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UNDERSTANDING THE REGENERATION OF ATLANTIC FFOREST UNDER CLIMATE CHANGE: SEED GERMINATION IN RESPONSE TO INCREASED TEMPERATURES

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UNDERSTANDING THE REGENERATION OF ATLANTIC FOREST UNDER CLIMATE CHANGE: SEED GERMINATION IN RESPONSE TO INCREASED TEMPERATURES:

Entendendo a regeneração florestal da Mata Atlântica sob as mudanças climáticas: germinação de sementes em resposta ao aumento de temperatura

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RESUMO

A Mata Atlântica é um hotspot mundial de biodiversidade e desempenha um papel crucial ao fornecer serviços ecossistêmicos essenciais para a sociedade. Dada a influência das mudanças climáticas na dinâmica ecológica desse bioma, é essencial entender a magnitude dos efeitos climáticos em processos como a regeneração por espécies nativas. Neste estudo, investigamos como as ondas de calor afetam a germinação e o estabelecimento de 10 espécies de árvores nativas na Mata Atlântica brasileira em um experimento em câmaras climáticas. Dez sementes por espécie foram submetidas a dois tratamentos de quebra de dormência (com/sem) e incubadas em dois níveis de temperaturas diurnas (25/35 °C). A germinação das sementes foi monitorada diariamente. Após a fase de germinação, (até) duas plântulas por espécie foram aclimatadas por 15 dias e, posteriormente, expostas a três eventos de ondas de calor (40 °C por 72 horas), com um intervalo de 5 dias entre cada evento. O impacto das ondas de calor no desenvolvimento das plantas (altura e número de folhas) foi monitorado semanalmente. Seis espécies germinaram em pelo menos um dos tratamentos a que foram submetidas. Apenas a identidade das espécies afetou significativamente a germinação das sementes. A dinâmica do processo de germinação se mostrou diferente entre as câmaras de 25°C e 35°C, mas o número total de sementes germinadas nos tratamentos foi semelhante ao final dos 49 dias. As espécies com melhor desempenho foram *Libidibia ferrea* (Mart. ex Tul.) e *Copaifera langsdorffii* Desf. As ondas de calor não afetaram a sobrevivência ou o desenvolvimento das plantas. Ressaltamos a necessidade de estudos específicos para cada espécie a fim de compreender a regeneração da Mata Atlântica diante os diferentes cenários de mudanças climáticas.

Palavras-chave: germinação de sementes; mudanças climáticas; ondas de calor; tamanho da semente

ABSTRACT

The Atlantic Forest is a global hotspot of biodiversity and plays a crucial role by providing essential ecosystem services to society. Given the impact of climate change on the ecological dynamics of this biome, it is essential to understand the magnitude of the effects of climatic extremes on processes such as the regeneration of native species. In this study, we investigated how heat waves affects the germination and establishment of 10 species of trees native to the Brazilian Atlantic Forest through a climate chamber experiment. Ten seeds per species were subjected to two dormancy-breaking treatments (with/without) and incubated at two levels of diurnal temperatures (25/35 °C). Seed germination was monitored daily. After the germination phase, up to two seedlings per species were acclimatized for 15 days and subsequently exposed to three heat wave events (40 °C for 72 hours), with a 5-day interval between each event. The impact of heat waves on plant development (i.e., height and leaf number) was monitored weekly. Six species germinated under at least one of the treatments to which they were subjected. Only the identity of the species significantly affected seed germination. The dynamics of the germination process were different between the 25°C and 35°C chambers, but the total number of seeds germinated in the treatments were similar at the end of the 49 days. The species with the best performances were *Libidibia ferrea* (Mart. ex Tul.) and *Copaifera langsdorffii* Desf. The heat waves did not affect the survival or development of the plants. We emphasize the need for species-specific studies to understand Atlantic Forest regeneration in the face of future climate changes.

Keywords: seed germination; climate changes; heat waves; seed size

1. INTRODUCTION

According to the latest IPCC report (2023), the continuous emission of greenhouse gases into the atmosphere will lead to an increase in the average global temperature exceeding 1.5°C, causing changes in rainfall patterns, rising sea levels, increased occurrence of extreme weather events (e.g., floods, severe droughts, heat waves), and landscape alterations. Such changes will result in ecosystem alterations in terms of species composition and community structures (Blowes et al., 2019; Thomas, 2020). Consequently, forested environments will undergo irreversible biodiversity loss, leading to the degradation of ecosystem services that are essential to humanity. For example, based on extinctions that have already occurred, recent projections suggest that the frequency of future species-level extinctions may be twice as high among tropical species compared to temperate species (Román-Palacios & Wiens, 2020).

Tropical rainforests have unique biodiversity. The Atlantic Forest, for example, is recognized as one of the 34 hotspots for global biodiversity conservation. It contributes to 70 % of the gross domestic product (GDP) and 2/3 of the industrial economy (Martinelli et al. 2013). These forests also store a significant amount of carbon both below- and aboveground (Dixon et al., 1994), thus acting as sinks for atmospheric CO2. Some climate models indicate that with the rising temperatures, rainfall patterns will change and may become more intense in some tropical areas (dos Santos et al., 2020; IPCC, 2023). Both temperature and precipitation play a crucial role in the forest structure (Medina, 2006), influencing biogeochemical cycles, which leads to changes in soil chemical content and nutrient supply for plants.

Germination is a growth and sensitive process, as such it is irreversible. While the physiological process of germination remains largely uniform across all plant species, there is considerable variation among different species in terms of the specific conditions and tolerance ranges associated with germination (Schmidt, 2007). For example, most tropical lowland species require temperatures between 20 and 28°C for germinate, while temperate species germinate at a lower temperature. Germination temperatures that are significantly above or below the optimal conditions for the species can result in poor germination and abnormalities in the emerged seedlings (Schmidt, 2007). In addition, the dormancy mechanism is also dependent on environmental temperature. Species with physical dormancy can break the dormancy in higher temperatures (Martin et al., 1975; Auld & O'Connell, 1991), and others require either stratification or periods of dry post-ripening at specific temperatures to overcome dormancy. Thus, changing the temperature regime can alter the seed's metabolism and consequently modify the germination process. Therefore, understanding the consequences of changes in temperature and rainfall is essential to understand the structure and dynamics of forests.

Heatwaves events will become more intense and frequent all over the globe (IPCC, 2023), which may cause damage to plants not adapted to extreme temperatures, altering species interactions, and leading to the local extinction of species with low plasticity and adaptability. Environmental fluctuation, such as temperature or light regime, and life-story strategy (i.e., pioneer vs. non-pioneer species), strongly influence seedling ecology and tolerance. This includes factors like light adaptation, shoot-root balance, and stress tolerance (Schmidt, 2007). Early developmental stages of plants are expected to be more sensitive to climate change, highlighting the importance of considering plant age in studies evaluating the effect of heat on seedling development (Lloret et al., 2004; Fay & Schultz, 2009; Dalgleish et al., 2010). Moreover, at the scale of the whole tree, excessive heat can cause a decrease in growth, leaf development, and leaf area. When combined with drought, it may lead to mortality (Teskey et al., 2015). On the other hand, in the absence of drought, heat waves may favor plant performance by increasing photosynthetic activity (Bokhosrt et al., 2011) and overall plant fitness through acclimation to warmer conditions (Bauweraerts et al., 2014).

Therefore, fast and decisive mitigation actions in this decade can reduce the impacts of climate change on such ecosystems. In this context, the main goal of this study was to assess how temperature increase scenario may affect the regeneration niche of species of trees native to the Brazilian Atlantic Forest. To address these questions, we conducted germination experiments in two temperature scenarios and applied two treatments related to seed dormancy. Our hypothesis was that an increase in temperature would have a negative impact on germination success, resulting in a reduction in the number of germinated seeds, and that the dormancy break treatment would enhance germination. Additionally, we investigated the effect of heat waves on the establishment of germinated seedlings, hypothesizing that plants would be adversely affected at the end of heat wave cycles. Finally, we test some functional traits and their contribution to the seed germination pattern. Our hypothesis for this analysis was that functional traits such as wood density, seed size, and seed weight would stand out compared to others.

2. MATERIALS AND METHODS

Plant species selection and seed material

Seeds of 10 tree species native to the Brazilian Atlantic Forest were chosen for inclusion in this study (refer to Table 1 for details and appendix 3 for pictures of each species): *Ormosia arborea* (Vell.) Harms; *Pleroma granulosum* (Desr.) D. Don*; Joannesia princeps* Vell.;

Copaifera langsdorffii Desf.; *Senna macranthera* (DC. ex Collad.); *Myroxylon peruiferum* L.f; *Handroanthus impetiginosus* (Mart. ex DC.) Mattos; *Handroanthus chrysotrichus* (Mart. ex DC.) Mattos; *Astronium urundeuva* (Fr. All.) Engl.; *Libidibia ferrea* (Mart. ex Tul.). The selection criteria included being native to the Brazilian Atlantic Forest, absence of threat of extinction, availability for purchase, and fit the wood density classification criteria. To this criterion, the density values for the potential list of species were referenced in the literature (Oliveira, 2014; Campos Filho & Sartorelli, 2015). Wood was categorized as soft when the mean density values was ≤ 0.8g/cm^3 and as hard when the values exceeded 0.8g/cm^3. Consequently, the selected species were further categorized into 5 softwoods and 5 hardwoods Fifty seeds of each species were obtained from nurseries and authorized seed producers in Southeastern Brazil in December of 2022. These seeds were stored at regular temperatures until the initiation of the experiment, approximately four months later.

Table 1: Information of each species used in the study. Mean longest length represents the seed size and mean weight represented the weight of the seeds.

Species	**Popular name in Brazil**	**Botanic family**	**Wood density trait**	**Mean longest length (mm)**	**Mean weight (g)**
Ormosia arborea (Vell.) Harms	Olho de cabra	Fabaceae	Soft (0.7g/cm^3)	12.72	6.04
Pleroma granulosum (Desr.) D. Don	Quaresmeira	Melastomataceae	Soft (0.4g/cm^3)	0.96	0.013
Joannesia princeps Vell.	Cutieira	Euphorbiaceae	Soft (0.5g/cm^3)	25.43	54.6
Copaifera langsdorffii Desf.	Copaíba	Fabaceae	Soft (0.5g/cm^3)	10.07	3.73
Senna macranthera (DC. ex Collad.) H.S.Irwin & Barneby	Pau fava	Fabaceae	Soft (0.5g/cm^3)	5.59	0.69
Myroxylon peruiferum L.f	Cabreúva	Fabaceae	Hard (0.9g/cm^3)	30.58	0.13
Handroanthus impetiginosus (Mart. ex DC.) Mattos	Ipe roxo	Bignoniaceae	Hard (0.8g/cm^3)	23.49	3.16
Handroanthus chrysotrichus (Mart. ex DC.) Mattos	Ipê Amarelo	Bignoniaceae	Hard (0.8g/cm^3)	23.93	0.58
Astronium urundeuva (M.Allemão) Engl.	Aroeira preta	Anacardiaceae	Hard (0.9g/cm^3)	3.91	0.15

Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	Pau ferro	Fabaceae	Hard (1g/cm^3)	10.13	1.59

2.1 Experimental design

Study area

The Atlantic Forest biome, a biodiversity hotspot that presents more than 90% of its original distribution in Brazil, occurring in several Brazilian states and in parts of Argentina and Paraguay (Mittermeier et al. 2004). It comprises two primary vegetation types: the Atlantic Rain Forest and the Atlantic Semi-deciduous forest. Predominantly covering the low to medium elevations (~1000 m elev.) along the eastern slopes of the mountain chain running parallel to the coastline from southern to northeastern Brazil, the Atlantic Rain Forest boasts a warm and wet climate without a dry season (Morellato & Haddad, 2000). On the other hand, the Atlantic Semi-deciduous Forest extends across the plateau (usually > 600 m elev.) in the central and southeastern interior of the country. This region experiences a seasonal climate characterized by a relatively severe dry season, typically occurring from April to September (Leitão Filho & Morellato 1997, Oliveira-Filho & Fontes 2000).

Germination experiment

The experiment was conducted in climate chambers at the Chair of Restoration Ecology (Technical University of Munich) from April to June 2023. Forty seeds of each species were used in the experiment, after being washed with chlorine (5%) for five minutes. Each species was divided into two treatments: dormancy break and no dormancy break, which were placed in Petri dishes with filter paper moisten with distilled water. The dormancy break treatment (hereafter referred as D) consisted in seed that underwent the break for dormancy mechanism, being the opposite to the treatment no dormancy break (hereafter referred as ND). The dormancy-breaking treatment consisted of a thermal shock (immersion in distilled water at 70 °C for 15 minutes) followed by pre-soaking in distilled water for 24 hours. Only *Ormosia* *arborea* (Vell.) Harms, *Libidibia ferrea* (Mart. ex Tul.)*, Joannesia princeps* Vell.*,* and *Copaifera langsdorffii* Desf. received also mechanical scarification before the thermal shock due to their hard seed coats. The species *Pleroma granulosum, Handroanthus chrysotrichus* and *Handroanthus impetiginosus* weren't washed with chlorine due to their sensible coat. Afterward, half of each group (i.e. 10 seeds from each species) was separated into two climatic chambers (Poly Klima® MN- Schrank). The first chamber simulated the optimal temperature incubation scenario for germination in the tropics (Brancalion et al., 2010), with a daily temperature of 25 °C and a night temperature of 20 °C, along with a photoperiod of 13 hours of light and 11 hours of darkness. The second chamber simulated a climate change scenario, where temperatures were increased in accordance with Nobre et al. (2019) with a daily temperature of 35 °C and night temperature of 30 °C, under the same photoperiod as previously mentioned. During five days a week, seeds were kept moist with distilled water, and their germination was recorded. A given seed was considered to have germinated when the first primary root was visible and growing continuously (Labouriau, 1983).

Heat waves simulation

If at least one seed of each species exhibited germination and developed the first pair of cotyledons, they were randomly selected for the heat wave cycles. This selection occurred regardless of the treatment or the temperature at which the seed was found. All seeds went through the 3 heat wave cycles, although they were not executed simultaneously due to different germination times.) Up to two seedlings for each species were transplanted into small pots filled with approximate 54g of gardening soil (Topfsubstrat ® grobe struktur). In cases where the same species germinated in both chambers (25°C and 35°C), the seedlings were planted separately. Such seedlings were acclimatized for 15 days before the simulation of the first heat wave event. Heat wave events were simulated in a third chamber by maintaining a temperature of 40°C for 72 hours and photoperiod of 13 hours of light and 11 hours of darkness. During the heat wave, no water was provided to the plants. Following the heat wave simulation, the seedlings were returned to their respective chambers for a resting period of 5 days before the next heat wave. Distilled water was provided during resting period to maintain the soil moisture. In total, three cycles of heat wave simulations were conducted (approximate duration of 30 days). Measurements of the maximum length of the longest branch of the plant (hereafter referred as plant height) was taken using a ruler (cm) and the number of leaves (visual counting) (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2013) were taken initially (before any heat wave simulation) and after all the heat wave simulations, for all the seedlings. Because of non-uniformity of germination rates for all species, some species only had one individual instead of two to experience the heat wave simulation (i.e. *Ormosia arborea* (Vell.) Harms *and Myroxylon peruiferum* L.f).

Functional traits measurements

Seed functional traits for each species were measured (Table 1). Ten seeds of each species were weighted (seed weight) and measured (seed size) with a digital caliper to measure the mean longest length (mm). Only for *Pleroma granulosum (Desr.) D. Don.* 20 seeds were weighted, due to the very small size and light weight of the seeds of this species.

2.2 Statistical analysis

Germination succession rates were calculated in percentage using MS Excel. To evaluate the effects of the temperature scenarios and of the dormancy break treatment on the probability of germination rates of each species as well as on the probability of total germination, we used generalized linear mixed-effects models with a binomial error structure implemented with the R-package *glmmTMB* (Brooks et al. 2017), as follow: *glmmTMB(cbind(germinated_seeds,non_germinated_seeds) ~ Temperature * Treatment + Species,family=binomial, data=germination.avg*). Likelihood ratio test (LRT) was used to test for the significance of the manipulated treatments and temperature scenarios. The same mixed-effects models but with Poisson error was used to (1) evaluate the effects of temperature of germination and the germination over time between germination temperatures (i.e climate chambers) (*glmmTMB(Germination ~ Temperature*Day + (Day|Species) +(1|Treatment), ziformula = ~1, family = poisson, data=dados*); (2) to test the heat wave cycles and the germination temperature on the number of leaves: *glmmTMB(log(Number_of_leaves) ~ Plant_age + Temperature*Amount_heat_wave + (1|spp_id), data=traits*. For the first model, contrasts tests for pairwise comparisons were used to test the significance between 25°C and 35°C temperature, with the R-package *emmeans* (Lenth, 2021). The effects of heat waves cycles and the germination temperature on plant height were assessed using the same models with a Gaussian error structure, as follow: *glmmTMB(log(Height_cm) ~ Plant_age + Temperature*Amount_heat_wave + (1|spp_id) + (Day|spp_id), data=traits*. Furthermore, two linear regressions were performed to assess: (1) the effect between the heat waves on the overall plant height and leaf number; (2) the correlation between seed weight and size with the germination success rates of all plants (regardless dormancy treatment or temperature germination).

Another generalized linear mixed-effects model was perform, in order to assess the significance of the functional traits used in this experiment on the total number of germinated seeds, with Poisson error structure (*glmmTMB(germinated_seeds ~ seed_weight + seed_size + wood_density + Botanic_family + (1|Species), data=dados, family = poisson(link = "log")*. Finally, a Factor analysis of mixed data (FAMD) analysis was performed with the R-package *Factoextra* (Le et al., 2020) to understand how the groups were distributed and related between the variables: seed size and weight, wood density, botanical family, and the variables manipulated in the experiment (treatment and germination temperature). Data analyses were performed using R version 4.2.1 (R Core Team, 2023).

3. RESULTS

Seed germination rates

After 49 days monitoring the germination experiment, six species germinated in at least one chamber (as shown in Table 2), while the species *Handroanthus chrysotrichus (Mart. Ex DC.) Mattos, Handroanthus impetiginosus (Mart. Ex DC.) Mattos, Joannesia princeps Vell., and Pleroma granulosum (Desr.) D. Don.,* did not. Germination percentages for each species by dormancy break treatment is given in table 2. *Libidibia ferrea* (Mart. Ex Tul.) had the highest germination, followed by *Copaifera langsdorffii* Desf., *Astronium urundeuva* (Fr. All.) Engl., *Ormosia arborea* (Vell.) Harms, and *Senna macranthera* (DC. Ex Collad.), respectively.

Table 2: Germination (in %) for 11 species of trees native to the Brazilian Atlantic Forest according to their germination temperature (25°C or 35°C) and treatment applied for dormancy break, where "D" represents the seed that received the treatment for break the dormancy and "ND" represent the seed that did not receive any treatment.

	25°C		**35°C**	
	D	**ND**	**D**	**ND**
Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	90%	80%	100%	100%
Copaifera langsdorffii Desf.	40%	20%	40%	0
Astronium urundeuva (FR. All.) Engl.	0	30%	0	30%
Ormosia arborea (Vell.) Harms	40%	0	10%	0
Senna macranthera (DC. ex Collad.) H.S.Irwin & Barneby	10%	10%	20%	10%
Myroxylon peruiferum L.f	0	10%	0	0

Handroanthus chrysotrichus (Mart. ex DC.) Mattos	0	0	0	0
Handroanthus impetiginosus (Mart. ex DC.) Mattos	0	0	0	0
Joannesia princeps Vell.	0	0	0	0
Pleroma granulosum (Desr.) D. Don	0	0	0	0

The total germination percentage in the 25°C and 35°C germination temperatures was 33% and 31%, respectively (Figure 1.B). In the dormancy break treatment, overall germination was 35% and in the treatment without dormancy break, it was 29% (Figure 1.A). Only the identity of species used in the experiment significantly affected the probability of total germination:

```
                   Chisq   Df  Pr(>Chisq)
Temperature        0.1603   1   0.6889
Treatment          1.4180   1   0.2337
Species           50.6510   9   8.124e-08 ***
Temperature:Treatment  0.0023  1    0.9614
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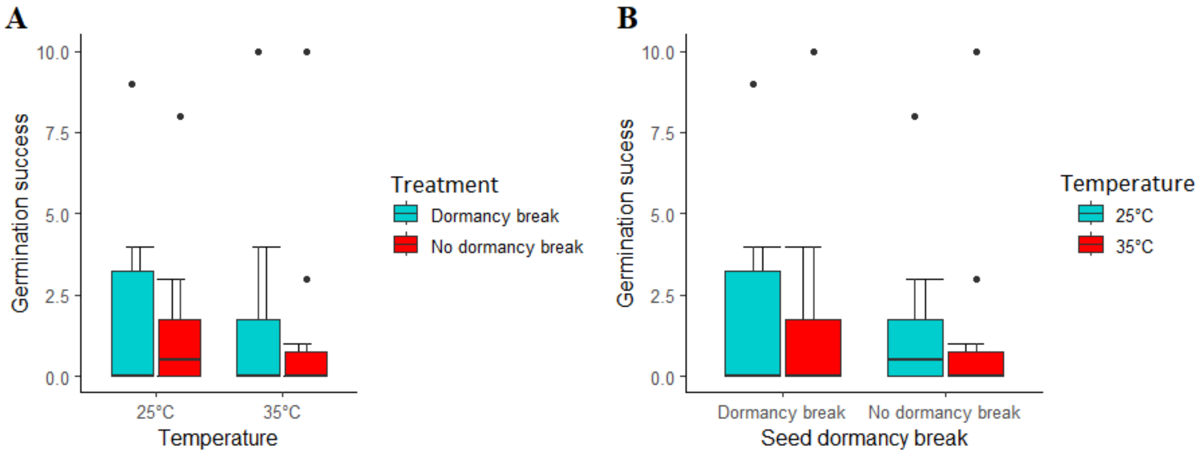

Figure 1: Germination success (represented between 0-10) plotted with experimental variables. In figure A, germination rates (y-axis) are plotted across the temperature (x-axis), where the first group of bars represented the 25°C chamber and the second group the 35°C chamber, simulating the climate change scenario. In figure B, the germination rates (y-axis) were plotted across the dormancy break treatments (x-axis), and the first group bar (Dormancy break) represents the treatment where the seeds underwent break dormancy, and the second group (No dormancy break) represents the treatment where the seeds had any treatment to break dormancy mechanism.

The germination temperature (i.e 25°C or 35°C) was significant for germination over time (i.e germination velocity) (DF=1; p-value= 0.003), specifically, germination at 35°C (z ratio= -2.0; p-value < 0.01), as shown in Figure 2: both curves showed an asymptotic behavior, not varying much between chambers (25°C or 35°C), however it is observed that at 35°C (climate change scenario) germination rates increase more quickly and tend to stabilize faster , when compared to the 25°C chamber (normal scenario)

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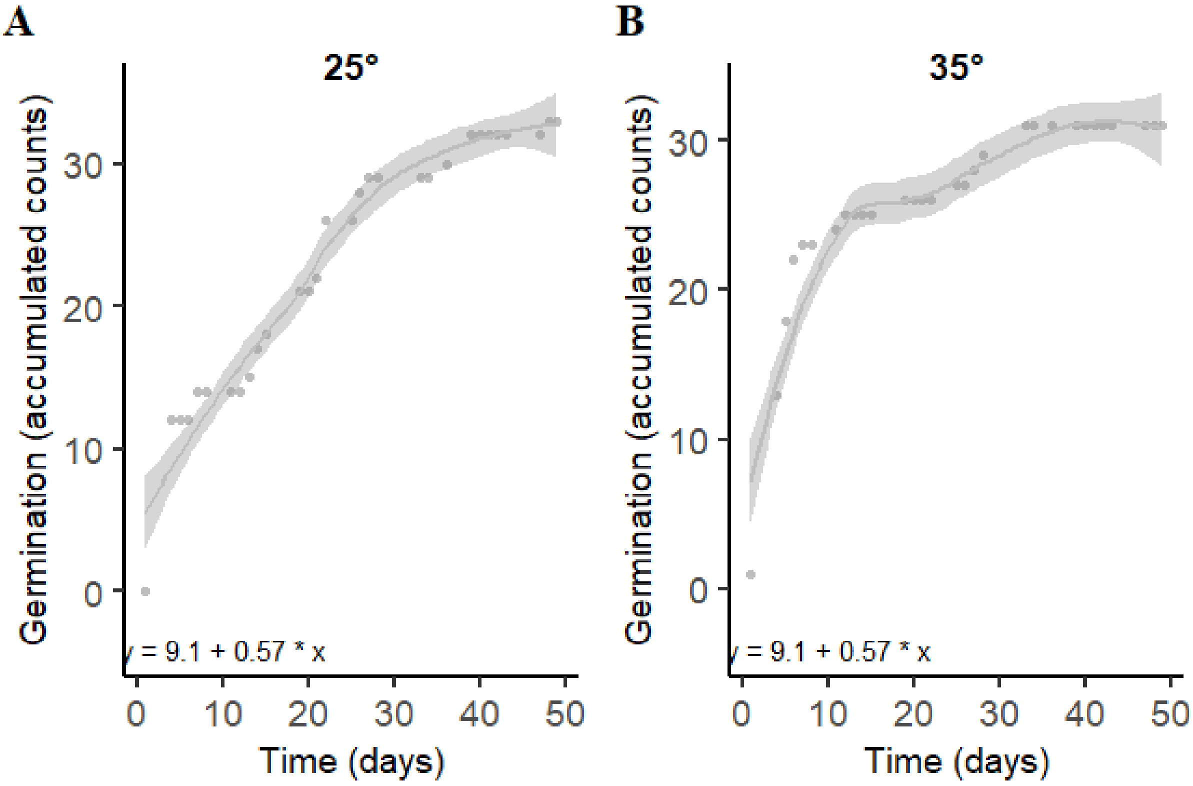

Figure 2: Dynamics of germination counts (y-axis) during the whole experiment time in days (x-axis) in (A) the 25°C chamber and (B) in the 35°C chamber (climate change scenario). In y axis, germination accumulated includes all seed that did and did not germinate during the whole experiment time.

When considering the performance of each species individually, the dormancy break treatment was significant for *Copaifera langsdorffii* Desf. (p=0.04, z rate= -2.06, DF=1), *Astronium urundeuva* (Fr. All.) Engl. (p=0.03, z rate=0, DF=1) and *Ormosia arborea* (Vell.) Harms (p=0.01, DF=1, z ratio= 0).

Heat waves and plant development.

Among the germinated seeds, 11 individuals were random selected for the acclimation period, before the heat wave simulations. Furthermore, two individuals of *A. urundeuva* did not survive during the acclimation period, thus only one individual remained for being used during the heat wave simulations. *Libidibia ferrea* (Mart. Ex Tul.) was the species with higher development after the 3 heat waves simulations, representing the higher height of 30.5cm and 39 cm and 12 and 8 leaves for the 2 individuals, respectively. Contrastively, *Senna Macranthera (*DC. ex Collad.) showed the lower development, with 4cm of height and 2 leaves by the end of the experiment.

All plants tested survived after three heat wave events over the course of the experimental period. The number of heat waves neither germination temperature affected the height or number of leaves of the plants (Figure 3 and Figure 2 on appendix B).

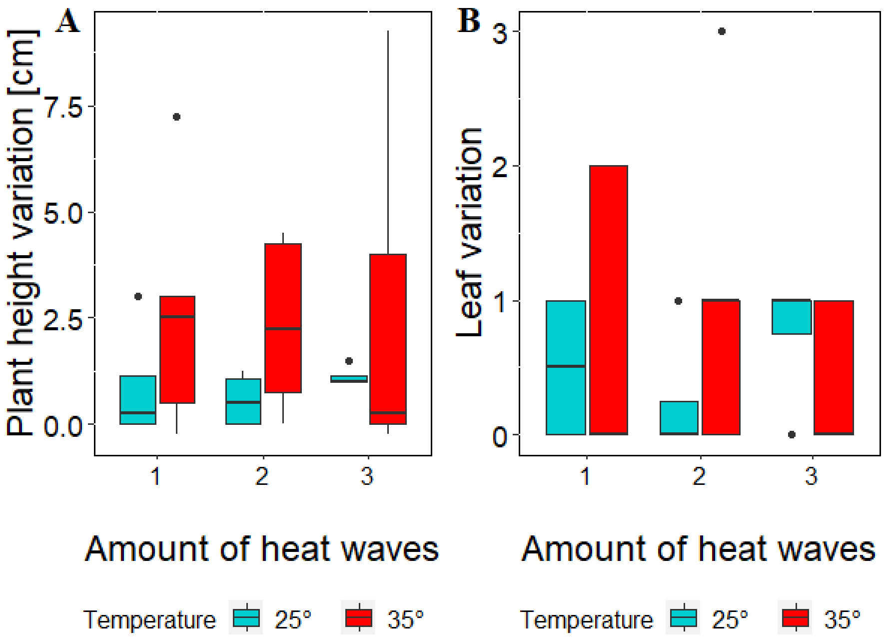

Figure 3: (A) Box plot representing the height variation between each heat wave cycle (1, 2 and 3), for each germination temperature (plants germinated at 25°C represented in blue and plants germinated at 35°C chamber represented in red). (B) Box plot of leaf variation between each heat wave cycle (1, 2 and 3), for each germination temperature (plants germinated at 25°C represented in blue and plants germinated at 35°C chamber represented in red).

Functional traits

The FAMD analyses (see appendix A) revealed that the variables tested (seed size, seed weight, wood density, species identity, botanical family, dormancy treatment used in the seeds and the germination temperature) were distributed into four groups. The first group, which made the major contribution to the data distribution, consisted of species identity and botanical family. The second group comprised only of seed size. The thirds group consisted of wood density and finally, the last group with almost no contribution was seed weight, treatment, and temperature. Regarding the generalized linear mixed-effects model performed, the following traits showed significance: wood density (p value < 0.01, DF=1), specifically the soft wood plants (p value < 0.01, DF=1, z rate= - 5.7) and botanical family (p value < 0.01, DF=4).

Linear regression analyses testing the effects of heat waves on plant height and leaf number did not yield any significant results. Additionally, seed weight did not show a significant correlation with germination ($p= 0.1$, DF=1, F value= 2.2). However, seed size showed a negative but weak significant relationship ($R^2=0.09$; $p=0.05$, F value= 4.03, DF=1, Fig. 4).

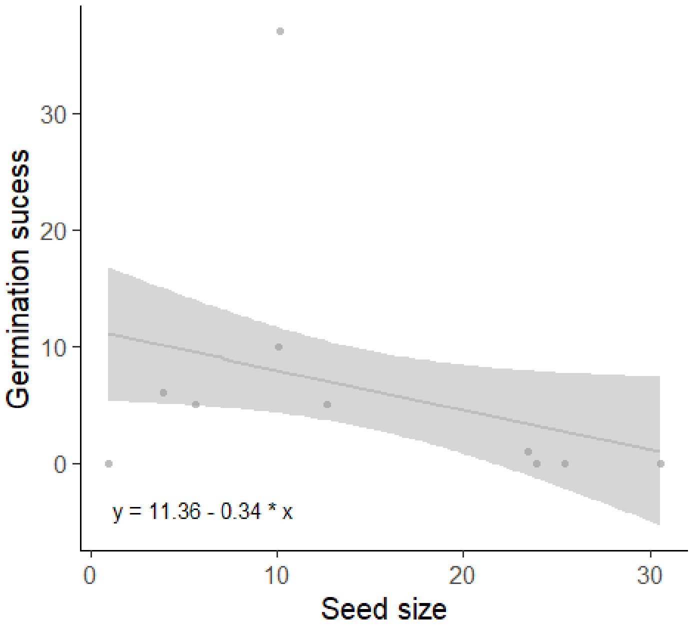

Figure 4: Linear regression between germination units (y axis) and seed size (mm) for all species (x axis). The line and its equation demonstrate a negative relationship between the overall germination rate and seed size of all species used.

4. DISCUSSION

Our findings reveal that six out of 11 species germinated under at least one of the treatments to which they were subjected. Only the identity of the species significantly affected seed germination probability, while the germination temperature 35°C was significant for the germination rate over time, even do it didn't affect the final number of germinated seeds (total counting), leading us to reject our first hypothesis. The species that showed the best performance were *Libidibia ferrea* (100% at 35 °C, regardless of dormancy break) and *Copaifera langsdorffii* (40% at both temperatures, with dormancy break). Heat waves did not affect the survival of the plants neither affected their development, thus, rejecting our second hypothesis. The functional traits wood density, botanical family and seed size showed to be significant, partially confirming our last hypothesis about functional traits. Additionally, the species' identity also proved to be important in the distribution of data among the predictor variables, reinforcing the previously found result.

Germination rates vary depending on the species.

Considering the behavior of germination rates between both chambers, we could not see differences between the final number of germinated seeds, but the significance of the interaction between temperature and time could indicate that velocity of the germination at 35°C is higher than 25°C. This may be because at higher temperatures, you can accelerate the seed germination process by increasing seed's metabolism, but otherwise, as we could see in Figure 2, those rates also established faster at 35°C. The implications of this accelerating will vary according to the environment and the community dynamics that the species is and the specific specie response, while some could respond germinating faster, others may be damage by this increase temperature, acquiring pathogens or becoming inviable. As a result, the community may change its structure over time.

In fact, a previous study found that the optimal germination temperature for tree species in the Atlantic Forest is around 25°C, with no discernible differences between pioneer and non-pioneer groups (Brancalion et al., 2010). Moreover, given the wide water availability in this biome, seeds can germinate across a broader range of temperatures, since moisture content also required for germination is not a limiting factor, aligning with the outcomes observed in our study. Temperature is one of the main factors limiting seed germination, thus controlling both germination intensity and velocity (Bewley and Black, 1982) as well as seed dormancy (Lambers et al., 2008). The optimal temperature for each species is related to favorable environmental conditions for its development and varies according to its geographical distribution and ecological group (Thompson, 1977; Brancalion et al., 2010). Thus, finding the optimal temperature range to accelerate germination is challenging.

Dormancy and germination mechanisms play pivotal roles in the preservation of long-lived seed banks. They achieve this by either delaying germination until favorable conditions emerge or by preventing simultaneous germination of the entire seed bank (Baskin & Baskin, 1998; Fenner & Thompson, 2005). This is because temperature may be more related to overcoming dormancy than favoring the germination process. However, when associated with the ecological group (pioneer vs. non-pioneer species), the shifting range of temperatures can be important in determining the composition of plant communities. Pioneer species typically require shifts in the biotic conditions to germinate under clearing forest conditions, which promotes the entry of light and changes the soil temperature, allowing pioneer seeds present in the soil to germinate (Dalling et al., 1998, Raich and Gong, 1990) and further benefit non-pioneer germination (Brancalion et al., 2010). Therefore, changes in the temperature and light regime (i.e. climate change) promote changes in germination patterns and speed, which can select species and alter species dynamics in ecological succession.

In our results, the dormancy break treatment influenced germination only marginally. The higher germination rates in dormancy break treatments reported by other studies (Beltrame, 2013; dos Santos, 2011; Filho et al., 2005; Negri et al., 2009; Teixeira et al., 2011) were not observed here, which might indicate that seeds maintaining dormancy were afforded a substantial amount of time to trigger their late germination mechanism, contrasting to seeds lacking dormancy in which the germination was reduced over time. Another possible explanation for this result is that the dormancy treatment applied to all seeds may not have been effective for all studied species. In contrast, this adverse, individual species response to a standardized dormancy-breaking treatment supports our result that germination was explained solely by species identity.

According to Walck and colleagues (2011), germination in some species occurs in a specific time, while in others, it is postponed due to dormancy until a favorable season, increasing the chances of seedling survival. However, the authors also stated that projected changes in ecological cues may either hinder, postpone, or enhance seed regeneration, depending on the species. Our results show that the germination dynamics varies among species, thus indicating the need for species-specific studies to evaluate potential ecological responses of different species to altered environmental conditions due to climate change. This suggests that in a biodiverse biome like the Atlantic Forest, characterized by high endemism rates, studies focused on plant characterization can provide insights into how species respond to adverse conditions. For economically significant species, having prior knowledge of their characteristics is fundamental for sustainable use in the economy. Moreover, these baseline studies are essential for developing conservation tools and strategies. For instance, for species that exhibit dormancy break in warmer environments, an increase in temperature may lead to a faster release from dormancy. Indeed, Ooi et al. (2009) observed that germination was enhanced for two out of four physiologically dormant plant species from Australian arid environments under increased temperatures while keeping other environmental conditions controlled.

The individual species models revealed that *Libidibia ferrea* (Mart. ex Tul.) was not significantly affected by any variable but exhibited higher germination rates and robust development. Lima et al (2006) reported similar high germination rates for this species (98.06% and 98.89% at 25°C and 35°C, respectively) using the same substrate, which was consistent with our results. *L. ferrea* demonstrated characteristics of a generalist species, performing well throughout the different conditions and treatments manipulated in the experiment. In addition, *Copaifera langsdorffii* Desf., *Astronium urundeuva* (Fr. All.) Engl., and *Ormosia arborea* (Vell.) Harms were influenced by the dormancy break treatment. These species have in common the fact that they also occur in high abundance in the cerrado, a predominantly xeric environment, indicating that the dormancy mechanism present in these species is fundamental for their survival in certain environments. Although all three species were also categorized as belonging to a secondary successional stage (develop in the environment after previous occupation by pioneer species) *A. urundeuva* seeds that germinated in both chambers did not undergo a dormancy break treatment. *A. urundeuva* seeds exhibit embryonic dormancy, thus being recommended to immerse seeds of this species in water for 24 hours at room temperature to trigger germination (Carvalho, 2014). Another study reported contrasting results, reporting that seeds of this species, after dormancy break treatment, exhibited germination rates between 79% and 93% at 25°C, with lower rates at 35°C (Pacheco et al., 2006). We believe that the divergent outcomes were likely associated with an extended storage period lacking temperature control. This prolonged storage may have diminished seed viability. Also, the dormancy-breaking process employed in this study, may had exerting a negative impact on the species. Notably, *A. urundeuva* was the only species that did not survive during the acclimatization period before the heat wave simulation, suggesting sensitivity to abrupt changes. For the remaining five species (*H. chrysotrichus, H. impetiginosus, J. princeps, and P. granulosum*) which did not exhibit any germination throughout the experiment, we attribute this behavior to factors such as seed viability and sensibility. It is plausible that these species may not remain viable after prolonged storage periods without controlled temperature. Additionally, the chlorine wash administered prior to incubation may have adversely affected seed germination, as even seeds subjected to no dormancy break treatment displayed no signs of germination.

Heat wave did not affect plant development.

The impact of heat waves on plant development has been evident in various moments, but the same was not observed in our results. The European heat wave of 2003 resulted in a substantial 30% reduction in ecosystem gross primary production (Ciais et al., 2005). Similarly, the extreme heat wave experienced in Russia during 2010 was the most severe for that region, leading to an estimated 50% reduction in gross primary production (Bastos et al., 2013).

Notably, a study on *Pinus taeda* and *Quercus rubra* seedlings exposed to repeated moderate (+6 °C) or extreme (+12 °C) heat waves in a greenhouse reported significant growth reductions caused by the +12 °C heat wave, but not the +6 °C heat wave (Bauweraerts et al., 2014).

The simulations of heat waves showed no significant effect on seedling development (see more in Figure 2 in appendix B). However, only three cycles of heat waves or the temperature 40°C appeared to be insufficient to reach the physiological limit of the species and disrupt their development. Alternatively, for both the number of leaves and the height of the plants, it was not possible to observe any pattern (decreasing or increasing values between species and the amount of heat waves) (Figure 3, appendix B). We believe this may represent stress-tolerant behavior, however, more studies are needed, as the absence of seedlings without any heat wave events (i.e. control treatments) in the experiment makes it difficult to predict the physiological limitations mentioned before.

Functional traits: seed size as an important variable

Studies focus on forest-monitoring networks in tropical forests have shown that high temperatures can result in lower tree growth and fecundity (Clark et al. 2010, Feeley et al. 2007, Teskey et al., 2015) and elevated mortality (Chazdon et al. 2005). However, to comprehend the impact of rising temperatures on species performance, the functional traits approach can help with understanding. An example lies in the correlation between wood density and various indicators of plant performance. Species characterized by slower growth and lower mortality rates tend to exhibit denser wood, whereas their fast-growing counterparts with higher mortality rates typically display traits associated with softer wood (Chave et al., 2009; Maynard et at., 2021).

Seed weight and size are crucial functional traits that influence the dynamics of the regeneration process (Leishman & Westoby, 1994). Seed size is related to seedling establishment, because it can dictate the dispersal strategy: large seeds have more reserve and thus, have more chance of emerging from deep soil depths and face unfavorable conditions (Busso and Parryman, 2005; Bruun and Ten Brink, 2008; Dalling & Hubbell, 2002). Yet, seed size and weight are related to seed dispersal via seed predation (Hillyer and Silman, 2010). Deb and Sundriyal (2017) studying 3 tree species of an Indian Tropical rainforest affirmed that seed size variation has an important ecological effect, by influencing the reproductive strategy of plant species. Species that colonize disturbed open sites with minimal competition tend to produce abundant, small seeds, typically located in the upper soil seed bank (Lambers, 2008). As a result, the initial growth of such species facilitates the arrival of later species, which are more deeply buried in the soil and require better conditions to establish (Lambers, 2008). Ultimately, the growth and establishment strategies in forest ecosystems are highly dependent on species-specific responses, collectively shaping the community dynamics. Furthermore, the stored seed bank can hold a wider genetic base compared to the adult standing vegetation (Barret et al., 2005; Shimono et al., 2006; Stearns & Olson, 1958), such that the seed bank can buffer against changes in the genetic composition of populations. In a warmer future scenario, those plants with small and abundant seeds may become more productive and more frequent on seed banks, as temperature can influence seed production (Jump and Woodward, 2003) and change the composition on seed banks, consequently changing the species and the genetic composition of plant communities.

Although seed size showed a significant relationship with germination rates, as exemplified by the linear regression, the same was not observed in the FAMD analysis. On the other hand, this analysis also confirmed previously reported results, where species identity was significant for germination rates. Furthermore, functional traits such as seed size, seed weight, and wood density are intrinsic to the species. Therefore, when reported in the analyses, they already encompass the characteristics of all species used in the study, reinforcing a species-specific response to environmental conditions.

5. FINAL REMARKS

These findings highlight the individualized responses of different species of trees to the impacts of increased temperatures in response to climate change, thus indicating a notable resilience to rising temperatures in both seed germination and plant initial establishment in tropical enviroments. It underscores the importance of conducting species-specific studies to gain a nuanced understanding of Atlantic Forest regeneration in the face of climate change and its associated implications. In a future characterized by warmer conditions, only those more resilient species may prove capable of successfully regenerating. This could lead to altered community dynamics across the ecological succession gradient. Given the Atlantic Forest's rich biodiversity, a generalized interpretation of these effects may be unrealistic. Considering the extensive coverage of this biome and its provision of essential ecosystem services, some linked to economic and food security, there is an urgent need for further research in this field.

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APPENDIX

Appendix A. Graphic result of FAMD analysis

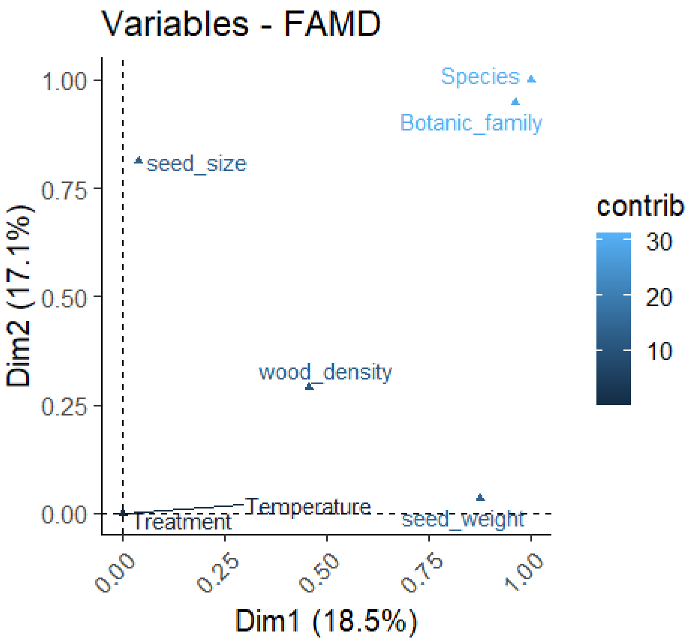

Figure 1: Graphic result of FAMD analysis. The blue color scale indicates the degree of contribution of that variable to the data distribution. The lighter the shade of blue, the greater its contribution to the

data. In this way, a well-defined grouping is observed between the traits "Species" and “Botanic family" in comparison to the others, in which it was responsible for the highest contribution.

Appendix B. Exploratory graphics: heat wave and germination temperature on plant development

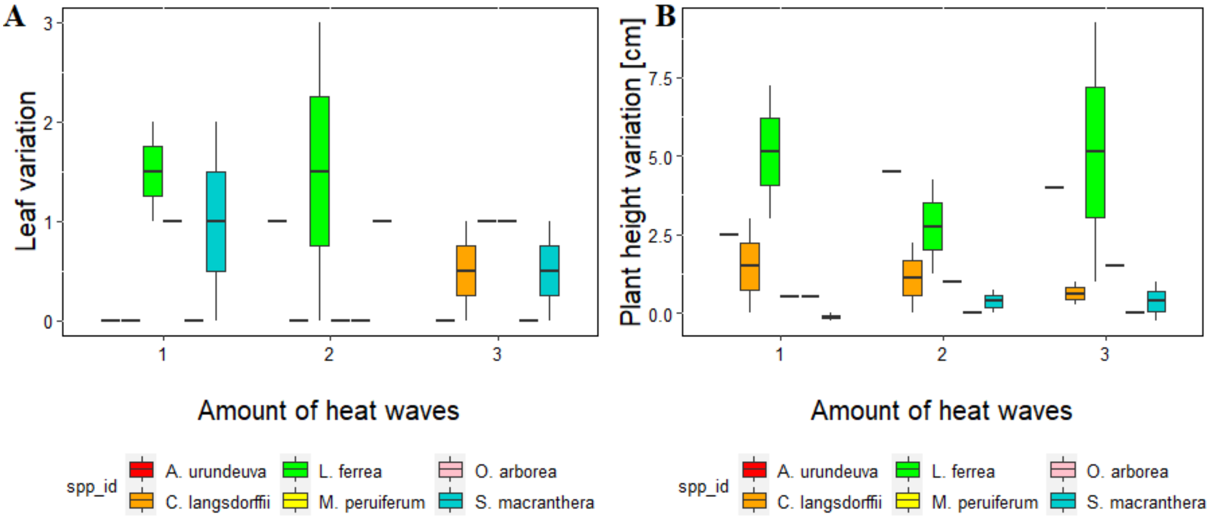

Figure 2: In this figure is represented the leaf variation (A) and the height variation (B) across the heat wave cycles in each species used in the study, as shown in the legend.

Appendix C. Seed pictures

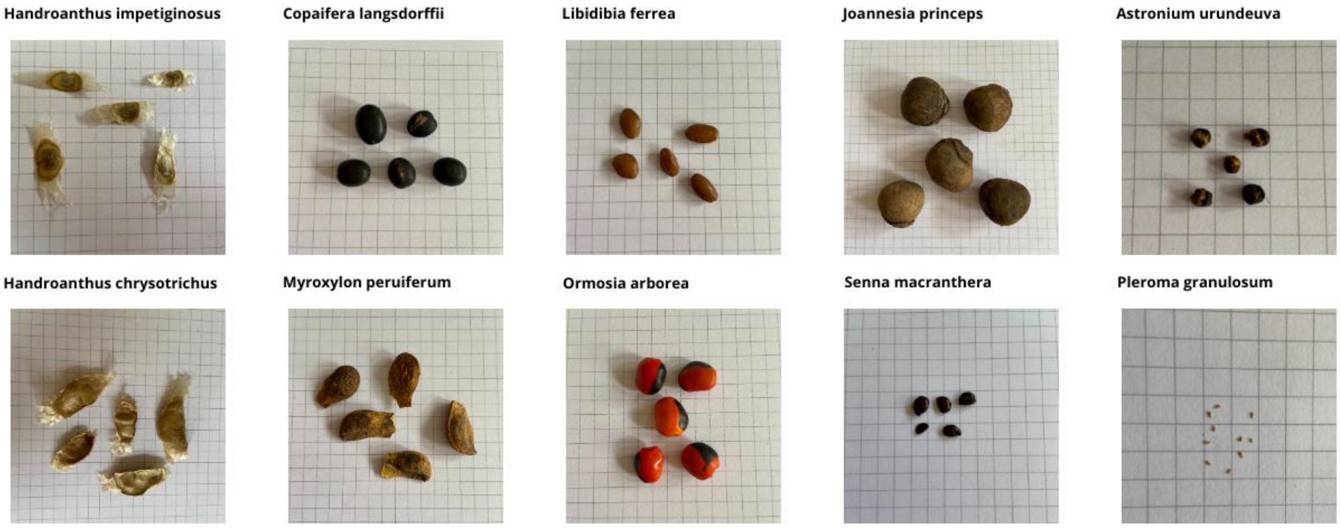

Figure 3: Picture of each species and seed used in the experiment.