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Germination behavior of *Seidlitzia rosmarinus* Boiss., a perennial halophyte of Arabian deserts

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Abstract

Seidlitzia rosmarinus, a C_4 perennial halophyte, is distributed in the deserts of the Middle East and Central Asia. This species has potential for rehabilitating salt-affected soils due to its high salinity resistance and soil-stabilizing ability. It produces seeds with wings attached to the perianth that facilitate their dispersal by wind. Both intact (winged) and de-winged seeds under different light, temperature and salinity conditions were tested to determine the role of the wings during seed germination. Both intact and de- winged seeds were able to germinate under all the tested temperature regimes, with better germination occurring at lower temperature than at higher temperature. De-winged seeds had higher germination percentages compared to the intact seeds. Light enhanced the germination of intact seeds. However, de-winged seeds germinated equally well under light and darkness. Both intact and de-winged seeds were able to germinate when exposed to saline solutions and were also able to recover their germinability once they were transferred from the saline solution to distilled water. This ability of *S. rosmarinus* seeds to germinate at lower salinity and remain germinable even at higher salinity could be due to its evolution to survive in unpredictable desert environments.

Introduction

Environmental factors such as drought, salinity, high evapotranspiration and irradiance are the major limiting factors for plant growth and survival in the desert (Yasseen, 2011). Therefore, plants inhabiting desert areas have developed various morphological, anatomical and physiological modifications that help them thrive under such adverse conditions (Abdel-Bari et al., 2007). Production of winged fruits under stressful environmental conditions is an adaptation to wind dispersal that helps the seed to escape by increasing offspring dispensability and colonization in favorable areas under the harsh and unpredictable desert conditions (Howe and Smallwood, 1982; Jurado et al., 1991; Venable and Brown, 1993; Brändel, 2007; Venable et al., 2008). Since wings contain abscisic acid and a higher amount of salt, they act as mechanical barriers for water absorption and subsequent radical growth, which inhibit germination (Takeno and Yamaguchi, 1991; Wei et al., 2007; Xing et al., 2013; El-Keblawy et al., 2013; Bhatt et al., 2016; Bhatt et al., 2017). However, they protect the seeds from salinity damage and also regulate the seed germination level and timing (Wei et al., 2007; Xing et al., 2013; El-Keblawy and Bhatt, 2015). Moreover, they also determine the proper place for seed storage and the time of germination and thus influence soil-seed bank dynamics (Xing et al., 2013).

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Seidlitzia rosmarinus Boiss (Synonym: *Salsola rosmarinus* [Bunge ex Boiss.] Eig) in the *Amaranthaceae,* is a perennial halophytic shrub that grows up to 80 cm in height and inhabits sandy plains, *sabkha* (salt flats), *wadi* (riverine gulches) and drainage channels that have alkaline and saline soils (Breckle, 1986; Jongbloed, 2003). It is widely distributed in Iran, Jordan, the United Arabic Emirates, Saudi Arabia, Kuwait, Qatar, Bahrain, Jordan, Afghanistan and Central Asia (Jongbloed, 2003; Hadi, 2009; Deymeh et al., 2012; Sagheb-Talebi et al., 2014). *S. rosmarinus* has been identified as one of the potential species that could be used for rehabilitating degraded desert rangelands and salt-affected soils due to its high salinity resistance and soil-stabilizing ability (Koocheki and Mahalati, 1994; Jafari et al., 2003; Amiraslani and Dragovich, 2011; Mahmoodi et al., 2013) besides being frequently grazed by camels (Koocheki and Mahalati, 1994). Considering the ecological and economic role played by *S. rosmarinus* in the desert ecosystem (Hadi and Sharif, 2003; Ashraf and Harris, 2004; Hadi, 2009), it is important to know how environmental factors influence seed germination in this species. Environmental factors such as light, water, temperature, salinity and their interaction control the seed germination of desert halophytes (Noe and Zedler, 2000; Gulzar et al., 2013; El-Keblawy et al., 2013; El-Keblawy and Bhatt, 2015; Bhatt and Santo, 2016). Therefore, initial establishment of a species under desert conditions mostly depends on the seed germination response.

S. rosmarinus produces seeds (fruits) that ripen during October and November with attached winged perianth that help their dispersal by wind (Burtt and Lewis 1954). Previous studies have examined the salinity tolerance of *S. rosmarinus* seeds during germination using different saline solutions, such as sodium chloride (NaCl), sodium nitrate ($NaNO_3$), potassium chloride (KCl) and potassium nitrate (KNO_3) (Kurkova et al., 2002; Hadi et al., 2007; Rasuoli et al., 2012). However, the role of the wing perianth (intact and de-winged) in germination, salinity tolerance and germination recovery has not been investigated to date. The current study hypothesized that these structures may have a role in regulating seed germination and salinity tolerance. Therefore, the effects were investigated of the wings (presence or absence) on the germination response of *S. rosmarinus* seeds under varying levels of light, temperature and salinity. The assessment also considered whether the seeds subjected to elevated levels of salinity were able to recover and germinate after being transferred to distilled water.

Materials and Methods

Seed collection and storage

Mature fruits of *S. rosmarinus* were collected in December 2016 from Julaia (28º 52’49”N, 48º 16’32”E), Kuwait. Seeds were collected from 20–25 individuals to represent population diversity. *Salsola imbricata, Suaeda vermiculata* and *Heliotropium bacciferum* are the common associated species of *S. rosmarinus* in its natural population. The collected seeds were air-dried, cleaned and stored in brown paper bags at room temperature (20 ± 2 °C) for 1 mth. The seed mass (mean ± SD) was determined for the intact and de-winged seeds of *S. rosmarinus* by weighing three replicates of 50 seeds each using a Sartorius analytical balance with an accuracy of 0.0001 g. Wings were removed from the seeds using a hand-made rubber thresher and care was taken not to scarify the seed coat while removing the wings (El-Keblawy et al., 2013).

Native habitat

The coastal location is hyperarid with a sporadic annual precipitation of 114 mm occurring mostly between October and March and the summer is hot and humid with daytime temperatures reaching above 50 °C (Omar et al., 2007).

Germination experiments

Germination of intact and de-winged seeds of *S. rosmarinus* was studied under two alternate temperature regimes (15/20ºC and 20/25ºC) and two illumination conditions (continuous darkness and 12 hr light photoperiod). Differences in the light regimes coincided with the higher temperatures. These temperature regimes are close to those that occur between October and March when the conditions for germination and seedling establishment are better due to the higher chance of rainfall in the study area (Omar et al., 2007). Darkness was achieved by wrapping Petri dishes in aluminum foil. The germination was conducted in tight-fitting Petri dishes (9 cm diameter) containing one disk of Whatman No. 1 filter paper moistened with 10mL of distilled water. Four replicates of 25 seeds each (intact and de-winged) were used for each treatment. Emergence of the radicle was the criterion for germination. Germinated seeds were counted and removed daily from the photoperiod treatments over a total 14 d test period and at the end of the day 14 for the darkness treatments. The experiment was stopped after 14 d because no new germination had occurred for a consecutive 3 d period.

Effect of salinity on seed germination

To assess the salinity tolerance on seed germination of *S. rosmarinus*, both intact and de-winged seeds were germinated under different salinity levels (100 mM NaCl, 200 mM NaCl, 400 mM NaCl, 600 mM NaCl). Seeds sown under the same conditions but in distilled water were used as the control. Four replicates, each of 25 seeds, were used for each treatment. Seeds were germinated in Petri dishes (9 cm diameter) containing a single disk of Whatman No. 1 filter paper moistened with 10 mL of salt solution. Petri dishes were sealed with parafilm to minimize evaporation and placed in 15/20°C under two illumination conditions (constant darkness and 12 hr light photoperiod). The highest temperature coincided with the light period. Seed germination was recorded as mentioned above.

Germination recovery

After 14 d, seeds (intact and de-winged) that had failed to germinate in both light and darkness and the different NaCl treatments were transferred to distilled water to test their ability for germination recovery. The recovery percentage (RP) was calculated using Equation 1:

$$RP = (a\text{-}b/c\text{-}b) \times 100 \quad (1)$$

where a is the number of seeds that germinated in the saline treatments after a 14 d period plus those that germinated after another 14 d period in distilled water; b is the number of seeds that germinated in the saline treatments and c is the total number of seeds tested (Gul and Weber, 1999; Yang et al., 2010).

Initial germination was determined using Equation 2 and the final germination was determined using Equation 3:

$$(b/c) \times 100 \quad (2)$$

$$(a/c) \times 100 \quad (3)$$

where b is the number of seeds that germinated in the saline treatments and c is the total number of seeds tested.

Data analysis

The effect of the temperature and light regimes on seed germination was evaluated by calculating the final germination percentage (mean ± SD) and mean germination time (MGT; mean ± SD, in days). The MGT was calculated using Equation 4:

$$MGT = \sum DN/\sum N \quad (4)$$

where D is the number of days counted from the date of sowing and N is the number of seeds germinated on day D. The values of germination percentages were normalized using an arcsine square-root transformation and then subjected to analysis of variance (ANOVA) and the least significant differences (LSD) *post hoc* test using the SPSS software package (version 17) SPSS Inc., Chicago IL, UDA) and the untransformed data are shown in tables.

The effects of light conditions (photoperiod and total darkness), temperature regimes (15/20ºC and 20/25ºC) and the two seed types (intact and de-winged) on the final germination percentage were analyzed using a three-way factorial ANOVA. The statistical analysis of MGT was analyzed using a two-way factorial ANOVA with temperature regime (two levels) and seed type (two levels) as the sources of variation. A three-way factorial ANOVA was used to test the effect of different concentrations of NaCl (five levels), light conditions (two levels) and seed type (two levels) on the final germination percentage.

Results

Seed mass

Wings constituted 60.4% of total seed weight. Their removal reduced the mean mass (± SD) of 50 seeds from 250.3 ± 0.1 mg to 99.3 ± 0.7 mg.

Effect of temperature and light regimes

The effect of incubation temperature and light regimes on the final germination percentage of intact and de-winged seeds and the ANOVA results are shown in Tables 1 and 2, respectively. Temperature, light and seed type (intact and de-winged seeds) had significant ($p < 0.05$) effects on seed germination. However, the effect of light on germination percentage was only marginally significant ($p = 0.047$) compared to the temperature ($p = 0.013$) and especially the seed type ($p < 0.001$). The two-way and three-way interactions among the different factors were not significant ($p > 0.05$) as shown in Table 2. A one-way ANOVA was used to compare the final germination percentages of intact and de-winged seeds. For all temperature and light regimes assayed, the germination percentages of intact seeds were significantly lower (p <0.01 and $p < 0.001$, depending on temperature and light conditions) than those of de-winged seeds (Table 1). Germination of intact and de-winged seeds ranged from 24% to 41% and from 76% to 88%, respectively. For each light condition and seed type, the highest germination percentages were reached at 15/20ºC. De-winged seeds exposed to 12 hr light photoperiod had the highest germination.

Germination speed was also significantly affected by temperature ($p = 0.004$) and seed type ($p < 0.001$) but their interaction (temperature × seed type) was not significant ($p = 0.567$) as shown in Table 3. For each temperature regime tested, germination speed was significantly ($p < 0.05$) higher for de-winged seeds (Table 1). The highest germination rate (i.e. the lowest MGT value) of intact and de-winged seeds was recorded at 20/25ºC.

Table 1 Germination percentage (mean ± SD) and mean germination time (MGT, mean ± SD) under the combination of two alternate temperature regimes and two light regimes (12 hr light photoperiod and total darkness) for *S. rosmarinus* intact and de-winged seeds

Light regime	Incubation temperature (ºC)	Germination (%)			MGT (d)		
		Intact	De-winged	*P*	Intact	De-winged	*P*
Darkness	15/20	28 ± 2.83	85 ± 2.96	***	---	---	---
	20/25	24 ± 1.41	76 ± 5.48	***	---	---	---
Photoperiod	15/20	41 ± 2.96	88 ± 2.45	***	4.42 ± 0.13	3.05 ± 0.30	*
	20/25	32 ± 3.74	78 ± 5.38	**	3.80 ± 0.15	2.17 ± 0.05	***

MGT could only be assessed in treatments subjected to light.

P = for each parameter (germination percentage and MGT), temperature and illumination condition, the significance level between values from intact and de-winged seeds are shown.

***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ns, not significant.

Table 2 Analysis of variance of germination percentages of *S. rosmarinus* affected by light regimes (total darkness and 12 hr light photoperiod), temperature regimes (15/20ºC and 20/25ºC) and wings (intact and de-winged).

Source of variation	df	MS	*F*	*P*
Light (L)	1	144.88	4.37	0.047
Temperature (T)	1	241.07	7.27	0.013
Wings (W)	1	7989.43	241.03	<0.000
L × T	1	9.17	0.28	0.604
L × W	1	39.58	1.19	0.285
T × W	1	17.86	0.54	0.470
L × T × W	1	1.18	0.04	0.852
Error	24	33.15		

df = degrees of freedom; MS = mean square; F = Fisher's test

Table 3 Analysis of variance of mean germination times (MGT) of *S. rosmarinus* affected by temperature regimes (15/20ºC and 20/25ºC) and wings (intact and de-winged).

Source of variation	df	MS	*F*	*P*
Temperature (T)	1	2.25	12.47	0.004
Wings (W)	1	9.00	49.88	<0.000
T × W	1	0.62	0.34	0.567
Error	12	0.18		

Df = degrees of freedom; MS = mean square; F = Fisher's test

Effect of NaCl concentration

In general, the highest germination percentages were recorded in distilled water (control seeds) and increasing NaCl concentrations caused a reduction in the germination percentage (Table 4). For all combinations of temperature, light and seed type, significant ($p < 0.05$) differences were found among germination from 0 (control) to the highest tested NaCl concentrations (400 mM and 600 mM). Germination was lower than 5% for these two highest NaCl concentrations (Table 4). Saline concentration and seed type (intact and de-winged seeds) had significant ($p < 0.001$) effects on seed germination (Table 5). However, the effect of light on germination percentage was not significant ($p = 0.700$). The two-way interactions between salinity and seed type and between salinity and light were significant ($p < 0.001$ and $p = 0.010$, respectively). On the contrary, the interactions between light and seed type and among the three factors considered were not significant ($p = 0.182$ and $p = 0.094$, respectively).

A proportion of ungerminated salt-exposed seeds was able to germinate when they were transferred to distilled water. Recovery germination decreased with an increasing NaCl concentration (Table 4). The recovery percentage (RP) ranged from 28% to 45% for intact seeds and from 31% to 75% for de-winged seeds. In general, the highest RP values were reached with 400m MNaCl.

Discussion

Every desert plant species has unique dispersal and germination mechanisms that determine its survival and development in desert environments (Gutterman, 1994; Baskin and Baskin, 1998; El-Keblway and Bhatt, 2015). Although the presence of a winged perianth inhibits seed germination in various species of the *Amaranthaceace,* their presence enhances their chances of being dispersed from the mother plant and colonizing a new habitat which will increase their chances for survival in unpredictable, harsh desert environments (Ungar and Khan, 2001; Bhatt et al., 2016; Bhatt et al., 2017). In the present study, de-winged seeds germinated more rapidly and also achieved significantly higher germination percentages (76–88%) compared to intact seeds (24–41%). These results suggested that the wings possibly did not contain germination inhibitors but might act as a physical barrier for radicle emergence because both intact and de-winged seeds of *S. rosmarinus* were able to absorb water equally well (data not shown). These results were in accordance with previous studies where the presence of wings reduced germination by acting as a mechanical barrier for radical emergence. However, their presence did not prevent water uptake by seeds (Wei et al., 2007; Xing et al., 2013; El-Keblawy et al., 2013; Bhatt et al. 2017). Therefore, it was presumed in the current study that besides facilitating seed dispersal, the presence of wings controls the timing of germination in order to enhance the chances for successful seedling establishment, for reducing inter plant competition and extending the germination period during winter (October to March), especially in desert environments. Furthermore, timing of seedling emergence has been reported to play an important role in determining the reproduction and fitness of plants under desert conditions (Donohue et al., 2010). Therefore, the differences in germination percentage between the intact and de-winged seeds might be helpful in responding to the risk associated with unpredictable environments. Furthermore, under natural conditions, wings may decay over time and release the seeds at different intervals in order to spread the germination over a longer duration to enhance the chances of survival and to maintain population viability under such extreme conditions.

Table 4 Germination percentages (mean ± SD) of *S. rosmarinus* seeds (intact and de-winged) after incubation in different NaCl concentrations for 14 d (initial germination) and germination percentages when non-germinated seeds were incubated for 14 d in distilled water (final germination). Seeds were incubated at 15/20ºC alternating on a 12 hr cycle and under two light conditions (continuous darkness and 12 hr light photoperiod).

Illumination condition	Salinity (mMNaCl)	Intact			De-winged		
		Initial germination (%)	Final germination (%)	Recovery percentage (%)	Initial germination (%)	Final germination (%)	Recovery percentage (%)
Darkness	0	28 ± 2.83^{c}	-	-	85 ± 2.60^{c}	-	-
	100	31 ± 5.89^{c}	57 ± 5.17$_{b}$	37.7	72 ± 3.74^{bc}	82 ± 2.24^{a}	35.7
	200	9 ± 2.18^{bc}	47 ± 4.33$_{ab}$	41.7	54 ± 3.00^{b}	80 ± 2.45^{a}	56.5
	400	2 ± 1.00^{ab}	46 ± 1.00$_{ab}$	44.9	4 ± 2.45^{a}	72 ± 5.10^{a}	70.8
	600	0^{a}	38 ± 1.73$_{a}$	38.0	0^{a}	68 ± 2.45^{a}	68.0
Photoperiod	0	40 ± 3.16^{c}	-	-	88 ± 2.45^{c}	-	-
	100	10 ± 1.73^{b}	50 ± 2.24^{b}	44.4	71 ± 1.66^{c}	80 ± 2.45^{a}	31.0
	200	8 ± 1.41^{b}	44 ± 3.16^{b}	39.1	49 ± 3.84^{b}	83 ± 1.66^{a}	66.7
	400	1 ± 0.87^{a}	37 ± 2.18^{ab}	36.4	4 ± 0.00^{a}	76 ± 5.10^{a}	75.0
	600	0^{a}	28 ± 2.83^{a}	28.0	1 ± 0.87^{a}	75 ± 1.66^{a}	74.7

Mean values in a column superscripted by the same letters are not significant different ($p < 0.05$).

Table 5 Analysis of variance of germination percentages of *S. rosmarinus* affected by salinity, light conditions and wings

Source of variation	df	MS	*F*	*P*
Salinity (S)	4	7912.29	301.97	<0.000
Light (L)	1	3.93	0.15	0.700
Wings (W)	1	8384.72	320.00	<0.000
S × L	4	95.45	3.64	0.010
S × W	4	941.10	35.95	<0.000
L × W	1	47.88	1.83	0.182
S ×L × W	4	54.68	2.09	0.094
Error	60	26.20		

Df = degrees of freedom; MS = mean square; F = Fisher's test
Salinity = 0 mM NaCl, 100 mM NaCl, 200 mM NaCl, 400 mM NaCl or 600 mM NaCl.
Light = total darkness or 12 hr light photoperiod.
Wings = intact or de-winged.

De-winged seeds of *S. rosmarinus* germinated equally well in the light and darkness, indicating that they are not light-dependent (neutral photoblastic) and have an equal chance of germination if they remain on the soil surface or are slightly buried in the soil. However, if they are buried too deep in soil, they might exhaust their resources before the seedlings could emerge from the soil surface. A similar trend was reported in other halophytes such as *Haloxylon salicornicum* (Kaul and Shankar, 1988), *H. ammodendron* (Huang et al., 2003) and *Salsola imbricata* (Zaman et al., 2010). These characteristics of *S. rosmarinus* seeds suggest that they cannot form a persistent soil seed bank (Pons, 2000; Fenner and Thompson, 2005). However, intact seeds of *S. rosmarinus* showed slightly better germination in light, indicating that they are able to germinate even at the soil surface when other environmental conditions are favorable for germination. It was presumed from the current study that intact seeds have less chance of being buried in the soil compared to de-winged seed. Therefore, they are mostly exposed to light which could induce the light requirement during their germination. Furthermore, it is possible that intact seeds are able to form a transit soil seed bank since they require light to induce their germination. Both intact and de-winged seeds achieved maximum germination at lower temperatures. This temperature range is often encountered during the early winter in Kuwait (November to December). Other halophytes have been shown to have similar optimal temperature ranges for germination in similar habitats (Mehrun et al., 2007; El-Keblawy et al., 2016). Seeds of *S. rosmarinus* mature during December when the temperature is low and the chances of rainfall are high. This might be how this species has evolved to prevent seedling recruitment in summer under such extreme conditions.

Both intact and de-winged seeds were able to germinate in up to 400 mM NaCl under both continuous darkness and a 12 hr light photoperiod but the highest salinity level (600 mM NaCl) reduced the germination percentage significantly ($p < 0.05$). Moreover, de-winged seeds showed higher germinability in the elevated salinity compared to the intact seeds. Similar results were reported by Hadi et al. (2007). Seeds of other halophytic species also germinated better and more rapidly in non-saline conditions and their germination progressively decreased with increasing salinity levels (Khan et al., 2000; El-Keblawy and Bhatt, 2015; Bhatt et al., 2016). De-winged seeds in most of the halophytic species germinate better under saline conditions because lesser amounts of salts were absorbed by de-wingeed seeds (Baskin and Baskin, 1998). However, in the current study, intact seeds were able to germinate slightly better under saline conditions, indicating that the presence of salt in the wing perianth of intact seeds did not affect germination in this species. Thus, low concentrations of sodium ions were effective in promoting the seed germination of this species.

Intact seeds of *S. rosmarinus* germinated better in complete darkness when they were exposed to different salinity levels; whereas de-winged seeds did not show any differences under a 12 hr photoperiod and in complete darkness. Further, the better germination noticed in intact seeds under complete darkness indicated that if they were buried in soil, they would experience dark conditions and probably would be less affected by salinity compared to those seeds that remained on the soil surface and, hence, they would germinate better in darkness even in saline habitats. The soil surface usually has higher salinity because of salt buildup (Blanco and Folegatti, 2002). A similar result was reported for halophytic *Sarcocornia fruticosa* seeds which had higher germination in darkness compared to light/ darkness (Redondo-Gómez et al., 2004). Both winged and de-winged seeds were able to recover and germinate once they were transferred to distilled water although the germination recovery was higher in de-winged seeds compared to intact seeds. The ability of *S. rosmarinus* seeds to remain viable even at higher salinity levels (up to 600 mM NaCl) could indicate that the seeds are highly tolerant to salinity and they are able to germinate once the salinity level decreases after rainfall (Qu et al., 2008; El-Keblawy and Bhatt, 2015; Bhatt et al., 2016; Bhatt et al. 2017). Therefore, this species has excellent potential to be utilized for the rehabilitation of salt-affected areas. De-winged seeds can germinate immediately whereas intact seeds might help in extending their germination period and will contribute to the formation of transit seed banks and to the control of germination timing. This strategy might be of ecological significance under harsh, saline, desert environmental conditions which will provide multiple opportunities for their establishment. However, removing wings (de-winged) from seeds could be practiced for the mass production of seedlings in the nursery.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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