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Seed Technology/ Original Article

Physiological and biochemical quality of paradise nut seed

Abstract – The objective of this work was to evaluate the physiological quality of *Lecythis pisonis* seed and their biochemical changes after being subjected to accelerated aging. Seed were arranged in a randomized block design consisting of seven accelerated aging durations (0, 24, 48, 72, 96, 120, and 144 hours), with four replicates of 25 seed each. Moisture content (%) was determined, and seed vigor, seedling emergence and growth (%), and the biochemical composition of seed were analyzed. Accelerated aging for 120 hours, at 40 °C, resulted in higher carbohydrate concentration and seedling emergence, and in one of the lowest lipid contents. Protein concentration decreased, whereas starch and fiber contents increased with accelerated seed aging. Seedling emergence from seed subjected to 144 hours of aging declined sharply, and seed moisture content rose significantly. Seed of *L. pisonis* exhibit high physiological quality.

Index terms: *Lecythis pisonis*, phenotypic plasticity, seed biochemistry, seed physiology.

Qualidade fisiológica e bioquímica de sementes de sapucaia

Resumo – O objetivo deste trabalho foi avaliar a qualidade fisiológica das sementes de *Lecythis pisonis* e suas alterações bioquímicas após serem submetidas ao envelhecimento acelerado. As sementes foram dispostas em delineamento de blocos ao acaso, composto por sete períodos de tempo de envelhecimento acelerado (0, 24, 48, 72, 96, 120 e 144 horas), com quatro repetições de 25 sementes cada uma. Determinou-se o teor de água (%), e analisaram-se o vigor, a emergência e o crescimento das plântulas (%) e a composição bioquímica das sementes. O envelhecimento acelerado das sementes por 120 horas, a 40 °C, resultou em maior concentração de carboidratos e emergência de plântulas, e em um dos menores teores de lipídios. A concentração de proteína diminuiu, enquanto os teores de amido e fibra aumentaram com o envelhecimento acelerado das sementes. A emergência de plântulas obtidas de sementes submetidas a 144 horas de envelhecimento declinou drasticamente, e o conteúdo de água das sementes aumentou acentuadamente. Sementes de *L. pisonis* apresentam alta qualidade fisiológica.

Termos de indexação: *Lecythis pisonis*, plasticidade fenotípica, bioquímica de sementes, fisiologia de sementes.

Caroline Palacio de Araujo (✉)
Universidade Federal do Espírito Santo, Jerônimo Monteiro, ES, Brazil.
E-mail: carolinepalacio@yahoo.com.br

Natasha Vieira de Oliveira
Universidade Federal do Espírito Santo, Jerônimo Monteiro, ES, Brazil.
E-mail: natashav.oliveira@gmail.com

Thuanny Lins Monteiro
Universidade Federal do Espírito Santo, Jerônimo Monteiro, ES, Brazil.
E-mail: thuannyer@gmail.com

Ingridh Medeiros Simões
Universidade Federal do Espírito Santo, Jerônimo Monteiro, ES, Brazil.
E-mail: simoes.ingridh@gmail.com

Joana Silva Costa
Universidade Federal do Espírito Santo, Jerônimo Monteiro, ES, Brazil.
E-mail: joanasilvacosta9@hotmail.com

Débora Pellanda Fagundes
Universidade Federal do Espírito Santo, Alegre, ES, Brazil.
E-mail: debora.pellanda@yahoo.com.br

Edilson Romais Schmildt
Universidade Federal do Espírito Santo, São Mateus, ES, Brazil.
E-mail: e.romais.s@gmail.com

José Carlos Lopes
Universidade Federal do Espírito Santo, Alegre, ES, Brazil. E-mail: jcufes@bol.com.br

Rodrigo Sobreira Alexandre
Universidade Federal do Espírito Santo, Jerônimo Monteiro, ES, Brazil.
E-mail: rodrigosobreiraalexandre@gmail.com

✉ Corresponding author

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Introduction

Lecythis pisonis Cambess. is an unconventional tropical tree with the capacity to produce functional nuts. More than 14 types of phenolic compounds have been observed in its nuts, and 22 types in its shells, making it a source of natural antioxidants with a significant abundance of flavonoids, phenolic acids, and essential nutrients (Demoliner et al., 2018). Seed of *L. pisonis* are oleaginous and rich in unsaturated fatty acids, making them valuable sources of palmitic, linoleic, and oleic acids (Araujo et al., 2023).

Oil-rich seeds have a high lipid content, which makes storage conservation difficult due to crystallization processes (Ballesteros et al., 2019). Lipids are essential sources of energy during seed germination; however, they also make seeds more susceptible to deterioration during natural aging, due to lipid peroxidation (Naghisharifi et al., 2024). The chemical composition of seed influences their longevity during storage, making it essential both to understand the deterioration impacts on these reserves during aging and how this affects germination over time (Nadarajan et al., 2023).

Seed of *L. pisonis* exhibit germination difficulties associated with physical and physiological dormancy (Araujo et al., 2020; Duarte et al., 2022). They also require many days for seedling emergence, which occurs unevenly (Araujo et al., 2024). Currently, they are classified as intermediate seed, as they tolerate embryo dehydration to low moisture contents (15, 10, and 4%). However, they are sensitive to storage of about three months at low temperatures (-20 and -86 °C), according to Araujo (2024), who also observed that *L. pisonis* seed can be stored for up to one year at 6 °C, when packed in kraft paper bags.

Environmental factors have a direct influence on seed germination and can compromise essential attributes such as vigor. This parameter is strongly associated with the ability of seed to resist physiological damage, such as that caused by the natural aging process. In this context, the importance of the accelerated aging technique stands out, as it allows of the simulation of natural aging effects, enabling the identification of physiological damage that directly impacts seed vigor (Huang et al., 2020). The application of accelerated aging technique to *L. pisonis* seed is especially relevant, considering the scarcity of studies on the sensitivity of this species to storage and natural aging. In addition, *L. pisonis* seed have characteristics that suggest a high vulnerability to deterioration, such as high lipid content and high humidity (Araujo, 2024), factors that contribute to reduce their viability over time.

Therefore, the objective of this work was to evaluate the physiological quality of *L. pisonis* seed and their biochemical changes during deterioration, when they are subjected to accelerated aging.

Materials and Methods

Seed of *L. pisonis* were harvested from two parent trees located in the municipality of Laranja da Terra, in Espírito Santo state, Brazil, at the following geographical coordinates: tree 1 (19º47'5.49"S, 41º9'16.53"W), and tree 2 (19º47'1.0" S, 41º9'18.41"W). Seed were disinfested with alcohol at 70% for 1 min, and sodium hypochlorite at 2% for 10 min, followed by triple rinsing with distilled water.

Subsequently, the accelerated aging test was conducted in BOD (biochemical oxygen demand) germination chambers, regulated at 40 °C, and seed were placed on screens in Gerbox acrylic boxes filled with 40 mL of distilled water.

The experiment was carried out in a randomized complete block design, consisting of seven accelerated aging times (0, 24, 48, 72, 96, 120, 144 hours) and four replicates of 25 seed each.

Seed moisture content was determined at all accelerated aging times. Seed mass was weighed in an analytical balance, and then placed in an oven at 105±3 °C until a constant dry mass was achieved. The averages were applied to the following equation: U (%) = (FM-DM)/FM×100, where: U (%) is the percentage of water lost; FM is the fresh mass; and DM is the dry mass (Brasil, 2009).

After each accelerated aging period, seed were sown in 280 cm³ polyethylene tubes filled with Vivatto Slim Plus substrate (Technes, São Paulo, SP, Brazil), which were placed on benches covered with black shade cloth that provided 50% light intensity in a forest nursery. For each accelerated aging time, 100 seed divided into four replicates of 25 seed each were sown. After sowing, the parameters seedling emergence, emergence speed index (Maguire, 1962), and the mean time of emergence (MTE, days) (Labouriau, 1983) were evaluated daily for 120 days. For emergence calculations, the methodological guidelines described by Brasil (2009) were followed, with adaptations, considering emergence as the proportion of the total number of normal seedlings that emerged above the substrate, using the following equation: Emergence (%) = (number of normal emerged seedlings/total number of seed sown)×100.

After 120 days, the following analyses were conducted: shoot length (cm), primary root length (cm), stem diameter (mm), number of lateral roots, number of leaves, shoot dry mass (g), root dry mass (g), total dry mass (g), and Dickson's quality index (DQI) (Dickson, 1960).

During the experiment evaluation period, the daily monitoring of climatic conditions was also performed (Figure 1) for the following data: maximum temperature (Tmax) and minimum temperature (Tmin), using an analog thermometer; relative humidity (RH, %) using a Lambrecht aspiration psychrometer (Göttingen, Germany); and precipitation measurement, using a 150 mm rain gauge for precipitation index calculation (mm).

The biochemical analysis was performed on endosperm samples from seed of each treatment, using the modified methodology of Bligh & Dyer (1959). Samples were weighed (0.250 g) and dried in an oven at 45 °C, with four replicates per treatment. Initially, ethanol series (98%, 80%, and 50%) were performed, followed by the addition of 1.5 mL of chloroform. The samples were then kept in water bath at 80 °C, for 20 min, followed by centrifugation at 10,000 rpm for 10 min to obtain a hydrophilic liquid phase and a hydrophobic phase.

The precipitated hydrophobic portion from the extraction was used for the measurement of lipid content (Bligh & Dyer, 1959); after 12 hours rest, it was placed in an oven at 60 °C until reaching a constant weight. The content of total soluble sugars content was determined by adding 80% ethanol and 0.2% anthrone to the hydrophilic solution, followed by a water bath at 100 °C, for 15 min, and measurement using a spectrophotometer (Femto 700 Plus) at 620 nm wavelength of (Yemm & Willis, 1954).

For total soluble phenolic content, the extraction solution was diluted twice in 80% ethanol, followed by the addition of 10% Folin-Ciocalteu, and 4% sodium carbonate. The samples were kept in a dark chamber for 30 min, after which they were analyzed using a spectrophotometer at 760 nm wavelength (Swain & Hills, 1959). Protein content was determined by adding 0.2 mol L^{-1} potassium hydroxide (KOH) to the pellet, followed by a water bath at 75 °C for two hours. After centrifugation at 10,000 rpm for 10 min, the supernatant was removed. The extract was then diluted in 0.2 mol L^{-1} KOH and Bradford solution and left to rest for 10 min (Bradford, 1976). The measurement was performed using a spectrophotometer at 595 nm wavelength.

Starch content was determined by adding 3% hydrochloric acid (HCl) to the pellet obtained from the protein extraction (Mello et al., 2022). The samples were incubated in a dark chamber for three hours, followed by centrifugation at 10,000 rpm for 10 min. The supernatant was used for measurement using a spectrophotometer at 620 nm wavelength. Fiber content was quantified by drying the pellet resulting

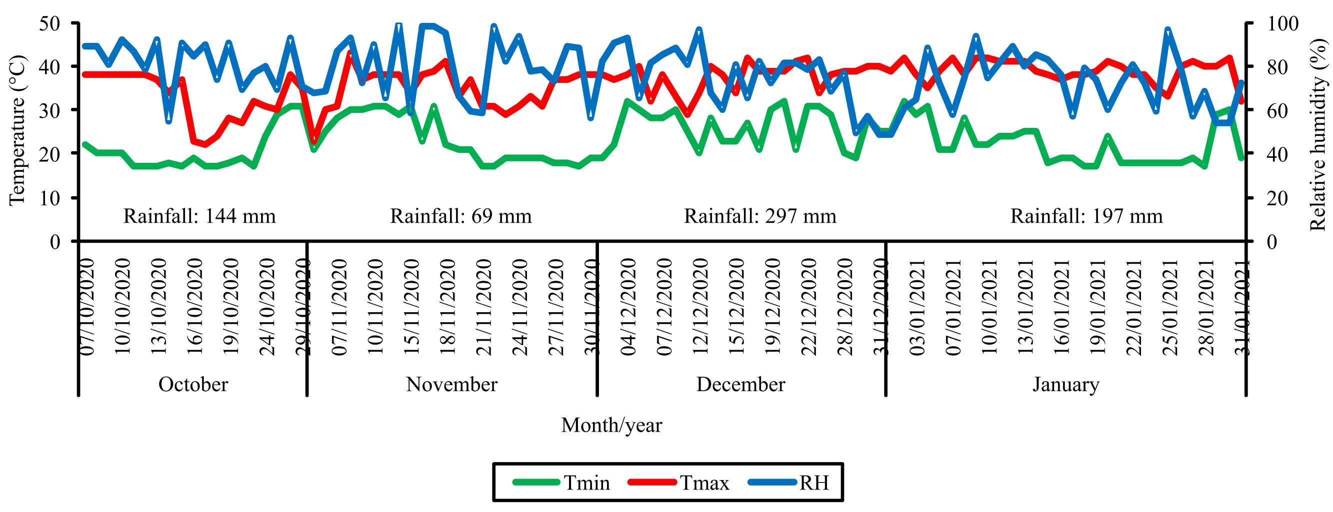

Figure 1. Climatic conditions during the evaluation period of seedling emergence in a forest nursery: Tmin, minimum temperature; Tmax, maximum temperature; RH: relative humidity.

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from starch extraction in an oven at 60 °C, until reaching a constant mass (Mello et al., 2022).

All characteristics were analyzed using the Dunnett's test, at 5% probability. This test was used for comparison because regression curves could neither be used to fit with linear nor nonlinear models. The means for the accelerated aging times from 24 to 144 hours were analyzed using the Scott-Knott's clustering test, at 5% probability level, using the 'Tratamentos.ad' package (Azevedo et al., 2022; R Core Team, 2022).

Results and Discussion

Lecythis pisonis seed showed the highest seedling emergence (92%) in the treatment of 120 hours of accelerated aging, surpassing that of the control (80%). In contrast, a drastic decline of seedling emergence (4%) was observed in 144 hours of aging (Figure 2).

The emergence speed index was higher in seed aged from 72 to 120 hours. The MTE was higher in the treatment of 144 hours of aging than that of the control, and the treatments of 24 and 48 hours had the shortest ones. The drastic decrease of emergence coincided with the increase of seed moisture content at the 144 hours' time point, which was 6.6% higher than the control.

The accelerated aging of *L. pisonis* seed acted as a stimulator of seedling emergence and vigor up to a certain period of time (120 hours) (Figure 2). One possible explanation is related to the resistance of *L. pisonis* seed to thermal stress conditions. These seed require thermal shocks at high temperatures, for short periods, to express their maximum vigor. However, the exposure to prolonged periods of stress leads to seed reduced viability and/or to abnormal seedling growth, with poorly developed root systems and shoots (Araujo et al., 2024).

The species *L. pisonis* exhibits slow and nonuniform seedling emergence, with low emergence rates (0 to 50%) when germinated at 25 °C (Rosa et al., 2020).

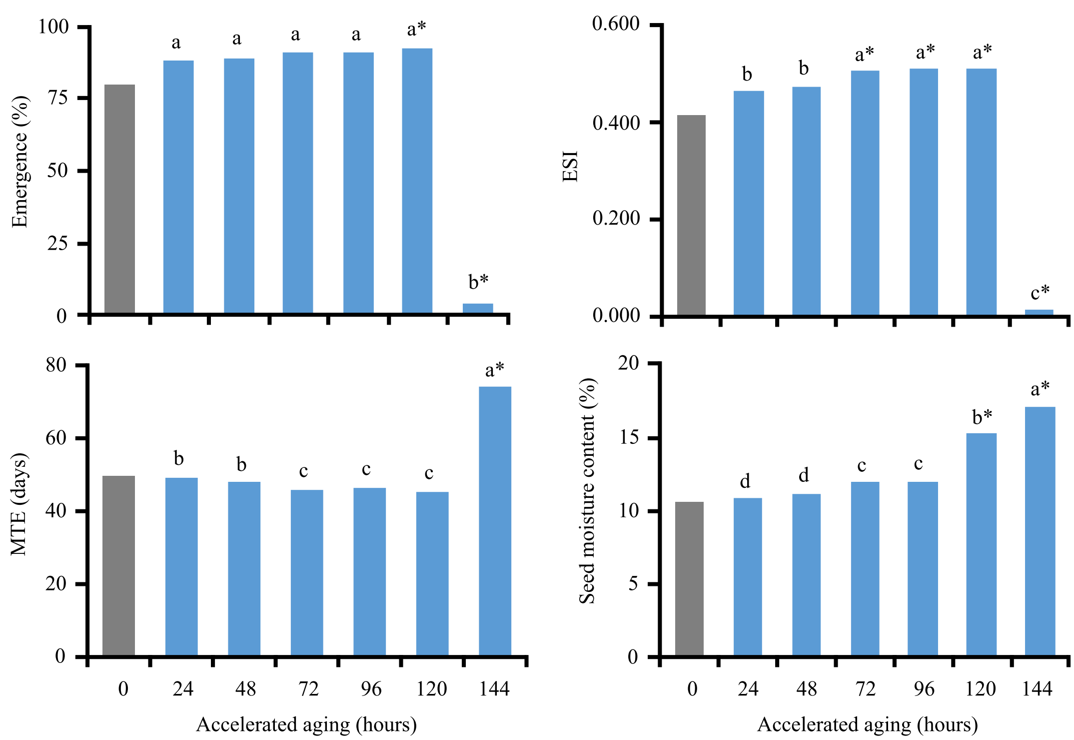

Figure 2. *Lecythis pisonis* seed aged at 40 °C, for periods of 0 (control), 24, 48, 72, 96, 120, and 144 hours: Emergence, seedling emergence (%); ESI, emergence speed index; MTE, mean time of emergence (days); and Seed moisture content (%). *Means differed significantly from the control, in the same column, by Dunnett's test, at 5% probability. Means for the accelerated aging times from 24 to 144 hours, followed by equal letters in the columns, do not differ significantly from each other, by Scott-Knott's mean grouping test, at 5% probability).

Some authors suggest that this may be due to physical and/or physiological dormancy of its seed (Araujo et al., 2020; Duarte et al., 2022), which have a hard and thick seed coat and are rich in lignin, which potentially hinders the germination processes (Rosa et al., 2020). Recent findings by Araujo et al. (2024) highlight that *L. pisonis* seed exhibit a high variation of seedling emergence (0 to 88%), depending on the applied germination temperature. For maximum emergence rate and vigor within a shorter period, the application of thermal shocks, under alternating temperatures of 30–45 °C (20 hours/4 hours, and 21 hours/3 hours) has been recommended (Araujo et al., 2024). These findings are consistent with the data observed in the present study, in which the controlled stress, up to a certain period, enhanced seed vigor.

Decrease of vigor and emergence of *L. pisonis* seedlings also coincides with the increase of seed water content, making them more susceptible to deterioration processes and pathogen proliferation. Increased moisture reduces the seed longevity and their metabolic activities, consequently raising the production of ROS, which causes cell damage (Farahani et al., 2025). The cytoplasmic viscosity decreases with increased water content, leading to metabolic processes related to seed deterioration, mainly through the oxidation of macromolecules such as proteins, lipids, and genetic material (Rej et al., 2024).

Seed accelerated aging of up to 120 hours did not negatively influence most of the growth characteristics analyzed in *L. pisonis* seedlings (Figure 3). The shoot length at aging times from 24 hours to 120 hours did not differ from the control, showing lower values at 144 hours. It was also observed that the root length was higher at 120 hours and 144 hours, with a higher number of lateral roots in the treatment of 120 hours. Stem diameter and leaf number did not differ among treatments, in comparison with the control, and total dry mass and DQI were not significant among seed aged from 24 hours to 120 hours, in comparison with the control, with lower values at 144 hours.

These results indicate that the accelerated aging of *L. pisonis* seed up to 120 hours did not cause a sufficient cellular damage to impair the normal growth of seedlings, which preserved their morphological and physiological characteristics. This can be explained by the high vigor of *L. pisonis* seed, whose enzymatic antioxidant system (catalase, peroxidase, and superoxide dismutase) proves to be effective under stressful high-temperature conditions (Araujo et al., 2024). Vigorous plants have a higher chance of success, when taken to the field, with the development of a well-formed root system and aerial parts (shoots) being essential (Guimarães et al., 2024).

In the context of seed conservation, reserve compounds play an important role in maintaining viability and vigor during storage (Nadarajan et al., 2023). In the present study, the highest concentration of carbohydrates was observed in 120 hours of aging, with 4.7 mg g^{-1} increase in comparison with the control (0.47%) (Figure 4). Seed aged for 120 hours may have exhibited an adaptive response to the controlled stress, increasing the metabolic activity and the conversion of reserve substances into carbohydrates, allowing of energy accumulation and promoting germination. Carbohydrates are associated with the desiccation tolerance in seed (one example of which is the raffinose family of oligosaccharides); they contribute to embryo desiccation tolerance and provide greater stability to cell membranes, thereby preventing oxidative damage (Cai et al., 2025).

Accelerated aging caused a decrease of the percentage of lipids in seed after 24 hours, in the comparison with that of the control, which also showed a significant lipid decrease for the treatments of 72, 96, and 120 hours. The fluctuations observed in lipid reserves during the accelerated aging suggest possible events of lipid peroxidation. Even under low humidity conditions, the lipids in dry seed can undergo auto-oxidation (Garg et al., 2022). The species *L. pisonis* is an oilseed, and its seed are rich sources of unsaturated fatty acids (Araujo et al., 2023) which are more sensitive to oxidation, particularly during storage (Garg et al., 2022).

Protein concentration decreased after 48 hours of accelerated aging. Under high-temperature conditions, protein degradation is thermally induced, which may affect seed longevity, primarily due to the loss of enzymatic functions that are essential for cellular function and repair (Cai et al., 2025). In the present study, the seedling emergence of *L. pisonis* was not affected by the reduction of protein content; however, this decrease indicates the onset of physiological deterioration of seed, which is likely due to oxidative stress.

Starch concentration significantly increased in the aging times from 72 hours to 144 hours in comparison with the control. Whether artificial or natural, accelerated seed aging can compromise essential metabolic pathways for mobilizing energy reserves, such as starch degradation pathways, through the inactivation of α-amylase and β-amylase enzymes (Zhang et al., 2022). Therefore, the increase of starch content in aged *L. pisonis* seed is an indication of energy mobilization blockage of this reserve, hindering its conversion into simple sugars.

The highest concentration of total soluble phenols occurred at 96 hours of aging in comparison with the control. The fiber content averaged 45.26% in the

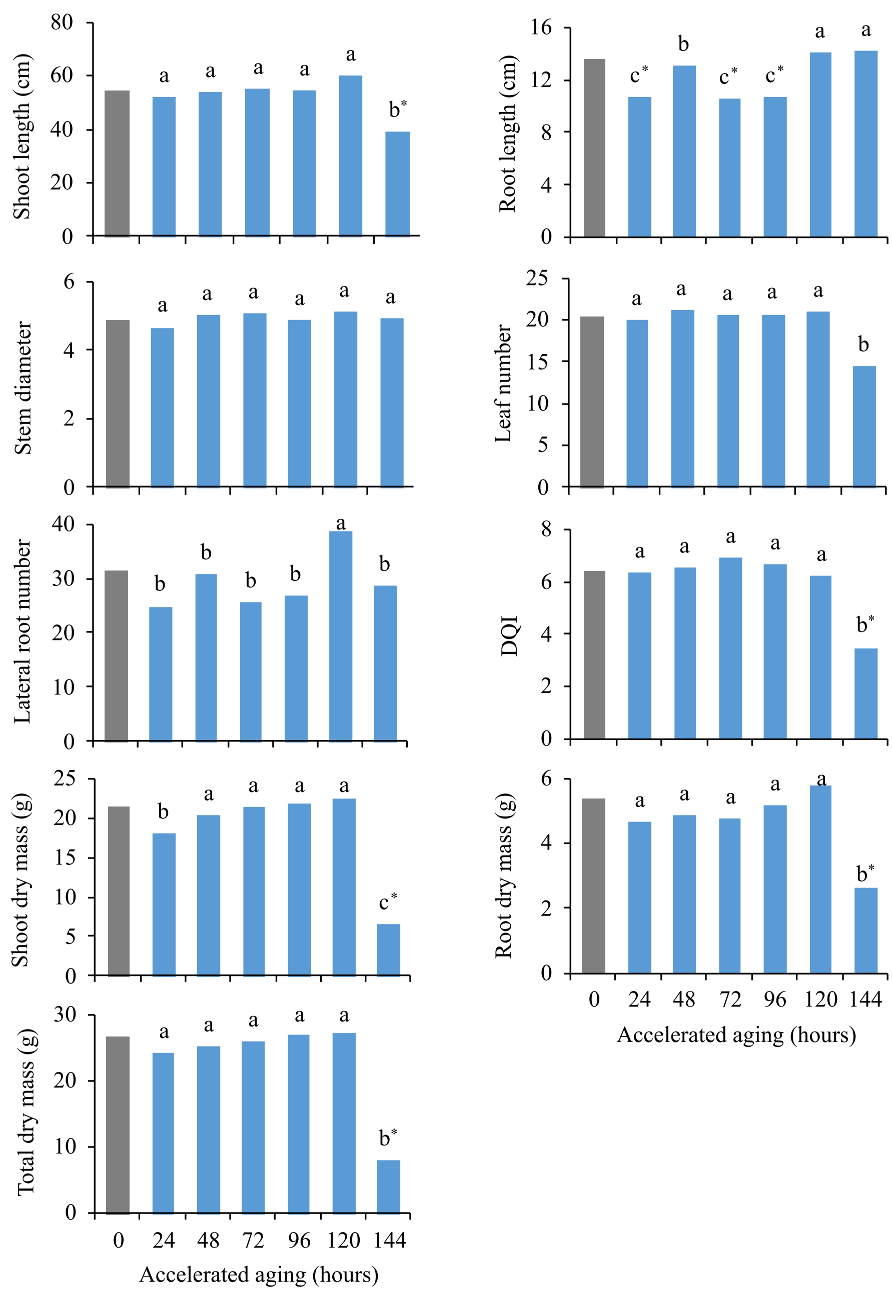

Figure 3. Growth characteristics of *Lecythis pisonis* seedlings whose seed were aged at 40 °C, for a period of 0 (control), 24, 48, 72, 96, 120, and 144 hours. *Means significantly differed from the control, in the same column, by Dunnett's test, at 5% probability. Means for accelerated aging times from 24 to 144 hours, followed by equal letters in the columns, do not differ significantly by Scott-Knott's mean grouping test, at 5% probability.

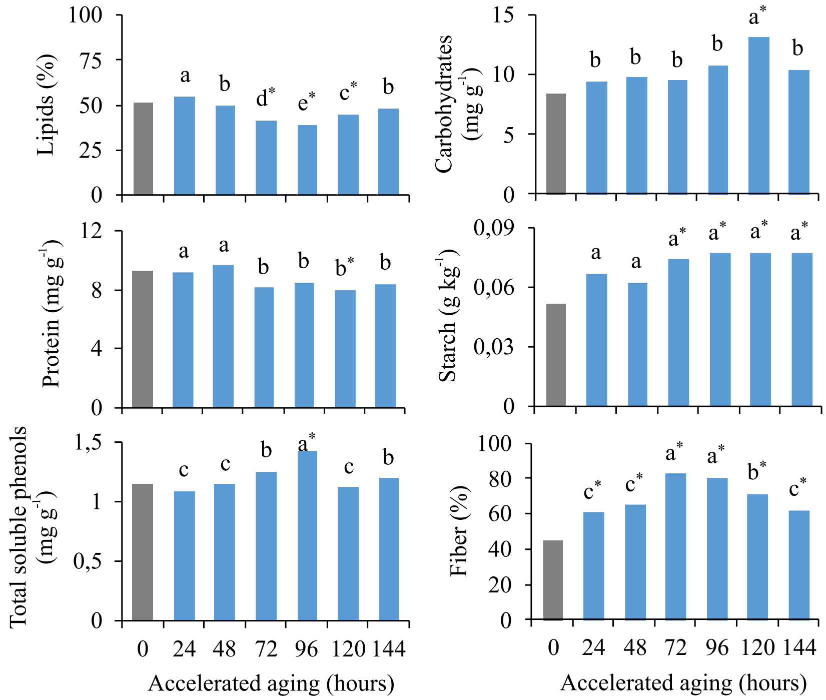

Figure 4. Biochemical characteristics of *Lecythis pisonis* seed aged at 40 °C, for a period of 0 (control), 24, 48, 72, 96, 120 and 144 hours. *Means differed significantly from the control, in the same column, by Dunnett's test, at 5% probability. Means for accelerated aging times from 24 to 144 hours, followed by equal letters in the columns, do not differ from each other, by Scott-Knott's mean grouping test, at 5% probability.

control, increasing significantly at 72 hours (83%) and 96 hours (81%) of aging. The increase of fiber content in aged seed, in comparison with the control, may be related to structural changes in the cell wall of the endosperm, which indicates a physiological stress response. Fibers are present at significant amounts in nuts and seeds, along with lipids and proteins (Santos et al., 2023). Seed endosperm is rich in storage hemicelluloses, and cellulose is present in smaller amounts. Hemicelluloses act as carbohydrate reserves, providing energy during germination. In some cases, they may also contribute to water retention in the post-imbibition phase and protection against mechanical shocks (Otegui, 2007).

Conclusions

1. *L. pisonis* seed exhibit high vigor under stressful conditions of high temperature (40 °C) for up to 120 hours.

2. *L. pisonis* seed exposed to stressful conditions of high temperature (40 °C), for up to 120 hours, invest their reserves in root growth and formation of new roots.

3. The increase of moisture content favors the physiological deterioration and, consequently, the mortality of *L. pisonis* seed exposed to stressful conditions at high temperature (40 °C) for 144 hours.

4. *L. pisonis* seed exposed to stressful conditions at high temperature (40 °C) show a reduction of lipid and protein contents, while carbohydrates, starch, phenols, and fibers increase, especially up to 96 hours of exposure.

5. *L. pisonis* seed have the ability to tolerate stressful storage conditions without an immediate loss of vigor.

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Author contributions

Caroline Palacio de Araujo: conceptualization, formal analysis, funding acquisition, investigation, methodology, writing – original draft, writing – review & editing; **Natasha Vieira de Oliveira**: investigation, methodology, writing – original draft; **Thuanny Lins Monteiro**: formal analysis, investigation, methodology, and writing – original draft; **Ingridh Medeiros Simões**: formal analysis, investigation, methodology, writing – original draft; **Joana Silva Costa**: formal analysis, investigation, methodology, writing – original draft, writing – review & editing; **Débora Pellanda Fagundes**: formal analysis, investigation, methodology, writing – original draft; **Edilson Romais Schmildt**: formal analysis, investigation, methodology, and writing – original draft; **José Carlos Lopes**: formal analysis, investigation, methodology, supervision, writing – original draft; **Rodrigo Sobreira Alexandre**: formal analysis, investigation, methodology, supervision, writing – original draft.

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No generative artificial intelligence (AI) was used in this study.

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