

Original Article

## Direct seeding as a recruitment alternative for the threatened tropical palm *Syagrus coronata* (Mart.) Beccari in Brazilian dry forest

Semeadura direta como alternativa de recrutamento para a palmeira tropical ameaçada *Syagrus coronata* (Mart.) Beccari em floresta seca brasileira

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### Abstract

Habitat loss reduces biodiversity and threatens ecological services. The use of techniques for vegetation restoration such as direct seeding seems promising, mainly because it reduces costs and labor. The aim of this study was to investigate which are the main ecological filters that can inhibit the success of direct seeding, using *Syagrus coronata* (Mart.) Beccari (Arecaceae), a species that has great ecological and extractive importance for the Brazilian semi-arid region, and is found in habitats with different management intensities. The following hypotheses were tested: (1) managed habitat (pasture) and natural habitat (caatinga vegetation) show differences in seed fate; and (2) defleshed fruits will have greater seed germination success compared to not defleshed. Seed fate was evaluated for two consecutive years, year I (2016–2017) and year II (2017–2018). Within these years, 800 mature fruits were buried along 300 m transects, half with defleshing treatment, and monitored during 240 days. The highest seed survival occurred in year II, this result may be associated with higher rainfall recorded during the experiment, considering that there was no difference in seed germination between habitats. Defleshing facilitated germination and reduced insect predation, likely by removing invertebrate larvae before they have reached the seed. Desiccation was the major cause of mortality in the entire study and was higher in the managed habitat. Water insufficiency may have caused the deactivation of antioxidant mechanisms and affected the embryo. Although defleshing may favor germination, this procedure would not be indicated for pastures as it favors desiccation. The study showed how habitat management and fruit defleshing can affect seed fate. More studies on ecological relationships need to be carried out to increase understanding of how habitat modification affects the functioning of arid ecosystems.

**Keywords:** Arecaceae, Caatinga, ecological filters, germination, habitat management.

### Resumo

A perda de habitat diminui a biodiversidade e ameaça os serviços ecológicos. A utilização de técnicas para recomposição da vegetação como a semeadura direta parece promissora, principalmente por diminuir gastos e mão de obra. O objetivo do estudo foi investigar quais são os principais filtros ecológicos que podem inibir o sucesso da semeadura direta, utilizando a espécie *Syagrus coronata* (Mart.) Beccari em habitat manejado e natural na Caatinga. Foram testadas as hipóteses: (1) habitat manejado (pastagem) e habitat natural (vegetação de caatinga) apresentam diferenças no destino de sementes; e (2) frutos despulpados terão maior sucesso germinativo comparado aos frutos com polpa. O destino das sementes foi avaliado por dois anos consecutivos, ano I (2016–2017) e ano II (2017–2018), no qual 800 frutos maduros foram enterrados ao longo de transectos de 300 m, metade com tratamento de despulpamento, e monitorados ao longo de 240 dias. A maior sobrevivência de sementes ocorreu no ano II, este resultado pode estar associado a maior pluviosidade registrada durante o experimento, considerando que não houve diferenças entre os habitats. A remoção da polpa facilitou a germinação e reduziu a predação, possivelmente, pela remoção de larvas de invertebrados, antes que elas alcançassem o endocarpo. A dessecação foi a maior causa de mortalidade em todo o estudo e foi maior no habitat manejado, a escassez hídrica pode ter causado a desativação de mecanismos antioxidantes e afetado o embrião. Embora a remoção de polpa possa favorecer a germinação, esse procedimento não seria indicado para pastagens por favorecer a dessecação. O estudo mostrou como as interações planta-animal podem agir diante da funcionalidade do habitat e tratamento do fruto. Mais estudos sobre as relações ecológicas precisam ser realizados para aumentar a compreensão de como a modificação do habitat afeta o funcionamento de ecossistemas de Caatinga.

**Palavras-chave:** Arecaceae, Caatinga, filtros ecológicos, germinação, habitat manejado.

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## 1. Introduction

Tropical ecosystems have undergone intense deforestation due to human activities (Silva and Barbosa, 2017; Espírito-Santo et al., 2020; Souza and Reis, 2020). Changes in land cover and use lead to a decrease in biodiversity, compromising ecological regulatory services such as pollination, seed dispersal and biological control (Silva et al., 2020). Environments with little forest cover, such as pastures, are characterized by a lack of vegetative propagules (Guarino and Scariot, 2014; Souza-Silva et al., 2015), high predation of seeds and seedlings by livestock (Hordijk et al., 2019), and high soil degradation (Souza and Reis, 2020). Additionally, competition with exotic grasses act as inhibitors of natural regeneration, restricting the restoration of native plants (Souza-Silva et al., 2015; Pereira et al., 2021).

Ecological restoration emerges as an important alternative to mitigate part of the negative impacts resulting from human actions (Espírito-Santo et al., 2020; Raupp et al., 2020). The Brazilian Caatinga is the largest remnant of tropical dry forest in South America, which has more than 60% of its area occupied by anthropogenic ecosystems and demand urgent ecological restoration actions (Silva and Barbosa, 2017; Silva et al., 2017). The loss of area in this ecosystem is mostly due to the removal of vegetation for the croplands (Souza and Reis, 2020), opening of pastures for livestock (Raupp et al., 2020), hunting and logging, causing intensive and extensive disturbances (Silva et al., 2017). This entire process leaves a legacy that in some cases can delay the natural regeneration of the ecosystem (Palma and Laurance, 2015; Espírito-Santo et al., 2020). There are different restoration techniques whose efficiency varies depending on the potential of the landscape site (Raupp et al., 2020). In order to scale up restoration efforts, it is important to develop inexpensive and effective methods (Holl et al., 2017; Raupp et al., 2020; Aniceto et al., 2021).

Direct seeding, in which seeds of native species are planted directly in habitats intended for restoration (Aniceto et al., 2021), is a strategy that has been recommended because it has a lower cost of implantation (Holl et al., 2017; Aniceto et al., 2021), which is 30 times lower than planting seedlings (Palma and Laurance, 2015; Freitas et al., 2019; Raupp et al., 2020). In addition, it is noteworthy for its practicality and speed, especially when the objective is to restore large areas (Oliveira et al., 2019). For direct seeding, species from different successional stages are used at high densities, facilitating the establishment of late succession plant groups (Oliveira et al., 2019). To optimize the success of the technique, it is recommended to bury the seeds in order to protect against possible predators and reduce desiccation by high temperatures on the soil surface (Oliveira et al., 2019; Freitas et al., 2019). However, some bottlenecks limit the effectiveness of this method (Holl et al., 2017; Raupp et al., 2020), such as the low germination rates of many seeds in the field (Freitas et al., 2019) and the impossibility of storing recalcitrant seeds (Rodrigues et al., 2019).

In this context, the present study aimed to investigate which are the main ecological filters that can inhibit

the success of direct seeding, using the species *Syagrus coronata* (Mart.) Beccari, known as licuri (Drumond, 2007). This species is a late successional colonizer and has greater growth when subjected to reduced levels of luminosity (Carvalho et al., 2006; Porto et al., 2018). Its seeds are considered recalcitrant, are highly sensitive to desiccation (Rodrigues, 2004), in which the burying is recommended (Pereira et al., 2021). Studies with species of the same genus achieved satisfactory results for field germination (Oliveira et al., 2019). Another positive factor is the nucleating potential of licuri, which due to its anatomical characteristics allows the fixation of native species, facilitating colonization and diversity in degraded areas (Leal et al., 2014).

Licuri has a high socioeconomic value for the Brazilian semi-arid region. It is an important Non-Timber Forest Product (Lima et al., 2020). It plays a vital role in the income of traditional populations and small farmers (Campos et al., 2019; Silva et al., 2020; Pereira et al., 2021). It is commonly used for the provision of fodder, food, fibers, oils and medicinal products (Campos et al., 2019). Due to its importance, its cutting was prohibited by federal law because it is listed in the Vulnerable to Extinction Category (IBAMA, 2008). It bears fruit throughout all months of the year (Barbosa et al., 2021; Noblick et al., 2020) and the fruit can be consumed by frugivorous animals both pre- and post-dispersal (Drumond, 2007). The Lear's Macaw, *Anodorhynchus leari* (Bonaparte 1856) (family Psittacidae), an endangered bird of the Caatinga, is the main primary consumer of licuri fruits (Martins et al., 2015). After dispersal, secondary consumers are rodents, especially Dasyproctidae (such as *Dasyprocta* and *Myoprocta*) and Equimiyidae (*Proechimys*) (Guimarães et al., 2005; Jansen et al., 2010; Aroucha and Aroucha, 2013; Fedriani and Delibes, 2013). Seed predation by the insect *Pachymerus nucleorum* (Fabricius) Bruchinae is quite common (Andrade et al., 2013; Benton, 2015; Silva et al., 2020; Melo et al., 2021). During the consumption of licuri fruits by rodents, it is common to manipulate the fruit, removing the exocarp and mesocarp, which is followed by burying of the seeds (Aroucha and Aroucha, 2013). Three hypotheses have been raised about this behavior (Guimarães et al., 2005; Jansen et al., 2010), in which defleshing allows: (1) the removal of predatory beetle larvae, before they reach the seed; (2) the decrease in post-dispersal predation by other mammals, since the odor released by the pulp increases detection by rodents; and (3) reduction of microbial infection and prolonged life of the stored seed. All these mechanisms point to a mutual benefit for the host plant and "dispersers-buriers".

In this study, the following hypotheses were tested: (1) managed habitat (pastureland) has higher seed mortality than natural habitat (caatinga vegetation); and (2) defleshed fruits will have greater germination success compared to not defleshed. The prediction that prolonged fruit exposure in deforested habitats can make seeds more sensitive to desiccation was tested (Souza-Silva et al., 2015; Porto et al., 2018), reducing germination rates (Caixeta, 2018). Furthermore, habitat disturbance will lead to low rates of seed removal by vertebrates, considering that pastures are often related to defaunation processes (Fedriani and

Delibes, 2013). Defleshed fruits will have greater survival due to the lower odor that makes it difficult for vertebrates to find them (Jansen et al., 2010), and consequently greater germination (Porto et al., 2018). The results of this study can allow the understanding of appropriate management strategies for the recruitment of licuri, which can be used in future restoration projects in arid regions.

## 2. Materials and Methods

### 2.1. Study area

This study was carried out at the Jiboia Settlement (1,045.44 ha), in the rural area of the municipality of Senhor do Bonfim, Center-North of the State of Bahia (10°32'54.7" S- 40°11'12.9" W) (IBGE, 2017). The original vegetation of this area is the tropical dry forest, mainly characterized by the presence of xerophytes and semi deciduous trees (Silva and Barbosa, 2017; Souza and Reis, 2020). The total annual precipitation varies from 750 to 800 mm, the dry season occurs between July and October with an average precipitation of 205 mm and an average precipitation of 392 mm in the summer rainy season, which occurs from December to April. The annual temperature varies between 25° and 29°C (Souza and Reis, 2020; Pereira et al., 2021).

The land structure of the settlement has a Legal Reserve area of 20% (209.09ha) with water availability from rivers, streams, lakes and water courses (Alves et al., 2014; Souza and Reis, 2020). The legal reserve consists of fragments of secondary vegetation, consisting of hypoxerophilous vegetation and tall trees, which reach up to 15 meters in height. It has not been selectively logged for 12 years, and it has been undergoing regeneration process for over 60 years (Pereira et al., 2021). Despite having maintained plant cover, it is possible to verify the free movement of cattle. The area also has managed habitats that have been deforested for the implementation of castor bean (*Ricinus communis*), beans (*Phaseolus vulgaris*), cassava (*Manihot esculenta*), corn (*Zea mays*) and cattle in pasture fields (Souza and Reis, 2020). Both systems, pastures and croplands, were implemented and abandoned at different times. In this study, the managed habitat used as pasture was selected.

*Syagrus coronata* is one of the few plant species maintained after deforestation and establishment of pastures in the study region. The presence of the species in human-managed habitats is justified by the protection by a Federal Law (IBAMA, 2008), which prohibits the cutting of the palm tree because it has great importance and extractive use in the region (Carvalho et al., 2016). Individuals of licuri in different ontogenetic stages are commonly found in the natural habitat (Pereira et al., 2021). The managed habitat is characterized by intense fruit harvesting and livestock raising (Souza and Reis, 2020), while the natural habitat is restricted to fruit harvesting, however, less frequently. The aforementioned areas of pasture and dry forest vegetation will be mentioned throughout the manuscript as managed habitat and natural habitat, respectively.

### 2.2. Studied species

The licuri is a monoecious, arborescent palm tree, reaching up to 12 m in height (Noblick, 2017). The palm tree is well adapted to semi-arid climate conditions, distributed in the regions of Caatinga and the Northern Atlantic Forest (Lima et al., 2020) with greater concentration in the municipalities of the state of Bahia (Carvalho et al., 2016). It has drupe-like fruits, with a light yellow to orange exocarp when ripe (Noblick, 2017; Moura et al., 2019) and fibrous-mucilaginous mesocarp with a sweet and edible flavor and lignified endocarp, which covers the white-yellowish endosperm with oleaginous properties (Moura et al., 2019). Seeds maintain viability for up to 180 days when stored in permeable bags and conditions of temperature (25° C) and relative humidity of 53-72% (Porto et al., 2018). The collection of its leaves, fruits and seeds is an important source of income and livelihood for rural communities and indigenous peoples in the semi-arid regions of northeastern Brazil (Campos et al., 2019). They are used for various purposes, for consumption by humans as well as domestic and wild animals, and are highly important for construction, handicrafts, fuel and medicinal use (Campos et al., 2019).

### 2.3. Sample design

In November 2016, at the beginning of the rainy season in the study region, two adult reproductive licuri individuals, with mature and recently fallen fruits, were arbitrarily selected in order to reduce the genetic variability. The fruits were collected and taken to the laboratory, and inspected for signs of pathogens and predation, and then stored at room temperature for five days (Figure S1). Among the fruits collected, 800 were selected, half of which were defleshed with the removal of the exocarp and mesocarp, simulating defleshes by rodents (Jansen et al., 2010).

The selected seeds were taken to the field and distributed among four fragments, two natural habitats and two managed habitats. In each fragment, 200 seeds were buried, 100 defleshed and 100 not defleshed, along two transects of 300 meters. Ten holes were dug (3 to 5 cm deep), similar to those made by rodents (Galetti et al., 2006; Pereira et al., 2021) and spaced 30 meters apart. At each excavated point, 10 seeds were buried. The space between the holes was far enough to guarantee sample independence (Jansen et al., 2010; Pereira et al., 2021). The location of the holes was marked with signal tape and numbered at chest level (1.30 m high). The seeds had their fate monitored after 10, 20, 40, 80, 160 and 240 days.

In subsequent years, 2017-2018, this entire procedure was repeated. The sampling that took place between 2016-2017 was called year I. The sampling that took place between 2017-2018 was called year II. The duration of the experiments was based on studies that indicated the germination of this species, with a variation between 15 days (Moura et al., 2019), 72 days (Caixeta, 2018; Porto et al., 2018), and 211 to 284 days (Aroucha and Aroucha, 2013). Total precipitation during the study months in year I was 299.9 mm and 459.34 mm during the months of year II (Pereira et al., 2021).

All seeds were classified into the following categories: (1) removal by vertebrates, when the seed was at least partially consumed, evidenced by vertebrate bite marks, or removed; (2) predation by insects, evidenced by the emergence hole of adult insects and the completely hollow seed; (3) germinated/surviving, when radicle emission was characterized; (4) desiccated, seeds that did not germinate at the end of the experiment and showed changes in color, texture and loss of viability were categorized as desiccated (Galetti et al., 2006; Jansen et al., 2010); and (5) attacked by pathogen (fungi). Because fungal attack is not readily visible on external field examination, this category was determined at the end of the study each year. The seeds that after the last measurement (240 days) did not have their outcome defined in the field were taken to the laboratory and broken in order to verify the mortality factor, and thus the category they fit (Figure S2).

#### 2.4. Statistical analysis

At the end of each year, the proportions of seeds in each category were calculated. The effects of habitat and defleshing treatments (explanatory variables) on seed fate (response variable) were determined using generalized linear mixed effects models (GLMMs). In these models, the seed burial points were considered replicates ( $n = 62$  points for year I and  $n = 73$  points for year II) and the nested structure (fragment/transsect) was used as a random effect. Each model was adjusted for binomial error distribution and compared to the null model, followed by residual inspection to test the model's suitability (Zuur et al., 2009). These models were performed using the "lmer" function of the "lme4" package (Bates et al., 2015) of the R<sub>3.6.0</sub> software (R Development Core Team, 2016).

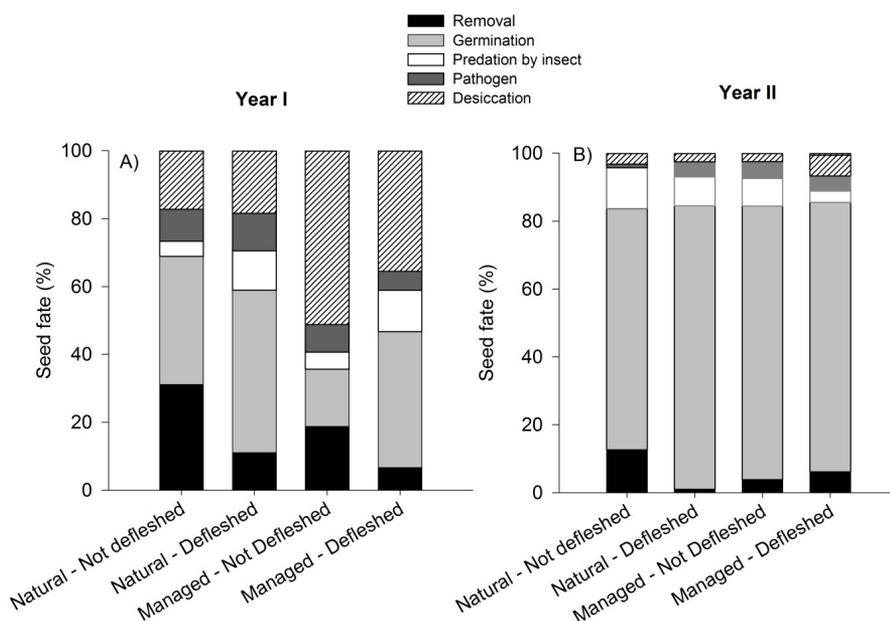
### 3. Results

Germination (60%) was the most likely fate of most seeds during the two years studied, regardless of habitat and defleshing treatments. When compared between habitats, 61% of the seeds germinated in the natural habitat, while 56% germinated in the managed habitat, we recorded absence of significant difference ( $F = 0.467$ ;  $P > 0.05$ ). On the other hand, defleshed treatment had higher germination (66%) than not defleshed (52%;  $F = 7.06$ ;  $P < 0.01$ ; see Figure 1). A higher percentage of germination was recorded in year II (77%) than in year I (51%;  $F = 22.39$ ;  $P < 0.0001$ ; Figure 1).

Desiccation was the major cause of mortality in the entire study (15%). The managed habitat had greater desiccation (22%) compared to the natural habitat (10%;  $F = 7.89$ ;  $P < 0.01$ ). The desiccated category constituted 20% of the seed fate experienced in year I and only 3% in year II ( $F = 18.47$ ;  $P < 0.0001$ ; Figure 1).

For comparisons within each year of the experiment, seed germination differed between habitats only in year I (Table 1), where the highest germination rates occurred in the natural habitat (38%). Defleshing increased seed germination for year I (Table 1), this effect was more pronounced for the natural (47%) compared to the managed habitat (40%) (Table 1; Figure 2A-2B).

Desiccation differed between habitats only in year I (Table 1), being higher in the managed habitat (Figure 2C-2D). The defleshing treatment did not affect desiccation in both years (Table 1), however, within the managed habitat, desiccation was higher on defleshed fruits in both years (Figure 2C-2D). These fruits had obvious evidence of dehydration, such as discoloration of the integument and dry tissues.



**Figure 1.** Effects of habitat and defleshing treatments on the seed fate of *Syagrus coronata* after 240 days during two years of experiment.

**Table 1.** Mixed-effect generalized linear models to test the effects of habitat (natural vs managed) and defleshing (defleshed vs not defleshed) treatments on seed fate of *Syagrus coronata* (Year I with n=62; Year II with n=73). Statistically significant variables ( $p < 0.05$ ) are highlighted in bold.

Response variable	Explanatory variable	Year I		Year II	
		F	P	F	P
Germination	Habitat	13.805	<b>0.001</b>	0.222	0.640
	Defleshing	6.879	<b>0.012</b>	3.924	0.055
	Habitat x Defleshing	1.173	0.291	1.523	0.226
Desiccation	Habitat	19.832	<b>0.001</b>	1.072	0.308
	Defleshing	0.126	0.724	0.004	0.951
	Habitat x Defleshing	1.814	0.192	1.1734	0.287
Removal	Habitat	2.148	0.157	0.227	0.637
	Defleshing	3.461	0.071	3.830	0.057
	Habitat x Defleshing	0.562	0.461	4.201	<b>0.048</b>
Predation	Habitat	0.001	0.999	4.589	<b>0.040</b>
	Defleshing	5.050	<b>0.031</b>	3.098	0.086
	Habitat x Defleshing	0.0237	0.879	0.074	0.787
Pathogen	Habitat	0.536	0.472	0.900	0.350
	Defleshing	0.006	0.937	1.865	0.180
	Habitat x Defleshing	0.391	0.538	0.998	0.325

Mortality categories: removal by vertebrates, predation by insects and attack by pathogens reached 11%, 8% and 6%, respectively, during the study (Figure 1). The vertebrate removal and pathogen attack categories did not differ between habitats and defleshing treatments in both years (Table 1). However, not defleshed within the natural habitat had a higher percentage of removal (Figure 2E-2F). Finally, insect predation differed between defleshing treatment for year I (Table 1; Figure 2G), being higher in not defleshed (47%) compared to defleshed (12%). Predation differed between habitats in year II (Table 1; Figure 2H), being higher in the natural (11%) than in the managed habitat (5.5%).

#### 4. Discussion

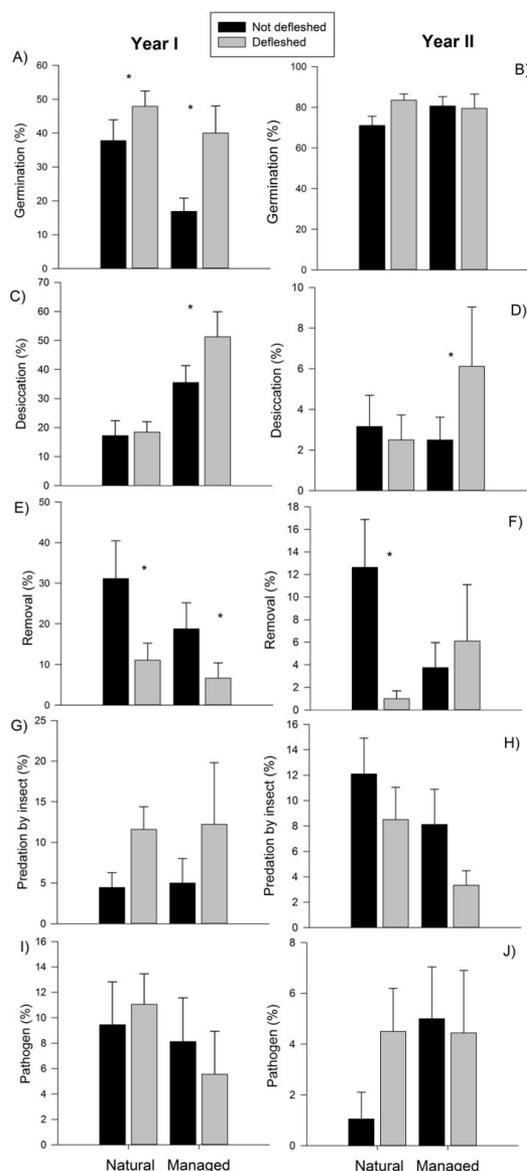
In general, the fate of *S. coronata* seeds differed between habitats. The highest mortality occurred in the managed habitat, mainly by desiccation (Figure 1A). It was evidenced that defleshing increased germination and reduced consumption by beetle *P. nucleorum* in year I, supporting our hypotheses.

The highest germination found in year II may be associated with rainfall (459.34 mm) recorded during the experiment (Pereira et al., 2021), during this year there was no difference in seed germination between habitats. In year I, marked by lower precipitation, germination was higher in the natural habitat. These results may be related to the milder microclimate, i.e. soil and air temperatures (Guarino and Scariot, 2014; Souza-Silva et al., 2015; Holl et al., 2017). Thus, possibly the shading acted to neutralize the lack of water during periods of low rainfall (Espírito-Santo et al., 2020). In fact, Lima et al. (2020) found that rainfall parameters may hinder the expansion of *S. coronata* in drier regions of the Caatinga.

Defleshing may have facilitated the penetration of water into the seed by the micropyle (Pivetta et al., 2005), in addition to eliminating germination-inhibiting substances present in the pulp (Almeida, 2018). Similar results were reported by Pivetta et al. (2005), who observed a positive effect of defleshing to *Syagrus schizophylla* (Mart.) Glassmann palm, which increased germination. Teixeira et al. (2011) confirm that the defleshing favored the preservation of the fruit, resulting in a greater germination power of the Australian Royal Palm *Archontophoenix alexandrae* H. Wendl. & Drude. However, Teixeira et al. (2011), point out that the effectiveness of manual defleshing, without additional treatment, can accelerate the loss of germination power and vigor of the seeds, being more advisable to use it immediately after harvesting the fruits.

Desiccation was the highest recorded mortality factor, it was high during year I (with lower precipitation) and higher in the managed habitat. The physiological conditions of licuri fruits are also a major challenge for the preservation and maintenance of the species (Rodrigues, 2004). Its fruits are considered recalcitrant and highly sensitive to desiccation (Rodrigues, 2004; Caixeta, 2018; Porto et al., 2018). The results of this study showed that the burying of seeds was not able to reduce desiccation in pastures. In addition, the defleshing treatment increased desiccation in the managed habitats (see Figure 2C-2D). The loss of moisture from fruits in water-scarce environments can possibly cause the deactivation of antioxidant mechanisms and the accumulation of toxic substances (Almeida, 2018), drastically affecting the embryo (Caixeta, 2018). Although licuri is a species adapted to regions with long periods of drought, defleshing has not been shown to be a viable technique for pasture environments.

Overall, seed removal did not differ between habitats. This category does not necessarily indicate mortality, as seeds may have been lost and may have survived



**Figure 2.** Mean values ( $\pm$  standard error) for seed fate of *Syagrus coronata* during two years of experiment. The charts in the left panel represent the results for year I, while the charts on the right represent the results for year II. Asterisks indicate statistically significant differences between defleshing treatment (defleshed vs not defleshing) within each habitat ( $p < 0.05$ ).

(Jansen et al., 2010; Pereira et al., 2021). It is suggested that rodent vertebrates may be absent or in low abundance in both habitats, with the natural habitat being characterized as an empty forest (Jansen et al., 2010). Only 11% of the fruits fell into the removed category. Licuri seeds were sensitive to desiccation (Rodrigues, 2004) making them less attractive to small rodents in both habitats (Jansen et al., 2010; Fedriani and Delibes, 2013).

Within each habitat, vertebrate removal was twice as high in not defleshed fruits for the two years of the study. This preference can be explained by the odor released

by the pulp increasing rodent detection (Galetti et al., 2006; Jansen et al., 2010; Silva et al., 2017). Licuri fruits can be primary energy sources for many rodent species (Pereira et al., 2021). In this case, especially the fruits not defleshed, showed an initial advantage in attracting rodents to the managed habitats, increasing visit frequency and consequently seed dispersal.

Predation by *P. nucleorum*, which is a great cause of seed mortality in palm populations (Grenha et al., 2008; Silva et al., 2020; Melo et al., 2021), was only 8% in this study. We recorded two-fold more predation in the natural habitat. The greater predation in the natural habitat can be sustained by the abundance of resources that favors the distinct feeding habits recorded for the different stages of *P. nucleorum* (Grenha et al., 2008; Benton, 2015; Barbosa et al., 2021). In the larval stage, *P. nucleorum* feeds exclusively on seeds, which represent a rich food that is well protected against environmental adversities (Rodrigues, 2004). In the adult stage, *P. nucleorum* feed on nectar and pollen (Benton, 2015) and act as pollinators (Barbosa et al., 2021), being more affected by the microclimatic fluctuations of the environment (Medeiros et al., 2019), mainly in pastures (Silva et al., 2020). In this way, natural habitats can support a greater variety of resources (e.g., pollen, nectar and fruits) for the different life stages of *P. nucleorum*. In addition, defleashes the fruit reduced predation by *P. nucleorum*, and therefore allowed the removal of predatory beetle larvae before they reached the seed. We emphasize that defleshing can be an efficient alternative for seed survival, especially in natural habitats, since it also increased germination.

The attack by pathogens corresponded to the lowest percentage of final seed fate. This category did not differ between habitat or defleshing treatments. Despite the low relevance of this category in this study, rainy years may favor prolonged exposure of seeds in the field and contribute to an increase in the incidence of fungi (Barnard et al., 2013). Further studies are important to understand how palm plantations will survive under environmental stress and climate change scenarios (Palma and Laurance, 2015; Noblick et al., 2020).

Thus, it is possible to highlight that interannual climatic variations can affect the fate of seeds. This is a reflection of the Caatinga's heterogeneity and how much the ecosystem dynamics is influenced by environmental conditions (Silva and Barbosa, 2017). Semi-arid regions such as the Caatinga are prone to desertification (Silva and Barbosa, 2017; Espírito-Santo et al., 2020), which can compromise seed survival, especially in managed habitats. However, the direct seeding technique proved to be viable and can be interesting for small farmers considering the low cost. In addition, the use of native species of economic value, such as licuri, with the potential to generate income, products and services, reconciling socioeconomic and environmental demands, is an incentive for farmers (Raupp et al., 2020).

### 5. Conclusion

Direct seeding with burial may be a recommended technique in order to favor the recruitment of individuals

of licuri in the Brazilian Caatinga, since 60% of the buried fruits germinated after 240 days. However, rainfall was an important bottleneck for seed germination, since in year II, with the highest rainfall, germination was similar in the two studied habitats. Fruit defleshing reduced vertebrate removal and *P. nucleorum* beetle attack, but increased desiccation, the major mortality factor in this study, especially in the managed habitat. In this way, the burying of defleshed seeds would be more suitable for areas covered by natural vegetation, while the burying of not defleshed would be indicated for pastures. Thus, studies evaluating seed fate in the field can help to elucidate the effects of habitat disturbance on the vital growth and survival rates of individuals and on the long-term persistence of populations.

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## Supplementary Material

Supplementary material accompanies this paper.

**Figure S1.** Treatment of the fruit in the laboratory, (A) mechanical removal of the pulp from the fruits of *Syagrus coronata*, (B) separation of the fruits with pulp in separate pots. The pots with not defleshed and defleshed fruits were stored for five days to verify the emergence of *Pachymerus nucleorum*.

**Figure S2.** *Syagrus coronata* seeds in different fate categories (A) *Pachymerus nucleorum* larva developing inside the seed, (B) Adult beetle emerging from the seed (C) Seeds classified as germinated due to radicular emission.

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