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STORAGE ON MATERNAL PLANTS AFFECTS LIGHT AND TEMPERATURE REQUIREMENTS DURING GERMINATION IN TWO SMALL SEEDED HALOPHYTES IN THE ARABIAN DESERTS

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Abstract

Seeds are either stored in a soil seed bank or retained on maternal plants until they are released (aerial seed bank). Though there are extensive studies on the germination requirements of seeds in soil banks of saline habitats, studies conducted for halophytes with aerial seed banks are rare. We assessed the impact of aerial and room-temperature storages on the light and temperature requirements during germination in two small-seeded halophytes: *Halocnmum strobilaceum* having a short-term aerial seed bank (less than one year) and *Halopeplis perfoliata* having a longer term aerial seed bank (up to two years). Seed storage in the aerial bank reduced the germination in *H. strobilaceum*, but either increased it (5-months storage) or had no effect (17-months storage) in *H. perfoliata*. Seeds of both species that were stored in aerial bank germinated to higher percentages in light than in darkness, indicating that considerable portions of the seed populations are light sensitive. Seeds of *H. perfoliata* attained less than 5.0% germination in darkness at higher temperatures, compared to more than 90.0% in light. The results support the hypothesis that the aerial seed bank is an adaptive strategy for survival in the saline habitats of the two species.

Key words: Aerial seed bank, Arabian deserts, Germination, Halophytes, *Halocnemum strobilaceum*, *Halopeplis perfoliata*.

Introduction

Seed banks are considered an important source of plant recruitment in desert environments (Kemp, 1989; Gunster, 1992). The distribution of different plant species is the result of their strategies of seed dispersal, dormancy and germination behaviour (Kos *et al.,* 2012). Seeds are either stored in the soil (i.e., soil seed bank), or retained above ground on maternal plants until they are released (i.e., aerial seed bank) (Gunster, 1992). It has been reported that many shrubby halophytes maintain a soil seed bank in saline soils (Zaman & Khan, 1992; Khan, 1993; Aziz & Khan, 1996). Persistent seed banks in halophytes are usually produced by enforced or induced dormancy and carry seeds over a predictable dry or hyper-saline period after which germination occurs (Gul & Weber, 2001). However, some other plants retain their seeds in the plant canopy as aerial seed bank, a phenomenon also known as serotiny that occurs in various species in North America, the Mediterranean and South Africa (Lamont *et al.,* 1991).

Aerial seed bank is a phenomenon described in many species of the unpredictable, harsh deserts of the arid and semi-arid regions (Kamenetsky & Gutterman, 1994; Van Rheede Van Oudtshoorn & Van Rooyen, 1999). In desert plants, aerial seed bank plays important roles in the protection of seeds against granivores, anchorage against surface run-off, bet-hedging risks by spreading seed dispersal in time, and retaining seeds in a favorable microhabitat (Ellner & Shmida, 1981). The major role for aerial seed bank is to protect seeds from unfavorable conditions in the soil and release them when conditions are favorable for germination and seedling growth (Lamont *et al.,* 1991). Recent studies have found that seeds released from aerial seed bank have little dormancy and germinate immediately after dispersal (Aguado *et al.,* 2011; 2012). Consequently, aerial seed bank would play the same role as the soil seed bank; both protect seeds from unfavorable conditions and release them when optimal field conditions for seed germination and seedling emergence are met (Thanos, 2004).

The environmental factors associated with seed in the soil seed bank differ from those in the aerial seed bank. Seeds in a soil seed bank are either buried at different depths or stored on the soil surface. Seeds stored on the soil surface are exposed to light and face diurnal fluctuations in the temperatures. Conversely, seeds buried in the soil are stored in darkness and face less diurnal temperature fluctuations. In the aerial seed bank, however, seeds are exposed to light and experience less fluctuation in diurnal temperatures.

Germination requirements are usually affected by the environmental conditions that seeds usually face during storage (Uhl & Clark, 1983; Pons, 2000; Ooi *et al.,* 2009). For example, seeds enter dormancy once they are buried in the dark (Wesson & Wareing, 1969; Pons, 1991). In addition, induction of dark dormancy was reported to be faster at higher temperatures in some species which are well known to form persistent seed banks (Pons, 1991). Consequently, we expect special light and temperature requirements for seeds stored in the aerial seed bank to differ from those of seeds stored at room temperatures or in soil seed banks.

Germination of halophytes under natural conditions is mainly controlled by light, temperature, moisture and salinity (Baskin & Baskin, 1998; Zia & Khan, 2004; El-Keblawy & Al-Rawai, 2005; Qu *et al.,* 2008). Typically, germination of halophytes commences in the Arabian deserts after effective rainfall dilutes the soil salinity (El-Keblawy, 2004, 2013; El-Keblawy *et al.,* 2007; El-

Keblawy & Al-Shamsi, 2008). Consequently, the effect of light and temperature and their interaction would be important at that time.

Temperature plays an important role in controlling germination, establishment and regeneration of desert species (Baskin *et al.,* 1999; Budelsky & Galatowitsch, 1999). It has been reported that germination depends on the temperature of incubation in some halophytes (Gul *et al.,* 2000; Khan *et al.,* 2001), but depends on both temperature and light and their interaction in other halophytes (De Villiers *et al.,* 1994; El-Keblawy & Al-Rawai, 2005; El-Keblawy *et al.,* 2007). Despite such extensive knowledge on germination requirements of seeds that form soil seed banks in saline habitats, almost no study has examined light and temperature requirements and their interaction in the germination of halophytes that form the aerial seed bank. The aim of the present study was to assess the light and temperature requirements during germination in *H. perfoliata* and *H. strobilaceum*. These two halophytes produce small seeds that are retained on maternal plants (i.e., form the aerial seed bank). *H. strobilaceum* has a short-term aerial seed bank (less than one year), but *H. perfoliata* has a longer-term aerial seed bank (extending up to two years). Both species produce seeds with little dormancy, but can stay viable for years at room temperatures (Ali El-Keblawy, unpublished data). The impact of aerial and room temperature storage on final germination and the germination rate index of the two species were assessed in different temperatures in both light and dark.

Materials and Methods

The halophytic *H. strobilaceum* and *H. perfoliata* are major components of the perennial hyper-saline vegetation of the United Arab Emirates (UAE). Seeds of the two species mature in December (early winter) and are retained on maternal plants in dry grooves in the joints between small stem segments. Seeds are present at the upper and lower stem joints in *H. strobilaceum*, but only at the upper stem joints in *H. perfoliata*. The aerial seeds of *H. strobilaceum* are released gradually within the first year of production, but stay for up two years in *H. perfoliata* (Ali El-Keblawy & Bhatt, 2015). Both species were categorized among the native halophytes that could be used to landscape urban areas, especially areas fringing coastal regions, according to the Qatar Sustainability Assessment System (QSAS) criteria (GORD, Qatar, personal communication).

Seed collection and storage: Seeds of both *H. strobilaceum* and *H. perfoliata* were collected from a saline habitat in Al-Hamryah, Sharjah Emirate, UAE (25°28'27.95"N and 55°31'46.8"E) during December 2012 and April 2013. Seeds were randomly collected from the whole population to represent its genetic diversity. In the December collection, the newly ripened fruits of both species (of a very light brown colour) were separated (hereafter referred to as 'five-month room temperature storage'). The April collection of *H. strobilaceum* had only light brown fruits that were matured by December 2012; hereafter these are referred to as 'five-month aerial seed bank storage'. The fruits of the April collection of *H. perfoliata* were separated according to their colours into light brown fruits (matured on December 2012) or very dark or almost back (matured on Dec 2011). Hereafter we refer to these two seed lots as five-month and 17-month aerial seed bank storage respectively. Seeds from different lots were air dried, cleaned and stored in brown paper pages at room temperature (20±2°C) until used for experiment in April 2013.

Germination experiment: To assess the effects of temperature and light and their interaction, seed germination was conducted in incubators set at daily 15/25, 20/30 and 25/35°C temperature regimes in either continuous darkness or 12 hrs light /12 hrs darkness, the light coinciding with the higher temperatures. In the dark treatment, the dishes were wrapped in aluminum foil to prevent any exposure to light. Three replicates of 25 seeds each were used for each treatment. Radical emergence was the criterion for germination. Germinated seedlings were counted daily for 14 days following seed soaking. Seeds incubated in the dark were only counted after 14 days. No germination occurred after 6 days in the non-saline solution and after 10 days in higher saline solutions.

Data analysis: The rate of germination was calculated with a modified Timson's germination velocity index: $\sum G/T$, where G is the percentage of seed germinated every day, and T is the total germination period (Khan & Ungar, 1997). The maximum value possible for our data using this index was 100. The higher the value, the more rapid the germination. The germination rate was only calculated for seeds incubated under light conditions.

Three-way ANOVA were used to assess the significance of the main factors (storage condition, temperature and light) and their interactions for the final germination percentages. Two-way ANOVAs were used to assess the impact of storage condition and the temperature of incubation and their interactions on the germination rate index. Tukey test (Honestly significant differences, HSD) was used to estimate the least significant range between means. The germination rate was log-transformed and germination percentages were arcsine-transformed to meet the assumptions of ANOVA and to achieve normal distribution of the data. These transformations improved the normality of the distribution of the data. All statistical methods were performed using SYSTAT, version 13.0.

Results

Germination of *H. strobilaceum*: The effects of storage conditions and light of incubation on the final germination percentage of *H. strobilaceum* were significant ($p<0.001$, Table 1). Seeds stored for five months at room temperatures germinated in significantly greater quantity (87.0%), compared to seeds stored for the same period in the aerial seed bank (61.5%). Germination in light (80.0%) was significantly greater as compared to those occurring in dark (68.0%, Fig. 1).

The effects of storage condition and temperature of incubation on the germination rate index (GRI) of *H. strobilaceum* were significant ($p<0.05$, Table 1). Germination of seeds stored at room temperatures was significantly faster (GRI = 81), compared with seeds retained in the aerial bank (GRI = 76). In addition, germination at the highest temperatures (25/35°C) was significantly faster (GRI = 82), compared with that at the lowest temperatures (15/25°C, GRI = 75) (Fig. 2).

Germination of *H. perfoliata*: Three-way ANOVA showed significant effects for the main factors (storage, temperature and light) on the final germination percentage of *H. perfoliata* ($p<0.05$, Table 2). Storage for five months in the aerial seed bank significantly increased germination (63.6%), compared with storage at room temperatures for the same period (58.4%) and storage in the aerial seed bank for 17 months (56.2%). Germination at 15/25°C (75%) was significantly greater, compared with 20/30°C (57%) and 25/35°C (46%). Germination in light (89.0%) was three times greater than that in darkness (29.8%).

The interaction between storage and light on the final germination of *H. perfoliata* seeds was significant ($p<0.05$, Table 2). Germination in darkness was significantly greater for seeds stored for five months in the aerial seed bank (37.3%), compared with seeds stored for 17 months in the aerial seed bank (28.0%) and for five months at room temperatures (24.0%). However, no significant difference was observed between the germination of the three storage conditions in light (Fig. 1).

Table 1. Three-way ANOVAs testing the effects of storage condition, and light and temperature of incubation on (a) final germination percentage and (b) germination rate index of *Halocnmum strobilaceum*.

Source of variation	df	Mean squares	F-Ratio	p-Value
(a) Final germination percentage				
Storage (S)	1	1.416	154.143	<0.001
Temperature (T)	2	0.002	0.246	ns
Light (L)	1	0.331	36.069	<0.001
S*T	2	0.033	3.67	ns
S*L	1	0.000	0.001	ns
T*L	2	0.026	2.831	ns
S*T*L	2	0.015	1.613	ns
Error	24	0.009		
(b) Germination rate index				
Storage (S)	1	0.015	67.551	<0.001
Temperature (T)	2	0.008	38.141	<0.001
S*T	2	0.001	4.393	<0.05
Error	12	0.000		

ns: Insignificant difference at p=0.05

Table 2. Three-way ANOVAs testing the effects of storage conditions, and light and temperature of incubation on (a) final germination percentage and (b) germination rate index of *Halopeplis perfoliata*.

Source of variation	df	Mean squares	F-Ratio	p-Value
(a) Final germination percentage				
Storage (S)	2	0.072	3.307	<0.05
Temperature (T)	2	0.636	29.381	<0.001
Light (L)	1	9.231	426.243	<0.001
S*T	4	0.012	0.531	ns
S*L	2	0.103	4.764	<0.05
T*L	2	0.192	8.877	<0.01
S*T*L	4	0.014	0.634	ns
Error				
(b) Germination rate index				
Storage (S)	2	0.000	0.397	ns
Temperature (T)	2	0.026	22.022	<0.001
S*T	4	0.002	2.043	ns
Error	18	0.001		

ns: Insignificant difference at p=0.05

The interaction between temperature and light on final germination of *H. perfoliata* seeds was significant ($p<0.01$), indicating that response to the temperature of incubation depended on light conditions. Germination in light was significantly greater than in darkness at all three temperatures; however, the difference was much smaller at the lower temperatures, compared to the difference at higher temperatures. Germination in light was greater than in darkness by 1.6 times at 15/25°C, but ca. 4 times at 20/30 and ca. 14 at 25/35°C (Fig. 1).

Two-way ANOVA showed a significant effect on the germination rate index for temperature of incubation ($p<0.001$), but not for storage condition and the interaction between storage and temperature ($p>0.05$, Table 2). Germination was significantly faster at 20/30°C (GRI = 77.1), compared with lower temperatures (15/25°C, GRI = 71.1) and higher temperatures (25/35°C, GRI = 69.6) (Fig. 2).

The results showed that seed storage for five months in the aerial seed bank of *H. strobilaceum* resulted in reduction of the final germination percentage and germination speed, compared with storage at room temperatures. In *H. perfoliata*, however, aerial storage either increased the germination ability (5-month storage) or did not affect it (17-month storage), compared with storage at room temperatures. This indicates that natural field conditions resulted in the deterioration of seed quality in the aerial seed bank of the former, but did not affect it in the latter species. Such patterns would explain the seed bank formation strategies of the two species. *H. strobilaceum* has a short-term aerial seed bank (less than one year), but *H. perfoliata* has a longer-term aerial seed bank that could extend up to two years (El-Keblawy & Bhatt, 2015). The release of the aerial seeds of *H. strobilaceum* within the first year of their production indicates their ability to survive higher salinities than the soil seed bank (Qu *et al.,* 2008). The seeds of this species tolerated up to 500 mM NaCl (Song *et al.,* 2006) and 800 mM NaCl (El-Keblawy & Bhatt, 2015) and most of the salinity-induced germination inhibition was alleviated when seeds were transferred to distilled water (Song *et al.,* 2006). Conversely, seeds of *H. perfoliata* that have a long-term aerial seed bank are sensitive to salinity (400 mM NaCl resulted in complete germination inhibition (El-Keblawy & Bhatt, 2015) and consequently would lose their viability if they entered the soil seed bank. The greater germination ability after 17 months for the aerial seed bank indicates that seeds of *H. perfoliata* are opted for aerial seed bank, rather than soil seed bank. It is possible that each species could have experienced a different selection regime that allows it to cope with habitats that differ in salinity levels.

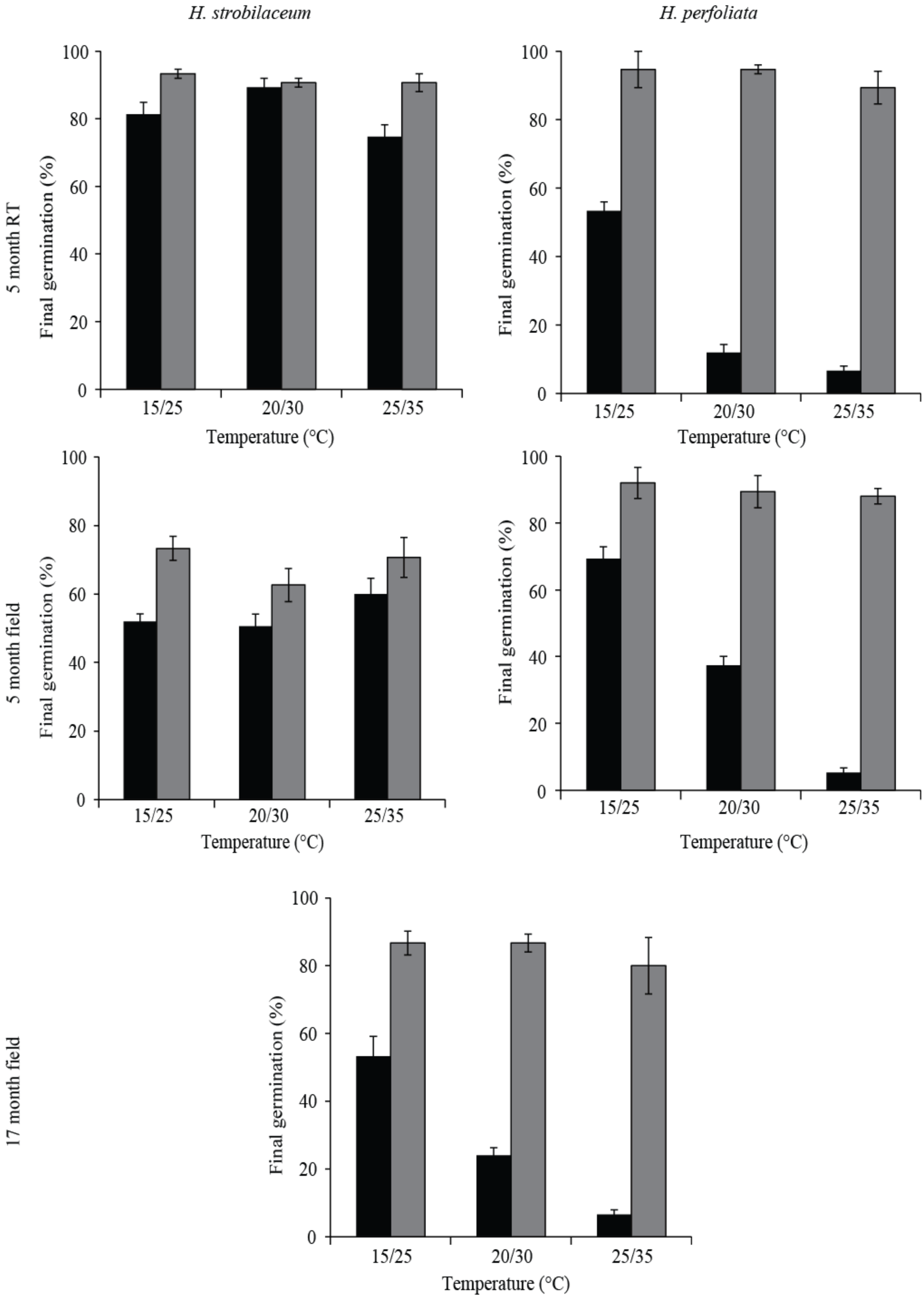

Fig. 1. Effect of seed storage, and light and temperature on final germination percentage of *H. strobilaceum* and *H. perfoliata*. Black bars = dark germination and light bars = light germination.

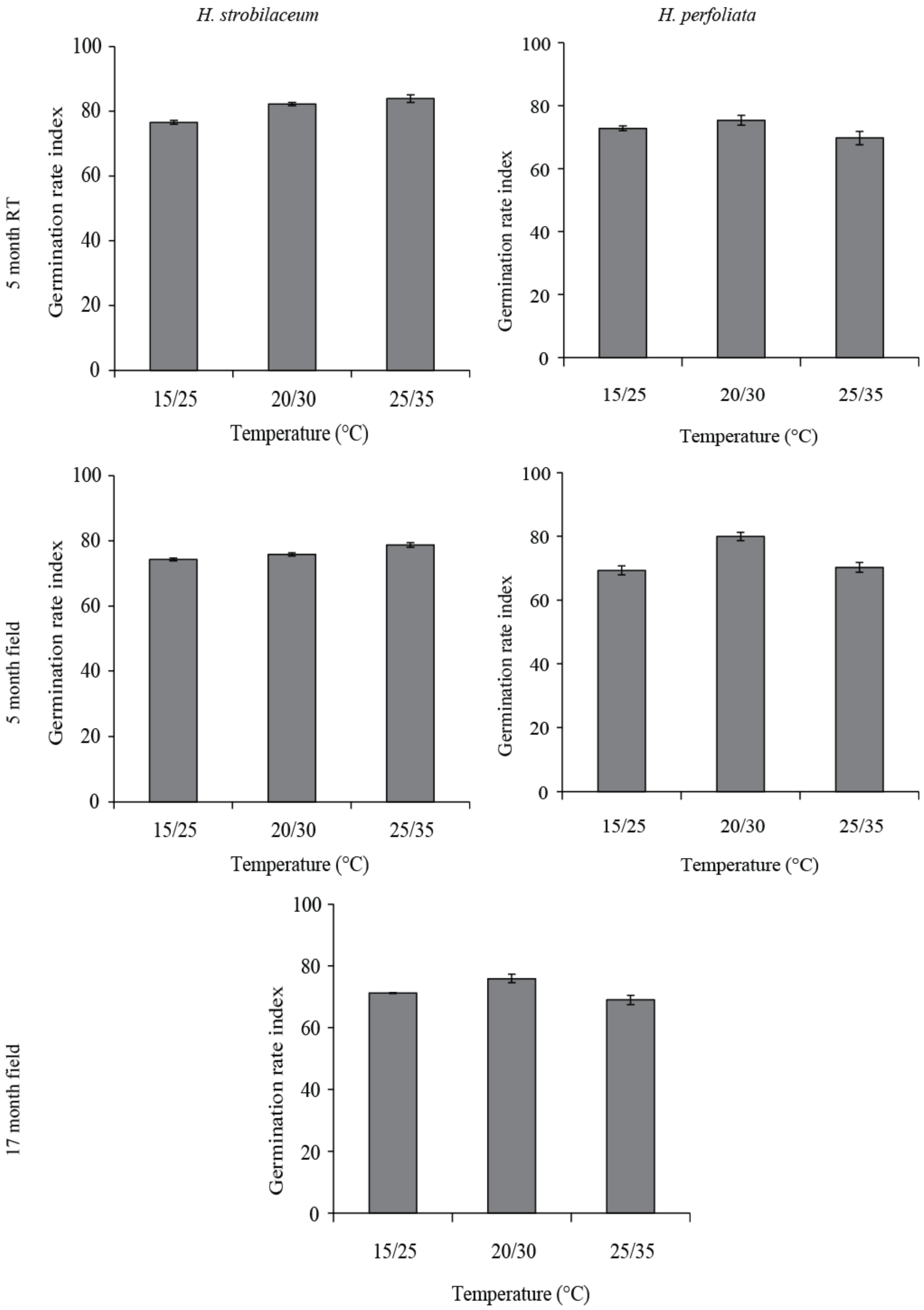

Fig. 2. Effect of seed storage and temperature on germination rate index of *H. strobilaceum* and *H. perfoliata*.

Discussion

Light and temperature are important factors determining seed germination (Bewley & Black, 1994). Halophytes vary in their response to light during germination. Some halophytes have an obligate light requirement for germination, while others germinate well under varying degrees of light and others having no light requirement for germination (Baskin & Baskin, 1995; 1998; Franklin & Whitelam, 2005). Seeds of both *H. perfoliata* and *H. strobilaceum* stored in the aerial seed bank germinated significantly more in light than in darkness, indicating that considerable portions of the seed populations are light-sensitive. Song *et al.* (2006) has documented similar results for *H. strobilacerum* in a Chinese population. A similar trend was reported in three small-seeded *Artemisia* species from the Negev deserts (*A. monosperma*, Huang & Gutterman, 1998; *A. phaerocephala*, Huang & Gutterman, 1999; and *A. ordosica*, Huang & Gutterman, 2000). Light requirement is particularly common in species with very small seeds, preventing germination at greater depths (Botto *et al.,* 1998; Scopel *et al.,* 1991). The two studied species have a very small seed size; the average weights of 100 seeds are 0.11 mg and 0.09 mg for *H. strobilacerum* and *H. perfoliata* respectively. The light requirement for germination of these two species ensures that they would germinate successfully on or near the soil surface when other environmental conditions are suitable for seedling emergence. If seeds are buried too deep in the soil where light cannot penetrate, they might become a part of a persistent soil seed bank (Pons, 2000).

In some species, the light sensitivity of seeds is dependent on phytochrome action and this sensitivity changes with temperature (Smith, 1975). In addition, the induction of dark dormancy has been reported to depend on temperature of incubation (Wesson & Wareing, 1969; Pons, 1991). For example, induction of dark dormancy was observed to be faster at higher than at lower temperatures in species that are well known to form persistent soil seed banks (Pons, 1991). In the present study, seeds of *H. perfoliata* attained very low germination in darkness at higher temperature (25/35^{o}C); less than 5.0% of the seeds germinated in darkness, compared to more than 90% in light. Once dispersed in soil, the small seeds of this species have a high chance of being buried and consequently undergo dark induction and could become a part of the soil seed bank (Bliss & Smith, 1985; Pons, 2000). Thus, germination at a soil depth is likely to be fatal for the resulting small seedlings, which cannot easily reach the soil surface (Pons, 1991).

The results of this study showed high germination for *H. strobilaceum* seeds in both light and darkness at the different temperatures. In *H. perfoliata*, however, germination was high at different temperatures in light, but few seeds germinated in darkness at lower temperatures. From such results, one may infer an adaptive strategy for germination and seedling survival in the natural habitats of the two species. It has been reported that seeds of *H. strobilaceum* tolerate higher salinities (Song *et al.,* 2006) compared to seeds of *H. perfoliata* (Mahmoud *et al.,* 1983; El-Keblawy & Bhatt, 2015). Similarly, adult plants of *H. strobilaceum* tolerate higher salinity levels under field habitats, compared to plants of *H. perfoliata* (Zahran, 1998; Anon., 2012). The ability of *H. strobilaceum* seeds to germinate to high proportions in both light and darkness under high temperature and their greater salinity tolerances during seed germination indicate that they could germinate even after summer rainfalls. The greater salinity tolerances of seedlings and adult plants enable seedlings recruited during summer to survive the increased salinity that results from high evaporation. In addition, the ability of *H. strobilaceum* seeds to germinate in both light and darkness at lower temperatures indicates that seedlings of this species could be recruited well in both summer and winter.

Conclusion

The ability of *H. perfoliata* seeds to germinate in darkness only at lower temperatures seems to concur with a lower sensitivity of both seeds and plants to salinity stress. The occurrence of dark germination mainly at lower temperature indicates that seeds could not germinate until autumn or winter, when saline habitats receive a suitable amount of rainfall that would reduce salinity levels. The lower temperatures associated with lower evaporation rate and the greater chances of rainfall during winter all confer a higher possibility of seedling survival. Conversely, germination of salinity sensitive seeds of *H. perfoliata* in darkness during summer would leave germinated sensitive seedlings at higher risk. At that time, salinity increases very fast because of the higher evaporation rate and the chances of another rainfall event that could extend the favorable period for seedling recruitment is low. More detailed studies on the morphology, dormancy and germination characteristics of seeds of *H. strobilaceum* and *H. perfoliata* are suggested in order to elucidate adaptive strategies of these desert halophytes in stressful saline habitats that have very high temperatures during summer and very rare summer monsoon rainfall. Further studies on germination over a saline gradient and seedling survival of these halophytes could confirm the hypothesis whether the aerial seed bank is an adaptive strategy for germination and seedling survival in the saline habitats of H. strobilaceum and H. perfoliata.

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