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ARTICLE

Storage duration, light, temperature, and salinity exposure influence germination of the glycophyte *Rhanterium epapposum*

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Abstract: Regeneration of native species is the first priority for biodiversity conservation and restoration. To this end, it is key to have seeds properly conserved in seed banks and knowledge of seed longevity and (or) dormancy alleviation at different storage time intervals. In addition, understanding the germination response of the stored seeds to environmental conditions improves the efficiency of restoration and rehabilitation projects. We investigated the influence of storage duration (1–5 years), light (0 or 12 h of illumination), thermoperiod (night/day temperatures of 15/20 and 20/25 °C), and salinity (0, 100, 200. and 400 mmol/L of NaCl) on seed germination of *Rhanterium epapposum*, a glycophytic species from the Arabian Peninsula. Seeds maintained viability after five years of storage indoors at room temperature. Three years of storage alleviated seed dormancy. Exposure to 12 h light per day and thermoperiods of 15/20 °C enhanced seed germination. The seeds were glycophytic; after-ripened seeds exposed to salinity exhibited reduced rates of germination that did not recover after the salinity was alleviated.

Key words: after-ripening, desert, glycophyte, restoration.

Résumé : La régénération des espèces indigènes est une priorité pour la conservation et la restauration de la biodiversité. À cette fin, il est essentiel de disposer de semences correctement conservées dans des banques de semences et de connaître la longévité et (ou) l'atténuation de la dormance des semences à différents intervalles de temps de stockage. En outre, la compréhension de la germination des semences stockées aux conditions environnementales améliore l'efficacité des projets de restauration et de réhabilitation. Les auteurs ont étudié l'influence de la durée de stockage (1 à 5 ans), de la lumière (0 ou 12 h de lumière), de la thermopériode (températures nuit/jour de 15/20 et 20/25 °C) et de la salinité (0, 100, 200 et 400 mmol/L de NaCl) sur la germination des semences de *Rhanterium epapposum*, une espèce glycophytique de la péninsule arabique. Les graines conservaient leur viabilité après cinq ans de stockage à l'intérieur, à température ambiante. Trois années de stockage permettaient de réduire la dormance des semences. L'exposition à 12 heures de lumière par jour et à des thermopériodes de 15/20 °C favorisait la germination des semences. Les graines étaient glycophytiques ; les graines post-maturées exposées à la salinité présentaient une germination réduite qui ne se rétablissait pas après la diminution de la salinité. [Traduit par la Rédaction]

Mots-clés : post-maturation, désert, glycophyte, restauration.

Introduction

The Arabian desert is one of the most inhospitable ecosystems in the world. Climate change is predicted to exacerbate temperature extremes and reduce the already low rainfall (Ribot et al. 2005; FAO 2010). Overgrazing, off-road driving, camping, and urban development pose further risks to desert plant biodiversity (Omar Asem and Roy 2010), leading some species to become endangered (Hawkins et al. 2008). The presumed erosion of plant diversity has increased calls for biological conservation (Arif et al. 2010) and restoration and rehabilitation strategies to minimise further biodiversity loss in desert ecosystems (Bisaro et al. 2014). Seed collection and ex-situ storage in seed banks is necessary to address the lack of available native seeds for use in restoration (Merritt and Dixon 2011; Elzenga et al. 2019; Baskin and

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Baskin 2020; León-Lobos et al. 2020) to assure the genetic heterogeneity of plant communities (Hay and Probert 2013).

Seed banking is one of the simplest and most efficient methods for ex-situ conservation because of its cost-effectiveness in facilitating the conservation of genetic resources for long periods (Walters et al. 2005; Cochrane et al. 2007). Seed banks are widely used for conservation, habitat restoration, and reintroduction of species by keeping seeds under controlled environments and increasing their longevity (Vitt et al. 2010; Hay and Probert 2013). They are effective for maintaining long-term seed viability in wild and threatened species and in agricultural crops (Walters et al. 2005; Cochrane et al. 2007). However, the use of seed banks in the conservation of Arabian desert species is relatively rare, and species viability under ex-situ storage conditions is not well known (Niane et al. 2013; Zaman 2013; Bhatt and Pérez-García 2016; Bhatt et al. 2018, 2019*a*). Seed longevity and dormancy during storage are influenced by temperature, seed moisture content, relative humidity, storage duration, and by the innate nature of the seed (Goodwin et al. 1995; Shaban 2013; Mahmood et al. 2016; Maighal et al. 2016; Baskin and Baskin 2020). There are broad interspecific differences in seed response to storage, making species-specific research essential for effective seed bank management. Seed banks require regular germination testing to minimise genetic erosion during storage (Ruiz et al. 1999).

Rhanterium epapposum Oliv. (Asteraceae) is a perennial dwarf shrub growing to 100 cm in height, native to Kuwait, Saudi Arabia, the United Arab Emirates, Iran, and Sudan (Chaudhary 2001; Hellyer and Aspinall 2005). It produces bright yellow flowers in March/April and mature fruit in April/May. The flower heads (capitula) contain 6–8 curved, glabrous one-seeded fruits (achenes) also known as cypsela. Capitula are dispersed by wind or animals (Thalen 1979); thus, achenes within a capitulum are dispersed together, and seeds can remain viable for up to five years (Zaman 2006). *Rhanterium epapposum* is drought-tolerant and stabilizes mobile sand (Halwagy et al. 1982), making it a useful native species for rangeland rehabilitation. It has economic value as fodder, fuel, medicine, and as an insecticide (Younis and Adam 2008; Phondani et al. 2016). Anthropogenic disturbance has pushed *R. epapposum* toward localised extinction in Kuwait (Brown 2003) and current populations are mostly confined to protected areas (Omar et al. 2001). In addition, some populations present low genetic differentiation, which may be a serious concern because the individual populations may suffer from a dramatic decline due to genetic drift (Al Salameen et al. 2020). Previous studies reported that freshly collected seeds of *R. epapposum* exhibit physiological dormancy, and thus have poor germination rates (Suleiman et al. 2009; Zaman et al. 2010). Additionally, the effects of dry heat, gibberellic acid, moist stratification and hydration/dehydration cycles on seed germination of *R. epapposum* were tested without removing the achene from its head (Suleiman et al. 2009; Zaman et al. 2010). However, the influence of environmental factors as well as storage period on seed germination has received scant attention. Temperature, light, and salinity are the main environmental factors regulating germination in many desert species (Bhatt and Santo 2016; Bhatt et al. 2016*a*, 2016*b*). Understanding the effect of these factors on seed germination will inform the best timing and conditions for seed sowing in vegetation restoration projects, and intraspecific seed storage time. However, there is no information on the effects of long-term seed storage on dormancy break and seed germination, nor is there information on salinity tolerance during germination of *R. epapposum*. The aims of this study were to examine seed germination response to (*i*) storage duration and incubation conditions during germination (i.e., light and temperature regimes), (*ii*) salinity, and (*iii*) prior exposure to salinity stress.

Materials and methods

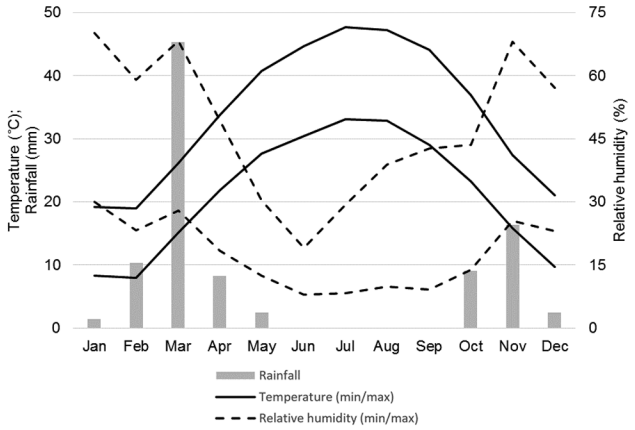
Seed collection

Mature *R. epapposum* heads were collected from naturally occurring populations in Sulaibiya, Kuwait (29°09′52″N, 47°43′30″E) each May from 2012 to 2016. Approximately 50–60 plants were randomly selected for seed collection to represent the genetic diversity of the population. After collection, the seeds were dried at room temperature for one week and stored at the Kuwait Institute for Scientific Research seed bank in brown paper bags under controlled conditions: temperature of 20 ± 2 °C and relative humidity of 15% ± 2%, until April 2017.

Storage duration, light, and temperature

Achenes (hereinafter referred to as seeds) were removed from the flower heads in April 2017, immediately prior to the experiment. Undamaged, healthy seeds were selected for germination, based on their external physical appearance. Seeds were germinated in 9-cm tight-fitting Petri dishes containing one disk of Whatman No. 1 filter paper moistened with 10 mL of distilled water. Four 25-seed replicates were used for each of 20 treatments, being each combination of five storage durations (1–5 years), two temperature regimes (12/12 h of 15/20 °C and 20/25 °C), and two light conditions (0 or 12 h illumination per day). These temperature regimes are close to those that occur between October and March (Fig. 1), when the probabilities of germination and seedling establishment are higher due to the higher chance of rainfall during that time of year (Omar et al. 2007). The 12 h of the higher temperature corresponded to the 12 h of light, when provided. For the dark treatments (0 h light per day), the Petri dishes were wrapped in aluminium foil. Germination was defined as the

Fig. 1. Climate data for Kuwait. Source: Sulaibiya meteorological station (from Kuwait Institute for Scientific Research — KISR).



emergence of a radicle by more than 1 mm. Germinated seeds in the light treatments were counted and removed daily for 30 days. Seeds in the dark treatments were only counted after 30 days. At this time, ungerminated seeds were evaluated for viability by dissection under a binocular microscope. Seeds with a white embryo were counted as viable, and those with a turgid/brown or absent embryo were counted as nonviable (data not shown).

Salinity

Salinity tolerance was assessed for seeds collected in 2012 and stored for 5 years, using four 25-seed replicates for each combination of four salinity levels (0, 100, 200, and 400 mmol/L of NaCl) and two light conditions (0 or 12 h illumination per day). The seeds were germinated in Petri dishes (9 cm diameter) on two layers of Whatman No.1 filter paper, moistened with 10 mL of salt solution. The Petri dishes were sealed with parafilm to minimize evaporation, and then incubated at 15/20 °C. Germinated seeds were counted and removed daily in the light treatments. Germination of the dark treatments was assessed at the end of the 30-day experiment.

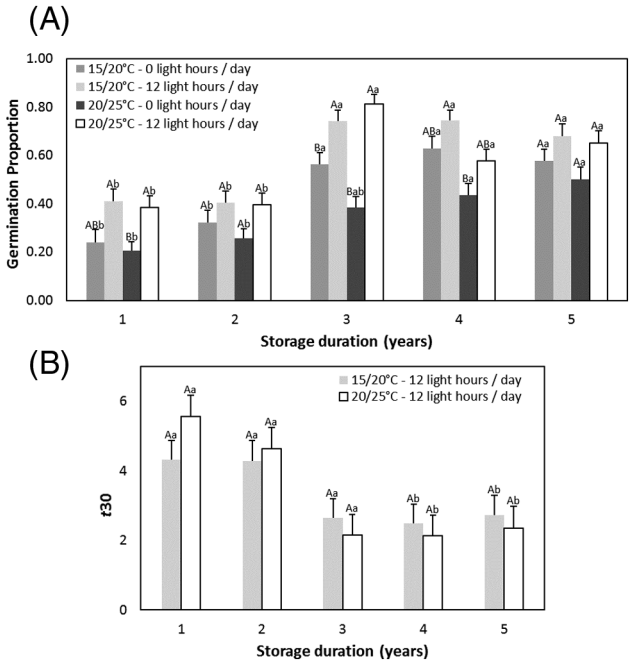
Recovery from salinity exposure

All ungerminated seeds from saline treatments were rinsed in distilled water and tested for germination in 0 mmol/L NaCl (distilled water), under conditions of 15/20 °C and 12 h daily illumination. Germinated seeds were counted daily for 30 days.

Data analysis

In the first trial, the germination proportion was tested as a function of storage time, temperature, and light regimes, and their two- and three-way interactions were tested using a binomial distribution model. The time it took for 30% of the seeds to germinate (*t*30) was evaluated as a function of storage time, temperature, and their interactions. The parameter *t*30 was chosen because it allowed us to include treatments producing a low rate of germination. The *t*30 was estimated with a

Fig. 2. Influence of storage duration, light, and temperature regime on germination proportion and time to 30% of seeds germinated (*t*30). Letters indicate significance of light and temperature conditions of each storage duration (upper case), and among storage years (lower case). Error bars indicate the standard errors.



curve fitting of the replicate with the '*drc*' (Ritz et al. 2019) and '*drcSeedGerm*' (Onofri et al. 2018) packages. In the second trial, the germination proportion was analysed as a function of salinity, light regime, and their two-way interactions, whereas *t*30 was evaluated as a function of salinity. In the third trial, the rate of germination for the seeds exposed to salt water was analysed as a function of both salinity and the light regime, and their two-ways interactions were examined.

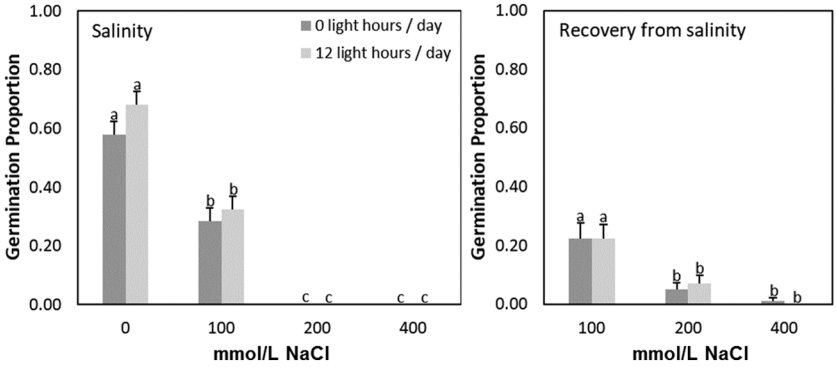
In all cases, the model with all of the factors and interactions was first fitted with all factors and interactions, and then the factors were analysed for significance using a likelihood ratio test (LRT) for the binomial data (proportion of germinated seeds) and on the scaled deviance for the Gaussian data (*t*30). Further multiple comparisons were conducted using least-squares means for multiple comparisons with the '*lsmeans*' package (Length 2016). All statistical analyses were performed with R software, version 3.5.3 (R Core Team 2019).

Results

Storage duration, light, and temperature

Seed germination was affected by all of the factors and the two-way interactions between storage time and light conditions. Germination proportion increased with storage duration, resulting in a 30% increase from the first to the fifth year (Fig. 2). Germination proportion was 18.6% higher in the light treatments (12 h

Fig. 3. Seed germination under variable light conditions during exposure to salinity (left) and after transferal to distilled water (right), of seeds stored for five years and germinated under a 15/20 °C (12 h/12 h). Letters indicate significant differences. Error bars indicate the standard errors.



illumination per day), and 7.8% higher in the colder temperature regime (15/20 °C), when compared with the warmer temperature (20/25 °C) and dark (0 h illumination per day) treatments (Fig. 2). The interaction between light and storage time was significant because the light treatment had a stronger effect on germination in the seeds stored for 3 years, but less of an effect on the seeds stored for 5 years (Fig. 2).

Germination timing ($t30$) was affected by storage time only, with germination occurring faster with each successive year of storage (Fig. 2).

Salinity

Germination proportion was strongly influenced by salinity level. Light regime had no effect in this experiment, which involved one storage duration. Germination proportion declined with increasing salinity, with no germination for seeds exposed to ≥200 mmol/L NaCl (Fig. 3).

Recovery from salinity exposure

Prior exposure to salinity had a lasting effect on germination when seeds were later exposed to distilled water. Only a few seeds germinated after exposure to ≥200 mmol/L NaCl, with the germination proportion correlating negatively ($b = -0.013 \pm 0.004$, $p < 0.001$) with increased salinity (Fig. 3). All of the ungerminated seeds exhibited imbibition when observed using the cut test (data not shown).

Discussion

Favourable conditions for germination are spatially and temporally unpredictable in desert systems (Rubio-Casal et al. 2003). Understanding the requirements for dormancy break and germination is key for desert rehabilitation and restoration projects. Most desert seeds are dormant at maturity and therefore require an after-ripening period to release dormancy (Baskin and Baskin 2014, 2020; Bhatt and Pérez-García 2016; Bhatt et al. 2018). Therefore, understanding how storage duration influences dormancy release can improve rehabilitation and restoration projects reliant on anthropogenic seed dispersion. The higher germination percentages for the old seed lots indicate that *R. epapposum* seeds not only maintain viability for extended periods under storage conditions (20 ± 2 °C and RH 15% ± 2%), but also that dry storage alleviates physiological dormancy. Previous researchers have reported that *R. epapposum* forms a persistent soil seed bank (Zaman 2006) and germinates after rain events exceeding 30 mm (Brown 2003). Zaman et al. (2010) reported that there is great variation in the germination proportion among years, and this variation correlated with the proportion of empty achenes as well as various climatic features.

Formation of a persistent soil seed bank improves long-term survival of species that grow in highly unpredictable environmental conditions by spreading germination over seasons and occurring under opportunistic suitable conditions (Cohen 1967; Caballero et al. 2003). As expected, most seeds remained dormant for two years, with 69.3% and 66.0% germination after 1 and 2 years of storage, respectively. Germination percentage increased during the first two years of storage, then remained constant to the fifth year. Seed dispersal in this species is proximal and synaptospermic, with multiple seeds contained within each dispersing capitulum, typically spreading just 3–93 cm from the mother plants (Zaman et al. 2010), resulting in spatial aggregation (Zohary 1950), which might facilitate the retention of seeds in a favourable microhabitat, especially under extreme desert conditions. Germination, nevertheless, varies temporally due to prolonged survival in the seed bank, during which time seeds could be subjected to further spatial dispersal. Dormancy heterogeneity among seeds within a capitulum produces temporal variation in germination (Watson and Renney 1974; Thalen 1979; Gutterman 2000).

Most seeds of desert species have physiological dormancy at the time of seed maturity, such that dry storage is effective at improving germination via after-ripening mechanisms (Kucera et al. 2005; Bair et al.

2006; Baskin and Baskin 2014; Bhatt and Pérez-García 2016). In our study, seeds germinated at a significantly greater proportion after two years of storage, indicating a deep physiological dormancy. However, seeds in the soil seed bank are subjected to extreme hot and dry environments during the summer, and mild winters. These conditions may result in a faster after-ripening of seeds in situ than seeds stored at room temperature (Baskin and Baskin 2020). Further study is needed to determine how the dormancy of *R. epapposum* seeds is broken, especially under natural conditions.

Light significantly enhanced the germination of *R. epapposum* seeds at both tested temperature regimes. This positive light response indicates that germination is more likely to occur at the ground or near the ground surface. The low rate of germination in darkness, i.e., indicative of burial, may favour its maintenance in the soil for the next germination season. Seeds of *R. epapposum* are very small (50 seeds weight 0.0506 mg) and are unlikely to contain sufficient reserves for epicotyl elongation to the soil surface if buried (Milberg et al. 2000). Generally, this species proliferates in shallow well-drained sandy habitats (Brown and Al-Mazrooei 2003; Vincent 2008). Seed burial can be intermittent in this type of habitat, thus a buried seed may not remain buried when the next rainfall occurs. Germination differences between temperature regimes were observed in seeds stored for three years, with a positive response when stored at 15/20 °C (12 h/12 h). These differences in the inherent physiological characteristics of seeds collected in different years might have affected the germination behaviour. The variation between consecutive years from the same populations might be caused by different maternal environments during ripening (Schütz and Rave 2003; Zaman et al. 2010). These findings are in accordance with Mishra (2009), who reported that temperature requirement may change with the age of seed and progress of after-ripening.

Rhanterium epapposum grows on dry soils and colonises arid environments where saline soils are common. Understanding the effect of salinity stress on germination is important for restoration of desert areas. Seeds were able to germinate when exposed to 100 mmol/L NaCl (<32%), but at higher salinity levels, none of the seeds were able to germinate. This result is consistent with the results reported for other desert glycophytes such as *Salvia aegyptiaca* (Gorai et al. 2011) and *Ochradenus baccatus* (Bhatt and Pérez-García 2016). Complete inhibition above 100 mmol/L NaCl could explain the higher abundance of *R. epapposum* in sandy habitats compared with saline habitats, because sandy habitats usually have lower salinity (Brown and Al-Mazrooei 2003; Vincent 2008). *Rhanterium epapposum* exhibited poor recovery of germination when the salinity stress was released. Recovery from salinity was significantly lower for seeds exposed to 200 mmol/L NaCl compared with seeds exposed to 100 mmol/L NaCl, and fell to zero germinated seeds at higher salinity levels. These results indicate that *R. epapposum* is a true glycophyte, in which secondary dormancy is induced by salinity, as reported for other species (El-Keblawy et al. 2016; Bhatt et al. 2016*c*, 2018, 2019*b*). In our study, none of the seeds germinated at the tested concentrations of NaCl, indicating that seeds of *R. epapposum* cannot germinate when the salinity is ≥100 mmol/L. Moreover, once transferred to distilled water, only 20% of the *R. epapposum* seeds recovered their germinability, indicating salt-induced dormancy. Therefore, for restoration and rehabilitation of *R. epapposum*, it is very important to avoid saline soil for successful germination. Nevertheless, adult plants of *R. epapposum* are tolerant of saline soils. Similar results have been reported for other Arabian desert glycophytes (Bhatt and Pérez-García 2016; Bhatt and Santo 2017; Bhatt et al. 2018, 2019*b*), in which germination is sensitive to salinity but mature plants are more tolerant (Mayer and Poljakoff-Mayber 1975). The seed germination of the glycophytes such as *R. epapposum* under saline conditions may occur in years with large individual rainfall events (Brown and Al-Mazrooei 2003; Omar and Bhat 2008), when the saline conditions are alleviated. Then, specialized root structures from mature plants may allow them to survival in saline soils. However, further investigation is needed to understand the establishment mechanism of this perennial shrub. In the present study, when exposed to saline solution, seeds germinated equally well under light and dark conditions, and germination recovery was unaffected by photoperiod during pre-treatment.

Conclusions

Rhanterium epapposum seeds have physiological dormancy that can be alleviated by long-term storage under room conditions. Germination percentages of *R. epapposum* seeds increased with the increasing storage duration, especially after two years. Under natural conditions, distributing seeds at the soil surface during winter and avoiding saline areas will enhance germination percentage and seedling establishment.

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