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Article

Orthodox vs. Recalcitrant? Germination and Early Growth of *Phoenix* Species (Arecaceae) Stored for up to Ten Years

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Abstract: This study investigated seed storage behavior and seedling development patterns in the genus *Phoenix* L. (*Arecaceae*), addressing the knowledge gap regarding orthodox versus recalcitrant characteristics in these ecologically and economically significant palms. We examined the germination capacity and subsequent growth in 31 seed samples from various *Phoenix* species stored for up to 10 years at approximately 5 °C, at the Germplasm Bank at the Escuela Politécnica Superior de Orihuela, comprising 465 seeds monitored over a one-year period. The seed germination trials involved planting seeds in pots placed in an open-air greenhouse after ambient temperatures consistently exceeded 20 °C, typically after mid-June. *Phoenix dactylifera*, *P. canariensis*, *P. theophrasti*, the hybrid *P. dactylifera* × *P. canariensis*, and *P.* × "Palmeri" demonstrated orthodox seed storage behavior, maintaining viability for up to nine years. Conversely, *P. sylvestris*, *P. pusilla*, *P. rupicola*, and *P. loureiroi* consistently failed to germinate despite previous germination success, suggesting potential recalcitrant characteristics. Statistical analyses revealed that species identity and geographic origin exerted greater influence on germination success than seed age. Seedling development exhibited a conserved seasonal pattern across all species, with synchronized leaf emergence in September and March–July, followed by winter dormancy. Significant intraspecific variation was observed, particularly within *P. dactylifera* varieties, in both leaf production and final leaf length. These findings provide valuable insights into germplasm preservation and cultivation strategies, demonstrating that while some *Phoenix* species are suitable for long-term seed banking, others may require alternative conservation approaches. The observed species-specific and variety-specific differences offer important selection criteria for horticultural applications and conservation efforts.

Keywords: conservation; development; dormancy; germplasm bank; seed biology; seedling

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1. Introduction

The genus *Phoenix* L. Sp. Pl. 2, 1753, comprises a group of palms belonging to the order Arecales. It is notable for its pinnate leaves, unlike the palmate leaves characteristic of other genera in the subfamily Coryphoideae.

Currently, between 14 and 20 species are recognized, distributed from the Macaronesian Archipelago and Cape Verde Islands, North Africa, to the Middle East, India, China, Vietnam, southern Europe, Thailand, and islands of the Indian Ocean [1–3] (Figure 1).

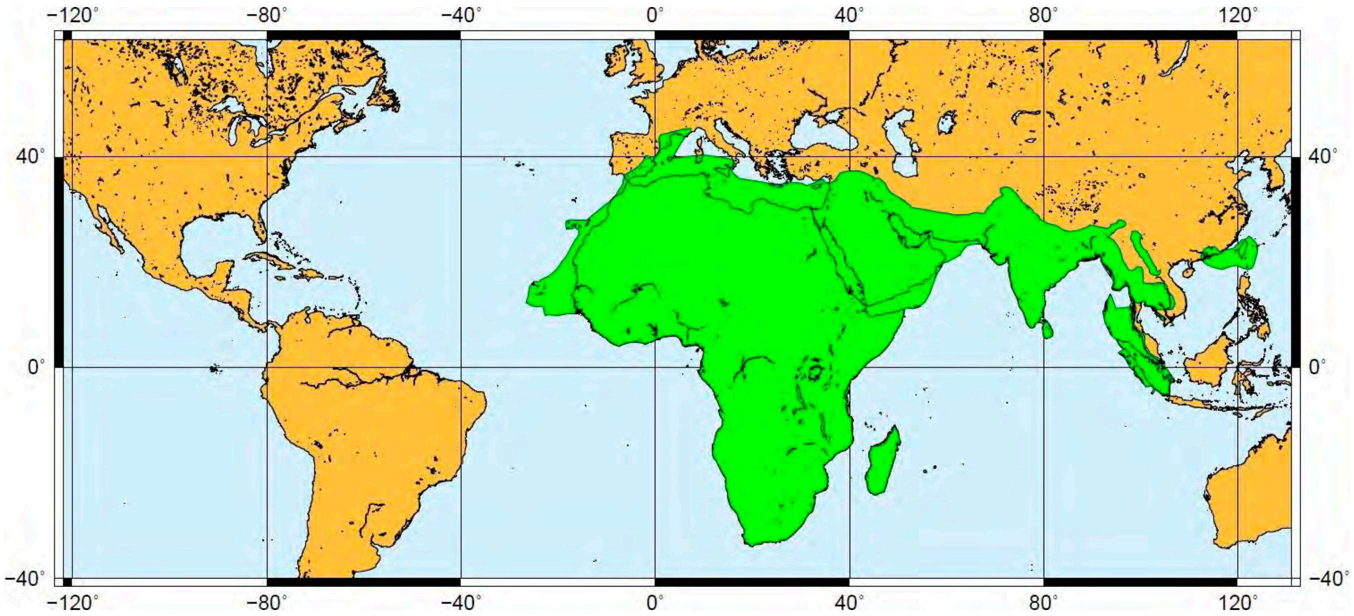

Figure 1. Primary distribution of the *Phoenix* genus in green. Image by Francisco Alcaraz, with permission.

Seedling date palms are prevalent in traditional cultivation regions and naturalized populations where intentional introduction occurred, notably in Spain and the Americas. These populations, particularly in Spain, Peru, and Mexico, represent valuable genetic repositories. Growing in diverse climatic conditions, these specimens may possess advantageous traits that, through biotechnological applications, could enhance elite cultivars' resistance, hardiness, salt tolerance, and fruit characteristics, thereby advancing commercial production [4].

Seed storage behavior is a crucial biological trait that significantly influences plant conservation strategies. Seeds are primarily classified into two categories based on their post-harvest physiology and storage potential: orthodox and recalcitrant. This classification reflects adaptations to diverse environmental pressures and has profound implications for ex situ conservation efforts [5].

Orthodox seeds can endure substantial desiccation, typically to 5–7% moisture content, and can be stored at low temperatures for extended periods, often lasting decades or more. Their longevity increases predictably with decreasing storage temperature and moisture content. Examples include most annual crops like wheat, rice, and corn, as well as many temperate species and plants adapted to seasonal dry periods [6,7].

In contrast, recalcitrant seeds are intolerant of desiccation, losing viability rapidly when their moisture content falls below a relatively high threshold, usually 20–30%. They cannot survive conventional seed bank storage conditions and remain metabolically active after shedding. Examples include many tropical tree species such as mango, cacao, and avocado, as well as aquatic plants and several economically important tree crops [6,8].

There is also an intermediate category of seeds that can tolerate some desiccation but not to the extent of truly orthodox seeds, denominated here "non-orthodox", representing a physiological continuum rather than strict categories [9,10].

The classification of seeds as orthodox or recalcitrant represents a fundamental criterion for germplasm preservation protocols [11,12]. About 75 to 80% of angiosperm species produce orthodox seeds that can survive drying and prolonged storage at −20 °C. By contrast, 5 to 10% of angiosperm species produce recalcitrant seeds that do not survive desiccation and are killed by freezing when ice crystals form [13]. While this functional dichotomy guides gene bank practices, the seed biology literature typically frames these categories in terms of desiccation tolerance: orthodox seeds survive significant dehydration, whereas recalcitrant seeds exhibit marked sensitivity to moisture reduction [12].

The distribution of seed storage behavior shows distinct patterns across plant taxonomy and biogeography:

- Orthodox seeds predominate in temperate regions, in arid environments, and among herbaceous plants.
- Recalcitrance is more common in tropical and subtropical regions, particularly in moist broadleaf forests [14,15].
- Within some families, such as Dipterocarpaceae, recalcitrance is the norm.
- Other families, like Fabaceae, exhibit a mix of both behaviors.
- Primitive seed plants often display recalcitrant characteristics.
- Some plant families show strong phylogenetic conservation of seed storage behavior.

This distribution suggests that recalcitrance may be an ancestral trait in seed plants, with orthodoxy evolving as an adaptation to seasonal or unpredictable environments where dormancy confers survival advantages.

The physiological differences between orthodox and recalcitrant seeds include the following:

1. Cellular and biochemical adaptations:
    - Orthodox seeds accumulate protective proteins (LEA proteins), sugars (especially oligosaccharides), and antioxidants during maturation and undergo cytoplasmic vitrification during drying.
    - Recalcitrant seeds lack sufficient protective mechanisms against desiccation damage and maintain high metabolic activity [9].
2. Water relations:
    - Orthodox seeds can survive equilibration with very dry air, with cellular water tightly bound [9].
    - Recalcitrant seeds maintain a high proportion of free water and experience lethal membrane damage upon drying [9].
3. Developmental pathways:
    - Orthodox seeds typically undergo a programmed drying phase during maturation.
    - Recalcitrant seeds are shed at high moisture content and remain metabolically active [16].

Genetic basis: Recent genomic studies have identified gene expression patterns associated with desiccation tolerance, including transcription factors that regulate LEA protein synthesis, antioxidant systems, and sugar metabolism pathways.

Ecological significance: Seed storage behavior reflects ecological adaptation and reproductive strategy as follows:

- Orthodox seeds are adapted to unpredictable or seasonal environments where dormancy increases survival probability and are often smaller with higher production numbers [17].
- Recalcitrant seeds are adapted to stable, humid environments where immediate germination is advantageous and are often larger with greater nutrient reserves.
- Seed sizes frequently correlate with storage behavior, with larger seeds tending toward recalcitrance [18,19].
- Dispersal mechanisms often align with storage behavior, with wind-dispersed seeds typically being orthodox.

- Pioneer species generally produce orthodox seeds, while climax forest species often produce recalcitrant seeds.

These ecological correlations reflect the tradeoffs between seed longevity, establishment success, and reproductive investment.

Implications for ex situ conservation: The physiological differences between orthodox and recalcitrant seeds create distinct challenges for conservation as follows:

Orthodox seeds:

- Well suited for conventional seed banking (dried and stored at −18 °C).
- Predictable longevity under proper storage conditions.
- Cost-effective conservation of genetic diversity.
- Large sample sizes can be stored in limited space.

Recalcitrant seeds:

- Conventional seed banking is ineffective.
- Alternative approaches are required, such as cryopreservation of embryonic axes or embryos, in vitro culture of embryos or embryonic axes, field gene banks (living collections), pollen storage and artificial pollination, and synthetic seed technology.

These limitations have significant implications for conservation priorities, particularly for tropical tree species with recalcitrant seeds that are disproportionately threatened by habitat loss and climate change.

Current research focuses on the following:

1. Identifying the molecular mechanisms underlying desiccation tolerance.
2. Understanding the genetic basis of seed storage behavior to potentially engineer greater storage tolerance.
3. Exploring the continuum of seed storage behaviors beyond the simple orthodox–recalcitrant dichotomy [10].
4. Predicting seed storage behavior based on phylogenetic and ecological information [15,17–20].
5. Developing improved techniques for preserving recalcitrant germplasm [21,22].

The distinction between orthodox and recalcitrant seeds represents a fundamental aspect of plant reproductive biology with critical implications for conservation. As habitat loss accelerates and climate change threatens natural ecosystems, effective ex situ conservation strategies must account for these physiological differences. The continued development of technologies for preserving recalcitrant germplasm remains a priority for global plant conservation efforts, particularly for tropical forest species that are both highly threatened and likely to possess recalcitrant seeds [5,23].

Seed longevity is a critical parameter in germplasm preservation facilities, guiding storage protocols, regeneration schedules, and viability testing. Although its biological importance was recognized in the early 20th century when Nicolai I. Vavilov identified the need for systematic conservation of threatened phytogenetic resources, research has since revealed significant variation in longevity both and within species [24]. Multiple factors influence ex situ seed longevity, including genetics, developmental stage at collection, processing methods, and environmental storage conditions—particularly relative humidity and temperature [25,26].

Cryopreservation, under specific parameters, facilitates the long-term conservation of plant germplasm. A remarkable demonstration of this phenomenon was observed in *Silene stenophylla* tissue specimens from Siberia, dating to the Late Pleistocene epoch (approximately 30,000 years before present), which were preserved in permafrost conditions. Through the application of in vitro culture techniques and micropropagation protocols, these ancient tissues were successfully regenerated into viable specimens capable of sexual reproduction [27].

Anhydrobiotic seeds of diverse plant taxa exhibit remarkable tolerance to adverse environmental conditions when maintaining a desiccated state. Under these conditions, their metabolic processes are downregulated to a minimal threshold of activity—a state of quiescence—while maintaining germination viability over extended temporal periods [28,29]. During ontogeny, orthodox seeds develop desiccation tolerance mechanisms through a complex maturation process. This developmental progression is characterized by the gradual acquisition of longevity—defined as the cumulative duration throughout which desiccated seeds retain their biological viability [9]. Francis E. Lloyd investigated seed ontogeny and histochemical changes that occur during germination in cultivars of *P. dactylifera* [30].

Various *Phoenix* species exhibit seed characteristics that fall between orthodox and recalcitrant, which we designate here as "non-orthodox". Studies of *Phoenix reclinata* demonstrate that although both embryonic and endospermic water content decrease during seed maturation, they maintain relatively high levels—a characteristic frequently associated with, although not exclusive to, non-orthodox seeds. The embryonic cellular ultrastructure and minimal water absorption requirements for germination initiation further support the non-orthodox classification of these seeds. Current evidence suggests that *P. reclinata* seeds display intermediate post-harvest behavior, placing them between orthodox and recalcitrant categories in terms of their storage characteristics [31].

Desiccation tolerance in *Phoenix* species appears to be associated with a form of seed dormancy, which can be alleviated through acid treatments or immersion in water at varying temperatures and durations. This phenomenon has been specifically investigated in *P. dactylifera* [32,33].

Very long-term preservation of *Phoenix dactylifera* seeds has a recent history. In 1963, archaeological excavations in southern Israel yielded a remarkable discovery: an undisturbed clay vessel containing several date palm seeds. The vessel, recovered from arid soil conditions, underwent radiocarbon dating analysis, which placed its chronological context between 155 BCE and 64 CE. The seeds were subsequently preserved at Bar-Ilan University in Tel Aviv. Four decades later, in 2003, agricultural specialist Elaine Solowey initiated germination trials with three of these ancient seeds. Notably, one seed successfully germinated, and by 2011, eight years post-germination, the specimen flowered [34,35]. This extraordinary case demonstrates the exceptional longevity potential of some *Phoenix* seeds under specific preservation conditions.

In 2007, the Valencian Regional Government commissioned a comprehensive study on date palm and wild palm populations within its territory. This led to the establishment of the Spanish Palm Germplasm Bank, funded by the National Institute for Agricultural Research (INIA). The bank was created to facilitate the collection, propagation, preservation, and characterization of *Phoenix* species and other related palms. Currently, the Palm Germplasm Bank houses over 600 living accessions, representing 19 species and subspecies and 4 interspecific hybrids [36]. As of 2024, the National *Phoenix* Collection has documented 1675 accessions, illustrating the extensive range of palm genetic resources stored in this repository (Figure 2). A key feature of the collection is that over 90% of the accessions were obtained from seeds, which are desiccated and stored at 4 to 5 °C. Consequently, evaluating the germination capacity of these seeds after long-term storage is crucial to determine the viability of this seed collection as a genetic resource.

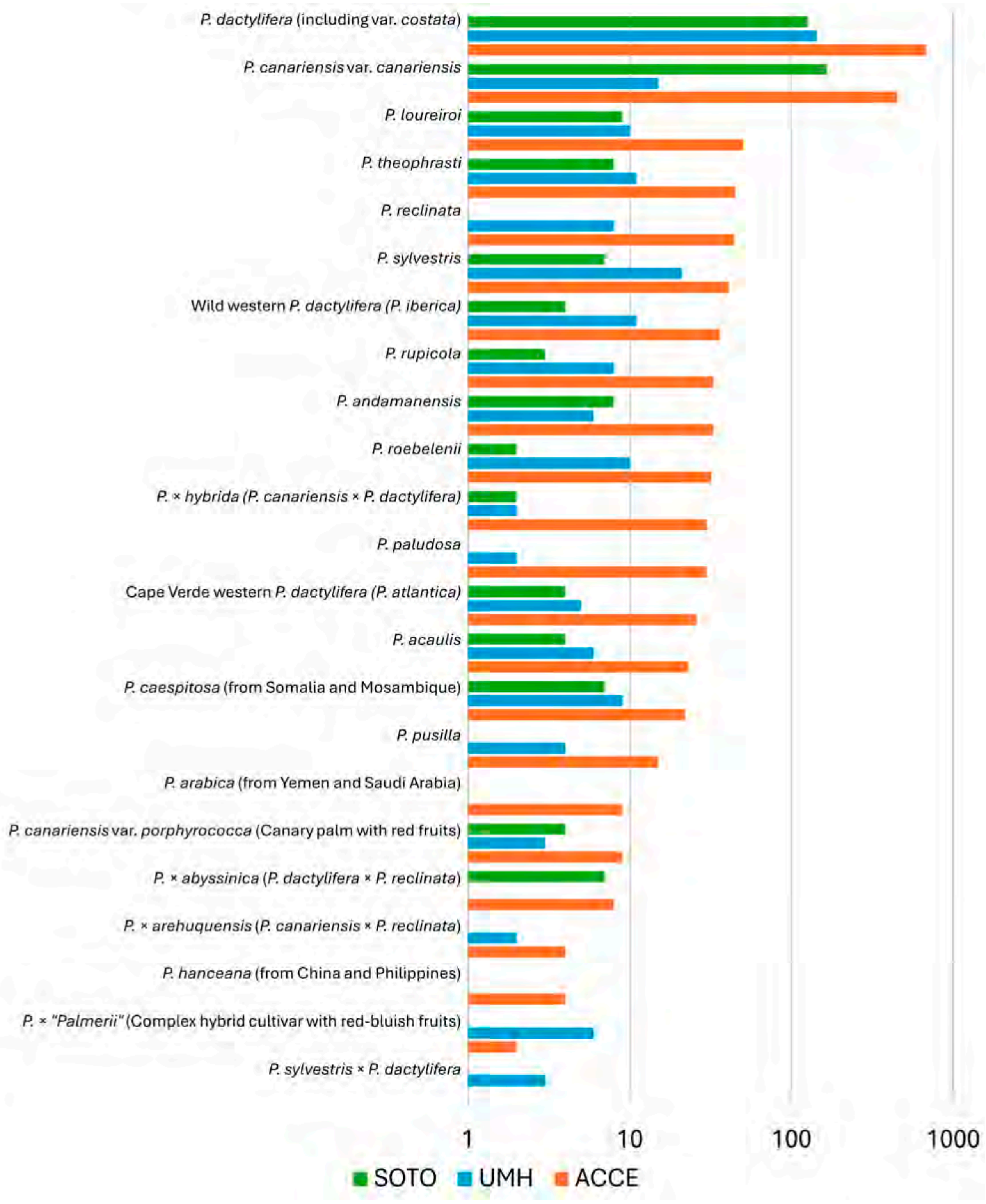

Figure 2. Number of accessions for each *Phoenix* taxon maintained in ex situ conservation at three sites in Orihuela, Spain, as per 2024. The *x*-axis indicates the number of accessions, while the *y*-axis lists the different *Phoenix* taxa. Bars represent the following: ACCE (green)—accessions conserved as seeds in the seed bank; SOTO (blue)—accessions cultivated as living palm trees in the 16-hectare Palmetum gardens of Orihuela; and UMH (orange)—accessions grown in the experimental fields (EPSO) of the Miguel Hernández University at Desamparados. A given taxon may be present in one, two, or all three locations, depending on germination success. Overall, most accessions are preserved in seed form, with approximately 50% also represented as living specimens in the field collections. Graph by Diego Rivera.

This extensive seed collection serves as a valuable resource for future studies on the morphological, genetic, and biochemical characteristics of the *Phoenix* genus, with significant potential for applications in horticulture and conservation.

This study investigated seed samples from the National *Phoenix* Collection to determine seed storage behavior (orthodox or recalcitrant) and analyze growth rates and developmental patterns across species during the first year. The specific objectives included (1) evaluating germination capacity after extended standardized storage, (2) assessing the influence of seed age and species on the percentage of germination, (3) analyzing seasonal patterns of growth rates, and (4) comparing vegetative development among species. This systematic approach contributes to a comprehensive understanding of *Phoenix* seed biology and development, informing both conservation and cultivation practices.

2. Materials and Methods

2.1. Plant Material

The present study was conducted using seed material from the *Phoenix* Germplasm Bank located at the Miguel Hernández University (UMH), specifically at the Escuela Politécnica Superior de Orihuela (EPSO), which is part of the global germplasm bank network and is supported by the Miguel Hernández University of Elche, the Municipality of Orihuela, and the National Institute of Agricultural Research (INIA).

Seeds from multiple *Phoenix* species and varieties were collected and maintained in controlled storage conditions, refrigerated chambers (Liebherr, Ochsenhausen, Germany) at 5 °C with silica gel with humidity indicator (orange, 2.5–6 mm, Scharlab S.L., Barcelona, Spain). This study utilized 31 seed samples (Table 1), representing a broad spectrum of *Phoenix* taxa. The sampling strategy prioritized Spanish localities, particularly the Valencia and Murcia regions, while also incorporating samples from the northern Iberian Peninsula (Asturias and Galicia). To achieve a comprehensive representation of *Phoenix* diversity, seeds from other Mediterranean countries and Southeast Asia were also included. The collection comprised the following taxa: *Phoenix dactylifera* L. (including cultivars "Negres", "Candios de mala clase", and "Rojos"), *P. dactylifera* var. *costata* Becc., *P. canariensis* H. Wildpret var. *porphyrococca* Vasc. & Franco, *P. loureiroi* Kunth, *P.* × "Palmeri" (identified as a hybrid through genetic analysis by Carreño [3]), *P. rupicola* T. Anderson, *P. sylvestris* (L.) Roxb., and *P. theophrasti* Greuter "Datça." The samples were acquired between 2008 and 2015 from diverse sources, including commercial suppliers, germplasm repositories, and field collections conducted across Spain and other relevant geographical locations. Seed ages ranged from 633 to 3440 days since collection.

Table 1. *Phoenix* accessions studied with their codes.

Repository Code	Species and Variety	Accessions Data (Date and Locality of Seed Collection)	Storage (Days) **	Previous Germination Results
	Phoenix canariensis H. Wildpret		1870 *	
E160-1677	*P. canariensis* var. *porphyrococca* Vasc. & Franco	24-11-2009; Espinardo (Murcia, Spain)	2771	30-11-2009, −
E160-1036	*P. canariensis* var. *canariensis*	26-08-2013; Colombres (Asturias, Spain)	1400	17-09-2013, −
E160-1478	*P. canariensis* var. *porphyrococca*	28-08-2013; Cambados (Pontevedra, Spain)	1398	20-06-2014, +
E160-1488	*P. canariensis* var. *porphyrococca*	29-10-2010; Valencia (Spain)	2432	20-06-2011, +
E160-1490	*P. canariensis* var. *macrocarpa* H. Wildpret	20-12-2014; Granada (Spain)	919	30-06-2015, +
E160-1496	*P. canariensis* var. *canariensis*	27-08-2013; Cudillero (Asturias, Spain)	1399	10-07-2014, +
E160-1676	*P. canariensis* var. *canariensis*	24-11-2009; Espinardo (Murcia, Spain)	2771	30-11-2009, −

Table 1. *Cont.*

Repository Code	Species and Variety	Accessions Data (Date and Locality of Seed Collection)	Storage (Days) **	Previous Germination Results
	Phoenix dactylifera L.		2591 *	
E160-1476	*P. dactylifera* var. *dactylifera*	28-01-2008; Fortuna (Murcia, Spain)	3437	none
E160-1477	*P. dactylifera* var. *dactylifera*	28-01-2008; Fortuna (Murcia, Spain)	3437	none
E160-1479	*P. dactylifera* var. *dactylifera*	25-09-2011; Elche (Alicante, Spain)	2101	30-06-2012, +
E160-1480	*P. dactylifera* var. *costata* Becc.	16-01-2011; Santomera (Murcia, Spain)	2353	30-6-2011, +
E160-1481	*P. dactylifera* var. *costata*	10-11-2010; Santomera (Murcia, Spain)	2420	30-6-2011, +
E160-1483	*P. dactylifera* var. *dactylifera*	03-12-2008; Ojós (Murcia, Spain)	3127	20-07-2009, +
E160-1484	*P. dactylifera* var. *dactylifera*	04-02-2013; Elche (Alicante, Spain)	1603	04-02-2013, −
E160-1485	*P. dactylifera* var. *dactylifera*	11-11-2011; Orihuela (Alicante, Spain)	2054	29-12-2011, −
E160-1486	*P. dactylifera* var. *dactylifera*	12-10-2010; Albatera (Alicante, Spain)	2449	30-06-2011, +
E160-1489	*P. dactylifera* var. *dactylifera* “Negres”	25-01-2008; Elche (Alicante, Spain)	3440	30-06-2009, −
E160-1491	*P. dactylifera* var. *dactylifera* “Rojos”	02-10-2015; Elche (Alicante, Spain)	633	20-06-2016, +
E160-1493	*P. dactylifera* var. *dactylifera* “Negres”	25-01-2008; Elche (Alicante, Spain)	3440	10-07-2016, +
E160-1495	*P. dactylifera* var. *dactylifera* “Negres”	25-01-2008; Elche (Alicante, Spain)	3440	10-07-2016, +
E160-1497	*P. dactylifera* var. *dactylifera* “Candios de mala clase”	23-01-2011; Elche (Alicante, Spain)	2346	20-06-2011, +
	Phoenix × “Palmeri”		1710 *	
E160-1482	*Phoenix* × “Palmeri”	18-06-2012; B & T World Seeds [1]	1834	10-07-2014, +
E160-1487	*Phoenix* × “Palmeri”	20-02-2013; KPR [2]	1587	10-07-2014, +
	Phoenix theophrasti Greuter			
E160-1492	*P. theophrasti* “Datça”	06-07-2013; Palmiye Merkezi [3]	1451	30-9-2013, +
	Phoenix × *hybrida* André (*Phoenix dactylifera* L. × *Phoenix canariensis* H. Wildpret)			
E160-1494	*P.* × *hybrida*	16-01-2011; El Siscar (Murcia, Spain)	2353	10-07-2011, +
	Phoenix pusilla Gaertn.			
E160-327	*P. pusilla*	22-11-2009; Kenibreed [4]	2773	24-12-2011, −
	Phoenix sylvestris (L.) Roxb.		2773 *	
E160-328	*P. sylvestris*	22-11-2009; Kenibreed [4]	2773	30-06-2010, +
E160-329	*P. sylvestris*	22-11-2009; Kenibreed [4]	2773	30-06-2010, +
	Phoenix loureiroi Kunth		*1650 **	
E160-712	*P. loureiroi*	25-12-2012; Kenibreed [4]	1644	30-06-2013, +
E160-714	*P. loureiroi*	12-12-2012; Kenibreed [4]	1657	30-06-2013, +
	Phoenix rupicola T. Anderson			
E160-713	*P. rupicola*	25-12-2012; Kenibreed [4]	1644	30-06-2013, +

Note: Seed sample details including mean ages in *italics* (*) of the group of samples from each species, identified by genus, species, and variety name. Samples included in the experiment are identified with their accession codes. (**) The column “Age (days)” records the number of days since seed collection until the experiment began. Germination results are displayed as “+” (successful germination) and “−” (no germination). Commercial seed sources: [1] B & T World Seeds (Aigues-Vives, France), [2] KPR Gardeners Club (Slovakia), [3] Palmiye Merkezi (Koycegiz, Mugla, Turkiye), and [4] Kenibreed Plant (West Bengal, India).

Seed samples were selected to prioritize species of research interest while ensuring sufficient seed quantities for germination experiments, minimizing depletion of the germplasm collection. Thirty-one samples, each containing 15 seeds, were chosen for this study (Table 1). These samples were stored in refrigerated chambers at 5 °C with silica gel desiccant to control humidity. Germination trials were conducted by planting seeds in pots, which were then placed in an open-air greenhouse after the ambient air temperatures consistently exceeded 20 °C, typically after mid-June in southeastern Spain. Germination of tropical *Phoenix* species presented greater challenges compared with arid-adapted species, even with fresh seed stock. Following selection, a standardized photographic protocol was implemented to document the dorsal and ventral surfaces of each seed sample (Supplementary Table S1). Images were captured using a Panasonic DMC-FZ50 camera under consistent lighting conditions. Millimeter paper and a 30 cm ruler were included in each photograph for accurate scale reference.

2.2. Planting Seeds

The germination protocol was selected based on the standard procedure routinely used by the *Phoenix* germplasm bank, which has successfully applied it to over 1500 seed-derived accessions representing the full diversity of the genus (Figure 1). Uniform conditions were preferred to ensure consistency across the samples analyzed in this study.

On 26 June 2017, the planting phase of the study was initiated. Fifteen seeds from each sample were directly sown into standardized black containers with the shape of an inverted pyramidal frustum, with commercial potting soil, each with a 3 L volume capacity and dimensions of 15 cm × 20 cm, without any pre-treatment or hydration. To maintain experimental uniformity, these containers were utilized across all treatments. Each container was meticulously labeled to record critical metadata, including the provenance, collection date, collector identification, and pertinent additional information, thereby ensuring accurate and comprehensive data collection and facilitating subsequent interpretation of results. This systematic methodological approach was implemented to ensure rigorous sample management throughout the initial phase of the study. Subsequently, on 2 April 2018, to encourage greater root development and ensure optimal adaptation for future field planting, plants were transplanted from the initial 3L pots to larger 13L pots.

2.3. Data Collection

Data collection commenced on 17 July 2017, with the initial observation of seed germination. The initial recorded data consisted of the total number of germinated seeds per pot. Subsequently, seedling growth was monitored using a 40 cm ruler. To ensure consistent longitudinal data, the first three germinated seedlings in each pot were measured at 15-day intervals from the onset of germination until 19 July 2018. Growth measurements were continued until the development of five leaves per seedling, with all data recorded in Excel.

Concurrent with growth measurements, environmental parameters were monitored. Air temperature, both internal and external to the greenhouse, was recorded using two "Six-Bellani" thermometers. The soil temperature within the pots was measured using a digital food thermometer (model "5989"), equipped with a 120 mm stainless steel probe and a measurement range of −50 °C to +150 °C, to investigate potential correlations between soil temperature and growth rates. These measurements were also taken at 15-day intervals, and comparative temperature data were obtained from the AEMET Orihuela observatory [37].

To evaluate early seedling development, a common method was employed: the assessment of plant growth rate during the first year through the measurement of plant length. Specifically, the length of the first leaf was recorded for three individuals per sample, as this metric serves as a reliable indicator of growth rate. All individuals were meticulously labeled to ensure accurate tracking and data association.

2.4. Data Analysis

The relationship between seed age and germination percentage was analyzed using Pearson's and Spearman's correlation coefficients. Population means were compared using Welch's t-test to accommodate potential heteroscedasticity. Species-specific germination patterns were evaluated using one-way ANOVA followed by post hoc analysis when appropriate. Statistical significance was established at $p < 0.05$. Effect sizes were calculated using

Cohen's d to quantify the magnitude of differences between groups. All statistical analyses were performed using standard statistical software in Python 3.11 and Claude 3.7 Sonnet, released in February 2025, analysis [38,39].

We also implemented a Bayesian framework to estimate the correlation coefficient (ρ) between seed age and germination rate. The bivariate relationship was modeled using a bivariate normal distribution with an uninformative prior on the correlation parameter.

For the prior distribution, we employed a uniform prior for ρ over the interval $[-1, 1]$, indicating no prior belief about the direction or strength of the correlation.

Posterior distributions were computed using Markov Chain Monte Carlo (MCMC) sampling with the No-U-Turn Sampler (NUTS) algorithm. We ran four independent chains, each with 2000 iterations, discarding the first 1000 iterations as warm-up.

Convergence was verified using the potential scale reduction factor ($\hat{R} < 1.05$) and effective sample size (>400 for all parameters).

From the posterior distribution, we calculated the mean posterior correlation coefficient, 95% credible intervals, the probability of a positive correlation ($P(\rho > 0)$), and the probability of a practically significant correlation ($P(\rho > 0.3)$).

The same Bayesian framework was applied separately to data subsets for *Phoenix dactylifera* and *Phoenix canariensis* to assess species-specific correlations.

This methodology provides a comprehensive probabilistic assessment of the relationship between seed age and germination, allowing for direct statements about the probability of correlations of different magnitudes rather than relying solely on significance testing.

3. Results

3.1. Phoenix Seed Age and Germination

Our results, as depicted in Figure 3, revealed an irregular pattern in seed germination.

Multiple variables influenced germination irregularity. Seed water content was essential during germination, while seed quality significantly affected germination rates. For instance, *P. canariensis* seeds from diverse origins demonstrated inconsistent behavior, with seeds in pot 27 exhibiting decomposition without germination. Seed quality typically peaked at harvest maturity before declining. Environmental conditions (temperature, moisture, and light) and physiological factors (dormancy status and nutrient reserves) further modulated germination patterns, with stronger dormancy or inadequate reserves potentially causing delayed or reduced germination.

In summary, the irregular germination pattern highlighted in our results was likely influenced by a combination of seed age, botanical source, seed quality, environmental factors, and physiological states. A comprehensive analysis considering these factors, and in particular age and botanical source, is essential to understand and address the observed variability in seed germination considering that we paid attention to work under uniform environmental factors and physiological states.

3.1.1. Seed Age and Germination Percentage: Pearson Correlation Coefficient

The Pearson correlation ($r \approx 0.215$, $p = 0.246$) between the seed age and germination percentage revealed a weak, non-significant positive relationship. Seeds averaged 2129 days (~5.8 years) in age with 49% mean germination rate, with substantial variation in both metrics (age SD ≈ 834 days; germination SD ≈ 37%). While older seeds demonstrated a slight tendency toward higher germination, this trend lacked statistical significance. Other factors appeared more influential, particularly the species of origin, as evidenced by *P. dactylifera* seeds both being older and exhibiting higher germination percentages (Table 1).

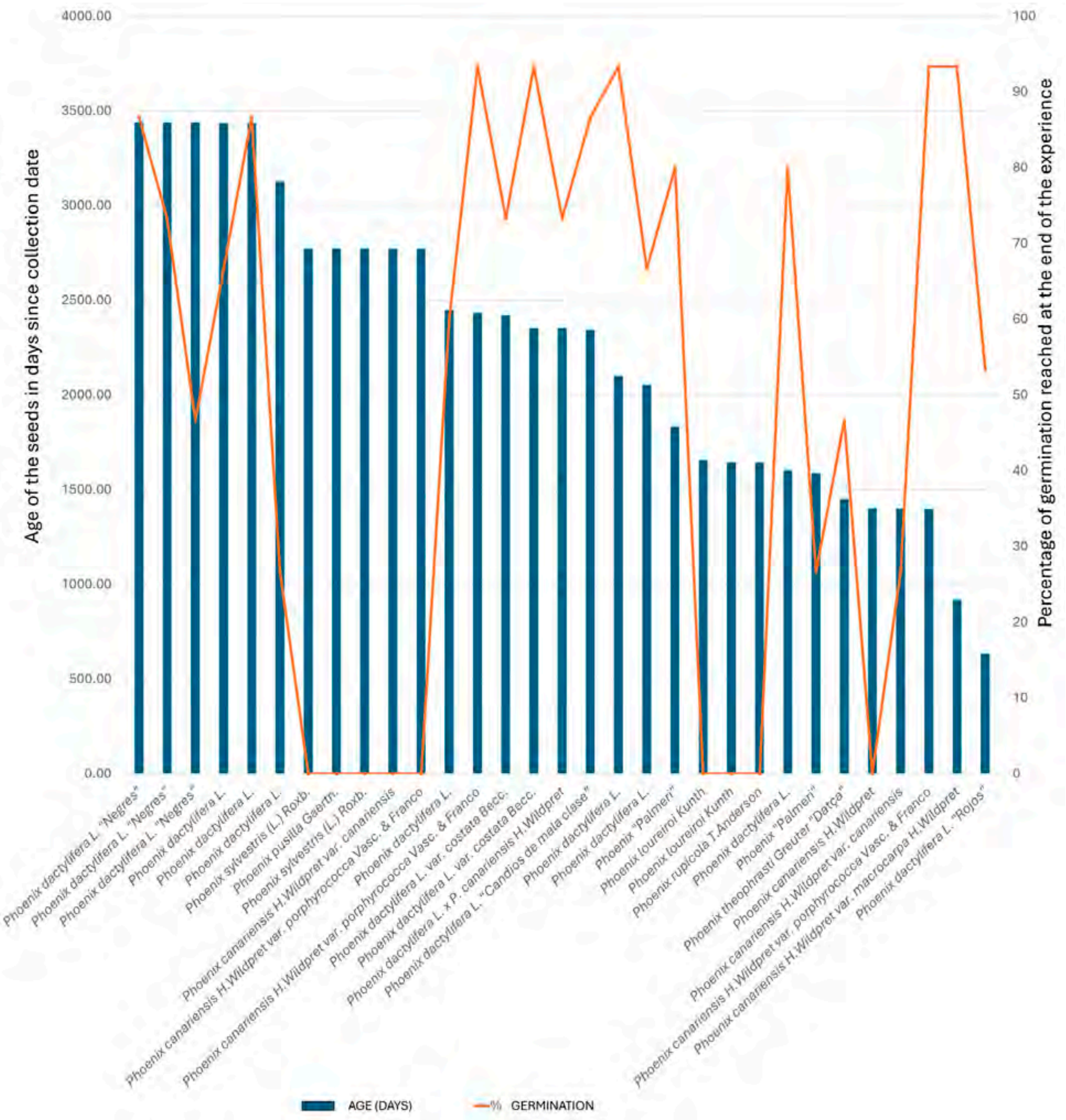

Figure 3. Comparison of seed age (blue bars) and germination percentage (orange line) across *Phoenix* plant species and varieties. The x-axis lists different *Phoenix* types described in Table 1 and Supplementary Table S1, while the left y-axis represents the seed age in days, and the right y-axis represents the germination percentage. The chart highlights variations in germination success relative to seed age and botanical origin. The names of local varieties or ethnovarieties are shown in quotation marks (“”).

3.1.2. Seed Age and Germination Percentage: Spearman Correlation Coefficient

The Spearman correlation ($\rho = 0.184$, $p = 0.323$) indicated a weak, non-significant monotonic relationship between the seed age and germination percentage. This result, slightly weaker than the Pearson correlation ($r = 0.215$, $p = 0.246$), suggested the relationship was neither strongly linear nor monotonic. Rank transformation failed to reveal patterns obscured in raw values. These findings confirmed that seed age was not a reliable predictor of germination percentage, with other factors likely exerting greater influence on germination outcomes.

3.1.3. Seed Age and Germination Percentage: *t*-Test

A *t*-test analysis was conducted by dividing samples at the median seed age (2346 days) into older (n = 16) and younger (n = 15) groups. Mean germination percentages were comparable between older (48.13%) and younger (50.89%) seeds, with a difference of −2.76%. Welch's two-sample *t*-test revealed no significant difference (t = −0.187, p = 0.853) with a negligible effect size (Cohen's d = −0.068). This analysis corroborated the correlation findings, confirming that seed age did not significantly influence germination rates in this dataset.

3.2. Phoenix Seed Age, Species, and Germination

3.2.1. Overall Species Comparison

Phoenix dactylifera had the highest number of samples with 12, a mean germination rate of 70.14%, and a wide range from 26.67% to 93.33%. The average seed age was approximately 2437 days or about 6.7 years.

Phoenix canariensis had seven samples with a mean germination rate of around 42.86%. The germination rate varied significantly, from 0% to 93.33%, and the seeds were younger on average, at approximately 1724 days or about 4.7 years.

Phoenix sylvestris, *P. loureiroi*, and *P. rupicola* all showed 0% germination. These seeds ranged from relatively young to older, with ages exceeding 1600 days.

Phoenix × "Palmeri", likely a hybrid, exhibited variable germination rates ranging from 26.67% to 80%. The seeds were relatively young, averaging around 1710 days.

Phoenix theophrasti had a single sample, with a germination rate of 46.67%. The seed age was 1451 days.

Statistical Comparisons:

A *t*-test comparing the germination rates of *P. dactylifera* and *P. canariensis* revealed no statistically significant difference, despite *P. dactylifera*'s higher mean germination rate. This suggested that the observed difference may be due to chance or the limited sample size.

Age–Germination Correlation by Species:

For species with sufficient samples, neither *P. dactylifera* nor *P. canariensis* showed a significant correlation between the seed age and germination rate.

Practical Implications:

P. dactylifera demonstrated the highest overall germination success, maintaining good viability even with older seeds.

Some species, such as *P. sylvestris*, *P. pusilla*, *P. loureiroi*, and *P. rupicola*, showed no germination. This suggested either inherently lower seed viability, poor tolerance to long-term storage, or specific germination requirements that were not met in the study conditions.

Varieties within the same species, such as different varieties of *P. canariensis*, exhibited variable germination rates, indicating that genetic factors played an important role in seed viability.

3.2.2. Bayesian Approach to Correlation Analysis

A Bayesian approach to correlation analysis offered several advantages for our seed germination data: The analysis provided the full posterior distribution of correlation values rather than a single coefficient, offering a more comprehensive view. We could make direct probability statements, such as "there is an X% probability that the correlation is positive", instead of relying on p-values. Credible intervals were intuitive; a 95% credible interval directly indicated the range containing 95% of the plausible correlation values. If we had prior information about seed germination patterns, it could be formally incorporated into the analysis.

The key findings from Bayesian analysis were as follows: For the overall dataset, the mean posterior correlation was approximately 0.21, with a 95% credible interval ranging from about −0.15 to 0.55. The probability of a positive correlation was around 85%, while the probability of a practically significant correlation ($\rho > 0.3$) was about 30%. This meant there was an 85% chance that the seed age and germination were positively correlated but only a 30% chance that this correlation was strong enough to be practically meaningful.

Species-Specific Analysis: For *Phoenix dactylifera*, the mean posterior correlation was approximately 0.18, with a 95% credible interval ranging from −0.35 to 0.67. The probability of a positive correlation was around 75%.

For *Phoenix canariensis*, the mean posterior correlation was about 0.30, with a 95% credible interval ranging from −0.54 to 0.89. The probability of a positive correlation was around 71%. These species-specific results suggested that both species showed more evidence for positive than negative correlations. *P. canariensis* may have had a slightly stronger correlation between seed age and germination. However, the wide credible intervals for both species indicated substantial uncertainty.

This Bayesian analysis complemented frequentist approaches, such as Pearson, Spearman, and *t*-tests, by providing a more nuanced understanding of the relationship between seed age and germination in *Phoenix* species.

3.2.3. Relationship Between the Year of Collection and the Germination Percentage of the Species

When examining the relationship between the year of collection and the germination percentage of the species, it was evident that the highest germination rates were observed in samples of *Phoenix dactylifera* from Spain, which belonged to the Western Group of this species, and in certain samples of *P. canariensis*. Remarkably, some *P. canariensis* samples, including both the typical variety and var. *porphyrococca*, failed to germinate throughout the observation period. Conversely, a hybrid between these two species, represented by a single sample, demonstrated over 70% germination (Figures 4 and 5).

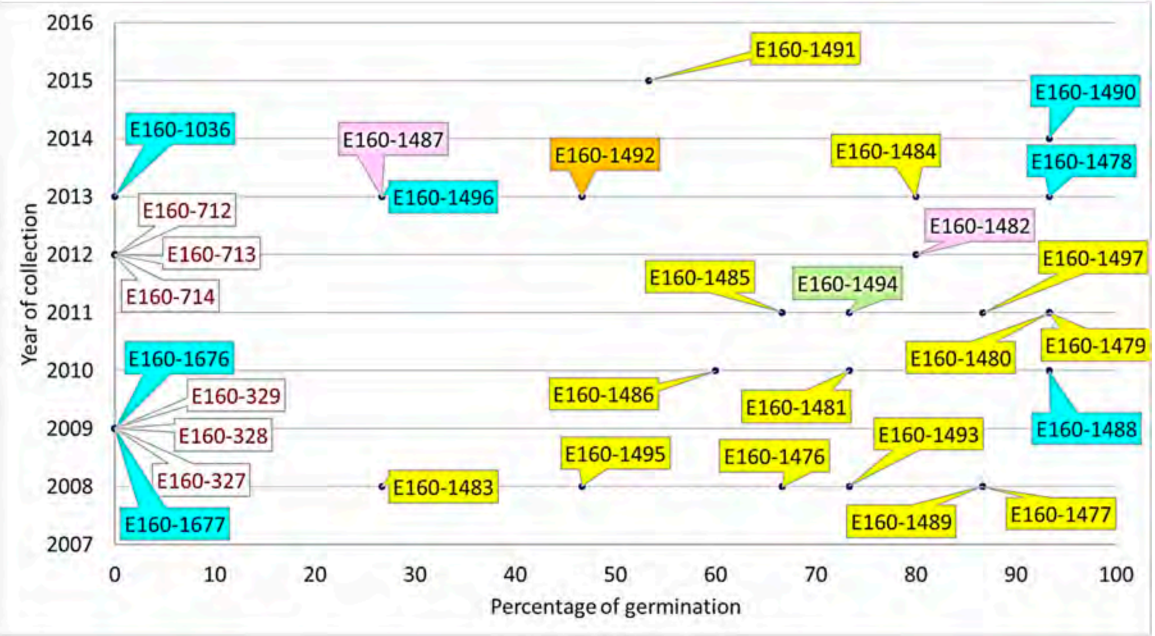

Figure 4. Germination percentage and year of collection across *Phoenix* samples. Color code: yellow—*Phoenix dactylifera*; blue—*Phoenix canariensis*; purple—*Phoenix* "Palmeri"; green—*Phoenix* × *hybrida* (*P. canariensis* × *P. dactylifera*); orange—*Phoenix theophrasti*; white—tropical *Phoenix* species of the Indian subcontinent. Note: Codes as in Table 1 and Supplementary Table S1.

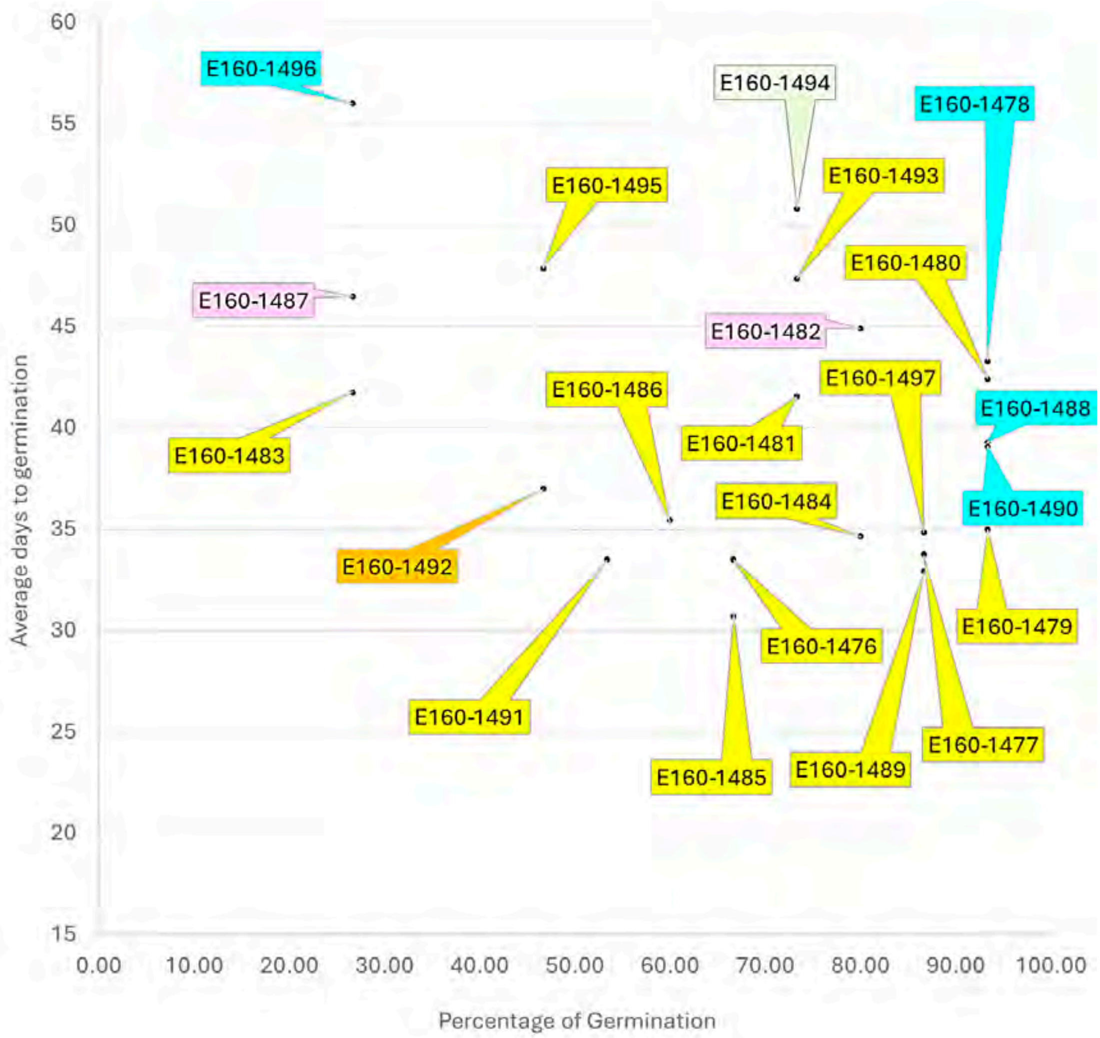

Figure 5. Germination percentage and average days to germination across *Phoenix* species. Color code: yellow—*Phoenix dactylifera*; blue—*Phoenix canariensis*; purple—*Phoenix* "Palmeri"; green—*Phoenix* × *hybrida* (*P. canariensis* × *P. dactylifera*); orange—*Phoenix theophrasti*. Note: Codes as in Table 1 and Supplementary Table S1.

It is noteworthy that the *P. canariensis* samples from the Espinardo Campus (E160-1676 and E160-1677) previously did not germinate in the year they were first planted (Table 1). This observation suggested a potential issue with the quality of the source material as the palms were already severely infested with *Rhynchophorus ferrugineus*, which may have adversely affected the normal development of fruits and seed viability. Similarly this occurred with *P. canariensis* var. *canariensis* from Colombres and among the Indian samples with *P. pusilla* (Table 1).

On the contrary, several samples with good gemination rates (Figure 4) failed previously to germinate: *P. dactylifera* var. *dactylifera* "Negres" (E160-1489) and two *P. dactylifera* var. *dactylifera* (samples E160-1476 and E160-1477) from Fortuna and *P. dactylifera* var. *dactylifera* from Orihuela (E160-1485).

The sample of *P. theophrasti* from Datça (Turkey), possibly a hybrid between *P. theophrasti* and *P. dactylifera* according to Carreño [3], displayed a germination rate close to 50%. Notably, none of the tropical species from the Indian subcontinent and Southeast Asia (*Phoenix sylvestris*, *P. loureiroi*, *P. roebelenii*, *P. rupicola*, and *P. pusilla*) germinated, except for two originally labeled *P. acaulis* samples. The unexpectedly high germination in samples initially attributed to *P. acaulis*, considering that this species belonged to the

Indian group, confirmed previous questions regarding their identity as thousands of seeds labeled *P. acaulis* circulated in Europe in the early 2000s, producing plants resembling the so-called *P.* × "Palmeri", which Carreño [3] identified as a complex hybrid involving multiple parental species. However, the samples of *Phoenix sylvestris*, *P. loureiroi*, and *P. rupicola* had successfully germinated in 2011 or 2013 (Table 1).

The data presented in Figure 4 demonstrated that the year of seed collection, and consequently the seed age, exerted a substantially lesser effect on germination capacity than other examined factors. Specifically, the botanical origin of the seeds, defined by species, and the geographic region of origin were shown to be significantly more influential determinants of germination success.

There did not appear to be a clear relationship between the average days to germination and the final germination percentage of the samples. However, all the most successful samples with high germination percentages had an average germination time of 35–43 days (Figure 5).

3.3. Phoenix Seedling Development

3.3.1. Leaf Number

The analysis of total leaf emergence patterns in *Phoenix* spp. seedlings revealed distinct species-level and variety-level trends, offering valuable insights for palm cultivation and breeding strategies.

Species-Level Patterns (Figure 6A):

All species exhibited synchronized major leaf emergence periods in September 2017 and March–July 2018. *P. dactylifera* demonstrated the most pronounced step pattern, with dramatic increases during these windows. The universal September emergence event suggested a strong seasonal trigger across species.

Growth rate differentiation was evident among species. *P. dactylifera* displayed three distinct growth phases: rapid growth from July to September 2017, a plateau from October 2017 to February 2018, and accelerated growth from March to July 2018. In contrast, *P. canariensis* showed a more constant, gradual increase throughout the year. The hybrid *P.* × "Palmeri" exhibited minimal winter growth but notable spring emergence.

Dormancy periods were observed in all species, with reduced or halted leaf production between November and February. *P. dactylifera* maintained the most stable plateau during this period, while *P. theophrasti* and the hybrid (*P.* × *hybrida*) showed nearly complete cessation of new leaf emergence.

Variety-Level Patterns (Figure 6B):

Significant intraspecific variation was noted within *P. dactylifera*. The standard *P. dactylifera* s.l. dramatically outperformed, in total leaf numbers, specialized varieties such as "Negres", "Candios de mala clase", and "Rojos", which showed substantially lower production rates. Similarly, *P. canariensis* varieties differed significantly, with var. *porphyrococca* performing better than var. *macrocarpa* or var. *canariensis*.

The response to seasonal triggers varied among varieties. The September leaf flush was strongest in *Phoenix dactylifera* L. s.l. and the hybrid *P dactylifera* × *P. canariensis*. Spring emergence timing varied slightly, with some varieties activating earlier in March compared with others in April–May. *P. canariensis* varieties showed a less pronounced seasonal response compared with *P. dactylifera* varieties.

The hybrid *Phoenix dactylifera* × *P. canariensis* exhibited intermediate behavior between its parent species, following the *P. dactylifera* emergence pattern but at a reduced magnitude. On a per-plant basis, considering only three individuals, this hybrid appeared quite productive. This hybrid exhibited growth and developmental rates analogous to

P. dactylifera; however, its leaf emergence frequency pattern more closely aligned with that of *P. canariensis*.

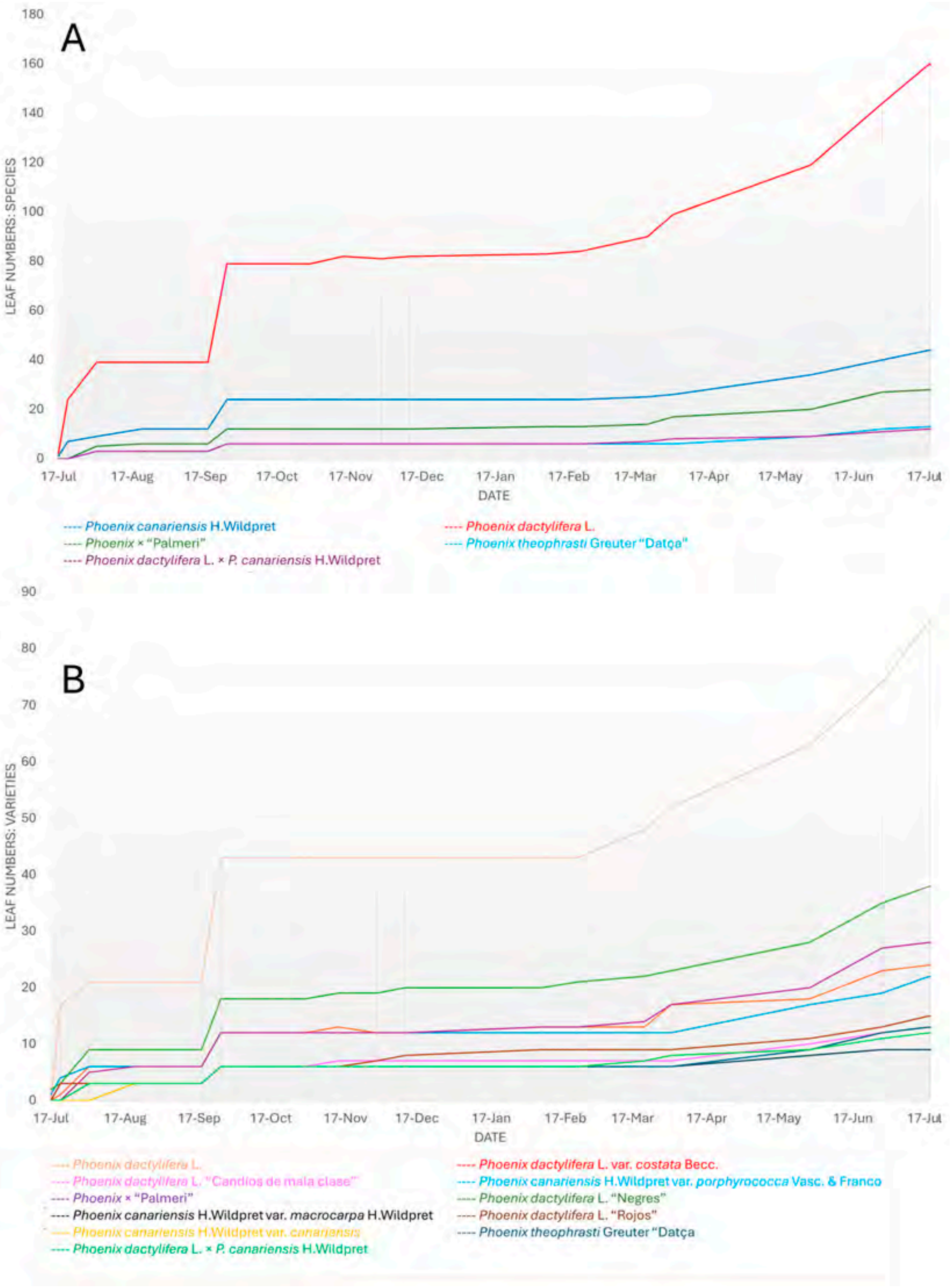

Figure 6. Leaf production dynamics in *Phoenix* spp. seedlings during the first 12 months post-germination, represented as total leaf count. (**A**) Total leaf production per species. The figure includes 42 of the 149 individuals germinated of *P. dactylifera*, 15 of 46 of *P. canariensis*, 6 of 16 of *P.* "Palmeri", 3 of 11 of *P. hybrida*, and 3 of 7 of *P. theophrasti*. (**B**) Total leaf production per variety. The figure includes 21 of the 72 individuals that germinated *P. dactylifera*. s.l., 6 of 31 of *P. dactylifera* "Negres", 9 of 28 of *P. canariensis* var. *porphyrococca*, 6 of 25 of *P dactylifera* var. *costata*, 6 of 16 of *P.* "Palmeri", 3 of 14 of *P. canariensis* var. *macrocarpa*, 3 of 13 of *P. dactylifera* "Candios de mala clase", 3 of 11 of *P. dactylifera* × *P. canariensis*, 6 of 8 of *P. dactylifera* "Rojos", 3 of 7 of *P. theophrasti* "Datça", and 3 of 4 of *P. canariensis* var. *canariensis*.

Species vs. Varieties—Key Insights:

The basic leaf emergence pattern, characterized by a September flush, winter dormancy, and spring flush, appeared genetically conserved across the *Phoenix* genus. However, the magnitude and duration of these flushes varied substantially between species and varieties. *P. dactylifera* genetics likely conferred greater leaf production potential regardless of variety.

All *Phoenix* palms responded to the same seasonal cues, albeit with varying sensitivity. The universal September flush suggested a response to late summer conditions, while the consistent winter dormancy indicated temperature or photoperiod sensitivity across the genus.

Hybrid vigor was not strongly evident in leaf production metrics in the case of *P.* × *hybrida*, suggesting that breeding for increased leaf production should focus on *P. dactylifera* genetics (Figure 7).

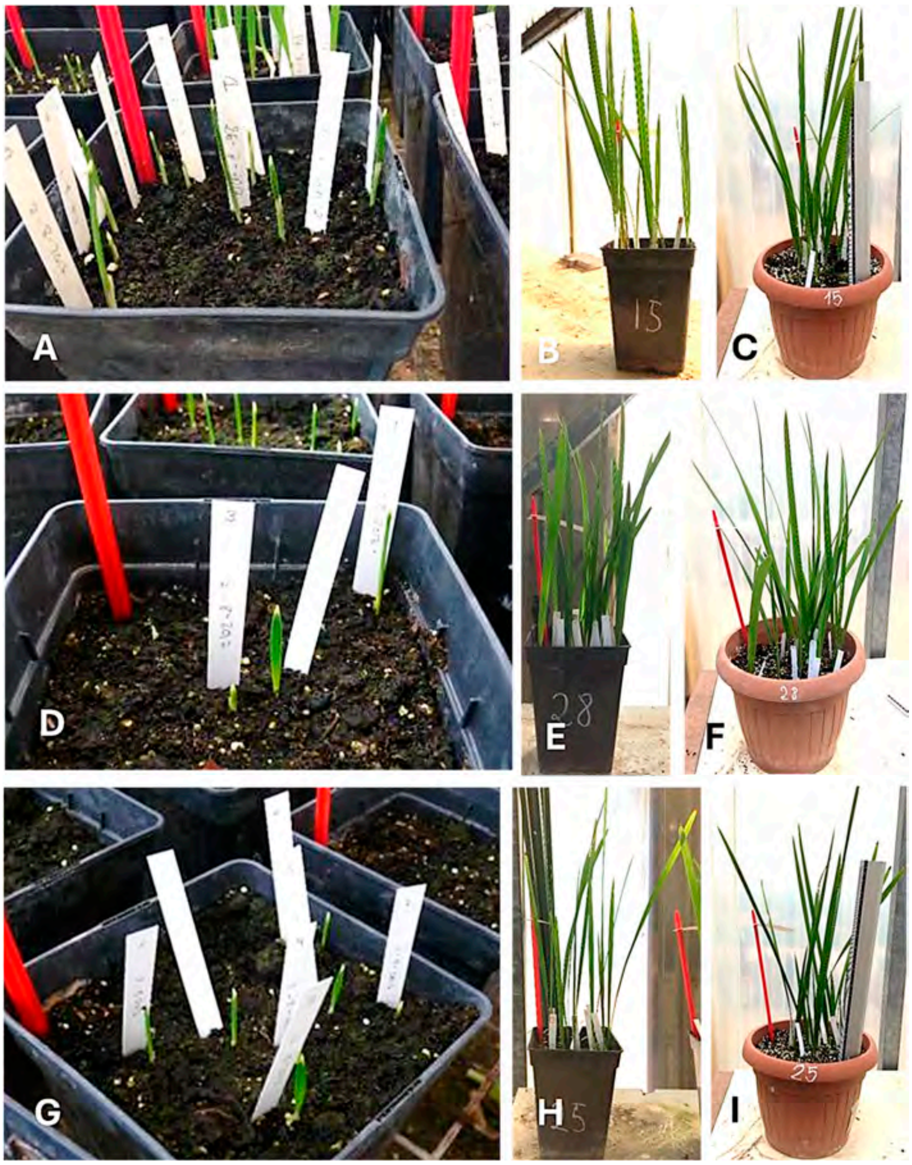

Figure 7. Leaf production dynamics in *Phoenix* spp. seedlings over the first 12 months. (**A**–**C**) E160-1486 *P. dactylifera* L., (**D**–**F**) E160-1494 *P.* × *hybrida* André (*P. dactylifera* L. × *P. canariensis* H. Wildpret), and (**G**–**I**) E160-1492 *P. theophrasti* Greuter "Datça". (**A**,**D**,**G**) 7-August-2017, (**B**,**E**,**H**) 7-February-2018, and (**C**,**F**,**I**) 30-May-2018. The black, square pots (**A**,**B**,**D**,**E**,**G**,**H**) were used in the first phase, germination and growth, until March 2018. In April 2018, they were transplanted into larger, round, brown pots (**C**,**F**,**I**).

Growth strategy differences were notable between species. *Phoenix dactylifera* demonstrated an "opportunistic" strategy with intense periodic leaf flushes, while *P. canariensis* showed a more "conservative" approach with steady, continuous leaf production. These strategies likely reflected adaptations to their native habitats.

Considering the mean number of leaves per individual, the analysis of key patterns and observations in *Phoenix* spp. seedlings also revealed the distinct growth phases and species-specific variations, offering insights into developmental biology and taxonomic relationships within the genus.

Growth Phases: Most taxa exhibited three distinct phases: initial emergence (Figures 6 and 7), a stable plateau period, and a final acceleration phase. The timing of these phases was relatively consistent across taxa, suggesting a conserved developmental program.

Species-Specific Patterns: *Phoenix dactylifera* varieties showed considerable variation. The "Negres" variety exhibited the most vigorous growth, reaching 6.33 leaves on average by the end, while the standard variety reached 4.05 leaves. In contrast, the "Rojos" variety showed remarkably slow development, producing only on average 2.50 leaves per individual. This suggested high intraspecific variability within *P. dactylifera*.

Phoenix canariensis varieties generally demonstrated slower leaf emergence, with all varieties having fewer leaves by the end compared with most *P. dactylifera* varieties. The variety *porphyrococca* showed particularly slow development, reaching only 2.44 leaves on average. The species average was 2.93 leaves by the final time point.

Hybrid Performance: *Phoenix* × "Palmeri" exhibited vigorous growth, reaching on average 4.67 leaves, suggesting possible heterosis or hybrid vigor. The *Phoenix dactylifera* × *P. canariensis* hybrid showed intermediate performance, with 4.00 leaves, falling between the two parent species, but it did not reach 5 leaves like its parents and was somewhat slower. The speed of its growth was more similar to *P. canariensis* since it was March when its third leaf developed, and in June its fourth final leaf appeared.

Initial Emergence Timing: *P. dactylifera* "Negres" uniquely started with a mean of 0.33 leaves at the first point, indicating earlier germination. In contrast, *P. canariensis* var. *canariensis* and *P. theophrasti* "Datça" showed delayed initial emergence.

Stability Periods: Most taxa demonstrated extended plateaus where the leaf number remained constant. The *Phoenix dactylifera* "Negres" showed the most continuous growth with fewer plateaus.

Final Growth Acceleration: All taxa exhibited accelerated leaf production in the final three to four time points, with the magnitude of this acceleration varying dramatically between taxa (Figure 7).

Taxonomic Significance: The analysis highlighted remarkable intraspecific variation within *Phoenix dactylifera*, with the final mean leaf counts ranging from 2.50 to 6.33 among its varieties, suggesting high genetic diversity or plasticity. Despite differences in growth rate, the overall pattern of initial emergence followed by a plateau and final acceleration was conserved across taxa, indicating a shared developmental program.

Hybrid performance suggested that leaf emergence traits may be inherited differently, with some hybrids showing intermediate inheritance and others possibly exhibiting heterosis. The patterns supported current taxonomic relationships, with varieties within species showing more similar patterns than between species, although notable exceptions existed, such as *P. dactylifera* "Rojos," which behaved more like a *P. canariensis* variety.

This analysis provides valuable insights into both developmental biology and taxonomic relationships within the *Phoenix* genus, highlighting the importance of seedling development traits in understanding palm evolution and classification.

3.3.2. Leaf Length

The growth patterns of *Phoenix* spp. seedlings were monitored over a 12-month period, revealing distinct variations among species and seasonal influences (Figure 8). *Phoenix dactylifera* varieties, notably "Rojos", exhibited the most vigorous growth, while *Phoenix theophrasti* "Datça" achieved the highest leaf length of 48 cm in April 2018. Conversely, *Phoenix canariensis* varieties showed slower but steady growth.

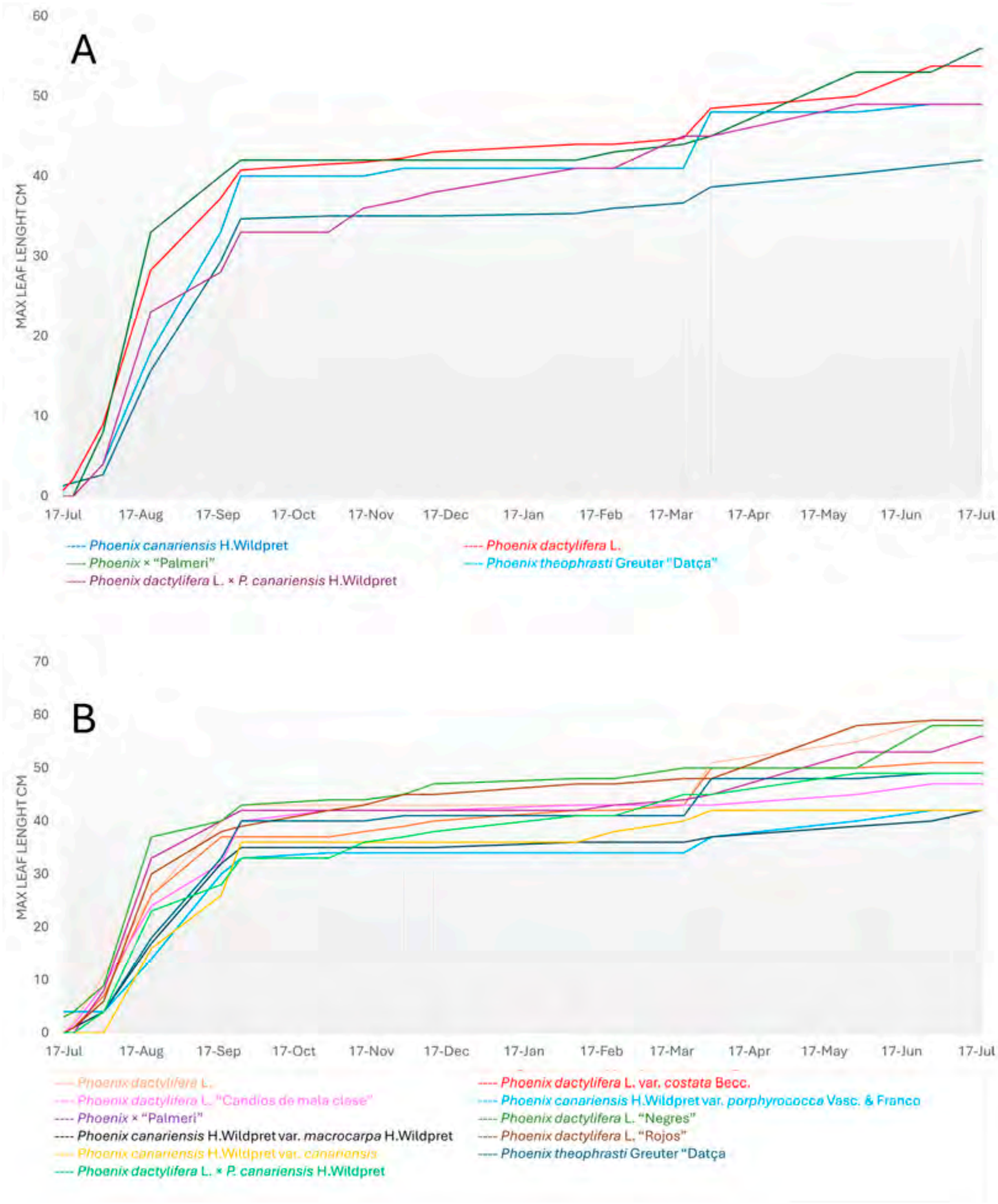

Figure 8. Temporal patterns of leaf development in *Phoenix* spp. seedlings during the initial 12-month post-germination period: maximum leaf length. (**A**) Maximum length per species. The figure includes 42 of the 149 individuals germinated of *P. dactylifera*, 15 of 46 of *P. canariensis*, 6 of 16 of *P. "Palmeri"*, 3 of 11 of *P. hybrida*, and 3 of 7 of *P. theophrasti*. (**B**) Maximum length per variety. The figure includes 21 of the 72 individuals that germinated *P. dactylifera*. s.l., 6 of 31 of *P. dactylifera* "Negres", 9 of 28 of *P. canariensis* var. *porphyrococca*, 6 of 25 of *P dactylifera* var. *costata*, 6 of 16 of *P.* "Palmeri", 3 of 14 of *P. canariensis* var. *macrocarpa*, 3 of 13 of *P. dactylifera* "Candios de mala clase", 3 of 11 of *P. dactylifera* × *P. canariensis*, 6 of 8 of *P. dactylifera* "Rojos", 3 of 7 of *P. theophrasti* "Datça", and 3 of 4 of *P. canariensis* var. *canariensis*.

Seasonal effects significantly influenced the growth patterns, with a noticeable slowdown during winter (December–February) and a growth surge in spring (March–April) (Figure 8). Some species exhibited slight decreases in average leaf length due to novel leaf emergence. This led us to instead represent the maximum length of the leaves in Figure 8.

By the final measurement on July 19th of the second year, most species reached mean leaf lengths between 28 and 38 cm, with *Phoenix dactylifera* "Rojos" and *Phoenix* "Palmeri" achieving the greatest average lengths. But this peak of leaf length was shared also with other *P. dactylifera* s.l. samples and the *P. dactylifera* "Negres" cultivar (Figure 8B). On average, the fastest-growing varieties were *P. dactylifera* "Rojos", *P.* "Palmeri," and *P. theophrasti* "Datça," while the slowest were *P. canariensis* var. *porphyrococca* and the hybrid *P. dactylifera* × *P. canariensis* (*P.* × *hybrida*).

The data suggested that different *Phoenix* species had distinctive growth patterns, which could inform selection for landscaping or agriculture. The hybrid did not exhibit hybrid vigor for leaf length, and there may be optimal times for interventions based on observed growth phases.

Key growth patterns included a rapid establishment phase from July to September, a winter plateau from November to February, a spring growth surge from March to April, and a maturation phase from May to July of the second year. The top performers in final leaf length were *Phoenix dactylifera* "Rojos" (mean 37.67 cm and maximum 59 cm), *P.* × "Palmeri" (mean 36.86 cm and maximum 56 cm), and *P. dactylifera* "Negres" (mean 33.63 cm and maximum 58 cm), while slower growers included *P. canariensis* var. *porphyrococca* (mean 26.82 cm and maximum 42 cm) and the hybrid (mean 28.08 cm and maximum 49 cm). Overall, *P. dactylifera* varieties achieved greater leaf lengths than *P. canariensis* varieties, with the hybrid showing intermediate performance.

4. Discussion

The diaspores of most palm species have morphophysiological dormancy. Date palm seedlings exhibit a "remote-tubular" germination pattern. The embryonic axis within the cotyledonary sheath extends downward via positive geotropism, allowing the seedling to develop at a distance from the seed. The persistent radicle breaks through the cotyledonary base, while the plumule emerges from the sheath's cleft or ligular extension. This remote germination strategy relocates the seedling from the original seed location [40–42].

Seed storage behavior can be orthodox or non-orthodox (intermediate or recalcitrant) [5–10,28]. We identified two distinct behavioral patterns regarding the influence of storage conditions involving seed desiccation and preservation at low temperatures, although above freezing, in the successful germination of seeds. The "tropical" group of species from the Indian subcontinent and Southeast Asia appeared unable to tolerate these storage conditions, rapidly losing germination capacity, likely due to their recalcitrant nature. This coincides with the generally accepted view that recalcitrance is more common in tropical and subtropical regions, particularly in humid broadleaved forests [14,15]. "Recalcitrant" seeds are desiccation intolerant. They are highly hydrated at shedding and do not survive drying below a moisture content between 30 and 65% depending on the species [7,43].

This finding is particularly relevant for the international seed trade as these species should ideally be sown from freshly harvested fruits. In contrast, the "Mediterranean-Saharan" group, broadly defined, includes species such as *Phoenix dactylifera* L., *P. canariensis* H. Wildpret, and *P. theophrasti* W. Greuter, whose seeds exhibit an apparently orthodox behavior. This, again, coincides with the generally accepted view that orthodox seeds predominate in temperate regions, arid environments, and dry forests [44,45]. Seeds that have better protection against damage that occurs under dry conditions survive longer;

hence, seed longevity is a manifestation of desiccation tolerance and is conventionally treated as a quantitative trait [28,46]. Obviously, other factors such as the degree of maturity of the fruit must be considered. In the case of *P. canariensis* it has been found that the best percentages of gemination are obtained from fully ripe fruits and under temperatures ranging between 20 and 30 °C and above [47]. Pre-treatments involving immersion in water at different temperatures can also improve germination rates [48]. In our experiment we worked with seeds of different species and varieties under uniform conditions without pre-treatment.

Archival botanical repositories, historical herbaria, and archaeological assemblages have yielded viable propagules with remarkable longevity, facilitating the regeneration of extinct germplasm and the restoration of extirpated taxa [49]. Documentary evidence provides the most robust validation of seed longevity, as exemplified by three notable cases: *Vachellia farnesiana* (L.) Wight & Arn. (*Acacia farnesiana* L.) and *Acacia melanoxylon* R.Br. collected in Egypt in 1856 and deposited in the Swedish Museum of Cultural History, which germinated after 151 years of storage; *Albizia julibrissin* Durazz. specimens, collected in 1793, which exhibited germination following inadvertent hydration during the British Museum's aerial bombardment of 1940; and *Nelumbium* specimens, originally accessioned in 1705 within the Hans Sloane collection at the British Museum, which demonstrated viability upon testing in 1942. However, seed age determination becomes substantially more problematic when derived from archaeological or geological contexts as both the absolute chronology of cultural or geological events may be imprecise and the temporal relationship between seeds and their encompassing matrix cannot always be definitively established [49–54].

However, from archaeological excavations in the Judean desert (1963–1991), 32 preserved date seeds from Masada, Qumran, Wadi Makukh, and Wadi Kelt sites were cultivated at Kibbutz Ketura. Six seeds were successfully germinated and named "Adam" (Masada), "Jonah", "Uriel", "Boaz", "Judith" (Qumran), and "Hannah" (Wadi Makukh) (Table 2). Radiocarbon dating was performed on seed shell fragments adhering to the seedlings' rootlets, including the previously germinated "Methuselah". After adjusting for modern carbon contamination (2–3%), the chronological distribution showed Methuselah, Hannah, and Adam (first to fourth centuries BCE), Judith and Boaz (mid-second century BCE to mid-first century CE), and Uriel and Jonah (first to second centuries CE) [34,35].

Table 2 provides a comprehensive overview of germination data for seeds of various date palm (*Phoenix*) species under different storage conditions and ages. The analysis reveals several key insights.

Ancient date palm seeds (*Phoenix dactylifera*) were discovered in archaeological sites in Israel, specifically Masada, Wadi Makukh, and Qumran. These seeds were approximately 1900–2200 years old. Remarkably, these ancient seeds exhibited a germination rate of around 19%, demonstrating their ability to retain viability over millennia under natural dry conditions.

In contrast, 144-year-old Kew Garden seeds, which included multiple varieties of *Phoenix dactylifera* collected from Baghdad in 1873, showed a 0% germination rate. These seeds were stored in sealed glass jars and later in acid-free boxes at approximately 16 °C at Kew Gardens, indicating a complete loss of viability under these conditions (Table 2).

Modern storage methods have yielded more promising results. Recent *Phoenix dactylifera* seeds, aged 9–11 years, exhibited an 88% germination rate when dried at 15% relative humidity and stored at −20 °C. Desiccated seeds stored at 5 °C showed a germination rate ranging from 47% to 87%. Similarly, *Phoenix canariensis* varieties stored for 2–17 years demonstrated variable germination rates, ranging from 52% to 93%. The best results were achieved through desiccated storage at 5 °C and low-humidity freezer storage.

Table 2. Longevity of viable *Phoenix* sp. seeds: Documented germination success following extended preservation.

Species	Varieties	Storage Conditions	Germination Percentage	Age of the Seeds (Years)	Refs
Phoenix dactylifera	"Methuselah" and "Hannah"	Dry archaeological, Masada	c. 19%	c. 2200	1,2
Phoenix dactylifera	"Adam"	Dry archaeological, Wadi Makukh	c. 19%	c. 2200	1
Phoenix dactylifera	"Judith" and "Boaz"	Dry archaeological, Qumran	c. 19%	c. 2000	1
Phoenix dactylifera	"Uriel" and "Jonah"	Dry archaeological, Qumran	c. 19%	c. 1900	1
Phoenix dactylifera	Baghdad, 1873, 35,988 ("Drah Subbah")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 35,990 ("Zadie")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 35,991 ("Brem")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 35,992 ("Makawieh Eshgar")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 35,993 ("Etchrisieh")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 36,006 ("Tiburzel")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 36,007 ("Sin Mufta")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 36,008 ("Khaderawieh")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 36,011 ("Makawieh Ahmur")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 36,012 ("El Washa")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 36,021 ("Sukri")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 36,024 ("Bedraieh")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 36,025 ("Khustawieh")	Sealed glass jars and later acid-free card boxes, at c. 16 °C, at Kew	0%	144	4,5
Phoenix dactylifera	Baghdad, 1873, 35,988 ("Drah Subbah")	Sealed glass jars and later acid-free card boxes, at c. 16 °C	0%	144	4,5
Phoenix dactylifera	Balqa, Jordan, 2003	Dried at 15% [RH], stored at −20 °C	88%	11	4
Phoenix dactylifera	"Negres"	Desiccated, stored at 5 °C	47–87%	9	3
Phoenix canariensis	var. *porphyrococca* Vasc. & Franco	Desiccated, stored at 5 °C	93%	7	3
Phoenix dactylifera	var. *costata* Becc.	Desiccated, stored at 5 °C	93%	6	3
Phoenix canariensis	var. *porphyrococca* Vasc. & Franco	Desiccated, stored at 5 °C	93%	4	3
Phoenix. canariensis		Dried at 15% [RH], stored at −20 °C	72%	17	6
Phoenix. canariensis		Dried at 15% [RH], stored at −20 °C	52%	6	6
Phoenix. canariensis		Dried at 15% [RH], stored at −20 °C	72%	2	6

[1] [35]; [2] [34]; [3] This research; [4] [49]; [5] [54]; [6] [55]. Abbreviation: RH—relative humidity.

The key findings from this analysis underscore the remarkable longevity potential of date palm seeds. Ancient seeds can retain viability for millennia under natural dry conditions, while modern cold storage methods with controlled humidity are effective for medium-term preservation. However, the 144-year-old seeds stored at moderate temperatures completely lost viability, highlighting the critical role of storage temperature and low humidity in maintaining seed viability. These data emphasize the importance of proper storage conditions for the preservation of date palm seeds.

We must clearly distinguish between the concept of seed orthodoxy as it pertains to long-term storage in germplasm banks following seed desiccation and orthodoxy as verified by experimental desiccation with immediate germination testing. These results may not always align, as seen with *P. roebelenii* seeds, which in our experience at the germplasm bank did not withstand storage, although Beltrame et al. [56] classify them as physiologically orthodox; unfortunately, we did not have samples with enough seeds to include this species in our study. Davis and Pritchard [57] report *P. dactylifera* seeds as orthodox and those of *P. reclinata* as doubtfully orthodox.

The preservation of viable seeds has been proposed as a potential mechanism for the restoration of extinct plant species through the utilization of historical specimens maintained in herbaria and natural history collections. The theoretical framework for plant species resurrection postulates that viable propagules—specifically seeds or spores—preserved within herbarium voucher specimens of extinct taxa could potentially facilitate de-extinction events. This paradigm suggests that botanical extinction is not ultimately determined by the demise of the final living specimen but rather by the loss of viability in the terminal propagule. Currently, the primary constraint in implementing plant de-extinction protocols lies in the methodological limitations of germination and in vitro cultivation techniques. This challenge is particularly acute given the irreplaceable nature of diaspores conserved in herbarium specimens of extinct taxa, which precludes experimental optimization through iterative attempts [58]. This potential restoration methodology holds particular significance for agricultural sciences, specifically in cases where the extinct taxa represent domesticated crops or their wild progenitors with agronomic importance.

Our findings, despite temporal and taxonomic constraints, indicate that *Phoenix* taxa indigenous to Mediterranean and Saharan regions, notably *P. dactylifera* and related taxa, demonstrate remarkable desiccation tolerance in their seeds. The data suggest that long-term seed viability can be maintained under relatively moderate storage conditions. Consequently, the potential exists for the recovery of near-extinct taxa, such as *P. arabica* and *P. caespitosa*, through the utilization of seeds from preserved herbarium specimens.

However, samples of *Phoenix sylvestris*, *P. loureiroi*, and *P. rupicola*, aged between 1644 and 2773 days (Table 1), which failed to germinate in this study, had successfully germinated four to six years earlier. This suggests a loss of viability under relatively moderate storage conditions and indicates that these species may exhibit recalcitrant behavior.

5. Conclusions

Our study revealed significant differences in seed behavior and seedling development across *Phoenix* species. *P. dactylifera*, *P.* × “Palmeri”, and *P. canariensis* demonstrated orthodox seed storage behavior with the seed age having minimal impact on germination success, while *P. sylvestris*, *P. rupicola*, *P. pusilla*, and *P. loureiroi* exhibited potentially recalcitrant characteristics. Species identity and geographic origin proved substantially more influential than seed age in determining germination outcomes, with notable intraspecific variation observed. Seedling development followed a conserved seasonal pattern across all species (September flush, winter dormancy, and spring flush), although with marked differences in magnitude and duration, particularly among *P. dactylifera* varieties where “Negres” displayed superior vigor. These findings provide valuable guidance for ex situ germplasm conservation strategies, suggesting that orthodox-behaving *Phoenix* species can be effectively preserved through conventional seed banking, while potentially recalcitrant species require alternative conservation approaches. Additionally, the observed growth patterns inform cultivar selection for ornamental horticulture and breeding programs, particularly in regions with pronounced seasonal temperature fluctuations. Future research should explore the physiological and biochemical mechanisms underlying seed recalcitrance in certain *Phoenix* species, investigate potential dormancy in *P. dactylifera*, characterize metabolic changes during prolonged storage, and test germination and growth responses across broader genetic pools and environmental conditions.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/horticulturae11050537/s1: Table S1: *Phoenix* seed samples for the germination and early development study.

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