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Short Communication

Seasonality, dispersal modes, and optimal germination times modulate the fruiting of tropical tree species

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Abstract

We investigated the associations of seasonality, dispersal modes and seed germination speeds with the fruiting of *Clusia nemorosa*, *Pleroma fissinervium*, and *Vochysia pyramidalis* in a gallery forest, Chapada Diamantina, Brazil. Observations of mature fruits with dispersing seeds were carried out from 2003 to 2006. Cross-correlation and circular statistics were performed to test the relationships among fruiting and abiotic factors, and phenological seasonality. Dispersion syndromes were defined and germination experiments were performed after seed collection (*n* =100/species), using four replicates. The species evidenced seasonal fruiting. *Clusia nemorosa* produced zoochoric seeds and *V. pyramidalis* anemochoric seeds, which were dispersed during the rainy season and positively correlated with precipitation; *P. fissinervium* produced autochoric seeds, released during the dry season to early rainy season, being positively correlated with insolation and negatively with humidity. The rotating wing seeds of *V. pyramidalis* were released in the rainy season and aided floating in watercourses, characterizing hydrochory. *Clusia nemorosa* and *V. pyramidalis* germinated (2–6 days) more rapidly than *P. fissinervium* (9 days). Seasonality, dispersal modes, and optimal germination conditions modulated the fruiting of the species examined, whose reproductive strategies responded to environmental drivers such as precipitation, favoring germination during the rainy season.

Key words: fruiting phenology, germination speed, seed dispersal.

Resumo

Investigamos a associação da sazonalidade, modos de dispersão e velocidade de germinação com a frutificação de *Clusia nemorosa*, *Pleroma fissinervium*, e *Vochysia piramidalis* em mata de galeria, Chapada Diamantina, Brasil. Frutos maduros com sementes em dispersão foram observados de 2003–2006. Correlação cruzada e estatística circular testaram relações entre frutificação e fatores abióticos e sazonalidade fenológica. Síndromes de dispersão foram definidas e experimentos de germinação ocorreram imediatamente após coleta das sementes (*n* = 100/espécie), utilizando quatro repetições. As três espécies apresentaram frutificação sazonal, *C. nemorosa* com sementes zoocóricas e *V. piramidalis* com sementes anemocóricas dispersas durante as chuvas, foram positivamente correlacionadas com a precipitação, e *P. fissinervium* com sementes autocóricas liberadas durante a estação seca ao início das chuvas, positivamente correlacionadas com insolação e negativamente com a umidade. Sementes de alas rotativas auxiliando a flutuação em cursos d'água, liberadas na estação chuvosa, definiram hidrocoria para *V. pyramidalis*. *Clusia nemorosa* e *V. pyramidalis* germinaram (2–6 dias) mais rapidamente que *P. fissinervium* (9 dias). Sazonalidade, modos de dispersão e condições ótimas de germinação modularam a frutificação das espécies, cujas estratégias reprodutivas responderam a fatores ambientais, como precipitação, favorecendo a germinação na estação chuvosa.

Palavras-chave: fenologia da frutificação, velocidade de germinação, dispersão de sementes.

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Seasonal tropical environments are currently being impacted by climate change in terms of precipitation, air temperature, humidity, and soil-water availability, which, in turn, affect the phenologies as well as the dispersal and germination modes of the plants growing there (Novaes *et al*. 2020; Morellato *et al*. 2016). Seasonal precipitation exerts a great influence on the traits of tropical species and affects fruiting and seed germination, and is therefore linked to the seasonality of frugivore dispersers and the optimal timing for abiotic dispersal (Schupp *et al*. 2010). In addition to precipitation, abiotic factors such as temperature, photoperiod (day length), moisture, and solar irradiation intensity (daily insolation) are also considered important variables in defining the fruiting, seed release patterns, and germination of tropical plants (Mendoza *et al*. 2017).

The timing of diaspore dispersal will reflect abiotic or biotic seed dispersal modes (Poschlod *et al*. 2010). The timing of germination is critical to other life-history traits, as seedlings will experience different environmental conditions depending on the timing of their emergence (Narita 1998). The phenology of fruiting and seed dispersal is therefore important to our understanding of the dynamics of forest ecosystems as well as to the management and conservation of tropical vegetation (Morellato *et al*. 2016).

We investigated the association of regional climatic seasonality, dispersal modes and seed germination speeds with the timing, intensity and seasonality of the fruiting (mature fruits with dispersing seeds) of *Clusia nemorosa* G. Mey (Clusiaceae), *Pleroma fissinervium* Schrank et Mart. *ex* DC. (Melastomataceae), and *Vochysia pyramidalis* Mart. (Vochysiaceae), tree species widely distributed in Brazil and abundant in gallery forest in Chapada Diamantina mountains in northeastern Brazil (Funch *et al*. 2008). To that end, we addressed the following questions: is the fruiting of those species seasonal? Which climatic variables are associated with fruiting? Do the dispersal modes (biotic/abiotic) of those species reflect their fruiting and seed dispersal seasons (dry/rainy)? Are their respective seed germination speeds associated with favorable times for their successful establishment? Abiotic diaspores (such as winged or xerocasic capsules) can only be successfully dispersed during the dry season - but must then wait for the first rains to germinate; on the other hand, species that produce zoochoric diaspores (and are predominant in tropical forests) fruit continuously - but maintain their fruiting peaks in the rainy season, with its favorable conditions for germination (Van Schaik *et al*. 1993; Mendoza *et al*. 2017). We therefore expected that species having abiotic seed dispersal would show strongly seasonal fruiting (during the dry season) and relatively longer germination times, while zoochoric species would fruit continuously (but with a fruiting peak in the rainy season) and would have more rapid seed germination.

The vegetation in the northern section of the Chapada Diamantina mountains (11°36'–13°56'S, 40°40'–43°56'W) is a mosaic of savannas, humid and dry forests, and open rocky-field vegetation (Funch *et al*. 2008). The gallery forest along the Lençóis River (12º33'38"S, 41º24'40"W, 400–500 m a.s.l.) has an evergreen canopy of trees reaching up to 15 m, and includes species such as *V. pyramidalis*, *C. nemorosa*, and *P. fissinervium* growing on dystrophic litholic neosols (Funch *et al*. 2008). The region experiences a relatively humid tropical climate (type Aw by the Köppen system), with a rainy season concentrated between December and April, and a dry season between July and October (Alvares *et al*. 2013). Rainfall, relative humidity, temperature, and daily insolation data were acquired from a local weather station (INMET 2021).

Fruiting phenology (determined by monitoring mature fruits with dispersing seeds) was accompanied on a monthly basis among 20–24 adult individuals / species from September/2003 to August/2006, using the Fournier (1974) approach to estimate phenophase intensity. For the analyses of seed dispersal modes, the species were described according to the morphological criteria formulated by Van der Pijl (1982). We evaluated, under laboratory conditions, the capacity of the seeds to germinate as well as their germination velocity. Mature seeds were collected during the fruiting peak of each species in 2006 (20 seeds/5 individuals/species). We tested fresh seeds, as recommended by Brasil (2009), with the germination experiments taking place immediately after seed collection, using four replicates (n = 25 seeds / species). The seeds were placed on sheets of germinating paper in a petri dish and moistened with distilled water (equivalent to 2.5 times the weight of the paper) (Brasil 2009), and then held in a Biochemical Oxygen Demand (B.O.D.) type chamber at 25 ^{o}C with relative humidity of 80% under a 12-hour photoperiod (160 W m^{-2}) for 30 days. Germination evaluations were carried out daily, adopting the criteria of radicle emission as indicative of germination, following Brasil (2009).

The normality of the phenological data was tested following Shapiro & Wilk (Zar 2010). We examined any correlations between fruiting and abiotic factors (precipitation, temperature, photoperiod, moisture, and daily insolation) using Spearman's correlation coefficients (r_s), calculated using R software version 4.0.3 (R Core Team 2020). We examined fruiting seasonality using circular statistics (to calculate the mean angle, mean date, length of the mean vector [*r*] as well as the Rayleigh test (*Z* and *P*). The fruiting frequency was based on the total number of individuals showing that phase per month; the months were subsequently converted into angles, at 30° intervals. The phenological events with significant mean angles ($P < 0.05$), as estimated using the Rayleigh test (*Z*) for circular distributions (Zar 2010), were transformed into mean dates. Phenophases whose vector lengths (*r*) were > 0.5, and whose Rayleigh tests were indicated as significant, were considered seasonal (Morellato *et al*. 2010). All circular analyses were performed using the "circular" package of R software, version 4.0.3 (R Core Team 2020).

All three species evidenced strongly seasonal fruiting (Tab. 1; Fig. 1). *Clusia nemorosa* produces seeds with zoochoric red aryls, with greater intensity and an average date of dispersal during the rainy season (between January and March) that was positively correlated with precipitation (0.59–0.70, $P < 0.05$) and temperature (0.60–0.62, $P < 0.05$) (Fig. 1a; Fig. 2). *Vochysia pyramidalis* produces hydrochoric winged seeds, with greater intensity, and with an average date of dispersal during the rainy season (between February and March) that was positively correlated with precipitation (0.56–0.69, $P < 0.05$) and humidity (0.63, $P < 0.05$) (Fig. 1b; Fig. 2). *Pleroma fissinervium* produces autochoric pulvinate seeds, with greater intensity, and with an average date of seed release during the dry to early rainy season (the first half of October) that was positively correlated with insolation (0.68–0.74, $P < 0.05$) and negatively correlated with humidity (0.63–0.84, $P < 0.05$) (Fig. 1c; Fig. 2). *Clusia nemorosa* and *V. pyramidalis* germinated more rapidly than *P. fissinervium*. The seeds of *V. pyramidalis* germinated after approximately two days, with a germination percentage of 82%. The seeds of *C. nemorosa* required from 2 to 6 days to germinate, with high viability (100% germination). The seeds of *P. fissinervium* required nine days to germinate, reaching 75% of germination at the end of the 10 day evaluation period (the lowest germination percentage among the species studied).

In tropical forests with dry and rainy periods, most tree species are zoochoric and tend to show fruiting/dispersal peaks in the rainy season (Mendoza *et al*. 2017). That strategy guarantees greater seedling survival, as moist soil conditions are favorable due to the release of nutrients (resulting from the decomposition of the litter during the rainy period) and the easy availability of water - offering a greater chance of

Table 1 – Circular statistics of the fruiting phenology of *Clusia nemorosa*, *Pleroma fissinervium*, and *Vochysia pyramidalis* in a gallery forest in the Chapada Diamantina mountains, northeastern Brazil.

Studied group (method)	Phenophases	Mean date	Mean angle	Length of the mean vector (*r*)
Clusia nemorosa	Year 1	9-Mar	68.18°	0.87*
	Year 2	30-Jan	29.57°	0.74*
	Year 3	26-Feb	56.47°	0.75*
Pleroma fissinervium	Year 1	4-Oct	274.05°	0.81*
	Year 2	4-Oct	274.55°	0.76*
	Year 3	10-Oct	280.01°	0.81*
Vochysia pyramidalis	Year 1	21-Mar	79.38°	0.88*
	Year 2	26-Feb	56.19°	0.89*
	Year 3	14-Mar	72.99°	0.92*

* = Rayleigh test (p) < 0.01

germination and successful seedling development (Van Schaik *et al*. 1993). In addition to seasonality, the timing of fruit production and seed dispersal are influenced by a plant's dispersal mode (Mendoza *et al*. 2017; Poschlod *et al*. 2010). Species with fleshy fruits require abundant water resources for fruit development, as was observed during the three years of monitoring of *C. nemorosa*, which produces fleshy capsular fruits containing arillate seeds sought after by animals (zoochory) (Riguete *et al*. 2012).

Vochysia pyramidalis, with capsular fruits and anemochoric winged seeds, likewise fruited and dispersed its seeds during the rainy season during the three years of our study - the opposite of what might be expected for an anemochoric species, as their seed dispersal is commonly associated with the dry season and low humidity (favoring the dispersal by wind of seeds with wings or seed plumes) (Novaes *et al*. 2020). *V. pyramidalis* is found exclusively in gallery forests close to river margins in the Chapada Diamantina mountains, or associated with areas of infiltration on valley sides (Funch *et al*. 2008). Van der Pijl (1982) pointed out the incidental and convergent characters of hydrochory and anemochory, with the rotating wing design of diaspores aiding floating in watercourses. As its seeds are released during the rainy season, hydrochory is indicated for *V. pyramidalis*, as it is adjusted to environmental conditions present at that time of the year (Poschlod *et al*. 2010).

The autochoric capsular fruits (poricidal) of *P. fissinervium* containing powder-like seeds are produced and mature in the dry season - a common characteristic among species with small fruits that become dehydrated (Van der Pijl 1982). Its seeds are released very close to the mother plant, without any dispersal agent (Poschlod *et al*. 2010), and low relative humidity has been indicated as the most

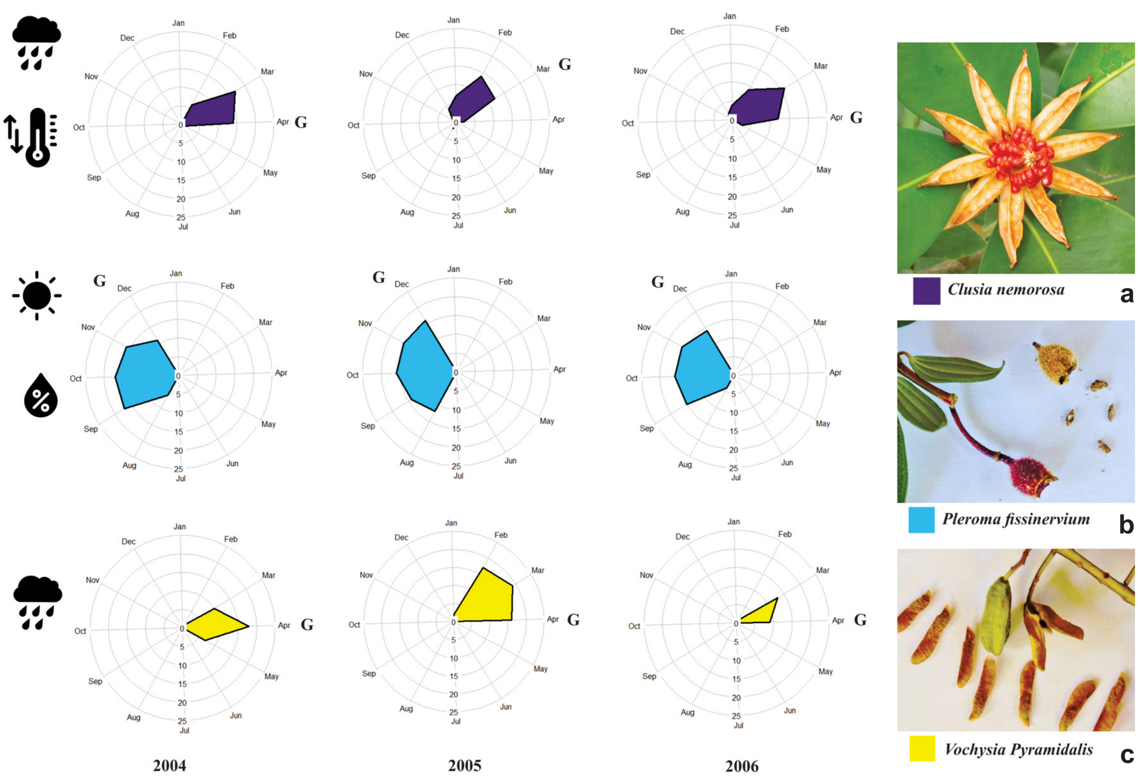

Figure 1 – a-c. Fruiting phenology and environmental variables in a gallery forest in the Chapada Diamantina mountains, northeastern Brazil – a. *Clusia nemorosa*; b. *Pleroma fissinervium*; c. *Vochysia pyramidalis*. Circular histograms of individual fruiting frequencies, with precipitation, temperature, insolation, and humidity influencing their fruiting phenologies. The times of seed germination (G) are indicated in the histograms. Photographs of their diaspores are provided next to histograms of each species. The climatic environments that influenced fruit set in the studied species are represented by the icons: = precipitation; = temperature; = insolation; = humidity.

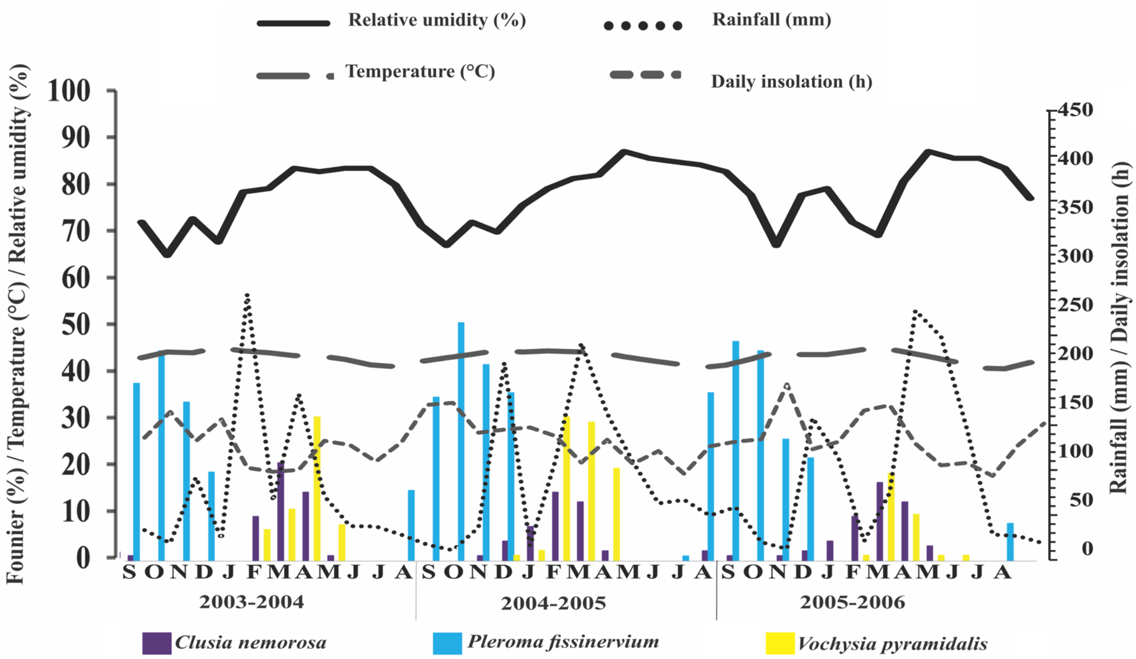

Figure 2 – Fruiting intensity (% Fournier) of *Clusia nemor*osa (orange bar), *Pleroma fissinervium* (blue bar), and *Vochysia pyramidalis* (yellow bar) and the environmental variables in a gallery forest in the Chapada Diamantina mountains, northeastern Brazil. Dotted line = rainfall; small dashed line = daily insolation; solid line = relative humidity; large dashed line = temperature. (Source: INMET).

determinant abiotic factor influencing the dispersal of autochoric species (Howe & Smallwood 1982). The low humidity during the dry season favors seed maturation, as in *P. fissinervium*, and their release from the fruits was observed during the transition period between the dry and rainy seasons during the three years of our study. Additionally, the delay in their germination helps ensure adequate conditions for seedling development at the beginning of the rainy season (Van Schaik *et al*. 1993).

Seasonality, dispersal modes, and optimal germination conditions modulate the fruiting of the species examined here. Each species has a reproductive strategy that responds to environmental driver, such as precipitation - strategies that have been selected for and better ensure the germination of their seeds at the beginning of the rainy season (which facilitates seedling establishment).

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