Desiccation Tolerance and Storage Characteristics of Seeds of the Rare and Endangered Plant *Garcinia paucinervis*: A Postprint

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Abstract

The germination of Garcinia paucinervis seeds at different dehydration levels, their water absorption rate after rehydration, changes in stress-resistance physiological indices during dehydration, and seed germination under various storage conditions were investigated to study the dehydration sensitivity and storage characteristics of G. paucinervis seeds. The results showed: (1) The initial water content of G. paucinervis seeds was 45.29%, and the water loss rate reached 45% after 35 days at room temperature. (2) When the water loss rate was below 18%, the germination rate and water absorption rate after rehydration showed no significant changes; when the water loss rate exceeded 18%, both the germination rate and water absorption rate after rehydration decreased significantly, with the germination rate reaching 0 at 42% water loss. The critical water content of the seeds was 27.29%, and the lethal water content for 50% mortality was 12.72%. (3) With increasing dehydration degree, the relative electrical conductivity, soluble sugar content, and proline content gradually increased; the malondialdehyde content showed little change when the water loss rate was below 24% but increased significantly when above 24%; the activities of both superoxide dismutase (SOD) and peroxidase (POD) exhibited fluctuating changes, reaching their maximum at 18% water loss. (4) Seeds stored dry at room temperature for 1 month and those stored wet at -1°C and -20°C for 1 month could not germinate; seeds stored by water immersion for 1 month showed significantly reduced germination rate; wet storage at 4°C for 1, 3, and 6 months significantly delayed seed germination but had no significant effect on the final germination rate. These results indicate that when the water loss rate is below 18%, G. paucinervis seeds can maintain normal cellular metabolism through stress-resistance regulation, tolerate certain degrees of dehydration and low temperature, and are classified as low-level recalcitrant seeds; when the water loss rate exceeds 18%, seed metabolism becomes imbalanced, leading to deterioration and eventual death. Wet sand storage at 4°C (with 7.5% water content) is a suitable method for short-term storage of these seeds. This study provides a theoretical basis for the conservation and utilization of the rare and endangered tree species G. paucinervis.

Full Text

Preamble

Dehydration Tolerance and Storage Characteristics of Seeds of the Rare and Endangered Plant *Garcinia paucinervis*

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Abstract

This study investigated the dehydration sensitivity and storage characteristics of *Garcinia paucinervis* seeds by examining germination at different dehydration levels, water absorption rates after rehydration, changes in resistance physiological indices during dehydration, and seed germination under various storage conditions. The results showed: (1) The initial moisture content of *G. paucinervis* seeds was 45.29%, and the dehydration rate reached 45% after 35 days at room temperature. (2) When the dehydration rate was below 18%, germination percentage and water absorption after rehydration showed no significant changes; however, both decreased significantly when dehydration exceeded 18%, with germination dropping to zero at 42% dehydration. The critical moisture content (CMC) was 27.29%, and the lethal moisture content for 50% mortality (LMC) was 12.72%. (3) As dehydration progressed, relative conductivity and soluble sugar and proline contents increased gradually. Malondialdehyde (MDA) content changed little below 24% dehydration but increased significantly above this threshold. Both superoxide dismutase (SOD) and peroxidase (POD) activities fluctuated, peaking at 18% dehydration. (4) Seeds stored dry at room temperature for one month or stored moist at -1°C and -20°C for one month failed to germinate. Water immersion storage for one month significantly reduced germination percentage, while moist storage at 4°C for 1, 3, and 6 months significantly delayed germination but did not affect final germination percentage. These findings indicate that *G. paucinervis* seeds can tolerate moderate dehydration and low temperatures through resistance regulation when dehydration is below 18%, classifying them as minimally recalcitrant seeds. However, when dehydration exceeds 18%, metabolic imbalance leads to deterioration and

death. Moist sand storage at 4°C (with 7.5% moisture content) represents an effective short-term storage method. This study provides a theoretical basis for the conservation and utilization of this rare and endangered species.

Keywords: seed moisture content, germination percentage, desiccation sensitivity, recalcitrant seeds, seed storage

Introduction

Understanding seed storage characteristics is crucial for plant germplasm preservation, introduction, and ex situ conservation (Costa et al., 2018; Wyse et al., 2017). Roberts (1973) classified seeds into recalcitrant and orthodox categories based on storage behavior. Recalcitrant seeds do not undergo maturation drying upon dispersal, typically maintaining high moisture contents of 30-60%, and are sensitive to dehydration and low temperatures. Most die when dried to 15-20% moisture content, with storage lifespans of only days to weeks under ambient ventilation, unlike orthodox seeds that can be dried and stored at low temperatures (Berjak & Pammenter, 2001). Consequently, recalcitrant seed storage requires careful moisture maintenance above the critical moisture content (CMC). Ellis et al. (1990) further defined intermediate seeds, which are damaged when moisture content falls to 7-12%, with tropical-origin intermediate seeds being cold-sensitive (Hong & Ellis, 1996).

Approximately 8% of species produce desiccation-sensitive seeds, with the highest sensitivity found among tropical and subtropical moist broadleaf forest plants (Wyse & Dickie, 2017). The primary cause of viability loss during dehydration is membrane lipid peroxidation, which damages membrane structure and function, coupled with declining antioxidant protection system activity and free radical accumulation, leading to cellular metabolic disorder (Greggains et al., 2001; Varghese et al., 2011). Global climate change threatens plants with recalcitrant seeds, making dehydration sensitivity and storage major research foci. Pelissari et al. (2018) assessed dehydration tolerance in 66 Brazilian tree species, suggesting evaluation should consider moisture content of embryos, endosperm, seed coats, and fruit peels. Tropical *Garcinia gummi-gutta* seeds germinate slowly, with germination percentage dropping sharply below 34% moisture content, and complete loss of viability after two months at -10°C or 5°C, characterizing them as tropical dormant recalcitrant seeds. However, these seeds maintained 90% germination after 18 months at 15°C in sealed plastic containers (Joshi et al., 2017). Other *Garcinia* species such as *G. indica* and *G. xanthochymus* also show desiccation sensitivity (Malik, 2005). The principle for storing recalcitrant seeds involves maintaining moisture and viability at the lowest tolerable temperature while preventing microbial damage (Berjak & Pammenter, 2007). *Butia capitata* seeds lose viability under freezing conditions, but isolated embryos can be cryopreserved in liquid nitrogen (Dias et al., 2015).

Garcinia paucinervis Chun et How, a member of the Clusiaceae family, is a nationally protected second-class endangered evergreen tree (Farm et al., 2003).

Endemic to karst mountains, it occurs in western and southwestern Guangxi and southeastern Yunnan at elevations of 194-830 m (Zhang, 2017), offering ornamental, ecological, medicinal, and economic values (Zhang et al., 2015a). Currently, wild populations are limited and fragmented, with few large fruit-bearing individuals, resulting in poor natural regeneration (Zhang et al., 2017). Deteriorating karst habitats have constrained socioeconomic development in these regions. As an excellent ecological restoration species, *G. paucinervis* remains rarely cultivated artificially, with limited reports on its propagation. Our preliminary research found that cuttings are difficult to establish and seeds exhibit dormancy characteristics (Zhang et al., 2018), losing viability after one month of ventilation storage. This storage challenge severely restricts seedling production. Therefore, this study systematically investigated germination at different dehydration levels, water absorption after rehydration, changes in resistance physiological indices during dehydration, and germination under various storage conditions to elucidate dehydration sensitivity and identify optimal storage methods, providing scientific guidance for *G. paucinervis* conservation and utilization.

Materials and Methods

1.1 Experimental Materials

Garcinia paucinervis seeds were collected in June 2016 from Nonggang National Nature Reserve (22°27 58 N, 106°57 18 E). After harvest, fruits were piled and fermented for approximately 10 days in the laboratory. Seeds were extracted by rubbing off pulp and flesh, then surface-dried for use.

1.2 Experimental Procedures

1.2.1 Seed Basic Characteristics and Moisture Content Determination The thousand-seed weight was measured using the 100-seed method. Fifty randomly selected plump seeds were measured for two-dimensional size. Seed viability was determined using the TTC method (Song et al., 2005). Moisture content was calculated on a fresh weight basis by randomly selecting three fresh seeds, slicing them into 1 mm sections, and oven-drying at 105±2°C for 17 hours (ISTA, 1999), with five replicates.

1.2.2 Seed Dehydration Treatment Seeds were weighed (W) and placed in a ventilated room (26-31°C, 72-82% RH) for natural dehydration. Weight was recorded periodically (W) to calculate dehydration rate: Dehydration rate (%) = (W -W)/W × 100%. Target dehydration rates were 6%, 12%, 18%, 24%, 30%, 36%, and 42% (allowing ±0.3% error). Fresh seeds (initial moisture content) and seeds at each dehydration level were flash-frozen in liquid nitrogen and stored at -80°C for physiological index determination.

1.2.3 Water Absorption Measurement After Rehydration Using fresh seeds as control, seeds dehydrated to 6%, 12%, 18%, 24%, 36%, and 42% were soaked in distilled water at 25°C. Seeds were weighed daily (W) with water changes until saturation. Water absorption rate (%) = [(W -W)/W] × 100%, with three replicates. The time required to reach saturation was recorded for each dehydration level.

1.2.4 Germination Test and Parameter Calculation Seven dehydration levels plus fresh controls were tested. Seeds were disinfected in 0.1% KMnO for 30 minutes and rinsed. Germination was conducted in 1000 ml plastic boxes (172×117×70 mm) containing 4 cm of sterilized river sand at 1 cm sowing depth. Each dehydration level had two boxes with 10 seeds each, replicated three times. Boxes were placed in an LRH-250-G incubator at 25°C with periodic illumination (3000 lx, 12 h/d), maintaining moist substrate. The 448-day test recorded germination (seedling emergence above sand) weekly after the first germination. Parameters calculated were:

- **Germination Time Lag (GTL)**: Days from test initiation to first germination.
- **Germination Percentage (GP)**: GP (%) = (germinated seeds / total seeds) × 100%.
- **Mean Germination Time (MGT)**: MGT = Σ(t ×n)/Σn , where t is day i and n is seeds germinated on day i (Liu et al., 2005).

1.2.5 Resistance Physiological Index Determination Seeds at 6%, 12%, 18%, 24%, 36%, and 42% dehydration (with fresh controls) were peeled. Relative conductivity of embryos and endosperm was measured by conductometry (Chai et al., 2018). Superoxide dismutase (SOD) and peroxidase (POD) activities were determined by NBT and guaiacol methods, respectively. Malondialdehyde (MDA), soluble sugar, and proline contents were measured by TBA, anthrone colorimetric, and sulfosalicylic acid methods, respectively (Li et al., 2000), with three replicates.

1.2.6 Seed Storage Trials Fresh seeds were stored using eight methods: (1) Dry storage at room temperature for 1 month; (2) Dry storage at 4°C for 1 month in kraft paper bags; (3) Water immersion at 25°C for 1 month with daily water changes; (4) Moist storage at -20°C (seeds mixed 1:3 v/v with river sand at ~7.5% moisture); (5) Moist storage at -1°C for 1 month; (6) Moist storage at 4°C for 1 month; (7) Moist storage at 4°C for 3 months; (8) Moist storage at 4°C for 6 months. Stored seeds were germinated following section 1.2.4 for 350 days.

1.3 Data Analysis

Data were processed using Microsoft Excel 2010 and analyzed with SPSS 19.0 via one-way ANOVA, with Duncan's test for multiple comparisons (germination percentages were arcsine-transformed for homogeneity). Values are presented as mean ± standard error (SE). Figures were prepared using SigmaPlot 11.0.

Results

2.1 Seed Size and Moisture Content

Garcinia paucinervis seeds are ovoid to broadly ovoid, with embryos enclosed in endosperm that is difficult to separate. Seeds measured (30.80±2.14) mm in length and (15.39±0.96) mm in diameter, with a thousand-seed weight of (4381.75±77.53) g. Mature seeds had initial moisture content of 45.29%±0.72% and viability of 95.56%±1.92%.

2.2 Effect of Room Temperature Storage on Seed Dehydration

The relationship between dehydration duration and water loss rate is shown in [Figure 1: see original paper]. Seeds dehydrated uniformly over time, reaching a stable water loss rate of approximately 45% after 35 days of natural air-drying.

2.3 Water Absorption of Dehydrated Seeds After Rehydration

Water absorption in *G. paucinervis* seeds was extremely slow, with fresh seeds requiring approximately 24 days to reach saturation at 14.55% absorption. When dehydration rate was below 18%, saturated water absorption and saturation time showed no significant difference from fresh seeds. As dehydration increased, both saturated water absorption and saturation time decreased progressively. Seeds dehydrated to 42% reached saturation in approximately 12 days with -6.69% absorption, indicating they could not regain original fresh weight after rehydration [Figure 2: see original paper].

2.4 Effect of Dehydration on Seed Germination

Seeds dehydrated to 42% showed zero germination. Germination dynamics and parameters for other dehydration levels are presented in [Figure 3: see original paper] and ; non-germinated seeds completely rotted. Seeds at 36% dehydration consistently showed lower germination than other treatments. GTL increased progressively with dehydration level. Fresh seeds achieved 93.33% GP, which remained unchanged below 18% dehydration but declined significantly above this threshold. The CMC was determined to be 27.29% based on the sharp viability decline beyond this point (Probert & Brierley, 1989; Pammenter et al., 1998). At 36% dehydration, GP dropped to only 21.67%. MGT showed fluctuating changes with dehydration, significantly extending to 242.88 days at 12% dehydration, showing no significant difference from controls at 18-24% dehydration, but dramatically increasing to 337.33 days at 36% dehydration.

The relationship between dehydration rate and germination rate is shown in [Figure 4: see original paper]. The LMC , defined as the moisture content at which germination falls to half that of fresh seeds (He & Song, 2003), was

12.72% for *G. paucinervis* (based on 93.33% fresh seed germination and 45.29% moisture content). According to [Figure 1: see original paper], this LMC is reached after approximately 19 days of indoor natural drying.

2.5 Changes in Resistance Physiological Indices During Dehydration

Relative conductivity increased linearly from 52.03% to 98.24% as seeds dehydrated from fresh to 42% water loss. MDA content increased by 34.43% from fresh seeds to 18% dehydration (non-significant), but rose significantly by 187.92% from 18% to 42% dehydration [Figure 5: see original paper]A.

SOD and POD activities fluctuated during dehydration, peaking at 18% water loss and declining significantly above 24% dehydration, though showing some recovery at 42% dehydration [Figure 5: see original paper]B.

Soluble sugar content remained stable below 6% dehydration, then increased linearly to 3.03 times that of fresh seeds at 42% dehydration. Proline content increased progressively with dehydration, reaching 7.10 times the fresh seed level at 42% dehydration [Figure 5: see original paper]C.

2.6 Effect of Storage Methods on Seed Germination

Seeds stored dry at room temperature or moist at -1°C and -20°C for one month completely rotted. Germination dynamics and parameters for remaining storage methods are shown in [Figure 6: see original paper] and . Final GP showed no significant difference from controls except for water immersion storage (WI1), which was significantly lower. GTL was significantly longer only for dry storage at 4°C (DS1) compared to controls. However, moist storage at 4°C for 1, 3, and 6 months (SH1, SH3, SH6) significantly delayed germination (increased MGT) without affecting final GP.

Discussion

Garcinia paucinervis seeds are large, heavy, and high in moisture content, exhibiting morphological characteristics of recalcitrant seeds. When dehydration was below 18%, saturated water absorption and saturation time showed no significant difference from fresh seeds, but both parameters declined sharply above 18% dehydration. Seeds dehydrated to 42% could not regain original weight after rehydration. This suggests that at low dehydration levels, seeds can repair membrane structure and enzyme modifications through imbibition, but severe dehydration causes irreversible changes to structural proteins and enzymes, reducing imbibition capacity and leading to viability loss.

Germination percentage remained stable below 18% dehydration but declined sharply above this threshold, indicating mild dehydration has minimal impact while severe dehydration significantly reduces viability. The highly significant negative correlation between dehydration rate and germination percentage ($P<0.01$) confirms dehydration sensitivity. Therefore, seeds with dehydration rates below 18% or stored under summer room ventilation for no more than 8 days are recommended for sowing. The prolonged germination process showed increasing GTL with dehydration, likely due to time required for physiological repair. The fluctuating MGT pattern with dehydration, also observed in recalcitrant *Ardisia punctata* seeds (Yang et al., 2013), may be related to endogenous hormone levels or enzyme activities within the 18-24% dehydration range.

Relative conductivity and MDA content are common indicators of seed deterioration and damage (Chen et al., 2016). MDA, as the end product of membrane lipid peroxidation, damages membrane systems, increases membrane permeability, causes metabolic disorder, and poisons cells by reducing antioxidant enzyme activities (SOD, POD) and altering protein structure and function (Ma et al., 2015), representing a primary cause of seed deterioration. Reactive oxygen species (ROS) accelerate lipid peroxidation and damage proteins and DNA (Farooq et al., 2009). Seeds accumulate ROS when normal metabolism is affected, and dehydration tolerance is associated with antioxidant defense systems. During early dehydration, water stress activates protective responses in *G. paucinervis* seeds, with increasing SOD and POD activities scavenging ROS and maintaining membrane stability (Zhang et al., 2015b), resulting in slow increases in relative conductivity and MDA. Between 18-36% dehydration, rapid MDA accumulation indicates intensified lipid peroxidation, with MDA and ROS accumulation exceeding tolerance limits, causing sharp declines in SOD and POD activities and ineffective ROS scavenging (Tang, 2012). This coincides with increased membrane permeability and cellular content leakage, manifested as rapidly increasing relative conductivity and accelerating deterioration. Below 36% dehydration, the trends of these four resistance indices in *G. paucinervis* align with those of recalcitrant *Panax notoginseng* and *Castanea mollissima* seeds (Duan et al., 2014; Zong et al., 2006). However, above 36% dehydration, POD may participate in ROS generation, poisoning cells or reacting with phenolic substances and H O to cause browning (Yang & Gao, 2001), accelerating deterioration of already damaged seeds and causing cell disintegration and death, as also observed in *Aesculus chinensis* seeds during late dehydration stages (Chen, 2006). The reason for increased SOD activity at late dehydration stages requires further investigation. Soluble sugars can form complexes with LEA proteins to control dehydration rate, while proline stabilizes metabolism and protoplasmic colloids (Li et al., 2000). These osmotic regulators assist POD and SOD in scavenging excess free radicals and protecting cells. The linear increase in soluble sugar and proline content with dehydration in *G. paucinervis* seeds demonstrates osmotic adjustment capacity through solute accumulation to maintain cellular osmotic balance. Collectively, these findings indicate that *G. paucinervis* seeds can maintain normal cellular metabolism through resistance regulation below 18% dehydration, but suffer metabolic imbalance and deterioration above this threshold.

Dry storage at room temperature and moist storage below 0°C for one month resulted in complete seed mortality, with some seeds shriveling during dry storage at 4°C, indicating unsuitability for dry storage and sensitivity to sub-zero temperatures. High moisture content causes intracellular ice formation below 0°C, damaging membrane systems during freeze-thaw cycles. Storage temperatures below 15°C are lethal for most tropical seeds (Bedi & Basra, 1993), such as *G. gummi-gutta* (Joshi et al., 2017). However, *G. paucinervis* seeds survived moist storage at 4°C for up to six months, with extended GTL and MGT but unchanged final GP, demonstrating that 4°C moist sand storage reduces metabolic rate and moisture loss, representing an effective short-term storage method. Water immersion storage likely reduced GP due to oxygen deficiency or microbial infection.

Based on dehydration tolerance and cold sensitivity differences, recalcitrant seeds are classified as highly, moderately, or minimally recalcitrant (Ntuli et al., 2015). Temperate recalcitrant seeds generally show greater dehydration and cold tolerance than tropical species (Pammenter & Berjak, 2000). *Garcinia paucinervis*, occurring in the tropical-subtropical transition zone, tolerates moderate dehydration and temperatures above 0°C, with CMC of 27.29% and LMC of 12.72%, but dies below 0°C. Its recalcitrance level is lower than the tropical congener *G. cowa* (initial moisture 50.1%, CMC 39%, mortality after one month at 4°C; Liu et al., 2005) and similar to minimally recalcitrant *Castanea mollissima* seeds (100% germination after 9 days natural drying, 53.5% after 15 days, tolerating 0-2°C or even -4°C moist storage; Tao & Zhu, 2004; Wang et al., 1999), but higher than intermediate *Magnolia sargentiana* seeds (CMC 15.3%, LMC 5.3-7.1%; Tang, 2014). Therefore, *G. paucinervis* seeds are classified as minimally recalcitrant.

According to Baskin and Baskin (2005), seeds with germination initiation exceeding four weeks exhibit dormancy. Due to high moisture content, recalcitrant seeds typically germinate rapidly and are considered non-dormant or viviparous (Tweddle et al., 2003). However, recent reports have documented dormancy in some recalcitrant seeds (Jayasuriya et al., 2012; Joshi et al., 2017), a finding supported by this study.

Garcinia paucinervis occurs in limestone forests of western Guangxi and southeastern Yunnan, where litter burial maintains seed moisture content and relatively low winter temperatures create natural moist storage conditions. The thin, drought-prone soils on rocky outcrops favor the minimally recalcitrant characteristic that maintains high viability under short-term mild drought. These results establish a foundation for conserving and utilizing this valuable resource, while long-term germplasm preservation via isolated embryo cryopreservation warrants further investigation.

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Note: Figure translations are in progress. See original paper for figures.