Seed Germination Behavior of Halophytes Distributed in Arid Arabian Deserts

A Review of Current Research

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Abstract

This article presents an overview of the seed germination research on halophytes and the factors influencing their germination. The influence of different environmental factors on germination behavior and salt tolerance of seeds was reviewed in 13 halophytes from the United Arab Emirates (UAE) to provide updates in this field of research and identify areas of future research. The literature review indicated that mostly there is a consistent pattern in seed germination behavior of studied halophytes. In the presence of light, a higher germinability was obtained at lower temperature (15/25 °C), as compared with higher temperatures (25/35 °C). In general, germination was relatively faster at 25/35 °C, which would favor faster seedling establishment if rainfall does occur by the end of the growing season in the arid deserts. Salinity treatments differently affected seed germination of halophytes included in this study. Seed germination decreases with increasing salinity; however, it was recovered after seeds were transferred to distilled water and showed species-specific recovery patterns. These patterns

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indicate that seeds can survive higher salinities in their soil seed bank. The seed biology information, including data gathered in the lab-based experiments, would significantly help in optimizing the germination of halophyte seeds for vegetation restoration in arid desert habitats.

Keywords

Halophyte · Salinity · Seed germination · Temperature · Recovery · Storage

1 Introduction

Research into the halophyte seed germination and salinity tolerance has gained momentum in recent years. Halophytes can vary in their salt tolerance and grow in saline environments in both coastal and inland areas, such as in mangrove swamps, salt marshes, seashores, and saline semi-deserts. These plants acquire different adaptation traits, through natural selection, like salt tolerance, resistance, and avoidance, and some species are capable of growing in seawater level salinity or higher (Brown 2019). Scientific literature suggests that the halophytic grasses tend to exclude salt from their tissues and are less salt-tolerant compared with the dicots. Dicots incorporate salt into their tissues to maintain osmotic potential and therefore tend to be succulent and can be very salt-tolerant. As halophytes can play increasingly important roles as models for understanding plant salt tolerance, it is well accepted that the salt tolerance threshold of plants differs and considerably depends on species. Flowers and Colmer (2008), Pirasteh-Anosheh et al. (2016), and González (2019) have provided a comprehensive overview of plant salt tolerance and adaptation strategies in halophytes to survive in diverse saline habitats. These reviews also highlighted that seed heteromorphism, maintenance of seed banks, dormancy, rapid germination, and recovery potential from earlier salinity exposure are among the essential strategies used by different halophytes.

Seed germination is an early life-history trait, which is a key component of a plant's response to the environment. Germination traits are reported to play a significant role in plant distribution in saline habitats (Ungar 1978). Many studies highlighted the variation in seed germination strategies among different species (Meyer et al. 1995; Petrů and Tielbörger 2008; Forbis 2010; Baskin and Baskin 2014; El-Keblawy and Gairola 2017; El-Keblawy 2017; Liu et al. 2018). Under variable spatially and temporally environmental conditions of arid deserts, the timing of germination is critical for successful seedling establishment that can affect plant growth and establishment. Salinity affects germination and emergence of many plant taxa distributed in arid and desert environments (El-Keblawy and Bhatt 2015; El-Keblawy et al. 2015). The majority of halophytes (of Amaranthaceae) belongs to saline habitats of subtropical regions adapted to fast germination strategy (Kadereit et al. 2017). From the available literature, it can be inferred that plants of highly unpredictable and stressful habitats use this strategy to minimize the chances of seedling mortality (Karrenberg et al. 2002; Gutterman 2003; Khan and Gul 2006; El-Keblawy et al. 2014; Bhatt and Santo 2018).

Data from germination-related studies in the laboratory or field conditions can be useful to explain timing and control of germination in seeds of natural habitats. From the functional significance of some of the observed germination characteristics, it could be concluded that certain regenerative mechanisms observed in the field conditions could be predicted from the laboratory examination of seeds. Seed germination-related research on halophytes from salinity-varying environments offers experimental information for restoration of salt-affected ecosystems by exploring patterns in germination traits. Thus, seed biology research has the potential to make significant contributions to the species conservation and restoration/revegetation programs (El-Keblawy et al. 2018c). Here, we present an update on the progress in seed germination research of halophytes in the UAE. This paper provides an overview of seed germination behavior of plant taxa with (1) faster germination, (2) high salinity tolerance at germination stage, and (3) faster recovery from salt stress. Such information is essential to understand the process of seedling establishment and regeneration of native plants, and will also be useful in developing future efforts and strategies for halophytes conservation, and the restoration of the salt-affected areas.

2 Geographical Distribution of Halophytes

The distribution pattern of halophytes varies according to their distinct differences in maximum salt tolerance and subsequent growth responses to salinity (Yuan et al. 2019). Halophytes distribution is generally affected by habitat characteristics such as edaphic and geomorphological factors and fluctuation of climatic factors. Recently, an overview of the halophyte vegetation of the Arabian Peninsula was provided by Ghazanfar et al. (2019). According to this overview, saline environments of the Arabian Peninsula are poor in species with 120 halophytes, which constitute about 4% of the total flora of the Peninsula. Halophytic vegetation in the UAE is distributed in coastal parts, near-coastal parts along the Arabian Gulf and inland Sabkha (Deil and Müller-Hohenstein 1996; Boer 2002; Böer and Saenger 2006; Brown et al. 2008). There are about 76 species of vascular plants considered as halophytes or species that can grow successfully on salty soils in the UAE (Boer 2002; Gairola et al. 2019).

From the eco-physiological and functional point of view, halophytes of the UAE are still under-explored. In this article, halophytes are arranged as per their geographical distribution in the UAE. Besides, their dispersal strategies and categorization in high-salinity and low-salinity groups by their natural habitats are presented; however, sometimes, it is hard to identify the actual group of a particular species (Fig. 1). Some species are predominantly found in salt marshes, but can also occur in saline sandy substrates in the inland desert-like sabkha. As shown in Fig. 1, two perennial species of the genus *Salsola*, *S. drummondii* and *S. rubescens*, and a grass *Halopyrum mucronatum* have comparatively restricted geographical distribution. However, *Haloxylon salicornicum* grows abundantly in almost every ecosystem, including gravel deserts and foothills. Other species, i.e., *Sporobolus spicatus* and *S. imbricata* are also widely distributed, owing to their tolerance to drought

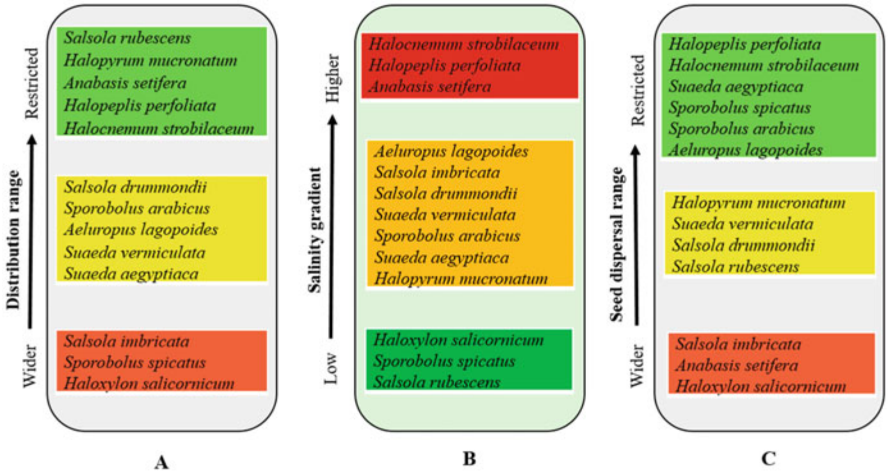

Fig. 1 General pattern of distribution of selected halophytes in UAE (**A**); along natural salinity gradients (**B**) spatial seed dispersal (**C**)

and salinity. *S. imbricata* is highly tolerant of aridity and saline-alkaline conditions. *Anabasis setifera* and *Halopeplis perfoliata* are mainly distributed on the edge of the salt marshes. *Halocnemum strobilaceum* grows primarily in salt marshes. Halophytic grasses are primarily distributed in coastal areas, while sometimes these are also found in inland saline soils. The fruiting season for most of these species is from September to January. The major threat to halophytic vegetation is a loss of natural habitats by urbanization and coastal development. Therefore, halophytic species in the UAE require more research attention given their utilization potential, and more importantly, considering the expansion of salt-affected areas worldwide.

3 Seed Characteristics of Halophytes

Literature suggests that the forms and shapes of seeds are highly varied as per the specific environmental requirements for their dispersal and plant establishment (Hilhorst et al. 2010). In many higher plants, seeds ensure dispersal of a particular species in space and time, for which plants have evolved different dispersal strategies. Seed dispersal, dormancy, and germination strategies contribute toward the geographic distribution of different plant species (Kos et al. 2012). Similarly, seed size and dispersal of diaspore units of halophytes could play an important role in regulating their dormancy, germination, establishment, and restoration (Ungar 1987; Hutchings and Russell 1989; Huiskes et al. 1995; El-Keblawy et al. 2018b). The type and morphology of diaspores and dispersal mode data of plant species were obtained from the literature and authors field notes and databases. Where the data was lacking, the taxa were assigned a dispersal mode based on that of their relatives with similar seed. Species belongs to family Amaranthaceae have the maximum average value of diaspore size compared to Poaceae. Among 13 studied species, *S. arabicus* and *S. spicatus* have the smallest diaspore unit “seed” (0.08 cm for each), while the biggest unit was recorded for *S. imbricata* “fruit” (0.8 cm). The diaspore traits may reflect different recruitment strategies of plants under harsh and unpredictable desert conditions. Research shows that morphology, mass, and diaspore size can influence important traits, including seed dispersal, dormancy, and germination of many desert halophytes (El-Keblawy et al. 2014, 2016; El-Keblawy and Bhatt 2015). Among halophytes of this study, *S. setifera*, *H. salicornicum*, *S. drummondii*, and *S. imbricata* have winged structures on seeds as a dispersal-enhancing character, which also contributes in regulating the dormancy and seed bank dynamics (El-Keblawy 2014; Shabana et al. 2018; Gairola et al. 2019). Other species, including *Aeluropus lagopoides*, *H. strobilaceum*, *H. perfoliata*, *H. mucronatum*, *S. arabicus*, *S. spicatus*, *S. aegyptiaca*, and *Suaeda vermiculata* produce small seeds, which lacks dispersal-enhancing characters (Khan and Gul 2006; El-Keblawy et al. 2015; Shabana et al. 2018). Generally, halophytes that produce seeds with winged perianths usually form a transient seed bank, and those that produce wingless seeds maintain persistent seed bank in soil (El-Keblawy 2013) (Table 1).

Seed maternal environment can also influence numerous traits related to seed germination (Wang et al. 2012; Yang et al. 2015; Liu et al. 2018). Literature indicates that certain halophytic species produce heteromorphic seeds to ensure optimum seedling establishment under high saline conditions (Liu et al. 2018, and references therein). A recent review by Liu et al. (2018) highlighted the role of maternal characters in the production of heteromorphic seeds under saline conditions. As one of the consequences of stressful saline conditions, mother plants may produce subsequent generations with different phenotypes (due to transgenerational effects), which is an adaptive strategy to survive under harsh conditions (Liu et al. 2018).

4 Temperature and Light Requirements for Germination

Seed germination in many desert plants is influenced by key environmental factors such as temperature, light, soil moisture, soil salinity, and seed burial depth (Gutterman 2000; Weber 2009; El-Keblawy et al. 2015). Hence, seeds of different desert plants show species-specific responses to the critical environmental factors. Gul et al. (2013) reported that salinity, temperature, and photoperiod are significant factors influencing seed germination responses in species of saline habitats. Desert halophytes employ different strategies to grow successfully under high saline conditions. Seeds of some halophytic species can germinate under high salinity and therefore has high tolerance at germination level. On the other hand, seeds of other species become dormant when exposed to high salinity and can germinate when rainfall lowered soil salinity (Weber 2009; Ahmed and Khan 2010). However, in deserts, annual rainfall varies substantially in both amount and timing; hence, it acts as a primary limiting factor for seed germination (Gutterman 1993). Besides water, temperature and photoperiod are often reported to influence salt tolerance and germination recovery of halophyte seeds (El-Keblawy 2004; Gul et al. 2013; Rasheed et al. 2019). In general, a

Table 1 Characteristics of the species included in this study

Species	Family	Growth form	Diaspore length (cm)	Dispersal mode	Diaspore appendages
Aeluropus lagopoides	Poaceae	Perennial, grass	0.12	Semachory	Absence
Anabasis setifera	Amaranthaceae	Perennial, shrub	0.50	Anemo-meteochory	Wings
Halocnemum strobilaceum	Amaranthaceae	Perennial, shrub	0.15	Barochory	Absence
Halopeplis perfoliata	Amaranthaceae	Perennial, shrub	0.30	Barochory	Absence
Halopyrum mucronatum	Poaceae	Perennial, grass	0.10	Semachory	Short appendage
Haloxylon salicornicum	Amaranthaceae	Perennial, shrub	0.70	Anemo-meteochory	Wings
Salsola imbricata	Amaranthaceae	Annual or perennial, shrub	0.80	Anemo-meteochory	Wings
Salsola drummondii	Amaranthaceae	Perennial, shrub	0.70	Anemo-meteochory	Wings
Salsola rubescens	Amaranthaceae	Perennial, shrub	0.50	Anemo-meteochory	Wings
Sporobolus arabicus	Poaceae	Perennial, grass	0.08	Semachory	Absence
Sporobolus spicatus	Poaceae	Perennial, grass	0.08	Semachory	Absence
Suaeda aegyptiaca	Amaranthaceae	Annual or short-lived perennial, herb	0.30	Barochory	Spongy perianth
Suaeda vermiculata	Amaranthaceae	Perennial, shrub	0.30	Barochory	Absence

thermoperiod is reported to play an important role in the seeds of desert plants to select a suitable time for germination and seedling establishment (Baskin and Baskin 2014). Photoperiod also influence germination and determine when and where the seed will germinate (Fenner and Thompson 2005).

Furthermore, it has been reported that the interaction between light and temperature during germination can influence the sensitivity of seeds to both thermoperiod and photoperiod (Baskin and Baskin 2014; El-Keblawy et al. 2016). Several studies have shown that in many halophytes, seed germination occurs when the optimal combination of key environmental factors meets. Generally, in the arid deserts of the UAE, the time of seed maturation usually coincides with the onset of rainfall when the temperature becomes relatively cooler, and conditions get favorable for seed germination and seedling recruitment of halophytes (El-Keblawy et al. 2016). The interaction of temperature and salinity affects the seed germination of many halophytes (Khan et al. 2001; El-Keblawy 2004; Rasheed et al. 2019). Different patterns of germination and salinity tolerance behavior have been found in halophytes. The topic related to

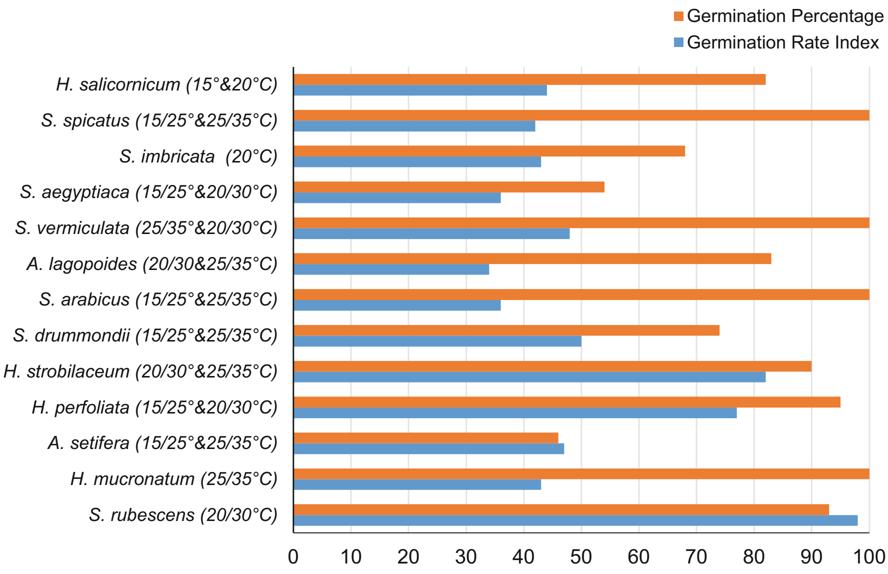

Fig. 2 Optimal temperature for seed germination and maximum germination rate index of the seeds of 13 species (indicated in brackets). The tested temperature range to seed germination for most species was 15/25 °C, 20/30 °C and 25/35 °C, and thermoperiod alternated with light (12-h photoperiod and 12-h dark), whereas for *H. salicornicum* it was constant temperatures of 15, 20, 25, and 30 °C and for *S. imbricata* it was a constant temperature of 20 °C. Studied halophytes: *H. salicornicum* (El-Keblawy 2013), *S. imbricata* (El-Keblawy et al. 2007), *S. aegyptiaca* (El-Keblawy et al. 2016), *S. vermiculata* (El-Keblawy et al. 2018a), *A. lagopoides*, *H. mucronatum* *S. arabicus*, *S. spicatus* (El-Keblawy 2017), *Anabasis setifera* (El-Keblawy et al. 2016), *H. perfoliata*, *H. strobilaceum* (El-Keblawy et al. 2015), *S. drummondii* (Elnaggar et al. 2019) and *S. rubescens* (El-Keblawy et al. 2014)

salinity tolerance at the germination stage and subsequent recovery of seeds is covered in the following section in detail. Studying seed germination of halophytes can provide valuable information about germination requirements and limit of salinity and other abiotic stress tolerance (Baskin and Baskin 1998; Gul et al. 2013; Manzoor et al. 2017), thereby helps in species selection for ecosystem restoration programs.

The halophytic species included in this article are commonly found in either coastal ecosystems or co-occurring in coastal ecosystems and inland salt flats of the UAE. Most of these halophytes exhibited high germination percentages under light and at lower temperature (Fig. 2). Grass species like *A. lagopoides* and *H. mucronatum* had maximum germination at higher temperature (20/30 °C and 25/35 °C). However, both species of *Sporobolus* reached higher germination at lower temperature (15/25 °C). Only *H. mucronatum* and *S. spicatus* seeds showed non-photoblastic behavior during germination with insignificant differences between germination percentages under light and dark, but the percentages were higher in the light. Germination was faster at higher temperatures for seven studied species. The seeds of *S. rubescens*, *H. strobilaceum*, *H. perfoliata*, and *H. mucronatum* germinated faster than the rest of the species, and their optimal temperatures were 25/35 °C, 20/30 °C and 25/35 °C, respectively (Fig. 2).

In this analysis, the optimum temperatures for maximum seed germination ranged from 15/25 °C to 20/30 °C. This result concurred with a previous study by Gairola et al. (2019), where the optimum temperatures for germination of some halophytes were found to be 15/25 °C. In addition, among all the studies, seed germination was stimulated by light at all temperature regimes; however, a proportion of seeds still germinated under dark. It is noteworthy that seeds of the studied species were partially positively photoblastic that showed relatively higher germination under light conditions than in darkness. Generally, a requirement for light implies that germination would occur when seeds placed onto or near to the surface of the soil (El-Keblawy et al. 2016). Our analysis also suggests that buried seeds are still capable of germination. Nevertheless, it is suggested that higher germination would occur when seeds located on the soil surface than buried in the soil, as reported by other researchers (Khan and Gul 2006; Gul et al. 2013; El-Keblawy et al. 2017; Liu et al. 2018). Our analysis indicated that higher temperatures (25/35 °C) resulted in both faster germination and a higher total number of germinated seeds in *H. mucronatum* (Fig. 2).

In a study assessing drought tolerance in *S. drummondii*, Elnaggar et al. (2019) reported that seeds of this species germinated over 40% under higher drought conditions (−1.2 MPa). Based on the results of this study, the authors highlighted that the broad window of germination for *S. drummondii* seeds indicate a lower risk of future warmer climate on seed germination attributes of this species. A study assessing the impact of aerial and room temperature storages on light and temperature requirements during germination of *H. strobilaceum* and *H. perfoliata* seeds showed that 17-month stored seeds of *H. perfoliata* had no difference in germination between the aerial seeds bank (~93%) and room temperature storage (~95%) (El-Keblawy and Bhatt 2015), whereas 5-month stored seeds of *H. strobilaceum* showed over 80% germination in room temperature (23 °C) storage seeds than aerial seed bank (61.5%) and seeds of room temperature storage maintained viability more than the field-stored seeds. Recently, seed germination of eight halophytes stored under ex situ storage conditions was evaluated. Results indicate that most of the halophytes maintained germination up to 3 years when stored at −18 °C (Gairola et al. 2019). Such results are encouraging in a way that maintaining the viability of seeds under long-term storage would help in the restoration of salt-affected habitats. Further, species with a reduction in seed germination during storage needs to be tested repeatedly to establish the re-collection plans.

5 Seed Germination Responses to Salinity

Seed germination under saline habitats is a complex process, and plants inhabiting these soils adopt interesting mechanisms to regulate germination (Liu et al. 2018). These adaptations ensure the survival and distribution of halophytes. Halophytes occur naturally in habitats with higher soil salinities, usually from sodium chloride (NaCl). A wide range of variability in salt tolerance among halophytic species have already been reported (Khan and Gulzar 2003; Khan and Gul 2006; Redondo-

Gómez et al. 2008; Fernández et al. 2016; El-Keblawy et al. 2015, 2017; Manzoor et al. 2017; Rasheed et al. 2019; Bhatt et al. 2020). Based on the available literature, it has been established that some halophytes show salt-tolerance, while others use a salt-avoidance strategy at seed germination level, and some other species represent both tolerance and avoidance mechanisms.

In present analysis, seeds of all studied species were non-dormant and germinated maximally in non-saline conditions. Relatively high seed germination was observed under low and moderate (15/25 and 20/30 °C) temperatures, which indicates that halophytes of arid zone are adapted to cope with stochastic and low rainfall by producing seeds (with high germination) mainly during winter rainfall season with low temperatures and less soil evaporation. This confers a longer growing period to newly emerged seedling for establishment (El-Keblawy et al. 2016). It is also observed that seed germination decreased with increasing salinity, and only a few seeds have been germinated at hyper-saline conditions. However, in some species, germination is recovered when ungerminated seeds transferred from high salinity to distilled water. The information on salt tolerance responses of halophyte seeds to temperature sensitivity and germination recovery from salinity is given in Table 2. For example, *A. setifera* (c. 6% germination at 800 mmol/L NaCl; El-Keblawy et al. 2015), *S. imbricata* (18% germination at 500 mmol/L NaCl; El-Keblawy et al. 2007), and *S. vermiculata* (7% germination at 400 mmol/L; El-Keblawy et al. 2018a) have been reported as most salt-tolerant halophytes species from the UAE. However, *S. rubescens* (yellow-winged seeds) do not germinate in mediums containing >100 mmol/L NaCl, hence regarded as salt-sensitive (El-Keblawy et al. 2014). Several studies reported that salt-induced inhibition of seed germination in halophytes could be related to low water potential (osmotic stress) or/and ionic toxicity (ionic stress) (Hameed et al. 2013; El-Keblawy et al. 2014; Lin et al. 2016; Manzoor et al. 2017). Higher salinity tolerance during germination has been reported for *S. drummondii* seeds, as some seeds of this species were able to germinate in extremely high salinity, i.e., 1000 mM NaCl (Rasheed et al. 2015). This indicates that salinity tolerance of halophyte seeds is a variable trait (Rasheed et al. 2019). In some halophytes, low salinity did not influence seed germination under different temperature regimes. It showed that halophyte seeds are able to germinate during summer rains, where they have to deal with combined stresses of temperature and salinity to survive under fluctuating environments.

Germination of *S. imbricata* and *S. vermiculata* seeds collected from non-saline habitats was inhibited at ≤500 mM NaCl; however, germination inhibition occurred at <800 mM NaCl for *H. salicornicum*, *H. strobilaceum*, and *A. setifera* (Table 2). Seed germination of *S. aegyptiaca* and *S. rubescens* was very low at 100–300 mM NaCl under both higher (25/35 °C) and moderate temperatures (20/30 °C), indicating that seeds were more sensitive to salinity than temperature. In further, seeds of *S. vermiculata* and *S. imbricata* are highly tolerant to salinity and temperature variations but are partially photoblastic in nature, hence do not germinate if buried under the soil. It is also observed that seeds of *S. vermiculata* and *S. imbricata* maintained their viability in saline solutions and showed maximum recovery (90% and 70%, respectively) when transferred to normal conditions (distilled water).

Table 2 Representative studies highlighting the responses to salinity tolerance during germination, temperature sensitivity, and recovery from salinity stress in different species

Species			Salinity tolerance (mM NaCl)	Temperature sensitivity		Recovery from salinity stress		Reference
				$\leq$30/20 °C	>30/20 °C	<600 mM	>600 mM	
Haloxylon salicornicum			800	LS	HS	HR	MR	El-Keblawy and Al-Shamsi 2008
Anabasis setifera			800	LS	HS	HR	LR	El-Keblawy et al. 2016
Suaeda vermiculata	Saline MH		300	LS	HS	HR	–	El-Keblawy et al. 2018a
	Non-saline MH		500	LS	HS	HR	–	
Suaeda aegyptiaca	Saline MH		200	LS	HS	LR	–	El-Keblawy et al. 2017
	Non-saline MH		200	LS	HS	HR	–	
Salsola imbricata			500	LS	HS	HR	–	El-Keblawy et al. 2007
Salsola rubescens	Red fruits	W	500	LS	HS	–	–	El-Keblawy et al. 2014
		DW	500	HS	LS	–	–	
	Yellow fruits	W	100	LS	LS	–	–	
		DW	500	LS	LS	–	–	
Halocnemum strobilaceum	RT-stored seeds (5 months)		600	LS	HS	HR	LR	El-Keblawy and Bhatt 2015
	Field-stored seeds (5 months)		800	LS	HS	LR	LR	
Halopeplis perfoliata	RT-stored seeds (5 months)		400	LS	HS	LR	–	
	Field-stored seeds (5 months)		400	LS	HS	HR	–	
	Field-stored seeds (17 months)		400	LS	HS	LR	–	

LS low sensitive, *HS* high sensitive, *LR* low recovery, *MR* medium recovery, *HR*: high recovery, *MH* maternal habitat, *W* winged, *DW*: de-winged, *RT* room temperature

However, seeds of *S. aegyptiaca* showed very less recovery (20%), indicating that seeds had lost viability under high salinity.

In general, salt-induced inhibition of seed germination of halophytes is a species-specific trait. For instance, a considerable reduction of seed germination percentage was observed in *S. aegyptiaca* at 100 mM NaCl, while this concentration did not affect seed germination in *S. vermiculata*. In annual or biennial halophyte like *S. aegyptiaca*, germination strategies are important for the plant's survival (Gul et al. 2013; Hajiboland et al. 2018). Comparing two annual/biennial halophytes, the germination of *S. aegyptiaca* was more susceptible than *S. imbricata* to varying salinity. Similar to other halophyte species (Khan and Gul 2006; Gul et al. 2013; Hajiboland et al. 2018), seeds of *S. vermiculata* and *S. imbricata* also sowed high germination recovery when transferred to distilled water, indicating that these seeds can maintain viability in soil seed bank even after exposing to higher salinity. Rasheed et al. (2019) provided an overview of seed germination and recovery responses of some sabkha and playa halophytes to varying salinity, temperature, and photoperiod. The authors found that seed germination of playa species was sensitive to low temperatures, whereas sabkha species were sensitive to high temperature under saline conditions. High salt-resistant species like *Halogeton glomeratus* and *Suaeda fruticosa* showed better seed germination percentage under salinity. These findings suggest that seed germination response to combined temperature and salinity could be an important strategy for halophytes to survive in variable saline environments. Debez et al. (2018) reported that as part of the plant survival strategy, annual halophyte *Cakile maritima* prevents germination and seedling establishment under high salinity (i.e. 200 mM NaCl). Authors further suggested that high salinity might pose a priming-like effect, by boosting seed germination and vigor of this species under post-stress conditions, sustained by active metabolic machinery. Bhatt et al. (2017) showed that salinity completely inhibited germination of two morphs (yellow and pink colored) of *Salsola vermiculata* when their perianth wings were intact. However, removal of perianth wing significantly increased germination percentage and rate of both morphs, which were decreased with increasing salinity. The authors further reported that de-winged pink seeds had better salinity tolerance and recovery than their yellow counterparts did. This indicates that *S. vermiculata* may use perianth color as an adaptive strategy to survive in a hostile desert environment.

Species-specific germination recovery responses of halophytes have been reported by several authors. For example, higher germination recovery at lower temperatures was reported for *S. imbricata* (El-Keblawy et al. 2007), *Salsola vermiculata* (Guma et al. 2010), *H. salicornicum* (El-Keblawy and Al-Shamsi 2008), and *Limonium stocksii* (Zia and Khan 2004), whereas *A. lagopoides* seeds recovered quickly at higher temperatures (Gulzar and Khan 2001). Bhatt et al. (2020) also found the highest recovery percentage for *A. lagopoides* seeds from hypersaline habitat when incubated at higher temperatures (25/35 °C). Thus, plants of the saline arid desert are adapted to maintain high seed viability despite facing a range of salinity and the ability to germinate upon arrival of suitable conditions. El-Keblawy and Bhatt (2015) reported greater salinity tolerance of *H. strobilaceum* seeds (800 mM NaCl); however, seeds of *H. perfoliata* can germinate up to 400 mM NaCl. Qu et al. (2008) also reported *H. strobilaceum* as a salt-resistant species, which can germinate up to 750 mM NaCl. On the other hand, Mahmoud et al. (1983) reported that seeds of *H. perfoliata* could germinate only up to 250 mM NaCl. However, Rasool et al. (2017) reported that seeds of *H. perfoliata* could germinate up to 600 mM NaCl, and hyper-salinity with high-temperature regime (25/35 °C) caused high seed mortality of this species. The higher germination recovery at lower to moderate temperatures could be a strategy of some species to prevent seedling formation in early summer when high temperature alongside high salinity would hinder the chances of seedling survival, in some cases, low germination recovery from high salinity, perhaps due to ion toxicity, as reported widely in the literature. In summary, salinity tolerance is a variable trait in halophyte seeds. The sensitivity of seeds to extremes of salinity, temperature, and darkness might indicate an adaptation strategy of the species to limit germination only under optimum conditions (e.g., after sufficient rainfall) to maximize the chances of seedling survival (Rasool et al. 2017; El-Keblawy et al. 2017; Rasheed et al. 2019; Bhatt et al. 2020).

6 Rapid Seed Germination Strategy of Halophytes

Seeds of arid zone halophytic plants are often characterized by faster germination to cope with infrequent and unpredictable rainfall. Thus, rapid germination is the dominant trait of many desert halophytes, which allows them to capitalize soils with less salinity after rainfall and favor seedling recruitment. For example, higher rate of seed germination was recorded in *S. imbricata* (El-Keblawy 2014), *H. salicornicum* (El-Keblawy and Al-Shamsi 2008), and *S. drummondii* (Rasheed et al. 2019). The Sharjah Seed Bank and Herbarium also supports the results of non-dormancy and faster germination rates in these species (unpublished data). In halophytes like species of *Salsola* and *Haloxylon*, seeds contain fully differentiated spirally coiled embryos. In these species, seed germination merely consists of the uncoiling of the spiral embryo after imbibition resulting in quick germination (Parsons 2012). Parsons (2012) also mentioned that seeds of a Sahara desert halophyte *Anabasis aretioides* imbibed after a rain shower and unfolded their embryos within 10 min to establish seedlings quickly (Grenot 1974).

In some cases, plant species producing large quantities of seeds might exhibit rapid germination across a range of diurnal temperatures to take advantage of rainfall events across all seasons. Literature suggests that several halophyte species in subtropical regions are characterized by high seed production and fast germination of recently dispersed seeds. As discussed by Duncan et al. (2019), such alternative regeneration traits allow them to capitalize on sporadic rainfall, and may have a crucial role in explaining population dynamics in arid desert ecosystems. Thus, the seed germination stage is a significant demographic bottleneck for the plant of saline environments because germination occurs mainly when seed dispersal coincides with appropriate environmental conditions that allow rapid germination and seedling establishment. Parsons (2012) reviewed that very fast germination is associated with plant families having small to tiny seeds and little or no endosperm. According to

Parsons (2012), seeds of these species have soft and thin seed coats that readily imbibe water. He suggested that species exhibiting fast germination are mainly from high-stressed habitats, e.g., arid or saline environments, which can be of profound ecological significance in minimizing seedling mortality in such habitats. Representative studies are required to test the relationship between germination speed and seed size with different halophytic species, including habitat indifferent species, to make general assumptions about this relationship.

7 Conclusion and Outlook

Literature suggests that seeds of selected halophytic species are non-dormant, positively photoblastic, and generally preferred low to moderate temperatures for germination. The increase in salinity decreased seed germination of halophytes included in this study. In most cases, maximum germination obtained at low temperature corresponds well to the temperature that prevails during the winter season in subtropical arid deserts. Such germination response indicates that seeds should be sown in the field at a time when habitat moisture and lower temperature conditions are most favorable for germination in arid desert environments. A high germination percentages and germination rates under higher salinity (e.g., *Anabasis setifera*) exhibits a typical salt-tolerance behavior of a species. In contrast, a salt-avoidance strategy in some species (e.g., *Suaeda vermiculata* and *Salsola imbricata*) has shown by a high percentage of germination recovery after the alleviation of salinity stress. Seeds that show fast germination recovery at lower temperature may indicate the best conditions, especially in dry years, for seed sowing of these species to restore degraded deserts. Species strategies of preventing seed germination under high temperature and salinity conditions coincided well with the unfavorable season for seedling growth and establishment during the summer period in arid deserts. The current knowledge on germination patterns of arid desert halophytes would have implications for improving future restoration outcomes in salt-affected habitats. However, additional studies on halophytes from the deserts of UAE considering their soil seed banks and seed heteromorphism, the effects of storage and abiotic stresses on germination and seedling growth, phytoremediation potential, medicinal properties, and applications in saline agriculture to improve food security, would be helpful in creating new knowledge and understanding.

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