Rodriguésia 75: e01222022. 2024
http://rodriguesia.jbrj.gov.br
DOI: http://dx.doi.org/10.1590/2175-7860202475002

Short Communication

Fruiting phenology in *Aspidosperma discolor* and implications for seed dispersal and population distribution

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Abstract

We investigated *Aspidosperma discolor* fruiting in three subpopulations in the inland Atlantic Forest of Northeastern Brazil, to better understand how local and global factors (such as the *El Niño* Southern Oscillation - ENSO) drive fruiting, and how functional traits are related to its dispersal potential and spatial distribution. Observations of mature fruits with dispersing seeds were carried out between 1993 and 2012. Dispersal potential was evaluated using seeds released at two different heights. Spatial distribution was analyzed using the Standardized Morisita dispersal index. *A. discolor* displayed seasonal fruiting during the dry season in all subpopulations, with variations in their average dates but without significant interannual variations in the proportions of fruiting individuals. The undulate seeds had average dispersal distances between 57.36 and 79.54 m. We found a random distribution pattern of the trees. The seasonal dry/rainy regime influenced fruiting and dispersal patterns, and seeds were released during the dry season (even in ENSO years). So, we demonstrate the importance of wind dispersal as a driving factor of fruiting, associated with an abiotic filter (low humidity) during the dry season. Additionally, the aerodynamic nature of the undulate diaspore and its dispersal potential influenced the random pattern of spatial distribution of *A. discolor*.
Key words: anemochoric seeds, seasonality, spatial distribution, tropical forest.

Resumo

Investigamos a frutificação de três subpopulações de *Aspidosperma discolor* em uma área Mata Atlântica no interior do nordeste do Brasil, para entender melhor como fatores locais e globais (*El Niño* Southern Oscillation - ENOS) impulsionam a frutificação, e como as características da espécie estão relacionadas aos seus potenciais de dispersão e distribuição espacial. Frutos maduros com sementes em dispersão foram observados entre 1993 e 2012. A dispersão foi avaliada por lançar sementes em duas alturas diferentes. A distribuição foi analisada usando o índice de dispersão padronizado de Morisita. *A. discolor* apresentou frutificação sazonal durante a estação seca nas três subpopulações com variações de suas datas médias, mas sem variações interanuais nas proporções de indivíduos frutificando. As sementes onduladas evidenciaram distâncias médias de dispersão entre 57,36 e 79,54 m. Encontramos padrão de distribuição aleatório das árvores. O regime sazonal seco/chuvoso influenciou os padrões de frutificação e dispersão, e sementes foram liberadas durante a estação seca (mesmo em anos ENSO). Assim, demonstramos a importância da dispersão anemocórica como fator impulsionador da frutificação, associada a um filtro abiótico (baixa umidade) durante a estação seca. Adicionalmente, a natureza aerodinâmica do diásporo ondulado e seu potencial de dispersão influenciaram a distribuição espacial aleatória de *A. discolor*.
Palavras-chave: anemocoria, sazonalidade, distribuição espacial, floresta tropical.

See supplementary material at <https://doi.org/10.6084/m9.figshare.c.6186679>

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The analysis of phenological data considering different populations growing under similar regional climate presents an interesting challenge, and the use of temporal and spatial replicates can contribute to a better understanding of phenological patterns and their relationships with annual climatic factors and interannual variations (Abernethy *et al.* 2018; Costa *et al.* 2021). Fruiting patterns in tropical trees may be affected by a variety of local factors, including rainfall (Dunham *et al.* 2018), insolation (Wright & Calderón 2018), certain species traits (Babweteera *et al.* 2018), micro-environmental factors such as canopy architectural and phenological patterns (Silva & Rodal 2009), and environmental edges (Menezes *et al.* 2018). Local environment factors can be affected by phenomena related to global climatic patterns such as the *El Niño* Southern Oscillation - ENSO, which can drastically change rainfall regimes and drought periods (Chapman *et al.* 2018; Menezes *et al.* 2018).

The time of fruit production is the main driver of the timing of diaspore dispersal, which is in turn influenced by exogenous factors and species traits, such as seed dispersal modes and plant habit (Mendoza *et al.* 2017; Poschlod *et al.* 2010). The majority of anemochoric species in tropical seasonal forests disperse their fruits during the dry season (*e.g.*, Novaes *et al.* 2020), and such species are a compelling group for investigating key functional traits, as their dispersal is mainly governed by physical factors such as wind (Augspurger *et al.* 2017). Furthermore, the individual characteristics of the seeds, such as mass, surface area and morphology of the diaspores, are the most important attributes that influence the dispersal and distribution of these species in space (Augspurger 1986; Greene & Quesada 2005). A tropical species with anemochory seeds is *Aspidosperma discolor* A.D.C. (Apocynaceae), this species is considered a hardwood species and is used for building houses. It is endemic to Brazil and distributed throughout the Atlantic Forest (Rainforest) and Caatinga (Seasonal Dry Tropical Forest and Woodland) domains (Castello *et al.* 2023) and is found in inland Atlantic Forest sites in the Chapada Diamantina mountain range in Bahia State (Funch *et al.* 2008). *Aspidosperma discolor* has been part of the focus of a forest tree monitoring project in Chapada Diamantina which was initiated in 1993 to accompany variations in the rhythms of leaf exchange, flowering and fruiting associated with environmental variables. We used phenological datasets for *A. discolor* collected by our research group in the Chapada Diamantina Mountain Range between the years 1993 and 2012 (Cerqueira, personal communication; Couto-Santos, personal communication; Funch *et al.* 2002). We sought to respond the following questions: Does the seasonal rainfall regime influence fruiting and seed dispersal? Are there significant interannual variations in fruiting related to *El Nino* events in the subpopulations studied? Does the aerodynamic nature of the diaspores and their dispersal potential influence the spatial distribution of *A. discolor*? We expected that fruiting and seed dispersal would be associated with the region's seasonal rainfall regime and with significant variations in fruit production due to *El Nino* events. Additionally, we expected that diaspore traits (*i.e.*, their aerodynamic nature associated with their dispersal potential) would exert significant influence on the spatial distribution of *A. discolor*.

Data collections were made at a regional scale in three subpopulations in a fragmented forest area [Appendix S1; Appendix S2 (available on supplementary material <https://doi.org/10.6084/m9.figshare.c.6186679>)] located between 12º27'06"–12º33'39"S and 41º23'14"–41º28'34"W, at 500–1,000 m a.s.l., on the eastern flank of the Chapada Diamantina range. The humid forest sites there have continuous evergreen canopies, with reproductive individuals of *A. discolor* approximately 10 m tall as well as emergent individuals reaching up to 20 m, considered late secondary, with importance value varying from 3.32 to 7.10 (Cerqueira, personal communication; Couto *et al.* 2011; Funch *et al.* 2008). The cloud forest site grows on a litholic neosols on the flank of Serra da Bacia and experiences consistent mistiness throughout the year, even during dry months; the gallery forest site along the Lençóis River experiences sporadic and rapid flooding during the rainy season; the tableland forest site occurs on red-yellow latosol (Funch *et al.* 2008). The region has an Aw type tropical climate (Alvares *et al.* 2014), with a rainy season concentrated between November and April and a dry season between July and October. Climatic data for the study period (1993–2012) were obtained from the National Institute of Meteorology (INMET 2020). Photoperiod data were obtained from the Astronomical Applications Department of the U.S. Naval Observatory website (<https://www.esrl.noaa.gov/psd/enso/mei/>) (Fig. 1). The region was affected during the study period by *El Niño* events between October and January of the years 1993, 1997–98, 2009, and 2012, resulting in scenarios of extreme drought (especially in 1993) (INMET 2020). *El Niño* Southern Oscillation Multivariate Index (MEI) values were obtained from the National Oceanic and Atmospheric Administration (<http://www.esrl.noaa.gov/psd/enso/mei>). The MEI consists of positive values for the warm phase (*El Niño*) and negative values for the cold phase (*La Niña*).

The fruiting (seed maturation/dispersal) of 19 tagged *A. discolor* trees were evaluated between 1993 and 2012, although there are some data collection gaps (Appendix S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.c.6186679>). Qualitative observations (*i.e.*, presence or absence of a phenophase) were performed at the end of each month (average intervals of 30 days). We tested seasonality phenological data using circular statistics (Morellato *et al.* 2010). The Kruskal-Wallis and Wilcoxon signed-rank tests were used to evaluate if there were inter-annual variations in the time intervals and the proportions of fruiting events in each subpopulation (Morellato *et al.* 2010; Zar 2010). We used the Generalized Linear Model (GLM), with the Binomial error distribution corrected with Quasi-Binomial when necessary, to examine the effects of the abiotic variables precipitation, insolation, and ENSO on the fructification of *A. discolor*. To avoid the effect of multicollinearity, relative humidity, monthly mean temperature and photoperiod were excluded from the analysis.

Follicle-type fruits (Castello *et al.* 2023) open and expose the seeds, and we classified the seeds/diaspores of *A. discolor* based on their morphological characteristics and aerodynamic behaviors according to Augspurger (1986). Seeds were taken from four trees. Seed mass was determined using a digital electronic balance, and a flatbed scanner was used to determine their areas, using QUANT software (Vale *et al.* 2003). Tests of the dispersal potentials of *A. discolor* seeds were carried out during the dry season by simulating the

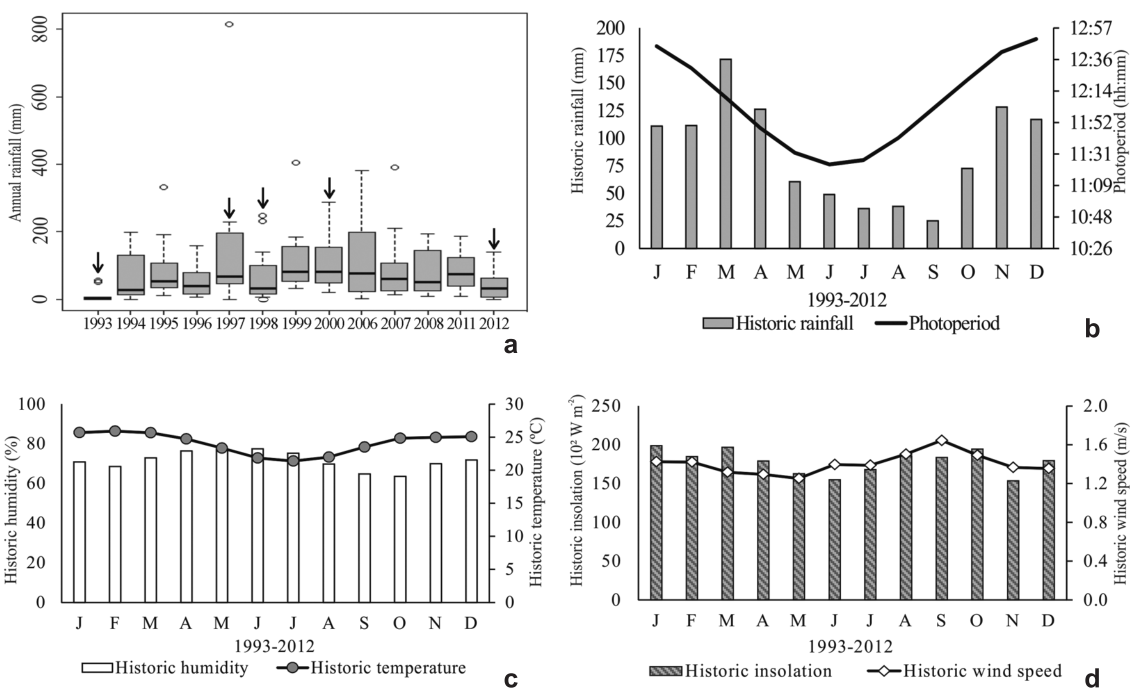

Figure 1 – a-d. Environmental data for the study region in the Chapada Diamantina mountains, Brazil, for the period between 1993 and 2012 – a. average (± SE) annual rainfall, black arrows indicate *El Niño* years; b. mean monthly rainfall and photoperiod; c. mean monthly humidity and temperature; d. mean monthly insolation and wind speed. (Source: National Institute of Meteorology - INMET station located in Lençóis / National Institute of Meteorology and Astronomical Applications Department of the U.S. Naval Observatory).

dispersal of 64 intact seeds under natural conditions. The seeds were released from two different heights (6 and 10 m, approximating the heights of the branches of adult individuals), and the time elapsed from their release until they reached the soil was determined using a digital chronometer. The seeds were released in the absence of any wind (0.0 m/s) or with wind speeds of 5 m/s (the maximum wind speed recorded in the study area during October) (INMET 2020). We adopted the methodology proposed by Augspurger (1986) to evaluate the dispersal potential of *A. discolor*. We calculated the relation between weight and diaspore area (wt/area) to examine wing-loading (Augspurger 1986; Augspurger *et al.* 2016, 2017). The descent rate (or *terminal velocity*) of the diaspore is related to its wing-loading (Sheldon & Burrows 1973). We used linear regression to evaluate the relationship between seed area and weight, and examined the association between the average durations of the falls from 6 m and 10 m using Spearman's correlation coefficient (r_s).

Plots of different sizes [160 plots (covering 6.25 m^2 each), 80 plots (25 m^2), and 50 plots (40 m^2)] were used in the sampling, and the numbers of individuals in each were counted (both young and adult) in each sampling unit (plot). To evaluate the distribution pattern of *A. discolor*, we sampled a total of 63 individuals in the study sites. We analyzed the distribution pattern of the population using the Standardized Morisita Dispersal Index (I_p), as it is independent of population density and sample size (Smith-Gill 1975).

We performed all analyzes using R software, version 4.0.2, with the addition of the "circular", "vegan" and "car" packages (R Development Core Team 2020).

As expected, fruiting phenology was strongly seasonal, occurring mainly during the dry season, with significant variations in terms of the proportions of individuals that fruited over the time in each subpopulation (Fig. 2; Tab. 1). We found variations in the time intervals of fruiting in the gallery forest subpopulation (Appendix S3, available on supplementary material <https://doi.org/10.6084/m9.figshare.c.6186679>), although there were no interannual variations in the proportions of individuals fruiting among the subpopulations when considered together (Appendix S4, available on supplementary material <https://doi.org/10.6084/m9.figshare.c.6186679>). Concerning all of the subpopulation together, most fruiting episodes occurred during the dry season (July and October), except for the years 2006–8, when fruiting events preceded the dry season, and in the year 2012, when no fruiting

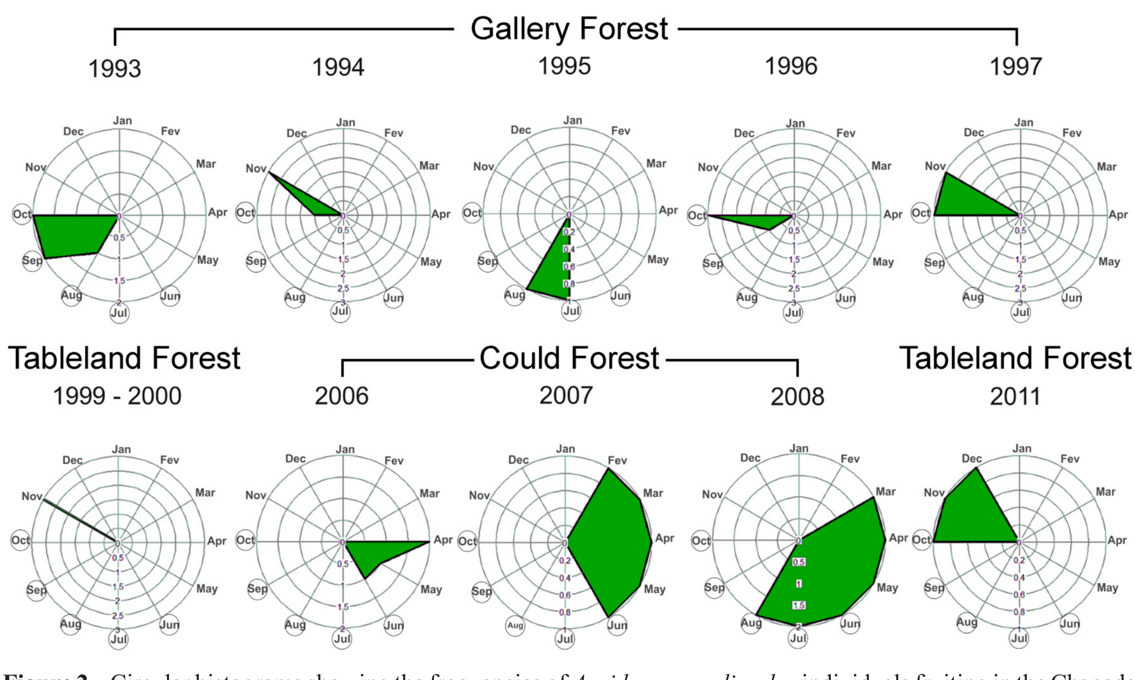

Figure 2 – Circular histograms showing the frequencies of *Aspidosperma discolor* individuals fruiting in the Chapada Diamantina mountains, Brazil. Dry season months are circled.

Table 1 – Circular statistical results for the seasonal fruiting of *Aspidosperma discolor* in an inland Atlantic Forest, Chapada Diamantina, Brazil. Phenological event observations (N).

Sites	Years	Observations (*N*)	Mean date	Mean angle	Length of the mean vector (*r*)	Angular standard deviation	Rayleigh test (*p*)
Gallery forest	1993	5	06/Sep	246.21°	0.92	22.18°	< 0.01
	1994	4	23/Oct	296.63°	0.97	12.92°	0.01
	1995	2	13/Jul	195°	0.96	14.96°	0.16
	1996	4	22/Sep	261.63°	0.97	12.92°	0.01
	1997	6	15/Oct	285°	0.96	14.96°	< 0.01
Tableland forest	1999-2000	3	16/Oct	300°	1	0°	0.03
	2011	3	31/Oct	300°	0.91	24.22°	0.07
Cloud forest	2006	4	23/Apr	112.10°	0.91	25°	0.02
	2007	5	30/Mar	90°	0.75	41°	0.05
	2008	12	16/May	135°	0.64	48°	< 0.01

was observed (Fig. 2). The GLM evidenced that fruiting was associated with ENSO oscillations in the gallery forest subpopulation; there were also significant interactions between ENSO oscillations and precipitation that influenced fruiting in this subpopulation (Tab. 2). Fruiting in the tableland forest subpopulation was associated with insolation (Tab. 2). In the cloud forest subpopulation, fruit set was not significantly associated with any environmental condition (Tab. 2).

Aspidosperma discolor seeds are elliptic, brownish, with a central seed nucleus surrounded by a dry membranous wing. The seeds have an average weight of 144.00 mg (± 7.00), an average area of 1.30 cm^2 (± 0.02), and an average wing-loading of 110.77 mg/cm^2 . A positive linear association could be observed between weight and area, demonstrating that as the area of the seed increases its mass increases significantly ($F = 452$, $R^2 = 0.89$, $p = 0.001$, $df = 62$). The diaspores were classified as the undulator type, although two types of behavior of the diaspores were identified during the dispersal potential experiments: 1- free fall, without any other kind of movement except sliding through the air, much like the glider type; and 2- an initial free fall movement, followed by rotation along the seed axis. The average dispersal distance found for this species was 57.36 m from a height of 6 m and 79.54 m from a height of 10 m (Appendix S5, available on supplementary material <https://doi.org/10.6084/m9.figshare.c.6186679>). A positive linear association was observed between the average duration of the fall from 6 m and the average duration of the fall from 10 m ($r_s = 0.80$, $p < 0.01$). *Aspidosperma discolor* showed a random spatial distribution pattern, regardless of plot size, in all of the sampled areas, as the Morisita dispersal index (I_p) varied from 0.19 to 0.37 (Appendix S6, available on supplementary material <https://doi.org/10.6084/m9.figshare.c.6186679>).

Environmental drivers varied enormously and irregularly throughout the study years in the region (Funch *et al.* 2002), being greatly affected by ENSO (Menezes *et al.* 2018). Such factors were seen to shift the average time intervals of phenological activities in the species studied, but did not seem to have any significant effect on interannual variations in the proportions of individuals fruiting in the three subpopulations during our study. In contrast to other studies that have highlighted the important role of ENSO in plant phenology (Chapman *et al.* 2018), only a strong *El Niño* predominating from July to December/1993, and providing only 357 mm of total rainfall, was observed to influence *A. discolor* fruiting. The irregularity and overall scarcity of rainfall during the years 1993–1994 also significantly influenced reproductive patterns otherwise observed in years of more consistent rainfall (Funch *et al.* 2002).

Table 2 – Generalized Linear Models (GLMs) results adjusted to an error distribution, showing the effects of total monthly rainfall, solar insolation, and the intensity of the *El Nino* Southern Oscillation (ENSO), on the fruiting of *Aspidosperma discolor* in forest sites at the Chapada Diamantina. When the variables are statistically significant are displayed significance codes for p-value: 0 '***' 0.001 '**' 0.01 '*' 0.05. (The complete results of full models are reported in Appendix 7, available in the supplementary material at <https://doi.org/10.6084/m9.figshare.c.6186679>).

Site	Explanatory variable	Distribution error	Deviance	p-value
Gallery forest	ENSO	Binomial	6.977	0.008256 **
	Rainfall: ENSO		4.6995	0.030171 *
Tableland forest	Solar Insolation	Binomial	14.512	< 0.001 ***
Cloud forest	Rainfall	Quasi-binomial	1.2384	0.3502
	Solar Insolation		0.1486	0.7445
	ENSO		3.8804	0.1037
	Rainfall: Solar Insolation		0.4004	0.5933
	Rainfall: ENSO		0.0052	0.9515
	Solar Insolation: Enso		0.8046	0.4502
	Rainfall: Solar Insolation: Enso		0.0042	0.9565

Most anemochoric fruits with orthodox seeds disperse during the dry season/beginning of the rainy season, as was observed with *A. discolor* (Cortés-Flores *et al.* 2020; Ibarra-Manriquez *et al.* 1991; Jara-Guerrero *et al.* 2011; Justiniano & Fredericksen 2000; Novaes *et al.* 2020; Salomão *et al.* 1997). Anemochory can also be observed in humid tropical forests among emergent trees with high investments in fruit production (Augspurger *et al.* 2017). Species traits, including tree height, canopy position, and the numbers of fruits produced, are important factors related to the distances to which tropical anemochoric diaspores can be dispersed, as their emergence above the canopy (where there is greater wind circulation) favors effective dispersal (Augspurger *et al.* 2017). In addition to those species characteristics in *A. discolor*, diaspores traits such as the presence of a central seed nucleus, a surrounding wing, and reduced mass favor dispersal even in dense forest vegetation (Augspurger 1986). The glider aerodynamic behavior described in this study for *A. discolor* was previously reported for *Aspidosperma cruenata* Woods. (Augspurger 1986) and *A. spruceanum* Benth. *ex* Müll.Arg. (Augspurger *et al.* 2017), with average wing-loading being similar between *A. discolor* and *A. cruenata* (Augspurger 1986).

ENSO oscillations and their association with precipitation were important for explaining the fruiting patterns in the gallery forest subpopulation, while the insolation of the tableland forest subpopulation was the best predictor of the observed fruiting patterns observed there; no environmental variable tested was found to be related to fruit set in the cloud forest subpopulation. We consistently documented strong seasonality in the timing of the dispersal of the anemochoric diaspores during the dry season or at the beginning of the rainy season. Wind dispersal, as a driving factor of fruiting, supports the hypothesis that dispersal is a relevantly associated with abiotic filters (Zobel 1997). Although dispersal is not easy to measure, our results demonstrated its association with the random distribution pattern of *A. discolor* (Augspurger 1986; Augspurger *et al.* 2017).

The expected average dispersal distance of *A. discolor* diaspores found here (79.54 m) was lower than that reported by Augspurger (1986) for *Aspidosperma cruenata* (129 m) (with a wind speed of 3.5 m/s) in a semi-deciduous forest on Barro Colorado Island, Panama. Wind dispersed seeds can attain distances of 100 m from the mother plant in undisturbed forests (although most do not attain distances greater than 30 m) (Guariguata & Pinard 1998). *Aspidosperma discolor* evidence a random pattern of spatial distribution, regardless of plot size, distinct from reports of aggregated distribution in other species of the genus, such as *A. polyneuron* Muell. Arg. (Silva *et al.* 2004). The spatial distribution of a plant population depends on the pattern of seed dispersal and on the probability of seedling survival, aggregated distribution patterns, on the other hand, reflect specific dispersal mechanisms (Janzen 1970), possibly related to autogyro and rolling-autogyro diaspores, which tend towards clumped dispersals (Augspurger 1986).

Long term studies in tropical phenology are somewhat rare (Mendoza *et al.* 2017). Thus, our results are extremely important for understanding phenological patterns of tropical trees, as they provide a long-term dataset. We emphasize, however, the importance of long-term phenological studies without gaps between years to obtain more consistent results. The results of this study highlight the importance of wind dispersal as a driving factor of fruiting phenology, related to abiotic filters associated with the dry season and the aerodynamic nature of the undulate diaspores of *A. discolor* and their dispersal potential as influencing its random spatial distribution. The study also sheds light on the behavior of tropical anemochoric tree species in relation to ENSO and their capacity for maintaining the intrinsic nature of their fruiting during the dry season even during *El Niño* events. Future studies should focus on longer periods of phenological data to obtain more consistent results, on testing the variability of the aerodynamic behaviors of those diaspores and their dispersal potentials, and examining plant mortality as well as germination rates during periods of prolonged drought associated with *El Niño* events - thus to contributing to a better understanding of the relative importance of *El Niño* and wind dispersal as driving factors of fruiting phenology in tropical plants.

Acknowledgements

The authors would like to thank the Graduate programs in Botany and Plant Genetic Resources/ Universidade Estadual de Feira de Santana (UEFS); Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 480508/2008-09); and the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB 5303/2009), for financing this research project; and the Chapada Diamantina Foundation (FCD), for assistance with the fieldwork.

Data availability statement

In accordance with Open Science communication practices, the authors inform that supplementary data is available to the reader at <https://doi.org/10.6084/m9.figshare.c.6186679>.

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Area Editor: Dr. André Rech

Received on November 10, 2022. Accepted on October 26, 2023.