UNIVERSIDADE FEDERAL DE UBERLÂNDIA
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PADRÕES FENOLÓGICOS E DISPERSÃO DE DIÁSPOROS DE ESPÉCIES ANEMOCÓRICAS REPRESENTATIVAS DO CERRADO

LETÍCIA RODRIGUES NOVAES

UBERLÂNDIA-MG

2020

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PADRÕES FENOLÓGICOS E DISPERSÃO DE DIÁSPOROS DE ESPÉCIES ANEMOCÓRICAS REPRESENTATIVAS DO CERRADO

Dissertação apresentada à Universidade Federal de Uberlândia, como parte das exigências para obtenção do título de Mestre em Ecologia e Conservação de Recursos Naturais.

Orientadora: Prof.ª Dr.ª Helena Maura Torezan Silingardi

Coorientador: Prof. Dr. Odenir de Almeida

UBERLÂNDIA-MG

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Reuniu-se na sala 14A, bloco 2D, Campus Umuarama, da Universidade Federal de Uberlândia, a Banca Examinadora, designada pelo Colegiado do Programa de Pós-graduação em Ecologia e Conservação de Recursos Naturais, assim composta: Professores Doutores: André Rosalvo Terra Nascimento - INBIO/UFU; Estevão Alves da Silva - IFGoiano; Helena Maura Torezan Silingardi - INBIO/UFU, orientador(a) do(a) candidato(a).

Iniciando os trabalhos o(a) presidente da mesa, Dr(a). Helena Maura Torezan Silingardi, apresentou a Comissão Examinadora e o candidato(a), agradeceu a presença do público, e concedeu ao Discente a palavra para a exposição do seu trabalho. A duração da apresentação do Discente e o tempo de arguição e resposta foram conforme as normas do Programa.

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APROVADA em 29 de janeiro de 2020.

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UBERLÂNDIA-MG

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ÍNDICE

RESUMO

Em ambientes sazonais os fatores bióticos e abióticos variam entre as estações do ano. As plantas evoluíram adaptações para expressar suas fenofases nas épocas com condições mais favoráveis. Os estudos de fenologia na savana brasileira têm descrito um padrão generalizado para todas as espécies, baseado principalmente na precipitação e temperatura, desconsiderando o vento, o modo de dispersão e a divisão entre as fenofases de frutos jovens e maduros. O vento é importante especialmente no momento da liberação dos diásporos e na distância de dispersão de espécies anemocóricas. A distância afeta o sucesso reprodutivo das plantas, o padrão de distribuição das espécies, a dinâmica das populações e a estrutura das comunidades. Apesar disso, não há um consenso quanto ao conjunto de fatores que, juntamente com o vento, determinam a distância de dispersão de espécies anemocóricas. Tem-se investigado os padrões de dispersão de espécies anemocóricas do hemisfério norte, mas pouco se sabe sobre elas no hemisfério sul, especialmente na savana brasileira ou Cerrado, as quais computam cerca de 30% de suas espécies. Além disso, raros estudos avaliam concomitantemente a influência de fatores bióticos e abióticos e suas interações na distância de dispersão, em condições naturais e controladas. Diante disso, o objetivo 1 desse trabalho foi descrever os padrões fenológicos de cinco espécies anemocóricas de Cerrado de acordo com as condições climáticas. Para isso foram elaboradas as seguintes hipóteses: (i) as espécies apresentam padrão fenológico similar entre si; (ii) a influência das variáveis abióticas (vento, precipitação, temperatura e umidade) é diferente entre as fenofases; (iii) a dispersão dos diásporos é relacionada à caducifolia. O objetivo 2 foi investigar a influência de fatores extrínsecos e intrínsecos aos diásporos na distância de dispersão em condições naturais e controladas. Para isso foi elaborada a seguinte hipótese: (iv) fatores extrínsecos (velocidade do vento e temperatura) e intrínsecos (tempo de queda, carga alar e grupo aerodinâmico) afetam a distância de dispersão das espécies anemocóricas de Cerrado. As espécies apresentaram padrão fenológico similar entre si, exceto para as fenofases de botão e flor (de duas espécies) e fruto jovem. A influência de cada variável abiótica depende da fenofase, mas em geral a precipitação e os ventos são os fatores mais importantes. O momento de dispersão dos diásporos está relacionado à queda das folhas. Os resultados mostraram ainda que fatores extrínsecos e intrínsecos aos diásporos influenciaram direta e indiretamente a distância de dispersão. O fator mais relevante foi o vento, seguido pelo tempo de queda. A distância de dispersão aumentou com o vento, a temperatura e o tempo de queda e diminuiu com o aumento da carga alar da semente. As variáveis também apresentaram interações entre si, influenciando indiretamente a distância. Esses resultados mostram a importância da inclusão do vento e das interações entre as fenofases ao avaliar padrões fenológicos. Sugerem ainda que é necessário considerar efeitos lineares e causais para determinar o potencial de dispersão das espécies anemocóricas.

Palavras-chave: Sementes; Savanna brasileira; *Aspidosperma*; *Dalbergia*; *Kielmeyera*; *Peixotoa*; *Pterodon*; *Qualea*.

ABSTRACT

In seasonal environments, biotic and abiotic factors vary between seasons. Plants evolved adaptations to express their phenophases in periods with more suitable conditions. Previous studies have described a generalized phenological pattern for all species in the Brazilian savanna, mainly based on rainfall and temperature, not considering the wind, the dispersal mode and the division between the phenophases of young and ripe fruits. The wind is important especially at the diaspore release and its dispersal distance, observed in anemocoric species. Distance affects plant reproductive success, species distribution pattern, population dynamics, and community structure. Despite this, there is no consensus about which factors are the most important in driving seed dispersal distance. Most studies are performed with Northern Hemisphere vegetation and few studies have attempted to observe anemocoric seed dispersal distances of plants from the Southern Hemisphere, especially at Savanna environments. The Brazilian Savanna, also called Cerrado, presents about 30% of anemocoric species. Furthermore, rare studies concurrently evaluate the influence of biotic and abiotic factors and their interactions on dispersal distance under natural and controlled conditions. In this context, the first aim was to describe the phenological patterns of five anemocoric plant species in the face of different climatic conditions. We addressed three hypotheses: (i) anemocoric plants are phenologically similar; (ii) the influence of abiotic factors (wind, rainfall, temperature, and humidity) differs between phenophases; (iii) diaspores dispersal is related to deciduousness. The second aim was to investigate the influence of extrinsic and intrinsic seed-related factors on the seed dispersal distances of anemocoric species under natural (field) and controlled (laboratory with wind tunnel) conditions. Our main hypothesis was that both extrinsic (wind speed and temperature) and intrinsic (falling time, wing-loading and aerodynamic group) diaspore-related factors influence diaspore dispersal distance of Cerrado anemocoric species. The results show that the species are phenologically similar, except for the floral bud and flower of two species and young fruit. The influence of each abiotic variable differs between phenophases, but in general rainfall and wind are the most important factors. The diaspore dispersal moment is related to the leaf fall. The results also showed that extrinsic and intrinsic factors to diaspores directly and indirectly influenced the dispersal distance. The most relevant factor was wind, followed by falling time. The dispersal distance was positively related to the wind speed, temperature and falling time and negatively related to the diaspore wing-loading. The variables also presented interactions with each other, indirectly influencing the distance. These results show the importance of include wind and the interactions between phenophases when evaluating phenological patterns. It also suggests that linear and causal effects should be considered in order to determine the dispersal potential of anemocoric species.

Keywords: Seeds; Brazilian Savanna; *Aspidosperma*; *Dalbergia*; *Kielmeyera*; *Peixotoa*; *Pterodon*; *Qualea*.

Introdução Geral

A dispersão de sementes consiste no rompimento da ligação do diásporo com a planta-mãe e seu transporte para um novo local, onde poderão ocorrer a germinação e o estabelecimento da plântula (Van Der Pijl, 1982; Levin et al., 2003). A dispersão, em especial à longas distâncias, possibilita o escape de predadores, parasitos e doenças, a diminuição da competição entre coespecíficos, o aumento das chances de sobrevivência e a colonização de novos locais favoráveis ao estabelecimento (Howe & Smallwood, 1982; Augspurger et al., 2016; Sullivan et al., 2018). Dessa forma, a distância de dispersão dos diásporos influencia os padrões de distribuição das espécies, o fluxo gênico, a manutenção da dinâmica espacial de populações e metapopulações e a estrutura das comunidades (Soons & Bullock, 2008; Maurer et al., 2013). Além disso, constitui uma estratégia importante para a persistência das espécies frente às mudanças climáticas globais (Hampe, 2011).

O processo de dispersão de diásporos pode ocorrer de diversas formas dependendo das interações das espécies vegetais com os agentes bióticos ou abióticos e são denominadas síndromes de dispersão. A autocoria é a dispersão dos diásporos por mecanismos próprios e a zoocoria é a dispersão feita por animais. A hidrocoria é a dispersão pela água e a anemocoria é a dispersão pelo vento (Van der Pijl, 1982; Quick et al., 2016). A distribuição dessas síndromes no ambiente é influenciada por diversos fatores, como a estrutura da paisagem e as condições climáticas locais. A maior riqueza de espécies anemocóricas é encontrada em ambientes mais abertos e/ou secos (Howe & Smallwood, 1982). Isso provavelmente ocorre pelo fato dos ventos serem mais intensos em áreas abertas do que em florestas densas, visto que em áreas abertas o bloqueio físico feito pelas plantas para a movimentação do vento e dos diásporos carregados por ele é menor, permitindo uma maior eficiência de dispersão (Nathan, 2001; Schupp et al., 2019). Ambientes secos permitem uma maior evaporação da água e consequente perda de peso dos diásporos, além de proporcionar o aumento da velocidade das massas de ar, o que também incrementa a dispersão (Heydel & Tackenberg, 2016).

A Savana Brasileira ou Cerrado apresenta vegetação predominantemente aberta e com duas estações climáticas bem definidas, o verão chuvoso e quente e o inverno seco e com temperaturas mais amenas (Coutinho, 2002). O Cerrado possui cerca de 13.670 espécies (Flora do Brasil, 2018) e aproximadamente 30% delas (segundo levantamento realizado na base de dados REFLORA: reflora.jbrj.gov.br) apresenta dispersão anemocórica, sendo esta a segunda síndrome mais recorrente nesse ambiente (Gottsberger & Silberbauer-Gottsberger, 1983; Peres, 2016).

As espécies que utilizam o vento para disseminação de seus diásporos geralmente apresentam adaptações morfológicas para permitir um maior tempo de queda, ou seja, mais tempo de voo entre a liberação da planta-mãe e o pouso no solo. Dessa forma, aumenta a probabilidade dos diásporos serem levados por rajadas de vento e alcançarem maiores distâncias de dispersão (Green, 1980; Howe & Smallwood, 1982; Augspurger, 1986; Nathan et al., 2011). As adaptações morfológicas estão relacionadas ao formato, à área de sustentação e à carga alar dos diásporos, que é a massa dividida pela área. Essas adaptações determinam o grupo aerodinâmico de cada diásporo, ou seja, o comportamento do diásporo no ar. As espécies que apresentam essas adaptações geralmente são classificadas em dois grupos morfológicos: plumosas ou aladas. Os diásporos plumosos são do grupo aerodinâmico flutuante, já os alados podem ser autogiros, autogiros-rolantes, planadores ou tipo helicóptero (Augspurger, 1986). Além dos traços dos diásporos, características da planta como a forma de crescimento e altura também podem influenciar o processo de dispersão (Thomson et al., 2011, Bullock et al., 2017).

As condições climáticas como a umidade, precipitação e temperatura são outros fatores relevantes na dispersão dos diásporos, visto que interferem na distribuição e intensidade dos ventos e também na massa das sementes, atuando assim na distância de dispersão alcançada (Tackenberg, 2003; Ozinga et al., 2004; Renner, 2004; Heydel & Tackenberg, 2016). Em ambientes sazonais as condições climáticas também afetam indiretamente a distância de dispersão por influenciar a fenologia das espécies (Williams et al., 1997, Damascos et al., 2005; Almeida et al., 2016). Por exemplo, muitas espécies anemocóricas tem a dispersão dos diásporos coincidindo com o final da estação seca (Oliveira, 2008), quando há menor umidade e maior intensidade de ventos (Soons & Bullock, 2008), o que pode aumentar as chances de dispersão a maiores distâncias e influenciar o sucesso reprodutivo das plantas.

Apesar da grande quantidade de estudos de dispersão de diásporos anemocóricos, não há um consenso em relação ao conjunto de fatores determinantes nesse processo (Soons et al., 2004; Wright et al., 2008; Zhu et al., 2015). Além disso, os trabalhos realizados estão concentrados no hemisfério norte (Augspurger et al., 2016; Masaki et al., 2019) e pouco é conhecido a respeito desse processo para as espécies de savana, especialmente a savana brasileira. É importante ressaltar ainda que os trabalhos muitas vezes avaliam os fatores de forma isolada ou apenas com modelos matemáticos teóricos. Somando-se a isso, pouco tem sido investigado acerca da fenologia completa das espécies anemocóricas, considerando tanto a fenologia vegetativa quanto a fenologia reprodutiva. Os estudos existentes são de espécies isoladas e não levam em consideração o modo de dispersão, a distinção entre as fenofases de fruto jovem e de fruto maduro na fase de dispersão, e as possíveis interações entre as fenofases.

Diante disso, o trabalho foi dividido em dois capítulos formatados como dois manuscritos que serão submetidos a revistas científicas:

1- Environmental variables drive phenological events of anemocoric plants and enhance diaspore dispersal potential: a new wind-based approach

O objetivo desse capítulo foi descrever os padrões fenológicos de cinco espécies anemocóricas comuns no Cerrado, considerando as variáveis climáticas.

(Capítulo no formato da revista*: Science of the Total Environment*)

2- Seeds in the wind: extrinsic and intrinsic seed-related factors determine seed dispersal distance in the Brazilian savanna

O objetivo desse capítulo foi investigar a influência de fatores extrínsecos e intrínsecos às sementes na distância de dispersão de espécies anemocóricas de Cerrado, em condições naturais e controladas.

(Capítulo no formato da revista: *Journal of Ecology*)

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Environmental variables drive phenological events of anemocoric plants and enhance diaspore dispersal potential: a new wind-based approach

ABSTRACT

Phenological studies of Brazilian savanna vegetation have described a generalized phenological pattern for all species, mainly based on rainfall and temperature. Few, if any, studies have considered wind as an explanatory factor; abiotic factors may differ between phenophases, and one phenophase may directly influence the expression of another. Thus, we aim to describe the phenological patterns of five anemocoric plant species (*Aspidosperma tomentosum*, *Dalbergia miscolobium*, *Kielmeyera coriacea*, *Peixotoa tomentosa* and *Qualea multiflora*) in the face of different climatic conditions, mainly evaluating the effects of wind on the ripe diaspore. We addressed three main questions: (1) What is the phenological behavior of each of these five anemocoric species in a seasonal environment? (2) Which climatic variables best explain each phenophase? And, (3) is the dispersal of ripe diaspores synchronized with leaf fall at the end of the dry season, since the presence of leaves may otherwise block the spread of diaspores? We found that (i) our focal species showed similar phenological patterns, except for the floral bud and flower phenophases of two species (*A. tomentosum* and *P. tomentosa*), and the young fruit phase; (ii) each abiotic variable has a specific level of influence for each phenophase, but the most important variables were rainfall and wind speed; and (iii) the dispersal moment of diaspores is related to deciduousness, occurring when plants have fewer leaves blocking wind passage and enabling dispersal over long distances. We conclude that the phenological patterns of these five anemocoric plants are similar, but that the patterns observed are not necessarily those described for Cerrado species. Additionally, we find that wind is an important factor in the expression of specific

phenophases, and that the expression of some phenological events depends on the expression of others, especially diaspore dispersal.

KEYWORDS: Phenology; Seed dispersal; Cerrado; Brazilian savanna; Phenophase.

1. Introduction

Phenology is the study of naturally recurring phenomena, such as animal and plant life cycle events, and their relationships to climate (Almeida et al., 2013; Almeida et al., 2016). The study of plant phenology points to the main factors that induce the temporal changes in phenological events of each species, such as leafing, deciduousness, budding, flowering, and fruiting (Morellato et al., 2010; Mariano et al., 2016). The timing, duration, and synchrony of phenological events, also called phenophases, influence plant reproductive success, community structure, and the quantity and quality of resources available for consumer organisms (Williams et al., 1999); that is, they are paramount for ecosystem dynamics.

Plants, like other organisms, have developed adaptations to express their phenophases in the most suitable seasons, when considering seasonal variation in biotic and abiotic natural factors (Batalha and Martins, 2004; Sanchez-Azofeifa et al., 2013; Wright et al., 2019). In seasonal tropical environments, plant phenological events are determined both by their internal rhythms and by seasonal climatic changes (Damascos et al., 2005). In temperate ecosystems, phenological events are caused primarily by seasonal changes in temperature and photoperiod, while in tropical ecosystems, studies have shown that phenological events are mainly caused by rainfall (Reich and Borchert, 1984; Wright et al., 2019).

From this perspective, we may notice that plant behavior (the specific adjustments in growth and development according to the environment; Van Loon, 2016) is closely linked to abiotic factors, which drive phenological events. However, these phenological events may also be changing due to climate change, which can directly affect the reproductive success of plants (Vilela et al., 2017). Also, phenological changes can indirectly affect the community dynamics (Memmott et al., 2007; Encinas-Viso et al., 2012; Velasque and Del-Claro, 2016), since plants are the basis of the food chain and act as links within ecosystems (Del-Claro and Torezan-Silingardi, 2012). Several studies have evaluated and shown the effects of climate change on abiotic factors, especially on temperature and rainfall. Vilela et al. (2017) showed that variation in temperature and rainfall in Brazilian savanna over a period of ten years affects the timing of flowering, altering the degree of synchrony among plant species and consequently their interactions with herbivores, pollinators and fruit set.

These effects of climate change on plant phenological events and community dynamics become even more important in seasonal ecosystems. The Brazilian Neotropical savanna, also called Cerrado, has a marked dry/cold season (April-September) and wet/warm season (October-March), and a high diversity of plants with different life forms and dispersal modes (Oliveira-Filho and Ratter, 2002). The Cerrado has approximately 14,000 plant species (Flora do Brasil, 2018), and anemocoric plants represent 30% of this total (according to our survey of the Reflora database: http://reflora.jbrj.gov.br/reflora/herbarioVirtual/, accessed 01/30/2018). Anemochory is the second most common dispersal syndrome (Gottsberger and Silberbauer-Gottsberger 1983; Peres, 2016), behind only zoochory, which is the first dispersal syndrome in Cerrado and in many other tropical areas (Escribano-Avila et al., 2018).

Phenological studies of Cerrado vegetation have described a generalized phenological pattern, mainly based on rainfall and temperature (Batalha and Mantovani, 2000; Lenza and Klink, 2006; Silva et al., 2011; Azevedo et al., 2014; Lacerda et al., 2018). According to this general pattern, leaf sprouting is common at the transition from dry to wet season, leaf fall occurs at the end of the dry season in deciduous species, flowering occurs mainly during the wet season, and fruit dispersal by animals occurs in the wet season, while wind dispersal is concentrated in the dry season. Few studies have shown how wind, or other related abiotic factors, affects the phenology of anemocoric plants, especially diaspore dispersal events. Specific wind conditions can determine the timing of abscission of anemocoric propagules and directly influence dispersal distance and indirectly affects plant fitness (Soons and Bullock, 2008; Maurer et al., 2013; Heydel et al., 2015; Escobar et al., 2018). In addition, the effects of climate change on one phenophase may affect the occurrence of another phenophase. For instance, new spaces are created in the canopy when leaves fall, which allow increased wind passage and may facilitate diaspore dispersal (Mantovani and Martins 1988; Donohue 1998; Maurer et al., 2013; Fu, 2019; Seale and Nakayama, 2019).

Thus, current climate changes can lead to a collapse of the plant community, and not only through developmental problems due to changes in temperatures and rainfall (Vilela et al., 2017). Plant community collapse may also happen through changes in wind speed patterns. Studies related to these changes in the wind speed or wind direction as influenced by climate change are considerably abundant, but all are mainly related to wind power production (Lucena et al., 2010; Miu et al., 2015; Karnauskas et al., 2017). Therefore, there is a clear need to study how environmental variables, especially wind, which is little studied from the perspective of climate change and ecosystem dynamics, can affect plant phenological events, which may then indirectly affect food chain structure and ecosystem functioning.

In this context, we aimed to describe the phenological patterns of five anemocoric plant species as affected by climatic conditions, mainly by evaluating the effects of wind on the ripe diaspore. We addressed three main questions: (1) What is the phenological behavior of these five anemocoric species in a seasonal environment? (2) Which climatic variables best explain each phenophase? And (3) is ripe diaspore dispersal synchronized with leaf fall at the end of the dry season, as the presence of leaves may otherwise block the spread of diaspores?

Each of our questions relates to a hypothesis, prediction and approach (see Table 1 for details).

Table 1. Hypotheses and predictions tested in this study to evaluate phenological patterns of anemocoric species in the Brazilian savanna.

Overview	Prediction	Approach	Resource
H1: Anemocoric plants are phenologically similar	Leaves sprout during the transition from dry to wet seasons	Analysis of phenological activity and intensity over the year	Fig. 1a; Supplementary Material (SM): Fig. S2a; Table 2
	Developed leaves occur year-round, but with a lower intensity at the end of the dry season		Fig. 1b; SM: Fig. S2b; Table 2
	Deciduousness occurs mainly at the end of the dry season		Fig. 1c; SM: Fig. S3; Table 2
	Floral buds, flowers and young fruits occur during the wet season		Fig. 2a-c; SM: Fig. S4a-b; Fig. S5a; Table 2
	Ripe diaspores occur mainly at the end of the dry season		Fig. 2d; SM: Fig. S5b; Table 2
H2: The influence of abiotic factors differs between phenophases	Vegetative phenophases are more conditioned by rainfall	Redundancy Analysis (RDA)	SM: Fig. S6 and S7; Table S1
	Production of floral buds, flowers and young fruits are mainly explained by rainfall and temperature		
	Ripe diaspores are mainly explained by wind speed		
H3: Diaspore dispersal is related to deciduousness	Ripe diaspores occur during deciduousness, since the presence of leaves decreases diaspore dispersal potential	Watson two-test analysis	Fig. S3 and S5b

2. Materials and Methods

2.1 Study site

Fieldwork was carried out from May/2018 to July/2019 at a tropical savanna reserve (18°57’45”S, 48°17’30”W) from “Clube de Caça e Pesca Itororó de Uberlândia”, Minas Gerais State, Brazil (Vilela et al., 2014). The vegetation consists of a variety of phytophysiognomies typical of the Cerrado (see Appolinario and Schiavini, 2002). We used plants from the cerrado *sensu stricto*, characterized by a dense scrub of shrubs and trees (Vilela et al., 2017). The climate at the study site is markedly seasonal, with a dry/cold season (April-September) and a wet/warm season (October-March) (Oliveira-Filho and Ratter, 2002; Vilela et al., 2017). The mean annual rainfall is 1500 mm and mean annual temperature is 22 °C (Bächtold et al., 2012). During the study, the climatic seasonality resembled the average climatic pattern, with an annual total rainfall of 1597 mm, but a higher annual mean temperature of 27ºC.

2.2 Species

We chose five anemocoric species common to the Cerrado (Flora do Brasil, 2018), each from a different family. *Aspidosperma tomentosum* Mart. (Apocynaceae), which has dry follicle type fruit; *Dalbergia miscolobium* Benth. (Fabaceae), which has samaroid type fruit; *Kielmeyera coriacea* Mart. & Zucc. (Calophyllaceae), which has septicidal capsule type fruit; *Peixotoa tomentosa* A. Juss. (Malpighiaceae), which has samarid type fruit; and *Qualea multiflora* Mart. (Vochysiaceae), which presents a loculicidal capsule type fruit (Barroso et al., 1999) (see species Fig. S1 in Supplementary Material). All species are trees when adult, but can also remain shrubby, except for *P. tomentosa,* whose individuals are only shrubs. The focal species also rank high on the Importance Value Index (IVI) in the Cerrado, where *D.*

miscolobium and *Q. multiflora* belong to the two most abundant families (Felfili and Silva, 1993; Bridgewater et al., 2004).

2.3 Data collection

Every month over a 14-month period, we evaluated the phenology of fifteen individual plants per species (total = 75 plant individuals). The phenological vegetative events were: the presence of (i) sprouting leaves, (ii) developed leaves and (iii) deciduousness; while the phenological reproductive events were: the presence of (iv) floral buds, (v) flowers, (vi) young fruits (fruits not ready for dispersal, usually small, newly formed, greenish and/or enclosed in capsule), and (vii) ripe diaspores (when diaspores are being dispersed; henceforth simply: ripe fruits), adapted from Azevedo et al. (2014). We determined the occurrence of each phenophase by the presence/absence and intensity of each phenophase per individual (adapted from Fournier, 1974; Ribeiro and Castro, 1986). Phenophase intensity was scored for each plant using an interval semi-quantitative scale from 0 until 3, with 0 if the event was absent; 1 if the event was sporadic (1-25% of the branches); 2 if it was frequent (26-75% of branches); and 3 if it was very frequent (76-100% of branches). We observed plants by eye and/or with binoculars, as needed to see the canopy of larger species (Mariano et al., 2016).

Moreover, we obtained climatic data (hourly wind speed, temperature and humidity) from the Airport Tenente Coronel Aviador Cesar Bombonato, Uberlândia, Minas Gerais, Brazil (located 18,8 km from the study site), on wunderground website, and rainfall from the Climate Station of the Geography Institute of the Federal University of Uberlandia (9 km). These data were used to calculate the average maximums for each month (see Table S1).

2.4 Data analysis

Statistical analyses and diagrams were performed in R software 3.6.1 (R Core Team, 2019) with 5% probability. Each analysis and the specific packages used are described below for each hypothesis of this study.

H1 – To describe the phenological behavior and verify the occurrence of seasonal patterns, we performed circular statistical analyses for each species using the package "circular" (Agostinelli and Lund 2017). We used 12 months of data to calculate the circular statistic parameters, due to repeating patterns. The months were transformed into angles, from 1° = January to 331° = December at intervals of 30°, due to monthly observations. The frequency of individuals in each phenophase for each species was used to calculate five parameters: (i) mean vector (μ), (ii) length of mean vector (r) that is a measure of concentration of frequencies around the estimated mean angle, which vary from zero (when there is dispersion of phenophase frequencies and the mean angle cannot be described) to one (when all the data are concentrated at the same direction or angle) (Morellato et al., 2010), (iii) median, (iv) circular standard deviation, and (v) Rayleigh test (z). The mean date for each phenophase was obtained by converting the mean angular directions into corresponding mean dates (see Morellato et al., 2000; Morellato et al., 2010; Vilela et al., 2017). Before conducting circular analyses, we examined unimodality by performing Watson's goodness of fit test. Furthermore, intensity diagrams were carried out to view intensity patterns over the year.

H2 – To verify the distribution of phenophases according to climatic variables and determine which one best explained each phenophase for each species, we performed a Redundancy Analysis (RDA), using the package "vegan" (Oksanen et al., 2013). RDA is a direct extension of regression analysis, used to model multivariate response data (Roy et al., 2014). The RDA was carried out after a Hellinger transformation, which gives low weights to variables with low counts and many zeros. The statistical significance of each analysis was tested by a randomization test with 999 permutations using the ‘envfit’ function, and we used permutation of residuals at a 5% significance level to select significant variables (Liu et al., 2015). Variation partitioning was carried out using only the significant variables. The ‘anova’ function was used to check the significance of models through the package “stats” (R Core Team, 2019). The results were presented in an ordination diagram (biplot), with variables represented by arrows. To determine the influence of abiotic variables on each phenophase, we considered three factors: (i) angle size between vectors of abiotic variables and phenophases (close to 90°= uncorrelated, close to 0°= positive correlated, and close to 180°= negative correlated); (ii) arrow direction (positive correlation when arrows are in the same direction and negative correlation when arrows are in opposite directions); and (iii) arrow length (Buttigieg and Ramette, 2014), which show a variable’s importance in explaining the variation of phenophases. Predictor abiotic variables entered into the model were: wind speed, rainfall, humidity and temperature; and phenophases were: sprouting leaves, developed leaves, deciduousness, floral buds, flowers, young fruits, and ripe fruits.

H3 – To evaluate whether the dispersal of ripe diaspores was related to deciduousness, for each species we performed a Watson two-test (Zar 1996) and evaluated circular diagrams to compare the mean vector (μ) and the length of the mean vector (r) between ripe fruits and deciduousness; ripe fruits and sprouting leaves; and ripe fruits and developed leaves. To corroborate our hypothesis, the mean vector (r) of ripe fruits needed to be located along or shortly after the mean vector of deciduousness, had to always come before the mean vector of leaf sprouting, and could not overlap with the developed leaves mean vector. If those conditions were met, it would confirm that diaspore dispersal will occur at the moment when the plant has fewer leaves, which would be fundamental for long dispersal distance and plant establishment.

3. Results

H1: Anemocoric plants are phenologically similar

For all species, leaves began sprouting at the end of the dry season and the beginning of the wet season, peaking between September and October (Fig. 1a, Table 2 and Fig. S2a in Supplementary Material). All species presented developed leaves all year-round, but at a low intensity at the end of the dry season, July-September (Fig. 1b, Table 2 and Fig. S2b). Deciduousness for all species peaked in the dry season, mainly at the end of the dry season (July-September) (Fig. 1c, Table 2 and Fig. S3a).

Concerning floral buds, *A. tomentosum* and *P. tomentosa* showed floral buds during the dry season (*A. tomentosum*: July-September; *P. tomentosa*: April-August) and flowers of the other three species budded in the wet season (*D. miscolobium*: January-February*;* *K. coriacea*: November-December; *Q. multiflora*: November-January; Fig. 2a, Table 2 and Fig. S4a). Flowers were often found at the same time as floral buds (*A. tomentosum*: August-October; *P. tomentosa*: May-August; *D. miscolobium*: January-February; *K. coriacea*: November-January; *Q. multiflora*: December-February; Fig. 2b, Table 2 and Fig. S4b).

Young fruits developed differently between species, occurring during both the dry and wet seasons, but more so in the dry season (Fig. 2c, Table 2 and Fig. S5a). Three species presented a long period with young fruits, beginning soon after flowering and remaining through the end of the next dry season (*A. tomentosum*: October-August; *K. coriacea*: January-August; *Q. multiflora*: January-October). The other two species had unripe fruits for just five months, *D. miscolobium* from February-May (Fig. 2c, Table 2 and Fig. S5a), and *P. tomentosa* from May to September, during the same dry season they were produced. Ripe fruits dispersed their diaspores mostly at the end of the dry season for all five species, especially between July and September (Fig. 2d, Table 2 and Fig. S5b).

H2: The influence of abiotic factors differs between phenophases

The results from the permutation tests revealed that among the four abiotic variables, the phenophase variation of *A. tomentosum* was better explained by wind speed (r^2=0.86), temperature (r^2=0.70), and rainfall (r^2=0.68) (Fig. S6a). For *D. miscolobium*, the most important explanatory abiotic variables were rainfall (r^2=0.70) and wind speed (r^2=0.64) (Fig. S6b). For *K. coriacea,* all abiotic variables were significant predictors: wind speed (r^2=0.80), temperature (r^2=0.77), rainfall (r^2=0.76) and humidity (r^2=0.70) (Fig. S6c). Similarly, all abiotic factors explained the phenophase variation of *P. tomentosa*: wind speed (r^2=0.86), rainfall (r^2=0.79), humidity (r^2=0.71) and temperature (r^2=0.59) (Fig. S7a). Finally, *Q. multiflora* phenophases were better explained by rainfall (r^2=0.67), wind speed (r^2=0.61) and temperature (r^2=0.57) (Fig. S7b). Then, rainfall and wind speed were the most determinant factors for explaining the phenophase variation.

In general, sprouting leaves were positively correlated with rainfall and wind speed (Fig. S6 and S7). *Kielmeyera coriacea* and *P. tomentosa* also showed a negative relationship with air humidity. Developed leaves were positively correlated with rainfall, and negatively correlated with wind speed and temperature. Deciduousness was better predicted by a negative correlation with rainfall and a positive correlation with temperature and wind speed.

Floral bud development was mainly explained by rainfall (Fig. S6 and S7). Floral budding for *Dalbergia miscolobium*, *K. coriacea* and *Q. multiflora* was strongly and positively correlated with rainfall, but *A. tomentosum* and *P. tomentosa* floral budding was negatively correlated with rainfall. Floral budding was correlated with wind speed and temperature for all species, albeit in different directions. Almost all species showed a negative correlation between floral budding and wind speed, except for *A. tomentosum,* which showed a positive correlation, and *P. tomentosa,* which showed no correlation between floral budding and wind speed. Regarding floral budding and temperature, the two factors were positively correlated in *A. tomentosum*, but negatively correlated in *K. coriacea* and *Q. multiflora*.

Flowers exhibited a similar pattern to floral buds. Flower phenophase was also correlated with rainfall (Fig. S6 and S7). Flowering and rainfall were positively correlated in *Dalbergia miscolobium*, *K. coriacea* and *Q. multiflora*, but negatively correlated in *P. tomentosa*, and not correlated in *A. tomentosum*. Flowering was also correlated with wind speed and temperature. Flowering in almost all species showed a negative correlation with wind speed, except for *A. tomentosum*, which presented a positive correlation, and *P. tomentosa* which did not exhibit any correlation between flowering and wind speed. Concerning flowering and temperature, were positively correlated in *A. tomentosum* and *P. tomentosa* and *K. coriacea* and were negatively correlated for *Q. multiflora*.

The presence of young fruits, in general, was weakly and negatively related to rainfall (Fig. S6 and S7). For *Aspidosperma tomentosum* and *D. miscolobium,* young fruits were also explained by a negative correlation with wind speed, and for *P. tomentosa* by a positive correlation. Ripe fruits were better explained by wind speed for all species, although species also showed a negative relationship with rainfall and a positive relationship with temperature.

H3: Diaspores dispersal is related to deciduousness

4. Discussion

Our results showed that the phenological patterns of the five evaluated anemocoric plant species are directly linked to climate variables, where different abiotic factors are more important than others to explain the expression of each phenophase. In detail, we observed that (i) our focal species showed similar phenological patterns, except for the floral bud and flowering phenophases of two species, and young fruit; (ii) each abiotic variable has a specific level of influence for each phenophase; and (iii) the dispersal moment of the diaspores is related to deciduousness. In this context, we corroborate most of our hypotheses and predictions by showing that plant phenological behavior, especially in seasonal environments, is more complex than previously thought, with specific climate variables acting in different ways and at different stages of the plant phenological cycle.

Sprouting leaves arose at the end of the dry season and beginning of the wet season for all species, which is in accordance with our prediction and studies conducted with these species in other Cerrado areas (Araújo, 2006; Pirani et al., 2009; Silvério and Lenza, 2010; Del-Claro and Marquis, 2015; Souto, 2017). Also, rainfall was the most relevant factor when predicting this phenophase. Rain increases the amount of water in the soil, and consequently the roots are able to get soil mineral nutrients that are critical for growth and tissue differentiation, required steps for the production of leaves (Davidson and Milthorpe, 1966; Pietro et al., 2012). In addition, we observed that wind also predicted sprouting leaves. Indeed, we expected that as intense winds occur in the Cerrado during the dry and early wet season, in particular, September (Table S1), when rainfall starts (Oliveira-Filho and Ratter, 2002) and leaves sprout. Thus, wind is working as a secondary factor, influencing the sprouting of leaves.

Fully developed leaves were present year-round for all focal species, but at a lower intensity at the end of the dry season when leaves fall and new leaves sprout, as expected. This pattern has also been found for *Peixotoa tomentosa* in the same area (Torezan-Silingardi, 2007) and for *Qualea multiflora* in another Cerrado area (Souto, 2017). However, our results for *Dalbergia miscolobium* differ from previous work on the species showing developed leaves only from October to January (Souto, 2017). Nonetheless, this difference could be due to variation between different locations, as that contrasting study took place in a Cerrado area 280 km from our study site (Souto, 2017). No data are found in the literature about the phenology of developed leaves for *Aspidosperma tomentosum* and *Kielmeyera coriacea*. This is the first study to evaluate these factors in detail. Maintaining fully developed leaves year-round can help maintain general plant activities such as photosynthesis (Liu et al., 2011). Also, the presence of developed leaves was positively related to rainfall and negatively related to wind speed and temperature. Soil water is required for leaf maintenance, and wind is an important environmental factor especially during the transition between dry and wet seasons (Table S1), when deciduous plants lose their developed leaves, often influenced by wind velocity (Soons and Bullock, 2008). Thus, a negative relationship of the developed leaves with the wind and a positive relationship with the rainfall is expected. In addition, a negative relationship between developed leaves and temperature was also expected. During the end of the dry season in the Cerrado, the temperature increase and amount of rainfall reach their lowest values (Table S1), which can be a trigger for leaf fall, preventing water loss in these environments during more hostile times (see a more detailed discussion below).

Deciduousness for all species was concentrated at the end of the dry season, as expected and according to findings for the same species in different Cerrado areas (Oliveira and Sazima, 1990; Jackson et al., 1999; Franco et al., 2005; Pirani et al., 2009; Silvério and Lenza, 2010; Pereira et al., 2018). Our plants showed similar patterns of deciduousness as those found by Hoffmann and Haridasan (2008), Scholz et al. (2008) and Vilela et al. (2017). *Aspidosperma tomentosum*, *K. coriacea* and *Q. multiflora* are deciduous species, while *D. miscolobium* and *P. tomentosa* are brevideciduous. Leaf fall at the end of the dry season may occur due to lower water availability (Gill and Mahall, 1986), increased temperature and wind. In the absence of rainfall and the presence of heat and wind, deciduousness can help the plant conserve water; otherwise, the release of water vapor to the atmosphere by evapotranspiration could compromise vital plant activities in the dry season (Goldstein et al., 2008). Thus, reducing the amount of mature leaves in certain savanna species may be a drought avoidance mechanism (Tomlinson et al., 2013).

The timing of floral buds and flowers varied among species. *Dalbergia miscolobium*, *K. coriacea* e *Q. multiflora* produced floral buds and flowers during the wet season, as expected by the pattern described for typical Cerrado species (Batalha and Mantovani, 2000; Lenza and Klink, 2006; Silva et al., 2011; Azevedo et al., 2014; Lacerda et al., 2018). However, *A. tomentosum* and *P. tomentosa* flowered in the dry season. Hence, our prediction was only partially corroborated. A possible explanation is that besides phenology affecting ecological interactions, ecological interactions also can affect phenology (Gezon et al., 2016; Lemoine et al., 2017; Vilela et al., 2017). The abundance and activity of many pollinator insects are greatest in the wet season (Wolda and Roubik, 1986). Therefore, many plants have adapted to take advantage of pollinators' abundance and activity. Furthermore, species diverge in their dependence on these pollinators (Rodger and Ellis, 2016). *Aspidosperma tomentosum*, *D. miscolobium, K. coriacea* and *Q. multiflora*, for example, are self-incompatible (Oliveira and Gibbs, 2000), while *P. tomentosa* is self-compatible (Vilela et al., 2017). In this context, due to reproductive strategy (self-compatible or self-incompatible), some plants depend less on pollinator abundance for fruit production than others (Rodger and Ellis, 2016). For instance, since *P. tomentosa* is self-compatible, this species is less pollen limited and less dependent on pollinators, and can flower at different periods of the year. Therefore, different factors drive the development of floral buds and flowers in these species throughout the year.

Further, we showed the abiotic variable most related to floral bud and flower production was rainfall, easily seen in *D. miscolobium*, *K. coriacea* and *Q. multiflora.* Rainfall can trigger further development, as an abundance of water facilitates the absorption of mineral nutrients from the soil. Blooming in the dry season can still be an adaptation to provide floral resources at a time when this product is scarce, thus increasing the chances of attracting pollinators and increasing the pollen exchange rate (Ne'eman et al., 2010; Silva et al., 2011). Also, some plants strategies are influenced by rainfall. For example, pollen deposited on the stigma can be removed by rain (Lawson and Rands, 2019). Thus, some plants have evolved pollen adhesion structures, allowing them to tolerate rainfall, while others do not have these structures and must flower during the dry season, as may occur for *A. tomentosum* and *P. tomentosa.* We did not evaluate these strategies, but we suggest that they be evaluated to explain such phenological variations. Finally, we also need to consider the effects of photoperiod on the triggering of floral budding, and how this differs for each plant species (Silva et al., 2011). In June we have the peak of the dry season and the smallest amounts of daily sunlight available, but the opposite is seen in December, when the availability of daylight is the highest of the year (Souza and Funch, 2016; Cordeiro et al., 2019).

Fewer young fruits were present in the wet season than in the dry season, but this pattern diverged among the species, not corroborating our prediction. *Aspidosperma tomentosum*, *K. coriacea* and *Q. multiflora* produced young fruit for long periods of time, beginning after the flowering of each species and remaining until the end of the subsequent dry season, encompassing in all these cases the wet and dry season. Such prolonged fruit presentation probably occurs to increase the chances of seeds maturing and dispersing in a period in which wind conditions are conducive to dispersal (Heydel and Tackenberg 2016), which can increase reproductive success. *Dalbergia miscolobium,* in turn, presented young fruits during the end of the wet season and the beginning of the dry season.

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Seeds in the wind: extrinsic and intrinsic seed-related factors determine seed dispersal distance in the Brazilian savanna

ABSTRACT

1. Seed dispersal distance directly influences plant reproductive success by enabling seeds to escape from predators, avoid competition and colonize new suitable sites. In the case of anemocoric plants, different climatic variables may influence seed dispersal distance, especially regarding anemocoric plants from regions with extreme seasonality, such as the Brazilian Cerrado savanna. Despite of this importance, there is no consensus about which factors (extrinsic and/or intrinsic to seeds) are the most important drivers of seed dispersal distance.
2. In this context, we evaluated the impacts of both extrinsic and intrinsic seed-related factors on the seed dispersal distance of Brazilian savanna anemocoric species under natural and controlled conditions. We hypothesized that both extrinsic (wind speed and temperature) and intrinsic (falling time, wing-loading and aerodynamic group) seed-related factors influence the seed dispersal distance. We carried out the study in a Brazilian Cerrado area, in 2018 and 2019. Seeds of six anemocoric plant species were released under field (natural) and wind tunnel (controlled) conditions.
3. Our results show that both extrinsic and intrinsic seed-related factors directly, and indirectly via interaction of the factors, influence the seed dispersal distance of the anemocoric species. Wind speed explained the most variation in dispersal distance, followed by falling time. Dispersal distance increased with wind speed, temperature, and falling time, and decreased with the increase of wing-loading. The rolling autogyro aerodynamic group presented greater dispersal potential. Temperature indirectly affected dispersal distance positively via wind speed, and negatively via

wing-loading, which in turn indirectly affected dispersal distance negatively via falling time. The aerodynamic group also indirectly and positively affected dispersal distance via falling time.

4. These results are innovative in indicating that a set of extrinsic and intrinsic seed-related factors influence directly and indirectly the dispersal potential of Brazilian savanna anemocoric species. The most important factors found were wind speed and falling time, despite the linear and causal relationships between the analyzed factors. These effects are extremely important, because many times we seek explanations for events in an isolated and direct way, but forget that many factors can act together, modifying the fundamental conditions that influence the ecosystem processes.

Key-words: aerodynamic group, anemochory, cerrado, colonization hypothesis, diaspore, falling time, Janzen-Connell hypothesis, wing-loading.

Introduction

Seed dispersal is a crucial biological event to plant recruitment, encompassing the rupture of a diaspore's connection with the parent plant and dynamic unidirectional transport to a possible establishment place of the new individual (Van der Pijl, 1982; Levin, Muller-Landau, Nathan & Chave, 2003). According to Janzen (1970) and Connell (1971), this recruitment is dependent on seed density and the distance traveled by seeds from the parent plant. This hypothesis suggests that seed and seedling density increase with parent proximity, as most seeds fall under the parent plant canopy or are only dispersed short distances, resulting in a greater competition between conspecifics. Moreover, the Janzen-Connell hypothesis predicts the activities of seed pathogens and predators will be concentrated in these aggregations, leading to elevated seed mortality due to high density (Howe & Smallwood, 1982). In this context, the Janzen-Connell model proposes that seed dispersal increases survival by helping seeds evade predators and competition, also called the escape hypothesis. On the other hand, the colonization hypothesis predicts that seed dispersal enables colonization of new sites suitable for seed germination and development, since environmental conditions change in time and space (Howe & Smallwood, 1982; Casas, Willis & Donohue, 2012). Several studies support the Janzen-Connell hypothesis and the colonization hypothesis and indicate they are not mutually exclusive (Clark & Clark, 1984; Stevenson, 2007; Swamy et al., 2011; Comita et al., 2014; Mariano & Christianini, 2016).

Seed displacement away from the parent plant is very important for the maintenance of community assembly from the metacommunity, especially in fragmented landscapes (Trakhtenbrot, Katul & Nathan, 2014). Furthermore, dispersal is fundamental for maintenance of gene flow and the spatial dynamics of populations and metapopulations; in the latter case, especially plants whose seeds reach long distances (Cain, Milligan & Strand, 2000; Levin, Muller-Landau, Nathan & Chave, 2003; Greene, 2005; Trakhtenbrot, Katul & Nathan, 2014). Efficient seed dispersal results in new individual plants, which can also influence patterns of species distribution, and vice versa (Soons & Bullock, 2008). Thereupon, defining the drivers of seed dispersal distance will be key to understanding seed fate and plant reproductive success in any environment.

One factor driving seed dispersal distance and the establishment of new individuals is weather (Hampe, 2011; Casas, Willis & Donohue, 2012). Climate variables are closely linked to plant phenology, with phenological events (e.g. sprouting leaves, or seed dispersal) occurring during the most favorable climatic conditions (Wright, Calderón & Muller-Landau, 2019). This becomes paramount to anemocoric plants (dispersed by wind) in regions with extreme seasonality, such as the Cerrado (Brazilian savanna). In this region, the climate is divided into two distinct seasons, one rainy and warm, and the other dry and cold, with higher winds mainly at the end of the dry season (Oliveira-Filho & Ratter, 2002; Wright et al., 2008).

Thus, anemocoric plants need to release their seeds during the end of the dry season, as high wind speeds increase the likelihood of reaching greater distances (Zhu, Liu, Xin, Zhao & Liu, 2015).

Although wind is the main dispersal vector of the anemocoric seeds, it is not the only relevant factor, and anemocoric seed dispersal might be influenced by other factors (Wright et al., 2008). Despite several studies assessing which factors and mechanisms are important for anemocoric dispersal distance (Levin, Muller-Landau, Nathan & Chave, 2003), but a consensus has not been reached, and relevant factors may vary with vegetation type and species. For instance, some studies show that plant traits such as growth form (Bullock et al., 2017), plant height (Thomson, Moles, Auld & Kingsford, 2011), seed position in the canopy (Thomson, Moles, Auld & Kingsford, 2011), dispersal phenology (Nathan, Safriel & Noy-Meir, 2001; Maurer, Bohrer, Medvigy & Wright, 2013; Escobar, Silveira & Morellato, 2018), and landscape characteristics, such as topography and vegetation structure (Auffret et al., 2017; Uroy, Mony & Ernoult, 2019; Wolfe, Macchiavelli & Van Bloem, 2019), can all influence dispersal distance.

Other studies have focused on seed traits that allow seeds to have a longer flight time. For example, studies have evaluated: (i) aerodynamic group (autogyro, rolling autogyro, undulator, floater), based on the behavior of each morphological type of seed in the air (Augspurger, 1986; Seale & Nakayama, 2019); (ii) wing-loading, which is defined as seed mass divided by seed area (Green, 1980; Nathan et al., 2011; Smith et al., 2015; Zhu, Liu, Xin, Zhao & Liu, 2015); (iii) falling time (Tackenberg, Poschlod & Bonn, 2003; Soons, Heil, Nathan & Katul, 2004; Wright et al., 2008); (iv) terminal velocity (Nathan, Safriel & Noy-Meir, 2001; Wyse, Hulme & Holland, 2019); and (v) roughness (Nathan et al., 2011). All these characteristics may affect a seed's dispersal potential (Poschlod et al., 2013). Moreover, studies have shown that atmospheric conditions, such as temperature and humidity, as well as wind conditions, such as wind direction, turbulence, updrafts and wind speed, can also influence dispersal distance (Tackenberg, 2003; Soons & Bullock, 2008; Wright et al., 2008). Nevertheless, there is no consensus about which factors are the most important in driving seed dispersal distance (Soons, Heil, Nathan & Katul, 2004).

Finally, studies have attempted to evaluate and show the dispersal potential of anemocoric species, in particular those with long dispersal distances, as a function of mathematical models based on laboratory or field experiments (Augspurger, 1986; Tackenberg, 2003; Tackenberg, Poschlod & Bonn, 2003; Nathan et al., 2011; Zhu, Liu, Xin, Zhao & Liu, 2015). However, previous studies did not evaluate the effects of seed attributes and abiotic factors concomitantly on anemocoric seed dispersal distance in both laboratory and field experiments. In addition, most studies are performed with vegetation from the temperate and tropical zones of the Northern Hemisphere (Augspurger, Franson & Cushman, 2016; Masaki et al., 2019). As far as we know, few studies have attempted to observe anemocoric seed dispersal distances of plants from the Southern Hemisphere. For instance, about 30% of Cerrado plants are anemocoric species, according to the Reflora database (reflora.jbrj.gov.br). Thus, anemocoric plants are an important component of the Cerrado flora, and understanding the drivers of seed dispersal distance in these plants will help understand and conserve a significant portion of this unique habitat.

In this context, we investigated the influence of extrinsic (i.e. wind speed, temperature) and intrinsic (i.e. falling time, wing-loading, aerodynamic group) seed-related factors on the seed dispersal distances of anemocoric species under natural (field) and controlled (laboratory with wind tunnel) conditions. Our main hypothesis was that both extrinsic and intrinsic seed-related factors would influence seed dispersal distance. We expected that (i) dispersal distance would increase with wind speed, temperature, and falling time; (ii) dispersal distance would decrease with the increase of wing-loading; and (iii) seeds in the autogyro aerodynamic group would achieve longer distances than other aerodynamic groups. We designed these three predictions based on the following information: since these seeds are anemocoric, higher wind speeds will carry the seeds greater distances (Zhu, Liu, Xin, Zhao & Liu, 2015). Concomitantly, rising temperatures decrease seed weight by evaporating water, decreasing wing-loading and then increasing the falling time. This is because a lower value of wing-loading increases the drag force on the seed in flight, and consequently increases travel time through the air, allowing seeds to reach greater distances (Augspurger, 1986; Stallings, Thill, Mallory-Smith & Lass, 1995; Nathan et al., 2011). Finally, seeds in the autogyro aerodynamic group travel longer distances than other aerodynamic groups, since autogyro seeds exhibit a single wing that increases falling time (fall more slowly) by spinning. The spinning wing produces lift that opposes the force of gravity, which is not shared by the other groups, except when wind turbulence occurs (Green, 1980; Augspurger, 1986; Wright et al., 2008).

Materials and Methods

Study area

Fieldwork was carried out in the Cerrado area (*sensu stricto* Oliveira-filho & Ratter, 2002) of a tropical savanna reserve located at 18°57’45”S, 48°17’30”W, within “Clube de Caça e Pesca Itororó de Uberlândia”, Minas Gerais state, Brazil (Vilela, Torezan-Silingardi & Del-Claro, 2014). The area comprises about 200 hectares with trees 2-8 m tall, shrubs and grasses (Del-Claro, Rodriguez-Morales, Calixto, Martins & Torezan-Silingardi, 2019). The climate of the region is seasonal, with well-defined rainy (October to March) and dry (April to September) seasons. Maximum wind speed values occur at the end of the dry season, when most anemocoric plant seeds are dispersed (Novaes, LR et al. unpublished data).

Seed species, collection and classification

We collected ripe and intact diaspores (henceforth simply: ‘seeds’) from individuals of six anemocoric species: *Aspidosperma tomentosum* Mart. (Apocynaceae), *Dalbergia miscolobium* Benth. (Fabaceae), *Kielmeyera coriacea* Mart. & Zucc. (Calophyllaceae), *Peixotoa tomentosa* A. Juss. (Malpighiaceae), *Pterodon pubescens* (Benth.) Benth. (Fabaceae) and *Qualea multiflora* Mart. (Vochysiaceae). Two species from each of three aerodynamic groups were chosen, using the classification system of Augspurger (1986). We classified *Peixotoa tomentosa* and *Q. multiflora* as autogyros, *D. miscolobium* and *K. coriacea* as rolling autogyros, and *A. tomentosum* and *P. pubescens* as undulators (Fig. S1 in Supporting Information). We had two rounds of data collection for each species, from July to September in 2018 and in the same period in 2019. We collected a total of 100 seeds from 15 individuals (~7 seeds per individual), of which we selected only 50 for the experiments. All 50 selected seeds for each species were individually numbered with a felt-tip marker pen before being stored in a plastic box (Augspurger, Franson, Cushman & Muller-Landau, 2016; Liang et al., 2019). The other 50 seeds were used as backups, in the case of any problems with the first 50 seeds selected.

Seed measurements

The mass (g) and area (cm^2) were measured for each seed with a precision analytical balance (Shimadzu ATY224) and ImageJ software 1.48v (Schneider, Rasband & Eliceiri, 2012), respectively. These traits were measured after being individually numbered with a pen to avoid any kind of influence of dye on the mass, which could indirectly affect the analyzed attributes (sensu Liang et al. 2019). Wing-loading was calculated by dividing mass (g) by area (cm^2) (Green, 1980; Nathan et al., 2011).

Dispersal potential in natural conditions (field experiment)

The seed release field experiment was conducted in two dry seasons when seeds were dispersed naturally, during August-September of 2018 and 2019. To assess dispersal potential, we individually released 300 seeds (50 per species), from the average crown height of each species (adapted from Soons, Heil, Nathan & Katul, 2004 and Smith et al., 2015). To determine the mean height for a species, we used the 15 individuals per specie from which we collected seeds, and measured them with a laser telemeter (Vonder VD 770). The average heights were 2.8m for *A. tomentosum*, 1.8m for *D. miscolobium*, 2.3m for *K. coriacea*, 0.65m for *P. tomentosa*, 6m for *P. pubescens* and 2m for *Q. multiflora*.

Seeds were released from a manually driven platform according to the mean height of each plant species. This experiment was conducted on a 3m-wide reserve trail to ease visualization of seed dispersal distance, at different time intervals from 8:00 h up to 16:00 h, encompassing the widest range of abiotic conditions in daylight. Every hour, five seeds of each species were released individually, one species at a time, in order to release 50 seeds per species. The wind speed (m/sec) and temperature (°C) were recorded at each moment of seed release using an anemometer (Instrutherm TAFR-180) (adapted from Soons, Heil, Nathan & Katul, 2004 and Smith et al., 2015). Thus, we collected the most locally accurate data on the relationship of abiotic factors and seed dispersal distance. Falling time was considered as the time (sec) from release of the seed until it reached the ground, and was recorded with a stopwatch. The linear dispersal distance (cm) was measured after the seed had landed, using a measuring tape (Soons, Heil, Nathan & Katul, 2004; Dunker, Bull, Keith & Driscoll, 2019). Damaged seeds were replaced by ones similar in weight and area, from the extra 50 collected seeds.

Dispersal potential in controlled conditions (wind tunnel experiment)

The same seeds released in the field were then launched in a 9 m x 2 m wind tunnel test-section at the Center for Experimental Aerodynamics Research (CPAERO) at the Faculdade de Engenharia Mecânica of Universidade Federal de Uberlândia. Wind speed was controlled by a digital thermo-anemo-manometer Kimo MP200 outside the wind tunnel and by a Pitot tube type-L inside the wind tunnel test-section. A pitot tube is a tubular instrument that quantifies the total pressure and the static pressure of the airflow to regulate the wind speed (Liang et al., 2019). This equipment allowed us to control wind speed and thus obtain precise values on the distance reached by seeds at specific wind speeds. We individually released ten seeds consecutively per species, until 50 seeds of each species had been released at each wind speed. We also recorded the falling time, temperature and dispersal distance. However, in this part of the study, seeds were released from the same height (~1.2 m) and with controlled wind speeds (1, 2, 3, 4, 5, 6, 10 and 14 m/sec). Speeds from 1 to 6 were used because they are common in the Cerrado (see Results), and 10 and 14 were used to simulate atypical events that can be very important to long-distance dispersal events (Nathan, 2006).

Data analysis

Statistical analyses and diagrams were performed in R software 3.6.1 (R Core Team, 2019) with 5% probability. For all analyses, we checked normality and homogeneity. Each analysis and the packages used are described below for each experiment.

Field experiment

To assess whether abiotic variables and seed morphology affect dispersal potential, and which variables better explain the variation of dispersal distance in the field, we fitted a generalized linear model (GLM) with a Gaussian error distribution using the package ‘stats’ (R Core Team, 2019). The model was conducted with dispersal distance as response variable, and wind speed, temperature, falling time, and the interaction between wing-loading and aerodynamic group as predictors. We used the interaction between wing-loading and aerodynamic group, as both are intrinsic seed traits that can influence each other as well as dispersal distance. We compared the models using Akaike's information criterion (AIC), selecting the best model for the distance variation that presented the lowest AICc value, delta < 2, and the highest value of weight using the package 'MuMIn' (Barto'n, 2018). After model selection, we verified significance by comparing our final model to a null model (Crawley, 2007) through the anova function of the 'stats' package. Next, we checked variable significance with a Likelihood-Ratio Chi-squared test using the package "car" (Fox & Weisberg, 2011). Pairwise comparisons were conducted using Tukey's HSD test with the "multcomp" package (Hothorn, Bretz, Westfall & Heiberger, 2008). Box plots were plotted with means to ease visualization and comparisons among groups. Moreover, since wing-loading influenced dispersal distance (see Results), we compared wing-loading between plant species using a GLM with Gaussian error distribution, observing if species of the same and different aerodynamic groups showed variation in their wing-loading.

We used a Structural Equation Model (SEM) to show the effects of the direct/indirect and positive/negative relations of the predictive variables on dispersal distance. This analysis presents the linear and causal relationship among the predictor variables and shows a *coefficient of determination* (R^2) that allows estimation of the fraction of the variance explained by each variable in the model. To verify the fit of our model, we used the Comparative Fit Index (CFI) and the Root Mean Square Error of Approximation (RMSEA). The CFI is equal to the discrepancy function adjusted for sample size, while RMSEA is related to residuals in the model. Both CFI and RMSEA values range from 0-1, with CFI values close to 1 indicating better model fit, and RMSEA values close to 0 indicating better model fit (Hu & Bentler, 1999).

Wind tunnel experiment

In order to analyze the wind tunnel experiment, we fitted a generalized linear mixed model (GLMM) with a Gaussian distribution error followed by a Wald Chi-squared test, using the package 'lme4' (Bates, Maechler, Bolker & Walker, 2015) and 'car', respectively. The model was conducted with dispersal distance as response variable, and wind speed, temperature, falling time, and the interaction between wing-loading and aerodynamic group as predictors. Here we added seed as a random effect to control temporal repeated measures (Crawley, 2007). We used model selection, significance procedures, pairwise comparisons, and SEM analysis similar to the field experiment.

Results

Field experiment

The best model to predict the dispersal distance of anemocoric seeds in natural conditions was the model with wind speed, falling time, wing-loading and aerodynamic group interaction (AICc=3473.6, delta=0, weight=0.392). Dispersal distance varied according to wind speed, falling-time, wing-loading and aerodynamic group (χ^2=3527098, df=7, P<0.001). Although the interaction between wing-loading and aerodynamic group did not influence dispersal distance, wing-loading was significant (χ^2=6.121, df=1, P=0.013) and aerodynamic group was marginally significant (χ^2=5.670, df=2, P=0.058). All factors of this model combined explained 66% of the total variation in dispersal distance. Wind speed was the most important variable in explaining seed dispersal distance (χ^2=209.074, df=1, P<0.001), followed by falling time (χ^2=120.308, df=1, P<0.001), wing-loading (χ^2=6.121, df=1, P=0.013) and aerodynamic group (χ^2=5.670, df=2, P=0.058).

Dispersal distance presented a positive relationship with wind speed (Fig. 1a) and falling time (Fig. 2a), and a negative relationship with wing-loading (Fig. 2c). No relation was found for temperature (Fig. 1c). Dispersal distance significantly varied according to aerodynamic group (χ^2=27.6, df=2, *P*<0.001), in which rolling autogyro and undulator did not differ from each other (Tukey's HSD: z=1.088, *P*=0.522), but both differed from autogyro (Tukey's HSD: rolling autogyro-autogyro: z=4.995, *P*<0.001; undulator-autogyro: z=3.907, *P*<0.001; Fig. 2e). Rolling autogyro presented the highest mean dispersal distance, followed by undulator and autogyro, respectively (Table 1). Similarly, the dispersal distance varied between species in the same aerodynamic group (χ^2=78.642, df=5, *P*<0.001; Fig. S2a). *Kielmeyera coriacea* (rolling autogyro) travelled the greatest distance, followed by *A. tomentosum, Q. multiflora*, *D. miscolobium*, *P. pubescens* and lastly *P. tomentosa* (Table 1).

The comparisons of wing-loading between plant species allowed us to verify if seeds from the same aerodynamic group vary in dispersal distances due to the seed characteristics, that is, wing-loading. Species showed different values for wing-loading (χ^2=154.79, df=5, *P*<0.001, Table 1); however, only species from the undulator aerodynamic group (*A. tomentosum* and *P. pubescens*) showed a significant difference when we compared species in each aerodynamic group (Fig. S2c). The highest wing-loading observed was in *P. pubescens*, followed by *Q. multiflora*, *P. tomentosa*, *D. miscolobium*, *K. coriacea*, *A. tomentosum*, respectively (Table 1).

The SEM analysis showed significant results in terms of model fit (χ^2=53.985, df=5, P<0.001; CFI=0.871; RMSEA=0.181) and linear and causal effects. We found a direct and significant effect of wind speed (explained 56% of the variation), falling time (50%) and wing-loading (11%) on dispersal distance (Fig. 3a, Table S1). Wind speed and falling time showed a positive effect, while wing-loading showed a negative one. Also, wing-loading indirectly and significantly affected dispersal distance via falling time. Temperature and aerodynamic group were not significant in our SEM analysis (Table S1).

Wind tunnel experiment

The complete model with wind speed, temperature, falling time, wing-loading and aerodynamic group interaction as predictors was the best model to explain dispersal distance in the wind tunnel experiment (AICc= 29271.2, delta=0, weight= 0.987). Dispersal distance varied significantly according to wind speed, temperature, falling-time, wing-loading and aerodynamic group (χ^2=2038.1, df=8, P<0.001). All factors combined explained 82% of the total variation in dispersal distance. Wind speed was the most important variable (χ^2=6882.766, df=1, P<0.001), followed by falling time (χ^2=470.639, df=1, P<0.001), aerodynamic group (χ^2=95.445, df=2, P<0.001), the interaction between wing-loading and aerodynamic group (χ^2=54.585, df=1, P<0.001), and temperature (χ^2=10.664, df=1, P<0.001).

Dispersal distance was positively related to wind speed (Fig. 1b), temperature (Fig. 1d), falling time (Fig. 2b) and varied with wing-loading and aerodynamic group interaction (Figs 2d and 2f). Dispersal distance significantly varied according to aerodynamic group (χ^2=65.4, df=2, P<0.001), in which the autogyro and undulator groups did not differ from each other (Tukey's HSD: z=0.005, P=1.000), but they differed from the rolling autogyro group (Tukey's HSD: autogyro-rolling autogyro: z=7.006, P<0.001; undulator-rolling autogyro: z=7.001, P<0.001; Fig. 2f). Autogyro seeds showed the highest wing-loading and traveled the shortest distance, while the rolling autogyro group presented the lowest wing-loading and the highest distance (Table 1). Undulator seeds presented intermediate values of wing-loading and dispersal distance, but close to the values of autogyro seeds (Table 1). Dispersal distance also varied between species from the same aerodynamic group in the wind tunnel experiment (χ^2= 103.33, df=5, P<0.001, Fig. S2b). *Kielmeyera coriacea* (rolling autogyro) presented the highest distance, followed by *D. miscolobium* (rolling autogyro), *A. tomentosum* (undulator), *P. tomentosa* (autogyro), *Q. multiflora* (autogyro) and *P. pubescens* (undulator), respectively (Table 1).

Discussion

Our results show that both extrinsic and intrinsic seed-related factors directly, and indirectly via the interaction of factors, influence the seed dispersal distance of Brazilian savanna anemocoric species. Thus, our main hypothesis was corroborated. Dispersal distance increases with wind speed, temperature, and falling time, as evidenced by the results of our wind tunnel and field experiments, except for distance and temperature in the field. Our results are consistent with many other studies that demonstrate a positive relationship between wind speed and dispersal distance, with wind speed explaining the greatest amount of variation in the dispersal distance of anemocoric species (Dorp, Hoek & Daleboudt, 1996; Savage, Borger & Renton, 2014; Zhu, Liu, Xin, Zhao & Liu, 2015). Wind is a limiting factor for anemocoric species since in its absence or at low speeds, seeds do not reach long distances and instead fall below or near the mother plant. Thus, a lack of wind reduces the performance of seed morphological characteristics that could otherwise increase dispersal distance, such as aerodynamic movement and falling time. Furthermore, wind is an important factor for seed bank formation, as higher wind speeds provide greater seed burial in the soil (Liang et al., 2019). However, recent studies have shown that under a scenario of continuous and high greenhouse gas emissions, climate change can alter wind intensities and distributions (Lucena, Szklo, Schaeffer & Dutra, 2010; Miu, 2015; Karnauskas, Lundquist & Zhang, 2017). In certain regions of the Southern Hemisphere, such as the Eastern portion of Brazil, an increase in winds is expected (Karnauskas, Lundquist & Zhang, 2017). Although an increase in winds may initially seem beneficial to anemocoric species, it may also negatively impact them. Wind can help seeds by facilitating dispersal to new, perhaps better, environments, thereby escaping temperature conditions, rainfall and, humidity that have become inadequate. However, strong winds can also take the seeds to places unsuitable for colonization by certain species.

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Supporting Information

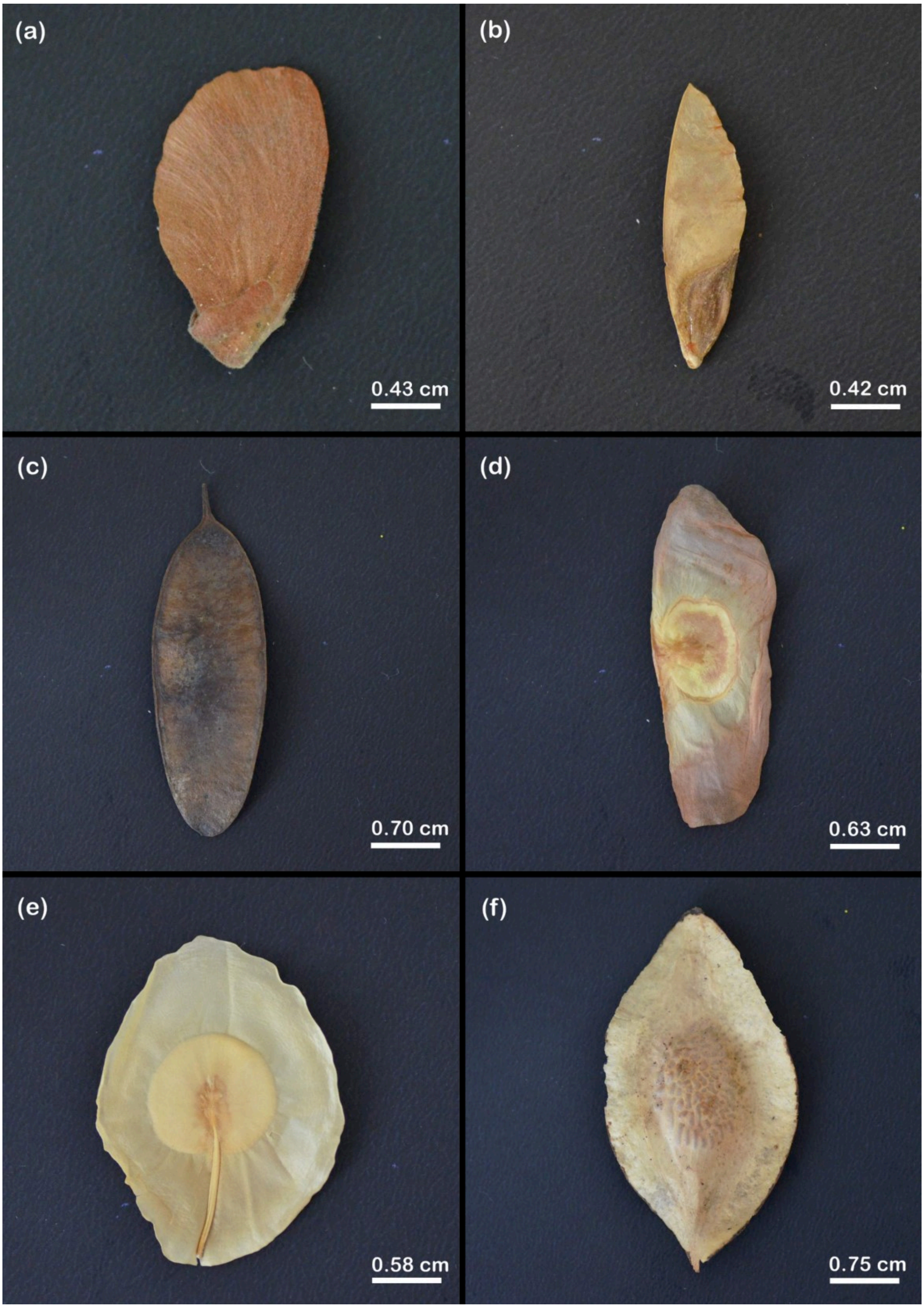

Figure S1. Diaspores of (a) *P. tomentosa* (autogyro) and (b) *Q. multiflora* (autogyro); (c) *D. miscolobium* (rolling-autogyro) and (d) *K. coriacea* (rolling-autogyro); and (e) *A. tomentosum* (undulator) and (f) *P. pubescens* (undulator).

Conclusão Geral

Conclui-se que as espécies anemocóricas estudadas apresentaram padrões fenológicos similares entre si, especialmente quanto à brotação, manutenção e queda de folhas, e quanto ao momento de dispersão das sementes. No entanto, os padrões encontrados não seguiram necessariamente o citado como padrão geral para as espécies de Cerrado. Isso mostra a relevância de se considerar o modo de dispersão das espécies e a divisão entre as fenofases do desenvolvimento do fruto. As principais variáveis que desencadearam as fenofases foram a precipitação e o vento, mostrando a importância de se incluir o vento como um novo fator chave ambiental nos estudos de fenologia das plantas, visto que até então ele tinha sido ignorado. A inclusão do vento nesses estudos é especialmente importante se considerarmos as mudanças climáticas que preveem alterações distintas na distribuição e intensidade do vento de acordo com a região da Terra. Além disso, há uma sincronia entre fenofases vegetativas e reprodutivas, como a caducifolia e a dispersão de diásporos maduros, a qual pode incrementar a distância de dispersão. O estudo mostrou também que um conjunto de fatores extrínsecos e intrínsecos às sementes interagem e afeta direta e indiretamente a distância de dispersão. Dentre os fatores extrínsecos estão a velocidade do vento e a temperatura, os intrínsecos foram o tempo de queda, a carga alar e o grupo aerodinâmico. A velocidade do vento e o tempo de queda das sementes foram as melhores preditoras para a distância de dispersão. As interações encontradas mostram a importância de se avaliar relações causais e lineares nos processos de dispersão de espécies anemocóricas em detrimento de fatores isolados. Novos estudos que foquem na dispersão anemocórica em ambientes de savana em outras regiões do globo, ou em outros ambientes, podem também evidenciar a importância do vento, como feito no presente estudo.