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ORIGINAL ARTICLE

Physiological and cytological responses to thermal stress in recalcitrant seeds of *Mauritia flexuosa* (Arecaceae)

Higor F. Salvador[1] · Hellen C. Mazzottini-dos-Santos[2] · Yule R. F. Nunes[2] · Leonardo M. Ribeiro[1]

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Abstract

Main conclusion **Recalcitrant seeds of *Mauritia flexuosa* show evidence of thermal stress tolerance, while germination is stimulated by a thermal regime typical of the rainy season.**

Abstract Recalcitrant seeds (sensitive to desiccation) are highly vulnerable to environmental changes, but little is known about their resilience to thermal stress, which will be particularly important in a scenario of climate change. *Mauritia flexuosa* L. f. is a neotropical palm of ecological and social importance that occurs in flooded environments. The species produces seeds with association of recalcitrance and dormancy (germination blockage) and has the ability to maintain persistent soil seed banks in ecosystems exposed to the markedly seasonal climate of the Cerrado biome. Thermal regimes (30/20, 35/25, 40/30, and 45/35 °C) were employed to investigate the role of temperature on seed physiology (viability, germination, respiratory activity, micropylar biomechanics, oxidative stress, membrane functionality) and cytology (micromorphometry, ultrastructure, and compound dynamics). Germination was stimulated by the 30/20 °C regime (typical of the rainy season), with reduction of the resistance of the tissues adjacent to the embryo, reserve mobilization, and cell expansion. The 40/30 and 35/25 °C regimes contributed to maintaining and increasing dormancy intensity, respectively. The 45/35 °C regime resulted in seed death due to reserve depletion and embryonic cell collapse. Tolerance mechanisms to moderate thermal stress include efficient antioxidant systems, cell homeostasis, and germination restriction. The capacity for differential responses to thermal regimes is important to the establishment of banks of recalcitrant *M. flexuosa* seeds and constitutes a factor in the adaptation of that species to the Cerrado seasonality. Nonetheless, rising global temperatures due to climate change and increasing local impacts pose risks to the species' reproductive success.

Keywords Abiotic stress · Antioxidant systems · Dormancy · Germination ecophysiology · Palms · Sensitivity to desiccation

Abbreviations

APX	Ascorbate peroxidase
CAT	Catalase
FM	Fresh mass
MDA	Malondialdehyde
ROS	Reactive oxygen species
SOD	Superoxide dismutase

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✉ Leonardo M. Ribeiro
leonardo.ribeiro@unimontes.br

[1] Departamento de Botânica, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Avenida Antônio Carlos, 6627, Pampulha, Belo Horizonte, Minas Gerais 31270-901, Brazil

[2] Departamento de Biologia Geral, Universidade Estadual de Montes Claros, Avenida Rui Braga, Vila Mauricéia, Montes Claros, Minas Gerais 39401-089, Brazil

Introduction

Recalcitrant seeds are intolerant to desiccation and low temperatures, and they therefore have low capacities for long-term viability and the formation of persistent soil seed banks (Hong and Ellis 1996; Marques et al. 2018). Recalcitrance is associated with moist environments, although plants that produce recalcitrant seeds can also occur under seasonal conditions (Tweedle et al. 2003; Berjak and Pammenter 2008). Most studies of recalcitrant seeds have emphasized their desiccation responses (Berjak and Pammenter 2008, 2013; Marques et al. 2018; Dias et al. 2024). The roles of

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other abiotic factors, such as temperature, are still only poorly understood, especially for tree species growing in tropical environments. Within this context, climate change (with increasing temperatures and greater rainfall instability) represents a real threat to the population dynamics of species that produce recalcitrant seeds (Marques et al. 2018; Pausas et al. 2022; Pritchard et al. 2022).

Temperature is one of the main environmental factors controlling seed germination, and provides indications of favorable periods for seedling establishment (Bewley et al. 2013; Baskin and Baskin 2014). This role is especially important in the case of recalcitrant seeds, which are dispersed in hydrated and metabolically active states (Berjak and Pammenter 2008). There are indications that high temperatures can increase germination rates of recalcitrant seeds but also reduce the available time for seedling establishment (Stevens et al. 2014). There have also been cases reported of associations between recalcitrance and dormancy (germination blockage due to intrinsic causes) (Tweddle et al. 2003; Silva et al. 2014). In those cases, seed-temperature interactions are more complex and directly involve viability control, in addition to the regulation of germination restriction (Baskin and Baskin 2014; Jaganathan 2021).

High temperatures intensify reactive oxygen species (ROS) production related to increased metabolic activity (Barreto and Garcia 2017; Marques et al. 2017; Bailly 2019). Imbalances between the production and elimination of these radicals can result in potentially fatal oxidative stress, especially in the case of recalcitrant seeds (Berjak and Pammenter 2008; Wojtyla et al. 2016; Bailly 2019). Temperature is the main environmental factor related to overcoming physiological dormancy (the most common type of dormancy observed among tropical seeds, Orozco-Segovia et al. 2003; Schlindwein et al. 2013; Baskin and Baskin 2014) as it acts to modulate endogenous hormone concentrations and weaken the tissues that restrict embryonic growth (Finch-Savage and Gerhard Leubner-Metzger 2006; Baskin and Baskin 2014). Some of these processes may be mediated by ROS levels, involving the antioxidant apparatus and other signaling and control mechanisms of cellular homeostasis (Pagano et al. 2002; Wojtyla et al. 2016; Bailly 2019). In-depth information concerning the effects of heat stress on the physiology of recalcitrant seeds has been scarce. Studies examining this approach will be essential to estimating the impacts of climate change on seed bank dynamics in humid environments, which also can represent important and highly threatened sequestered carbon deposits (Long et al. 2015; Bastos et al. 2017; Marques et al. 2018; Cristaudo et al. 2019; Esser et al. 2019; Rajendran et al. 2021).

Mauritia flexuosa L. f. ("buriti") is a palm tree of Amazonian origin that is widely distributed throughout tropical South America (Dransfield et al. 2008) and associated with swampy environments (Lorenzi et al. 2010; Lima et al. 2014; Melo et al. 2018). The species occurs in flooded environments (known as "veredas") in the Brazilian Cerrado—a biome with a markedly seasonal climate (Lorenzi et al. 2010; Lima et al. 2014; Melo et al. 2018). Buriti is considered the most abundant palm tree in Brazil and a key species for vereda ecology, in addition to being an important source of income for traditional populations and raw material for the cosmetic industry (Lorenzi et al. 2010; Endress et al. 2013; Nunes et al. 2022). This palm produces recalcitrant seeds that show morphophysiological dormancy (Silva et al. 2014; Veloso et al. 2016; Dias et al. 2024). This class of dormancy is typical of seeds that have small embryos with hormonal imbalance, which results in low growth potential (Baskin and Baskin 2014). After hormonal adjustment (a process usually induced by changes in temperature), the embryos require a growth phase inside the seed before germination is complete. Some studies have indicated that *M. flexuosa* has a reproductive strategy that combines the establishment of seedling banks and the maintenance of persistent soil seed banks in microenvironments subject to dry and constant humid conditions, respectively (Porto et al. 2018; Salvador et al. 2022; Almeida et al. 2024). However, there are no studies on changes in the thermal regime on the reproduction of the species.

The survival of the buriti palm in the Cerrado biome is threatened by habitat destruction due to human actions as well as climate change (Endress et al. 2013; Silva et al. 2014; Virapongse et al. 2017; Nunes et al. 2022). The Brazilian Cerrado is predicted to experience increased temperatures and high-frequency extreme heat events, and is considered the biodiversity hotspot that will be most affected by climate change in South America (IPCC 2022)—which highlights the importance of studies on the potential impact of thermal stress on *M. flexuosa* seed bank dynamics.

The present study was therefore designed to evaluate the influence of thermal stress on *M. flexuosa* seeds by addressing the following questions: (i) What is the role of temperature in controlling seed germination? (ii) What are the physiological and cytological responses of those seeds to thermal stress? We also examined ecophysiological aspects related to thermal stress tolerance and the implications for seed behavior in that environment under current and future climatic conditions.

Materials and methods

Collections and preliminary procedures

Mauritia flexuosa fruits were collected, in February 2021, after abscission, in a natural population located in the Rio Pandeiros Environmental Protection Area (APA-Pandeiros),

in the municipality of Bonito de Minas, in northern Minas Gerais State, Brazil (15°22′ 4.14″ S; 44°55′ 8.33″ W). The fruits were manually pulped and any seeds showing evidence of insect attacks and/or the presence of fungal mycelium were discarded. Four replications of 10 seeds and embryos (excised using a guillotine and stylet) were used to evaluate their water contents, considering the differences between fresh and dry masses (the latter obtained by drying the seeds in an oven at 105 °C for 24 h). Additionally, five replicates of 10 embryos were tested for viability by immersing them in a 1% solution 2,3,5-triphenyl tetrazolium chloride, incubating them in the dark (at 35 °C for five hours), and then visually inspecting them for staining (Spera et al. 2001; Ribeiro et al. 2010). The seeds were stored in plastic bags in an air-conditioned chamber at 20 °C (Veloso et al. 2016) for up to one month before the start of the experiment. Climatological data (Fig. 1) were obtained from a weather station maintained by the National Institute of Meteorology (INMET 2024) in the municipality of Januária, approximately 70 km from the study area; the sites there have the same geomorphological (Sanfransciscana depression) and climatic conditions (type Aw, Köppen).

Induction of thermal stress

The seeds were first disinfected by immersion in 6% sodium hypochlorite for 15 min, followed by three rinses with distilled water. The seeds were then set to germinate in polyethylene containers (22 × 16 × 5 cm, with lids) containing autoclaved sand that was moistened to retention capacity (Silva et al. 2014; Veloso et al. 2016). Five replications of 20 seeds were held in germination chambers (under a 12/12 h light/dark cycle, 50 mmol m^{-2} s^{-1}) and exposed to 30/20, 35/25, 40/30, and 45/35 °C temperature regimes for 60 days. The temperature regimes used were selected to represent daily temperature fluctuations under local climatic conditions as recorded in recent decades (Fig. 1), thus creating a moderate to severe thermal stress gradient while simulating current environmental conditions. Substrate moisture was controlled by monitoring the mass of an additional container (within each type of treatment regime) containing only moistened autoclaved sand, replacing lost water when necessary. Germination was evaluated daily, considering the protrusion of the cotyledonary petiole (Ribeiro et al. 2011; Silva et al. 2014). At the end of 60 days, the seeds exposed to all of the different temperature regimes were transferred to the 30/20 °C incubation regime (typical rainy season conditions, Fig. 1) and were maintained there for 30 additional days. The opercula (seed tissues that limit embryo growth, Silva et al. 2014) of seeds that had not germinated in the final evaluation were manually removed using a stylet and the seeds were left again under the same 30/20 °C conditions for an additional 15 days. At the end of the experiment, embryos still not germinated were excised from the seeds and subjected to the tetrazolium test to assess their viability (Spera et al. 2001; Ribeiro et al. 2010).

Biometric, physiological, and cytological evaluations, to be described below, were carried out using additional seed samples in the initial condition as well as after being subjected to the thermal conditions described above.

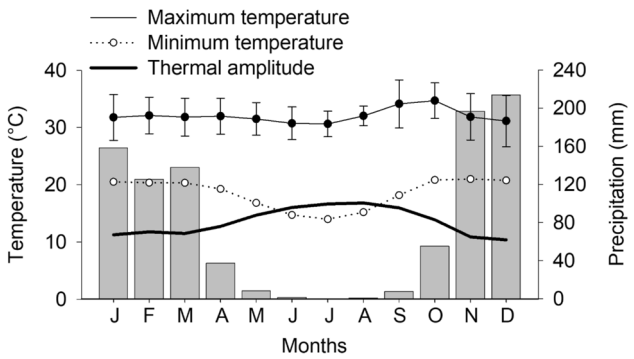

Fig. 1 Monthly averages of maximum and minimum temperatures, thermal amplitude and rainfall in the municipality of Januária, state of Minas Gerais, Brazil, in the years 1991–2021. Vertical bars indicate the deviation from the maximum daily temperatures recorded in this period

Biometric evaluations

Five replicates of 10 intact seeds (endosperm plus seed coat and isolated embryos) were evaluated at the beginning of the experiment (initial condition) and again after 30, 60 and 90 days of exposure to each thermal regime. The fresh and dry masses (after drying in an oven at 105 °C for 24 h) of the seeds and isolated embryos were determined and their water contents measured (Brasil 2009).

Estimation of embryo respiratory activity

Four replications of 10 embryos from seeds in the initial condition and those subjected to heat stress treatments for 90 days were weighed to determine their fresh mass (FM), immersed in a 1% solution of 2,3,5-triphenyl tetrazolium chloride, and subsequently incubated in the dark at 35 °C for five hours. The material was then washed three times in distilled water and immersed in 5 mL of absolute ethanol for 14 days. The supernatants from the absolute ethanol treatments were collected, centrifuged at 1000*g* for 30 s, and the absorbances of the solutions were evaluated in a spectrophotometer at 490 nm against a white reagent (using dead boiled embryos). The respiratory activity indicator was expressed in absorbance (A) g^{-1} FM (Harding and Benson 1995, with adaptations).

Estimation of membrane integrity—solute leaching

Four replications of 20 embryos obtained from seeds in their initial condition, as well as from seeds subjected to each heat stress treatment for 90 days, had their fresh masses determined and then immersed in ultrapure water and subsequently kept in a germination chamber for 4 h at 30 °C. The electrical conductivity of each solution was read using a bench conductivity meter (AK83, AKSO, São Leopoldo, Rio Grande do Sul, Brazil https://loja.akso.com.br/) and the results expressed in μS cm^{-1} g^{-1} FM [equivalent to the total conductivity after 4 h and subtracting blank conductivity (ultrapure water)] (Gonçalves et al. 2020).

Oxidative stress evaluation

Hydrogen peroxide (H_2O_2—one of the principal ROS) concentrations present in the embryos of seeds subjected to each thermal treatment were determined after the initial treatment as well as after 30, 60 and 90 days of exposure to the various heat stress conditions. To that end, four replicates of 30 mg of embryo tissue were macerated in liquid nitrogen in 2 mL tubes; 400 μL of trichloroacetic acid (TCA 0.1% m/v) was subsequently added. The plant extracts were then homogenized by vortexing for 1 min and centrifuged at 9500*g* for 15 min at 4 °C. A 250 μL aliquot of the supernatant was extracted and added to 250 μL of 100 mM sodium phosphate buffer (pH 7.5) and 1000 μL of 1 M potassium iodide. The tubes with the samples were then placed on ice (in total darkness) for one hour. The samples were subsequently maintained in the dark at room temperature (25 °C) for 10 min (to stabilize the reaction) and then analyzed in a spectrophotometer (UV-1800, Shimadzu, Tokyo, Japan https://www.shimadzu.com/) at 390 nm. The amount of H_2O_2 identified was expressed in μmol g^{-1} of fresh mass, based on a pre-established standard curve (Alexieva et al. 2001).

The activities of the main enzymes of the antioxidant system catalase (CAT), superoxide dismutase (SOD), and ascorbate peroxidase (APX), were evaluated. Plant extracts were obtained by macerating (in liquid nitrogen) four repetitions of 20 mg of embryo tissues in the initial condition and after each thermal treatment (of 30, 60, and 90 days). The samples were homogenized in polyvinylpyrrolidone (PVPP, 10% w/v), 500 μL of sodium phosphate buffer (50 mM, pH 6.8), 10 μL of ethylenediaminetetraacetic acid (EDTA, 100 μM), and 490 μL of deionized water by vortexing for 1 min. The extracts were then centrifuged at 9500*g* at 4 °C for 15 min. SOD activity was determined by adding 100 μL of the extract supernatant to a solution containing methionine (13 mM), nitro blue tetrazolium (NBT, 75 μM), 100 μM riboflavin EDTA (2 μM), and sodium phosphate buffer (50 mM pH 7.8). The tubes were then illuminated with fluorescent light (15 W tubes) for 10 min at 25 °C. Enzyme activity was terminated by interrupting the illumination. Control reactions were kept in the dark for 10 min. The blue formazan compound formed was analyzed at 575 nm using a spectrophotometer (UV-1800, Shimadzu). One unit (U) of SOD was defined as the amount of enzyme required to inhibit 50% of NBT photoreduction; the results were expressed as U min^{-1} mg^{-1} protein (Giannopolitis and Ries 1977). To determine CAT activity, 100 μL of the extract supernatant was added to sodium phosphate buffer (50 mM, pH 7.0) together with freshly prepared H_2O_2 (12.5 mM); the reaction was followed for one minute at 240 nm in a spectrophotometer. CAT activity was estimated using the molar extinction coefficient (ε) equal to 39.4 mM^{-1} cm^{-1} and expressed as μmol of H_2O_2 min^{-1} mg^{-1} protein (Cakmak and Horst 1991). APX activity was determined by adding 100 μL of the extract supernatant to sodium phosphate buffer (50 mM, pH 6.8) with freshly prepared ascorbate (0.25 mM) and H_2O_2 (1.0 mM). The oxidation rate of ascorbic acid was monitored every 10 s for 1 min at 290 nm in a spectrophotometer. APX activity was determined using ε equal to 2.8 mM^{-1} cm^{-1}, and the results expressed as μmol ascorbate (AsA) min^{-1} mg^{-1} protein (Nakano and Asada 1981).

Quantification of the lipid peroxidation indicator malondialdehyde (MDA) was also carried out. Four replicates of 30 mg of embryo tissue from seeds in the initial condition and those subjected to thermal treatments for 30, 60 and 90 days were used. The samples were macerated in liquid nitrogen and 1.5 mL of 0.1% (w/v) TCA was subsequently added. The samples were vortex homogenized for 1 min and subsequently centrifuged at 13700*g* for 15 min. A 1 mL aliquot of the supernatant was then added to a 3 mL aliquot of 0.5% (w/v) thiobarbituric acid solution (prepared in 20% TCA). The solution was maintained at 95 °C for 60 min and then cooled in an ice bath for 10 min. The samples were subsequently analyzed at 532 and 660 nm in a spectrophotometer. Interferences were eliminated by subtracting the two values (532–660), and the quantities of malondialdehyde (MDA) were expressed in nmol g^{-1} of fresh mass (Health and Packer 1968, adapted).

Operculum resistance to displacement

Four replications of 10 seeds each in the initial condition as well as seeds subjected to thermal stress for 60 and 90 days were sectioned parallel to the operculum, maintaining it intact; the embryos were removed with the aid of a hypodermic needle. The force required to displace the operculum (seed tissues that limit embryo growth, Silva et al. 2014) was then measured using a digital dynamometer (IP-90DI, Impac, Vargem Grande Paulista, São Paulo, Brazil https://impac.com.br/) coupled to a probe with a diameter corresponding to that of the embryos' cotyledonary petiole. The

probe was inserted into the embryonic cavity, through the sectioned part, and pushed until the operculum was displaced; the force required was recorded in N cm^{-2} (Mazzottini-dos-Santos et al. 2018).

Micromorphometric, histochemical, and ultrastructural evaluations

Fragments of the cotyledonary petiole and the haustorium plus adjacent endosperm excised from seeds from each thermal treatment were used. Samples were collected in the initial condition and after 30 and 60 days. The samples were fixed in Karnovsky solution (Karnovsky 1965) for 24 h, dehydrated in an ethanol series, and embedded in 2-hydroxyethyl methacrylate according to the protocol described by Paiva et al. (2011). Cross and longitudinal sections (3 µm thick) were obtained using a rotary microtome, stained with 0.05% toluidine blue, pH 7.4 (O'Brien et al. 1964, modified), and mounted on permanent slides using acrylic resin.

The regions of the embryos evaluated were selected considering those that exhibited pre-germination cellular morphological changes associated with overcoming dormancy in *M. flexuosa* seeds (based on previous work by Moura et al. 2019; Salvador et al. 2022). The lengths and diameters of 10 cotyledonary petiole cells (chosen at random) were measured in the medullary region of the radicle, in the meristem adjacent to the radicle, in the protodermis, in the ground meristem of the ligule (the region adjacent to the embryonic axis), in the protodermis, and in the ground meristem of the region opposite the ligule. The thickness of the digestion zone (the layer of collapsed endosperm cells adjacent to the haustorium), and the lengths and diameters of 10 cells in the protoderm, subprotoderm, and ground meristem of the haustorium were likewise determined. Assessments were carried out on sections (obtained as described above) from 10 fragments of each structure per treatment, using image analysis software (Zen, Zeiss, Jena, Germany; https://www.micro-shop.zeiss.com/en/de).

For histochemical evaluations, histological sections were obtained as described above. The sections were subjected to periodic acid-Schiff-PAS tests (O'Brien and McCully 1981, adapted) to detect neutral polysaccharides, and exposed to toluidine blue (O'Brien et al. 1964, modified) to detect of phenolic compounds. Photographic documentation was carried out using a photomicroscope (Scope A1/Axiocam 105 Color, Zeiss).

For ultrastructural evaluations, fragments of the peripheral region of the cotyledonary petioles of embryos from seeds in the initial condition, as well as those subjected to thermal treatments for 60 days, were fixed in Karnovsky's solution (Karnovsky 1965) for 48 h and post-fixed in 1% osmium tetroxide in 0.1 M phosphate buffer, pH 7.2 (Roland 1978). Ultrathin sections were subsequently treated with uranyl acetate and lead citrate and examined under a transmission electron microscope (Tecnai G2-12-Spirit, Philips/FEI Company, Eindhoven, Netherlands) at 80 kV.

Short-term effects of the 45/35 °C thermal regime

To evaluate the short-term effects of exposure to a lethal temperature after 60 days (defined based on the results of the previously described evaluations), seeds from newly dispersed fruits were subjected to a 45/35 °C thermal regime. After 2, 5, 10, 15, 20, and 30 days of exposure, biometric characteristics, viability, germination, estimation of respiratory activity and membrane integrity, concentrations of H_2O_2 and MDA, and the activities of antioxidant system enzymes were evaluated, following the procedures described above. Seeds not subjected to heat stress were considered as the control.

To evaluate the maintenance of germination capacity during the evaluation periods described above, the opercula of seeds kept at 45/35 °C were removed to subsequently germinate for 15 days at 30 °C in the dark. Ultrastructural analyses were subsequently carried out in the peripheral regions of the cotyledonary petiole of embryos subjected to thermal stress for 5, 15, and 30 days, as previously described.

Statistical analysis

Quantitative data on the biometry, biodynamics (operculum resistance), physiological (germination, viability, embryonic respiratory activity, solute leaching, oxidative stress indicators) and micromorphometric parameters (cellular dimensions) were tested for normality and homogeneity variance.

The data were subjected to analysis of variance, considering a factorial scheme, with thermoperiods and analysis times (30, 60 and 90 days) as factors, and the initial condition as an additional treatment. Means were compared using the Tukey test ($P < 0.05$). In the case of data relating to seeds subjected to the lethal thermoperiod (45/35 °C), the means were compared using the t test ($P < 0.05$). The analyses were carried out using the R software statistical package (version 3.4.4).

Results

Germination

Seeds incubated at 30/20 °C began to germinate after 21 days, and attained 31% germination in 30 days, which was a higher average than the other thermoperiods ($P < 0.001$). The germination percentages of the other thermoperiods did not significantly diverge from each other, with all of them having averages below 5% (Fig. 2). This pattern remained

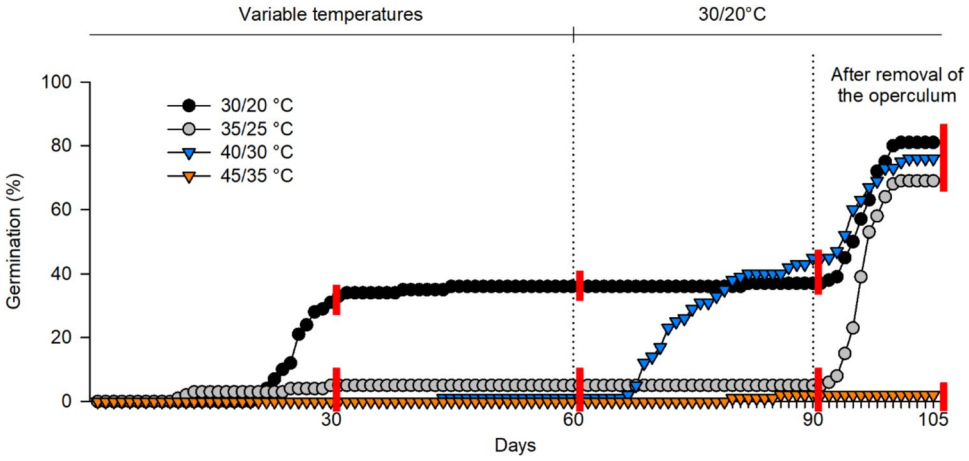

Fig. 2 Germination percentages of *M. flexuosa* seeds. The seeds were subjected to different temperature regimes for 60 days, and then transferred to a temperature of 30/20 °C for 30 days, followed by removal of the operculum of non-germinated seeds, and incubation at 30/20 °C for 15 additional days. Red vertical lines indicate no statistical difference between treatments, using the Tukey test ($P \leq 0.05$)

constant for 60 days ($P = 0.002$). The 30/20 °C thermoperiod (when applied to all of the seeds from all treatments for 60 and 90 days after the initiation of the experiment) was observed to stimulate the germination of seeds initially incubated at 40/30 °C, although that cooler thermoperiod did not affect seeds subjected to other thermoperiods. At 90 days, there was no statistical difference between the germination percentages of the initial 30/20 °C treatment (37%) and the initial 40/30 °C thermoperiod (45%). Thus, the 30/20 °C treatment was the most efficient in reducing the seed dormancy intensity [the level of restriction to germination, a concept derived from Finch-Sagave and Leubner-Metzger (2006) and Carvalho et al. (2015)], while the 35/25 °C treatment favored the maintenance of dormancy. The removal of the operculum, carried out at 90 days, promoted a drastic increase in the germination percentages of the 30/20, 35/25, and 40/30 °C thermoperiods (81, 69, and 76%, respectively) at 105 days. These means did not differ statistically from each other. Seeds from the 45/35 °C thermoperiod demonstrated only 2% germination, and the non-germinated seeds from this treatment did not show viable embryos by the tetrazolium test. Together, these results indicate that, except for the 45/35 °C treatment, the thermoperiods tested did not cause lethal stress levels in the seeds.

Biometric evaluations

The water contents of the seeds in their initial condition was 47.74% and, at the end of the experiment, was higher for seeds subjected to 45/35 °C (48.31%, $P = 0.0005$) (Fig. 3a). The dry mass of the seeds (7.72 g in the initial condition) became progressively reduced over time ($P = 0.0168$) (Fig. 3b), without the influence of temperature. Embryos from seeds maintained at 45/35 °C evidenced lower dry masses (8 mg, $P < 0.0001$) (Fig. 3c, d), while their water contents were always higher than in the initial condition

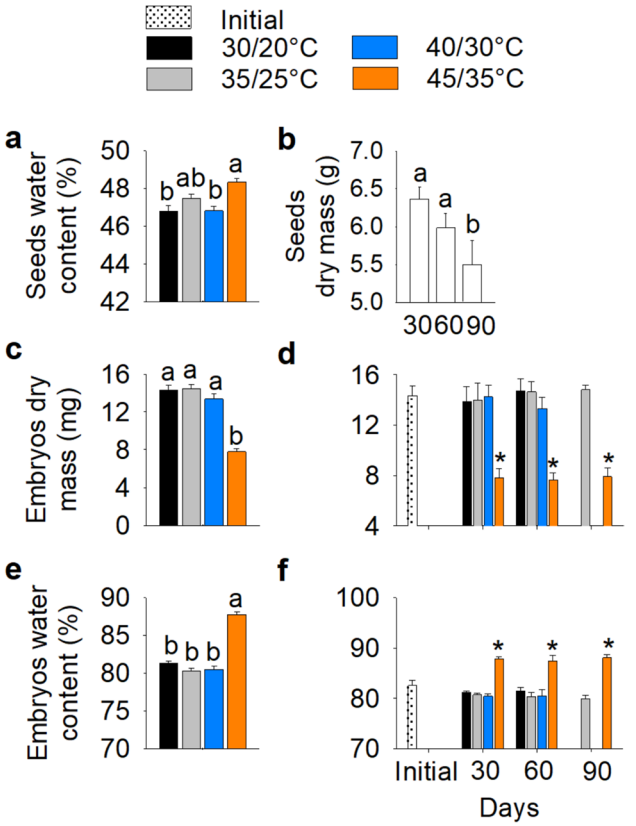

Fig. 3 **a-f** Effect of time and temperature on biometric characteristics of seeds and embryos of *M. flexuosa*. The seeds were subjected to different temperature regimes for up to 60 days, and then transferred to the temperature 30/20 °C for another 30 days. Vertical bars indicate the standard error of the mean ($n = 5$). Asterisks (*) indicate difference in relation to the initial condition. Different lowercase letters indicate differences between treatments, using the Tukey test ($P \leq 0.05$)

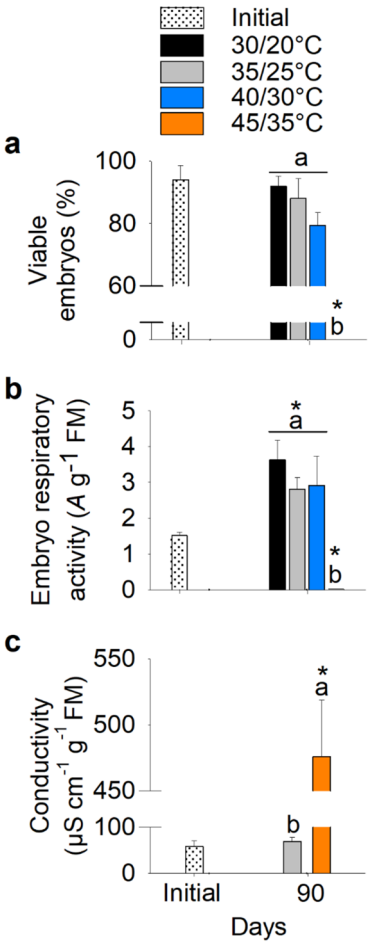

Fig. 4 Percentage of viability (**a**), estimated respiratory activity (**b**), and electrical conductivity of water after immersion (**c**) of *M. flexuosa* embryos. The seeds from which the embryos were extracted were subjected to different temperature regimes for 60 days, and then transferred to the temperature 30/20 °C for another 30 days. Vertical bars indicate the standard error of the mean ($n=4$). Asterisks (*) indicate difference in relation to the initial condition. Different letters indicate differences between treatments within time, using the Tukey test ($P \leq 0.05$)

and higher also than those of embryos maintained in other thermoperiods (average of 87.8%, $P<0.0001$) (Fig. 3e, f).

Viability, respiratory activity, and cell membrane functionality

Initial seed viability was 94% (Fig. 4a). Seed viability did not become altered after exposure to the 30/20, 35/25, and 40/30 °C thermoperiods during the entire experimental period (91, 88, and 79.3%, respectively), while seed viability after exposure to the 45/35 °C thermoperiod dropped to zero ($P<0.0001$) (Fig. 4a). There was an increase in the respiratory activity from 1.5 $A\ g^{-1}$ FM in the initial condition, to 3.6, 2.8, and 2.9 $A\ g^{-1}$ FM after 90 days of exposure to the 30/20, 35/25, and 40/30 °C thermoperiods, respectively; the respiratory activity of embryos in the 45/35 °C treatment was essentially zero (0.01 $A\ g^{-1}$ FM, $P<0.0001$) (Fig. 4b). The electrical conductivity of embryos in the initial condition was 57.9 µS g^{-1} FM, and was not statistically different from that recorded for the 35/25 °C treatment at the end of the experiment (68.7 µS g^{-1} FM) (Fig. 4c). The 45/35 °C treatment affected membrane permeability more intensely, resulting in an approximately seven-fold increase in electrical conductivity in relation to the initial condition (405.1 µS g^{-1} FM, $P<0.001$). It was not possible to carry out similar tests for the 30/20 and 40/30 °C treatments, as the breaking of dormancy and subsequent germination of the majority of the seeds in both treatments led to a reduction in samples available for conductivity evaluations.

Oxidative stress evaluation

The initial average H_2O_2 level of the embryos was 2.86 mM g^{-1} FM (Fig. 5c), with reductions in the concentrations of H_2O_2 after 60 and 90 days (1.62 and 1.54 mM g^{-1} FM, respectively; $P=0.0053$) (Fig. 5a). The 45/35 °C thermoperiod evidenced the lowest H_2O_2 value after 90 days (1.06 mM g^{-1} FM) in relation to the other thermoperiods, which did not differ from each other (Fig. 5b). After 30 days of exposure to the different thermoperiods, H_2O_2 levels in the embryos remained statistically similar to the initial level, regardless of the thermoperiod ($P=0.0260$) (Fig. 5c). There were pronounced reductions in H_2O_2 levels at 30/20 and 45/35 °C at 60 days (1.53 and 0.78 mM g^{-1} FM, respectively) in relation to the initial condition ($P<0.0001$) (Fig. 5c). A similar pattern was observed at the end of the experiment in terms of the 45/35 °C treatment (Fig. 5c). Due to the lack of samples (as a result of the germination of most seeds), it was not possible to evaluate the H_2O_2 levels of the 30/20 and 40/30 °C treatments after 90 days.

The initial CAT activity was 15.95 µmol min^{-1} g^{-1} protein. The activity of this enzyme varied over time ($P=0.0003$) (Fig. 5d), but no thermoperiod effects were observed ($P=0.1928$). The activity of that enzyme increased to 11.05 and 12.85 µmol min^{-1} g^{-1} protein after 30 and 60 days, respectively, and then to 19.40 µmol min^{-1} g^{-1} protein after 90 days, associated with reductions of H_2O_2 levels in the embryos (Fig. 5a). In the initial condition, SOD activity was 0.30 U min^{-1} g^{-1} protein, and did not vary over time ($P=0.7067$); likewise, no differences were observed among thermoperiods tested ($P=0.8279$). APX activity

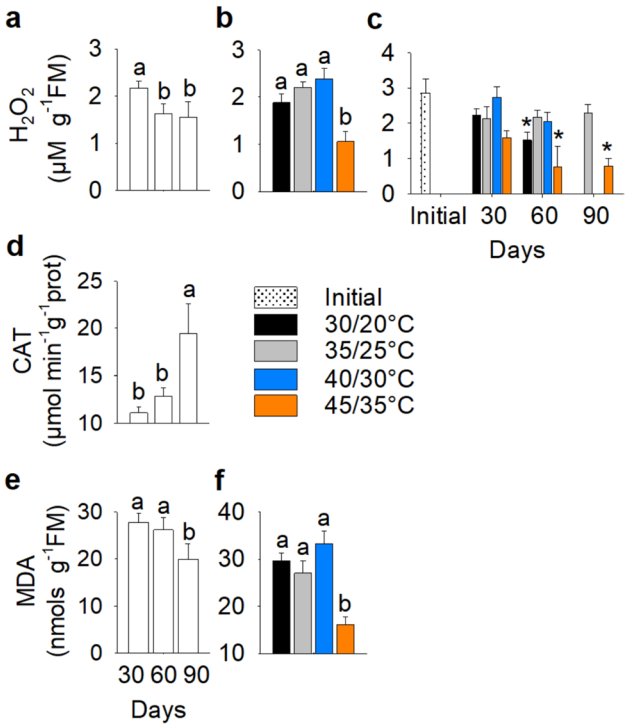

Fig. 5 Effect of time and temperature on H_2O_2 (**a**–**c**), malondialdehyde (MDA) (**e**–**f**) contents, and the enzymatic activity of catalase (CAT) (**d**), in embryos obtained of *M. flexuosa* seeds subjected to different thermal regimes for up to 60 days, and then transferred to a temperature of 30/20 °C for another 30 days. Vertical bars indicate the standard error of the mean ($n=4$). Asterisks (*) indicate difference in relation to the initial condition. Different lowercase letters indicate differences between treatments, using the Tukey test ($P \leq 0.05$)

was 6.30 µmol AsA min^{-1} mg^{-1} protein at the beginning of the experiment, and enzyme activity did not vary over time ($P=0.3796$) nor in relation to the different thermoperiods applied ($P=0.2869$).

Time ($P=0.0325$) and temperatures ($P<0.0001$) influenced MDA activity levels, without, however, there being any interaction between these factors (Fig. 5e, f). The MDA concentration in embryos in the initial condition was 26.90 nmols g^{-1} FM. At 30 days, the concentration was 27.73 nmols g^{-1} FM, a value that did not change significantly until day 60 of the experiment (Fig. 5e). By 90 days, MDA concentrations had decreased to 19.87 nmols g^{-1} FM. The 45/35 °C thermoperiod evidenced the lowest value for this parameter (average of 16.12 nmols g^{-1} FM) in relation to the other treatments, which did not differ from each other (Fig. 5f).

Operculum resistance to displacement

In the initial condition, the force required to displace the operculum was 88.13 N cm^{-2} (Fig. 6b). Operculum resistance became reduced throughout the course of the experiment in the different thermoperiod treatments of 30/20, 40/30, and 45/35 °C (66.0, 75.3, and 75.5 N cm^{-2}, respectively) (Fig. 6a). Only the seeds in the 35/25 °C treatment (which led to dormancy intensification, Fig. 2) maintained their operculum resistance equal to that observed in the initial condition (77.8 N cm^{-2}) until the end of the experiment (Fig. 6b). At 60 days, the 30/20 °C thermal regime (the treatment that favored germination, Fig. 2) provided the greatest reduction in operculum resistance (66.0 N cm^{-2}, $P=0.0330$). After 90 days, there were slight reductions in operculum resistance in the 40/30 and 45/35 °C treatments (72.37 and 69.19 N cm^{-2}, respectively), with no statistical difference between them (Fig. 6b). Operculum resistance was related to the dormancy intensity observed in seeds subjected to the 35/25 °C thermoperiod, and its reduction was related to the breaking of dormancy as a result of the 30/20 °C treatment (Fig. 2, 6a).

Micromorphometric evaluations

The effects of the different thermal regimes on micromorphometric and histochemical characteristics of *M. flexuosa* embryos are presented in Supplementary Fig. S1, S2 and S3, respectively, and summarized in Fig. 7. The embryo has two morphological regions: (i) a proximal region consisting of the cotyledonary petiole, facing the micropyle, where the embryo axis is inserted; (ii) a distal region consisting of the haustorium, which constitutes the cotyledonary limbus and is responsible for mobilizing endospermic reserves (Fig. 7). The embryo axis is composed of the hypocotyl-radicle axis and the plumule, which is surrounded by the ligule, a lateral region of the cotyledonary petiole.

Cell expansion in the radicle and peripheral regions of embryos was observed at 30 days in seeds subjected to the 35/25 and 40/30 °C thermoperiods, respectively (Fig. 7). The 45/35 °C thermoperiod caused cell expansion in both regions. At 60 days, cell expansion occurred in embryos subjected to all treatments, although with different patterns. The 30/20 °C thermoperiod (more favorable to germination) evidenced cell expansion in the radicle, peripheral regions of the cotyledonary petiole, and (in a pronounced way) in the peripheral and internal regions of the haustorium. The thermoperiods of 35/25 and 40/30 °C led to less cell expansion in the haustorium, compared to the 30/20 °C treatment. The 45/35 °C thermoperiod, on the other hand, resulted in significant expansion of the peripheral cells of the cotyledonary petiole and the central region of the haustorium. None of the treatments affected the thickness of the layer of collapsed cells (digestion zone) of the endosperm adjacent to the haustorium.

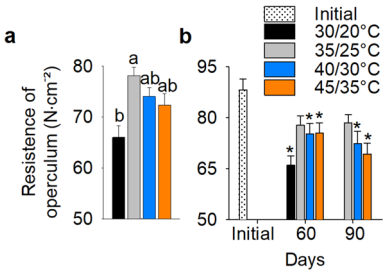

Fig. 6 Force required to displace the operculum of *M. flexuosa* seeds subjected to different thermal regimes for 60 days and then transferred to the temperature 30/20 °C for another 30 days. **a** Isolated effect of temperature on the resistance of the operculum. **b** Variation in the resistance of the operculum as a function of time and temperature. Vertical bars indicate the standard error of the mean ($n = 4$). Asterisks (*) indicate difference in relation to the initial condition. Different lowercase letters indicate differences between treatments, using the Tukey test ($P \leq 0.05$)

Histochemical evaluations

The embryonic cells in their initial condition evidenced abundant mucilage reserves (Supplementary Fig. S3a–b, h). Reserve consumption generally intensified in the cotyledonary petiole and haustorium regions after 30 days, as evidenced by mucilage content and transient starch deposition reductions (Fig. 7 and Supplementary Fig. S3c–d, i). Metabolite translocation towards the embryonic axis was notable (Supplementary Fig. S3). Mucilage consumption and starch deposition were greater in the cotyledonary petioles of embryos subjected to the 30/20 °C thermal regime (the more favorable regime for germination) and in the haustorium of embryos subjected to higher temperatures (40/30 and 45/35 °C); those alterations were lower in embryos subjected to the 35/25 °C thermal regime (associated with greater dormancy intensity) (Fig. 7). The cells of the ligule and haustorium of embryos maintained at 45/35 °C showed signs of cellular disorganization at 30 days (Supplementary Fig. S2 e–g and S3j). At 60 days, mucilage reserve mobilization and starch deposition were intense in the cotyledonary petioles of embryos subjected to all treatments, except in the 45/35 °C thermoperiod. Starch deposition was only observed in the haustorium of embryos subjected to the 30/20 °C regime (Fig. 7). Endosperm reserve mobilization was more evident in embryos maintained at higher temperatures (Supplementary Fig. S3f-g). At 60 days, embryos from seeds incubated at 45/35 °C exhibited collapsed cells, with vacuolar contents dispersed in the cytoplasm (Supplementary Fig. S2 j–m).

The accumulation of phenolic compounds was observed at the proximal end of the cotyledonary petiole in embryos in the initial condition, without significant differences among the 30/20, 35/25, and 40/30 °C treatments throughout the duration of the experiment (Fig. 7 and Supplementary Fig. S2d). Increases in phenolic compound accumulations (including in the plumule) were observed in embryos maintained at 45/35 °C at 30 days; at 60 days, more significant quantities of these compounds were observed at the apex of the cotyledonary petiole and extravasated from the ruptured cells (Fig. 7 and Supplementary Fig. S2 h, i, m, n).

Ultrastructural evaluations

The protodermal cells in the cotyledonary petiole exhibited a thicker external periclinal wall compared to the others (Fig. 8a, d, e, g). In the initial condition, the cytoplasm of those protodermal cells was thin, and peripheral, has flocculated content, small mitochondria and lipid droplets (Fig. 8b). Flocullar material (mucilage, confirmed by testing for neutral polysaccharides) was abundant in the vacuoles (Fig. 8a–c). The 30/20 °C thermoperiod treatment provoked small deformations of the cell wall (Fig. 8d); a proliferation of mitochondria around the nucleus, associated with poorly differentiated plastids, was observed in the cytoplasm (Fig. 8e, f). Invaginations were observed in the plasma membrane as well as the formation of vesicles to transport compounds originating from the endosperm (Fig. 8d–f). There was a slight accumulation of phenolic compounds in the vacuoles of the innermost cells of the ground meristem (Fig. 8f). The cells of embryos subjected to the 35/25 °C thermoperiod (the more restrictive treatment for germination) did not undergo evident changes in relation to their initial state (Fig. 8g–i), except that their cell walls showed sinuosities (Fig. 8g). Cells of the ground meristem evidenced dense protoplasts almost entirely filled with vacuoles containing mucilage, both in the initial condition and in embryos maintained at 35/25 °C (which were also rich in lipid droplets) (Fig. 8c, i). Protodermal cells from embryos subjected to the 40/30 °C treatment showed cytoplasm rich with organelles associated with the nucleus, the formation of autophagic vacuoles, and notable reductions in their mucilage reserve (electron translucent protoplast) the same was observed in the 30/20 °C treatment (Fig. 8d–f, j, k). The cells of the ground meristem evidenced the accumulation of phenolic compounds in their vacuoles, and small sinuosities in their cell walls (Fig. 8l).

Short-term effects of severe thermal stress (45/35 °C) on seeds

The dry masses of embryos subjected to the 45/35 °C thermoperiod regime became reduced after five days of evaluation, with the lowest values being observed at 30 days (Fig. 9a). The initial water content of the embryos was 82.3%, but increased after 5 days at 45/35 °C (85.0%),

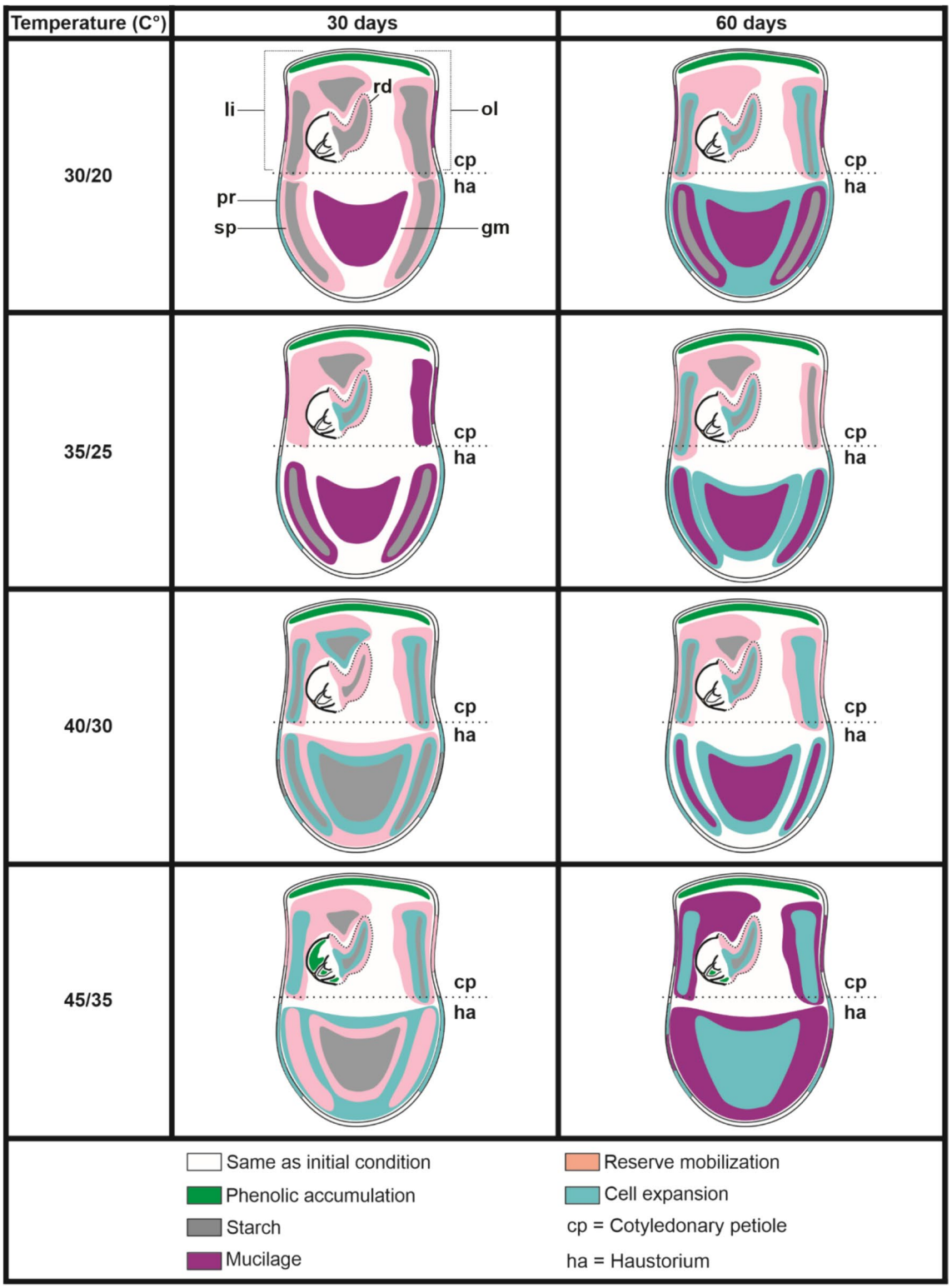

Fig. 7 Scheme of micromorphometric changes and histochemical evaluations in *M. flexuosa* embryos from seeds kept under thermoperiods of 30/20, 35/25, 40/30 and 45/35 °C, for 30 and 60 days. The evaluations were carried out on longitudinal sections of the cotyledonary petiole and cross sections of the embryos' haustorium. The cell expansion dynamics represented are relative to the dimensions of the cells in the initial condition. *cp* cotyledonary petiole, *ha* haustorium, *gm* ground meristem, *li* ligule, *ol* region opposite the ligule, *pr* protoderm, *rd* radicle, *sp* subprotoderm

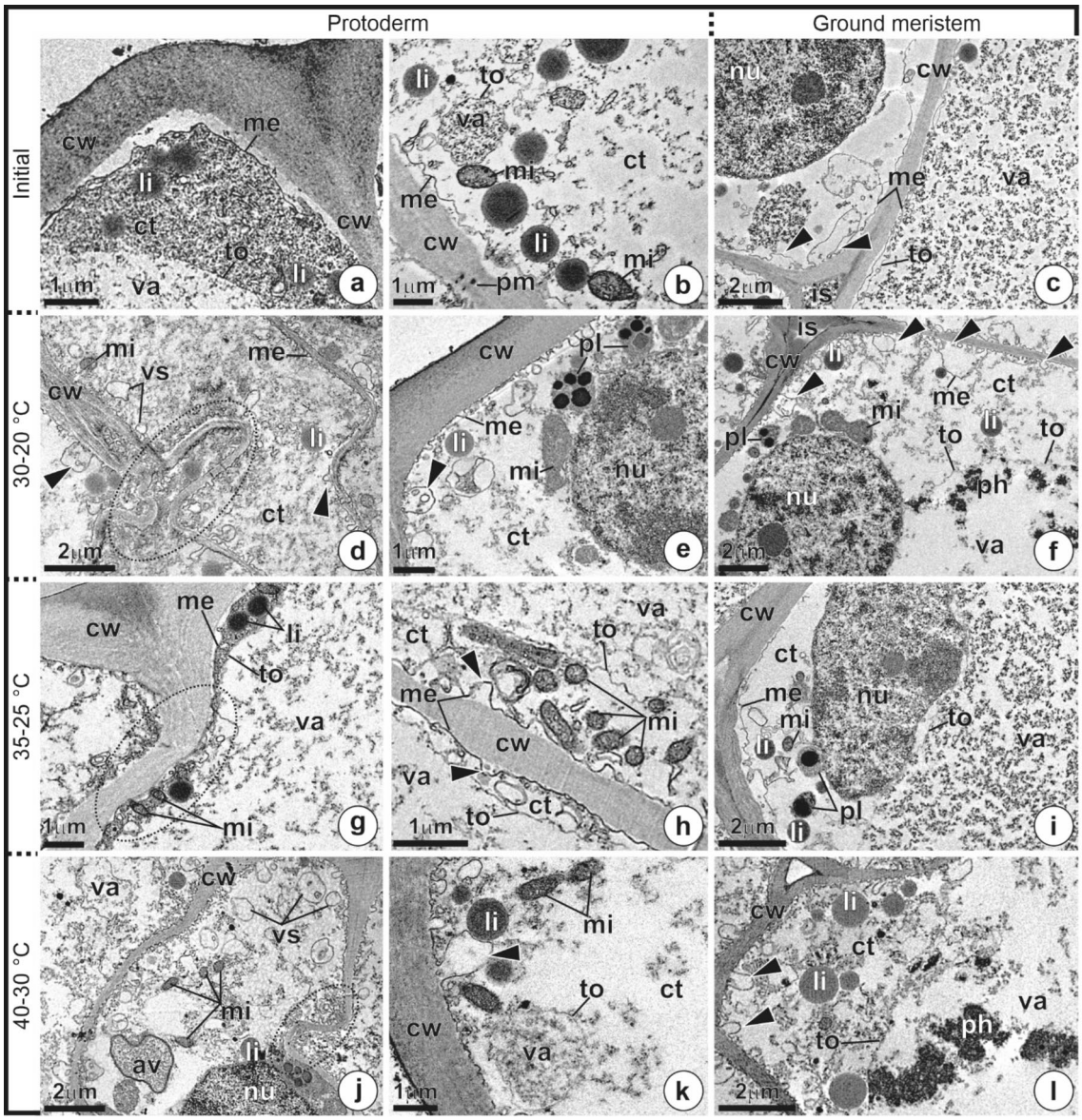

Fig. 8 TEM images of the cotyledonary petiole obtained from *Mauritia flexuosa* seeds grown at different temperatures (indicated on the left) for 60 days. **a** Protodermal cell of newly dispersed embryos with a thick external cell wall and cytosol containing a floccular-looking substance. **b** Mitochondria and lipid droplets arranged peripherally. **c** Ground meristem cells with prominent electron-dense vacuoles and sinuosities in the plasma membrane (arrowheads). **d** Pronounced sinuosity of the cell wall (ellipse) and the plasma membrane (arrowheads). **e** Proliferation of mitochondria, plastids and vesicles (arrowheads) in protodermal cells. **f** Accumulation of phenolic compounds and abundant vesicles (arrowheads) in cells of the fundamental meristem. **g** Sinuosity of the cell wall and large vauoles with floccular material. **h** Numerous mitochondria and sinuosities in the plasma membrane (arrowheads). **i** Large vacuole rich in mucilage and lipid accumulation in plastids in the peripheral cytosol. **j-k** Formation of autophagic vacuole and vesicles. **l** Reduced amounts of mucilage and accumulation of phenolic compounds in the vacuole *av* autophagic vacuole, *ct* cytosol, *cw* cell wall, *er* endoplasmic reticulum, *is* intercellular space, *li* lipids, *me* plasma membrane, *mi* mitochondria, *nu* nucleus, *ph* phenolic compounds, *pl* plastids, *ps* periplasmic space, *to* tonoplast, *va* vacuole, *vs* vesicles

continuing to increase until 30 days, when it reached 86.1% (Fig. 9b).

Maintaining the seeds at 45/35 °C for up to 30 days did not affect embryo viability (92.5% in the initial condition, $P = 0.1158$). The seeds also demonstrated the maintenance of their ability to germinate after being transferred to 30 °C, with an average germination percentage of 68.6%, without divergence from the initial condition ($P = 0.0702$). However, the respiratory activity of the embryos increased from 1.85 $A\ g^{-1}$ FM in the initial condition to 3.80 $A\ g^{-1}$ FM ($P < 0.001$) at 20 days (Fig. 9c). The electrical conductivity of embryos observed in the initial condition was

131.8 µS g^{-1} FM, which was the same as observed for embryos from seeds kept at 45/35 °C ($P = 0.3583$).

The initial average H_2O_2 concentration in the embryos was 2.86 mM g^{-1} FM; this average did not change throughout the experimental period ($P = 0.7983$). The initial activities of CAT and APX were 1.13 µmol min^{-1} g^{-1} protein and 1.15 µmol AsA min^{-1} mg^{-1} protein, respectively; no differences were observed due to thermal stress. Superoxide dismutase activity was detected after 5, 10, and 30 days at 45/35 °C (0.054; 0.060; 0.042 U min^{-1} g^{-1} protein,

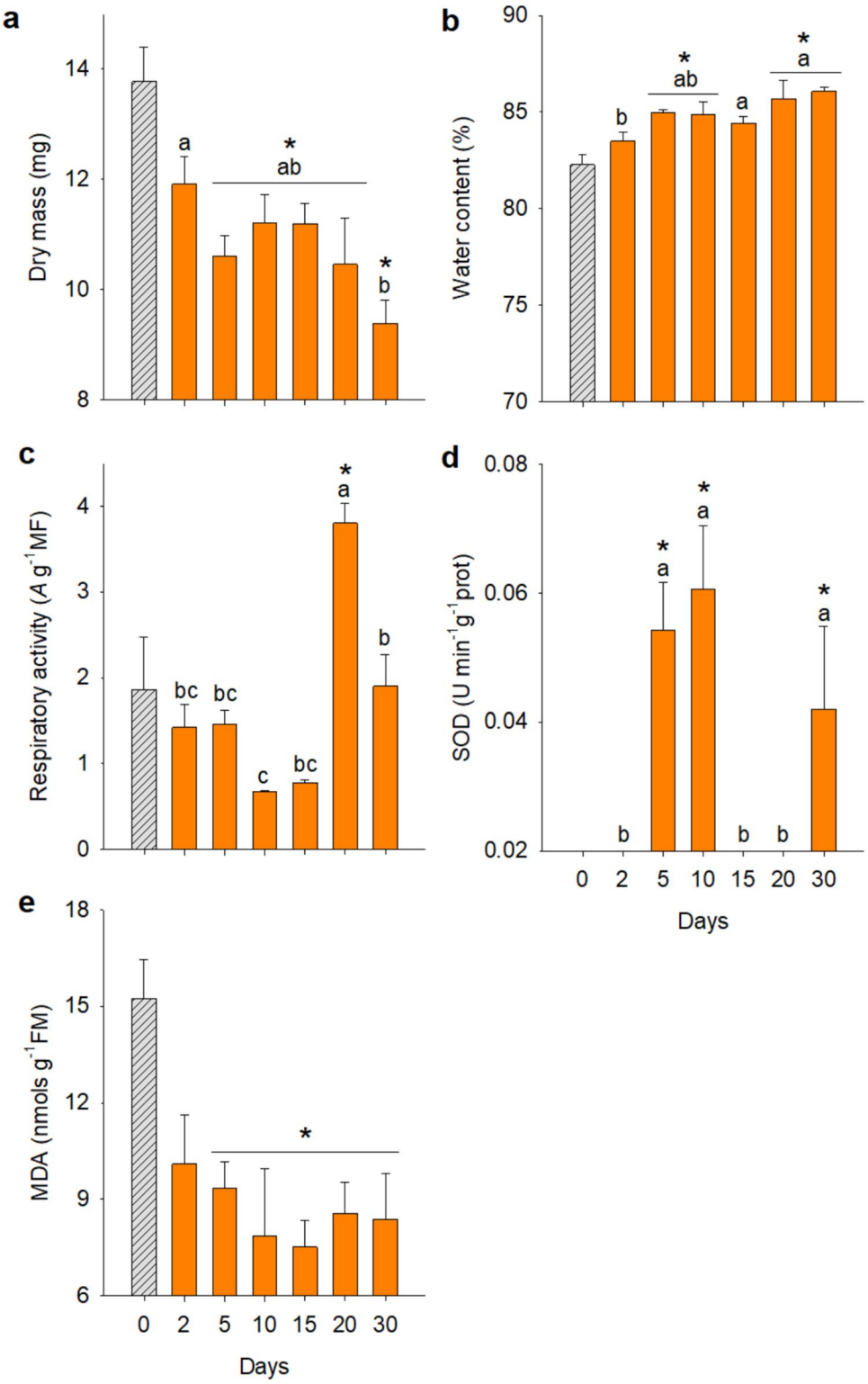

Fig. 9 Dry mass (**a**), water content (**b**), estimated respiratory activity (**c**), SOD activity (**d**) and MDA content (**e**) of embryos obtained from *M. flexuosa* seeds before and after being subjected to 45/35 °C, for up to 30 days. Vertical bars indicate the standard error of the mean ($n = 4$). Asterisks (*) indicate difference in relation to the initial condition, using the Tukey test ($P \leq 0.05$)

respectively) at levels higher than the initial condition (Fig. 9d). The MDA concentration in the initial condition (15.24 nmols g^{-1} FM) became reduced after 5 days of incubation, reaching 9.35 nmols g^{-1} FM and remaining lower than the initial condition throughout the course of the experiment ($P = 0.0051$) (Fig. 9e).

Cytological changes indicative of cell collapse occurred gradually between 5 and 30 days of cultivation under the 45/35 °C thermoperiod regime (Fig. 10a–l), culminating in cell death at 60 days (Fig. 10m–p). At five days, the cytoplasm of the protoderm cells remained rich in organelles that were markedly differentiated, with a notable proliferation of vesicles (Fig. 10a, b). From 15 days onwards, however, it was possible to identify intense deformity of the cell wall (Fig. 10e, m) and intense retraction of the plasma membrane, with the accumulation of substances in the periplasmic space (Fig. 10f, j). At 30 days, vacuolar contents were partially mobilized, with visible phenolic deposition (Fig. 10 i). The cells of the ground meristem likewise maintained a protoplast rich in organelles and lipid droplets, and the vacuoles contained remnants of mucilage and evidenced the gradual accumulation of phenolic compounds as well as the formation of autophagic vacuoles (Fig. 10c, d, g, h). At 30 days, there was a notable retraction of the plasma membrane and accumulations of substances in the periplasmic space (Fig. 10k, l). At 60 days, the protoplast evidenced widespread degradation, with the disintegration of the plasma membrane and organelles, with only the remnants of flocculated material, phenolic compounds, autophagic vacuoles, and vesicles dispersed in the cytosol (Fig. 10m-p).

Taken together, the results revealed the ability of seeds to buffer the effects of thermal stress for short periods, but were highly vulnerable to prolonged exposure to extreme conditions – associated with reserve depletion and the collapse of the embryonic cells.

Discussion

High temperatures and germination control

Exposure to high temperatures affects the germination of *M. flexuosa* seeds, causing maintenance or intensification of dormancy or loss of viability (Fig. 11). The most extreme thermal regime tested in the present work (45/35 °C, which has not yet been recorded in historical climate records in the study region; Fig. 1) caused the loss of seed viability when continued for 60 days. On the other hand, seeds respond to non-fatal high-temperature situations by halting germination (Fig. 2). The 40/30 °C thermoperiod contributed to maintaining the initial dormant state of the seeds, as some of the seeds quickly germinated when transferred to the 30/20 °C regime. The 35/25 °C thermoperiod regime induced an increase in dormancy intensity, as the seeds did not germinate when transferred to a 30/20 °C regime. Such thermoperiods normally occur in the transition between dry/rainy periods (September and October, the austral Spring), when rainfall is irregular and scarce, or during heat waves associated with drought (known as '*veranicos*', which frequently occur during the austral summer rainy season in December and January). These periods of low water availability limit germination and pose risks to seedling survival. It is important to note that the Cerrado veredas phytophysiognomy (where *M. flexuosa* occurs) is generally a humid environment, but shows accentuated cross-stratification and soils subject to humidity fluctuations throughout the year, especially at the edges of the veredas (Araújo et al. 2002; Porto et al. 2018; Almeida et al. 2024). High temperatures likewise inhibit the germination of *Euphorbia* sp. (Euphorbiaceae) seeds during occasional rains in the Mediterranean region (Cristaudo et al. 2019).

The germination of *M. flexuosa* seeds was favored by the 30/20 °C thermal regime (the typical regime of the rainy season; Fig. 1, 2). So adjusting the germination rate in response to temperature appears to represent a viable strategy favoring seedling recruitment during the rainy season. A similar pattern was observed with the orthodox seeds of *Annona crassiflora* (Annonaceae) and *Acrocomia aculeata* (Arecaceae) that show morphophysiological dormancy in soil seed banks in the same biome (Silva et al. 2007; Souza et al. 2022).

Previous research pointed to the control of buriti palm germination by pronounced seed dormancy, the capacity to maintain seed banks, and environmental temperatures (Silva et al. 2014; Salvador et al. 2022). According to these studies, the seeds of *M. flexuosa* will germinate in a wide range of temperatures after dormancy is overcome naturally as the seeds pass through the soil bank. In the present work, additional evidence was found that temperature acts to reduce the resistance of tissues adjacent to the embryo (Fig. 6) in seeds exposed to seasonal cycles in seed banks, thus overcoming the physiological component of morphophysiological dormancy and increasing their growth potential (Fig. 7) (concepts by Baskin and Baskin 2014). The 30/20 °C treatment appeared as more effective in reducing the resistance exerted by the operculum, a critical mechanical restriction that maintains dormancy in palm seeds (Neves et al. 2013; Silva et al. 2014; Carvalho et al. 2015; Mazzottini-dos-Santos et al. 2018). Furthermore, significant cytological changes were observed in embryos while breaking dormancy (when exposed to 30/20 °C), such as cell expansion and reserve mobilization towards the embryonic axis (Fig. 7).

Variations in dormancy intensity are common within seed populations (Finch-Savage and Leubner-Metzger 2006; Baskin and Baskin 2014; Carvalho et al. 2015), and the resulting uneven germination represents a strategy to

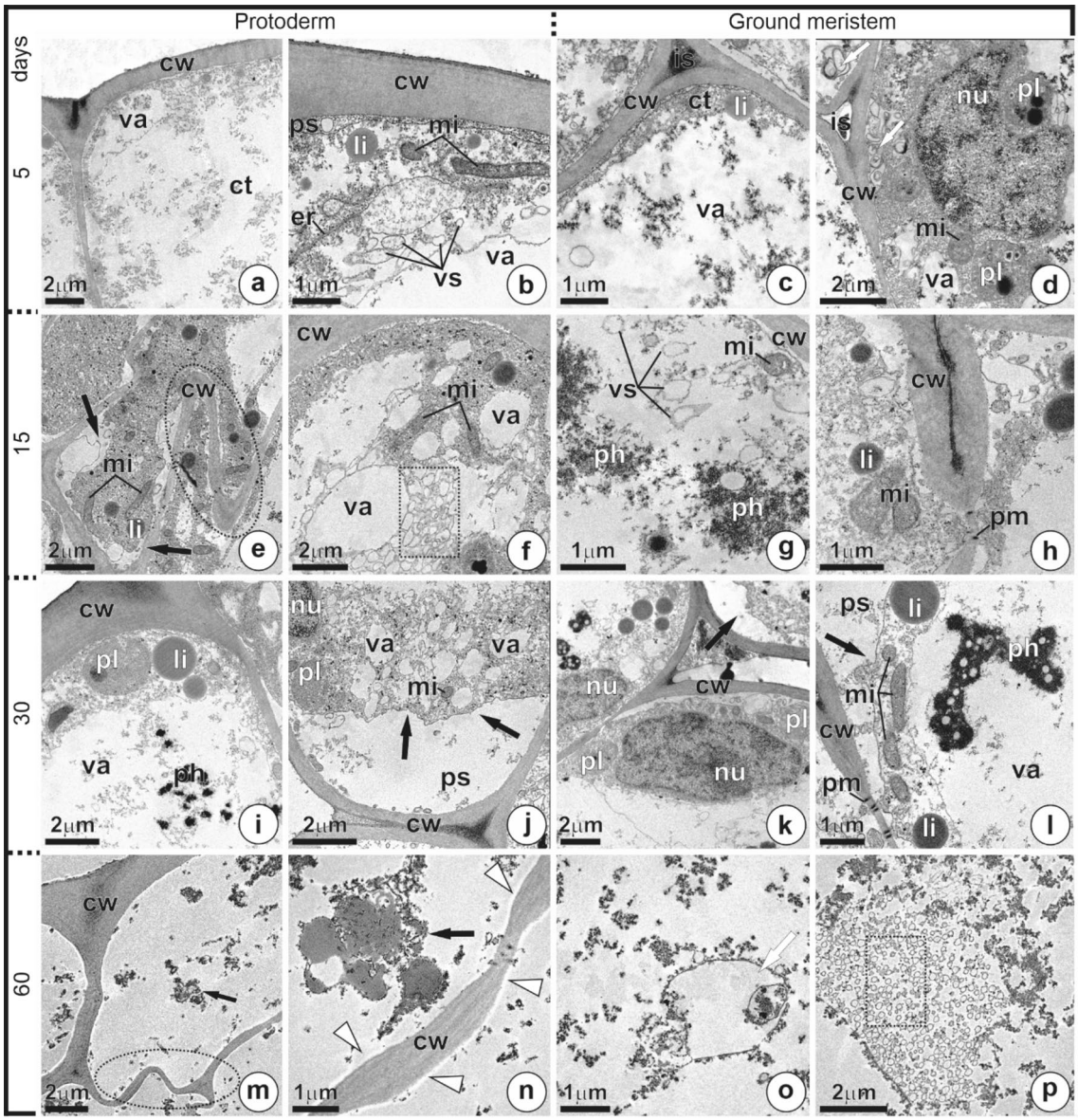

Fig. 10 TEM images of the cotyledonary petiole obtained from *Mauritia flexuosa* seeds cultivated at 45/35 °C at different times (indicated on the left). **a** Accumulation of a floccular-looking substance in small vacuoles and in the cytosol. **b** Periphery of the cell showing small accumulation of substances in the periplasmic space; the cytoplasm is dense, containing mitochondria, vesicles from the endoplasmic reticulum and some lipid droplets. **c** Peripheral cytoplasm and voluminous vacuole containing remnants of substances with a flocculated appearance. **d** Periphery of the cell indicating dense cytoplasm, with a conspicuous nucleus, mitochondria, plastids and proliferation of autophagic vacuoles (arrows). **e** Large sinuosities in the cell wall (ellipse) and retraction of the plasma membrane (arrows). **f** Periphery of the cell with evident vacuolation (rectangle). **g** Beginning of accumulation of phenolic compounds in the vacuole. **h** Periphery of the cell with intact mitochondria and lipid droplets. **i** Accumulation of phenolic compounds in the vacuole. **j** Strong retraction of the plasma membrane (arrows) and proliferation of small vacuoles in the cytosol. **k**, **l** Retraction of the plasma membrane (black arrows) and accumulation of phenolic compounds in the vacuole and substances in the periplasmic space; in the peripheral cytoplasm, mitochondria and plastids are intact. **m** Sinuosity of the wall (ellipse) and protoplast with remnants of flocculated substances (arrow). **n** Periphery of cells indicating damage to the plasma membrane (arrowheads) and protoplast remnants (black arrows). **o**, **p** Remnants of the protoplast with autophagic vacuole (white arrow) and proliferation of vesicles (rectangle). *ct* cytosol, *cw* cell wall, *di* dictyosome, *er* endoplasmic reticulum, *is* intercellular space, *li* lipids, *mi* mitochondria, *nu* nucleus, *ph* phenolic, *pl* plastids, *pm* plasmosdemata, *ps* periplasmic space, *va* vacuole, *vs* vesicles

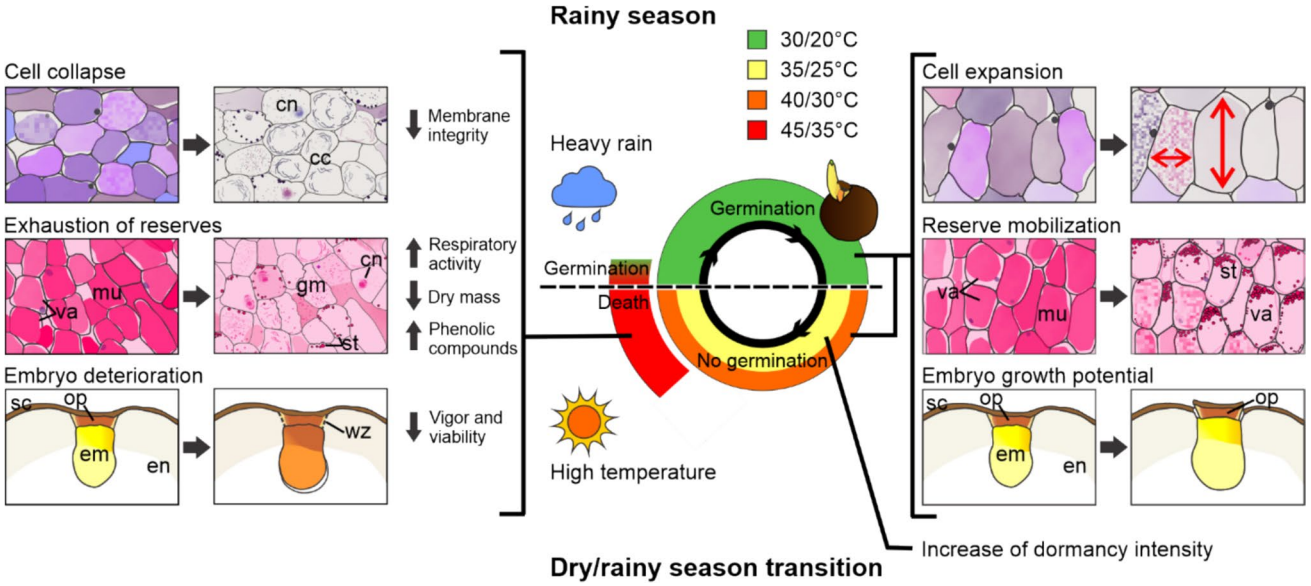

Fig. 11 Synthesis scheme of *Mauritia flexuosa* seed responses to different thermal regimes. *cc* collapsed cells, *cn* collapsed nucleus, *em* embryo, *en* endosperm, *gm* ground meristem, *mu* mucilage reserve, *op* operculum, *sc* seed coat, *st* starch, *va* vacuoles, *wz* weakness zone

distribute seedling emergence over time (*bet-hedging*) and thus maximize the chance of survival under unfavorable climatic conditions (Ooi et al. 2007; Silva et al. 2007; Long et al. 2015; Pausas et al. 2022; Zhang et al. 2022). Our results indicate that *M. flexuosa* seeds overcome dormancy during the rainy season, while seeds that do not germinate can increase their dormancy intensity (through exposure to high temperatures), being capable of germination only in subsequent rainy periods. Temperatures as high as 45/35 °C, which are predicted to occur in the region in the future due to climate change (Cristaudo et al. 2019; Oliveira et al. 2019; IPCC 2022), may exceed seed tolerance limits and become lethal (Fig. 4a).

Cytological and physiological responses to thermal stress

Buriti palm seeds are capable of high levels of cellular homeostasis in response to thermal stress, although they appear highly vulnerable to a 45/35 °C regime (Fig. 11). None of the other treatments presented severely stressful conditions to the seeds. Progressive cell expansion and reserve mobilization were observed during the evaluation periods, associated with high germination rates, especially in the 30/20 °C treatment (Figs. 2, 7). Additionally, buriti seeds respond well to short periods of high temperatures, maintaining levels of cellular metabolism that, in due course, will contribute to germination. Exposure to a 40/30 or 40 °C thermal regime, followed by 30 °C, was also found to promote high germination rates among seeds of the Brazilian palm *Butia odorata* (Schlindwein et al. 2013).

The high temperatures used in the present work promoted rapid cell expansion and the activation of reserve mobilization processes. Ultrastructural changes (cell expansion, vacuolization, reserve mobilization) that occur in recalcitrant seeds during storage (or the maintenance of dormancy) are comparable to germination initiation events in orthodox seeds (Farrant et al. 1985; Moothoo-Padayachie et al. 2016; Veloso et al. 2016). This increased metabolic activity contributes to preparing the seed for rapid germination when appropriate environmental conditions are available. In the present work, the states of the embryos kept at 35/25 °C (a treatment that favors the maintenance of dormancy), however, were more similar to that observed in the initial condition (Figs. 7, 8). In a study with simulated seed banks of *A. crassiflora* (Annonaceae), Silva et al. (2007) likewise observed the absence of significant changes at the cellular level in non-germinated seeds after an emergence peak, suggesting a relationship between cellular status and the level of dormancy.

Oxidative damage associated with active metabolism is normally the main cause of viability losses in recalcitrant seeds (Berjak and Pammenter 2008). On the other hand, the negative impacts of ROS tend to remain reduced in seeds exhibiting physiological dormancy, due to the presence of antioxidants and hormones associated with dormancy (Long et al. 2015; Moothoo-Padayachie et al. 2016). We verified here that enzymatic antioxidant systems were important for controlling oxidative stress in buriti seeds subjected to high temperatures, and that those systems have fundamental

roles in the persistence of seeds in soil banks (Salvador et al. 2022). The concentration of H_2O_2 became reduced over time, indicating that CAT activity was efficient in preventing lipid peroxidation from reaching harmful levels (Fig. 5a, d). Furthermore, SOD activity increased rapidly in response to the intensification of cellular metabolism (Fig. 9d), demonstrating its relevant role in the immediate containment of ROS in seeds under severe heat stress. Another important aspect is that groups of compounds showing antioxidant activities present in buriti fruits and seeds (e.g., phenolics and vitamin E; Siles et al. 2013; Silva et al. 2014) are effective as protective mechanisms against oxidative damage (Bailly 2019). In the present work, we identified greater accumulations of phenolic compounds in embryonic tissue subjected to high temperatures (Fig. 9, 10g, l), thus reinforcing the importance of these substances under stress conditions.

The 45/35 °C condition caused seed death in a short period of time, as seen by the high levels of cellular degradation observed from 30 days onwards (Fig. 10e–p). Before that time, oscillations of the evaluated physiological parameters were noted, reflecting homeostatic attempts to adjust the physiological status of the embryos exposed to high-temperatures and maintain short-term viability. Our short-term evaluation of the effects of the 45/35 °C regime did not allow us to associate cell death with oxidative stress, as H_2O_2 and MDA levels remained controlled for 30 days (Fig. 9e). Reserve exhaustion was evident, however, as a result of high respiratory activity (9c), and was associated with irreversible cellular disorganization (Fig. 10m–p).

No studies were found in the literature relating thermal stress to oxidative stress in recalcitrant seeds, however, similarities can be noted between cell damage caused by thermal stress and damage resulting from seed dehydration (Veloso et al. 2016; Gonçalves et al. 2020; Dias et al. 2024). Veloso et al. (2016) reported collapsed protoplasts in embryonic cells in *M. flexuosa* seeds dehydrated to 20% water content, with the disintegration of organelles and the leaching of cellular contents into the periplasmic space. In the present work, treatments that did not promote cell death maintained cell integrity, with large mucilaginous vacuoles and cytoplasm rich in organelles and reserve compounds (Fig. 8d–l). Buriti seeds, therefore, evidence resistance mechanisms that can withstand high temperatures, restrict germination, but maintain an active metabolism—although these resistance mechanisms can be overcome by drastic temperature increases.

Ecophysiological implications of high temperatures on recalcitrant *M. flexuosa* seeds

The differential responses of seeds to thermal regimes represent an important adaptive factor for *M. flexuosa* in the highly seasonal Cerrado environment (Fig. 11), although its seeds are vulnerable to extreme temperatures and may impact its conservation in future scenarios. Temperature cycles were shown to be important in controlling the germination of the Cerrado palms *A. aculeata* (Souza et al. 2022) and *Butia capitata* (Gonçalves et al. 2020; Soares et al. 2021), which are tolerant to desiccation and high temperatures. For these palms, temperature is a factor for overcoming morphophysiological dormancy and an indicator of the allocation of germination during the rainy season. Doubts, however, persist in the case of the buriti palm, considering that the species produces recalcitrant and dormant seeds and is native to the same seasonal environment—although restricted to humid environments (veredas).

Veredas sites experience the same climatic regime as neotropical savanna formations (Cerrado), but their edaphic characteristics are quite unique (Ribeiro and Walter 2008; Ávila et al. 2021). Veredas are quite long and narrow (associated with shallow runoff), with a permanently humid central region but a considerable border area subject to drying (a drying that would intensify as a result of irregular precipitation rates and rising temperatures). Our research has shown that *M. flexuosa* seeds use thermal cycles as indicators, which may help explain why it is one of only two species of palm trees of Amazonian origin (along with *Mauritiella armata*) that have adapted to semi-arid environments (Nunes et al. 2022; Almeida et al. 2024). The long-term persistence of buriti in Cerrado veredas, however, remains uncertain. The increased temperatures expected due to climate change will likely alter regional precipitation patterns (IPCC 2022), upsetting the interactions established between the seeds and their environment, thus putting the maintenance of natural populations at risk (Stevens et al. 2014; Pausas et al. 2022). Species with high degrees of specialization tend to be more sensitive to climate change (Borges et al. 2019), and their persistence will depend on both seed and habitat resilience.

Recent studies have drawn attention to the potential collapse of veredas ecosystems, as they are highly vulnerable to human local impacts and climate change (Silva et al. 2014; Ávila et al. 2021; Nunes et al. 2022; Almeida et al. 2024). In this sense, the prospect of rising global temperatures and increased occurrences of extreme weather events is worrying, as they could impact seed bank dynamics and the reproduction of this iconic South American palm tree. Our results therefore highlight that investigating the effects of environmental variables on seed physiology will be important for predicting future ecological dynamics and for proposing appropriate conservation practices.

Conclusions

Temperature affects the viability and germination of *M. flexuosa* seeds. Germination is stimulated by the thermal regime typical of the Cerrado rainy season (30/20 °C) and is associated with the reduction of the mechanical resistance exerted by the seed operculum, the mobilization of metabolic reserves, and embryo cell expansion. The seeds react preventively to high temperatures, restricting germination while maintaining an active metabolism, and relying on mechanisms of resistance to thermal stress (including an enzymatic antioxidant system efficient in controlling oxidative stress at high temperatures). The extreme thermal regimes expected to occur in the future, however, would cause extensive seed deaths if prolonged. The responses of buriti seeds to temperature cycles are important for controlling the dynamics of the species' seed banks, so that any significant increases in local temperatures will put the reproductive success of the species at risk.

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Author contributions LMR conceived the work. HFS collected the samples, conducted the experiments, and wrote the initial text. HCM-S performed the anatomical assessments and interpreted the related results. LMR and YRFN interpreted the ecophysiological data. HFS and LMR wrote the final text. All authors read the final version of the manuscript and agreed to its submission.

Data availability All data generated or analyzed during this study are included in this published article and its supplementary information files.

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

References

Alexieva V, Sergiev I, Mapelli S, Karanov E (2001) The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. Plant Cell Environ 24:1337–1344

Almeida TS, Ribeiro LM, De Paula Santos Martins C, Barbosa TL, Mercadante-Simões MO, De OliveiraVieira E, Nunes YRF, Lopes PSN (2024) Structural and physiological responses to water availability provide insights into the maintenance of *Mauritia flexuosa* (Arecaceae) seedling banks. For Ecol Manag 561:121881. https://doi.org/10.1016/j.foreco.2024.121881

Araújo MG, Barbosa AAA, Arantes AA, Amaral AF (2002) Composição florística de veredas no Município de Uberlândia, MG. Rev Bras Bot 25:475–493

Ávila MA, Mota NM, Souza SR, Santos RM, Nunes YRF (2021) Diversity and structure of natural regeneration in swamp forests in Southeastern Brazil. Flora (Jena) 28:1–7

Bailly C (2019) The signalling role of ROS in the regulation of seed germination and dormancy. Biochem J 476:3019–3032

Barreto LC, Garcia QS (2017) Accelerated ageing and subsequent imbibition affect seed viability and the efficiency of antioxidant system in macaw palm seeds. Acta Physiol Plant 39:72. https://doi.org/10.1007/s11738-017-2367-z

Baskin CC, Baskin JM (2014) Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego

Bastos LLS, Ferraz IDK, Lima Junior MJV, Pritchard HW (2017) Variation in limits to germination temperature and rates across the seed-seedling transition in the palm *Oenocarpus bataua* from the Brazilian Amazon. Seed Sci Technol 45:1–13

Berjak P, Pammenter NW (2008) From *Avicennia* to *Zizania*: seed recalcitrance in perspective. Ann Bot 101:213–228

Berjak P, Pammenter NW (2013) Implications of the lack of desiccation tolerance in recalcitrant seeds. Front Plant Sci 4:478. https://doi.org/10.3389/fpls.2013.00478

Bewley JD, Bradford KJ, Hilhorst HWM, Nonogaki H (2013) Seeds: physiology of development, germination and dormancy. Springer, New York

Borges FJA, Ribeiro BR, Lopes LE, Loyola R (2019) Bird vulnerability to climate and land use changes in the Brazilian Cerrado. Biol Conserv 236:347–355

Brasil – Ministério da Agricultura, Pecuária e Abastecimento (2009). Regras para análise de sementes. MAPA, Brasília, DF, Brazil

Cakmak I, Horst WJ (1991) Effect of aluminium on lipid peroxidation, superoxide dismutase, catalase, and peroxidase activities in root tips of soybean (*Glycine max*). Physiol Plant 83:463–468

Carvalho VS, Ribeiro LM, Lopes PSN, Agostinho CO, Matias LJ, Mercadante-Simões MO, Correia LNF (2015) Dormancy is modulated by seed structures in palms of the cerrado biome. Aust J Bot 63:444–454

Cristaudo A, Catara S, Mingo A, Restuccia A, Onofri A (2019) Temperature and storage time strongly affect the germination success of perennial *Euphorbia* species in Mediterranean regions. Ecol Evol 9:10984–10999

da Silva EAA, Melo DB, Davide AC, Bode N, Abreu GB, Faria JRM, Hilhorst HWM (2007) Germination ecophysiology of *Annona crassiflora* seeds. Ann Bot 99:823–830

de Lima NE, Lima-Ribeiro MS, Tinoco CF, Terribile LC, Collevatti RG (2014) Phylogeography and ecological niche modelling, coupled with the fossil pollen record, unravel the demographic history of a Neotropical swamp palm through the Quaternary. J Biogeogr 41:673–686

de Oliveira VA, de Mello CR, Beskow S, Viola MR, Srinivasan R (2019) Modeling the effects of climate change on hydrology and sediment load in a headwater basin in the Brazilian Cerrado biome. Ecol Eng 133:20–31

Dias GP, Ribeiro LM, Mazzottini-dos-Santos HC, Nunes YRF, França MGC (2024) Water stress resilience in *Mauritia flexuosa* (Arecaceae) embryos: new insights into the persistence of recalcitrant seed banks. Environ Exp Bot 226:105930. https://doi.org/10.1016/j.envexpbot.2024.105930

Dransfield J, Uhl NW, Lange C, Baker WJ, Harley M, Lewis C (2008) Genera Palmarum. The evolution and classification of palms. Royal Botanic Gardens, Kew

Endress BA, Horn CM, Gilmore MP (2013) *Mauritia flexuosa* palm swamps: composition, structure and implications for conservation and management. For Ecol Manag 302:346–353

Esser LF, Neves DM, Jarenkow JA (2019) Habitat-specific impacts of climate change in the Mata Atlântica biodiversity hotspot. Divers Distrib 25:1846–1856

Farrant JM, Berjak P, Pammenter NW (1985) The effect of drying rate on viability retention of recalcitrant propagules of *Avicennia marina*. S Afr J Bot 51:432–438

Finch-Savage WE, Leubner-Metzger G (2006) Seed dormancy and the control of germination. New Phytol 171:501–523

Giannopolitis CN, Ries SK (1977) Superoxide dismutases. I. Occurrence in higher plants. Plant Physiol 59:309–314

Gonçalves BG, Ribeiro LM, Dias DS, Mazzottini-dos-Santos HC, Martins CDPS, Lopes PSN, Mercadante-Simões MO (2020) Embryo responses to extreme water events provide insights into the behavior of *Butia capitata* (Arecaceae) seed banks during hydration cycles. Environ Exp Bot 169:103904. https://doi.org/10.1016/j.envexpbot.2019.103904

Harding K, Benson EE (1995) Biochemical and molecular methods for assessing damage, recovery and stability in cryopreserved plant germplasm. In: Grout BWW (ed) Genetic preservation of plant cells in vitro. Springer, Berlin, pp 113–167

Heath RL, Packer L (1968) Photoperoxidation in isolate chloroplasts: I. Kinetics and stoichiometry of fatty acid peroxidation. Arch Biochem Biophys 125:189–198

Hong TD, Ellis RH (1996) A protocol to determine seed storage behavior. IPGRI. Technical Bulletin No. 1. International Plant Genetic Resources Institute, Rome

INMET 2024 Instituto Nacional de Metereologia. https://portal.inmet.gov.br/

IPCC (2022) Climate change 2022 impacts, adaptation and vulnerability. In: Pörtner H-O, Roberts DC, Tignor M, Poloczanska ES, Mintenbeck K, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A, Rama B (eds) Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change Cambridge University Press. Cambridge University Press, Cambridge, p 3056

Jaganathan GK (2021) Ecological insights into the coexistence of dormancy and desiccation-sensitivity in Arecaceae species. Ann for Sci 78:10. https://doi.org/10.1007/s13595-021-01032-9

Karnovsky MJA (1965) A formaldehyde-glutaraldehyde fixate of high osmolality for use in electron microscopy. J Cell Biol 27:137A-138A

Long RL, Gorecki MJ, Renton M, Scott JK, Colville J, Goggin DE, Commander LE, Westcott DA, Cherry H, Finch Savage WE (2015) The ecophysiology of seed persistence: a mechanistic view of the journey to germination or demise. Biol Rev 90:31–59

Lorenzi H, Noblick L, Kahn F, Ferreira E (2010) Flora Brasileira: Arecaceae (Palmeira). Nova Odessa, São Paulo

Marques ER, Vaz TAA, Rodrigues-Junior AG, Davide AC, José AC (2017) In situ germination of two tropical recalcitrant seeds and changes in activity of ROS-scavenging enzymes. Trees 31:1785–1792. https://doi.org/10.1007/s00468-017-1584-9

Marques A, Buijs G, Ligterink W, Hilhorst H (2018) Evolutionary ecophysiology of seed desiccation sensitivity. Funct Plant Biol 45:1083–1095. https://doi.org/10.1071/FP18022

Mazzottini-dos-Santos HC, Ribeiro LM, Oliveira DMT (2018) Structural changes in the micropylar region and overcoming dormancy in Cerrado palm seeds. Trees 32:1415–1428

Melo WA, Freitas CG, Bacon CD, Collevatti RG (2018) The road to evolutionary success: insights from the demographic history of an Amazonian palm. Heredity 121:183–195

Moothoo-Padayachie A, Varghese B, Pammenter NW, Govender P, Sershen (2016) Germination associated ROS production and glutathione redox capacity in two recalcitrant-seeded species differing in seed longevity. Botany 94:1103–1114

Moura ACF, Ribeiro LM, Mazzottini-dos-Santos HC, Mercadante-Simões MO, Nunes YRF (2019) Cytological and histochemical evaluations reveal roles of the cotyledonary petiole in the germination and seedling development of *Mauritia flexuosa* (Arecaceae). Protoplasma 256:1299–1316

Nakano Y, Asada K (1981) Hydrogen peroxide is scavenged by ascorbate-specific peroxidase in spinach chloroplasts. Plant Cell Physiol 22:867–880

Neves SC, Ribeiro LM, Cunha IRG, Pimenta MAS, Mercadante-Simões MO, Lopes PSN (2013) Diaspore structure and germination ecophysiology of the babassu palm (*Attalea vitrivir*). Flora 208:68–78

Nunes YRF, Souza CS, de Azevedo IFP, de Oliveira OS, Frazão LA, Fonseca RS, dos Santos RM, Neves WV (2022) Vegetation structure and edaphic factors in veredas reflect different conservation status in these threatened areas. For Ecosyst 9:100036. https://doi.org/10.1016/j.fecs.2022.100036

O'Brien TP, McCylly ME (1981) The study of plant structure: principles and selected methods. Termarcarphi PTY, Melbourne

O'Brien TP, Feder N, McCully ME (1964) Polychromatic staining of plant cell walls by toluidine blue. Protoplasma 59:368–373

Ooi MKJ, Auld TD, Whelan RJ (2007) Distinguishing between persistence and dormancy in soil seed banks of three shrub species from fire-prone southeastern Australia. J Veg Sci 18:405–412

Orozco-Segovia A, Batis AI, Rojas-Aréchiga M, Mendoza A (2003) Seed biology of palms: a review. Palms 47(2):79–94

Pagano A, Folini G, Pagano P, Sincinelli F, Rossetto A, Macovei A, Balestrazzi A (2002) ROS accumulation as a hallmark of dehydration stress in primed and overprimed *Medicago truncatula* seeds. Agronomy 12:1–16. https://doi.org/10.3390/agronomy12020268

Paiva EAS, Pinho SZ, Oliveira DMT (2011) Large plant samples: how to process for GMA embedding? In: Choarini-Garcia H, Melo RCN (eds) Light microscopy: Methods and protocols. Springer/Humana Press, New York, USA, pp 37–49

Pausas JG, Lamont BB, Keeley JE, Bond WJ (2022) Bet-hedging and best-bet strategies shape seed dormancy. New Phytol 236:1232–1236. https://doi.org/10.1111/nph.18436

Porto KCN, Nunes YRF, Ribeiro LM (2018) The dynamics of recalcitrant seed banks of *Mauritia flexuosa* (Arecaceae) reveal adaptations to marsh microenvironments. Plant Ecol 219:199–207

Pritchard HW, Tsan FY, Wen B, Jaganathan GK, Calvi G, Pence VC, Mattana E, Ferraz ID, Seal CE (2022) Regeneration in recalcitrant-seeded species and risks from climate change. In: Baskin CC, Baskin JM (eds) Plant regeneration from seeds. Academic Press, pp 259–273

Rajendran PA, Avarachan SE, Krishnannair SK (2021) Desiccation studies in seeds of *Arenga wightii* Griff., an endemic vulnerable palm of Southern Western Ghats. Res J Biotechnol 16:168–173

Ribeiro JF, Walter BMT (2008) As principais fitofisionomias do bioma Cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds) Cerrado: ecologia e flora. Embrapa Informação Tecnológica, Brasília, pp 89–166

Ribeiro LM, Garcia QS, Oliveira DMT, Neves SC (2010) Critérios para o teste de tetrazólio na estimativa do potencial germinativo em macaúba. Pesq Agropec Bras 45:361–368

Ribeiro LM, Souza PP, Rodrigues-Junior AG, Oliveira TGS, Garcia QS (2011) Overcoming dormancy in macaw palm diaspores, a tropical species with potential for use as bio-fuel. Seed Sci Technol 39:303–317

Roland AM (1978) General preparations and staining of thin sections. In: Hall JL (ed) Electron microscopy and cytochemistry of plant cells. Elsevier, New York, USA, pp 1–62

Salvador HF, Mazzottini-dos-Santos HC, Dias DS, Azevedo AM, Lopes PSN, Nunes YRF, Ribeiro LM (2022) The dynamics of

Mauritia flexuosa (Arecaceae) recalcitrant seed banks reveal control of their persistence in marsh environments. For Ecol Manag 511:120155. https://doi.org/10.1016/j.foreco.2022.120155

Schlindwein G, Schlindwein CCD, Tonietto A, Dillenburg LR (2013) Alleviation of seed dormancy in *Butia odorata* palm tree using drying and moist-warm stratification. Seed Sci Technol 41:1–11

Siles L, Cela J, Munné-Bosch S (2013) Vitamin E analyses in seeds reveal a dominant presence of tocotrienols over tocopherols in the Arecaceae family. Phytochemistry 95:207–214. https://doi.org/10.1016/j.phytochem.2013.07.008

Silva RS, Ribeiro LM, Mercadante-Simões MO, Nunes YRF, Lopes PSN (2014) Seed structure and germination in buriti (*Mauritia flexuosa*)—the swamp palm. Flora 209:674–685

Soares JR, Ribeiro LM, Mercadante-Simões MO, Lopes PSN (2021) Hydration cycles and overcoming dormancy in *Butia capitata* (Arecaceae) diaspores. Trees 35:1511–1524. https://doi.org/10.1007/s00468-021-02132-9

Souza JN, Mazzottini-dos-Santos HC, Dias DS, Lopes PSN, Ribeiro LM (2022) Seasonality and the control of longevity and dormancy in macaúba palm diaspores. Ind Crops Prod 177:114475. https://doi.org/10.1016/j.indcrop.2021.114475

Spera MRN, Cunha R, Teixeira JB (2001) Quebra de dormência, viabilidade e conservação de sementes de buriti. Pesq Agropec Bras 36:1567–1572

Stevens N, Seal CE, Archibald S, Bond W (2014) Increasing temperatures can improve seedling establishment in arid-adapted savanna trees. Oecologia 175:1029–1040

Tweedle JC, Dickie JB, Baskin CC, Baskin JM (2003) Ecological aspects of seed desiccation sensitivity. J Ecol 91:294–304

Veloso VHS, Ribeiro LM, Mercadante-Simões MO, Nunes YRF (2016) Cytological aspects of recalcitrance in dormant seeds of *Mauritia flexuosa* (Arecaceae). Acta Physiol Plant 38:171. https://doi.org/10.1007/s11738-016-2194-7

Virapongse A, Endress BA, Gilmore MP, Horn C, Romulo C (2017) Ecology, livelihoods, and management of the *Mauritia flexuosa* palm in South America. Glob Ecol Conserv 10:70–92

Wojtyla Ł, Lechowska K, Kubala S, Garnczarska M (2016) Different modes of hydrogen peroxide action during seed germination. Front Plant Sci 7:1–16

Zhang Y, Liu Y, Sun L, Baskin CC, Baskin JM, Cao M, Yang J (2022) Seed dormancy in space and time: global distribution, paleo- and present climatic drivers and evolutionary adaptations. New Phytol 234:1770–1781

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