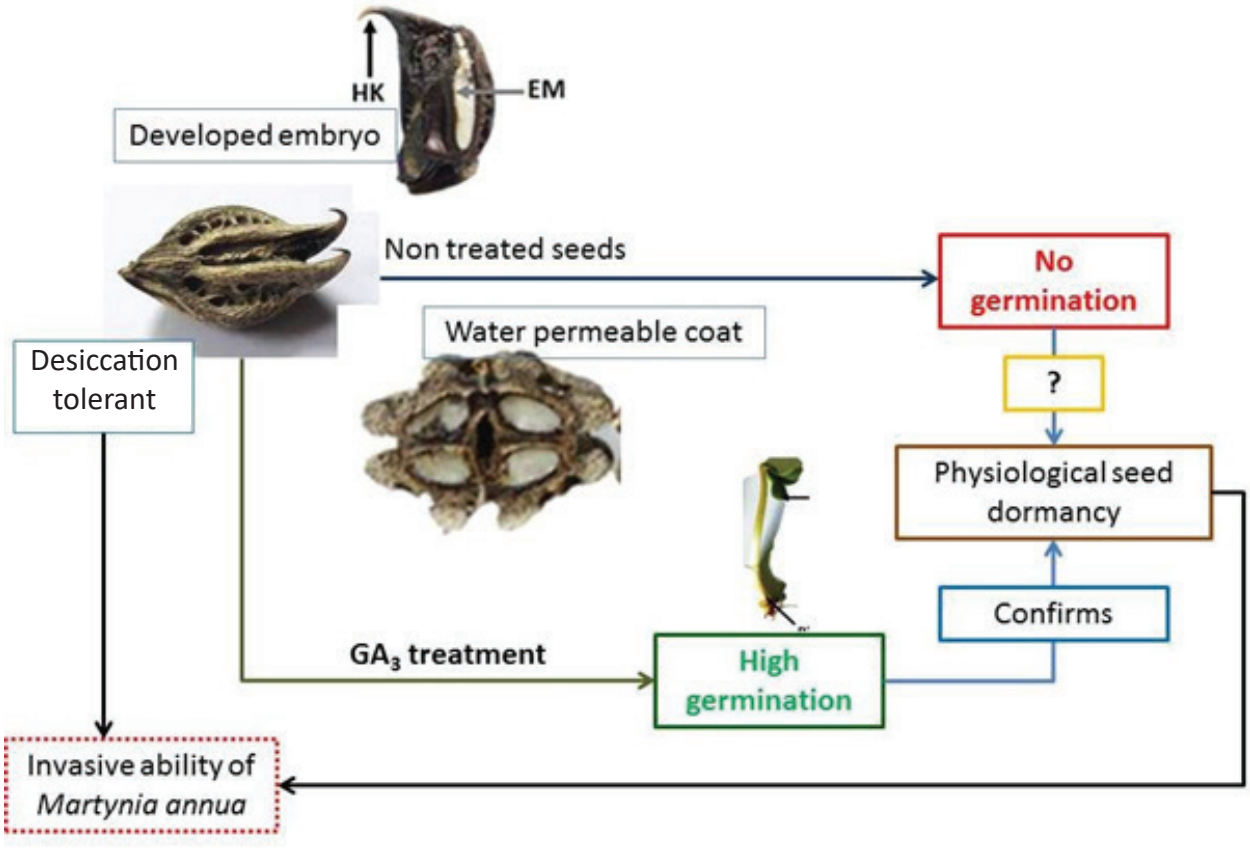
RESEARCH ARTICLE

Seed Germination Behaviour and Dormancy of *Martynia annua*: First Confirmed Report of Physiological Dormancy in Martyniaceae

Deshika L. Muthuthanthirige, K.M.G. Gehan Jayasuriya* and Shyam S. Phartyal



Highlights

- *Martynia annua* produces desiccation-tolerant and physiologically dormant seeds.
- First confirmed evidence of physiological dormancy reported in the Martyniaceae family.
- Physiological dormancy in *M. annua* seeds is effectively alleviated by 500 ppm Gibberellic Acid treatment.
- Desiccation tolerance and physiological dormancy of *M. annua* seeds may enhance its invasive potential.

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RESEARCH ARTICLE

Seed Germination Behaviour and Dormancy of *Martynia annua*: First Confirmed Report of Physiological Dormancy in Martyniaceae

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Abstract: Despite its medicinal value and invasive nature, the ecophysiology of seed germination in *Martynia annua* remains poorly understood. Thus, a study was conducted to explore the seed germination behaviour of this species. Diaspores were collected from the dry zone of Sri Lanka and brought to the University of Peradeniya, Sri Lanka. Seed moisture content and seed coat: seed mass ratio were determined. Imbibition and germination of fresh seeds were evaluated. The effect of dry storage and gibberellic acid (GA_3) on germination was tested. Seeds with and without woody endocarp imbibe water readily and their seed mass increased to 61 and 104% within 10 days of imbibition. Water-permeable seeds with fully developed embryos suggest that germination of *M. annua* seeds was not affected by the presence of the woody endocarp, indicating the absence of physical, morphological and morphophysiological dormancy in its seeds. However, seeds with and without endocarp failed to germinate under control (distilled water) treatment, whereas 500 ppm GA_3 treated seeds germinated >90% both with and without endocarp. Removal of endocarp considerably enhanced germination speed as GA_3-treated seeds completed germination within 11 days, while GA_3-treated seeds with intact endocarp took 1 month. Dry-stored seeds retained >90% viability even after 12 months of storage. These results confirm that *M. annua* produces desiccation-tolerant seeds with physiological dormancy, enabling long-distance dispersal across both spatial and temporal scales. This trait likely contributes to the species' successful distribution and invasion.

***Keywords*:** Physiological dormancy; Invasive species; Seed storage behaviour; Woody endocarp

INTRODUCTION

Martyniaceae is a unique monophyletic family under the order Lamiales (Angiosperm Phylogeny Group – APG III, 2009). Due to the uniqueness of the fruit, the family is known as the unicorn-plant family (Thieret, 1977). The fruit is characterized by the presence of incurved hooks that assist in epizoochory (Sorensen, 1986; Horbens et al., 2014). Thus, the fruit is highly adapted to disperse by large mammals (Gormley et al., 2015). Martyniaceae is native to the New World (Bretting, 1981) and comprises five genera: *Craniolaria, Holoregmia, Ibicella, Martynia* and *Proboscidea* (Kadereit, 2004). Although the structure of the fruit has gained the attention of biologists, the seed biology of Martyniaceae species in general, has not been studied in detail (Riffle et al., 1988). A few studies have been reported on germination and seed production of *Proboscidea louisianica* (Riffle et al., 1988), which is the largest genus in the family (Gutierrez, 2011). Based on the information reported by Riffle et al. (1988), Baskin & Baskin (2014) have speculated that *Proboscidea louisianica* possesses physiological dormancy (PD). However, dormancy was not confirmed using a systematic experimental procedure. Thus, we know little about seed dormancy and germination ecology in Martyniaceae.

Martynia annua L. is the most commonly distributed species among Martyniaceae species. Although it is native to Mexico, Central America, and the Caribbean (Gutierrez, 2011), the species has widely been introduced as an ornamental and medicinal herb in Australia, New Caledonia, South-eastern Asia, China, tropical Africa and in the Indian subcontinent (from Sri Lanka to Nepal) where it is currently designated as an invasive or naturalized weed (Rojas-Sandoval, 2018). In many of the introduced countries, *M. annua* has widely been used as a potential medicinal plant under the traditional system of alternative medicine (Bretting, 1981; Gupta & Deogade, 2018). Several studies have highlighted the antioxidant, wound-healing, antibacterial, and antidiabetic properties of this plant (Gupta & Deogade, 2018; Lodhi & Singhai, 2013; Malik & Katare, 2020), demonstrating its strong pharmacological potential. More recently, the seeds of *M. annua* were proposed to be an excellent source of raw material for biofuel production (Kumar et al., 2020). In Sri Lanka, *M. annua* is the only known species in Martyniaceae and occurs as a weed mainly in dry parts of the country (Theobald & Grape, 1981).

Fruits of all the Martyniaceae species are covered with a leathery exocarp which is later dropped due to dryness, exposing the woody endocarp at maturity (Horbens et al., 2014; Kadereit, 2004). *M. annua*, like the other members of the family, has a seed covered with endocarp and incurved hooks for epizoochory. Thus, the natural dispersal unit of *M. annua* contains 3-4 seeds surrounded by a hard woody endocarp. In Martyniaceae, the hard endocarp imposes mechanical constraints that can significantly delay germination, even after dormancy has been broken under

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the right environmental conditions (Chia et al., 2016). Fruit dispersal of Martyniaceae especially *Ibicella, Martynia,* and *Proboscidea* is facilitated by curved hooks in the fruits, through passive transportation, attaching to the hooves or ankles of animals (Thieret, 1977; Sorensen, 1986). After fruit dispersal, seeds of *Martynia* can only be released from its hard endocarp either trampling by a large animal or rotting of the endocarp (Thieret, 1977).

Martynia annua is a seed-propagated species and it commonly grows during the warm and wet season of the year along with disturbed sites like roadsides, moist thickets, riverbanks, floodplains, waste areas, and pastures (Rojas-Sandoval, 2018). Despite being an invasive species and used extensively as an ornamental and medicinal plant in different parts of the world, surprisingly, we know very little about its seed germination and storage ecophysiology. The seeds of Martyniaceae are known to possess a fully developed investing embryo, i.e., embryo erect, and stalk invested by cotyledons for half its length or more (Baskin & Baskin, 2014), and thick cotyledons lacking an endosperm (Martin, 1946). Kew-Seed Information Database listed its seed under the probable orthodox (desiccation-tolerant) category of seed storage based on information available on the storage physiology of other taxa of *Martynia* (SID, 2023). Since no information on the seed biology of *M. annua* is currently available, the first aim of our study was to investigate the presence/absence of dormancy in its fresh mature seeds, and if dormancy is present then identify the class and level of dormancy. The second objective was to confirm the seed storage physiology of *M. annua* suggested by Kew-SID (2022).

MATERIALS AND METHODS

Study species and fruit collection

Martynia annua is an annual or perennial branched herb that grows up to 1-2 m in height (Theobald & Grape, 1981). The study species grows as a weed along roadsides in Sri Lanka. In January 2020, mature fruits of *M. annua* were collected from six individual plants growing at least 2 m apart from each other in Medawachchiya town of Anuradhapura District, north-central province – belongs to the dry zone of Sri Lanka. Fruits were stored in labelled polythene bags and brought to the University of Peradeniya, Sri Lanka where the experiments were initiated within 3 days of the collection.

Fruit, seed, and embryo morphology and dimensions

This species bears fruits with upwardly curved two hooks (shorter than the fruit body), which contain four oblong, laterally compressed seeds (Gutierrez, 2011; Theobald & Grape, 1981). External and internal fruit characteristics were examined visually to determine seed arrangement and embryo characteristics. The Vernier caliper was used to measure seed dimensions, whereas a micrometer was used to measure the embryo length.

Determination of seed storage behaviour

Seed moisture content

The moisture content of freshly harvested seeds (with and without endocarp) was investigated to determine seed storage behaviour, i.e., sensitivity/tolerance to desiccation (Hong & Ellis, 1996) using an oven-dry method for 3 h at 120 °C (ISTA, 2008).

Seed coat ratio

Covering structures including endocarp and papery structure covering the embryo of ten *M. annua* seeds were separated individually from the embryo. These structures were oven-dried at 103 °C for 17 hours (ISTA, 2008) and the dry mass of each component was measured using digital chemical balance to the nearest 0.001 g. Seed coat ratio (SCR) was calculated using the equation given below and the SCR was used to predict the probability of the seed being desiccation sensitive or tolerant according to the method proposed by Daws et al. (2006).

$$\text{SCR} = \frac{\text{dry weight of the covering structures (endocarp and testa)}}{\text{dry weight of the total dispersal unit}}$$

Determination of seed dormancy

Germination of fresh seeds

This test was conducted to determine whether the fresh seeds of *M. annua* are non-dormant or dormant. Three replicates each of ten intact seeds (with endocarp). Four replicates each of eight endocarp-removed seeds (without endocarp) were placed on wet tissue papers moistened with distilled water and kept in boxes at ambient laboratory temperature (~ 26 °C) and 12/12 h light/dark conditions (white florescent light and diffused sunlight from windows during the daytime and complete darkness during nighttime) for incubation as a control treatment. Seeds were observed for germination initially at 2-day intervals, and thereafter at weekly intervals for 6 months.

Imbibition

The water imbibition test was performed to investigate the water permeability and/or impermeability of the endocarp and seed coat of *M. annua.* Ten seeds with intact endocarp and ten isolated seeds (without endocarp) were weighed individually to determine their initial weight using a digital balance to the nearest 0.001 g. Each seed sample was placed on wet tissue papers moistened with distilled water at ambient laboratory temperature (~26 °C). Isolated seed samples (without endocarp) were kept in a Petri dish while the seeds with intact endocarp were in a transparent box (12 cm × 6 cm × 5 cm). Seeds from both samples were then removed, blotted dry, kept back on wet tissue papers, and reweighed after 24 h (1 d), 5 d, and 10 d intervals (Jayasuriya et al., 2010). The moisture content of 10 d imbibed seeds (with and without endocarp) was evaluated and compared with the moisture content of fresh seed samples.

Effect of Gibberellic acid treatment on seed germination

This test was initiated with the standard germination tests to identify the response of *M. annua* seeds (with and without endocarp) to gibberellic acid (GA_3) to evaluate the class and level of seed dormancy, if any. Three replications each of ten seeds with intact endocarp and two replications each of six seeds without endocarp were, respectively, placed on wet tissue papers moistened with 500 ppm GA_3 solution and kept in boxes for incubation under similar ambient

laboratory temperature and light conditions.

Effect of dry storage on seed germination

Four samples, each with 48 seeds of *M. annua* were placed in paper bags and kept for dry storage on a laboratory bench at ambient room temperature (26 ºC) for 5 and 12 months, respectively. Two samples were retrieved after each storage period. During each storage period, the samples were divided into four replications, each with 12 seeds, and placed on wet tissue papers in four boxes. The first sample was moistened with distilled water (as a control) while the second sample was moistened with 500 ppm GA_3, and both samples were kept for incubation under similar ambient laboratory conditions as mentioned above. Additionally, a tetrazolium test was performed to determine seed viability (Phartyal et al., 2003) on two seeds taken randomly from each replicate of retrieved samples (a total of 8 seeds from each storage period).

RESULTS AND DISCUSSION

Fruit, seed, and embryo morphology and dimensions

The germination unit of *M. annua* (seed plus endocarp) consists of the black-thick, woody endocarp, papery seed coat, and an investing embryo (Figure 1). *Martynia. annua* fruit was 3.40±0.53 cm long, 1.94±0.22 cm wide, and 1.4±0.2 cm thick. However, the incurved fang-like claws, which are believed to be an aid in dispersal, were 0.54±0.20 cm long. The embryo of this species is composed of two thick overlapping cotyledons which auriculate at the base (length: 1.10±0.14 cm, 0.45±0.11 cm width) and with a small stalk.

Seed storage behaviour

The initial moisture content of intact fruit (seeds with endocarp) at the dispersal was 7.5±0.8%, whereas isolated seeds (without endocarp) had a moisture content of 11.3±2.1%. After 10 d of water imbibition, the moisture content of the seed both with and without the endocarp increased by 6.3 and 2.7-fold, respectively (Table 1). The moisture content of *M. annua* seeds at dispersal is within the range of desiccation-tolerant (orthodox) seeds but lower than the range suggested for recalcitrant seeds (Hong & Ellis, 1996). Thus, the observations suggested that *M. annua* seeds are desiccation-tolerant.

Further, the average seed coat ratio (SCR) of *M. annua* was 0.86±0.27. Daws et al. (2006) reported that recalcitrant seeds generally have an SCR < 0.5, and the probability of desiccation-sensitivity (P) is > 0.5. Based on the SCR, the probability of *M. annua* seeds being desiccation-sensitive (recalcitrant) is very low (0.0047), as ~0.5 is the threshold for desiccation-tolerant seeds. Thus, SCR further confirms the desiccation tolerance of *M. annua* seeds. This confirms Kew-SID (2022) speculation that seeds of *M. annua* must show orthodox storage behaviour. Orthodox seeds can maintain soil seed banks for considerably long periods. This trait may be one of the contributing factors to the invasive success of *M. annua*.

Table 1: Percentage of moisture contents (mean ± SE) of *Martynia annua* seeds with and without endocarp soon after dispersal and after 10 days of water imbibition.

	% Moisture Content	
	Soon after dispersal	After 10 days of imbibition
Seeds with endocarp (fruit)	7.5±0.8	47.7±4.0
Seeds without endocarp	11.3±2.1	30.2±3.7

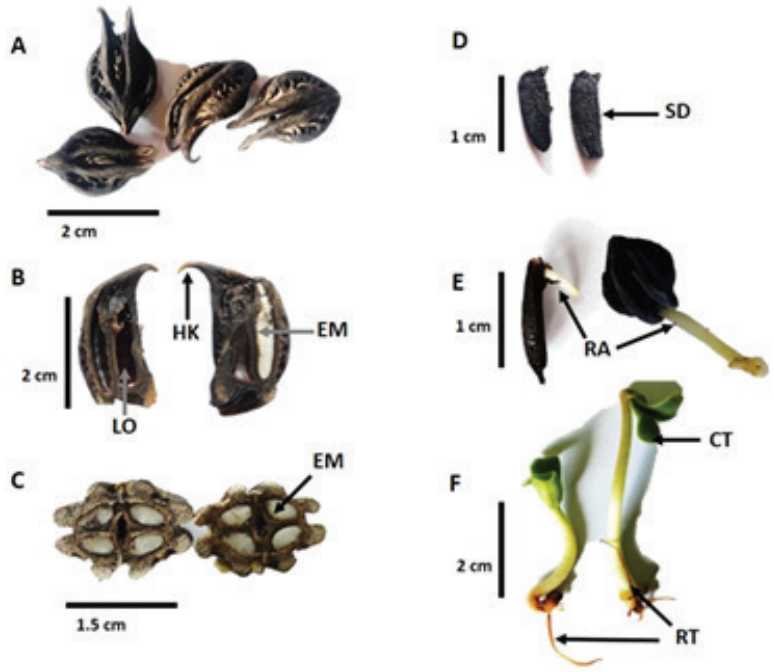


Figure 1: (A) *Martynia annua* fruits with characteristic upwardly curved two hooks; (B) longitudinal section and (C) cross-section of the fruit showing four locules; (D) laterally compressed seeds with black papery cover; (E) emergence of radicle; (F) seedling with cotyledons (CT, Cotyledons, EM; embryo, HK; hooks, LO; locules, RA; radicle, RT; root, SD; seed)

Seeds with a high SCR germinate slowly (Pritchard et al., 2004) and seeds with high SCR invest more in the seed coat, i.e., more in physical defense (Dalling et al., 2011 & 2020). Thus, as *M. annua* seeds have high SCR, it can be concluded that they depend on physical defense against seed predators and pathogens while they stay in the soil seed bank for extended periods. Pitt (1998) has reported that *M. annua* is difficult to control weeds as it creates a persistent soil seed bank. Gardener et al. (2010) devote *M. annua* invasion potential to its long-range dispersal ability by attaching through curved hooks.

Seed dormancy

None of the fresh mature seeds (with and without endocarp) incubated on tissue papers moistened with distilled water (as a control) under the ambient laboratory conditions germinated during the experimental period of 6 months. However, almost all the seeds had white, firm embryos when the experiment was terminated at the end of the germination period. Thus, it revealed that *M. annua* seeds have seed dormancy.

The mass of imbibed seeds with intact endocarp increased slowly by 27.6±1.8% in the initial phase (24 h), thereafter rapidly by 104.1±8.7% in 10 d. On the other hand, the mass of imbibed seeds without endocarp increased rapidly by 48.3±4.7% in the initial 24 h, thereafter slowly by 61.1±6.3% in 10 d (Figure 2). This experiment showed that both scarified (without endocarp) and non-scarified (with intact endocarp) seeds can take up considerable amounts of water within 24 h. Moisture content analysis of these imbibed seeds also showed that water has readily reached the embryo, i.e., there are no water-impermeable barriers within the endocarp. Thus, seeds have no physical dormancy.

Furthermore, the seeds possess a fully developed investing embryo that fills the entire seed, indicating that *M. annua* seeds do not exhibit morphological dormancy (for a detailed classification of seed dormancy, see Baskin & Baskin, 2014). Thus, there is only a possibility that *M. annua* seeds must have a physiological component to dormancy. Seed dormancy of *M. annua* has not been categorized previously, though it is a common invasive weed in many parts of the world (Gardener et al., 2010).

Gibberellic acid-treated seeds (with and without endocarp) germinated >90% within a month of incubation. Seeds without endocarp germinated to 100% within 11 days, while seeds with endocarp took 1 month to achieve 93.3±6.7% germination. Hundred percent of the embryos of five and 12 months stored seeds stained well during the tetrazolium test (an indirect test for seed viability). However, these stored seeds failed to germinate when incubated with and without endocarp in distilled water for 3 months. In contrast, both seed (with and without endocarp) samples of the same storage periods, incubated on GA_3 germinated >90% within a month, similar to the germination of GA_3-treated fresh seeds.

Results of our dormancy-breaking experiments confirmed that *M. annua* seeds have PD as this class of dormancy is caused by mechanical constraints posed on the embryo by the layers covering it, like seed coats and endosperm and also by the low growth potential of the embryo (Baskin & Baskin, 2014). According to the experiments, removal of the endocarp failed to facilitate the seed germination of *M.*

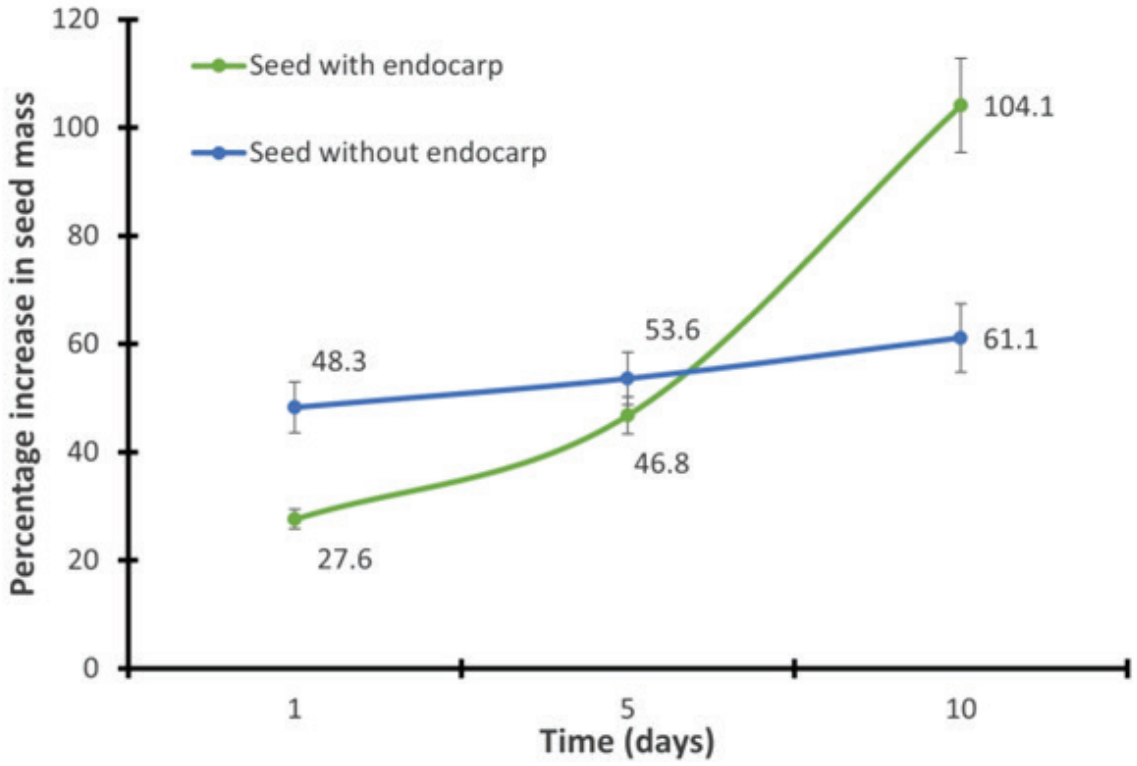


Figure 2: Time course for percentage increase in mass of *Martynia annua* seeds with and without endocarp. Bars indicate standard deviation.

annua, indicating that the endocarp constraint and the low growth potential of the embryo are responsible for the PD of this species. As seeds with and without endocarp have germinated significantly to a higher percentage (> 90%) within 30 days when incubated on GA_3, it can be concluded that the lack of embryo growth potential is the leading cause of PD in this species. GA_3 application on seeds without endocarp considerably increased the seed germination speed, as most seeds germinated within 10 days (20 days earlier than seeds with endocarp). External GA_3 application is known to change the hormone concentration ratio (especially GA_3: ABA; Yan & Chen, 2020) and enhance the expression of genes involved in increasing embryo growth potential.

Dry storage of seeds has not weakened the degree of dormancy, as no seeds germinated under control (distilled water) treatment within 3 months of incubation. Similarly, dry storage did not enhance the degree of dormancy, as >90% of 12-month-old, stored seeds germinated when incubated on a 500 ppm GA_3 solution, similar to the germination behaviour observed in the fresh seeds. When these results were considered, it was hard to define the level of PD of *M. annua*. As per the hierarchical classification system of seed dormancy, PD can be divided into 3 levels, i.e., nondeep, intermediate, and deep PD (Baskin & Baskin, 2014). Nondeep PD can be alleviated by dry storage for < 3 months and responds positively to the GA_3 treatment. Dry storage for 3-6 months could alleviate the intermediate PD. However, GA_3 may or may not alleviate intermediate PD. Over 6 months of dry storage is required to break deep PD and is not responsive to GA_3. Further, isolated embryos of seeds with deep PD do not produce normal seedlings (Baskin & Baskin, 2014). Our results indicate that the dormancy of *M. annua* seeds could not be alleviated even after 12 months of dry storage. However, both fresh and stored seeds germinated well on the GA_3 solution. Thus, *M. annua* seeds showed characteristics of both nondeep and deep PD. Thus, we categorize its seed as having an intermediate PD - closer to deep PD end of the continuum of PD from non-deep to deep.

According to a study conducted on *M annua* in the Gregory National Park, Australia, it was found that seeds take 2 years to germinate (Gardener et al., 2010; Pitt, 1998) and can be viable from 3.5 to 5 years. Therefore, understanding the seed germination pattern and dormancy behaviour is important to control the infestations of this species and its newly invaded ranges worldwide.

CONCLUSIONS

The results confirmed that seeds of *M. annua* possess physiological dormancy and the level of dormancy is most probably intermediate. Experimental findings also indicate that the seed display orthodox storage behaviour. However, to better understand the germination ecophysiology of *M. annua*, more field-based studies on its germination phenology are needed. Such studies should aim on identifying natural dormancy-breaking cues to clarify the soil seed bank dynamics and further explain the species' invasive potential.

DECLARATION OF CONFLICT OF INTEREST

The authors confirm that they have no conflicts of interest to declare.

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No funding is received for this work.

AUTHOR CONTRIBUTION

Conceptualisation: **K.M.G.G.J., D.L.M., S.S.P**.; design of experiments: **K.M.G.G.J., D.L.M.**; execution of experiments, data collection: **D.L.M.**; Statistical analysis: **K.M.G.G.J., D.L.M.**; data interpretation: **K.M.G.G.J., D.L.M., S.S.P**.; writing the first draft: **D.L.M.**; Manuscript editing and reviewing: **K.M.G.G.J., D.L.M., S.S.P.**; All authors have accepted responsibility for the content of the manuscript, reviewed all results, and approved the final version

DATA AVAILABILITY STATEMENT

The datasets generated during the current study are not publicly available as the study is ongoing; however, they are available from the corresponding author upon reasonable request.

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