



Imbibition and vigor curves as a function of *Copaifera arenicola* seed size

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Abstract - Seed imbibition typically follows a triphasic pattern; however, variations may occur depending on the species and seed traits such as size. This study aimed to determine the imbibition curve and evaluate seed vigor as a function of seed size in *Copaifera arenicola*. The imbibition curve was assessed based on moisture content on a dry basis, and seed vigor was estimated by electrical conductivity (EC) and total dissolved solids (TDS). The completely randomized design was adopted with three seed size classes and four replicates. The imbibition process did not exhibit a triphasic pattern, presenting only phases I and III. Small and medium seeds reached phase III earlier than large seeds. Seed vigor varied among size classes, with medium seeds showing lower EC and TDS values after 72 hours, which indicates higher physiological quality. These results suggest that seed size influences the dynamic imbibition and vigor of *C. arenicola*, although larger seeds did not demonstrate superior performance.

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Curvas de embebição e vigor em função do tamanho de sementes de *Copaifera arenicola*

Resumo - A embebição de sementes normalmente segue um padrão trifásico; no entanto, variações podem ocorrer dependendo da espécie e das características da semente, como o tamanho. Este estudo teve como objetivo determinar a curva de embebição e avaliar o vigor da semente em função do seu tamanho em *Copaifera arenicola*. A curva de embebição foi avaliada por meio da umidade em base seca, e o vigor da semente foi estimado usando condutividade elétrica (CE) e sólidos totais dissolvidos (STD). O delineamento inteiramente casualizado foi adotado com três classes de tamanho de semente e quatro repetições. O processo de embebição não exibiu um padrão trifásico, mostrando apenas as fases I e III. Sementes pequenas e medianas atingiram a fase III mais cedo do que sementes grandes. O vigor das sementes variou entre as classes de tamanho, com sementes medianas apresentando valores de CE e STD mais baixos após 72 horas, indicando maior qualidade fisiológica. Esses resultados sugerem que o tamanho da semente influencia na dinâmica e no vigor da embebição em *C. arenicola*, embora sementes maiores não tenham demonstrado desempenho superior.

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Introduction

The behavior of seeds in relation to water availability can be analyzed through imbibition, a process that strongly influences the physiological mechanisms underlying germination (Bewley et al., 2013). As seeds hydrate, cellular events are triggered that shift them from a quiescent to a metabolically active state (Dhaliwal & Angeles, 2022), promoting reserve mobilization, the activation of respiration, and the mobilization of energy and substrates required for embryo development (Bewley et al., 2013; Marcos Filho, 2015; Popinigis, 2023).

Imbibition is a physical process characterized by an increase in seed volume, leading to the subsequent rupture of the seed coat. As water uptake proceeds, a characteristic triphasic pattern becomes evident (Bewley et al., 2013; Dhaliwal & Angeles, 2022). Phase I involves rapid water uptake driven by a water potential gradient between the seed and the surrounding medium, continuing until the limit imposed by matric forces is reached (Bewley et al., 2013; Dhaliwal & Angeles, 2022).

Water absorption subsequently declines as the seed approaches equilibrium and metabolic activity intensifies. Phase II is characterized by slow water uptake, balanced between osmotic and pressure potentials, during which germination-related metabolic processes are activated (Bewley et al., 2013; Farooq et al., 2021). In this phase, membranes, mitochondria, and enzymes regain their functionality, accompanied by reserve mobilization and enzyme synthesis (Guimarães et al., 2008; Farooq et al., 2021). Phase III is marked by radicle protrusion and renewed rapid water uptake (Bewley et al., 2013).

These transitions define a curve that is fundamental for identifying atypical or restrictive germination behaviors (Bewley & Black, 1994; Bewley et al., 2013). During this process, especially in dry seeds with low water potential, membrane integrity may be compromised upon rehydration, resulting in the leakage of ions, sugars, organic acids, and amino acids into the imbibition medium (Matthews et al., 2012; Dhaliwal & Angeles, 2022). Such solute leakage is widely recognized as an indicator of seed quality and vigor, reflecting underlying biochemical and cellular conditions and providing insights into the acquisition of vigor during seed development (Corbineau, 2012; Marin et al., 2018).

Seed vigor encompasses the suite of properties that determine the potential for rapid and uniform germination under diverse environmental conditions (Marcos Filho, 2015). Together with viability, vigor establishes the physiological potential of seeds, playing a crucial role in global seed trade, crop production, and germplasm conservation (Matthews et al., 2012), although its expression is species-specific (Marcos Filho, 2015).

Among the methodologies for assessing vigor, the electrical conductivity (EC) test is widely used as an indirect proxy for membrane integrity (Parreño-de-Guzman et al., 2011), which reflects the overall metabolic status of the seeds (Marcos Filho, 2015). These protocols align with the standardized analytical guidelines established by the national *Regras para Análise de Sementes* (Brasil, 2025), which govern seed testing procedures in Brazil.

EC is based on the ability of a solution to conduct electrical current as a function of ionic concentration, which, in seeds, is determined by electrolyte leakage (Marin et al., 2018; Rusydi, 2018). These electrolytes, consisting mainly of inorganic are collectively expressed as total dissolved solids (TDS), which serve as a proxy for the ionic concentration solution. Thus, EC and TDS are often used as complementary parameters for evaluating seed quality (Rusydi, 2018).

Changes in seed vigor may be associated with genetic traits, degree of maturity, longevity, environmental conditions during seed formation, mechanical damage, sanitary status, packaging, storage conditions, and seed size (Rodrigues et al., 2020). Seed size is considered a physical indicator of quality that can influence germination and plant performance, potentially leading to uneven establishment due to heterogeneity in vigor (Vidak et al., 2022).

In wild species, variation in seed size is often pronounced as a result of genetic factors and environmental interactions (Leishman et al., 2000; Fenner & Thompson, 2007). According to Popinigis (2023), seeds may deteriorate during development, resulting in reduced germination capacity or even embryo death under adverse conditions. In some production contexts, the practical expression of seed quality may be lower than expected for high-germination lots (Matthews et al., 2012), which can be associated with heterogeneity in seed size and consequent differences in physiological quality.

Given that seed germination performance and vigor directly influence seedling establishment (Reed et al., 2022) and are associated with natural regeneration processes in tropical ecosystems (Silva et al., 2018), understanding the factors influencing these processes, particularly seed size and imbibition dynamics, is essential for improving seedling establishment, supporting restoration practices, and guiding conservation and management strategies (Pompelli et al., 2023; Mao et al., 2025).

Copaifera arenicola (Ducke) J. Costa & L. P. Queiroz, an endemic species of the Caatinga biome, has experienced population declines in the mesoregion of Northeast Bahia, Brazil, due to high demand for fuelwood, which potentially affects ecosystem balance (Gama et al., 2020) and threatens its long-term survival. This status reinforces the need to understand seed-related traits that underpin species regeneration and establishment.

Based on the premise that seed size may influence germination behavior depending on species-specific morphological and physiological properties (Bewley et al., 2013; Joshi, 2018; Mao et al., 2025), this study hypothesized that seed size may be associated with variations in vigor in *C. arenicola*, with larger seeds potentially exhibiting lower solute leakage (EC/TDS) and more efficient imbibition dynamics compared to smaller ones.

Therefore, this study aimed to determine the imbibition curve and estimate seed vigor as a function of seed size in *C. arenicola* (Ducke).

Material and methods

Plant material and experimental site

The experiment was conducted at the Seed Analysis Laboratory of the Federal University of Recôncavo da Bahia. Seeds were collected between August and October 2023 from 116 mother trees across five populations of *Copaifera arenicola* located in Caatinga remnants within the Northeast Bahia mesoregion, Brazil. The collected seeds were pooled into a single composite lot and stored in transparent polyethylene bags under refrigeration (5 ± 0.5 °C; $54 \pm 5\%$ RH), with a moisture content of 10.2% (Gama et al., 2025b). A working sample was subsequently obtained through random sampling, and the seeds were categorized by size.

Seeds were categorized based on individual length into small seeds (SS; < 11.8 mm), medium

seeds (MS; 11.8-14.6 mm), and large seeds (LS; > 14.6 mm) (Gama et al., 2025b). To overcome dormancy, the seeds were subjected to mechanical scarification by rubbing the region opposite the hilum with 100-grit sandpaper until the cotyledon became visible (Gama et al., 2025a). Subsequently, the seeds were surface-disinfected in a 3% sodium hypochlorite solution for five minutes, rinsed under running water for one minute, and dried on paper towels. Each size class was divided into four replicates of 25 seeds each and weighed on an analytical balance (0.001-g precision) to determine their initial mass.

Imbibition curve

The seed imbibition curve was determined for each seed size class (SS, MS, and LS) based on weight gain (WG, %), which served as an estimate of water uptake relative to the initial seed weight. This approach allowed the identification of the water absorption phases according to the model proposed by Bewley & Black (1994).

Seeds were weighed on an analytical balance (0.001-g precision) at successive intervals: 12 measurements at 60-minute intervals, 11 measurements at six-hour intervals, and 12 measurements at 12-hour intervals, totaling 35 evaluations at the following times: 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 18, 24, 30, 36, 42, 48, 54, 60, 66, 72, 78, 90, 102, 114, 126, 138, 150, 162, 174, 186, 198, 210, and 222 hours.

At each evaluation time, seeds were removed from the germination boxes, blotted with paper towels to remove excess surface water, weighed, and immediately returned to the containers. The evaluations were concluded when radicle protrusion occurred in at least 50% of the seeds in each subsample, allowing identification of imbibition phases. Weight gain was calculated according to Equation 1:

$$WG = \left(\frac{F_w - I_w}{I_w} \right) \times 100 \quad (1)$$

where: WG = weight gain (%); F_w = final seed weight (g) after imbibition at each evaluation time; I_w = initial seed weight (g) before imbibition.

Subsamples of 25 seeds were placed between two sheets of blotting paper moistened with distilled water at 2.5 times the dry paper weight and arranged in acrylic germination boxes (11 × 11 × 3 cm), which were sealed to prevent moisture loss. The boxes were randomly distributed in Biochemical

Oxygen Demand (BOD) germination chambers, maintained at an alternating temperature of 20-30 $\pm$ 2 $^{\circ}$ C with a 12-hour photoperiod (light), according to the Regras para Análise de Sementes (Brasil, 2025). The experimental design was completely randomized, with three seed size classes and four replicates per treatment.

Electrical conductivity and total dissolved solids measurements

For the electrical conductivity (EC) test and total dissolved solids (TDS) analysis, the mass method was used. Twenty-five seeds from each treatment (SS, MS, and LS) were placed in 100 mL plastic containers with lids, each containing 75 mL of distilled water. The containers were maintained in BOD-type germination chambers at an alternating temperature of 20-30 $\pm$ 2 $^{\circ}$ C, with a 12-hour photoperiod (white light) for 72 hours. A completely randomized design was used, with three treatments and four replicates of 25 seeds each.

During the 72-hour period, EC and TDS values of electrolytes released into the imbibition solution were measured at 2, 4, 6, 8, 12, 24, 48, and 72 hours using a multiparameter probe with an accuracy of $\pm$ 2% full scale (FS). The results were normalized by seed mass and expressed as μ S cm^{-1} g^{-1} (EC) and ppm g^{-1} (TDS).

Statistical analysis

The data obtained from the imbibition curve total dissolved solids (TDS), and electrical conductivity (EC) measurements were evaluated for normality of residuals using the Shapiro-Wilk test ($p > 0.05$) and graphical inspection. Simple linear and polynomial regression analyses were performed at a significance level of 5% ($p < 0.05$) using the SISVAR software (Ferreira et al., 2011), according to Equations 2 and 3:

$$Y_i = a + bx_i + \varepsilon_i \quad (2)$$

where: Y_i = dependent variable; a = intercept; b = slope; x_i = independent variable; and ε_i = random error.

$$Y_i = ax_i^4 + bx_i^3 + cx_i^2 + dx_i + e + \varepsilon_i \quad (3)$$

where: Y_i = dependent variable; a, b, c, d, e = regression coefficients ($a \neq 0$); x_i = independent variable; and ε_i = random error.

Results

Table 1 presents the analysis of variance summary and regression parameters for the best-fit models fitted to the imbibition curve (polynomial model) and total dissolved solids (TDS), and electrical

Table 1. Analysis of variance summary and regression parameters for the imbibition curve (polynomial model), total dissolved solids, and electrical conductivity (linear models) across different seed size classes of *Copaifera arenicola*.

Imbibition curve (Moisture content - MC%)									
ANOVA			Parameters					Statistics	
SV	F	Pr > F	α	b	c	d	e	R ²	SE (±)
SS	7,085.80	1.14E-25	1.90E-09	-9.27E-07	1.26E-04	1.70E-03	9.60E-03	0.9989	0.053
MS	16,312.06	2.02E-23	2.47E-09	-1.13E-06	1.40E-04	3.00E-03	5.10E-03	0.9996	0.072
LS	3,598.46	1.24E-29	4.69E-10	-2.41E-07	3.00E-05	2.00E-03	7.50E-03	0.9979	0.020
Total dissolved solids - TDS (ppm g ⁻¹)									
ANOVA			Parameters					Statistics	
SV	F	Pr > F	α	b				R ²	SE (±)
SS	506.3538	5.04E-07	0.273298	0.167086				0.9883	0.8107
MS	365.7183	1.32E-06	0.211228	0.607966				0.9839	0.7373
LS	894.4965	9.27E-08	0.253455	0.362466				0.9933	0.5657
Electrical conductivity - EC (µS cm ⁻¹ g ⁻¹)									
ANOVA			Parameters					Statistics	
SV	F	Pr > F	α	b				R ²	SE (±)
SS	698.3146	1.94E-07	0.651246	- 0.798773				0.9915	1.6451
MS	414.8535	9.1E-07	0.431899	0.933104				0.9857	1.4154
LS	710.0956	1.84E-07	0.521261	0.515443				0.9916	1.3057

SV = source of variation; F = F-statistic (F-test); Pr > F = p-value; a, b, c, d, e = regression coefficients; R^2 = coefficient of determination; SE = standard error; SS = small seeds; MS = medium seeds; LS = large seeds.

conductivity (EC) (linear model) across different seed size classes of *Copaifera arenicola*. Model selection was based on statistical significance ($p \leq 0.05$) and high goodness of fit ($R^2 > 0.99$).

Seed size classes did not differ in moisture gain during the first 12 hours of imbibition. After this period, differences became evident; medium seeds (MS) showed higher moisture gain compared to small (SS) and large seeds (LS), with LS exhibiting the lowest values (Figure 1).

The imbibition curve exhibited a biphasic pattern (phases I and III), whereas no clear plateau corresponding to phase II was observed. SS and MS reached phase III earlier (166 hours), whereas

LS reached this stage later (186 hours), indicating slower imbibition dynamics.

On a dry weight basis, MS, SS, and LS showed average weight increases of 108%, 96%, and 55% during phase I, respectively, indicating greater initial water uptake in intermediate-sized seeds.

TDS and EC increased linearly over time for all seed sizes (Figure 2). At the final evaluation (72 hours of imbibition), MS exhibited lower TDS ($16.4 \pm 1.65 \text{ ppm g}^{-1}$) and EC ($33.2 \pm 2.72 \text{ } \mu\text{S cm}^{-1} \text{ g}^{-1}$) compared to SS ($19.2 \pm 7.36 \text{ ppm g}^{-1}$ and $47.7 \pm 9.31 \text{ } \mu\text{S cm}^{-1} \text{ g}^{-1}$) and LS ($18.8 \pm 3.83 \text{ ppm g}^{-1}$ and $38.7 \pm 7.61 \text{ } \mu\text{S cm}^{-1} \text{ g}^{-1}$), indicating higher membrane integrity and physiological quality in MS.

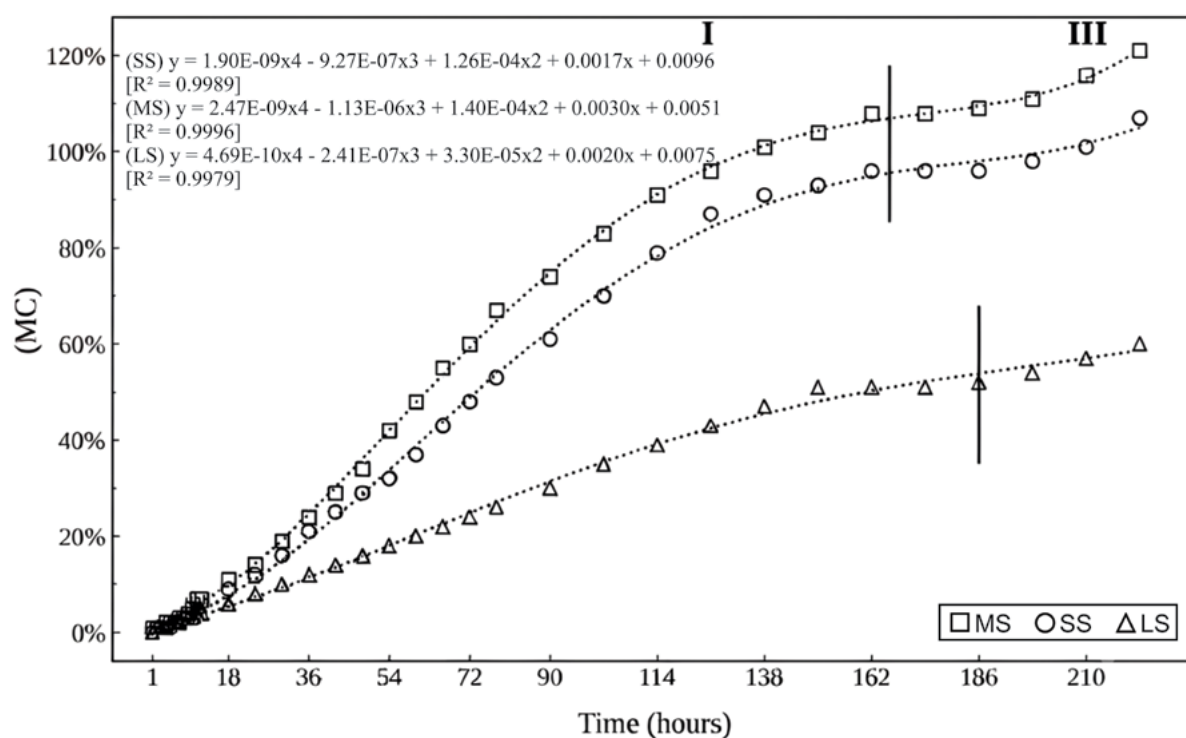


Figure 1. Imbibition curves of *Copaifera arenicola* seeds across different size classes: small (SS), medium (MS), and large (LS). Vertical lines represent the onset of Phase III, determined by the time required for 50% radicle protrusion. MC = moisture content.

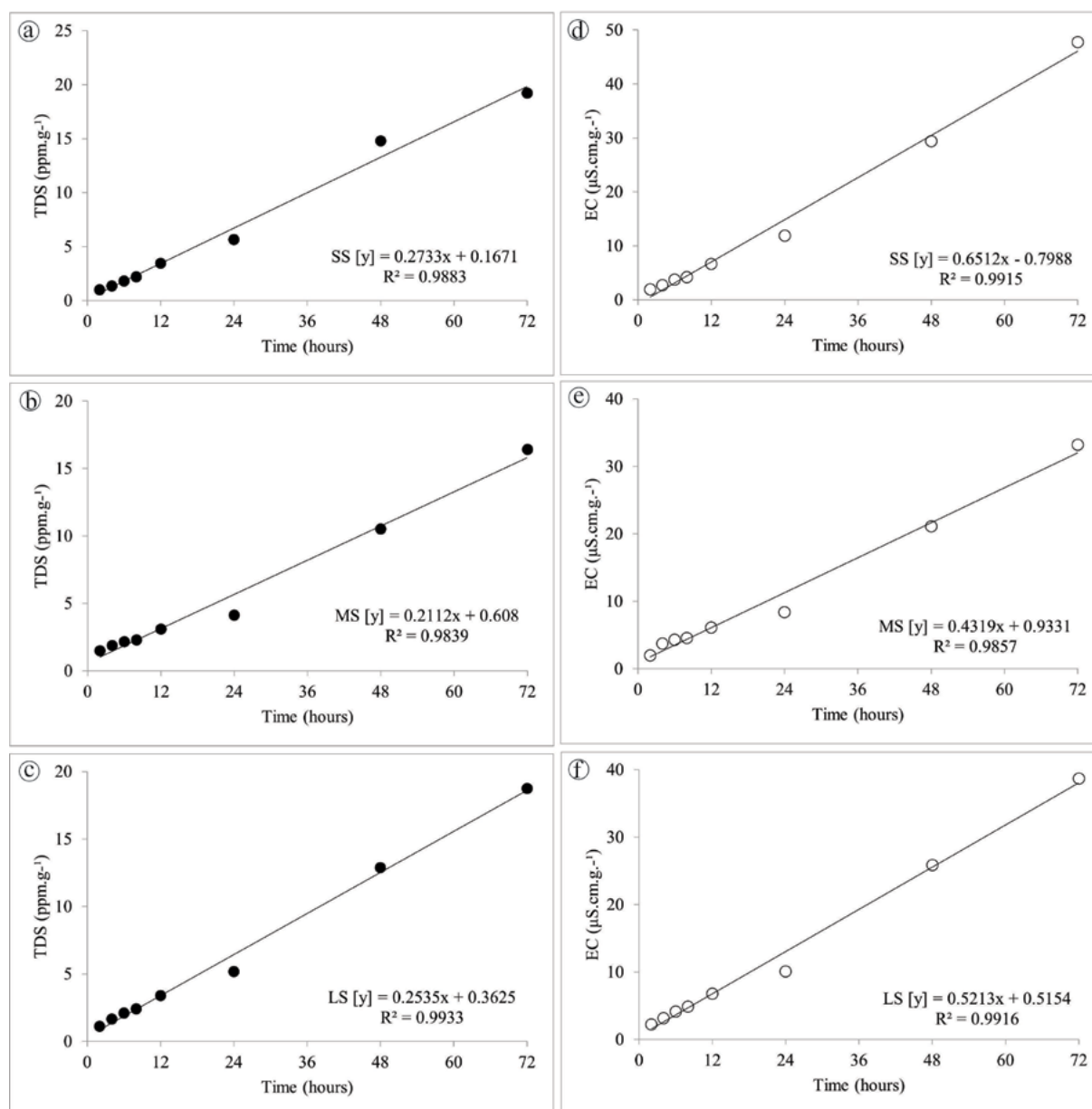


Figure 2. Linear regression of total dissolved solids (TDS;●) and electrical conductivity (EC;○) in *Copaifera arenicola* seeds across size classes: small (SS: a, d), medium (MS: b, e), and large (LS: c, f).

Discussion

In general, regardless of seed size, imbibition in *Copaifera arenicola* occurred slowly during the initial phase, lasting up to 12 hours. Although Phase I is generally characterized by rapid water absorption, this rate can vary among species. According to Wiraguna (2022), dry, mature seeds (viable and non-dormant) typically absorb water and oxygen more quickly during this initial stage.

However, the slow imbibition observed in *C. arenicola* seeds may be associated with residual

physical restrictions to water entry after mechanical scarification and structural limitations of the seed coat.

After this initial period, water absorption increased and moisture content (MC) differed among seed sizes, indicating that seed physical characteristics influenced imbibition. medium seeds (MS) consistently exhibited higher MC, followed by small seeds (SS), whereas large seeds (LS) absorbed water more slowly.

These differences may be partly related to differences in surface-to-volume ratio and other physical characteristics of the seeds. Popinigis

(2023) explains that differences in surface-to-volume ratio influence seed-water contact, which helps explain the slower imbibition of LS.

Conversely, in LS, slower water uptake and lower MC were sufficient to achieve 50% germination. This suggests an efficient metabolic activation even under reduced hydration, allowing the rapid development of the embryonic axis once a minimum water threshold is reached.

Similar results were reported for *Copaifera langsdorffii* Desf., in which Pereira et al. (2017) observed 50% germination after approximately 120 hours, with seeds at 55% MC germinating more slowly. These findings reinforce that the minimum water content required for germination is species-specific (Popinigis, 2013; Gómez-Maqueo et al., 2020).

According to Dhaliwal & Angeles (2022), once seeds reach approximately 50% of their dry weight in water, enzymes involved in reserve mobilization, organelle differentiation, and metabolite transport become activated.

Differences in surface-to-volume ratio may influence water and oxygen availability to the embryo, potentially affecting metabolic activation and germination (Wiraguna, 2022). Furthermore, according to Steinbrecher & Leubner-Metzger (2017) and Popinigis (2023), the embryonic axis is the structure that absorbs water more rapidly and continuously, promoting cell elongation; as new cells expand, the absorbed water becomes incorporated into their structure. Thus, the slower hydration observed in LS may be partly related to their lower surface-to-volume ratio and greater diffusion distance for water and oxygen.

The absence of a clearly defined triphasic pattern in the imbibition curve of *C. arenicola*, with a direct transition from phase I to phase III, may be attributed to slower mobilization of stored reserves, which maintains osmotic activity and continuous water uptake. According to Bewley et al. (2013), phase II is typically characterized by a reduced rate of water uptake associated with reserve mobilization.

These authors also state that elongation of the embryonic axis may begin before complete imbibition of storage tissues, indicating that seeds can enter phase III before fully completing phase I. However, they emphasize that it is difficult to predict the stage of germination based solely on MC prior to radicle protrusion.

Similarly, Pereira et al. (2017) observed only a minimally defined phase II in *C. langsdorffii*, indicating that the transition between hydration

and embryo growth may not always be clearly expressed in the imbibition curve. However, the duration and expression of imbibition phases may vary among species (Bewley & Black, 1994; Moret-Fernández et al., 2024).

From an ecological perspective, differences in MC and hydration rates among seed sizes may contribute to variation in the timing of germination, which could be advantageous for establishment under unpredictable water availability in semi-arid environments. This variation may also reflect genetic and phenotypic heterogeneity within populations, resulting in differential responses to environmental conditions (Fenner & Thompson, 2007; Bewley et al., 2013).

The imbibition curve alone was insufficient to explain seed vigor. Although MS and SS reached phase III earlier due to higher MC, TDS and EC increased linearly across all treatments.

At the final evaluation (72 hours), MS exhibited the lowest TDS and EC values, indicating greater vigor. According to Marin et al. (2018) and Wiraguna (2022), more vigorous seeds release fewer exudates because their cell membranes maintain structural integrity more effectively during hydration.

This suggests that membrane systems in MS remained more stable during hydration, effectively limiting solute leakage, in agreement with Marin et al. (2018), Rusydi (2018), and Popinigis (2023). In contrast, the delayed radicle protrusion observed in LS (approximately 20 hours later than in MS and SS) may be related to membrane damage caused by greater electrolyte leakage, possibly due to abrupt initial water uptake, as suggested by Vidak et al. (2022), although Lamichhane et al. (2018) reported that the causes of variation in seed exudation remain uncertain and that seed size alone is not a determining factor.

Finally, a direct relationship among MC, TDS, and EC was observed, as lower MC values during the initial hours corresponded to lower TDS and EC readings. Subsequently, both variables increased linearly over time for all seed size classes. However, as noted by Rusydi (2018), this relationship is not always strictly linear, as it depends on ionic strength and the specific activity of dissolved ions.

Conclusions

The imbibition curve of *Copaifera arenicola* demonstrated a biphasic pattern, characterized by

the occurrence of phases I and III without a distinct phase II. This behavior was consistent across all seed sizes, although medium (MS) and small (SS) seeds reached phase III earlier than large seeds (LS).

Seed size influenced imbibition dynamics and vigor, with MS showing greater physiological quality, as indicated by lower electrical conductivity (EC) and total dissolved solids (TDS).

These results suggest that seed size is associated with variations in vigor in *C. arenicola*, although larger seeds did not exhibit superior performance, thereby partially refuting the initial hypothesis.

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Conflict of interest

The authors have no conflict of interest to declare.

Authors' Contributions

Dráuzio Correia Gama: Conceptualization, investigation, formal analysis, methodology, writing original draft. **Emerson Dechechi Chambó:** Supervision, formal analysis, writing - review & editing. **Teresa Aparecida Soares de Freitas:** Methodology, writing - review & editing. **Raiana Bonfim Moreira Vidal:** Investigation.

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