









## INFLUENCE OF SEED MASS IN BIOMASS ALLOCATION OF A PALM VULNERABLE OF EXTINCTION

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This paper is a tribute to our dear Eduardo Arcoverde de Mattos.

**Abstract:** Seedling vigor, defined here as total seedling biomass, is directly related to seedling performance in the face of environmental harshness. Additionally, differential portioning between shoot and root biomass can be a determinant of seedling survival under conditions of resource scarcity. We aimed to determine the biomass allocation pattern of *Euterpe edulis* seedlings and test the hypothesis that heavier seeds produce more vigorous seedlings. We followed a germination protocol that produced 50 seedlings, 32 of which were used to calculate the total seedling biomass investment, relative growth rate (RGR), specific leaf area (SLA), and root/shoot ratio (R/S). A linear regression showed that the root/shoot ratio (R/S) increased with increasing seed mass ( $p = 0.03$ ). This result may be a consequence of differing seed reserves accumulated by seeds of different masses. Seed mass was also directly related to seedling vigor ( $p = 0.03$ ). Despite the lack of relationship between seed mass and RGR ( $p = 0.553$ ), the positive relationship between seed mass and SLA ( $p = 0.03$ ) suggests that heavier seeds have a slow-growth strategy, whereas lighter seeds have a fast-growth strategy. As heavier seeds produce more vigorous seedlings, they should be preferred when planning restoration plantations since their seedlings have greater chances of survival under harsh conditions and may present more satisfactory performance. Additionally, since the population studied is already located at the upper thermal limit of the species, we suggest that future studies focus on how seedlings of different sizes perform at different temperatures.

**Keywords:** fast-slow growth; initial seedling growth; Restinga; seed mass.

## INTRODUCTION

The seed and seedling stages are the most sensitive periods of the entire plant life cycle (Lei, 2010). Initial seedling growth is highly dependent on seed reserves, which creates a tendency for heavier seeds

to produce more vigorous seedlings (Westoby *et al.*, 1996). Seedling vigor, defined here as seedling size, and measured as total biomass (Westoby *et al.*, 2002), is positively related to seedling resistance to environmental harshness and disturbance due to potential deep root growth, which leads to better

water and nutrient uptake and growth in height, conditions that favor the photosynthetic process (Westoby *et al.*, 1996).

Seed mass can also be a determinant of growth strategy, since lighter seeds must grow faster to compensate for low seed reserves (Paz & Martínez-Ramos, 2003). Because of the rapid consumption of seed reserves, seedlings developed from lighter seeds need greater investment in photosynthetic tissues (greater specific leaf area – SLA), whereas seedlings produced from heavier seeds can allocate more biomass to the roots, prioritizing storage, anchorage, and nutrient and water uptake (Poorter & Rose, 2005). After the depletion of seed reserves, seedlings are completely dependent on environmental resources and on their ability to absorb light, water and nutrients (Haig & Westoby 1991; Neuburger *et al.* 2010). In addition to the ecological implications, understanding the effect of seed mass on seedling performance is crucial for restoration efforts, as it aids in the selection of propagules and ensures more successful outcomes. Therefore, many studies have focused on understanding seedling performance under gradients of resource availability (Baraloto *et al.*, 2005; Reich *et al.*, 1998; Silvestre *et al.*, 2016), of which one of the main interests was the tradeoff in the allocation of biomass between shoots and roots (Robinson, 2022).

The optimal partitioning theory states that biomass partitioning between shoots and roots occurs in response to environmental conditions (Gedroc *et al.*, 1996). Based on this theory, we can expect more biomass to be allocated to optimize the absorption of scarce resources, to support seedling development. In other words, under low light conditions, plants prioritize allocation to shoots (Poorter *et al.*, 2012), whereas under conditions of poor nutrient and water availability, greater biomass is allocated to roots (Villar *et al.*, 2004). These patterns may be potentialized by climate change, as they directly affect environmental resources and plant growth (Thabeet *et al.*, 2009), which in turn can compromise seed quality production and a different investment in the two components of the plant and seedling performance as a whole (da Silva Alabarce & Dillenburg, 2017). In this case, populations located in harsh habitats create interesting opportunities for the study of species responses in the face of changes in environmental conditions and extreme weather events. *Euterpe*

*edulis* Mart. is a keystone palm (Galetti *et al.*, 2013) with a vast geographic distribution (Lorenzi *et al.* 2010) that encompasses several ecosystem types, such as Dense Ombrophylous Forest, Deciduous Forest, and Restinga (coastal scrub) (Souza and Prevedello 2019). In coastal plain vegetation, *E. edulis* populations occur in periodically flooded forests with greater litter production and nutrient availability than other coastal plain formations do (Gripp *et al.*, 2023). However, due to sandy soils and water logging, the *E. edulis* populations studied in coastal plain forests (periodically flooded) usually occur at low densities (Reis 2006). Populations under these harsh conditions are more sensitive to extreme weather events, as corroborated by studies that show that *E. edulis* individuals at the Restinga de Jurubatiba National Park (PARNARJ) have reached their upper thermal limit (Marques Feliciano da Silva *et al.*, 2024).

The *E. edulis* population in PARNARJ faces severe environmental conditions, with higher mortality rates observed as the temperature increases (Silva *et al.*, 2023). For this reason, this population at PARNARJ is a good model for understanding seedling responses to harsh conditions. The species is predominantly distributed in shaded and humid forests; therefore, studying the initial regeneration of this species in harsh environments is a necessary assessment. In this context, we aimed to characterize the biomass allocation pattern of *E. edulis* seedlings. Additionally, we tested the hypothesis of the effect of seedling size proposed by Westoby *et al.* (1996), which states that heavier seeds produce more vigorous (measured by total biomass) seedlings. We expected to confirm this hypothesis and predicted a faster growth of seedlings from lighter seeds because of their lower reserves. Additionally, a negative influence of seed mass on specific leaf area was expected, suggesting that seedlings from lighter seeds need greater amount of photosynthetic tissue to support their fast growth.

## MATERIALS AND METHODS

### Target species

*Euterpe edulis* Mart., known as *palmito-jussara*, is a monoecious palm with a solitary stem that can reach 20 m in height and 15 cm in diameter

(Henderson, 2002). Native to the Atlantic Rainforest and the Brazilian Savanna (Cerrado) (dos Reis *et al.* 2000), *Euterpe edulis* has significant ecological relevance, since the fruits are part of the basic diet of the frugivore assembly (Fadini *et al.*, 2009). In addition, their natural high density and prolific seed production play a fundamental role in the natural regeneration of forests (Schorn *et al.* 2012). However, the intense exploitation of jussara palm-hearts has reduced the species distribution to protected areas (Souza & Prevedello, 2020), which has resulted in the species being classified as Vulnerable on the Red List of Threatened Species of Brazilian Plants (Martinelli & Moraes, 2013).

**Study area**

The study was conducted in the Restinga de Jurubatiba National Park (PARNARJ) (22° 16'S, 41° 39' W *datum* WGS84), in the north of Rio de Janeiro state, Brazil. The climate is tropical wet, with an annual precipitation of 1,300 mm and annual temperature ranging from 19 to 27 °C (Montezuma & Araújo, 2007, INMET 2025). PARNARJ covers 11 vegetation types but is mainly represented by coastal scrub (*restinga*). The study was conducted in a periodically flooded forest with an open canopy that can reach 20 meters in height and gets waterlogged during the wet season (Araújo *et al* 1998).

**Data collection**

Infructescences were collected from 10 mature palms (one from each palm) randomly selected during the seed dispersal period in March 2019 and taken to the laboratory. In the laboratory, these fruits were manually depulped using a sieve. One hundred seeds were individually weighed with a precision balance accurate to 0.0001 g to determine fresh mass. These seeds were then oven-dried at 78° C to lose water until a constant mass was obtained. Afterward, the seeds were individually weighed to determine the dry mass. The relationship between the wet and dry masses was obtained performing a linear regression to estimate the dry mass of the seeds in the germination experiment, which was later used in the vigor analyses.

**Germination experiment**

Another one hundred seeds were randomly selected, and the individual seed fresh mass was obtained by weighing them with a precision balance accurate to 0.0001 g. We previously determined the initial dry mass of the seeds used in the germination experiment by the linear regression equation of the relationship between the seed's fresh and dry mass ( $R^2 = 0.98$ ). Posteriorly, the 100 seeds were cleaned with three immersions of three minutes in a solution of 1% sodium hypochlorite, and three additional immersions of three minutes in a solution of 5 mL of nystatin diluted in 1 L distilled water. The seeds were arranged in Petri dishes with filter paper, humidified with 5 mL of 0.5% (V/V) nystatin and placed in a germination chamber at 25° C (de Andrade, 2001). The seeds were hydrated with the same nystatin solution once a week and monitored daily.

When 50 seeds had germinated (*i.e.*, emergence of the germinal bud), they were transplanted to individual 1.7 L vases and humidified to the point of field saturation. These vases were placed in a room at controlled temperature (23 to 25° C) and light conditions (100  $\mu\text{mol m}^2 \text{s}^{-1}$ , with 12h photoperiod). To avoid fungal proliferation, the vases were watered weekly with the nystatin solution. After the emergence of the first leaf, which marks the exhaustion of seed reserves and the inability of the seedling to photosynthesize (Belin & Queiroz, 1988), a macro and micronutrient solution (Table 1) was added to the substrate weekly.

**Table 1.** Nutrient composition of the macro and micronutrient solution used throughout the germination experiment.

Nutrient	Dosage (g/L)
Nitrogen	113.4
Potassium	75.6
Phosphorus	37.8
Calcium	12.6
Magnesium	12.6
Boron	2.52
Manganese	2.52
Zinc	5.04
Iron	1.26
Copper	1.01
Molybdenum	0.63

### Seed measurements and seedling trait calculation

We calculated the RGR (rate of dry mass increase per unit of dry mass present), the specific leaf area (SLA: leaf area/leaf dry mass) and the root/shoot ratio (root biomass/shoot biomass) of the seeds. The RGR calculation followed the protocol proposed by Evans (1972), in which a set of two similar seeds are paired according to their weight, and the RGR is calculated for each pair using seedlings from two measurement events.

At each event, destructive measurements were performed to obtain the seedling biomass (here used as a *proxy* of seedling investment). After each event, we determined the leaf dry mass and root dry mass, which resulted in the total dry mass. The leaf area (LA) was obtained from the Image J program.

The first measurement event was taken 165 days after starting the experiment, when more than half of the seedlings had more than two completely open leaves, which marks the exhaustion of seed reserves (Venturi & Paulilo, 1998; Neuburguer *et al* 2010). At this time, 18 seedlings were randomly selected, cleaned and cut into two parts: shoot (aerial part, that for *E. edulis* seedlings is only the leaves) and root. The material was oven-dried at 78° C until a constant mass was obtained, meaning that all the water had been lost, and then, the parts were weighed to determine the dry mass.

The second measurement was taken 228 days after seeding, when all the seedlings had at least three completely open leaves. Eight of the remaining 32 seedlings died, two were used as a pilot to test the method (the results were discarded) and 20 were used for the second measurement. The measurements followed the same protocol used for the first event.

The seedling traits were calculated by classical plant growth analysis as described by Hunt *et al.* (2002):

$$RGR_{(mg.g^{-1}.day^{-1})} = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1}$$

$$SLA_{(cm^2.g^{-1})} = \frac{L_A}{L_W}$$

where  $W_1$  represents the total dry biomass of the seedlings harvested in the first event,  $W_2$  represents the total dry biomass of the seedlings harvested in the second event,  $L_A$  represents the leaf area,  $L_W$  represents the leaf dry mass, and  $t_2$  and  $t_1$  represent the length of the experiment (63 days). To minimize the influence of outliers, the highest and lowest plants from each harvest were eliminated (Poorter 1989), leaving the experiment with 16 observations. Throughout the entire experiment, the individuals remained classified as seedlings (Portela & dos Santos, 2011). This means that no individual produced pinned leaves, and the ontogenetic stage of all individuals was the same at the time they were harvested for measurement.

### Data analysis

Before performing the following analysis, we performed a Shapiro-Wilk Test to test the data distribution pattern and, when needed, a Levene Test to test the data homoscedasticity (R base package) (R Core Team 2020). To test the hypothesis that heavier seeds produce more vigorous seedlings (Moles & Westoby, 2004), we performed a linear regression with initial seed mass as a predictor variable and total seedling mass as a response variable. Additionally, we performed five linear regressions using seed mass as a predictor and SLA, the root/shoot ratio, the root mass, the shoot mass and RGR as response variables. After constructing the models, we performed a Shapiro-Wilk test to test the normality of the residuals and a Breusch-Pagan test to test the homoscedasticity of the residuals (package “lmtest”) (Zeileis & Hothorn, 2002), all of which were met. Since the SLA and root/shoot are ratios rather than absolute values, we used all the seedlings (*i.e.*, seedlings from the first and second measurements), resulting in 32 observations. Because root mass and shoot mass produce absolute values, only seedlings from the second measurement were considered, resulting in 16 observations. All statistical analyses were performed in R *software* (R Core Team 2020).

## RESULTS

The seed dry mass ranged from 0.332 to 0.688 g, while total seedling dry mass ranged from 0.716 to 2.307 g. The linear regression showed a positive trend

between initial seed dry mass and total seedling dry mass ( $p = 0.03$ ;  $R^2 = 0.21$ ) (Figure 1).

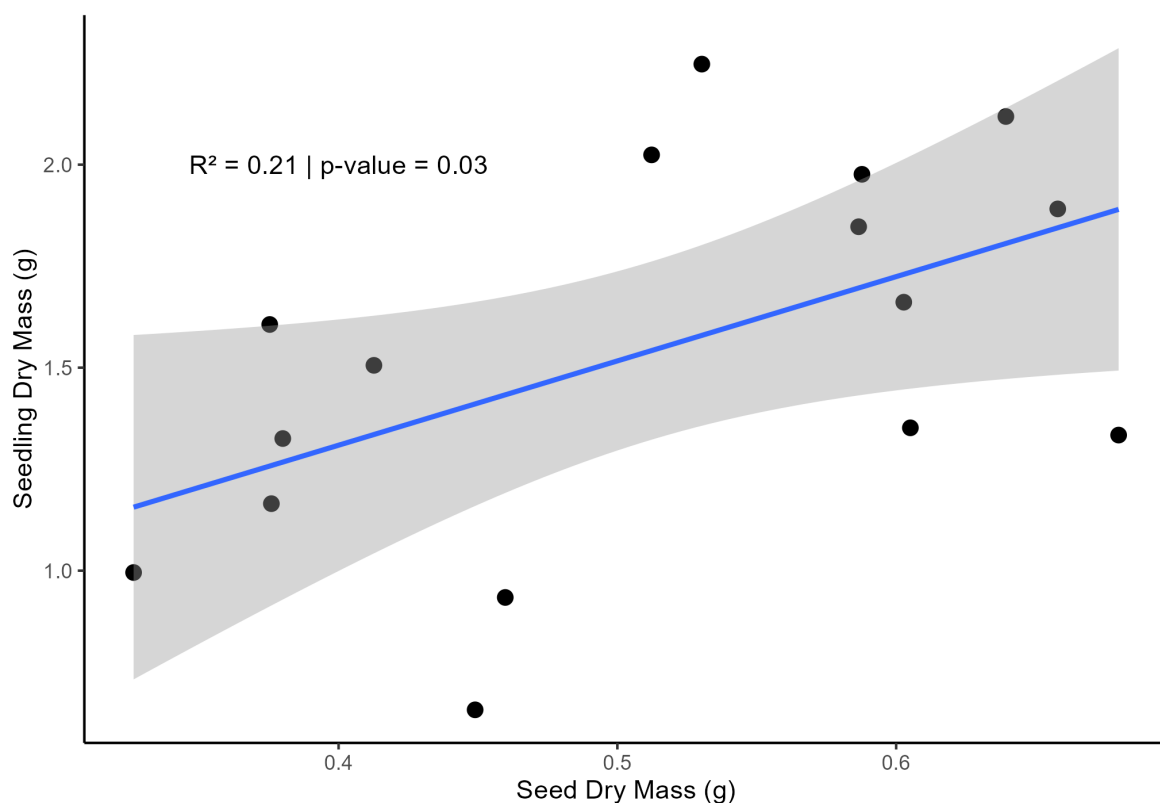
Seed dry mass was significantly related to three out of the four growth parameters measured (Figure 2). Heavier seeds had lower SLA (ranging from 189.01 to 337.86  $\text{cm}^2\text{g}^{-1}$  – Figure 2A), but greater root/shoot ratio (ranging from 0.14 to 0.48 – Figure 2B) and greater root (ranging from 0.08 to 0.61g) and shoot (ranging from 0.57 to 1.65 g) biomass (Figure 2C). However, a significant relationship was not observed between seed dry mass and RGR (Figure 2D).

## DISCUSSION

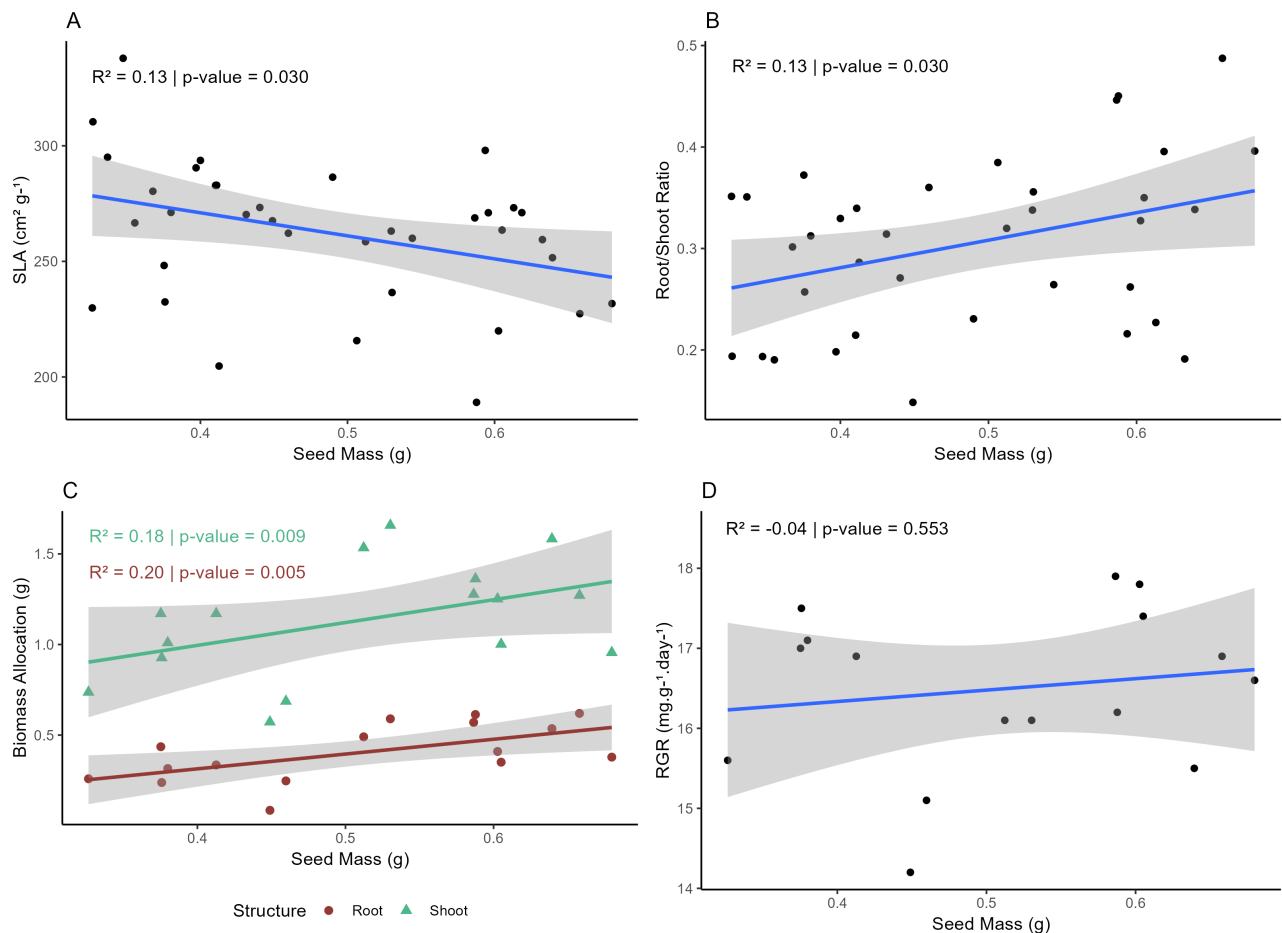
We found that seedlings from heavier seeds have a more balanced root/shoot ratio, however, due to the phylogenetic characteristic of palms, the total shoot biomass is always greater than the total root biomass. Additionally, the positive relationship between seed mass and seedling dry mass suggests that heavier seeds can produce more vigorous seedlings, as predicted by Westoby *et al* (1996).

A more balanced root/shoot ratio due to the increase in seed dry mass was previously verified by Fleig & Rigo (1998). This finding suggests that heavier seeds, but not lighter ones, can invest in aerial and photosynthetic structures without seriously compromising the biomass of roots and absorption tissues. As heavier seeds have more reserves, seedlings can invest more biomass in roots in early growth stages than lighter seeds can (Jurado & Westoby, 1996). Additionally, allometric relationships are not static throughout seedling development (Alves *et al.*, 2004). The root/shoot ratio varies significantly during the life history of an individual, which can influence the growth rate (Nakazono *et al.*, 2001) and the potential to tolerate harsh environmental conditions (de Oliveira *et al* 2017).

Even though heavier seeds develop a more balanced root/shoot ratio, in our findings, it did not surpass 0.48. In other words, the allocation of biomass to shoots was always greater than that to roots. A reasonable explanation is that the investment is driven by adverse conditions. Although



**Figure 1.** Linear regression showing the relationship between seed mass (predictor variable) and seedling vigor (response variable) of *Euterpe edulis* at Restinga de Jurubatiba National Park, state of Rio de Janeiro, Brazil. The blue line highlights the positive trend between the two variables. The gray shade indicates the 95% confidence interval of the regression.



**Figure 2.** Linear regressions between the seed mass (predictor variable) and the growth parameters of *Euterpe edulis* seedlings (response variables) at Restinga de Jurubatiba National Park, state of Rio de Janeiro, Brazil. Seed mass vs A) Specific Leaf Area (SLA,  $\text{cm}^2\text{g}^{-1}$ ); B) Root/Shoot Ratio; C) Biomass Allocation Pattern (g), Root in brown, Shoot in green; D) Relative Growth Rate (RGR) ( $\text{mg.g}^{-1}\text{day}^{-1}$ ). The blue, green, and brown lines highlight the positive trends between the variables. The gray shade indicates the 95% confidence interval of the regressions.

the individuals studied here were not subjected to adverse conditions, the PARNARJ population is at the upper thermal limit of the species (Marques Feliciano da Silva *et al.* 2024). Some studies have pointed out that maternal environmental conditions such as temperature, light, water, and nutrient availability, can significantly affect seed genetic parameters, seed traits, germination processes and even seedling vigor (maternal effects) (Cerqueira *et al.*, 2022; da Silva Alabarce & Dillenburg, 2017; Donohue, 2009; Li *et al.*, 2001).

The periodically flooded forest, that is the maternal environment, accumulates a thick litter layer and develops a closed canopy with plants reaching 12 meters in height (Gripp *et al.*, 2023; Kurtz *et al.*, 2012). Therefore, the amount of light available for seedling growth is scarce, requiring greater

investment in photosynthetic tissues (Gedroc *et al.*, 1996). In addition, the main nutrient sources in these forests are litterfall and litter decomposition (Bonilha *et al.*, 2012), which could explain the low investment in roots.

Based on these results and in the optimal partitioning theory (Gedroc *et al.*, 1996), which states that more biomass will be allocated to optimize the absorption of scarce resources, it is logical to consider that seedlings from periodically flooded forests are more affected by low light conditions than by nutritional scarcity. However, a recent study reported that root and shoot growth are not necessarily balanced and coordinated, thus, this differential allocation may be not an adaptive response, but rather constraints imposed by resource availability (Robinson, 2022). Moreover, before

arriving at any conclusions, a phylogenetic point of view must be considered, since palms naturally allocate more resources to shoot development than to root development (Henderson 2002). However, the studied palm species *Syagrus weddelliana* has an investment in biomass of approximately 90% and 77% of its roots, depending on the population (Oda *et al.* 2016). Therefore, these relationships are very interesting to study in the family.

In addition to influencing the root/shoot ratio, we found that seed dry mass also plays a very important role in seedling vigor (seedling total biomass). This relationship has already been well discussed in the literature (Moles & Westoby, 2004), but unlike other studies (Paz & Martínez-Ramos, 2003; Poorter *et al.*, 2008), we did not observe any influence of seed dry mass on the RGR. Lighter seeds usually have a higher RGR, which is expected, as they must grow faster to compensate for lower seed reserves (Paz & Martínez-Ramos, 2003). However, although this process is commonly reported in studies across different species, studies within a single species often show more contrasting results. (Castro *et al.*, 2008).

Our results suggest that intraspecific variation in RGR is not defined only by seed mass but may be influenced by external stressors (Castro *et al.*, 2008). However, even if the RGR did not vary with seed mass, the negative relationship between SLA and seed mass observed in our study suggests that the seedling growth strategy (resource usage strategy) is positively influenced by seed mass. Seedlings from heavier seeds had a small SLA, which suggests a slower-growth strategy (conservative resource usage), whereas seedlings from lighter seeds had a large SLA, which is related to the fast-growth strategy (acquisitive resource usage) (Reich *et al.*, 1997). A greater SLA allows for more light capture and photosynthetic ability, favoring growth (Poorter & Rose, 2005). Thus, given the negative relationship between seed mass and SLA, seedlings that develop from lighter seeds may take advantage of dry periods between flood events and grow faster in comparison to seedlings from heavier seeds, improving their probability of survival (Zamith & Scarano, 2010). The faster growth of lighter seeds may be a way to overcome a low reserve disadvantage (Paz & Martínez-Ramos, 2003). Moles and Westoby (2006) pointed out that even though heavier seeds produce more vigorous seedlings, slow growth exposes them to environmental harshness for a longer period of

time than do lighter seeds. Considering that the population studied faces harsh conditions (Marques Feliciano da Silva *et al.* 2024) because it occurs in an area periodically subjected to flooding (Kurtz *et al.*, 2012) and that more vigorous seedlings are less vulnerable to environmental harshness (Oliveira *et al.*, 2017) in populations subjected to harsh conditions, a faster growth strategy may be more advantageous in the long term.

However, generally, Reich (2014) pointed out the negative relationship between stress resistance traits and SLA, in other words, despite slow-growth, seedlings from heavier seeds may be more resistant to harsh conditions related to light, temperature and water availability. Therefore, our findings are highly relevant for the conservation of both *E. edulis* and the Atlantic Forest. It is estimated that only 13% of the original area of the Atlantic Forest remains today (Carlucci *et al.* 2021) and, alongside illegal exploitation of palmheart, the loss of the Atlantic Forest is the major reason why *E. edulis* is considered vulnerable to extinction (Martinelli & Moraes, 2013). When planning the restoration of Atlantic Forest areas, managing *E. edulis* is highly recommended because of its key-resource status (Cerqueira *et al.* 2022; Galetti *et al.* 2013). In this regard, we suggest that heavier seeds of *E. edulis* should be preferred to plantations because of their greater probability of producing more vigorous, and therefore resistant, seedlings. The *E. edulis* seedling plantations can not only help in the restoration of the Atlantic Forest (Andivia *et al.* 2021), but also, improve the *E. edulis* conservation efforts.

In this study, we verified the differential biomass allocation between *E. edulis* root and shoot seedlings growing in a coastal plain forest, but it is important to highlight that our experiment was conducted under controlled conditions of light and nutrients. Therefore, these results may not represent natural growth conditions. We suggest that future studies compare initial growth and seedling development stages using seeds from different environments to better understand how the allocation tradeoff is influenced by resource availability and environmental conditions. We also verified that heavier seeds produce more vigorous seedlings, which are more resistant to environmental harshness. These findings suggest that seed mass is an important trait influencing the natural regeneration process at PARNAJ since it is



closely related to the likelihood of seedling survival. This finding can also be applied to restoration efforts and improving *E. edulis* plantations, since heavier seeds can produce seedlings with more satisfactory performance. Additionally, since the population studied is at the upper thermal limit of this species, we suggest that future studies focus on how seedlings of different sizes perform at different temperatures. These findings will contribute to the prediction of how *E. edulis* seedlings will respond to the effects of climate change in coastal plain forests.

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