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DEHYDRATION TOLERANCE AND STORAGE SENSITIVITY OF *Campomanesia adamantium* SEEDS

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Abstract

Cultivating native fruit species depends on the existence of technical and scientific information. In this context, studies on propagation are the basis for other investigations. *Campomanesia adamantium* is propagated by seeds, and quality seeds guarantee the formation of high-performance plants in the field. This study aimed to analyze the dehydration tolerance and storage sensitivity of *Campomanesia adamantium* seeds. Experiment 1 evaluated the physiological quality of seeds with moisture contents of 43, 30, 26, 23, 18, 15, and 5%. Experiment 2 determined the seed moisture content, germination, and vigor of seeds depulped and immediately stored at 16 and 25°C, for 25 and 50 days. Seed viability was not affected by dehydration up to 15% of moisture content but decreased at 5%. Drying was accompanied by reduced seed vigor and seedling mass. The germination of unstored seeds was superior to stored ones. Storage at 16°C for 25 days was promising to maintain seed viability. The seeds showed intermediate recalcitrant behavior. Dehydration below 30% reduced vigor, while 5% affected viability. *Campomanesia adamantium* seeds can be stored for 25 days at 16°C in permeable packaging that maintains approximately 10% of moisture, with germination higher than 60%.

Keywords: Cerrado plants. Desiccation tolerance. Viability. Vigor.

1. Introduction

Campomanesia adamantium (Cambess.) O. Berg. belongs to the Myrtaceae family, is native to Brazil, and is found mainly in the Cerrado biome, featuring tropical savannah vegetation. The fruit of this plant is popular *in natura* because of its aroma, flavor, and high vitamin C concentration. The leaves are used in homeopathic treatments for intestinal problems and urinary tract infections. The fruit can also be used to make preserves, ice cream, and flavoring in distilled alcohol (Vallilo et al. 2006; Coutinho et al. 2010).

Seed germination is the most common way to propagate species of the *Campomanesia* genus. However, *C. adamantium* seeds have shown low germination rates, sensitivity to drying and storage, and slow seedling development in the field and were classified as recalcitrant (Melchior et al. 2006; Dresch et al. 2014, 2015a).

Seeds are classified as recalcitrant when they undergo less drastic drying processes during maturation and do not have defined limits between maturation and germination. They are characterized by a low tolerance to moisture content reductions and low-temperature storage, therefore, presenting limited storage potential (Barbedo et al. 2013; Marcos-Filho 2015). Approximately 8% of the world's plant species produce seeds sensitive to water loss (Wyse et al. 2017), while humid tropical and subtropical rain forests have the highest incidence (18.5%) of this type of seeds.

Dehydration tolerance depends on the drying rate, seed development stage, and species, among other factors (Berjak and Pammenter 2000; Marcos-Filho 2015). According to Marcos-Filho (2015), seeds with lower dehydration tolerance can be classified as either recalcitrant or intermediate. Recalcitrants are typically sensitive to water loss (e.g., *Avicennia marina*), while intermediates are more tolerant to dehydration but less resistant to low temperatures (e.g., *Coffea*).

Studies from recent decades have shown more diverse seed behavior after drying, revealing that the criteria used to define orthodox and recalcitrant seeds may be too limited (Walters 2015). Intermediate seeds have characteristics of both orthodox and recalcitrant seeds, as initially reported by Ellis et al. (1990).

Intermediate-recalcitrant seeds tolerate desiccation of approximately 10 to 13% but become less viable at lower moisture levels (Fonseca and Freire 2003). This "new category" shows that seed response to water loss is complex and, according to Barbedo et al. (2013) and Walters (2015), should not be simplified to the point of establishing only two opposite seed categories.

Seeds called recalcitrant, which are sensitive to dehydration, can germinate immediately after being released from the plant, mainly because of their high water content at maturity. This condition relates to an absence of mechanisms that provide tolerance to water loss, causing shorter periods of seed viability. Consequently, seeds with high moisture levels at maturation can only be stored for short periods under conditions that prevent dehydration. The length of hydrated storage is limited by the germination that may occur without additional water and the seed-related fungi that proliferate in this moist environment (Berjak et al. 2013; Castro et al. 2017).

Alternative methods for storing recalcitrant seeds, such as the partial dehydration to tolerable moisture levels (Scalon et al. 2012), which is a simple and inexpensive technique with the disadvantage of allowing short storage times and cryopreservation (Endoh et al. 2017), have appeared to reduce the harmful effects of high moisture contents, allowing long storage times but without success for large seeds. Also, the efficiency of this protocol requires knowing the desiccation tolerance limits of each species and the seed development stage, among other factors (Marcos-Filho 2015).

The literature reports that *C. adamantium* has recalcitrant seeds, but viable seeds with water content below 5% have been identified (Dresch et al. 2014, 2015b). Therefore, the physiological behavior of *C. adamantium* seeds was analyzed after dehydration, and germination and vigor were evaluated after storage.

2. Material and Methods

C. adamantium fruits were collected from 360 previously identified matrices (plant age ~13 years), between October and November 2016. The plants were located in Ipameri, GO, Brazil (17º43'19''S, 48º09'35''W, altitude 820 m). The climate of the region is classified as Cwa mesothermal humid, with an annual rainfall of 1,450 mm and an average annual temperature of 25ºC.

The flowers were marked at anthesis, and the fruit was collected intact between 50 and 65 days after flowering. The pulp was manually removed from the fruit after breaking the skin with a pincer. The seeds were fermented for 48 hours in a 25% ammonium hydroxide solution. After fermentation, the seeds were washed under running water for five minutes, spread out in a single layer on germination paper, and placed in a darkened area to dry superficially for 30 minutes. This process took place in the laboratory at 25°C and 53% of relative humidity.

Experiment 1 – Seed dehydration tolerance

Immediately after the superficial drying, the moisture content of the seeds was determined. This characteristic was expressed as a percentage of wet weight and determined from two replicates of 20 seeds dried in an oven at 105°C ± 3°C for 24 hours (Brasil 2009).

Seven samples of approximately 400 seeds each were selected. One of the samples was reserved for the treatment with the highest predetermined moisture content (43%).

Seed moisture levels were reduced to test dehydration sensitivity. Therefore, the seeds of the remaining six samples were dried under single-layer stainless steel screens in a forced-air oven (32°C ± 3°C, 27% of relative humidity) until reaching moisture levels of 30, 26, 23, 18, 15, and 5%. The moisture levels were determined by monitoring the seed mass at regular intervals. The final mass was predetermined using pre-established moisture levels (Eq. 1) (Sacandé et al. 2004):

$$\text{Eq. 1} \quad \text{Final mass (g)} = \frac{[(100 - \text{initial moisture level}) \times \text{initial mass}]}{100 - \text{desired moisture level}}$$

After dehydration, the seeds were sealed in polyethylene packages for 48 hours until reaching hygroscopic equilibrium in a laboratory at 25°C and 53% of relative humidity. Next, the moisture content of each sample was determined with the previously described oven method.

Seeds from each moisture level (43, 30, 26, 23, 18, 15, and 5%) were used to evaluate the physiological quality. Eight replicates of 25 seeds were placed on two sheets of germination paper, covered by a third sheet, and placed in germination boxes. The papers were moistened with deionized water equal to 2.5 times the dry mass of the paper. The boxes were maintained in a germination chamber at a constant temperature of 25ºC and under white light. The number of seeds with primary root protrusion and the number of normal seedlings were evaluated (Brasil 2009). These evaluations were performed every three days to determine the germination speed index (GSI). First count (FC) data were obtained at 20 days, and the final germination count (G) at 42 days, expressed as percentages.

Seedling fresh mass (SFM) was determined with eight replicates of 10 seeds and by wetting the germination papers as described in the germination test. The mass of individual normal seedlings was measured after 42 days in the germination chamber under white light and at a constant temperature of 25°C. Means per plant were expressed as mg seedling^{-1}.

There was no sign of germination (root protrusion) at the 5% moisture level, indicating a complete loss of viability. Thus, data from the 5% moisture content were excluded to avoid compromising the analysis. The experiment was completely randomized with six treatments and eight replicates. The model residuals were submitted to the Shapiro-Wilk normality test and Bartlett's homoscedasticity test. Having met all assumptions, G, FC, GSI, and SFM were submitted to analysis of variance and polynomial regression.

Experiment 2 – Seed storage

Five other samples (approximately 400 seeds each) were taken from the superficially-dried seeds with 43% of initial moisture content.

One of these samples was used as a control (test) and tested without storage. The remaining four samples were stored and sealed in 0.08-mm polyethylene bags for 25 and 50 days in two environments: approximately 16 and 25°C.

The temperature in the first environment was controlled by air conditioning, while the temperature of the other laboratory environment fluctuated with the tropical climate of the region. These temperatures were verified daily with a digital thermohygrometer. In the air-conditioned room, the temperature averaged 16.4°C and ranged from 14.4°C to 19.3°C, while relative humidity ranged from 31% to 99%. In the non-air-conditioned laboratory environment, the temperature averaged 25.7°C and ranged from 13.0°C to 34.6°C, while relative humidity ranged from 30% to 96%. The average temperatures were used to identify the treatments.

After 25 and 50 days of storage, the moisture content of the seeds was evaluated, and G and FC were determined as in Experiment 1.

The experiment was completely randomized in a 2 × 2 + 1 factorial scheme (two temperatures, two storage periods, and one control). Model residuals were submitted to the Shapiro-Wilk normality test and Bartlett's homoscedasticity test. Having met all assumptions, G and FC were submitted to analysis of variance and evaluated at 95% confidence intervals.

3. Results

Experiment 1 – Seed dehydration tolerance

The seed moisture content reached after drying was close to the desired levels, varying by at most 0.94 percentage points (Table 1), thus demonstrating the efficiency of the seed-drying methodology for this species.

Table 1. Targeted and actual moisture levels after drying *Campomanesia adamantium* seeds.

Target moisture level (%)	Actual moisture level (%)	Standard deviation (%)
43.00	43.33 a	1.18
30.00	29.66 b	1.83
26.00	25.76 c	1.35
23.00	23.06 c	0.09
18.00	18.47 d	0.54
15.00	15.90 d	2.10
5.00	5.94 e	1.40

Means followed by the same letter do not differ from each other by the SNK (Student-Newman-Keuls) test.

Root protrusion and normal seedling formation were higher than 90% at 42 days after sowing (G) for all moisture levels (except 5%) (Figure 1A). Seed viability was lost at the 5% seed moisture level. However, the seed viability evaluated with the germination test was not compromised by moisture reductions up to almost 15%, as demonstrated by insignificant regression coefficients.

Germination tests provide a snapshot of seed health but do not provide information on the viability thresholds that define seed longevity (Fleming et al. 2017). Therefore, other tests, such as vigor tests, are needed to predict potential losses from dehydration in seeds that tolerate moisture loss. Therefore, germination speed (FC and GSI) and seedling development (SFM) were also evaluated.

Regression models of the first germination count (FC) showed that reduced moisture content did not affect seed vigor as measured by root protrusion. In other words, there was no characteristic behavior that explained root protrusion according to seed moisture content for this species (Figure 1B). Additionally, as in G, root protrusion in the FC was higher than 90% for seeds with moisture content as low as 15%.

Conversely, the percentage of normal seedlings in FC declined continuously with decreases in seed moisture. Thus, seed vigor was strongly affected by dehydration. Only seeds with moisture content higher than 26% maintained high vigor (nearly 80% of normal seedlings in the FC). Seed vigor was highly reduced at 15% moisture content with only 54% of normal seedlings.

Seed vigor of *C. adamantium*, as indicated by GSI, was strongly affected by seed moisture levels (Figure 1C). Progressive dehydration levels were accompanied by sharp linear reductions in GSI, as indicated by primary root protrusion. This reduction was already substantial at 30% moisture. However, regarding the formation of normal seedlings, GSI fell linearly but less markedly, with decreasing seed moisture.

Reduced seed moisture content was associated with lower seedling mass (Figure 1D), which shows that the deleterious effects of seed dehydration continue to seedling development. The mass of seedlings grown from seeds with 15% moisture was markedly lower.

For all variables (G, FC, GSI, and SFM), 5% seedling moisture content did not produce seedlings or even start the germination process. Despite the continuous drop in seed physiological quality with dehydration, as shown by seed vigor and seedling development tests (Figure 1B, C, and D), seedlings continued to form at moisture levels as low as 15%. Figure 1A shows that at 15% moisture content, more than 90% of the seedlings were normal in the germination test.

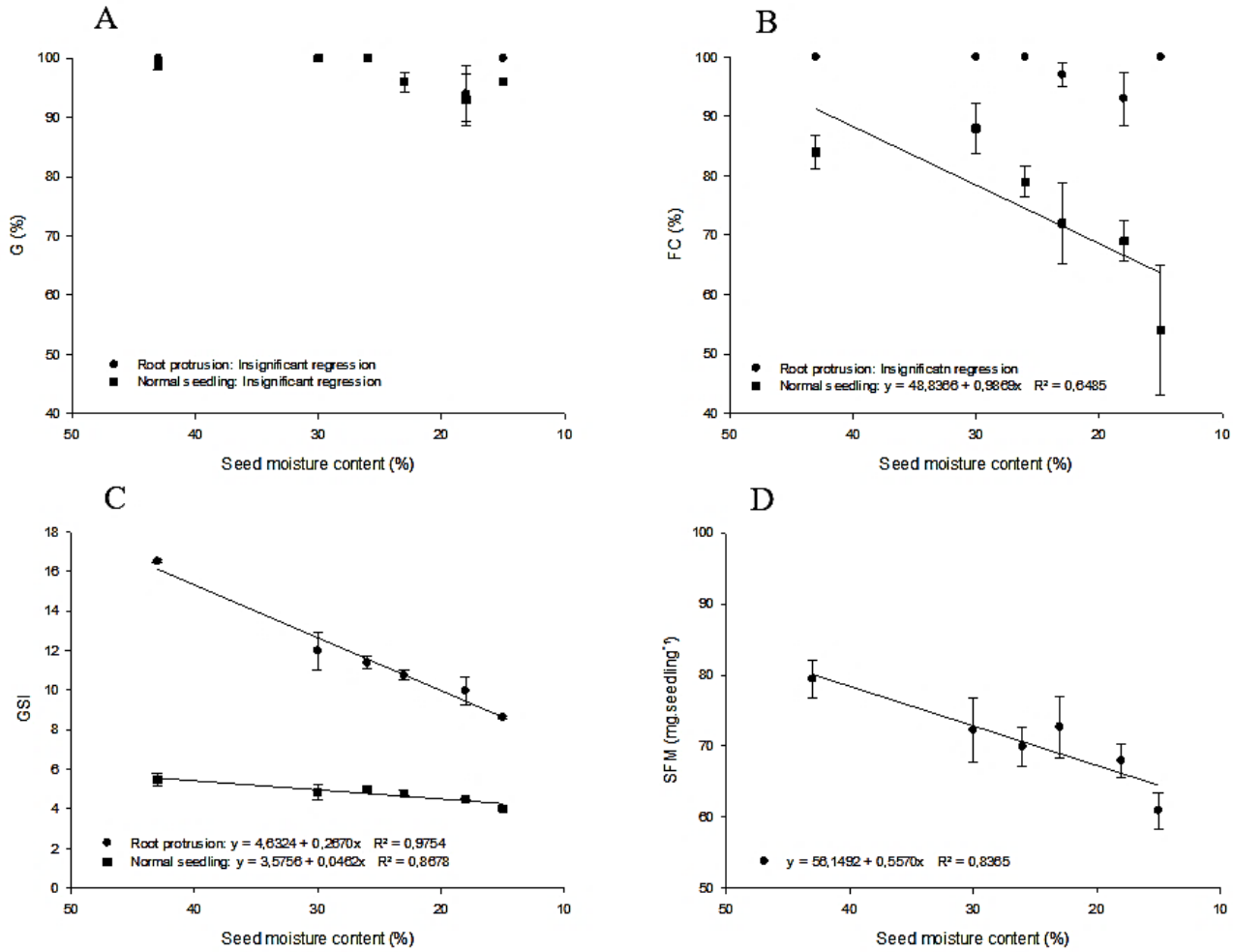

Figure 1. A - Germination (G), B – First germination count (FC), C – Germination speed index (GSI), and D – Seedling fresh mass (SFM) of *Campomanesia adamantium* seeds according to seed moisture content.

Experiment 2 – Seed storage

The moisture content of the seeds stored for up to 50 days was reduced between 9.34 and 5.79% (Table 2). These values show that the seed packaging allowed exchanging water vapor with the external environment until reaching hygroscopic equilibrium.

Table 2. Initial moisture levels and after storing *Campomanesia adamantium* seeds at two temperatures (16 and 25°C) and for two periods (25 and 50 days).

Storage conditions (Temperature - °C: Period - days)	Initial moisture level (%)	Moisture level after storage (%)
Control (ctrl)	43.06	*
16:25	43.06	9.34
16:50	43.06	6.85
25:25	43.06	7.11
25:50	43.06	5.79

* No storage.

Unstored seeds (test) had G values higher than 80% for root protrusion and normal seedlings. However, regarding FC, this behavior was maintained only when evaluating root protrusion. When FC was evaluated based on normal seedlings, unstored seeds showed values higher than 70% (Figure 2).

Combining the lower temperature (16°C) and shorter storage time (25 days) may be promising for *C. adamantium* seeds. This combination yielded G values of 74 and 64% for root protrusion and normal seedlings, respectively (Figure 2A and B).

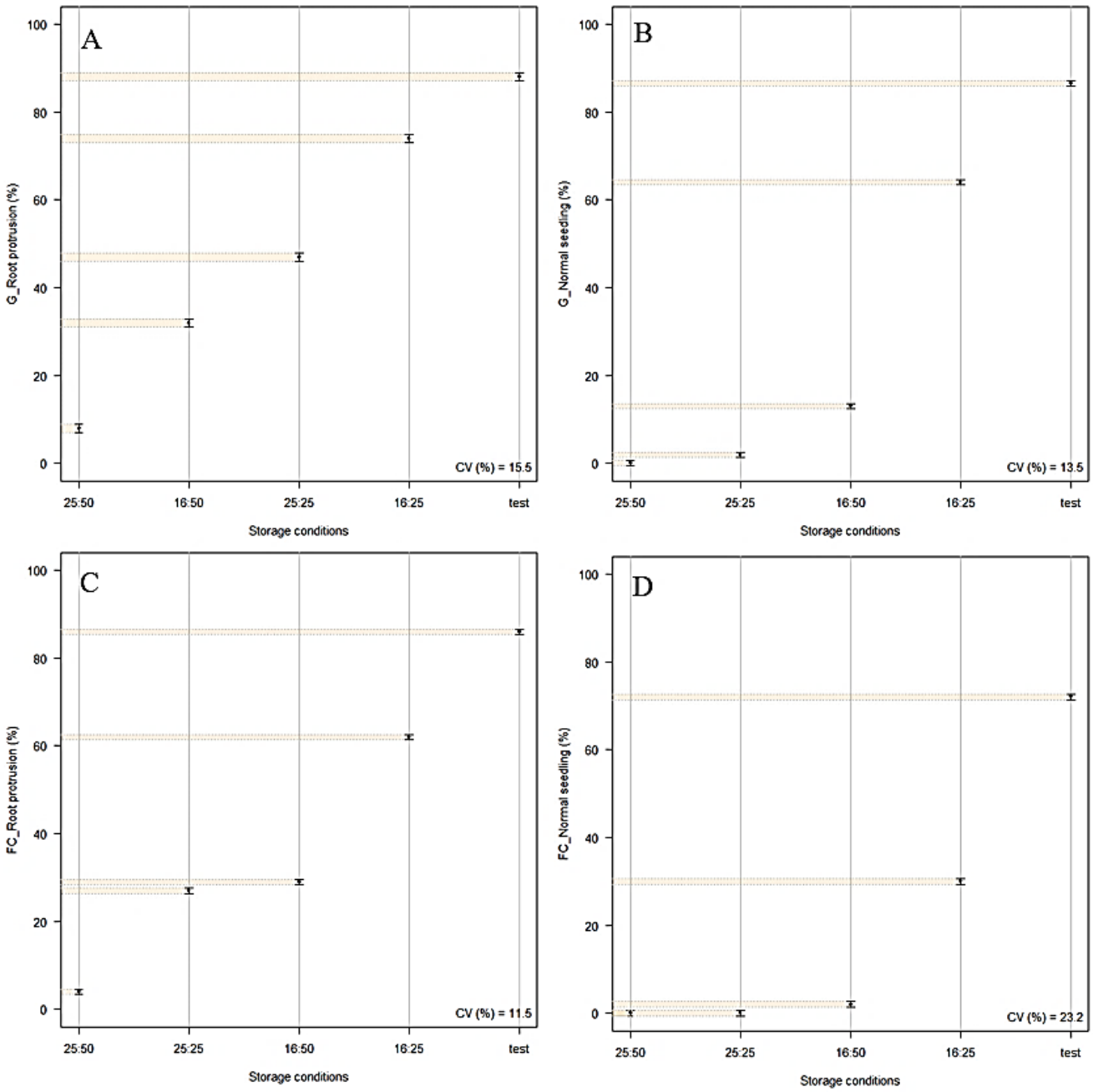

Figure 2. A - Germination (G) determined by root protrusion, B - Germination (G) determined by normal seedling formation, C – First germination count (FC) determined by root protrusion, and D - First germination count (FC) determined by the normal seedling formation of *Campomanesia adamantium* seeds either unstored (ctrl) or according to storage combinations at two temperatures (16 and 25°C) and for two periods (25 and 50 days).

Combining 25°C and 50 days produced G values close to zero, probably due to the moisture content (5.79%) obtained under these conditions. According to Walters (2000), moisture levels may be lethal when viability is completely lost. Therefore, experiments 1 and 2 showed that 5% is the lethal moisture level for *C. adamantium* seeds.

Figures 2C and D show that seed vigor was strongly affected by storage conditions. At the beginning of the germination process (root protrusion), the germination rate was higher than 70% for the storage combination of 16°C and 25 days and higher than 60% when evaluating normal seedlings.

Damage to seed vigor (FC) was high for all other storage combinations, showing the deleterious effects of long-term storage on *C. adamantium* seeds, regardless of the temperature. The formation of normal seedlings was nearly zero after storage of 50 days at 16°C and equal to zero after storage of either 25 or 50 days at 25°C.

4. Discussion

Experiment 1 – Seed dehydration tolerance

It took approximately 10 hours to dry the seeds to the lowest target moisture level. This is significant because, according to Marcos-Filho (2015), the dehydration rate affects seed tolerance to moisture loss. The same author defines rapid drying as a process that lasts a few hours. The faster the drying, the lower the water content tolerated by the seed without affecting viability (Pammenter et al. 2000).

Dresch et al. (2014, 2015b) evaluated the survival of seedlings from *C. adamantium* seeds with 10 and 5% moisture contents and found that these levels compromised seedling development after 30 days of storage. However, when the seeds were not stored, the seedlings did form at these same moisture levels. Our study showed that seeds with 5% moisture did not initiate germination, probably because dehydration tolerance depends on the stage the seeds are removed from the mother plant. Tolerance increases during the accumulation of reserves in recalcitrants that dehydrate during maturation (Finch-Savage 1996). Furthermore, some of the dehydration tolerance results from LEA protein accumulation, which occurs in the final stages of seed development (Long et al. 2015). Thus, studies on dehydration tolerance must harvest seeds according to the maturation process of the species, which in the present study was between 50 and 65 days after floral opening. Moreover, differences between the moisture content of the reserve material and the embryonic axis may complicate the comparison of results from different studies (Marcos-Filho 2015).

Moisture in recalcitrants relates to the structure of macromolecules and cell membranes. Thus, moisture losses change metabolic systems and damage, especially, cell membranes (Farrant et al. 1988; Marcos-Filho 2015), which may affect the speed of reactions to seedling formation. Consequently, seed vigor is reduced to zero viability when seeds are dried to levels not tolerated by the species.

The physiological quality of *Campomanesia pubescens* seeds was affected at dehydration levels below 30%. Decreasing moisture content from 35 to 4% reduced germination and vigor (Dousseau et al. 2011). Similarly, the first germination count of *Euterpe edulis* seeds was drastically affected by drying, and only undried seeds had higher vigor (Martins et al. 2009).

Dresch et al. (2015a) also studied *C. adamantium* and showed a similar linear decrease in GSI after both rapid (days) and slow (hours) drying processes. Similar data were also obtained by Martins et al. (2009), who worked with *Euterpe edulis* seeds (considered sensitive to drying) and concluded that GSI was sufficiently sensitive to detect gradual reductions in seed vigor with increased drying times. Alves et al. (2008) also showed lower GSI in *Talisia esculenta* seeds after 44 hours of drying.

The present study performed vigor tests to determine the speed of the germination process (FC and GSI). The effects of reducing seed moisture content are more readily shown by seed vigor because high moisture levels in seeds that tolerate dehydration are associated with protein integrity maintenance, endonuclease activation, and DNA conformation. Thus, dehydration leads to protein denaturation, cell membrane damage, and other effects that contribute to slower germination (Farrant et al. 1988; Osborne 2000).

The data of reduced seed moisture content associated with lower seedling mass agree with those obtained by Goodman et al. (2005), which showed reduced seedling development (shoots and roots) from red oak seeds with moisture content below 30%. The same study also showed that this reduction in seedling development was further accentuated at moisture levels below 20%. Alves et al. (2008) also reported reduced seedling length in *Talisia esculenta* grown from seeds submitted to natural drying for up to 120 hours.

Orthodox seeds tolerate reductions in moisture content below 6% (wet basis), while recalcitrants tolerate moisture contents above 16% (wet basis). Recent studies on seeds susceptible to desiccation showed that limiting this classification to either orthodox or recalcitrant oversimplifies a complex issue (Walters 2015). A third category (intermediate) must be added to classify seeds that can be dried to moisture levels lower than those tolerated by typical recalcitrants but not as low as those by orthodox seeds (Ellis et al. 1990; Pérez et al. 2012).

Dresch et al. (2014, 2015b) studied the same species and found that even at 5% moisture, viability was not completely lost. These data show that *C. adamantium* seeds do not fit the definition of recalcitrants but are described better as intermediates.

According to Marcos-Filho (2015), the minimum moisture content tolerated by recalcitrants ranges from 20 to 35%, but these levels should be assessed carefully because differences between the moisture content of the embryonic axis and the reserve tissues of the seeds may affect interpretation.

Eugenia pleurantha seeds with high moisture content germinated at 87%, while seeds with approximately 10% moisture germinated at 36%, and seeds at 7.4% did not germinate at all, suggesting intermediate behavior. Thus, DNA degradation occurred at the 7.4% level (Masetto et al. 2008).

Moisture content limits are not direct measures of the stress intensity tolerated by seeds, nor are they measures of cellular response to water stress (Walters 2015). Considering there are species that do not fit the orthodox and recalcitrant classifications, further studies on seeds sensitive to dehydration should be cautious about assigning categories and, most importantly, use tools that can quantify the damage caused by drying. The more seed behavior is analyzed and understood, the more difficult it is to categorize seeds (Barbedo et al. 2013).

Experiment 2 – Seed storage

Maintaining high moisture content would protect against membrane disorganization, support repair mechanisms and important enzymes, and lower the incidence of imbibition damage. Nevertheless, maintaining high moisture content is one of the main challenges in storing recalcitrant seeds (Marcos-Filho 2015).

Unstored seeds were superior to stored seeds regardless of storage time and temperature, demonstrating the dehydration sensitivity of these seeds. According to Walters (2015) and Michalak et al. (2015), seeds with short longevity, regardless of drying or cooling procedures, can also be classified as intermediate.

Santos et al. (2010) determined that moisture levels below 12% were lethal for *Hancornia speciosa* seeds. The loss of viability after dehydration and storage may result from the desiccation process that causes cytoplasm solidification and newly-formed spatial relationships between molecules that determine whether and for how long viability is maintained (Walters 2015).

However, these levels should be used with caution because they depend heavily on metabolic activity, dehydration rates, and other seed-specific factors (Pammente and Berjak 2000; Walters, 2015). This finding could help understand why other studies on *C. adamantium* have not shown a complete loss of viability at the 5% moisture level (Melchior et al. 2006; Dresch et al. 2014, 2015a, b).

In our study the seed vigor was strongly affected by storage conditions, this makes sense because moisture-sensitive seeds can be stored successfully with partial dehydration to levels tolerated by the species and in vapor-impermeable packaging (Marcos-Filho 2015; Vieira et al. 2008). In the present study, partial dehydration was successful at 16°C and 25 days, but moisture levels were not maintained during storage, as evidenced by the storage combination of 16°C and 50 days.

Similar results of survival near zero of seeds were found when storing *C. adamantium* seeds at a moisture level below 15% for 30 days (Dresch et al. 2015b).

5. Conclusions

C. adamantium seeds show intermediate dehydration sensitivity. Reductions in seed moisture below 30% compromise seed vigor, while 5% moisture content affects viability.

C. adamantium seeds should be stored for 25 days at 16°C in permeable packaging that maintains moisture content close to 10%, with germination higher than 60%.

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