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Seed Germination of *Garberia heterophylla* (W. Bartram) Merr. & F. Harper, a Pollinator Plant with Ornamental Appeal

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Abstract: Seed propagation is the primary means of reproducing many native and endemic species, including garberia [*Garberia heterophylla* (W. Bartram) Merrill & F. Harper]. This attractive pollinator plant, native to Florida, is scarcely found in nursery production and largely unknown to the gardening community. To better understand the seed biology of garberia, a series of experiments were conducted to evaluate the effects of population on seed viability and germination response to four seasonal temperatures, as well as the effects of time on seed storability. Initial seed viability was 49% and 60% for Central and North Florida populations, respectively. Seeds germinated readily, indicating non-dormancy, with significant effects of population and temperature observed. Overall, on day 28, a greater germination proportion was observed from seeds collected from North Florida than Central Florida across temperatures, except for winter (11/22 °C), where responses were similar. The greatest germination proportion for seeds collected from North Florida was observed at 15/27 °C (fall) and 19/29 °C (spring), whereas the greatest germination from Central Florida was observed at 11/22 °C (winter), with the steepest decline observed at summer temperatures (24/33 °C). Further, it was observed that garberia seeds are intolerant of long-term storage, losing viability as early as 3 months under conventional cold or room temperature storage and decreasing substantially more after 6 months. These findings contribute to the overall understanding of the seed biology of underutilized species such as garberia, key to the development of efficient and reliable propagation systems for our nursery industry.

Keywords: Asteraceae; native plants; propagation; xeric species; seed storage

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1. Introduction

In response to the many positive attributes native species can bring to urban gardens [1,2], growth in consumer interest and demand for residential and commercial native landscaping is expected to continue in an upward trajectory [3]. In a 2023 survey, 50% of respondents agreed that native plants were very or extremely important to include in landscapes [4].

Consumers value native plants for their tolerance of local climate, resistance to drought [5,6], and ecological value [4,7]. There is evidence that native plants support a broad array of native pollinators [8–10] and other wildlife, with the percentage of native vegetation in urban spaces a strong predictor of abundance and diversity for bats,

native birds, and beetles [11]. Other studies have highlighted the positive impact of native landscapes in providing habitat for migratory bird species, hosting a broader range of foraging and feeding behavior when compared to conventional landscapes [12]. Despite the overwhelming evidence of the beneficial role natives play in landscapes, they remain grossly underutilized in commercial and residential landscapes, comprising only 10% of the ornamental plant sales in the U.S. [13]. A 2022 survey of homeowners across four regions of the continental U.S. found that 58% of respondents reported purchasing native plants in the prior year [14]. Among respondents identified as "native-averse", a lack of availability of native plants was frequently cited as a reason to choose non-native species and cultivars for their landscapes. The consensus that diverse, native plant availability is a bottleneck for expanded sales is consistent with estimates revealing only 26% of native, vascular plant species in the U.S. are commercially available [15]. As a result, consumers often have a wider selection of forms, textures, and colors among the many non-native species and cultivars readily available in retail nurseries.

To address this need, efforts are underway to support a widely available and diverse palette of native plants for commercial-scale production [5] and to develop efficient propagation systems for novel species [16]. Propagation practices for native species, such as squareflower [*Paronychia erecta* (Chapm.) Shinners], coastalplain honeycombhead [*Balduina angustifolia* (Pursh) BL Robl), wireweeds (*Polygonella* spp.)], goldenasters [*Chrysopsis* spp. (Nutt.) Elliott] woody goldenrod [*Chrysoma pauciflosculosa* (Michx.) Greene], wild coffees (*Psychotria* spp.), sweet acacia [*Vachellia farnesiana* (L.) Wight & Arn var. *Farnesiana*], and gopher apple [*Geobalanus oblongifolius* (Michx.) Small], have been explored to optimize the year-round production of natives by seed [16,17], cuttings [18–20], and tissue culture [21].

One such species also meriting consideration for wider production and landscape use is garberia [*Garberia heterophylla* (W. Bartram) Merrill & F. Harper], a low-growing, woody shrub belonging to a monotypic genus of Asteraceae (Figure 1A). This native species is naturally found in xeric scrub ecoregions of oak hammock and pine flatwood plant communities in Florida [22]. A pollinator plant, garberia attracts a range of butterflies, bees, and moths [23]. Endemic to North and Central Florida, garberia spans USDA cold hardiness zones 9A, 9B, and 10A [22].

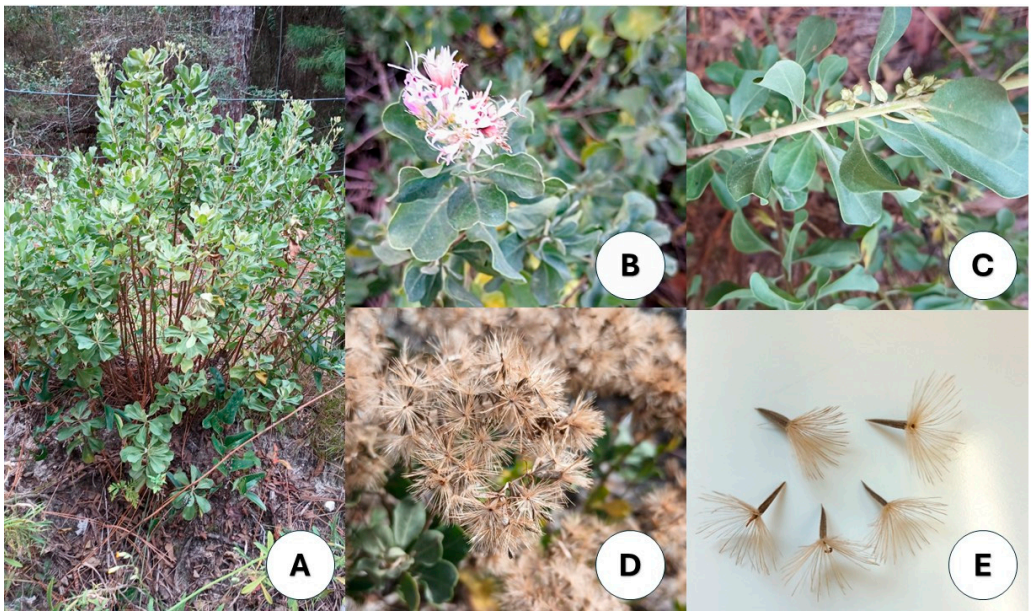


Figure 1. General appearance of *Garberia heterophylla* including its (**A**) growth habit; (**B**) inflorescence; (**C**) leaf arrangement; (**D**) infructescence; and (**E**) cypselae.

Garberia is best known for its showy inflorescences in late fall, which overwhelm the small plant in a stunning display, held in broad, flat clusters above the foliage (Figure 1B). Soft pink to lavender tubular disk florets terminate in sharp-cornered geometric stars at their apex, with slender stylets extending and twisting above for additional height and visual interest. Obovate leaves are gray-green with a pubescent and glandular surface, sometimes with a retuse apex, with two-ranked alternate phyllotaxy (Figure 1C). The dense and distinctive foliage presents year-round visual interest, offering texture and color variety to landscapes. The inflorescence is followed by the infructescence (Figure 1D), which holds dense clusters of cypselae, fringed with pappi that allow for wind dispersal (Figure 1E).

Despite its many desirable traits, this species is carried by less than a handful of nurseries in Florida [24], and its seed viability and germination requirements are largely unknown. Thus, the overall goal of this study was to develop optimal seed propagation practices for this underutilized species. The specific objectives were to (1) determine the influence of population (seed origin) and temperature on seed viability and germination and (2) assess seed storage longevity over time.

2. Materials and Methods

2.1. Seed Collection and Site Descriptions

Mature cypselae (hereafter referred to as "seeds") were collected from two natural populations situated on the periphery of Chiappini Farm Native Nursery (North Florida, USDA cold hardiness zone 9a) and the Natives Nursery (Central Florida, USDA cold hardiness zone 9b) within two weeks of each other in mid- to late December 2023. The central population (Davenport, FL, USA) can be described as a sand pine and oak scrub habitat with white sandy soils, full sun to part shade, growing alongside native plants such as coastal honeycombhead, Georgia calamint (*Clinopodium georgianum* R.M.Harper), saw palmetto [*Serenoa repens* (W. Bartram) Small], and scrub mint (*Conradina canescens* A.Gray). The northcentral population (Hawthorne, FL, USA) can be described as mixed hardwood and pine situated along a dirt road and fence line with sandy soils, full sun to part shade, growing alongside coral bean (*Erythrina herbacea* L.), Elliot's lovegrass (*Eragrostis elliottii* S. Watson), beautyberry (*Callicarpa americana* L.), yaupon (*Ilex vomitoria* Aiton), and coontie (*Zamia integrifolia* L.f.). Both populations were naturally established, absent of fertilizer or irrigation inputs, having at least 20 plants in each area, and used as a reliable stock plant seed source for their respective nurseries. Upon collection, seeds were stored at room temperature (25.5 $\pm$ 2 °C) on a lab bench in paper bags for two weeks prior to experimentation.

2.2. Pre-Germination Viability and Imaging

Ten representative seeds from each population (Central and North Florida) were measured using a digital caliper and photographed. Next, a subsample of seeds from each population was sent to an independent seed testing facility to assess initial pre-germination seed viability and embryo fill (US Forest Service National Seed Laboratory, Dry Branch, GA, USA). First, seeds were non-destructively imaged using an UltraFocus X-ray system equipped with the Vision software (Faxitron® Bioptics, LLC, Tucson, AZ, USA) to determine embryo development. Then, two replicates of 100 seeds per population were cut laterally, removing the distal end of the cotyledons, and stained overnight at 37 °C in a 1.0% TZ (2,3,5-triphenyl-2H-tetrazolium chloride) solution in accordance with the Association of Official Seeds Analysts (AOSA) rules for TZ testing of Asteraceae [25]. Seeds were considered viable when firm embryos stained evenly red under 10× magnification.

2.3. Seed Germination

Seeds from each population were visually sorted, removing debris and damaged or undersized material; surface sterilized with 10% bleach solution (Clorox®; 0.75% NaClO a.i., The Clorox Company, Oakland, CA, USA) for 5 min; and then triple rinsed with sterile deionized (DI) water. Four replications of 100 seeds were placed in 10.9 × 10.9 cm transparent polystyrene germination boxes with lids (Hoffman Manufacturing, Albany, OR, USA) containing two sheets of 10.16 × 10.16 cm white blotter paper and one sheet of 10.16 × 10.16 cm unbleached crepe germination paper (Hoffman Manufacturing, Albany, OR, USA). The germination boxes were moistened with 20 mL of sterile DI water and then placed in light- and temperature-controlled incubators (Percival I30VL, Percival Scientific, Perry, IA, USA) set at 11/22 °C (winter), 15/27 °C (fall), 19/29 °C (spring), and 24/33 °C (summer). These temperatures were selected to mimic local seasonal temperatures, consistent with other studies exploring Florida natives [19,26]. Light was provided by cool, white, fluorescent bulbs providing an average of 40 μmol·m^{-2} s^{-1} at each shelf level for 12 h, followed by 12 h of darkness. Germination boxes were opened only as needed to provide moisture and prevent seeds from desiccating. Germination progress was recorded at the first sign of radical emergence every three days. At the end of a 28-day period, the final germination percentage (FGP) and inflection point ($T50_{FG}$, days to 50% of FGP) were determined for each treatment.

2.4. Seed Storability

The remainder of the seeds collected from the Central Florida population were divided and held in paper bags, with one set placed on a bench shelf in the laboratory at room temperature (25.5 ± 2 °C) and another set placed in a standard refrigerator (4.5 ± 0.5 °C). These conditions were chosen to mimic practices typically employed by small-scale native nurseries. After 0-, 3-, and 6-month storage intervals, a subsample of 50 seeds was removed from each treatment and placed in four germination boxes lined with moistened blotter and crepe germination paper as previously described. Seeds were germinated in an incubator set to 19/29 °C (spring), as this temperature was pre-determined to be most suitable for this species. Germination was recorded every 3 days with final germination recorded after 28 days.

2.5. Experimental Design and Statistical Analysis

Experiments utilized a modified randomized block design, with each of the four shelves of each incubator considered a pseudo-block. Seed germination data were analyzed using Generalized Non-Linear Model procedures as implemented in SAS® PROC NLMIXED (SAS/STAT 15.2, SAS Institute, Cary, NC, USA) through a 3-parameter logistic growth model:

$$\text{Proportion germinated} = \frac{c}{(1 + Exp(-a \cdot (DAS - b)))}$$

where a = growth rate, b = days to half max germination, c = asymptotic final germination, and DAS = days after the start of the experiment. Storage condition × storage duration daily means were predicted from the fitted curve and plotted. Storage condition × storage duration regression parameters (maximum estimated germination and days to half-max germination) were compared using simple pair-wise t-tests ($\alpha = 0.05$).

3. Results

3.1. Seed Size, Pre-Germination Viability, and Visual Embryo Presence

On average, seeds collected from the North Florida population were larger (1.2× the length) than seeds collected from Central Florida (Figure 2). Initial pre-germination tetrazolium tests and X-ray analysis revealed seed viabilities were 49% and 60% for the Central and North Florida populations, respectively, with fully developed embryos present in 62% of the seeds from each population.



Figure 2. Representative image taken at 5× magnification showing the size of garberia seeds collected from North and Central Florida populations. Means of seed length were averaged across 10 replications.

3.2. Germination Response

The seeds germinated readily, as early as 3 days after placement, indicating a lack of dormancy (Figure 3). Within the first week, 25.2 to 48.6% germination was achieved among temperatures and populations. Germination was completed between 14–21 days, ranging from 37.5% to 61.5% on day 28.

The greatest final germination of seeds collected from Central Florida occurred in the winter temperature (59.5%), followed by spring (56.5%), fall (52.0%), and then summer (37.5%). For seeds collected from North Florida, the greatest final germination occurred in the summer and fall temperatures (61.0–61.5%) compared to the winter and spring temperatures (59.5–59.0%) (Figure 4). Overall, seeds collected in North Florida had a more consistent germination proportion across the temperature treatments (Figures 3 and 4).

The germination speed was also influenced by population and temperature treatments (Figure 5). A population effect was only observed for the inflection point (T50FG) of the winter treatment, where Central Florida seeds had an earlier inflection point (8.9 days) than North Florida seeds (10.2 days). For both populations, seeds germinated earliest in the summer temperature (3.2 days) and then in spring (4.2 days) and fall (5.3 days).

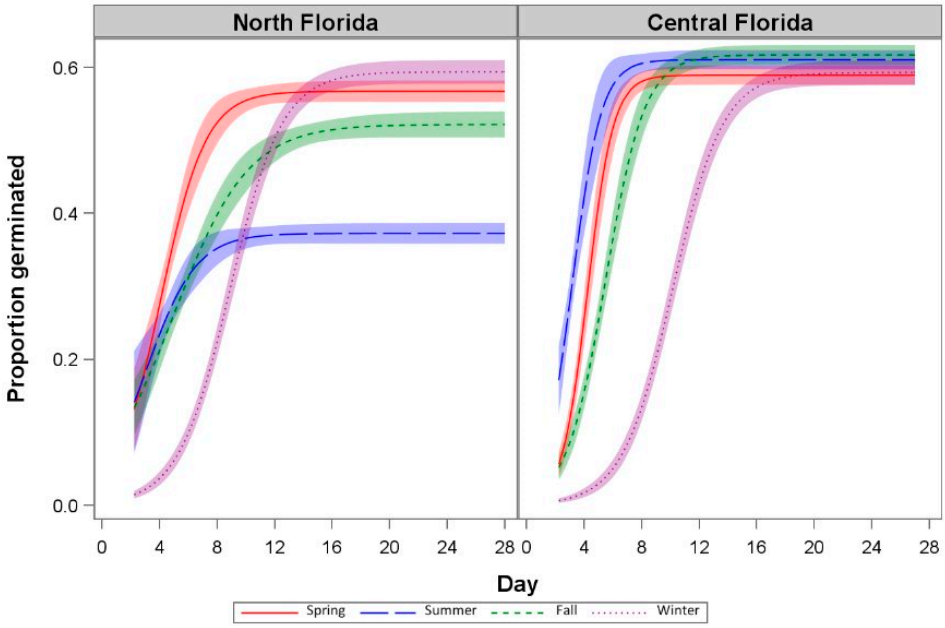


Figure 3. Germination of garberia seed from Central Florida (**left**) and North Florida (**right**) over 28 days across four temperatures: 19/29 °C (spring); 24/33 °C (summer); 15/27 °C (fall); and 11/22 °C (winter). Predicted germination proportion (symbols), fitted non-linear regression line (line), and 95% CI for the predicted mean response (colored areas) are shown.

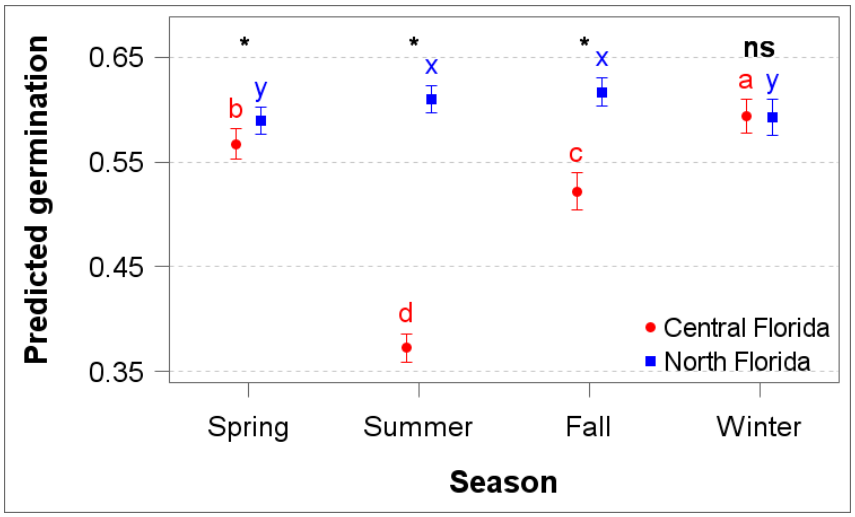


Figure 4. Final germination proportion after 28 days for garberia as predicted by a logistic growth model for seed collected in Central Florida (red) and North Florida (blue) across four temperatures: 19/29 °C (spring); 24/33 °C (summer); 15/27 °C (fall); and 11/22 °C (winter). The colored letters indicate statistically meaningful differences between seasons within a location ($\alpha = 0.05$). The * symbol indicates statistically meaningful differences between locations within a season ($\alpha = 0.05$); ns = nonsignificant.

3.3. Seed Storability

A significant effect for each storage duration (3 and 6 months) was observed for the germination of seeds maintained in cold and room temperature storage conditions (Figures 6 and 7). After 3 months of cold storage, predicted germination decreased by 15.6% when compared to the predicted germination of non-stored seeds. After an additional 3 months of cold storage (6 months total storage), predicted germination decreased even more dramatically by 52.0% when compared to 3 months of storage and 59.5% when compared to 0 months (non-stored seed). Likewise, a similar trend was observed for seeds

stored at room temperature (Figure 7), with significant responses observed between 0-, 3-, and 6-month intervals displayed by a 16.0% reduction in predicted germination between 0 and 3 months of storage, a 57.6% reduction in predicted germination between 3 and 6 months, and a 64.6% reduction in predicted germination between 0 and 6 months.

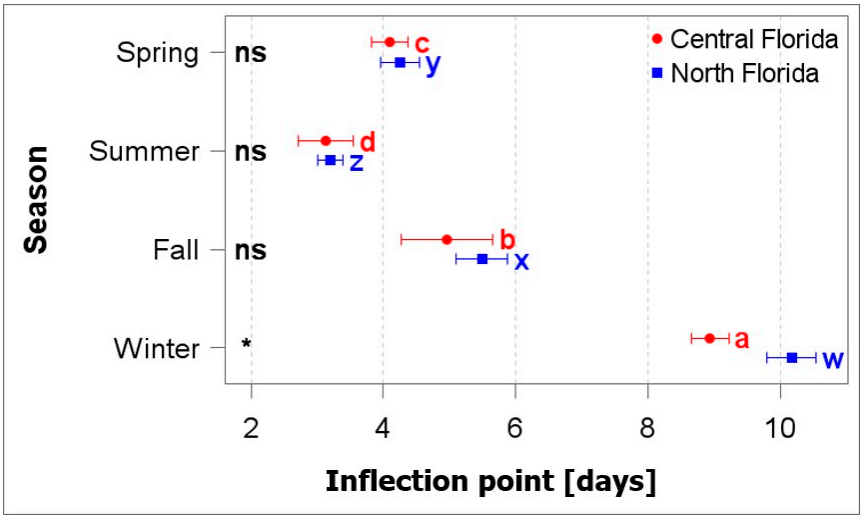


Figure 5. Germination speed for garberia seed collected in Central Florida (red) and North Florida (blue) across four temperatures: 19/29 °C (spring); 24/33 °C (summer); 15/27 °C (fall); and 11/22 °C (winter). The inflection point in this logistic growth model represents the days to half-maximum germination. Means ± 95% confidence intervals are presented. Within each population, the different letters indicate statistically meaningful differences between seasons ($\alpha = 0.05$). Within each season, the * symbol indicates statistically meaningful differences between locations ($\alpha = 0.05$); ns = nonsignificant.

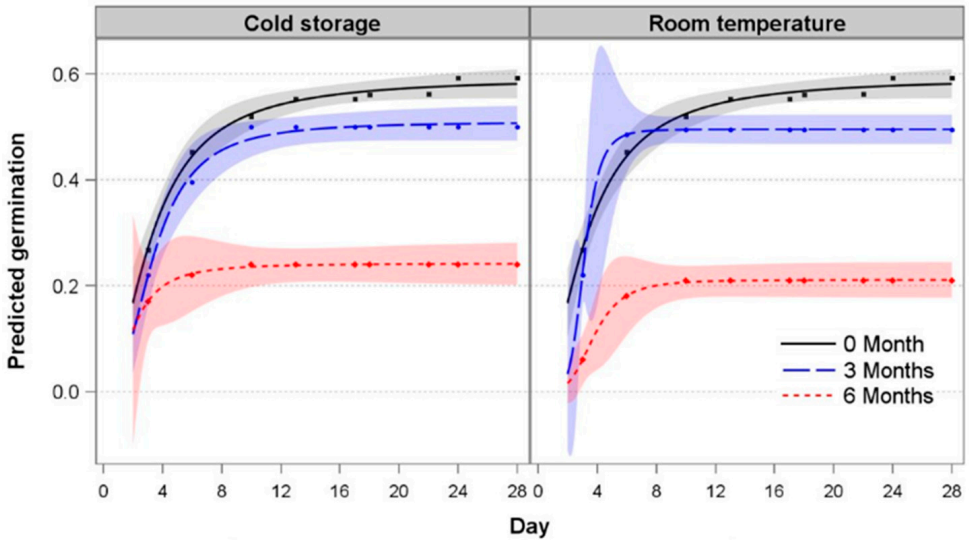


Figure 6. Germination response of garberia seed (Central Florida population) stored at room temperature (25.5 ± 2 °C) and in refrigerated conditions (4 °C) for 0-, 3-, and 6-month intervals. Predicted germination proportion (symbols), fitted non-linear regression line, and 95% CI for the predicted mean response (colored areas) are shown.

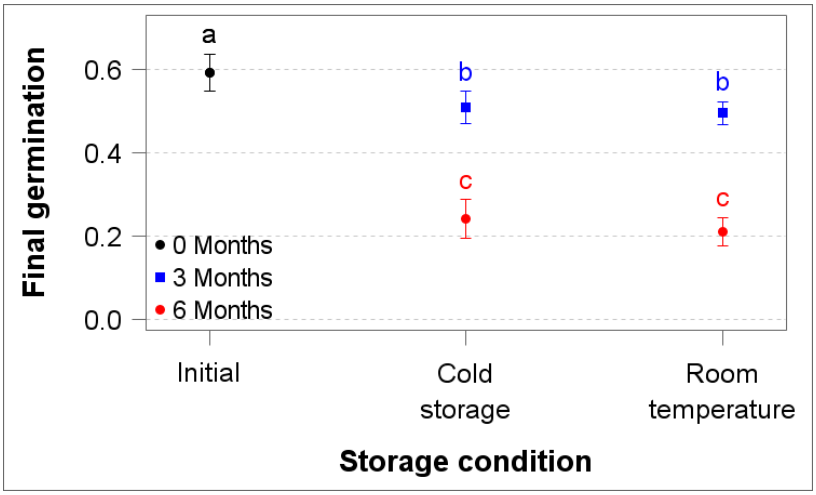


Figure 7. Final germination proportion of garberia as predicted by a logistic growth model for seed (Central Florida population) stored at room temperature (25.5 ± 2 °C) or in refrigerated conditions (4.0 ± 0.5 °C) for 0-, 3-, and 6-month intervals. Seeds germinated in the spring incubator (19/29 °C) for 28 days. The colored letters indicate statistically meaningful differences between storage durations ($\alpha = 0.05$).

4. Discussion

Understanding the seed biology of native species allows nursery growers to determine the optimal sowing rate and to predict how germination responses may be influenced by the collection site (seed provenance) and season (temperature). Likewise, knowledge of a species' ability to tolerate seed storage can help guide decisions regarding collection times and production scheduling. For threatened native species of ecological value like garberia [22], this work provides foundational knowledge that can be used to promote its use in restoration and other conservation efforts.

4.1. Initial Seed Fill and Viability

Our results showed that up to 40% of garberia seeds lacked embryo fill upon collection. Factors contributing to empty seeds include deterioration of the zygote and embryotic death [27], mutation [28,29], the degeneration of the unfertilized ovule [30,31], and insect feeding [32,33]. In our study, garberia seeds were collected from robust populations, and at an ideal time soon before their natural seed dispersal. This rules out the likelihood of inbreeding depression found in small or impacted populations [34] and inadequate harvest maturity [35]. The low proportion of seed fill could be intrinsic to this species, a trait that some studies have found to be an ecological benefit associated with reduced seed predation [36] or a consequence of age-related plant decline in unmanaged populations [37]. Others have reported the low seed viability (45–56%) of other wildflower species, such as seaside heliotrope (*Heliotropium curassavicum* L.), coastalplain honeycombhead, and bush goldenrod [*Chrysoma pauciflosculosa* (Michx.) Greene] [38]. These results suggest seed handling provisions may be beneficial for the commercial propagation of garberia to compensate for low seed viability. Feasible recommendations may include using specialized seed density separation equipment [39] or increasing the planting density per cell [40].

4.2. Seeds Are Non-Dormant

Although an ecological benefit, the dormancy of native seeds can be a time-consuming obstacle that growers must overcome to develop efficient propagation protocols [41]. In our studies, we found that garberia seed germinates readily once collected from the mother plants, thereby lacking both physical and physiological dormancy. Of the family Asteraceae,

species may exhibit a wide range of non-deep physiological dormancy types or lack dormancy altogether. Non-dormant seed types are commonly found in evergreen and semi-evergreen vegetation zones [42,43], consistent with the growth form of garberia. Additionally, perennial asters such as garberia are less likely to exhibit seed dormancy, as they have multiple seasonal opportunities to set seed and encounter favorable conditions, reducing the need to evolve seed dormancy mechanisms to ensure germination [43]. From a commercial nursery perspective, the lack of dormancy in garberia is conducive to its propagation and production, a trait very useful in its expanded use for restoration projects, as well as urban landscapes and gardens.

4.3. Population and Temperature Affect Germination Response

In this study, seeds from the two populations differed in their seed vigor, as evidenced by the North Florida population having greater pre-germination viability and the ability to germinate under a range of temperatures [44]. Also of note was the dramatic population response to the warm summer temperature (24/33 °C) treatment. Where the North population seed experienced the greatest germination proportion in the summer and fall temperatures, the Central Florida population seed had the least germination in the summer. Dell et al. [45] also observed this effect when germinating a different Asteraceae species, Eggert's sunflower (*Helianthus eggertii* Small), under warm temperatures (20/35 °C) compared to colder temperatures, as did Graves et al. [46] for goldenaster, and Trigiano et al. [47] for whorled sunflower (*Helianthus verticillatus* Small). This germination decline in warm conditions has also been observed in other Florida endemic taxa outside of Asteraceae [48]. For a number of species, germination rates increase with temperature until an upper limit is reached, after which, germination is sharply reduced [49]. Factors contributing to lower germination at warm temperatures include the hardening of the endosperm preventing radicle emergence [50,51], increased seed deterioration [52], metabolic effects including the up-regulation of ABA biosynthesis genes and the down-regulation of catabolism genes [53], and the transformation of germination promoting photosensitive pigments to their inactive forms [51]. While it remains unclear why the Central Florida seeds rather than the North Florida seeds had minimal germination in the warmer summer temperature, it was likely influenced by the environmental conditions of the population and reduced seed vigor. Population fitness can be influenced by several factors, including genetics [54,55], maternal age [55], and environmental characteristics such as light intensity and temperature [56]. Additionally, seed size has been shown to affect germination [57,58] and subsequent seedling vigor [59]. Interestingly, seeds collected from the Central Florida population were on average one to two millimeters shorter than seeds collected from the North Florida population. Consistent with our findings, population effects for germination under a range of temperatures have been observed for other native species such as coastalplain honeycombhead [60] and wild lime [*Zanthoxylum fagara* (L.) Sarg] [19], while LeFait and Qaderi, 2022 [56] found that differences in the day and night temperatures during maternal seed development influenced subsequent germination rates even within the same population. Though our collection sites were similar in terms of plant maturity, the number of individuals, sun exposure, and soil type, genetic variations, or differences in the abiotic conditions under which the seeds developed may have influenced traits like seed size and seed vigor.

The practical applications of these findings may be helpful to growers in deciding seed propagation timing for garberia. Naturally, garberia flowers from late to early fall (September to October) and sets seeds from late fall to early winter (November–December). Seed harvest times typically occur in mid-winter to late winter and are freshly sown within 2 weeks. Our temperature results suggest growers may extend their germination window

to fall and spring if necessary, and perhaps summer depending on the seed vigor. These results also underscore the importance of considering the role of population effects when evaluating the seed propagation of garberia and other native species for nursery production.

4.4. Seeds Lose Viability After Room Temperature or Cold Storage

Lastly, this study provided important insight into the storability of garberia seed. We observed that seeds began to lose viability within 3 months of room temperature or cold storage, with a dramatic decline after 6 months. This was sooner than expected, as many Asteraceae species can survive at least a year of dry storage [61], with maintained viability through cold storage [62]. Likewise, Adegbola and Perez [63] found seeds of blanketflower (*Gaillardia pulchella* Foug.) to be tolerant to desiccation and accelerated-aging-related stress. Seed bank tests of other Asteraceae species have further revealed that viability can be retained for 10 or more years [64,65]. Tolerance to postharvest desiccation can be important not only for providing seed storage recommendations for growers but also for the conservation of rare or endangered species. For example, Salazar et al. [66] evaluated 53 species from a Rockland ecosystem in South Florida to determine their ability to withstand dry and freezing storage conditions to assist with their long-term conservation. They found that species that are desiccation-sensitive or intolerant of freezing tended to be more common in plants native to subtropical and tropical regions. Morgan and Salmon [67] also observed that seeds from tropical species lacked dormancy more than seeds from temperate species. Other studies have found that recalcitrant seeds from tropical species require higher relative humidity and temperature in storage, with the ideal temperature ranging from 7 to 17 °C, while temperate species require lower temperatures ranging from −3 to 5 °C [52]. It is possible that for subtropical species like garberia, the ideal storage temperature falls between these ranges. Notably, commercial storage methods typically require drying seeds to 8–10% moisture before packaging them in air-tight containers and storing them in temperature- and humidity-controlled rooms [68]. We observed that fresh garberia seeds stored in a desiccator for 3–14 days had 7.8% moisture, revealing that this could have aided in seed longevity. However, sophisticated storage equipment is not practical for most native growers. To compensate for the potential postharvest loss of seed vigor, practitioners do not commonly use stored seed from the prior year's collection. Future studies may be warranted to determine if garberia seeds are tolerant to long-term storage options such as cryopreservation, which has been found to be successful for native species such as wild lime [19]. Studies seeking to expand on the population effect observed for germination should include more than two disparate populations if possible and could explore the genetic determinants of seed vigor. Given the narrow seed collection window and lack of seed longevity for garberia, further studies exploring the cutting propagation of this species are underway to ensure year-round nursery availability. Notable limitations of this study were the incorporation of a third storage treatment representing seed storage under commercial conditions and a longer duration of seed storage at 12 months. However, low seed quantities limited the collection of this data.

5. Conclusions

Research exploring the germination responses of underutilized species is vital in developing propagation protocols and establishing best practices in the collection and storage of native seeds. The results presented herein suggest that garberia is an excellent candidate for nursery production by seed. We recommend using freshly collected, mature seeds from healthy stock plant populations; seed sorting if possible; and sowing at 3–4 seeds per cell in late winter (or early spring in colder climates) to ensure maximum seed vigor and germination.

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