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RESEARCH ARTICLE

Is the endemic *Phoenix canariensis* H. Wildpret an orthodox species? Implications for its conservation

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ABSTRACT
Seed banks (gene banks) have become essential for the conservation of genetic biodiversity in natural ecosystems. Seed preservation is especially important for threatened species, since seeds are the primary genetic material used to reintroduce plant species. Knowledge of the desiccation tolerance of each species is relevant for selecting the best method for *ex situ* conservation, but it is not always available. Currently, the categorisation of the seed storage behaviour of the Phoenix species as orthodox, recalcitrant or intermediate, remains uncertain. This study uses four accessions of the endemic species from Canary Island *Phoenix canariensis* H. Wildpret, with storage times ranging between 2 and 28 years. Germination tests were carried out to measure seed viability over time, desiccation tolerance and the possible impact of seed storage on viability. The germination results differed for seeds after 192 days in a greenhouse. Accessions stored in the seed bank at −20°C and 15%RH for 17 years showed a high germination percentage (72%). In contrast, accessions stored under unsuitable conditions showed a 0% germination. These results indicate the orthodox seed storage behaviour of *P. canariensis*. In addition, it supports the good state of conservation of the material stored in the Seed Bank of the Botanical Garden Viera y Clavijo and the reliability of the temperature and humidity conditions in which the seeds of *P. canariensis* have been stored. In addition, the results are relevant in order to manage the conservation of this endemic species from the Canary Islands.

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Introduction

Recent studies have shown that the current global plant diversity extinction is 100–1000 times higher than during the recent geological past (Pimm et al. 1995; Humphreys et al. 2019). An average of 2.3 species has become extinct each year for the past 2.5 centuries. The ongoing plant extinction is of particular concern to isolated oceanic islands because of the vulnerability of the island biota (Humphreys et al. 2019).

Conservation seed banks have become essential for the genetic biodiversity conservation of natural ecosystems (Walsh et al. 2024). Seed preservation is especially important

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for threatened species since seeds are the primary genetic material used for reintroducing plant species (Broadhurst et al. 2008; Nadarajan et al. 2023). The maintenance of *ex situ* seed viability over long periods in seed banks is a key element for conserving plant genetic resources (FAO 2014; Fu et al. 2015; Walters and Pence 2021). However, it is essential to establish germination protocols for each species stored in the seed bank (pre-treatment, seed dormancy) (Baskin and Baskin 2014). In addition, storage conditions (humidity and temperature) must be optimised to guarantee seed viability (Harrington 1972; Bacchetta et al. 2008; Hay et al. 2023; Nadarajan et al. 2023).

Seeds of the majority of modern angiosperm species (90%) tolerate dehydration to very low water content (orthodox seeds), hence these seeds are desiccated (15%RH) and stored at low temperature (−20°C) (Tweddle et al. 2003; FAO 2014; Wyse and Dickie 2017; Ballesteros et al. 2019). However, not all seeds tolerate desiccation (recalcitrant seeds) and have been preserved in a different way (cryopreservation) (Berjak et al. 2017; Pritchard et al. 2017). In this sense, some essays have been carried out on *Phoenix* seeds under cryogenic conditions (Al-Madeni and Tisserat 1986). On the other hand, there are seeds that are classified as intermediate because may dry to some extent *in situ*, but not as much as orthodox seeds and/or embryo moisture content may remain high (Walters 2015; Hay et al. 2023). Desiccation tolerance is the ability of an organism, to survive extreme dehydration without sustaining irreversible damage. This capability allows the organism to resume normal metabolic functions when rehydrated. Knowledge of the desiccation tolerance of each species is relevant for selecting the best method for *ex situ* conservation (Walters 2015).

Phoenix canariensis H. Wildpret (Arecaceae) is an endemic and very representative palm species in the Canary Islands. The Canarian date palm is a diploid ($n = 18$), long-lived, slow-growing, arborescent monocot with a solitary trunk that grows up to 20 m, but most frequently between 5 and 10 m (Saro et al. 2014; Sosa et al. 2021). Fruits are fleshy, monospermous berries with an ovoid shape approximately 2 cm long, which take between 10 and 11 months to bear fruit, can overlap with the flowering cycle of the following year, and reach their optimal state of ripening from May to July (Saro et al. 2015).

This *Phoenix* endemic species grows between 300 and 900 m above sea level, depending on the ecosystem and geographical orientation (Saro et al. 2014; Sosa et al. 2021). The current natural distribution of *P. canariensis* consists of palm groves that remain of a wide natural distribution, mainly restricted to the bottom of ravines and slopes with high moisture. Currently, Canarian palm groves are catalogued as priority habitats of European Union Natura 2000 network of protection areas (European Habitat Directive 92/43/EEC), and the Canarian Government has recognised its threatened status (BOC 1991*). Phoenix canariensis* has most recently been assessed for The IUCN Red List of Threatened Species in 2017 listed as Least Concern (Beech 2017).

Although *Phoenix dactylifera* seeds have been recorded as one of the most long-lived, since they germinate even after 2000 years (Sallon et al. 2008, 2020), the categorisation of *Phoenix* species as orthodox or recalcitrant seed storage behaviour is still uncertain. Previous reports on *Phoenix* species considered seeds of *P. dactylifera* as orthodox and *P. canariensis, P. rupicola, P. sylvestris* and *P. reclinata* as probably non-orthodox (Pritchard et al. 2004). However, Berjak et al. (2017) considered *Phoenix* species as orthodox (*P. dactylifera*), probably orthodox (*P. canariensis, P. rupicola* and *P. sylvestris*), and as intermediate seeds (*P. reclinata*). In this sense, the seed information database (https://ser-sid.org/) has data for five *Phoenix* species reported as orthodox (*P. dactylifera*) and probably orthodox (*P. canariensis, P. reclinate, P. rupicola* and *P. sylvestris*). In addition, seed storage behaviour of Arecaceae species available data represent only c. 7%–10% of the species (Jaganathan 2021).

This uncertainty in palm seed categorisation generally reflects gaps in the information about seed water concentrations at shedding, storage parameters, seed survival in storage, and germination characteristics and conditions. The evaluation of seed longevity during natural aging requires a long period of time. In this sense, there are few studies that have tested the viability of *Phoenix canariensis* seeds after long periods of storage (Pimenta et al. 2010; Pardo-Pina 2019). Pardo-Pina (2019) conducted germination tests on seeds dried and stored in a freezer for nine years, suggesting an orthodox seed storage behaviour for this taxon.

The objectives of our study were (i) to evaluate the effect of time and storage conditions on the germination of *Phoenix canariensis* seeds, (ii) to determine the seed longevity of *P. canariensis* (iii) to determine the factors influencing the viability of the seeds of this species, and (iv) to determine the effectiveness of the current seed storage conditions in the Seed Bank of Jardín Botánico Canario Viera y Clavijo (JBCVC) to maintain the viability of *Phoenix canariensis* seeds.

Material and methods

Plant material

In order to test the effect of storage time and conditions, four accessions of *Phoenix canariensis* with different storage history were selected from the Seed Bank JBCVC (Table 1); (1) an accession sampled *ex horto* from the JBCVC, which has been stored for 28 years (1177/B) under unsuitable conditions, at room temperature from 1995 to 2005 (average annual temperature of 22°C) in a tube hermetically sealed with silicagel; (2) an accession from the natural population of La Sorrueda (Santa Lucía de Tirajana, Gran Canaria Island) and stored for 17 years at −20°C/15% RH in the Seed Bank (2850/B); (3) an accession sampled in Camino Largo (San Cristóbal de La Laguna, Tenerife Island) stored at −20°C/15% RH for six years (4804/B); and (4) a recent accession, stored for only two years, from the natural population of Casas Blancas (Santa Lucía de Tirajana, Gran Canaria Island) (6104/B) (Table 1). From each accession, 25 seeds were surface-sterilised with 2% hydrogen peroxide for three minutes, rinsed with distilled water, and soaked in water for 72 h.

Table 1. Collection data of seeds from four accessions of *Phoenix canariensis*. GC: Gran Canaria Island, TF: Tenerife Island.

Accession number	Collection date	Collection site	Altitude (m asl)	Time of storage (years)	Storage conditions
1177/B	1995	JBCVC *ex horto* (GC)	293.34 m	28	uncertain
2850/B	07/06/2006	La Sorrueda (GC)	1,513.99 m	17	−20°C, 15% RH
4804/B	19/12/2017	Camino largo (TF)	552.15 m	6	−20°C, 15% RH
6104/B	13/07/2021	Casas Blancas (GC)	540.15 m	2	−20°C, 15% RH

Morphological study

The polar and equatorial axes of 20 seeds from each accession were measured under a stereoscopic microscope (Olympus SZX12) following the method described in the International Seed Morphological Association. Pictures were taken with a digital camera (Nikon DSFi2), and the resulting images were analysed using NIS Elements v 4.0. Seed mass was determined by weighing four replicates of 100 seeds on an analytical balance with 0.001 g precision (Sartorius Quintix 65-1S).

Germination test

A germination test was performed to measure seed viability for each of the accessions with different storage histories. Seeds were then sowed in plastic pots (12 cm x 9 cm) filled with a mixture of peat moss, vermiculite, and coconut coir (5:3:1) and kept in a greenhouse with environmental control (natural light conditions, relative humidity of 60% and an average temperature of 27°C) and automatic spray irrigation of water of 15 min once a week.

The seeds were considered to have germinated when the cotyledons (the first leaves) emerged above the substrate. The final germination percentage was recorded after six months of sowing. In addition, the number of viable seedlings was counted after that period of time.

Data analysis

The germination percentage (%G), time to 25% final germination (T_{25}), germination speed (GS), and germination speed coefficient (CV), were calculated according to Coolbear et al. (1984) and Gavassi et al. (2014). The percentage of seedlings viability was also estimated.

Seed biometric data and germination parameters were subjected to ANOVA and multiple range test analysis using Excel (Microsoft Office Standard 2016) to test for significant differences between different accessions. Pearson's correlation between seed size and germination percentage, and between germination percentage and storage time was calculated using XLSTAT ver. 3.02, 2008.

Results

The polar axis length of the seeds ranged from 12.42 (6104/B) to 14.4 mm (4804/B), whereas the equatorial axis ranged from 8.43 (2850/B) to 8.84 mm (4804/B). In addition, the mass of 100 seeds ranged from 61.76 g (1177/B) to 106.27 g (4804/B) (Table 2). Therefore, accession 4804/B had the largest and heaviest seeds. In contrast, the most recent accession (6104/B) had the smallest seed size (Table 2).

Table 2. Seed morphological parameters mean and standard deviation of *Phoenix canariensis* from four different accessions from Canary Islands.

Accession number	Mass of 100 seeds (g)	Polar axe length (mm)	Equatorial axe length (mm)
1177/B	61.76	12.55 ± 1.11	8.48 ± 0.56
2850/B	69.38	13.44 ± 0.85	8.43 ± 0.34
4804/B	106.27	14.40 ± 1.16	8.84 ± 0.44
6104/B	60.41	12.42 ± 1.36	8.66 ± 0.39

Table 3. Percentage of germination (%G), germination speed (GS), germination speed coefficient (CV), time to 25% of final germination (T_{25}) and percentage of viable seedlings (%VS) of *Phoenix canariensis* seeds from four different accessions.

Accession number	%G	GS (seeds/day)	CV (%/day)	T_{25} (days)	% VS
1177/B	0	–	–	–	–
2850/B	72	63.27	12.329	1.90	100
4804/B	52	40.41	12.871	4.75	100
6104/B	72	67.33	18.367	2.10	100

ANOVA analysis detected significant differences among accessions with regard to the polar ($p < 0.001$) and equatorial axes ($p < 0.05$) (Supplementary Material, Table S1). Significant differences in seed morphological parameters (polar and equatorial axes) were detected among the analysed accessions (Supplementary Material, Table S2).

Germination ranged from 0% (1177/B) to 72% (2850/B and 6104/B) after 192 days (Table 3). The most recent accession analysed, 6104/B, showed the highest germination speed (GS) of the four accessions of *P. canariensis* germinated. However, we did not find any correlation between the germination percentage and biometric data (seed polar axis, seed equatorial axis or seed mass). After four months in the greenhouse, the percentage of viable seedlings of all accessions was 100% (Table 3).

Germination started 65 days after sowing for accessions 2850/B and 6104/B, while seeds from accession 4804/B germinated 67 days after sowing. However, after 192 days, none of the seeds from accession 1177/B germinated (Figure 1). The peak daily germination occurred between days 65 and 77 after sowing. The last seeds that germinated did so after 176 days (2850/B).

Germination speed (GS) ranged from 40.41 (4804/B) to 67.33 seeds/day (6104/B). On the other hand, the time to 25% of final germination (T_{25}) was approximately 2 days for

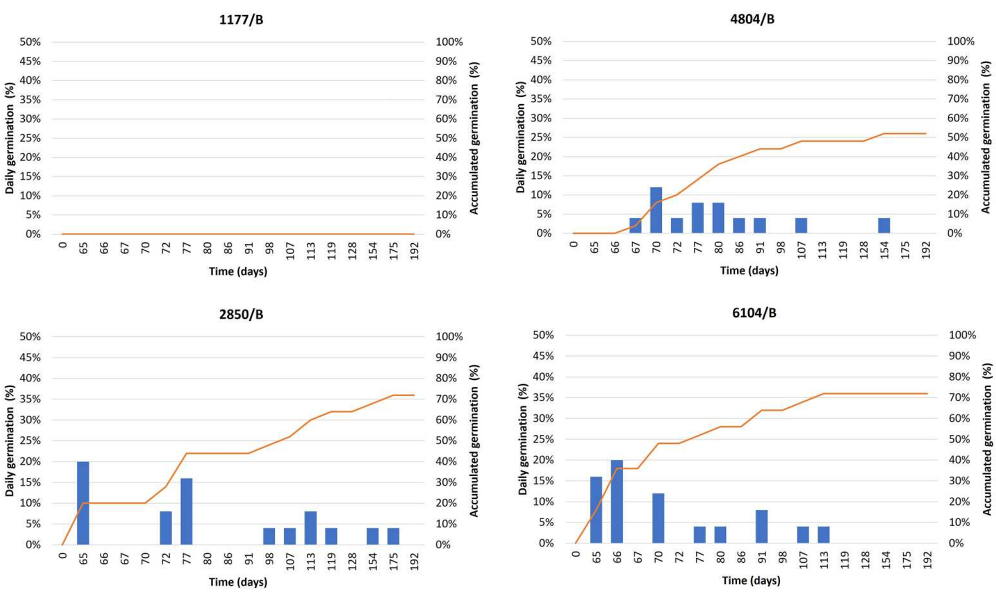

Figure 1. Accumulated germination rate (red line) and daily germination rate (Blue bars) of the four accessions of *Phoenix canariensis* analysed.

2850/B and 6104/B, and 5 days for accession 4804/B, and the germination speed coefficient had a maximum value of 18.367%/ day (6104/B) and a minimum of 12.329%/day (2850/B) (Table 3).

Discussion

Few studies have tested the viability of *Phoenix canariensis* seeds after long periods of storage (El-Tarawy et al. 1989; Pimenta et al. 2010). Pardo-Pina (2019) germinated seeds of *P. canariensis* after nine years of storage. *Phoenix canariensis* seeds have shown their capacity to germinate after a long period of storage at −20°C and 15% RH. After 17 years of storage, *Phoenix canariensis* seeds maintained their germination capacity. These results eradicated any doubt about seed desiccation tolerance and the orthodox character of the endemic palm from the Canary Islands.

The only accession that had not germinated (1177/B) was deposited in the seed bank 28 years ago under unsuitable conditions for a long period of time. The absence of germination may be due to: (i) the loss of seed viability over time, (ii) seeds that were not harvested at the optimal time and have never been viable, and (iii) suboptimal storage conditions. In this case, uncertain storage conditions could be the main factor affecting the seed viability of this accession.

The germination process was not immediate but lasted four months, which agrees with germination ecology studies in *Phoenix canariensis* (He et al. 2022). He et al. (2022) suggested that the delay to germination in underdeveloped embryos allows secondary dispersal of these seeds to a different environment, whereas the dispersal range of fully developed seeds is limited by immediate germination.

The low germination percentage of the accession stored for six years (4804/B; 52% germination) in relation to the accession stored for 17 years (2850/B; 72% germination), both stored and germinated under the same conditions, may suggest that the former was not collected at the optimal time. In this sense, the accession 4804/B was sampled in December, whereas accessions 2850/B, as well as accession 6104/B (72% germination) were sampled in June and July, respectively, which is in agreement with their optimal state of ripening time (from May to July; Saro et al. 2015). On the other hand, the population of Camino Largo (San Cristóbal de La Laguna, Tenerife Island), accession 4804/B, characterised to show red-bluish dates, has been identified as *P. canariensis* var. *porphyrococca* (Rivera et al. 2014), which could explain the different sizes, mass and germination percentages recorded for this accession. In addition, other authors suggested that these red-bluish dates could be hybrids between *P. canariensis* and *P. dactylifera* (Gros-Balthazard 2013; Rivera et al. 2019). However, morphometric studies of seeds from hybrids (2.0–2.5 cm) have shown an intermediate seed size between that of *P. dactylifera* (2.5–3.0 cm) and *P. canariensis* (1.0–1.5 cm) (Gros-Balthazard 2013). Nevertheless, seeds from accession 4804/B had a seed size of 1.4 cm (Table 2) within the *P. canariensis* range. Therefore, to clarify the taxonomic uncertainty of these palms with red-bluish dates, a genetic study with a higher number of molecular markers should be carried out.

Although some author suggested that the considerable variation in drupe size detected in *Phoenix canariensis* results in variations in seed size and germination potential (Spennemann 2019), we did not find any correlation between the germination percentage and biometric data (seed polar axis, seed equatorial axis or seed mass).

Currently, we do not know the maximum time at which *Phoenix canariensis* seeds are viable. However, considering that a seed from a congener (*P. dactylifera*) germinated after 2000 years (Sallon et al. 2008), it is more likely that *P. canariensis* seeds could maintain their viability for more than 17 years. Pardo-Pina (2019) found that storage time was not the main factor for maintaining *Phoenix* seed viability, since older seeds could have better germination percentage than new ones. Although storage conditions and harvest timing appear to be the main factors affecting the viability of *P. canariensis* seeds, there are other factors to consider (Hay et al. 2022).

Confirmation of the orthodox seed behaviour of *Phoenix canariensis* has relevant repercussions for its conservation. Desiccation tolerance allows us to store seeds for a long period of time in a seed bank for *ex situ* conservation. In addition, a better understanding of seed longevity will contribute to improved gene bank management (Hay et al. 2022). Therefore, we can implement the *Phoenix canariensis* genetic representation into the seed bank by carrying out an exhaustive sampling of most Canary Island date palm populations, in order to capture the greatest genetic diversity. In addition, we must consider harvest time in sampling strategy since it has showed as an important factor on germination (Hay and Smith 2003).

In this sense, nowadays, there are only twelve accessions from two islands (Gran Canaria and Tenerife islands) of *Phoenix canariensis* in the Seed Bank – JBCVC. Therefore, we should improve the representation of date palm populations on these islands, as well as incorporate new accessions from other islands where *P. canariensis* is present.

We conclude that sampling and storage conditions following the Seed Bank protocol from the JBCVC (15%RH and −20°C) showed a high potential for producing seedlings from seeds stored for long periods, which is essential for creating an *ex situ* collection that contributes to the species conservation.

Data availability statement

The data that support this study will be shared upon reasonable request to the corresponding author.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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