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Timing of seed dispersal and seed dormancy in Brazilian savanna: two solutions to face seasonality

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- **Background and Aims** The relationship between fruiting phenology and seed dispersal syndrome is widely recognized; however, the interaction of dormancy classes and plant life-history traits in relation to fruiting phenology and seed dispersal is understudied. Here we examined the relationship between fruiting season and seed dormancy and how this relationship is modulated by dormancy classes, dispersal syndromes, seed mass and seed moisture content in a Brazilian savanna (cerrado).
- **Methods** Dormancy classes (non-dormancy and physical, morphological, morphophysiological, physiological and physiophysical dormancy) of 34 cerrado species were experimentally determined. Their seed dispersal syndrome (autochory, anemochory, zoochory), dispersal season (rainy, dry, rainy-to-dry and dry-to-rainy transitions), seed mass and moisture contents, and the estimated germination date were also determined. Log-linear models were used to evaluate how dormancy and dormancy classes are related to dispersal season and syndrome.
- **Key Results** The proportions of dormant and non-dormant species were similar in cerrado. The community-estimated germination date was seasonal, occurring at the onset of rainy season. Overall, anemochorous non-dormant species released seeds during the dry-to-rainy transition; autochorous physically dormant species dispersed seeds during the dry season and rainy-to-dry transition; zoochorous species dispersed non-dormant seeds during the dry and rainy seasons, while species with morphological, morphophysiological or physiological dormancy dispersed seeds in the transitional seasons. Seed mass differed among dispersal seasons and dormancy classes, but seed moisture content did not vary with dispersal syndrome, season or dormancy class.
- **Conclusions** The beginning of the rainy season was the most favourable period for seed germination in cerrado, and the germination phenology was controlled by both the timing of seed dispersal and seed dormancy. Dormancy class was influenced by dispersal syndrome and season. Moreover, dormancy avoided seed germination during the rainy-to-dry transition, independently of dispersal syndrome. The variability of dormancy classes with dispersal syndrome allowed animal-dispersed species to fruit all year round, but seeds germinated only during the rainy season. Conversely, seasonally restricted wind-dispersal species dispersed and germinated their non-dormant seeds only in the rainy season.

Key words: Cerrado, dispersal syndromes, dormancy classes, fruiting phenology, germination phenology, neotropical savanna.

INTRODUCTION

In tropical regions with a seasonal climate, water availability in the soil is the main factor limiting seedling establishment and growth (Ray and Brown, 1995; Franco, 2002; Baskin and Baskin, 2014). Seasonality affects patterns of seed production and seed germination, as well as seedling development and survival, and the period favouring plant growth is restricted to the rainy season, when seed germination and seedling establishment are most likely to occur (Garwood, 1983; Khurana and Singh, 2001; Oliveira, 2008; Salazar *et al.*, 2011). Thus, in such ecosystems, germination at the beginning of the rainy season is a characteristic that has evolved independently in many lineages (Garwood, 1983; Blakesley *et al.*, 2002; Sautu *et al.*, 2007; Oliveira, 2008; Salazar *et al.*, 2011; Ramos *et al.*, 2017), and is crucial for plant recruitment as it maximizes the favourable period for establishment, allowing seedlings to develop an efficient root system or to store enough resources to survive the subsequent dry season (Franco, 2002; Oliveira, 2008).

In seasonal tropical ecosystems, the time when seeds germinate is regulated by the relationship between fruiting phenology and seed dormancy. In general, species that disperse seeds at the beginning of the rainy season have non-dormant seeds that germinate quickly if the soil moisture content for seedling development is adequate (Silveira *et al.*, 2012; Ramos *et al.*, 2017). However, seeds dispersed at the end of the rainy season and beginning of the dry season, a period during which the climatic conditions for seedling establishment are inadequate (but moisture still allows seed germination), are generally dormant and germinate only at the onset of the subsequent rainy season (Garwood, 1983;

Probert, 2000; Blakesley *et al.*, 2002; Sautu *et al.*, 2007; Salazar *et al.*, 2011; Ramos *et al.*, 2017). Even though seed dormancy is considered the main mechanism controlling the timing of seed germination in seasonal ecosystems (Baskin and Baskin, 2014), a few studies carried out at the community level have suggested that seed germination is controlled by both seed dormancy and the seed dispersal period (Garwood, 1983; Blakesley *et al.*, 2002; Sautu *et al.*, 2007; Salazar *et al.*, 2011).

Seed dormancy is related to fruiting phenology, but it also depends on other characteristics of the life history of the species, such as seed dispersal syndromes, seed mass and phylogeny, which are essential for the understanding of the evolutionary ecology of seed dormancy (Wang *et al.*, 2009; Yang *et al.*, 2013; Dayrell *et al.*, 2017; Ramos *et al.*, 2017). The few studies that have quantified dormancy classes at the community level and its relationships with life-history characteristics and seed traits have shown that seeds dispersed during the dry season usually have low moisture contents and physical dormancy, while those dispersed late in the rainy season have high moisture contents and physiological dormancy and are animal-dispersed (Sautu *et al.*, 2006, 2007; Salazar *et al.*, 2011).

The relationship between fruiting phenology and dormancy in the tropics has been tested at the community level for forest ecosystems (Ng, 1978; Garwood 1983; Blakesley *et al.*, 2002; Sautu *et al.*, 2007; Yang *et al.*, 2013), but studies in savannas are scarce, mostly restricted to certain clades (Silveira *et al.*, 2012; Ramos *et al.*, 2017) or species (Salazar *et al.*, 2011), hindering the understanding of general regeneration patterns for this biodiversity hotspot. Moreover, such studies are deficient as they do not consider different dormancy classes and dispersal syndromes. Therefore, the relationship between dormancy classes and both life-history characteristics of species (e.g. dispersal season and dispersal syndrome) and seed traits (e.g. seed mass and seed moisture content) are not fully understood for savannas, which may or may not follow the patterns described for other seasonal ecosystems (Sautu *et al.*, 2007).

Here we present the first comprehensive study addressing the ecology of seed dormancy in a woody cerrado community, aiming to evaluate the relationship between fruiting phenology and seed dormancy and how this relationship is modulated by dormancy classes, dispersal syndromes, and seed mass and moisture content. Specifically, we aimed to: (1) evaluate cerrado fruiting phenology at the community level, using an unprecedented phenology database of 11 years to accurately estimate the dispersal season of each species; (2) estimate the germination date of cerrado species and how it is affected by dispersal syndromes; (3) evaluate the proportion of dormant species in the community and how it varies according to dispersal season and syndrome; and (4) examine the relationship between dormancy classes, dispersal season and syndrome, and the seed mass and moisture content.

In seasonal tropical ecosystems, seed dormancy is related to seed dispersal at the end of the rainy season and during the dry season, or to limited seed dispersal (Garwood 1983; Sautu *et al.*, 2007; Wang *et al.*, 2009; Salazar *et al.*, 2011; Yang *et al.*, 2013; Ramos *et al.*, 2017). Therefore, we hypothesize that the proportion of dormant species in the cerrado depends on both fruiting phenology and dispersal syndromes. The cerrado fruiting patterns are characterized by ripe fruit production throughout the year, but a great proportion of species are fruiting at the end of the dry season and beginning of the rainy season (Tannus *et al.*, 2006; Oliveira, 2008; Pirani *et al.*, 2009; Silva *et al.*, 2011; Camargo *et al.*, 2013). Thus, we expect the timing of seed dispersal and seed dormancy to be equally important in controlling the timing of seed germination in cerrado communities. Moreover, fruiting peak varies with dispersal syndrome, with anemochorous species showing a restricted dispersal season, limited to the end of the dry season, autochorous species fruiting mainly during the dry season, and zoochorous species fruiting throughout the year, but peaking at the beginning of the rainy season (Batalha and Mantovani, 2000; Oliveira, 2008; Pirani *et al.*, 2009). Consequently, we expect an interaction between dispersal syndrome and season to modulate seed dormancy. For example, zoochorous species that disperse seeds at the end of the rainy season should be dormant and anemochorous species dispersing seeds at the end of the dry season should have non-dormant seeds, whereas a vast number of autochorous species dispersing seeds during the dry season should be dormant (Wang *et al.*, 2009; Yang *et al.*, 2013; Ramos *et al.*, 2017). Although the relationships between seed dormancy class and life-history characteristics are not fully understood for seasonal ecosystems, we expected that the cerrado community would show patterns similar to those described for other seasonal ecosystems. Therefore, we expected to find an interaction between dispersal during the dry season, physical dormancy and seeds with low moisture contents, while seeds dispersed late in the rainy season would tend to show zoochoric dispersal, physiological dormancy and seeds with high moisture contents (Sautu *et al.*, 2006, 2007; Salazar *et al.*, 2011).

MATERIAL AND METHODS

Study area

The study was conducted in a private reserve area of 260 ha and 770 m altitude, located at Itirapina county, south-eastern Brazil (22°10′52″ S, 47°52′25″ W). The vegetation of the study area is predominately the cerrado *sensu stricto* (woodland savanna), characterized by a dominant woody layer (discontinuous tree canopy heights of ~7 m) and a scattered herbaceous layer; for a detailed description of vegetation structure and plant species composition see Reys *et al.* (2013). The climate is characterized by a dry season from April to September and a rainy season extending from October to March (Reys *et al.*, 2013), with mean monthly temperatures of 18 °C in July and 32 °C in February, mean annual temperature of 20.7 °C and mean total annual precipitation of 1524 mm (Fig. 1A). The pattern of fruiting in the study area is characterized by ripe fruit production throughout the year, but fruiting peak varies with dispersal syndrome (Fig. 1B; Camargo *et al.*, 2013). Fruiting of anemochorous species is concentrated at the end of the dry season, for autochorous species fruiting occurs mainly during the dry season, while for zoochorous species fruiting occurs throughout the year, peaking at the beginning of the rainy season (database from Phenology Laboratory at UNESP; Fig. 1B).

Historical climatic data

We divided the year into seasons based on analyses of 30 years of climatic information (1982–2012) from the Centro de Recursos Hídricos e Estudos Ambientais (CRHEA–EESC/USP)

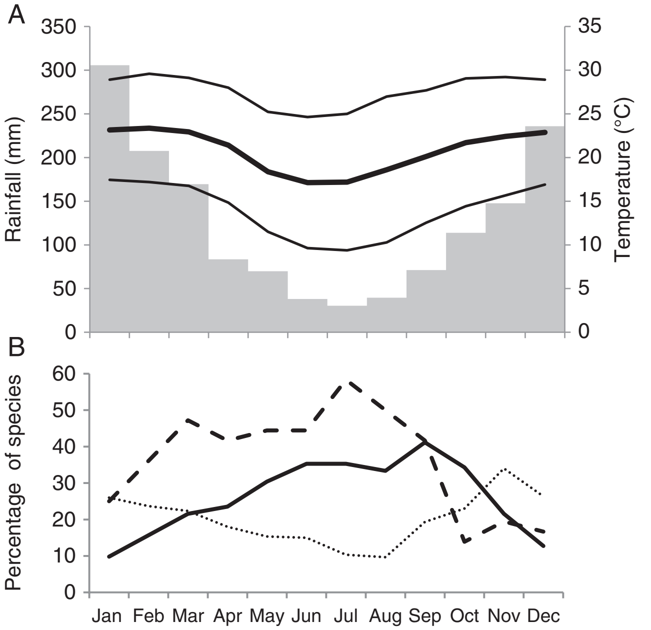

FIG. 1. Climate and fruiting phenology for the cerrado study site at Itirapina, south-eastern Brazil. (A) Average monthly temperatures and rainfall over a period of 30 years (1982–2012) (CRHEA–EESC/USP meteorological station). Maximum, mean and minimum temperatures (solids lines) and rainfall (bars). (B) Percentage of species fruiting per month according to the seed dispersal syndrome based on the total of 73 species monitored (6 autochorous, dashed line; 17 anemochorous, solid line; and 50 zoochorous, dotted line) during 11 years of phenological observations (Phenology Laboratory at UNESP, unpubl. data).

meteorological station, located ~6 km from the study site. The seasons were defined after a cluster analysis using Euclidian distance and unweighted pair group method with arithmetic mean (UPGMA) carried out with the Pvclust package (Suzuki and Shimodaira, 2006) in R software (R Core Development Team, 2016). We used the mean and coefficient of variation of the following variables for each month for the period of 30 years: maximum, minimum and mean temperatures; precipitation; number of rainy days; potential evapotranspiration; and precipitation minus potential evapotranspiration. Variables were standardized using the standard deviation. The values of potential evapotranspiration were calculated according to Thornthwaite and Mather (1955) and Rolim *et al.* (1998) with a field capacity of 100 mm.

The cluster analysis showed a high cophenetic coefficient (0.87) and divided the year into four seasons: rainy season (November to March), rainy-to-dry transition (April), dry season (May to August) and dry-to-rainy transition (September to October) (Fig. 2). The months during the dry season were characterized by low temperatures, low precipitation, few rainy days and low and variable evapotranspiration; the rainy season months were characterized by elevated temperatures, high precipitation, many rainy days and a significant difference between precipitation and potential evapotranspiration. The transitional months showed intermediate values between the dry and rainy seasons (Supplementary Data Table S1).

Fruit and seed collection

Mature fruits were collected every 15 d between March 2015 and March 2016 from 34 species (Table 1). We randomly followed trails inside the reserve, collecting all fruiting species available. Fruits of at least ten individuals per species were collected, except for *Qualea dichotoma*, *Virola sebifera* and *Kielmeyera coriacea*, for which we collected fruits of only one individual per species. Fruits of all individuals of a given species were put into paper bags and taken to the laboratory, where seeds were removed up to 48 h after harvesting. Seeds were then dried for 48 h at 25 °C and 40 % relative humidity. Seeds were stored in such conditions for <3 weeks prior to the germination experiments, except for seeds with moisture contents >30 %, with which germination experiments were set up to 7 d after seeds were harvested.

Dispersal syndrome

We used three sources to classify species dispersal syndromes: (1) morphological characteristics of the diaspore as proposed by Van der Pijl (1982); (2) information extracted from the literature (Morellato and Leitão-Filho, 1992; Oliveira

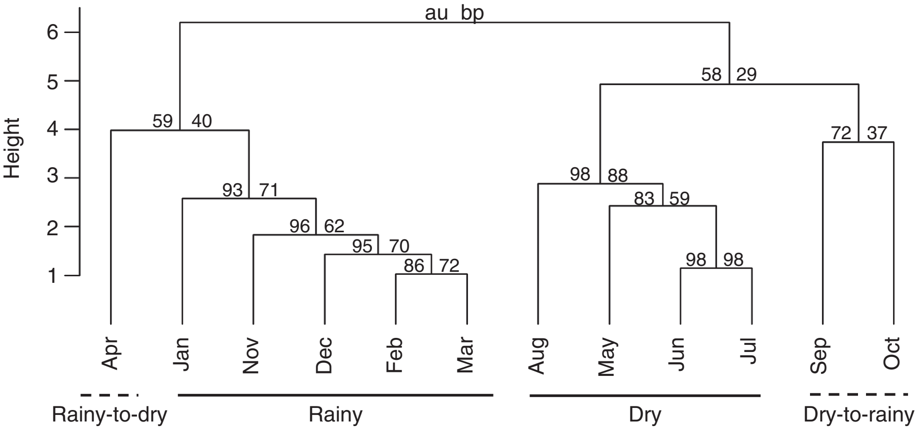

FIG. 2. Dendrogram from UPGMA cluster analysis based on Euclidian distances showing the months clustered by season according to the climatic variables used: rainy season from November to March, dry season from May to August, rainy-to-dry transition in April and dry-to-rainy transition from September to October. The height scale represents within-dataset Euclidean distance. Data are the average for a period of 30 years (1982–2012) (CRHEA–EESC/USP meteorological station).

and Moreira, 1992; Batalha and Mantovani, 2000; Weiser and Godoy, 2001; Camargo *et al.*, 2013); and (3) field observations. The zoochorous species had fleshy fruits or fleshy structures partially or totally involving seeds; anemochorous species had winged or flat diaspores with a large area:volume ratio; autochorous species did not have fleshy structures, neither did they show structures known to facilitate wind dispersal (Table 1).

Fruiting phenology

A long-term phenological study has been conducted by the Phenology Laboratory at UNESP since September 2004 in 36 transects of 25 × 2 m established throughout the study site with a distance of at least 50 m from each other (Camargo *et al.*, 2013; Reys *et al.*, 2013). In each transect, all individuals with circumference at 30 cm from ground level >3 cm were tagged and have been monitored for changes on reproductive and vegetative phenology at monthly intervals. The intensity of the phenophase for each tagged individual was registered using a semi-quantitative index with three classes: 0 (absence); 1 (≤50 % of branches with ripe fruits); and 2 (>50 % of branches with ripe fruits) (Opler *et al.*, 1976; Vogado *et al.*, 2016).

For 24 out of the 34 species collected in the present study, the fruiting peak was determined based on the 11-year database (2005–15) detailed above. The mature fruiting peak date of each of those 24 species was defined as the month with the maximum number of individuals fruiting (score >1) or with the higher score sum. For the remaining species, the fruiting peak was determined based on the dates of the seed collection, carried out fortnightly throughout 2015–16 (Table 1). The fruiting peak date was therefore used to classify the seed dispersal season of the species as the dry season, rainy season, dry-to-rainy transition or rainy-to-dry transition.

Data regarding the fruiting phenology of all species were then analysed using circular statistical parameters, where we considered the years of phenological observation as independent and the date or month of fruiting peak as the phenological variable. All analyses follow the procedures described by Morellato *et al.* (2000, 2010). Given that the circular data are on a scale with no true zero (Zar, 1999), the month of peaking fruiting was converted to angles, where January corresponds to the 30° circular interval and is assigned the angle 15° and so on up to December, corresponding to the last interval of 330° or 345°. We estimated the average fruiting peak date or the average angle for each species based on the frequency of fruiting peak dates each month over 11 years. The mean angle corresponds to the mean date of the year around which most individuals had their mature fruiting peak (Morellato *et al.*, 2010). With the average fruiting peak date for each species, we calculated the average angles for the community (34 species) and for each dispersal syndrome. The Rayleigh test was applied to determine the significance of the average angle (Zar, 1999). When significant, we can infer the occurrence of a seasonal pattern, since the Rayleigh test is confirming that fruiting peaks are significantly clustered around the average angle (here representing a month of the year), and we use the length of the r vector to infer the degree of seasonality (Morellato *et al.*, 2000, 2010). The r vector has no unit and ranges from 0 for no concentration around the mean date (no seasonality) to 1 for all unities concentrated at the same date (the highest degree of seasonality). The analyses were carried out with the Oriana 4 software (Kovach, 1994).

Classification of seed dormancy

For the germination experiments, seeds were placed in Petri dishes with two layers of filter paper saturated with distilled water under 24-h white light (≈32 µmol m^{-2} s^{-1}), and up to five constant temperatures (Table 1). For each species, we used six replicates containing 20–25 seeds for each temperature according to seed availability. Germination was determined by radicle curvature or protrusion of aerial structures (e.g. cotyledons or plumules; Northam and Callihan, 1994). The experiments were monitored three times a week for 1 month, after which germination was monitored weekly for a maximum of 12 months or until the germination curve was stabilized (at least 4 weeks without germination; Sautu *et al.*, 2006). At the end of the experiment, viability of non-germinated seeds was analysed by means of the tetrazolium test, using 1 % solution at 30 °C for 48–72 h (ISTA, 2007). The optimal temperature for germination for each species was determined as the temperature or array of temperatures with the highest germination percentage and germination rate. The percentage of germination, mean germination time and germination rate were calculated according to Ranal and Santana (2006).

We adopted the dormancy concept and classification system proposed by Baskin and Baskin (2014), where dormant seeds show one of the following characteristics: seeds with undifferentiated or undeveloped embryos, water-impermeable diaspores; or seeds that, when incubated under favourable environmental conditions for germination, show a mean germination time >30 d. Non-dormant seeds (ND) have a mean germination time of <30 d, water-permeable seed coats and totally developed embryos.

Dormancy classes

Species were classified as ND or into five dormancy classes according to Baskin and Baskin (2014): physical dormancy (PY), species with impermeable seed coats, well-developed and non-dormant embryos (germination occurs within 30 d after physical scarification); morphological dormancy (MD), species with seeds containing undeveloped embryos and a mean germination time of <30 d; morphophysiological dormancy (MPD), seeds with undeveloped embryos and mean germination time >30 d; physiological dormancy (PD), seeds that are permeable to water, with well-developed embryos and a mean germination time >30 d; and physiophysical dormancy (PYPD), seeds that are impermeable to water and have physiological dormancy.

Seed permeability to water was determined by imbibition tests with intact, fresh seeds. One hundred recently harvested seeds were weighed individually (when each seed had a weight of >0.001 g) or in six groups of 25 seeds each (for seeds weighing <0.001 g). Seeds were then placed in germination boxes with two layers of filter paper saturated with distilled water and incubated at 25 °C under white light for 48–72 h. Another layer of filter paper saturated with distilled water

Table 1. *List of cerrado species sampled for the germination tests at Itirapina, south-eastern Brazil (ordered by family and species name) and the respective ecological and experimental information: seed collection date, fruiting peak date (see Materials and methods section for calculations), growth form (tree, shrub, forb), dispersal syndrome (zoochory, anemochory, autochory), dispersal season (rainy, November to March; dry, May to August; rainy–dry transition, April; dry–rainy transition, September to October), dormancy class (ND, non-dormant; PD, physiological dormancy; PY, physical dormancy; MD, morphological dormancy; MPD, morphophysiological dormancy) and temperatures of the germination experiments, which were set up according to seed availability*

Family	Species	Seed collection date	Fruiting peak date	Growth form	Dispersal syndrome	Dispersal season	Dormancy class	Temperature (°C)
Annonaceae	*Xylopia aromatica* (Lam.) Mart.	April	April	Tree	Zoochory	Rainy–dry	MPD	25
Araliaceae	*Schefflera vinosa* (Cham. & Schltdl.) Frodin & Fiaschi	October	September	Shrub	Zoochory	Dry–rainy	MD	15, 20, 25, 30, 35
Bromeliaceae	*Ananas ananassoides* (Baker) L.B.Sm.*	March	March	Herb	Zoochory	Rainy	MD	15, 20, 25, 30, 35
Calophyllaceae	*Kielmeyera coriacea* Mart. & Zucc.*	September	September	Shrub	Anemochory	Dry–rainy	ND	20, 25, 30
Erythroxylaceae	*Erythroxylum cuneifolium* (Mart.) O.E.Schulz	November	November	Shrub	Zoochory	Rainy	ND	25, 30
Fabaceae	*Anadenanthera falcata* var. falcata (Benth.) Altschul	October	September	Tree	Autochory	Dry–rainy	ND	15, 20, 25, 30, 35
Fabaceae	*Chamaecrista desvauxii* (Collad.) Killip*	April	April	Subshrub	Autochory	Rainy–dry	PY	15, 20, 25, 30, 35
Fabaceae	*Dalbergia misculobium* Benth.	May	August	Tree	Anemochory	Dry	ND	25
Fabaceae	*Dimorphandra mollis* Benth.	August	June	Tree	Autochory	Dry	PY	15, 20, 25, 30, 35
Fabaceae	*Machaerium acutifolium* Vogel	July	August	Tree	Anemochory	Dry	ND	20, 25, 30
Fabaceae	*Mimosa sommians* Humb. & Bonpl. ex Willd.*	April	April	Forb	Autochory	Rainy–dry	PY	25
Fabaceae	*Plathymenia reticulata* Benth.*	August	August	Tree	Anemochory	Dry	PY	15, 20, 25, 30, 35
Fabaceae	*Stryphnodendron rotundifolium* Mart.	August	August	Tree	Autochory	Dry	PY	15, 20, 25, 30, 35
Lauraceae	*Ocotea pulchella* (Nees & Mart.) Mez	November	October	Tree	Zoochory	Dry–rainy	ND	25
Loganiaceae	*Strychnos* sp.*	October	October	Shrub	Zoochory	Dry–rainy	PD	20, 25, 30
Malpighiaceae	*Byrsonima intermedia* A.Juss.	April	February	Shrub	Zoochory	Rainy	PD	25
Melastomataceae	*Leandra solenifera* (DC.) Cogn.	November	December	Shrub	Zoochory	Rainy	ND	20, 25, 30
Melastomataceae	*Miconia albicans* (Sw.) Triana	November	December	Shrub	Zoochory	Rainy	ND	20, 25, 30
Melastomataceae	*Miconia chamissois* Naudin *	September	September	Shrub	Zoochory	Dry	ND	20, 25, 30
Melastomataceae	*Miconia fallax* DC.	November	November	Shrub	Zoochory	Rainy	ND	20, 25, 30
Melastomataceae	*Miconia ligustroides* (DC.) Naudin	March	March	Tree	Zoochory	Rainy	ND	20, 25, 30
Melastomataceae	*Miconia rubiginosa* (Bonpl.) DC.	March	March	Tree	Zoochory	Rainy	ND	20, 25, 30
Myristicaceae	*Virola sebifera* Aubl.	October	October	Tree	Zoochory	Dry–rainy	MPD	15, 20, 25, 30, 35
Myrtaceae	*Myrcia guianensis* (Aubl.) DC.	November	November	Tree	Zoochory	Rainy	ND	15, 20, 25, 30, 35
Myrtaceae	*Myrcia splendens* (Sw.) DC	January	January	Tree	Zoochory	Rainy	ND	25
Primulaceae	*Myrsine guianensis* (Aubl.) Kuntze	May	November	Tree	Zoochory	Rainy	PD	15, 20, 25, 30, 35
Rubiaceae	*Amaioua guianensis* Aubl.	July	June	Tree	Zoochory	Dry	ND	15, 20, 25, 30, 35
Rubiaceae	*Palicourea rigida* Kunth	March	March	Shrub	Zoochory	Rainy	PD	25
Rubiaceae	*Psychotria hoffmannseggiana* (Willd. ex Schult.) Müll.Arg *	April	April	Forb	Zoochory	Rainy–dry	PD	15, 20, 25, 30, 35
Rubiaceae	*Coccocypselum* sp.*	April	April	Forb	Zoochory	Rainy–dry	PD	15, 20, 25, 30, 35
Siparunaceae	*Siparuna guainensis* Aubl.	March	February	Shrub	Zoochory	Rainy	PD	25
Vochysiaceae	*Qualea dichotoma* (Mart.) Warm.*	July	July	Tree	Anemochory	Dry	ND	20, 25, 30
Vochysiaceae	*Qualea grandiflora* Mart.	September	September	Tree	Anemochory	Dry–rainy	ND	15, 20, 25, 30, 35
Vochysiaceae	*Vochysia tucanorum* Mart	September	September	Tree	Anemochory	Dry–rainy	ND	20, 25, 30

*Species for which the fruiting peak and dispersal season were determined according to the seed collection date. For the remaining species, dispersal season refers to the mean fruiting peak date determined based on 11 years of phenological data from the study site (see Materials and methods section for details).

was placed over the seeds in each germination box (ISTA, 2007). We recorded the percentage increase in fresh weight ($P\%$) for each seed or group of seeds for every time interval with the formula $P\% = [(P_2 - P_1)/P_1] \times 100$, where P_1 and P_2 represent the fresh weights at times t_1 and t_2, respectively, and thus determined the percentage of seeds that did imbibe (Paiva *et al.*, 2006; Orozco-Segovia *et al.*, 2007; Sautu *et al.*, 2007). For species belonging to families or genera that are known to have water-impermeable seeds (Willis *et al.*, 2014), we compared the percentage of imbibed seeds, germination percentage and mean germination time between intact seeds and mechanically scarified seeds. For species belonging to families or genera that have seeds with undeveloped embryos (Baskin and Baskin, 2014), we determined embryo growth before germination by comparing the embryo:seed size ratio of 20 seeds (ten fresh seeds and ten seeds imbibed for 30 d) cut longitudinally.

Estimated germination date

The estimated germination date was determined differently for dormant and non-dormant species, given that non-dormant species that dispersed during the dry season and the dry-to-rainy transition germinated promptly under laboratory conditions, but the low soil moisture and temperature in the field during this period are most likely insufficient to stimulate germination (Goldstein *et al.*, 2008; Ramos *et al.*, 2017).

For dormant species, the estimated germination date was determined by adding the average fruiting peak date (see the Fruiting phenology section, above) to the germination time for each species. The species germination time was calculated as the sum of the mean germination time in the optimum germination temperature with its standard deviation. For instance, the estimated germination date of a species with a seed dispersal peak at the beginning of June and a germination time of 90 d would be at the beginning of September. For species with non-dormant seeds, the estimated germination date was determined in two ways: for species dispersing seeds in the rainy season we added the average fruiting peak date to the germination time for each species, and for species dispersing seeds in the dry season and the dry-to-rainy transition we added the germination time for each species to the onset of the rainy season (beginning of November).

We only used the 28 species that had a germination percentage >50 % (Supplementary Data Table S2), given that the mean germination time tends to be underestimated with low germination percentages. The estimated germination date was thus considered as the month when most seeds of that species would germinate. Using the estimated germination date for each species, we calculated the average estimated germination date (average angles) for the community and for each dispersal syndrome. The Rayleigh test was applied to determine the significance of the average angle (Zar, 1999) and to infer the occurrence of seasonal patterns of germination timing as described above (Morellato *et al.*, 2000, 2010).

Seed mass and moisture content

To determine the seed mass for each species, 100 recently harvested seeds were weighed individually (for seeds weighing >0.001 g) or in eight groups of 100 seeds each (for seeds weighing <0.001 g). The moisture content was calculated using the formula MC% = $[(M_2 - M_3)/(M_2 - M_1)] \times 100$, where M_1 is the mass of the container, M_2 is the mass of the container with fresh seeds and M_3 is the mass of the container with dried seeds. The seeds were oven-dried at 80 °C until weight stabilization, for at least 72 h, using two replicates of at least 1 g each. Seeds >1 cm were cut before weighing (ISTA, 2007).

Data analyses

To examine whether fruiting phenology, seed dormancy and dispersal syndrome are related, we carried out two log-linear analyses. Log-linear models treat cell frequencies as counts distributed as a Poisson random variable, and these models do not distinguish response and predictor variables; all the variables are considered equally as response variables (Quinn and Keough, 2002). One log-linear analysis was run to test whether seed dormancy (presence/absence) is related to dispersal season and dispersal syndrome (full model: ~dormancy + dispersal season + dispersal syndrome + dispersal syndrome × dormancy + dispersal syndrome × dispersal season + dispersal season × dormancy), and another to test the relationship between dormancy classes, dispersal season and dispersal syndrome (full model: ~dormancy class + dispersal season + dispersal syndrome + dispersal syndrome × dormancy class + dispersal syndrome × dispersal season + dispersal season × dormancy class).

In both analyses, first we contrasted all possible models (full and reduced models) and chose the models that had the lowest Akaike information criterion (AIC) and likelihood ratio (LR) values. We then tested which interactions in the chosen model were significant by contrasting all models of conditional interactions with the model of homogeneous interactions (Quinn and Keough, 2002). All analyses were carried out using the package MASS (Venables and Ripley, 2002) in R software (R Core Development Team, 2016).

We conducted two factorial analysis of variance with permutations to evaluate the relationship of both seed moisture content and seed mass with dormancy class, dispersal season and dispersal syndrome; these analyses were done using the lmPerm package (Wheeler, 2010) in R software (R Core Development Team, 2016). *Post hoc* Tukey's tests were performed for multiple comparisons among variables.

RESULTS

Life history and seed traits

Seeds from 34 species belonging to 28 genera and 16 families were sampled in the present study, including 31 woody species and three herbaceous species (Table 1). The proportions of cerrado dormant and non-dormant species were similar (47.1 and 52.9 %, respectively). Zoochory was the most common dispersal syndrome (64.7 %), followed by anemochory (20.6 %) and autochory (14.7 %; Fig. 3). Among the studied species, 38.2 % dispersed their seeds during the rainy season, 14.7 % in the rainy-to-dry transition, 20.6 % during the dry season and 26.5 % in the dry-to-rainy transition (Fig. 3).

Seed dispersal occurred throughout the year and no seasonal patterns were observed for the studied cerrado community ($r = 0.13$; Rayleigh test $P = 0.585$; Fig. 4A, Supplementary Data Table S3). However, fruiting patterns differed according to dispersal syndrome (Fig. 4). For anemochorous species the fruiting peak was very seasonal, concentrated in August and September, at the end of the dry season and dry-to-rainy transition ($r = 0.93$; Rayleigh test $P < 0.001$; Fig. 4B, Supplementary Data Table S3). For autochorous species the fruiting peak was not significantly seasonal and occurred mainly from April to September, from the rainy-to-dry transition up to the

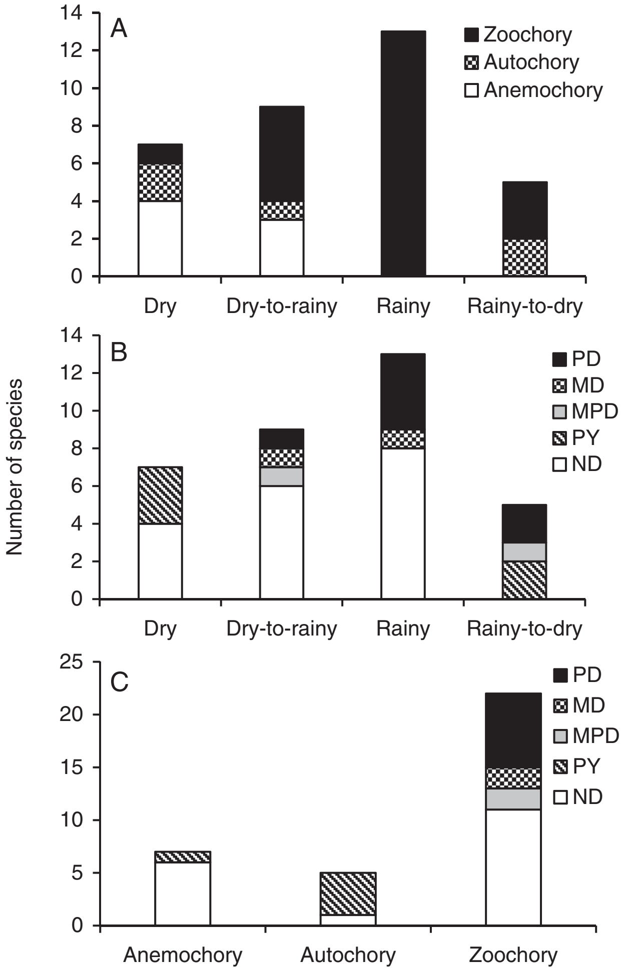

Fig. 3. Number of species fruiting in each dispersal season according to (A) dispersal syndrome, (B) dormancy class and (C) number of species in each dispersal syndrome according to dormancy class in a cerrado community in south-eastern Brazil. ND, non-dormant; PY, physical; MPD, morphophysiological; MD, morphological; PD, physiological.

dry-to-rainy transition (Fig. 4C, Supplementary Data Table S3). Finally, zoochorous species also did not show a significantly seasonal pattern of peak fruiting, although seed dispersal was higher during the rainy season (Fig. 4D; Supplementary Data Table S3).

The estimated germination date was significantly seasonal and occurred with the onset of the rainy season, between November and December, both at the community level ($r = 0.56$; Rayleigh test $P < 0.001$), for anemochorous ($r = 0.96$; Rayleigh test $P < 0.001$) and zoochorous species ($r = 0.46$; Rayleigh test $P < 0.031$) (Fig. 4, Supplementary Data Table S4). Autochorous species did not show a significant seasonal pattern of germination dates, with germination occurring between August and December (Fig. 4, Supplementary Data Table S4).

Seed mass had a frequency distribution that was positively asymmetrical (3.04) and concentrated (kurtosis 11.51), in which 82 % of seeds weighed between 0.01 and 0.1 g. Seed mass differed according to dispersal season and dormancy class but did not vary significantly with dispersal syndromes and interactions among traits (Supplementary Data Table S5, Fig. 5A–C). Seeds dispersed during the dry season and the dry-to-rainy transition were heavier (mean seed mass of 0.067 and 0.193 g, respectively) than those dispersed during the rainy season and the rainy-to-dry transition (mean seed mass of 0.021 and 0.014 g, respectively; Tukey test $P < 0.01$; Fig. 5B). Species with MPD had a greater seed mass than those in other dormancy classes (Tukey test $P < 0.05$; Fig. 5A).

Seed moisture content showed an asymmetrical frequency distribution (1.39) and positive kurtosis (0.69), with 70 % of species having low moisture contents (<20 %). Seed moisture content did not differ among dispersal syndromes, dispersal seasons, dormancy classes or any interaction among variables (Fig. 5D–F, Supplementary Data Table S6).

Relationships between seed dormancy, fruiting phenology and dispersal syndrome

The proportion of dormant species varied with dispersal season: 33.3 % of species dispersing in the dry-to-rainy transition, 38.5 % of species dispersing during the rainy season, 43 % of species dispersing throughout the dry season and all species dispersing in the rainy-to-dry transition had dormant seeds (Fig. 3).

The log-linear model (~dormancy + dispersal syndrome + dispersal season + dispersal syndrome × dispersal season), chosen according to the AIC and LR values (Table 2), and the contrasts between the conditional and homogeneous association models (Table 3) indicated that dormancy was related to the interaction between dispersal syndrome and season. Thus, anemochorous species were related to the absence of dormancy and dispersal during the dry season and the dry-to-rainy transition. For autochorous species, dispersal during the dry-to-rainy transition was related to absence of dormancy, while dispersal during the rainy-to-dry transition was related to dormancy. For zoochorous species, dispersal during the dry and rainy seasons was related to absence of dormancy and dispersal in the transitional seasons was related to dormancy, especially in the rainy-to-dry transition (Fig. 3, Supplementary Data Table S7).

According to the log-linear model (~dormancy class + dispersal season+ dispersal syndrome + dispersal syndrome × dormancy class + dispersal syndrome × dispersal season), chosen by the AIC and LR values (Table 4), and the contrasts between the conditional and homogeneous association models (Table 5), dispersal syndrome was related to dormancy class and dispersal season. Classes MD, MPD and PD were present exclusively among zoochorous species, while PY was detected in anemochorous and autochorous species and ND species were found among all dispersal syndromes (Fig. 3). The MD class was related to dispersal during the dry-to-rainy transition, MPD to dispersal in both transitional seasons, especially the rainy-to-dry transition, and PD to dispersal in the rainy-to-dry transition. In general, zoochorous species had a negative relationship between dispersing during the dry and rainy seasons and dormancy (MD, MPD and PD), and a positive relationship between dispersing in the rainy-to-dry transition and all dormancy classes, except MD (Fig. 3, Supplementary Data Table S8). For autochorous species, PY was related to dispersing

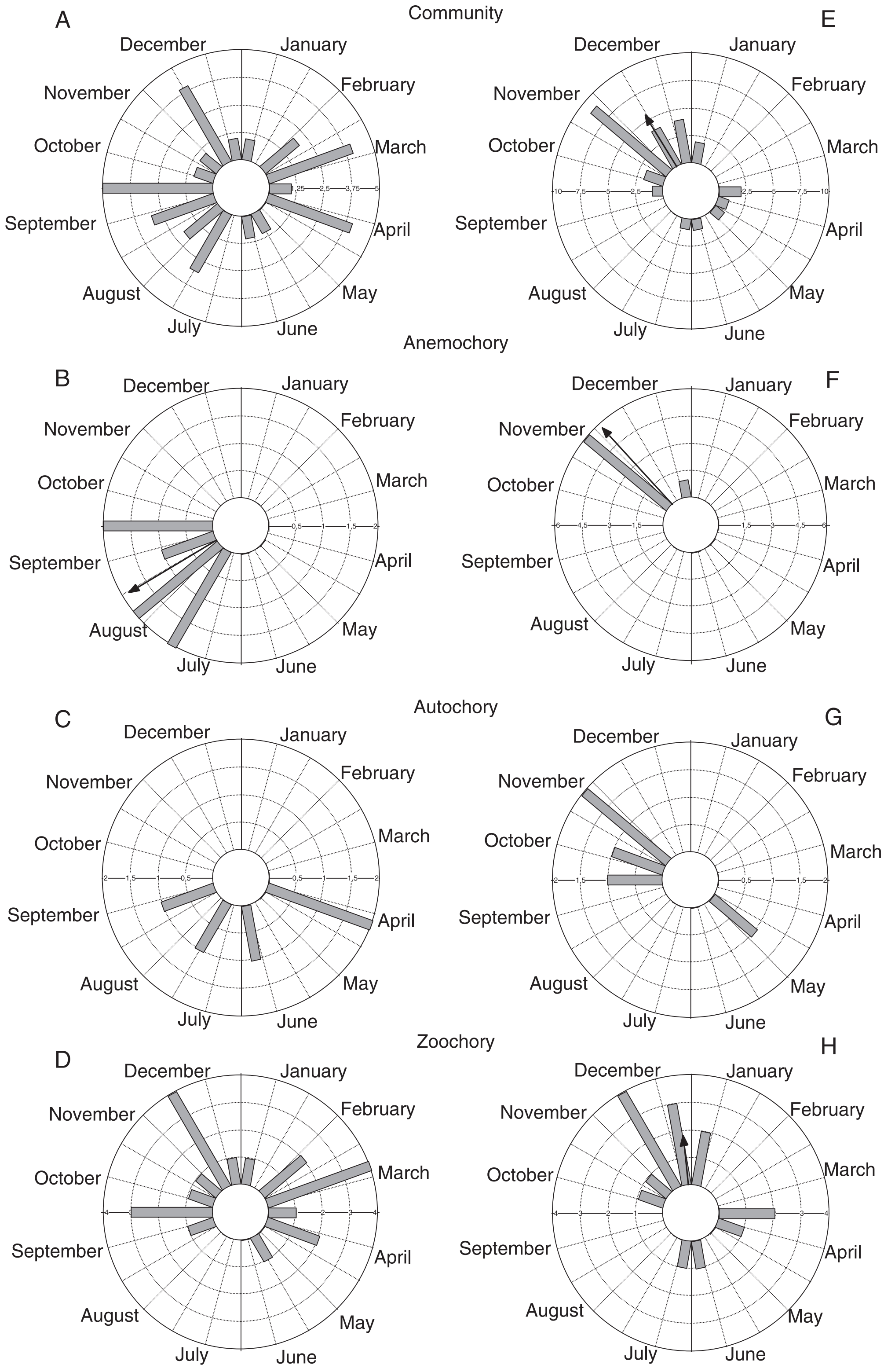

Fig. 4. Circular histograms for the frequency of fruiting peak dates (A–D) and estimated germination dates (E–H) for the community and for each dispersal syndrome in a cerrado community in south-eastern Brazil. Black arrows indicate the mean angle (mean date) and arrow length corresponds to the mean vector (*r*) value, or the degree of seasonality. Absence of a black arrow in a histogram indicates that the mean angle was not significant and pattern is not significantly seasonal (for details see the Materials and methods section and Supplementary Data Tables S2 and S3).

during the dry season and rainy-to-dry transition. Finally, for anemochorous species PY was related exclusively to dispersing during the dry season. For both anemochorous and autochorous species, we observed a positive relationship between dispersing in the dry-to-rainy transition and ND (Fig. 3, Supplementary Data Table S8).

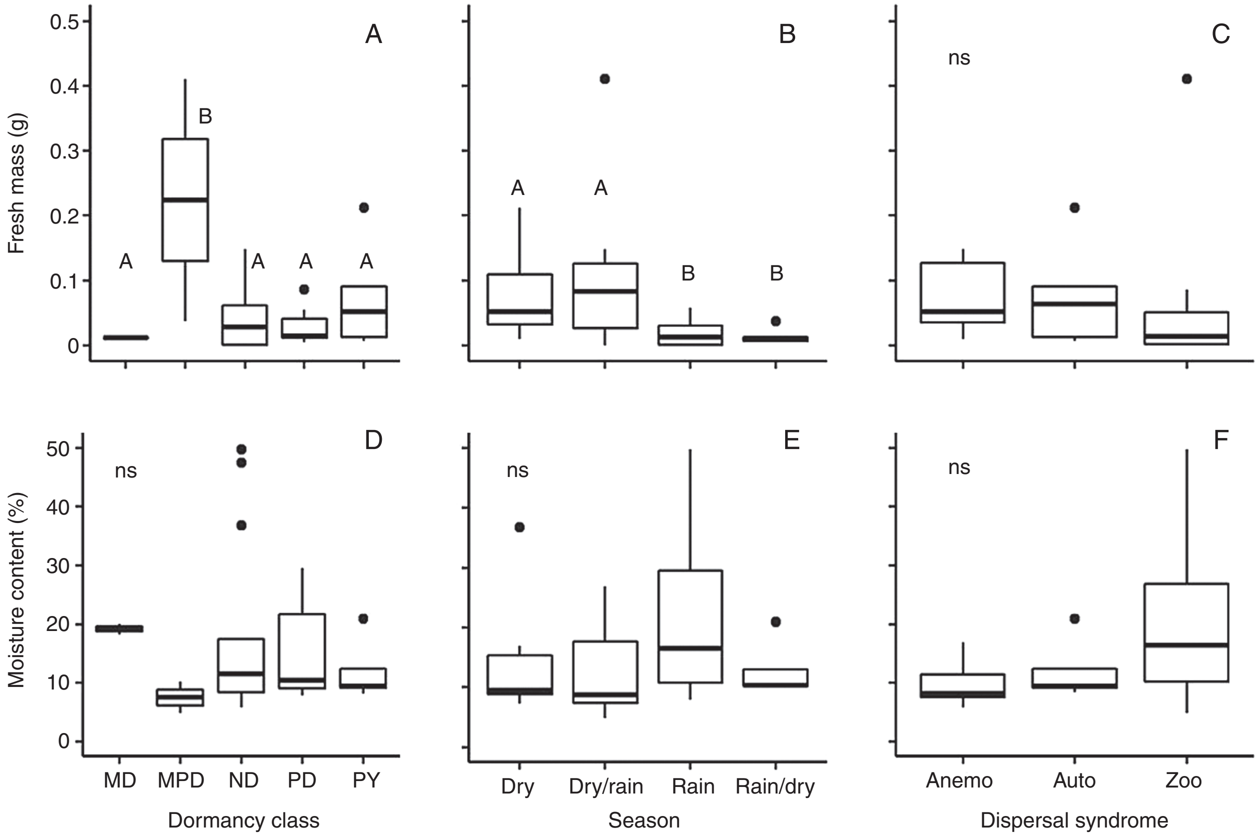

FIG. 5. Relationship between seed mass (A–C) and moisture content (D–F) according to dormancy class, seed dispersal season and dispersal syndrome for a cerrado community in south-eastern Brazil. Different capital letters indicate significant differences (Tukey test $P \leq 0.05$); ns, not significant. ND, non-dormant; PY, physical; MPD, morphophysiological; MD, morphological; PD, physiological; Anemo, anemochory; Auto, autochory; Zoo, zoochory.

DISCUSSION

Our results indicated that seed dormancy was dependent on the interaction between a species's dispersal syndrome and the seed dispersal season. Thus, species with limited seed dispersal (autochorous) tend to produce dormant seeds, while species with long-distance seed dispersal (anemochorous and zoochorous) presented dormant seeds only when dispersal occurred in unfavourable seasons, such as the rainy-to-dry transition. The harsh environmental conditions that follow seed dispersal likely reduce the probability of seedling establishment in cerrado species. Moreover, the relationship between dormancy and dispersal season was consistent among different dormancy classes, and varied with the dispersal syndrome. For instance, PY was related to anemochory and autochory, while MD, MPD and PD were related to zoochory. The proportion of species in our cerrado community dispersing dormant seeds during the dry season (43 %) was similar to what is described for humid tropical forests (Sautu, 2007). We also demonstrated that cerrado species germinate seasonally at the beginning of the rainy season, consistent with our expectations and other seasonal ecosystems (Garwood, 1983; Veenendaal *et al.*, 1996; Blakesley *et al.*, 2002; Marod *et al.*, 2002). We therefore suggest that germinating during the rainy season was selected across seasonal ecosystems, independent of phylogenetic groups, growth forms, dispersal syndrome or degree of seasonality. Further investigation including a larger number of species and growth forms is needed to test our assumption and investigate phylogenetic restrictions and the evolution of seed dormancy in cerrado.

Synchronizing germination with the onset of the rainy season, as observed in the cerrado community and for anemochoric and zoochoric species, may increase plant success as it maximizes the first growth period, allowing seedlings to develop an efficient rooting system and/or to accumulate enough storage reserves in order to survive the subsequent dry season (Frankie *et al.*, 1974; Garwood, 1983; Franco, 2002; Oliveira, 2008). On the other hand, the lack of seasonal germination in autochorous

TABLE 2. *Competing log-linear models tested to evaluate the relationship between seed dispersal season, dispersal syndrome and dormancy (presence/absence) for a cerrado community in south-eastern Brazil*

Model	LR	d.f.	P	AIC
(1) Season + syndrome + dormancy	41.94	17	0.006	53.265
(2) Season × syndrome + season × dormancy	**9.789**	**8**	**0.28**	**41.789**
(3) Season × dormancy + syndrome × dormancy	27.493	12	0.007	51.493
(4) Season × syndrome + syndrome × dormancy	12.692	9	0.177	42.692
(5) Season × syndrome + season × dormancy + syndrome × dormancy	6.015	6	0.421	42.015
(6) Full model (saturated model)	0	0		48

The chosen model, with the lowest AIC and LR values, is shown in bold.

TABLE 3. *Hierarchical comparisons of models to determine significant interactions between seed dispersal season, dispersal syndrome and dormancy (presence/absence) for a cerrado community in south-eastern Brazil*

Term	Models compared	LR	d.f.	*P*
Season × dormancy	4 versus 5	6.686	3	0.083
Syndrome × dormancy	2 versus 5	3.783	2	0.151
Season × syndrome	**3 versus 5**	**21.487**	**6**	**0.0015**

The significant conditional interaction, according to *P* values, is shown in bold.

TABLE 4. *Competing log-linear models tested to evaluate the relationship between seed dispersal season, dispersal syndrome and dormancy class for a cerrado community in south-eastern Brazil*

Model	LR	d.f.	*P*	AIC
(1) Season + syndrome + dormancy class	66.366	50	0.06	76.719
(2) Season × syndrome + season × dormancy class	16.519	32	0.989	72.519
(3) Season × dormancy class + syndrome × dormancy class	14.348	30	0.993	74.348
(4) Season × syndrome + syndrome × dormancy class	**17.243**	**36**	**0.997**	**65.243**
(5) Season × syndrome + season × dormancy class + syndrome × dormancy class	0.168	24	1	72.168
(6) Full model (saturated model)	0	0		120

The chosen model, with the lowest AIC and LR values, is shown in bold.

TABLE 5. *Hierarchical comparisons of models to determine the significant conditional interactions between seed dispersal season, dispersal syndrome and dormancy class for a cerrado community in south-eastern Brazil*

Term	Models compared	LR	d.f.	*P*
Season × dormancy class	4 versus 5	17.24	12	0.141
Syndrome × dormancy class	**2 versus 5**	**16.52**	**8**	**0.036**
Syndrome × season	**3 versus 5**	**14.35**	**6**	**0.026**

Significant conditional interactions, according to *P* values, are shown in bold.

species suggests that, for these cerrado species, dormancy was more related to distributing germination throughout the year rather than synchronizing germination with the most favourable period for seedling establishment. In fact, the results showed that the mean germination time of autochorous species was more variable than for anemochorous and zoochorous species (coefficient of variation of 29.4 % versus 10.6 and 12.3 %, respectively; Supplementary Data Table S2), confirming that in species with limited seed dispersal distance, dormancy is more related to spreading germination through time. Such distribution of germination time across seasons might enhance the chances for seedling establishment in autochorous species by ensuring that germination of some seeds would occur when environmental conditions are suitable for seedling establishment, and by decreasing competition between sibling plants (Hyatt and Evans, 1998; Wang *et al.*, 2009; Volis and Bohrer, 2013; Ramos *et al.*, 2017).

The timing of seed germination in the cerrado community was controlled both by dispersal season (beginning of the rainy season) and by dormancy, differing from other studies in seasonal ecosystems (Jurado and Flores, 2005), including savannas (Baskin and Baskin, 2014), which recognize dormancy as the main mechanism controlling germination. The relatively lower percentage of dormant species in the community is consistent with other studies in open cerrado and seasonal grasslands which have also reported <50 % of dormant species (Dayrell *et al.*, 2017; Ramos *et al.*, 2017; Zupo, 2017). The cerrado, unlike the semi-arid savannas of Africa (Veenendaal *et al.*, 1996) and Australia (Mott, 1978), is considered a mesic savanna with a highly predictable rainy season (Oliveira-Filho and Ratter, 2002), which allows the coexistence of both mechanisms: seed dispersal when climatic conditions are favourable for seedling establishment, and delaying germination (dormancy) to a point in time when climatic conditions are suitable for seedling establishment (Freas and Kemp, 1983). Moreover, >50 % of species in the community dispersed seeds between the end of the dry season and beginning of the rainy season, suggesting that the fruiting peak of cerrado species was related to the period in which seedling establishment and growth is most likely to succeed.

In the cerrado community, all species dispersing seeds in the rainy-to-dry transition were dormant, contrasting with <43 % of dormant seed species dispersing in the other seasons. Additionally, the relationship between dormancy and dispersal during the rainy-to-dry transition was maintained by different dormancy classes, which varied with dispersal syndrome. The pattern just described suggests that dormancy in cerrado species is associated with dispersal season and that the dry season is a strong filter restricting seedling establishment. The climatic conditions (temperature and rainfall) during the rainy-to-dry transition could stimulate germination, but are unsuitable for seedling establishment, as it is a short and highly unpredictable period followed by a marked drought. Therefore, the evolution of dormancy in seeds dispersed throughout this period is favoured, as it avoids germination during unfavourable conditions for seedling establishment (Jurado and Flores, 2005; Silveira *et al.*, 2012; Ramos *et al.*, 2017).

Furthermore, dormancy in cerrado species was mostly controlled by the interaction between dispersal season and dispersal syndrome, rather than by dispersal season or dispersal syndrome alone. Thus, species with limited dispersal (autochorous) tend to be dormant, while those with moderate to long dispersal (anemochorous and zoochorous) show dormancy when the seeds are dispersed during harsh conditions or periods of great climatic uncertainty. According to Venable and Lawlor (1980) and Freas and Kemp (1983), species with moderate dispersal distance dispersing seeds under predictable climatic conditions tend to be non-dormant, given that seeds will likely reach sites suitable for germination and establishment. On the other hand, dormancy is favoured in species with limited dispersal, dispersing seeds during periods of great environmental uncertainty, as the odds of reaching sites suitable for germination are reduced (Cohen, 1968).

The expected interactions between dispersal during the dry season, low seed moisture content and physical dormancy, and also between dispersal during the rainy-to-dry transition, zoochory, high seed moisture content and physiological dormancy (Sautu *et al.*, 2006, 2007; Salazar *et al.*, 2011), were partially corroborated in our work. Seed moisture content did not differ with dispersal syndrome, dispersal season or dormancy class, but species that had high moisture contents (>36 %) were dispersed mainly during the rainy season and germinated quickly. The interaction between high moisture content, prompt germination and dispersal during the rainy season may be advantageous as it reduces the probability of seed desiccation and contributes to faster development of the seedling during its initial growth period (Pritchard *et al.*, 2004). We observed, however, that most species (70 %) had low seed moisture contents (<20 %), a feature commonly found in environments with dry seasons, as in the cerrado, since seeds with low moisture content usually tolerate dry periods better than those with high moisture content (Murdoch and Ellis, 2000; Tweddle *et al.*, 2003; Pritchard *et al.*, 2004).

However, the relationship of dormancy class with dispersal syndrome was stronger than with dispersal season, given that dormancy allows seeds to avoid germinating during the rainy-to-dry transition and the mechanism used (dormancy class) varied with dispersal syndrome. Thus, in species with dry fruits (autochorous and anemochorous), the only mechanism avoiding germination is PY, while in species with fleshy fruits many mechanisms for avoiding germination were observed (MD, MPD, PD). According to Kuhlmann and Ribeiro (2016), there is a strong relationship between fruit type and dispersal syndrome in the cerrado, which is determined phylogenetically. Therefore, the diversity of dormancy classes found among zoochorous species might be related to the fact that fleshy fruits evolved many times among angiosperms, fleshy fruits are considered thus as a labile character (Eriksson, 2016; Kuhlmann and Ribeiro, 2016). On the other hand, fruits with autochory and anemochory are phylogenetically restricted (Kuhlmann and Ribeiro, 2016). To further test this assumption, germination experiments with a larger and more diverse species pool are needed.

Seed mass varied with dispersal season and dormancy class, but not with dispersal syndrome. Seeds dispersed in the dry season and in the dry-to-rainy season transition had greater seed mass than seeds dispersed in the rainy season and in the rainy-to-dry transition. Moreover, species with MPD had greater seed mass than species in other dormancy classes. Only two species had MPD, *Xylopia aromatica* and *Virola sebifera*, and the largest seeds in the community belonged to *V. sebifera* (7.5 times heavier than the community's mean seed mass). Thus, the difference in seed mass between dormancy classes is clearly influenced by the great seed mass of *V. sebifera*. Studies in seasonally dry environments found that seedlings from larger seeds are more likely to survive than seedlings from smaller seeds (Moles, 2018). However, seed mass is strongly affected by growth form, increasing with plant height (Moles, 2018). Therefore, the difference we detected in seed mass may be related to differences in growth form, since most species dispersing in the dry season and in the dry-to-rainy transition were trees, while species dispersing in the rainy season and in the rainy-to-dry transition also included shrubs and forbs.

In conclusion, most cerrado species germinated at the beginning of the rainy season and both dispersal season and seed dormancy controlled the timing of seed germination. The likelihood of a species being dormant depended upon the interaction between dispersal season and syndrome, where species with limited dispersal (autochory) tended to be dormant, while species with long-distant seed dispersal (anemochory and zoochory) tended to be dormant if dispersal occurred during the rainy-to-dry transition. Therefore, dispersal during the rainy-to-dry transition favours the evolution of seed dormancy as the environmental conditions are favourable for germination but not for seedling establishment. Avoiding germination during the dry season was a convergent character, since all species dispersing seeds during this period had dormant seeds independent of taxonomy or dispersal syndrome. On the other hand, dormancy in autochorous species may be related to distributing the risk of seedling mortality through time, which is supported by the lack of a seasonal germination pattern and a high coefficient of variation found in the mean germination time of these species. Additionally, dormancy class was related to dispersal season and syndrome, but not to seed mass and moisture contents. Aside from showing patterns of fruiting and germination phenology at a community level in cerrado, our results clarify how dormancy and dormancy classes are modulated by the interaction between dispersal season and syndrome, allowing a better understanding of the evolution of seed dormancy in seasonally dry tropical habitats such as the cerrado.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Table S1: climate characteristics of the four different seasons in a cerrado community in south-eastern Brazil. Table S2: seed germination traits of 28 species used for determining the estimated germination date in a cerrado community in south-eastern Brazil. Table S3: circular statistics parameters from fruiting phenology for the community and for each dispersal syndrome in a cerrado community in south-eastern Brazil. Table S4: circular statistics parameters from estimated germination date for the community and for each dispersal syndrome in a cerrado community in south-eastern Brazil. Table S5: summary of the factorial PERMANOVA to evaluate the effects of dormancy class, dispersal season, dispersal syndrome and their interactions on seed mass in a cerrado community in south-eastern Brazil. Table S6: summary of the factorial PERMANOVA to evaluate the effects of dormancy class, dispersal season, dispersal syndrome and their interactions on seed moisture content in a cerrado community in south-eastern Brazil. Table S7: standardized residues of the log-linear model evaluating the relationship between dispersal syndrome, dispersal season and dormancy in a cerrado community in south-eastern Brazil. Table S8: standardized residues of the log-linear model evaluating the relationship between dispersal syndrome, dispersal season and dormancy class in a cerrado community in south-eastern Brazil.

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