



## Reproductive phenology and germination of *Guapira hirsuta* (Choisy) Lundell

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**Abstract** - The objective of this study was to characterize the reproductive phenology, classify seeds desiccation tolerance, and model the germination curve of the *Guapira hirsuta*. For the phenological study, 17 individuals were monitored monthly from October 2021 to September 2022 for the presence or absence of flowers and fruits. Desiccation tolerance was assessed using seeds from eight individuals of *G. hirsuta*, collected in August 2021 in the Lago da Pedra do Cavalo Environmental Protection Area (Bahia, Brazil). Four treatments (15%, 12.5%, 10%, and 5% moisture content) were tested, with four replicates of 25 seeds each. Germination tests were conducted in a germination chamber. Logistic and Gompertz models were tested to fit the germination curve of the fresh seeds. *G. hirsuta* flowering occurred in June, with fruiting from July to September. The timing of seed dispersal at the study site coincided with the period of low water availability. *G. hirsuta* seeds are recalcitrant and exhibit slow germination, requiring 150-days for germination to stabilize and 92-days to reach 50% germination.

## Fenologia reprodutiva e germinação de *Guapira hirsuta* (Choisy) Lundell

**Resumo** - O objetivo deste estudo foi caracterizar a fenologia reprodutiva, classificar as sementes quanto à tolerância à dessecação e modelar a curva de germinação de *Guapira hirsuta*. Para o estudo fenológico, 17 indivíduos foram monitorados mensalmente de outubro de 2021 a setembro de 2022, quanto à presença ou ausência de flores e frutos. A tolerância à dessecação foi avaliada utilizando sementes de oito indivíduos de *G. hirsuta*, coletadas em agosto de 2021 na Área de Proteção Ambiental da Lagoa da Pedra do Cavalo, Bahia, Brasil. Testaram-se quatro tratamentos correspondentes aos teores de água (15%, 12,5%, 10% e 5%), com quatro repetições de 25 sementes cada. Os testes de germinação foram conduzidos em câmara de germinação. Modelos logísticos e de Gompertz foram testados para ajuste da curva de germinação das sementes frescas. A floração de *G. hirsuta* ocorreu em junho e a frutificação de julho a setembro. O período de dispersão das sementes no local de estudo coincidiu com o período de baixa disponibilidade hídrica. As sementes de *G. hirsuta* são recalcitrantes e apresentam germinação lenta, necessitando de 150 dias para estabilização da germinação e 92 dias para atingir 50% de sementes germinadas.



## Introduction

Among the different stages of the angiosperms life cycle, germination is the most critical point for successful establishment. Once dispersed, seeds often do not immediately encounter ideal conditions for germination (Bewley et al., 2013). We consider fruit dispersal timing and seed desiccation tolerance are factors of influence on the establishment of species in the natural environment. For species with seeds of slow germination and that do not tolerate desiccation, the synchronization of the dispersal time with the period of greater water availability is decisive for the germination and establishment of seedlings (Finch-Savage, 2003; Berjak & Pammenter, 2008; Marcos-Filho, 2015).

Integrating the germination curve with seed desiccation tolerance data and historical rainfall patterns provides insight into plant establishment and the potential impacts of climate change on species survival.

By characterizing the reproductive phenology of a species at a given site, it is possible to identify whether the time of fruit dispersal is consistent with the ideal conditions for seed germination and post-seminal development. Vegetative growth and reproduction of plants are regulated mainly by the water regime, which has led to generalizations related to vegetation with seasonal characteristics, such as fruit maturation, which usually occurs in the dry season or in the subsequent rainy season, when winds and fauna activity favor dispersal (Luna-Nieves et al., 2022). When orthodox seeds are dispersed in the dry season, they employ mechanisms to remain viable until the environmental conditions are favorable to germination. For recalcitrant seeds, low water availability will cause irreversible damage to the embryo (Salvador et al., 2022; Oyerinde et al., 2023).

*Guapira hirsuta* is native species from Brazil, belonging to the family Nyctaginaceae, and can be found in the form of subshrub, shrub or tree (Rossetto et al., 2023). This species occurs in the phytogeographic domains of the Amazon, Caatinga, Atlantic Forest, Cerrado and Pantanal, in the phytophysionomies of rupestrian grassland, riparian forest, seasonal forest, ombrophilous forest and restinga (Rossetto et al., 2023). Despite the wide geographic distribution of *G. hirsuta*, scientific publications containing information about the species are restricted, so far, to taxonomic (Furlan & Giulietti, 2014) and floristic studies (Peixoto et al., 2005; Camargos et al., 2008; Rochelle et al., 2011; Estevan et al., 2016; Oliveira-Neto et al.,

2017; Souza et al., 2018; Costa et al., 2021). An exception is the study conducted by Rocha-Santos et al. (2020), who surveyed the vegetation of 20 areas of Atlantic Forest in northeastern Brazil and observed reproductive aspects of 423 species. For *G. hirsuta*, these authors identified pollination by small insects, dioecious sexual system, a mating system characterized by cross-fertilization and zoochorous dispersal. Therefore, there is no information on the germination aspects and phenology of *G. hirsuta*.

Understanding flowering and fruiting patterns involves ecological and evolutionary insights, which are central to biodiversity conservation, especially in the context of climate change (Morellato et al., 2016). Therefore, to promote the conservation of native species, it is necessary to understand their reproductive phenology and seed traits, such as the cardinal germination temperatures, seed desiccation tolerance patterns, and the distribution of germination over time. To contribute to the conservation of *G. hirsuta* in the Lago da Pedra do Cavalo Environmental Protection Area (Bahia, Brazil), this study aimed to characterize its reproductive phenology, classify its seeds regarding desiccation tolerance, and model its germination curve.

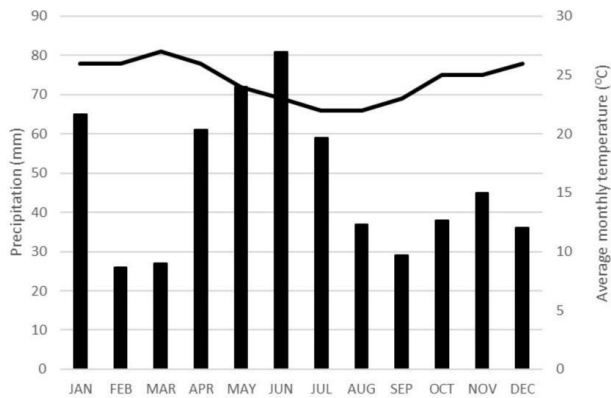
## Material and methods

### Study area

The study was conducted in a fragment of seasonal semideciduous forest within the Lago da Pedra do Cavalo Environmental Protection Area (EPA) (Bahia, Brazil), located in the municipality of São Gonçalo dos Campos, Central-North region of Bahia, Brazil. The site encompasses approximately 6.2 hectares, and coordinates 38°58'38.1" W and 38°58'46" W/12°19'53.9" S and 12°20'0.7" S).

The Lago da Pedra do Cavalo EPA is located in a transition zone between the Atlantic Forest and the Caatinga. The climate is classified as megathermal, with winter rains and hot summer (As, according Köppen), featuring average annual minimum and maximum temperatures of 22.4 to 27.2 °C, respectively, and an average annual rainfall of 720.7 mm (Santos et al., 2018). Meteorological data (2010-2021) were obtained from the National Institute of Meteorology (INMET) automatic station A413, located in Feira de Santana, less than 10 km from the seed collection site (Figure 1).

### Reproductive phenology



**Figure 1.** Annual distribution of precipitation and average monthly temperature, obtained from the National Institute of Meteorology (INMET) automatic weather station A413.

To evaluate reproductive phenology, 17 individuals of *Guapira hirsuta* (Choisy) Lundell (eight females and nine males) were monitored monthly for twelve months, from October 2021 to September 2022, for the presence or absence of flowers and fruits. We employed the semiquantitative methods of Fournier (1974), which consists of evaluating the phenological intensity on a scale from zero to four, according to the percentage of flowers and fruits present in the crown (Neves et al., 2017). Botanical specimens were collected from each sampled individual, herborized, and incorporated into the Herbarium of Recôncavo da Bahia (HURB).

Phenological analysis data was performed using circular statistics, with the months of the year converted into 30° angular intervals (Morellato et al., 2010). For each phenophase, the following parameters were calculated: (i) mean angle, which represents the average date of the phenological activity considered; (ii) vector length, which represents the aggregation of dates (synchrony of events) and seasonality ( $r > 0.5$  indicates aggregation); and (iii) Rayleigh test ( $z$ ), which determines the significance of seasonality. In the rejection of the null hypothesis, it is assumed that the data are not evenly distributed throughout the year, and the vector ( $r$ ) is calculated and used as a measure of the magnitude of the effect of seasonality on phenology. Thus,  $r$  ranges from 0 (phenological activity is evenly distributed throughout the year) to 1 (phenological activity is concentrated in a certain period of the year) (Nogueira et al., 2013). Spearman's correlation was used to analyze the correlation between average monthly temperature and precipitation in relation to the number of individuals with flowers and fruits. The analyses were performed

using *R* software (R Core Team, 2022) and the “circular” package (Lund et al., 2022).

### Seed desiccation tolerance

The experiment was conducted at the Laboratory of Ecology and Forest Restoration of the Federal University of Recôncavo da Bahia (UFRB), Cruz das Almas campus. During the phenological study, fruits of eight individuals of *G. hirsuta* were collected on August 27, 2021, within the forest fragment of the Lago da Pedra do Cavalo EPA.

Immediately after collection, the seeds were extracted from the fruits to perform the tests to define the degree of tolerance to desiccation. Moisture content was determined by the oven method at  $105 \pm 3$  °C for 24 hours (Brasil, 2009). Additionally, a germination test was performed to characterize the germination potential of the freshly collected seeds.

Desiccation tolerance was evaluated according to the methodology proposed by Hong & Ellis (1996). Four treatments, corresponding to moisture contents of 15%, 12.5%, 10% and 5%, were tested, with four replicates of 25 seeds each. The seeds were dried with blue gel silica (1-3 mm) inside 700 cm<sup>3</sup> polystyrene boxes, sealed with PVC film, and placed in Biochemical Oxygen Demand (B.O.D.) chamber at a temperature of 20 °C. From the moisture content (%) and initial mass (g) of the seeds, the final mass (g) was estimated for each sample, corresponding to the moisture content of the proposed treatments. Each polystyrene box contained one replicate with 25 seeds for the germination test, plus an additional 4 g of seeds for final moisture measurement. To monitor the drying process, seeds were weighed every three hours during the first 24 hours and daily after this period. Upon reaching the determined moisture contents (15%, 12.5%, 10% and 5%), the seeds were subjected to the germination test. The time to reach 15% moisture was approximately 18 hours, with ~24 hours to reach 12.5%, ~48 hours to reach 10% and ~262 hours to reach 5%.

For the germination tests, the seeds were arranged in paper rolls moistened with distilled water at a ratio of 2.5 times the dry paper weight (g) (Brasil, 2009). The rolls were placed inside transparent plastic bags to minimize evaporation and placed in a B.O.D.-type germination chamber at a constant temperature of 25 °C, with a 12-hour photoperiod.

Daily counts were performed to evaluate the number of germinated, hard and dead seeds and normal seedlings. Germination was defined by radicle protrusion (Bewley et al., 2013). Seeds that

failed to germinate but maintained visual integrity were classified as hard, whereas those with a deteriorated appearance were considered dead. Normal seedlings were identified by the presence of all well-developed essential structures. At the conclusion of the experiment, the viability of hard seeds was evaluated by the 0.5% tetrazolium test. The time of exposure of the seeds to the 0.5% tetrazolium solution was 24 hours, at a temperature of 30 °C (Silva et al., 2016). The duration of the germination experiment was determined by germination stabilization, defined as 10 consecutive days without radicle protrusion.

The effect of different moisture contents on the formation of normal seedlings and on germinated, dead, and hard seeds was evaluated using generalized linear models with a binomial distribution and a logit link function. Inferences from the analysis of deviance were based on the Chi-square test.

The proportion of dead seeds (%DS) determined through regression analysis, according to the following expression:  $\%DS = (\exp(4.76374 + (-0.117025*x))/1 + \exp(4.76374 + (-0.117025*x))) * 100$ ,  $R^2 = 0.96$ ;  $\exp$  = base of the natural logarithm;  $R^2$  = coefficient of determination.

Germination and normal seedlings formation curves were constructed to characterize the germination of newly collected seeds of *G. hirsuta*. To fit these curves, Logistic and Gompertz models were tested (Sousa et al., 2014) (Table 1), employing the least squares method and Gauss-Newton iterative procedures, using the nls function in R software (R Core Team, 2022).

**Table 1.** Nonlinear regression models describing germination curves over time.

Models	Functions
Logistic (Sousa et al., 2014)	$Y = a / (1 + \exp(-b(x - c)))$
Gompertz (Sousa et al., 2014)	$Y = a * \exp(-\exp(-b * (x - c)))$

Model assumptions were tested using the Shapiro-Wilk test for residual normality and the Breusch-Pagan test for homoscedasticity, using the bptest function of the lmtest package (Hothorn et al., 2022). Residual autocorrelation was assessed with the Durbin-Watson test, using the durbinWatsonTest function from the car package (Fox et al., 2023). When assumptions were not met, the generalized least squares method was applied, incorporating the first-order autocorrelation parameter (AR1) into the residuals, using the gnls function of the nlme package (Pinheiro et al., 2023) in R software (R Core Team, 2022). AIC and BIC criteria were used to evaluate model selection; lower values indicated a better fit.

In the Logistic and Gompertz models,  $a$  = maximum accumulated germination;  $b$  = growth relative to the inflection point;  $Y$  = germination accumulated over time;  $\exp$  = base of the Natural logarithm; and  $x$  = independent variable (time required for germination). For the Logistic model,  $c$  = time required to reach 50% germination and for the Gompertz model,  $c$  = time to reach 37% germination.

## Results

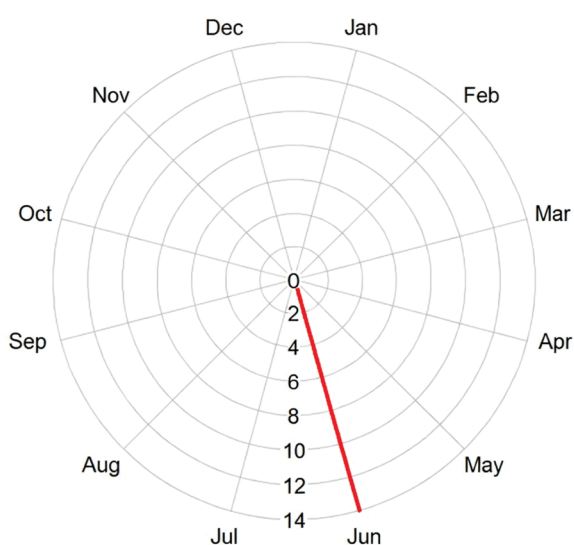
### Reproductive phenology

Of the 17 individuals observed, 14 (82.3%) produced flowers and fruits. Flowering and fruiting in *Guapira hirsuta* were seasonal. Circular statistics were used to calculate the mean angle, indicating the peak date of occurrence for the phenological events. The vector length ( $r$ ) for both phenophases was close to 1, that phenological activity was concentrated in a single period of the year. The Rayleigh test ( $Z$ ) confirmed the seasonality of both flowering and fruiting phenophases (Table 2).

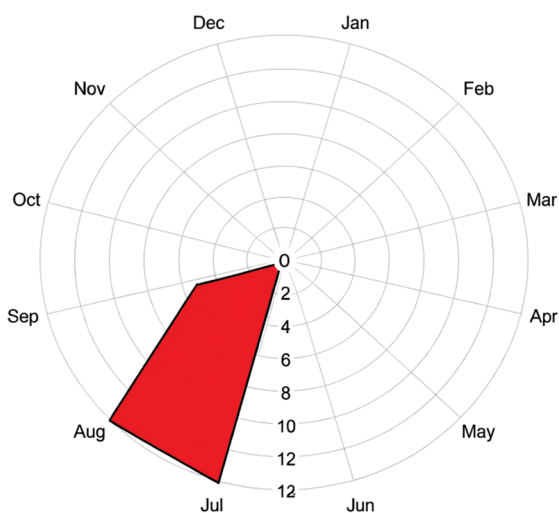
Mean flowering and fruiting dates occurred on June 1 (Figure 2) and July 22 (Figure 3), respectively. The beginning of fruiting occurred in July, with nine individuals retaining fruits until August and five extending until September. Fruit dispersal took place between August and September.

**Table 2.** Circular statistics of reproductive phenological events of *Guapira hirsuta* in the Lago da Pedra do Cavalo Environmental Protection Area, São Gonçalo dos Campos, State of Bahia, Brazil.

Phenophase	Mean angle ( $\mu$ )	Circular standard deviation	Mean day	Mean vector length ( $r$ )	Rayleigh Test ( $\rho$ )
Flowering	150.9	0	Jun 1	0.99	<0.001
Fruiting	201.6	0.3727602	Jul 22	0.96	<0.001



**Figure 2.** Circular histogram showing the relative frequency of the flowering phenophase of *Guapira hirsuta*, from October 2021 to September 2022.



**Figure 3.** Circular histogram showing the relative frequency of the fruiting phenophase of *Guapira hirsuta*, from October 2021 to September 2022.

The peak of the flowering phenophase occurred in June (Figure 2), while the highest fruiting intensity was observed between July and August (Figure 3). These results suggest that average monthly temperatures above 22 °C (Figure 1) may not favor fruiting. However, long-term annual monitoring of the species' phenological events is required to more clearly establish the relationship between temperature and fruiting.

#### Seed desiccation tolerance

The moisture content of the newly collected seeds was 52.4%, CI95%(μ): [51.2;53.6%]. The moisture content of seeds subjected to the drying procedures is presented in Table 3.

**Table 3.** Confidence interval ( $\alpha=0.05$ ) for the moisture content of seeds subjected to germination tests.

Target moisture content (%)	Observed moisture content (%)
15	14.7 ± 1.3
12.5	12.1 ± 0.7
10	10.0 ± 0.8
5	4.3 ± 0.8

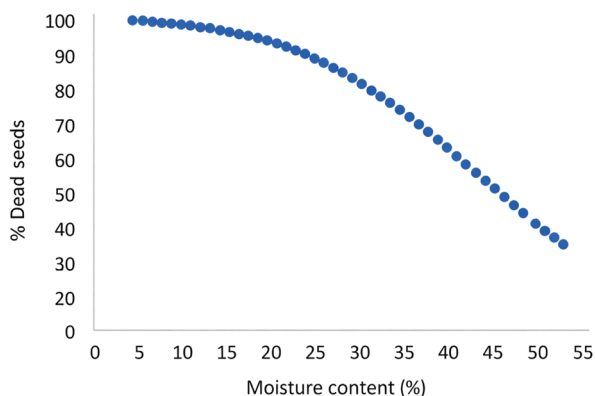
*G. hirsuta* germination was zero for seeds with moisture contents of 12.5%, 10% and 5%. When the seeds were dried up to 15% moisture content, the germination proportion was substantially lower than in those not subjected to drying. The chance of a newly collected seed, with moisture content around 52%, germinating was equal to 68% ( $M_{52\%} = \exp(0.7538) / (1 + \exp(0.7538))$ ), whereas for seeds dried to 15%, this probability dropped to 5.5% ( $M_{15\%} = \exp(-2.8445) / (1 + \exp(-2.8445))$ ). Similar estimates were obtained for normal seedlings formation (Table 4).

In the observed data, which gave rise to these estimates, at 52% moisture, germination and normal seedling formation ranged from 16 to 72%. At 15% moisture, germination ranged from 0 to 24% and normal seedling formation ranged from 0 to 16%.

**Table 4.** Estimated coefficients of the generalized linear models for germination and normal seedlings formation of *Guapira hirsuta* in response to seed moisture content.

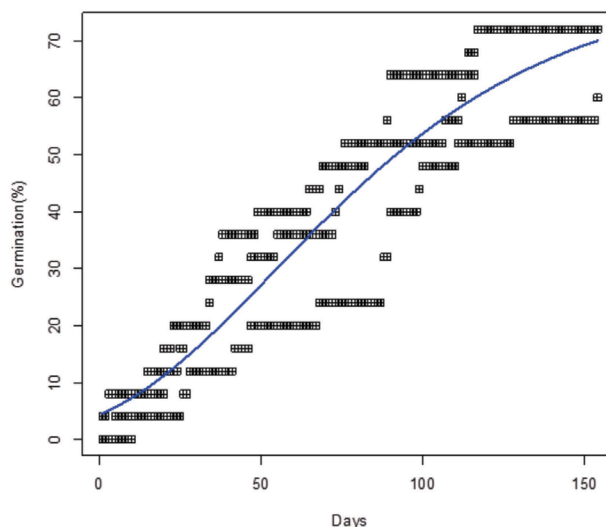
	Germination			Normal seedlings		
	Coefficients	p	p-value	Coefficients	p	p-value
Moisture 52%	0.7538	0.68	2.33E-03	0.6931	0.67	4.66E-03
Moisture 15%	-2.8445	0.055	1.97E-12	-2.8904	0.052	2.80E-12

The proportion of dead seeds was significantly influenced by moisture content. Most of the seeds that did not germinate were dead (Figure 4).



**Figure 4.** Proportion of dead seeds of *Guapira hirsuta* (%DS) in response to seed moisture content (x).

Based on Akaike (AIC) and Schwarz's Bayesian Information Criteria (BIC), the most appropriate model to describe the germination curves (Figure 5) and normal seedlings formation was the Gompertz model, incorporating a first-order autocorrelation parameter (AR1) (Table 5).



**Figure 5.** Germination curve of *Guapira hirsuta* seeds: black squares represent the observed values, and blue curve represents the estimated values.

Seed germination was slow and uneven. According to parameter "c" of the Gompertz model, 54 days were required to achieve 37% germination, while 63 days were needed for 37% normal seedling formation (Table 5).

**Table 5.** Parameters and evaluation criteria for the models used to fit germination and normal seedling formation curves of *Guapira hirsuta*.

	Models	a	b	c	%S	AIC	BIC	R <sup>2</sup>
<b>Germination</b>	Logistic	72.45	0.0338	67.31	21.35	3301.91	3318.45	0.859
	Logistic (AR1)	72.48	0.0338	67.34	21.34	3244.29	3264.97	0.858
	Gompertz	80.32	0.0198	54.12	21.12	3291.85	3308.39	0.862
	Gompertz (AR1)	80.37	0.0198	54.18	21.11	3222.72	3243.40	0.861
<b>Normal</b>	Logistic	71.13	0.0342	75.06	21.76	3114.20	3130.55	0.864
	Logistic (AR1)	71.15	0.0342	75.09	21.75	3073.88	3094.32	0.862
	Gompertz	79.76	0.0198	62.72	21.32	3096.20	3112.55	0.869
	Gompertz (AR1)	79.80	0.0198	62.77	21.31	3038.15	3058.60	0.868

Where: a = maximum accumulated germination; b = growth relative to the inflection point; c = time required to reach 50% of the germination (for the Logistic model), and c = time to reach 37% of the germination (for the Gompertz model); %S = standard deviation; AIC = Akaike criteria; BIC = Schwarz's Bayesian criteria; R<sup>2</sup> = coefficient of determination.

## Discussion

According to the reproductive phenology of *Guapira hirsuta*, fruiting peaked in July, with seed dispersal occurring in August and September (Figure 3). Lacerda et al. (2018), in a study of species from a savannah in northeastern Brazil, found that peak fruiting occurred during the transition from the rainy to the dry season. The authors state that this pattern ensures

water supply for fruit development while dispersal is facilitated by the subsequent dry period. During this time, reduced leaf cover increases fruit visibility for animal dispersers. This pattern of leaf senescence associated with the dry season is common in Brazilian dry forests (Amorim et al., 2009).

According to Hong & Ellis (1996), when most seeds desiccated up to 10-12% moisture content lose viability, they are classified as recalcitrant. For seeds

with moisture content around 12%, germination was zero and the proportion of dead seeds was 100% (Figure 4). Therefore, *G. hirsuta* seeds are recalcitrant. Such seeds are metabolically active when dispersed and rapidly lose viability as they dehydrate (Salvador et al., 2022; Oyerinde et al., 2023). The duration seed dehydration in the natural environment depends on the climatic conditions of the dispersal season, as well soil moisture and soil-holding capacity.

In the study region, *G. hirsuta* seed dispersal occurs in August, at the onset of the dry season (Figure 1). Santos et al. (2018), in study of the climate in Feira de Santana (approximately 30 km from the study site), reported that the lowest water deficit occurs between May and July. However, based on a 22-year historical series, no water surplus occurs in the region at any time. Consequently, given their recalcitrance, these seeds do not tolerate prolonged dehydration. Therefore, the establishment of *G. hirsuta* individuals is more likely if seeds reach sites near water bodies where soil moisture is better maintained.

*G. hirsuta* is among the prominent species in the structural analysis of the Atlantic Forest remnants in Serra da Capoeira, RJ (Peixoto et al., 2005) and Ubatuba, SP (Souza et al., 2018). These remnants are located in areas with no periods of water deficit. In the study by Menino et al. (2015), *G. hirsuta* was classified as a riparian forest indicator species. Although *G. hirsuta* has a wide geographic distribution (Rossetto et al., 2023), it occurs at higher densities in regions with greater water availability, which is consistent with the recalcitrant nature of its seeds.

At least 35 days were required for the newly collected seeds to begin germination, with stabilization at 150 days. Thus, germination was slow and uneven. Based on the Gompertz model,  $Y = 80.37 * \exp(-\exp(-0.0198 * (x - 57.18)))$  (Figure 5 and Table 5), approximately 92 days are required to reach 50% germination. According to Santos et al. (2020), under natural conditions, precipitation pulses trigger plant growth and development. For *G. hirsuta*, which exhibits slow and asynchronous germination, isolated precipitation peaks may promote the germination process, depending on the capacity of the seeds to germinate under low water availability. Therefore, to more conclusively elucidate the species' initial establishment strategies, further studies on the effects of water stress on germination and post-seminal development are necessary.

When studying the dynamics of recalcitrant seeds of *Mauritia flexuosa* L. f. in the seed bank, Salvador et al. (2022) classified them as persistent, as they remain

viable for periods longer than one year. According to these authors, despite their recalcitrance, *M. flexuosa* seeds form a persistent seed bank in humid environments due to their homeostatic capacity, which involves oxidative stress control and water retention. Thus, mechanisms similar to those elucidated for *M. flexuosa* are likely involved in maintaining the viability of *G. hirsuta* seeds during the 150-day germination test. Therefore, depending on soil water availability, recalcitrant seeds may maintain viability for extended periods. To better understand seed bank dynamics and the ideal storage conditions for *G. hirsuta*, it is necessary to define the substrate osmotic potential capable of maintaining seed homeostatic capacity, as well as their responses to rehydration after different levels of desiccation.

## Conclusions

*Guapira hirsuta* germination is slow and asynchronous, and its seeds are recalcitrant. Despite this, the species thrives in environments where dispersal occurs during periods of reduced rainfall. Such ecological paradoxes drive scientific inquiry toward answers that are essential for wildlife conservation. Although knowledge regarding the germination and initial establishment of *G. hirsuta* has not yet been fully elucidated, although the provides study presents information on this species that was previously unknown.

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## Conflicts of Interest

The authors declare no conflict of interest.

## Authors' Contributions

**Karine Pacheco de Jesus:** investigation, writing - original draft. **Manuela Oliveira de Souza:** investigation; conceptualization, methodology, writing - review & editing. **Dráuzio Correia Gama:** writing - review & editing. **Tamires**

**Santiago de Souza**: investigation. **Grênivel Mota da Costa**: writing - review & editing. **Andrea Vita Reis Mendonça**: conceptualization, formal analysis, methodology.

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