áreas de estudo

Barreirinhas-MA

Parque Estadual de Mirador-MA

ANEXO 2

NORMAS DO BRAZILIAN JOURNAL OF BOTANY (CAPÍTULO I)

Brazilian Journal of Botany – Instructions for authors

This journal is a member of, and subscribes to the principles of COPE.

The *Brazilian Journal of Botany* considers for publications original articles, short communications, and reviews.

Original articles should not exceed 30 doubled-spaced pages, including tables, figures, and references.

Longer articles might be considered, provided they are concise and its length is needed to properly convey its results. The sections of original articles should be:

- Abstract
- Introduction
- Material and methods
- Results
- Discussion
- Authors' contributions
- Acknowledgements
- References

Short Communications are handled rather flexible. The average article in this category has 4-6 printed pages (including references) and the "Results" and "Discussion" section are usually combined.

Reviews should be submitted by invitation only.

2. Submission Fee

The submission fee is not applicable to members of São Paulo Botany Society. For non-members, a nonrefundable fee is required for each manuscript submitted to the journal, as follows:

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To proceed with payment: http://botanicasp.org/en/journal-submission

3. Manuscript Submission

Submission of a manuscript implies: that the work described has not been published before; that it is not under consideration for publication anywhere else; that its publication has been approved by all co-authors, if any, as well as by the responsible authorities – tacitly or explicitly – at the institute where the work has been carried out. The publisher will not be held legally responsible should there be any claims for compensation.

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- The name(s) of the author(s)
- A concise and informative title (in bold)
- The affiliation(s) and address(es) of the author(s)
- The e-mail address, and telephone number(s) of the corresponding author
- We highly encourage authors to provide the 16-digit ORCID number (www.orcid.org)

7. Abstract

Please provide an abstract of 150 to 250 words. The abstract should not contain any undefined abbreviations or unspecified references.

8. Keywords

Please provide 4 to 6 keywords for indexing purposes. These key-words should appear in alphabetic order. Please do not include words already used in the article title.

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- Use a normal, plain font (e.g., 12-point Times Roman) and double line for text.
- Use the automatic page numbering function to number the pages (do not use line numbering function).
- Do not use field functions.
- Use tab stops or other commands for indents, not the space bar.
- Use the table function, not spreadsheets, to make tables.
- Use the equation editor or MathType for equations.
- Save your file in docx format (Word 2007 or higher) or doc format (older Word versions).
- Manuscripts with mathematical content can also be submitted in LaTeX (LaTeX macro package (zip, 182 kB)
- The use of footnotes is highly discouraged.
- Apply italic fonts only for scientific names, descriptions or diagnosis of new taxa, the names and numbers of collectors, and for genetic or statistical symbols.
- Numbers up to nine should be written in full, except if followed by units, or if indicating tables or figures (Examples: 21 L, 20.32 mg, Table 1);
- Separate units from values by placing a space (except for percentages, or geographical degrees, minutes and seconds). Use abbreviations whenever possible.

10. Headings

Headings should be numbered following the decimal system, a maximum of three levels is allowed (e.g. 1.1; 1.2; 1.2.1)

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Abbreviations should be defined at first mention and used consistently thereafter.

12. Scientific Style

- Please always use internationally accepted signs and symbols for units (SI units).
- Genus and species names should be in italics.
- Taxonomic authorities should be cited for all taxon names at the species level rank and below at their first usage in the text.
- Please use the standard mathematical notation for formulae, symbols etc.
- For compound units, use exponentiation; do not not slash. Example: mg day$_{-1}$ instead of mg/day, µmol min$_{-1}$ instead of µmol/min)
- Use Italic for single letters that denote mathematical constants, variables, and unknown quantities

- Use roman/upright for numerals, operators, and punctuation, and commonly defined functions or abbreviations, e.g., cos, det, e or exp, lim, log, max, min, sin, tan, d (for derivative)
- Use bold for vectors, tensors, and matrices.
- Manuscripts submitted to the journal are expected to adhere to internationally accepted nomenclature for receptors (www.guidetopharmacology.org) and enzymes (International Union of Biochemistry and Molecular Biology)

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References within the main text should appear in parenthesis as in the examples below. For multiple citations, use ascending chronological order:

- Negotiation research spans many disciplines (Thompson 1990).
- This result was later contradicted by Becker and Seligman (1996).
- This effect has been widely studied (Abbott 1991; Barakat et al. 1995a, b; Kelso and Smith 1998; Medvec et al. 1999, 2000).

14. Author Contribution Statement

Authors must provide a short description of the contributions made by each listed author (please use initials). This will be published in a separate section before the Acknowledgments.

15. Acknowledgments

Acknowledgments of people, grants, funds, etc. should be placed in a separate section before the reference list. T. The names of funding organizations should be written in full.

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The list of references should only include works that are cited in the text and that have been published or accepted for publication. Personal communications and unpublished works should only be mentioned in the text. Do not use footnotes or endnotes as a substitute for a reference list. Entries should be alphabetized by the last names of the first author of each work. Order multi-author publications of the same first author alphabetically with respect to second, third, etc. author. Publications of exactly the same author(s) must be ordered chronologically.

Always use the standard abbreviation of a journal's name according to the ISSN List of Title Word Abbreviations, see ISSN LTWA. If you are unsure, please use the full journal title.

○ **Journal Article**

Gamelin FX, Baquet G, Berthoin S, Thevenet D, Nourry C, Nottin S, Bosquet L (2009) Effect of high intensity intermittent training on heart rate variability in prepubescent children. Eur J Appl Physiol 105:731-738. doi: 10.1007/s00421-008-0955-8

Ideally, the names of all authors should be provided, but the usage of "et al" in long author lists will also be accepted:

Smith J, Jones M Jr, Houghton L et al (1999) Future of health insurance. N Engl J Med 965:325–329

○ **Article by DOI**

Slifka MK, Whitton JL (2000) Clinical implications of dysregulated cytokine production. J Mol Med. doi:10.1007/s001090000086

○ **Book**

South J, Blass B (2001) The future of modern genomics. Blackwell, London

○ **Book chapter**

Brown B, Aaron M (2001) The politics of nature. In: Smith J (ed) The rise of modern genomics, 3rd edn. Wiley, New York, pp 230-257

- **Online document**

Cartwright J (2007) Big stars have weather too. IOP Publishing PhysicsWeb. http://physicsweb.org/articles/news/11/6/16/1. Accessed 26 June 2007

- **Dissertation**

Trent JW (1975) Experimental acute renal failure. Dissertation, University of California, Berkeley.

- **Personal communications and unpublished works** should only be mentioned in the text

Example: (SE Sanchez, unpublished data).

- **Events**

Döbereiner J. 1998. Função da fixação de nitrogênio em plantas não leguminosas e sua importância no ecossistema brasileiro. In: Anais do IV Simpósio de Ecossistemas Brasileiros (S Watanabe, coord.). Aciesp, São Paulo, v.3, pp.1-6

- **In taxonomic papers,** cite botanical material in detail in the following sequence: place and date of collection, collector's name and number, and herbarium abbreviation, according to the samples below (except for historical collections in which location data is vague lacking):

BRAZIL. Mato Grosso: Xavantina, s.d., HS Irwin s.n. (HB3689). São Paulo: Amparo, 23-XII-
1942, JR Kuhlmann & ER Menezes 290 (SP); Matão, BR 156, 8-VI-1961, G Eiten et al. 2215 (SP, US).

BRAZIL. São Paulo: São Paulo, Jardim Botânico, Lago das Ninféias, 23$_o$38'20.5"S, 43$_o$37'18"W, 23-XII-1942, FC Hoehne s.n. (SP)

17. Tables

- Tables should be submitted separately from the text.
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- For each table, supply a table caption (title) explaining the components of the table.
- Identify any previously published material by giving the original source in the form of a reference at the end of the table caption.
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- Avoid abbreviations (except for units).
- Do not insert vertical lines.
- Use horizontal lines only to stress the header and close the table.

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- Supply all figures electronically, saved as eps, tif, or similar format.
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- Vector graphics containing fonts must have the fonts embedded in the files.
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- All lines should be at least 0.1 mm (0.3 pt) wide.
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- Halftones should have a minimum resolution of 300 dpi.

A

18.3. Combination Art

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- Spreadsheets should be converted to PDF if no interaction with the data is intended.
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Flora 236–237 (2017) 100–106

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Do conspecific populations exhibit divergent phenological patterns? A study case of widespread savanna species

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ARTICLE INFO

Edited by Fei-Hai Yu

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Phenology
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Temperature

ABSTRACT

Widespread savanna tree species can grow and survive at sites that diverge in water availability and seasonality, thus these species may be able to adjust their phenology in response to site variations. Here we evaluated vegetative and reproductive phenology in five woody species whose populations grow at two savannas sites under divergent climatic regimes, inserted in a large transitional zone between the Amazon forest and the semi-arid region. Patterns of leaf fall, leaf flush and flowering were recorded monthly for five woody species growing under longer (LDS) and shorter (SDS) dry seasons. We evaluated the seasonality, the start and peak dates for phenological events and the associations between phenophases and climatic data. We found a close relationship between phenological events and site temperatures, with phenological peaks in the LDS occurring, in general, about one to three months later than at the SDS site. Leaf fall coincides with warmer and drier periods when the day length is shorter. Leaf production and flowering were associated with increased day length in some populations. Our results support the hypothesis that the conspecific populations have a high degree of association with climatic variables, especially temperature and day length, showing distinct phenological responses associated to the local climatic differences.

1. Introduction

Phenological events are associated with a wide variety of ecological processes (Forrest and Miller-Rushing, 2010), and are therefore important to our understanding of species-level relationships (Goulart et al., 2005; Zalamea et al., 2011; Dalmolin et al., 2015) and adaptive mechanisms (Grogan and Schulze, 2012; Worbes et al., 2013; Guan et al., 2014). Phenology can also explain the temporal organization of plant communities (Stevenson et al., 2008; Kushwaha et al., 2011; Diez et al., 2012; Hawes and Peres, 2016; Ryan et al., 2017), because phenological events are linked to climatic and biotic factors (Pau et al., 2011; Tang et al., 2016), affecting the capacity of plants to acquire resources for growth and reproduction (Nord and Lynch, 2009; Nord et al., 2011).

Phenological responses of plant communities may diverge between sites, even if those sites are similar in species composition (Forrest et al., 2010). This suggests that climatic parameters are a stronger influence than species identity in determining phenological behavior (Pau et al., 2011). This may be especially evident for plant communities of the Brazilian savanna (Cerrado), where it is possible to find a great variety of phenological patterns following climatic variations along an extensive latitudinal and altitudinal gradient (Bulhão and Figueiredo, 2002; Batalha and Martins, 2004; Pirani et al., 2009; Silva et al., 2011; Rossatto 2013). The wide climatic variations in the Cerrado are due to its occurrence in disjunctive areas in the Amazon; in a continuous strip that runs from Brazil's Northeast to Center-South regions; and in the Southeast region of the country (Bridgewater et al., 2004). This continental occurrence subjects Cerrado plant communities to distinct regimes of dry season duration and annual rainfall amount (Alvares et al., 2013).

In tropical and sub-tropical regions, the amplitude in phenological events is often correlated with different climatic variables, including water availability (Dalmolin et al., 2015), photoperiod and light intensity (Young, 2007; Zimmerman et al., 2007) and temperature

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0367-2530/

variations (Pau et al., 2013). For savannas in particular, water availability – especially its decrease during the end of the wet season – is cited as one of the main factors driving leaf fall patterns (Bulhão and Figueiredo, 2002; Lenza and Klink, 2006; Rossatto et al., 2009; Guan et al., 2014). Flowering and leaf renewal are concentrated during the dry period; but especially during the transition from the late dry to the rainy season, a time of the year when day length and temperatures increase and first rains begin to fall (Figueiredo, 2008; Lenza and Klink, 2006; Pirani et al., 2009; Borges and Prado, 2014; Dalmolin et al., 2015; Ryan et al., 2017). The production of leaves and flowers during this transitional period has some advantages for savanna plants: the canopy reaches full development and is ready for maximal carbon gain just as the first rains start (Franco et al., 2005); an early flowering allows sufficient time for the complete fruit production and seed dispersal, which increases the success of seed germination and establishment (Batalha and Martins 2004). However, if the rainy period was delayed, and plants were not plastic enough to adapt their strategies, they would suffer from prolonged drought.

Although a typical regime of alternation between dry and rainy periods prevails in the savannas, the duration of the dry season, distribution of precipitation, average air temperatures and day length duration are highly variable (Rivera et al., 2002; Silva et al., 2008; Alvares et al., 2013). Temperature and day length are considered important drivers for phenological events in savanna species (Rivera et al., 2002), especially for vegetative growth. Ascertaining how species respond to such differences enables the predictions of changes in phenological events and of population dynamics, and contributes importantly to the assessment of how climate change affects natural populations (Franco et al., 2014). The use of conspecific populations (represented by individuals of the same species, but growing at different sites) is an interesting approach to comprehend local adaptations to climatic aspects (Panchen and Gorelick, 2016).

In the present study, we evaluated vegetative and reproductive phenology in five species whose populations grow at two savannas sites (Cerrado), under distinct climatic regimes, in a large transitional zone between the Amazon forest and the semi-arid region. These sites exhibit differences in the duration of the dry season: one of them shows higher total rainfall, but a longer dry season, while the other have lower rainfall, but a shorter dry season. Additionally, short dry season site shows the highest temperature and longest day length variations earlier than the long dry season site. This study aimed to answer whether: 1) differences in the seasonal climatic patterns of these sites influence the period, start and peaks, of the phenological events, 2) phenological events are associated with temperature and day length independently of the dry season duration. We hypothesize that if phenological phenomena are intrinsically linked to climatic variables at these sites, the shorter dry season will promote phenological events to occur earlier in comparison to the longer dry season. These responses will occur because leaf events and flower production are supposedly related to temperature and day length, which increase from mid to late dry season on each site and are indicative of the following rainy period.

2. Material and methods

2.1. Study sites and climate

We conducted our study at two savanna sites (regionally known as Cerrado *sensu stricto*) in the northeastern region of Brazil: the first site is located at Barreirinhas municipality (03°01′17″S, 43°06′28″W) and the second at the Mirador State Park (06°37′55″S, 45°52′38″W), both in Maranhão State, Brazil (Fig. 1). The climate is *As* in Barreirinhas, and *Aw* in Mirador State Park (Alvares et al., 2013), both of which are classified as tropical with two distinct seasons – dry and rainy – but differing in terms of total rainfall and in the dry season length, as

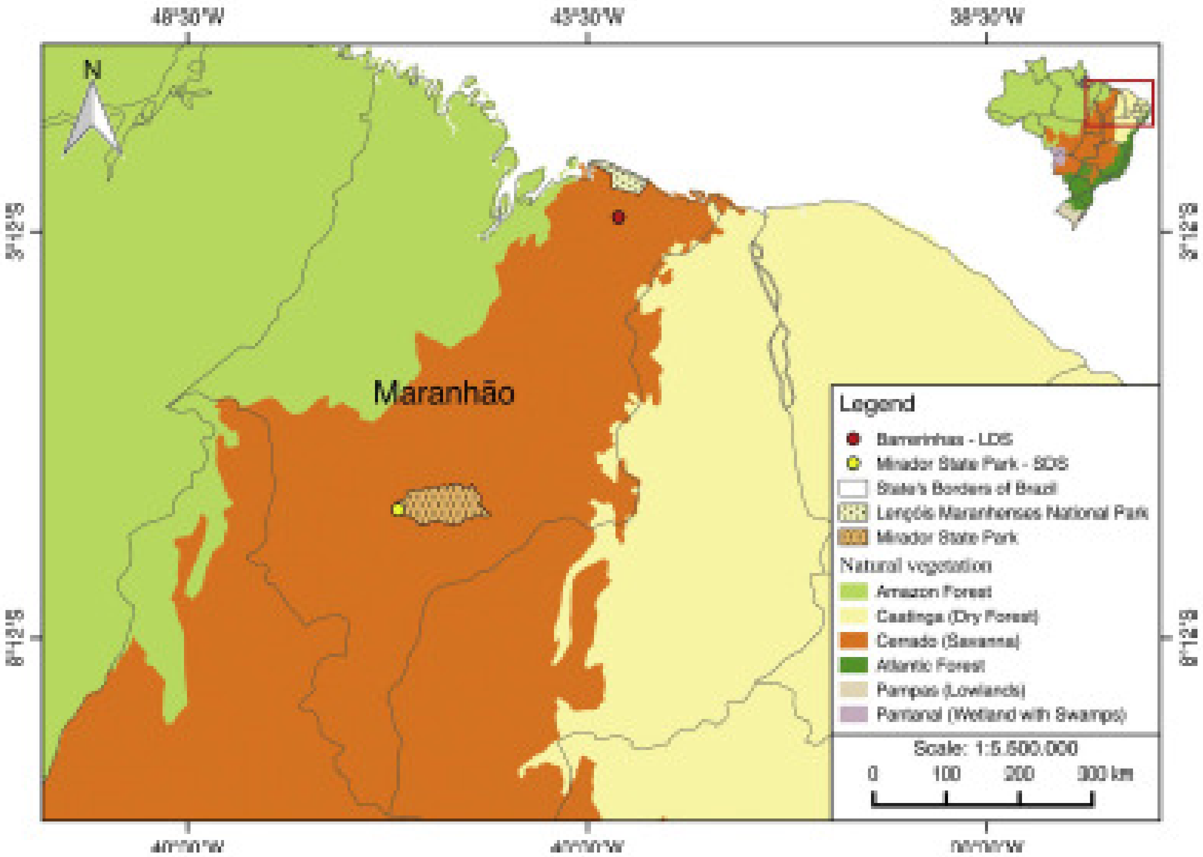

Fig. 1. Sites selected for phenological observations: Barreirinhas (longer dry season – LDS) and Mirador State Park (shorter dry season – SDS), Maranhão State, Brazil.

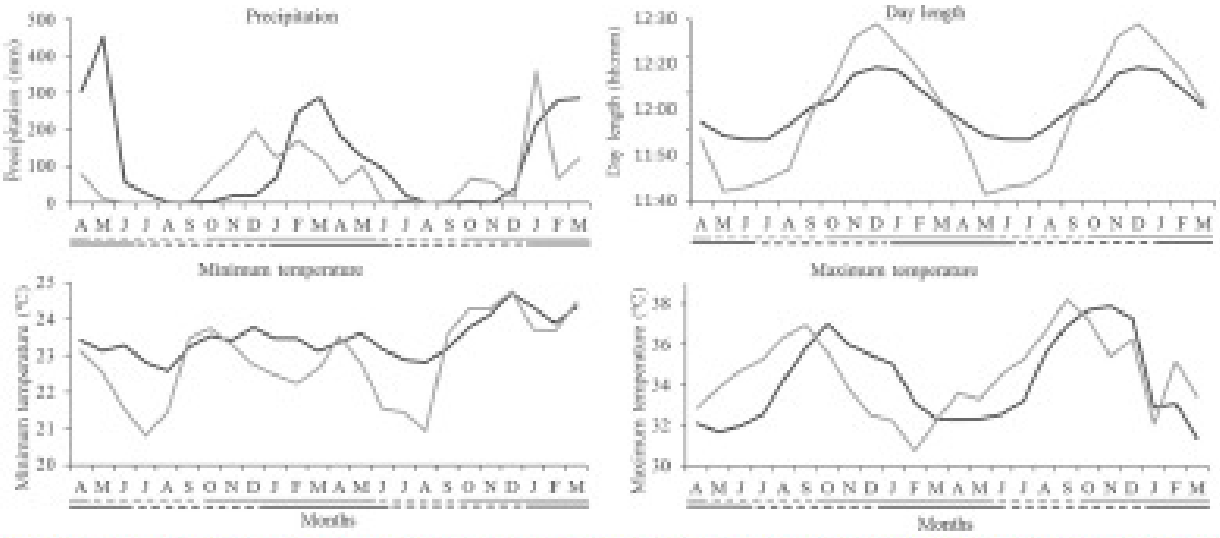

Fig. 2. Climatic data (April 2014 to March 2016) for LDS – longer dry season site (dark gray lines) and SDS – shorter dry season site (light gray lines), Maranhão State, Brazil. Rainy season indicated by continuous lines below the x axis; dry season indicated by dashed lines below the x axis.

observed during the study period (Fig. 2). For the sake of simplification and to clearly associate each study site with its respective climate, the Barreirinhas region will be referred to as the longer dry season (LDS) region, and Mirador State Park, as shorter dry season (SDS) region (Fig. 2).

The annual historical rainfall average for a 30-year period in LDS (from 1986 to 2016) was 1,700 mm; average monthly air temperature is around 27 °C, with a mean maximum of 34 °C, mean monthly minimum of 23 °C, and a dry period between July and late December, when the first rains begin to fall. The thermal amplitude, considering mean monthly data, varies from 8 to 14 °C (INMET-Instituto Nacional de Meteorologia/Chapadinha Station (n° 82382), 2017). The day length varies from 11 h and 57 min in June to 12 h and 18 min in December (Source: http://www.sci.fi/~benefon/sol.html). Altitudes around 90 m are predominant and the soils are sandy yellow latosols, with a high content of coarse sand and clay, being generally poorer than SDS soil (Appendix A, Supplementary material).

In SDS, the annual historical average rainfall was 1,200 mm; the monthly mean air temperature of 27 °C, monthly mean maximum of 33 °C and monthly mean minimum of 22 °C. Although SDS and LDS sites show similar ranges of mean temperature variation, mean monthly data show that the SDS region has a greater thermal amplitude – from 7 to 16 °C (INMET, Balsas Station (n° 82768), 2017) –, and a dry period extending from May to September. Despite little variation, the day length also has greater amplitude earlier in SDS area, going from 11 h and 44 min in June, to 12 h and 31 min, in December (Source: http://www.sci.fi/~benefon/Sol.html). The altitude ranges from 300 to 600 m, and the predominant soils in the region are litholic and yellow latosols, of the sandy loam type, with a high content of fine sand, and about 10% clay (Appendix A, Supplementary material). The monthly climatic data of total precipitation, mean maximum and mean minimum air temperatures (Source: http://www.inmet.gov.br/portal/) and day length (Source: http://www.sci.fi/~benefon/sol.html), for the period from April 2014 to March 2016, were obtained for association with the phenological data.

2.2. *Phenological study*

The vegetative (leaf fall and flush) and reproductive (flowering) phenology were recorded monthly in populations of five woody species that are common to the study sites and widely distributed in typical savanna areas of the Brazilian territory: *Byrsonima crassifolia* (L.) Rich. (Malpighiaceae), *Caryocar coriaceum* Wittm. (Caryocaraceae), *Hirtella ciliata* Mart. & Zucc. (Chrysobalanaceae), *Qualea grandiflora* Mart. (Vochysiaceae) and *Plathymenia reticulata* Benth. (Fabaceae). We marked and monitored all individuals of these species in 20 plots (20 × 20 m), covering 1.6 ha at each site. We sampled individuals with a minimum of 10 cm of trunk circumference at the ground level. Conspecific populations presented different densities in each area, implying a different number of individuals sampled per species. The number of individuals in LDS and SDS were, respectively: 69 and 11 for *B. crassifolia*; 13 and 26 for *C. coriaceum*; 19 and 27 for *H. ciliata*; 28 and 48 for *Q. grandiflora* and 140 and 11 for *P. reticulata*. Vouchers for these species are deposited in the Universidade Federal do Maranhão herbarium (Herbarium MAR).

Over a period of two years (between April 2014 and March 2016), we made monthly visual estimates of the percentage of crown area in each individual that presented the following signs: losing brown leaves (for leaf fall); flushing new leaves (for leaf flush); flower buds and/or open flowers (for flowering). Estimates for leaf fall, leaf flush and flowering were made using a scale of five categories: 0, 1, 2, 3 and 4, at intervals of 25% (0: 0%; 1: 1–25%; 2: 26–50%; 3: 51–75% and 4: 76–100%), following the methodology described by Fournier (1974). We calculated monthly averages of the percentage for each studied population, using the sum of the intensity values obtained for all individuals and dividing by the maximum possible value (number of individuals multiplied by four). This value was converted into a percentage.

2.3. *Statistical analysis*

We applied circular statistics to detect seasonal trends at the start (the mean date in which each population manifested the phenophase for the first time) and peak dates (the mean date in which each population showed the highest value for intensity) for a given phenological event. We also compared phenological patterns between the conspecific populations at both sites. For this, the months were converted to angles at 30° intervals. The circular parameters were estimated for each conspecific population (mean start and peak dates and length of mean vector (*r*)). To test the occurrence of seasonality, the Rayleigh Z test was applied. If the probability value is significant, the concentration intensity around the mean angle, represented by the vector *r*, is considered as a measure of the degree of seasonality, ranging from zero to one. It was not possible to determine the mean date of leaf fall start, since the activity in this phenophase was continuous in all individuals of the evaluated species, though it differed in intensity of occurrence.

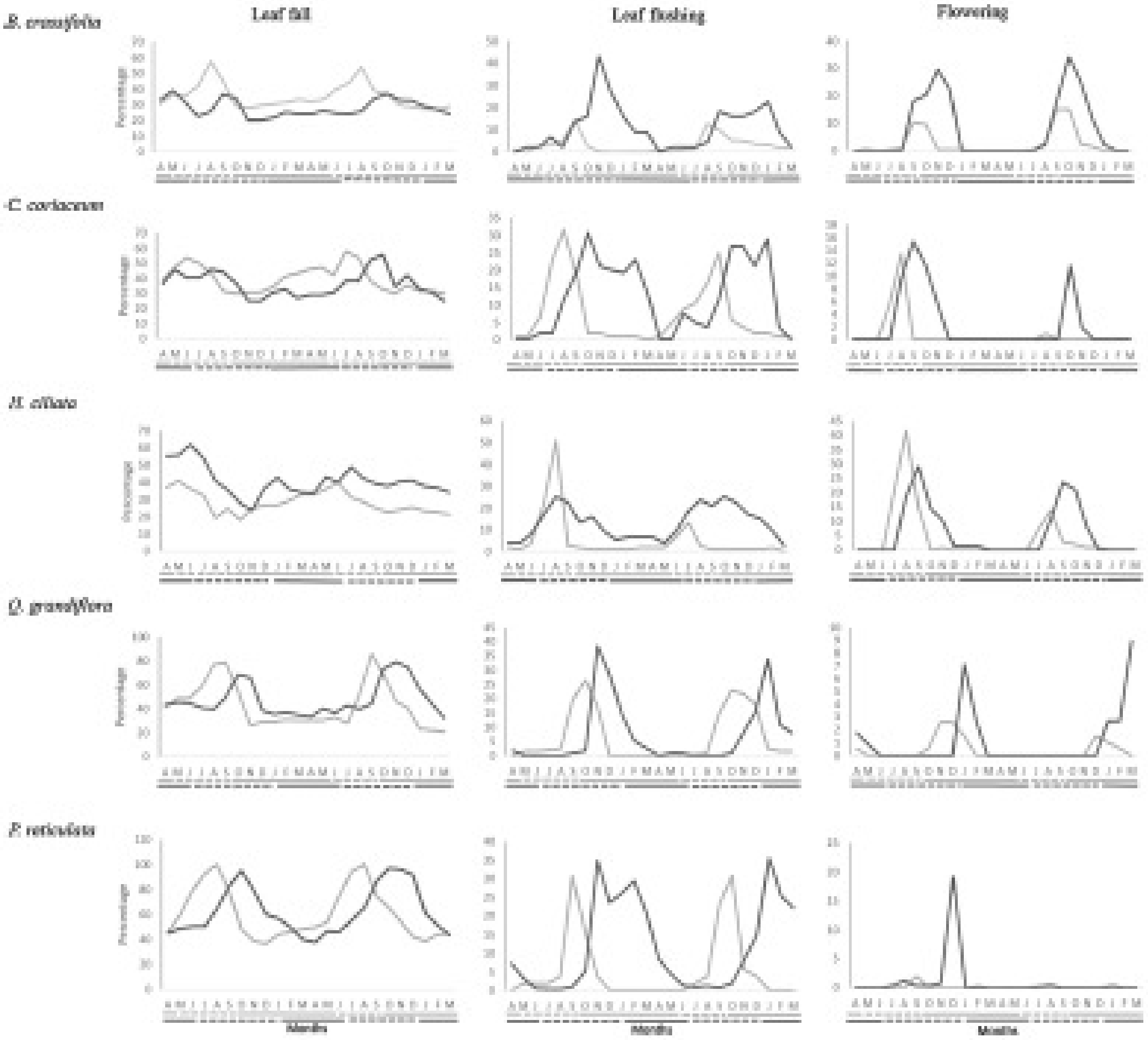

Fig. 3. Fournier intensity (percentage) for leaf fall, leaf flushing and flowering in the species *B. crassifolia*, *C. coriaceum*, *H. ciliata*, *Q. grandiflora* and *P. reticulata*, for LDS – longer dry season site (dark gray lines) and SDS – shorter dry season site (light gray lines), Maranhão State, Brazil. Rainy season indicated by continuous lines below the x axis; dry season indicated by dotted lines below the x axis.

We performed the Watson-Williams two-sample (F) test when the mean angle was significant, to determine whether conspecific populations exhibit a similar seasonal pattern across areas (Zar, 2010). The analyses related to circular statistics were performed in the software ORIANA 4.0 (Kovach, 2011). The species *P. reticulata* had only one flowering record in SDS and was therefore excluded from the statistical evaluations of this phenophase. In addition, we used multiple regression analysis to evaluate the association between phenological events (dependent variables) and monthly climatic variables, such as total precipitation, mean maximum and minimum air temperatures, and day length (independent variables). For these analyses, we showed only the significant relationships and the respective beta values (the effect of the independent variable on the dependent variable) (Zar, 2010).

3. Results

All species exhibited seasonal behavior on their peak dates of leaf fall as well on the start and peak dates of leaf flushing and flowering (Fig. 3 Table 1). In LDS, these phenomena were concentrated between July and December, whereas in SDS, they occurred from August to October, predominantly in the driest months. Independently of the species, the phenological phenomena tended to occur about one to three months earlier in SDS than in LDS (Fig. 3 Table 1).

For *B. crassifolia*, the mean start and peak dates occurred from October to December at LDS, and from August to October in SDS. The events showed significantly different start and peak dates (Table 2), with a delay of few days to two months at LDS (Table 1). The intensity of events exhibited the same trend, with uneven distribution between sites and higher proportions occurring earlier in SDS than in LDS. The duration of leaf flushing and flowering was longer in LDS than in SDS (Fig. 3).

For *C. coriaceum*, the mean dates of phenophases occurred from September to November in LDS, and from August to September in SDS (Table 1), with all phenophases showing significant differences between sites (Table 2). In LDS, start and peak events for this species occurred about one to two months later than in SDS (Table 1), and the duration of leaf flushing and flowering was longer. In SDS, higher intensity percentages of all phenophases occurred earlier than in LDS (Fig. 3).

For *H. ciliata*, the mean dates occurred from July to October in LDS, and from June to August in SDS. The events followed a pattern similar to those reported for the previous species, with a delay of one to two months in LDS (Table 1), except to leaf flushing start. As for the distribution of the phenophases percentages, leaf fall had the most irregular pattern throughout the year. The highest proportions of leaf flushing and flowering intensities in SDS preceded those in LDS, where their duration was prolonged (Fig. 3).

Between *Q. grandiflora* populations, the mean dates of phenophases

Table 1
Circular statistics for seasonality occurrence and mean dates for leaf fall peak and the start and peak for leaf flushing and flowering in savanna woody species subjected to longer dry season (LDS) and shorter dry season (SDS), Maranhão State, Brazil. LMV: length of the mean vector; LF = leaf fall; LFl = leaf flushing; Flw = flowering; P = peak; S = start; na = not available. Significance levels: * P < 0.001.

Sites	Statistics	LDS					SDS				
Species		LF-P	LFl-S	LFL-P	Flw-S	Flw-P	LF-P	LFl-S	LFL-P	Flw-S	Flw-P
B. crassifolia	Mean date	Oct (295.8°)	Oct (270.1°)	Dec (330.2°)	Oct (284°)	Nov (308.7°)	Aug (233.6°)	Sep (263.9°)	Oct (279.5°)	Oct (269.9°)	Oct (282.8°)
	LMV (r)	0.92	0.72	0.84	0.89	0.89	0.82	0.83	0.82	0.9	0.93
	Rayleigh Test (Z)	17.74*	11.37*	15.54*	16.81*	16.62*	72.04*	91.13*	87.68*	66.78*	71.85*
C. coriaceum	Mean date	Sep (268.5°)	Sep (263.6°)	Nov (304.1°)	Oct (279°)	Oct (287.5°)	Aug (210.9°)	Aug (220.4°)	Sep (244.5°)	Aug (225.2°)	Aug (220.8°)
	LMV (r)	0.86	0.75	0.65	0.87	0.92	0.85	0.71	0.75	0.96	0.99
	Rayleigh Test (Z)	17.86*	14.74*	9.59*	8.89*	10.07*	31.6*	24.08*	26.8*	6.49*	6.92*
H. ciliata	Mean date	Jul (199.6°)	Jul (197.6°)	Sep (252.6°)	Sep (249.7°)	Oct (274.7°)	Jun (176.6°)	Aug (212.4°)	Aug (222.4°)	Aug (223.3°)	Aug (236.9°)
	LMV (r)	0.45	0.67	0.8	0.96	0.91	0.94	0.87	0.92	0.94	0.96
	Rayleigh Test (Z)	6.02*	17.86*	23.02*	29.51*	25.77*	7.95*	32.72*	35.66*	30*	32.36*
Q. grandiflora	Mean date	Nov (317.9°)	Dec (348.9°)	Jan (8.1°)	Feb (53.7°)	Feb (55.12°)	Sep (261.5°)	Oct (269.9°)	Nov (312.3°)	Dec (345.8°)	Dec (339.7°)
	LMV (r)	0.89	0.81	0.86	0.91	0.9	0.88	0.72	0.79	0.93	0.52
	Rayleigh Test (Z)	34.6*	37.01*	38.93*	19.03*	18.86*	72.8*	50.36*	54.83*	12.05*	3.84*
P. reticulata	Mean date	Nov (304.8°)	Dec (350.6°)	Jan (0.9°)	Dec (356.9°)	Dec (358.2°)	Ago (216.9°)	Set (257.4°)	Oct (276.7°)	na	na
	LMV (r)	0.95	0.86	0.85	0.93	0.98	0.94	0.84	0.91		
	Rayleigh Test (Z)	64.09*	52.98*	51.35*	62.51*	69.50*	23.43*	17.87*	21.72*		

Table 2
Watson Williams test results for comparisons among the mean start and peak dates for leaf fall, leaf flushing and flowering in savanna species subjected to longer (LDS) and shorter dry season (SDS), Maranhão State, Brazil. LF = leaf fall; LFl = leaf flushing; Flw = flowering; S = start; P = peak; na = not available. F = circular statistical value, p = probability value.

Species	Statistics	LF-P	LFl-S	LFl-P	Flw-S	Flw-P
B. crassifolia	F	61.219	0.45	36.856	3.528	20.243
	p	< 0.001	0.503	< 0.001	0.063	< 0.001
C. coriaceum	F	47.601	14.405	22.015	16.67	16.096
	p	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
H. ciliata	F	1.155	2.584	18.046	33.029	54.258
	p	0.289	0.112	< 0.001	< 0.001	< 0.001
Q. grandiflora	F	115.156	116.974	78.434	65.327	20.071
	p	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
P. reticulata	F	76.517	63.753	67.109	na	na
	p	< 0.001	< 0.001	< 0.001		

were concentrated between November and February in LDS, and between September and December in SDS. The delay for this species was about two to almost three months (Table 1), with different mean start and peak dates (Table 2). The highest proportions of all SDS phenophases preceded those of LDS (Fig. 3). The leaf flushing and flowering pattern in LDS, referring to the phenophases duration, was not verified for this species (Fig. 3).

Phenological events in *P. reticulata* differed between sites (Table 2), with start and peak dates distributed from November to January in LDS and from August to October in SDS, with a delay of three months for all phenophases in LDS (except to Flow-S and Flow-P) (Table 1). Considering the intensity of events, we observed the same pattern of earlier occurrence in SDS and a longer leaf flushing duration in LDS (Fig. 3).

We found that maximum (positive trend) or minimum air temperatures (mostly negative trend) and day length were significantly associated with the intensity of the phenophases (Table 3). For most species, leaf fall, increased as maximum temperature increase at both sites, but it was also associated with a decrease of minimum temperatures in SDS. Day length also had a negative association with leaf fall in *C. coriaceum* and *H. ciliata*, for both sites (Table 3). For all species in SDS, except to *H. ciliata*, leaf flushing was related to the temperature (positive trend). In LDS, *B. crassifolia*, *Q. grandiflora* and *P. reticulata* showed association between leaf flushing and day length (positive trend), while for *C. coriaceum* and *H. ciliata*, maximum temperature (positive trend) and precipitation (negative trend) were, respectively, more associated with leaf flushing (Table 3). Flowering was not associated with climatic variables in *C. coriaceum* and *P. reticulata* (Table 3). For *B. crassifolia*, flowering was related to increase in maximum temperature at both sites. For *H. ciliata*, this event was associated with the decrease of the minimum temperature in SDS and an increase of the maximum temperature in LDS. *Q. grandiflora* exhibited significant relationship between flowering and day length in SDS (Table 3).

4. Discussion

Our results support the hypothesis that phenological phenomena are intrinsically linked to climatic variables, especially temperature and day length, independent of the site. We also confirm that a shorter dry season, in comparison to a longer dry season, promotes earlier occurrence of phenological patterns, because temperature and day length reaches a greater variation earlier at SDS site than at the LDS. The conspecific populations of the five evaluated species showed distinct behavior for all phenological events between the two sites, with differences in the start and peak dates. Peak dates generally occurred about one to three months later in LDS. This difference may represent levels of local adaptation and a high degree of phenotypic plasticity related to adjustments for the selective abiotic pressures driving leaf and flower production (Pellissier et al., 2014; Panchen and Gorelick, 2016; Silva Moraes et al., 2017).

The start and peak dates and the highest proportions of leaf fall intensity for the conspecific populations occurred at different times during drought in each area, accompanying the variations in temperature and/or decrease in day length at both sites. The association between temperature and leaf fall is presumably related to the increase in evaporative demand and water stress, with consequent loss of leaves, which was already reported for some savanna areas in Brazil (Bulhão and Figueiredo, 2002; Silvério and Lenza, 2010). As for the relationship with day length, this variable decreases during the early dry period, and may also function as a factor associated with leaf fall (Garcia et al., 2017), signaling climatic changes. Day length is the only variable correlated with leaf fall in *H. ciliata* at both sites, and was included among the variables related to leaf fall in *C. coriaceum*. The species *B. crassifolia*

Table 3
Multiple regression analyses results assessing the effect of climatic variables on phenology in savanna species subjected to longer dry season (LDS) and shorter dry season (SDS), Maranhão State, Brazil. NA – not available, NS – not significant. R^2 = *coefficient of determination; p = probability value and β = standardized regression coefficients*. Variables: MinT = mean minimum air temperature; MaxT = mean maximum air temperature; DL = day length; Ppt = precipitation.

Species	LDS			SDS		
	Leaf fall	Leaf flushing	Flowering	Leaf fall	Leaf flushing	Flowering
B. crassifolia	$R^2 = 0.70$ $p \le 0.01$ MaxT $\beta = 4.3$ MinT $\beta = 7.3$	$R^2 = 0.71$ $p \le 0.01$ DL $\beta = 97.27$	$R^2 = 0.74$ $p \le 0.01$ MaxT $\beta = 7.3$	$R^2 = 0.77$ $p \le 0.01$ MaxT $\beta = 2.82$ MinT $\beta = -4.35$	$R^2 = 0.63$ $p \le 0.01$ MaxT $\beta = 2.65$	$R^2 = 0.62$ $p \le 0.01$ MaxT $\beta = 2.69$
C. coriaceum	$R^2 = 0.57$ $p \le 0.01$ MaxT $\beta = 6.0$ DL $\beta = -13.2$	$R^2 = 0.75$ $p \le 0.01$ MaxT $\beta = 4.4$	NS	$R^2 = 0.77$ $p \le 0.01$ MinT $\beta = -3.23$ DL $\beta = -26.61$	$R^2 = 0.72$ $p \le 0.01$ MaxT $\beta = 4.7$ MinT $\beta = -4.6$	NS
H. ciliata	$R^2 = 0.44$ $p \le 0.05$ DL $\beta = -81.56$	$R^2 = 0.55$ $p \le 0.01$ Ppt $\beta = -0.01$	$R^2 = 0.61$ $p \le 0.01$ MaxT $\beta = 4.12$	$R^2 = 0.62$ $p \le 0.01$ DL $\beta = -31.64$	NS	$R^2 = 0.47$ $p \le 0.05$ MinT $\beta = -5.02$
Q. grandiflora	$R^2 = 0.67$ $p \le 0.01$ MaxT $\beta = 5.57$	$R^2 = 0.71$ $p \le 0.01$ DL $\beta = 178.3$	NS –	$R^2 = 0.67$ $p \le 0.01$ MaxT $\beta = 11.52$	$R^2 = 0.73$ $p \le 0.01$ MaxT $\beta = 4.44$	$R^2 = 0.65$ $p \le 0.01$ DL $\beta = 0.45$
P. reticulata	$R^2 = 0.92$ $p \le 0.01$ MaxT $\beta = 11.32$	$R^2 = 0.91$ $p \le 0.01$ DL $\beta = 0.55$	NS	$R^2 = 0.92$ $p \le 0.01$ MaxT $\beta = 7.66$ MinT $\beta = -10.9$	$R^2 = 0.59$ $p \le 0.01$ MaxT $\beta = 4.64$	NA

NS = not significant.

shows different degrees of leaf deciduousness, with greater crown cover and smaller variations in the proportions of leaf fall in LDS. The *H. ciliata* species also showed lower seasonality for this event (shorter length of vector *r*) in this area. We can postulate that these differences in the degree of intraspecific deciduousness among Cerrado species are indicative of high levels of plasticity against climatic aspects (Kuster et al., 2017), which allows them to cope with very distinct climatic regions of the Brazilian territory.

Leaf flushing showed generally consistent differences in the start and peak dates with distinct distribution of the intensity percentage throughout the year for both sites. This confirms the occurrence of the pre-rain green-up phenomenon reported for some savanna species in Central Brazil (Rivera et al., 2002; Franco et al., 2005; Silvério and Lenza, 2010; Dalmolin et al., 2015). This phenomenon is characterized by the appearance of new leaves before the rainy season. This strategy is reported to avoid plant nutrient losses due to herbivory or leaching (Van Schaik et al., 1993); to maximize carbon gain by increasing CO_2 assimilation (Rossatto et al., 2009; Dalmolin et al., 2015) and to make the best use of available nutrients in the soil as rainfall increases (Scholes and Walker, 2004; Noel and Lynch, 2009). During the pre-rain green-up, plants take advantage of the higher temperatures to quickly produce and expand their leaves. The influence of temperature on leaf flushing has been reported in tropical seasonally dry regions, such as savannas in Brazil (Pirani et al., 2009; Silvério and Lenza, 2010) and Africa (Seghieri et al., 2012) and may be a key variable for this process (Chambers et al., 2013). The delayed leaf production at LDS site (compared to plants in SDS) may be an adjustment to avoid overexposure of leaves produced during the dry season, which can decrease productivity in savanna plants.

The influence of day length has been reported as a trigger factor for leaf flush and flowering events in tropical regions, including savanna areas (Rivera et al., 2002; Young, 2007; Renner, 2007; Zimmerman et al., 2007; Pau et al., 2013; Borchert et al., 2015; Ryan et al., 2017). Although the results of the multiple regression did not show a clear relationship between the phenophases and day length, the leaf flush for all the species in LDS, except *H. ciliata*, increased considerably during the end of the dry period, when day length increases. In SDS, the increase in leaf flushing during the middle and end of the dry period occurs when there is a decrease in clouds and a higher incidence of solar radiation. Thus, as photosynthetic rates are higher in young leaves, the production of new leaves during the period of greater day length and/or irradiance favors photosynthesis and carbon gain (Wright and Van Schaik, 1994), since savanna plants has specific mechanisms to use and store water during the dry season (Goldstein et al., 2008). Therefore, the occurrence of production and growth phenophases during the period of low or no precipitation, indicates the existence of mechanisms that allow plants to rehydrate or maintain internal water levels (Worbes et al., 2013) and are favored by the transfer of assimilated products, which link directly to the growth organs and promote the production of leaves (Ryan et al., 2017) flowers and fruits (Pau et al., 2013; Zimmerman et al., 2007; Camargo et al., 2011; Borchert et al., 2015).

Flowering, which followed the trend of earlier occurrence in SDS, was less related to the climatic variables of each site. However, in *B. crassifolia* and *H. ciliata*, flowering was associated with variations in temperature during the dry period, and in *Q. grandiflora*, it was associated with the increased day length in SDS during the early rainy season. Although the populations of other species did not show significant results in relation to climatic variables, they showed a degree of seasonality compatible with different flowering strategies. Flowering occurred in *C. coriaceum* at both sites during the dry period, under higher irradiance and temperatures, and in *Q. grandiflora* in LDS, during early rainy season, with increased day length. *P. reticulata* in LDS had its flowering peak in the final days of the dry period. Thus, for both the evergreen species and the deciduous species, the water restriction in the environment does not limit flowering in general (Lenza and Klink, 2006; Tannus et al., 2006; Figueiredo, 2008; Pirani et al., 2009; Camargo et al., 2011; Silva et al., 2011; Barbosa et al., 2012). Regarding temperature, it is widely recognized as a variable that affects plant distribution and metabolism, and is an important requirement for flowering (Grace, 1987). Its influence on leaf production and flowering in savannas appears to be more important than the influence of water availability in dry and wet season (Seghieri et al., 2012).

In summary, we characterized the phenological responses in conspecific populations under distinct climates, showing that temperature and day length are the major drivers for phenological events, independent of the site. The duration of the dry season does not limit growth phenomena, but shorter dry seasons allows plants to produce leaves and flowers earlier than under longer dry seasons, because temperature and day length start to increase earlier in SDS site. This strategy indicates higher phenotypic plasticity in savanna woody plants, aligned with adjustments to maximize carbon gain and reproductive success.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.flora.2017.10.001.

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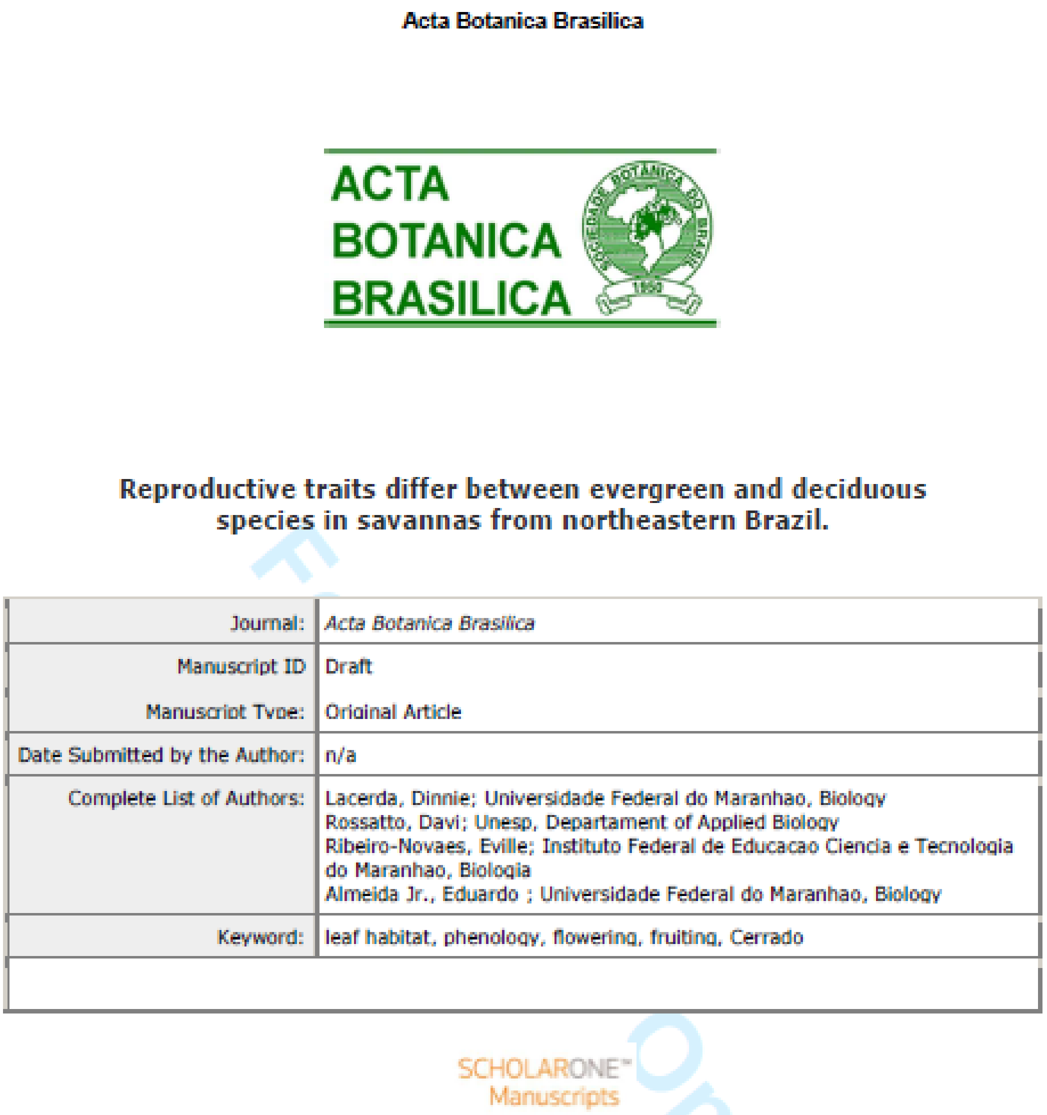
ANEXO 4

CONFIRMAÇÃO DE SUBMISSÃO DO ARTIGO REFERENTE AO CAPÍTULO III PARA A REVISTA ACTA BOTANICA BRASILICA.



Acta Botanica Brasilica

ACTA BOTANICA BRASILICA

Reproductive traits differ between evergreen and deciduous species in savannas from northeastern Brazil.

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Keyword:	leaf habitat, phenology, flowering, fruiting, Cerrado

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ANEXO 5

NORMAS PARA SUBMISSÃO NA REVISTA ACTA BOTANICA BRASILICA (CAPÍTULO III)

Language editing

If English is not your first language, it is strongly recommended to have your manuscript edited for language before submission. This is not a mandatory step, but may help to ensure that the academic content of your paper is fully understood by journal editors and reviewers. Language editing does not guarantee that your manuscript will be accepted for publication. Authors are liable for all costs associated with such services.

Types of articles

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Preparing the article file

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The first page should state the type of article (Original Article, Review, Viewpoint, Method or Short communication) and provide a concise and informative full title followed by the names of all authors. Where necessary, each name should be followed by an identifying superscript number (1, 2, 3 etc.) associated with the appropriate institutional address to be entered further down the page. Only one corresponding author should be indicated with an asterisk and should always be the submitting author. The institutional address(es) of each author should be listed next, each address being preceded by the superscript number where appropriate. The address must be synthetic, just enough to send a letter. Titles and positions should not be mentioned. This information is followed by the e-mail address of the corresponding author

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The Abstract should be followed by between five and ten Key words. Note that essential words in the title should be repeated in the key words.

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Title page
Abstract
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Materials and Methods
Results
Discussion
Acknowledgements
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Material and Methods and Results should be clear and concise. The Discussion section should avoid extensive repetition of the results and must finish with some conclusions. This section can be combined with results (Results and Discussion), however, we recommend authors consult the Editoral Board for a previous evaluation.

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Citations in the text should take the form of Silva (2012) or Ribeiro & Furr (1975) or (Mayer & Wu 1987a; b; Gonzalez 2014; Sirano 2014) and be ordered chronologically. Papers by three or more authors, even on first mention, should be abbreviated to the name of the first author followed by et al. (e.g. Simmons et al. 2014). If two different authors have the same last name, and the article have the same year of publication, give their initials (e.g. JS Santos 2003). Only refer to papers as 'in press' if they have been accepted for publication in a named journal, otherwise use the terms 'unpubl. res.', giving the initials and last name of the person concerned (e.g., RA Santos unpubl. res.).

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Smith GM. 1938. Cryptogamic botany. Vol. II Bryophytes and Pteridophytes. 2nd. edn. New York, McGraw-Hill Book Company.

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Research papers

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Alves JJ, Sampaio MTY. 2015. Structure and evolution of flowers. Acta Botanica Brasilica (in press). doi: 10.1590/0102-33062015abb3339.

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We acknowledge the Center of Microscopy (UFMG) for providing the equipment and technical support for experiments involving electron microscopy. We also thank J.S. Santos for assistance with the statistical analyses. This work was supported through a research grant from the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq (ID number).

For SHORT COMMUNICATIONS note that the editorial guidelines applying to original papers must also applying here. In general, the difference between original papers and short communications is the lack of subsections in the text and limited space for illustrations in the latter. Figures and tables can be present, assuming that the overall size of the manuscript does not exceed the five printed page limit (supplementary material can be added). The abstract (as described for original articles) must be followed by a "running text" (a single section, without subheadings), followed by the acknowledgments and references.

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All figures (photographs, maps, drawings, graphs, diagrams, etc.) and tables must be cited in the text, in ascending order. Citations of figures in the text should appear in an abbreviated, capitalized form (e.g., Fig. 1, Fig. 2A-D, Fig. 3A, Figs. 3A, 4C, Tab.1).

The maximum dimensions of individual figures should be 170 × 240 mm. The width of an individual component can be 170 mm or 85 mm, without exception, whereas the height can be ≤ 240 mm. For continuous tone images (e.g., photographs), please supply TIFF files at 300 dpi. More complex drawings, such as detailed botanical illustrations will not be redrawn and should be supplied as 600 dpi TIFF files.

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