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Germination ecology of heteromorphic seeds of slender Russian thistle (*Salsola collina*)

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Abstract

Slender Russian thistle (*Salsola collina* Pall.) is a troublesome weed distributed mainly in the cropping regions of northern China that produces heteromorphic seeds in the same plant. However, limited information is available on the germination ecology of heteromorphic seeds in *S. collina*. Thus, the present study was conducted to verify the effect of alternating temperature conditions, light conditions, winged perianth, salt concentrations, water stress, and burial depths on the seed germination or seedling emergence of *S. collina.* The results showed that *S. collina* produced two different types of fruits/seeds that significantly differed in seed size, seed color, external structure, and germination/dormancy behavior. The type A seeds (green seeds) were nondormant, and the germination percentage was >96% at all alternating day/night temperatures and light conditions; whereas type B seeds (yellow seeds) exhibited dormancy characteristics and poor germination (≤1%). Moreover, the winged perianth did not inhibit the germination of *S. collina* green seeds. The germination of green seeds declined rapidly when NaCl concentration exceeded 100 mM, and only 2.22% germination was observed at 600 mM NaCl. About 62.00% of green seeds germinated at −0.6 MPa, and 8.00% germination was obtained at −1.2 MPa. The seedling emergence declined with an increase of burial depth, and decreased sharply when the burial depth exceeded 1.0 cm. Only 8.33% seedling emergence occurred at a burial depth of 4.0 cm. The results gathered from present study will help to illustrate the ecological adaptation strategy of *S. collina* and indicate that shallow tillage can effectively minimize the seedling emergence of *S. collina*.

Introduction

Slender Russian thistle (*Salsola collina* Pall.) is a common annual herb that belongs to the genus *Salsola* within the Amaranthaceae family. It is native to southeastern Europe, southern Siberia, and arid regions of Central Asia (Mosyakin 1996), but has also successfully invaded the United States (Mosyakin 1996) and Canada (Crompton and Bassett 1985). Until now, *S. collina* has been listed as an important agricultural weed by the Global Compendium of Weeds (https://hear.org/gcw/species/salsola_collina). *Salsola collina* is distributed mainly in northeastern, northwestern, northern, and central China and parts of eastern China, and usually grows in waste places, roadsides, and cultivated fields in saline-alkaline soils (Zhu et al. 2003). As a troublesome weed, it produces serious deleterious effects in oat (*Avena sativa* L.) fields (Gu et al. 2011), no-tillage wheat (*Triticum aestivum* L.) fields (Lu et al. 2013), and cultivated licorice (*Glycyrrhiza uralensis* Fisch.) fields (Zuo et al. 2011).

It is well known that the fruit of the genus *Salsola* is an utricle and surrounded by five ovate-lanceolate, membranous perianth segments with abaxially crested humps or wings. Only one type of utricle in *S. collina* is recorded in the Flora of China, and it is described as being horizontal or oblique, surrounded by persistent perianth segments with abaxially crested humps or wings (Zhu et al. 2003). However, Crompton and Bassett (1985) and Mosyakin (1996) found that *S. collina* contained two different types of fruits/seeds in the same plant. In addition to the previously mentioned fruit type, they observed that some flowers in leaf axils located in lower portion of the branch produced a new type of fruit at maturity that formed gall-like balls in a nut-like casing (Figure 1A). These two fruits are referred to as type A and type B fruits/seeds (Figure 1B) in this study, respectively. Seed heteromorphism in the genus *Salsola* has also been reported in *Salsola affinis* C. A. Mey. (Wei et al. 2007), *Salsola ferganica* Drobow (Ma et al. 2018), *Salsola rubescens* Franch. (El-Keblawy et al. 2014), *Salsola korshinskyi* Drobow (Li et al. 2012), *Salsola brachiata* Pall. (Wang et al. 2007), *Salsola volkensii* Asch. & Schweinf. (Negbi and Tamari 1963), and *Salsola komarovii* Iljin (Yamaguchi et al. 1990), and exhibits different germination/dormancy behavior between heteromorphic seeds. However, no information has been obtained on the germination and dormancy requirements of heteromorphic seeds in *S. collina*.

Seed germination is the beginning of plant life history and directly impacts seedling establishment and subsequent growth. It is well known that the genus *Salsola* is widely distributed in temperate regions, as well as in arid and semi-arid environments (Rasheed et al. 2013). In these regions, the environmental conditions, such as temperature, availability of water, and soil salinity, are major limiting factors during the seed germination stage (Baskin and Baskin 2014; Noe and Zedler 2000). Among these factors, temperature plays a vital role in seed germination and early seedling growth (Baskin and Baskin 1989; Gutterman 1994). Previous studies showed that different species in the genus *Salsola* exhibited divergent responses to temperature regimes at the germination stage (Gremer et al. 2016; Gul et al. 2013). For example, Ma et al. (2018) found that germination of *S. ferganica* was promoted by lower temperature regimes (15/5, 20/10, and 25/15 C), while a higher temperature regime (30/20 C) inhibited germination. In contrast, Mehrun-Nisa et al. (2007) found that germination of *Salsola imbricata* Forssk. seeds was inhibited by a temperature regime of 20/10 C, compared with 25/15 C. Salinity is also considered to be one of the crucial limiting factors affecting seed germination and seedling establishment (Fernández et al. 2016; Tlig et al. 2008). Khan et al. (2002) found that the upper limit of salt tolerance in the different species of the genus *Salsola* varied at the germination stage. For example, Khan et al. (2002) reported that *Salsola iberica* Sennen & Pau seeds could germinate at 1,000 mM NaCl, while the germination of *Salsola kali* L. seeds was reduced at 60 mM NaCl (Ignaciuk and Lee 1980). In addition, soil moisture is a key environmental factor regulating seed germination and seedling establishment (Bradford 2002; Hu et al. 2015). Although a few reports have been obtained about the effects of temperature and light on the germination of *S. collina* seeds (Kinugasa et al. 2016; Zhang et al. 2015), the effects of salinity, osmotic potential, and burial depth on the germination of *S. collina* seeds have not been identified.

Studies on seed germination behavior and seedling emergence of *S. collina* will help us to understand its ecological adaptation strategy and formulate effective weed management practices for controlling its spread. In the present study, we found that *S. collina* produced two different types of fruits/seeds. Therefore, we hypothesized that different germination requirements existed in the heteromorphic seeds of *S. collina*. To illustrate the species-specific germination characteristics of *S. collina*, we (1) clarified the differences in the seed traits of heteromorphic seeds in *S. collina*; (2) investigated the effects of temperature regimes and light conditions on the germination of heteromorphic seeds of *S. collina*; (3) determined the effects of winged perianth on the germination of type A seeds of *S. collina*; and (4) examined the effects of salinity, osmotic potential, and burial depth on the germination of type A seeds of *S. collina*.

Materials and Methods

Seed Collection and Morphological Observation

Fifty mature *S. collina* plants were collected in October 2018 from a naturalized population growing on Yingchengzi Beach in Dalian City, Liaoning Province, China (121.36°E, 38.99°N). All plants were packed into plastic woven sacks and then brought back to the laboratory and air-dried at room temperature for 1 wk. The fruits/seeds were collected and then separated based on their morphological characteristics (Figure 1). All fruits/seeds were put into the paper bags and stored in a refrigerator at 4 C until the experiment.

The fruit of the genus *Salsola* is an utricle surrounded by five ovate-lanceolate, membranous perianth segments with abaxially crested humps or wings. Thus, in the genus of *Salsola*, the unit of dispersal and germination comprises the seed, utricle, and winged perianth or bract. *Salsola collina* produces two different types of dispersal units in the same plant: type A dispersal unit and type B dispersal unit. Because the type B utricle is hard to distinguish from the lignified bracts, we refer to the type A and type B dispersal units as type A and type B "fruits" (Figure 1B) and use them to study the effects of temperature and light and winged perianth on seed germination. In addition, the type A utricle (green color) and type B utricle (yellow color) are customarily referred to as "green seeds" and "yellow seeds," respectively (Figure 1B). Of the two, type A seeds (green seeds) are used in the effect of NaCl, osmotic potential, and burial depth on seed germination.

The seed sizes (including height, length, and width) of 40 seeds of each type (type A and type B) were determined using a Vernier caliper (MNT-150, Shanghai MNT Tools, Shanghai, P.R. China). The mean seed mass of 40 seeds of each type was weighed by using an analytical balance (Sartorius BP 221S, Sartorius, Germany).

General Germination Test Protocol

Germination tests were completed with fruits or seeds. Forty fruits or seeds of each type (type A and type B) were placed on two layers of filter paper (Whatman No. 1, Whatman International, Ltd., Maidstone, Kent, UK) in 90-mm-diameter petri dishes. About 5 ml of distilled water or the corresponding test solution was used to moisten the filter paper. Parafilm® PM-996 (Bemis Company, Inc., Sheboygan Falls, WI, USA) was used to seal the petri dishes to minimize water evaporation. The petri dishes were incubated in incubators set to alternating day/night temperatures of 20/10 C with 12-h light/12-dark conditions (MGC-100P, Shanghai Yiheng Scientific Instrument, Shanghai, P.R. China), unless otherwise indicated. For light treatments, light irradiation with an intensity of 150 μmol $m^{-2}s^{-1}$ was obtained using fluorescent lamps. Seeds were considered germinated when the length of the emergent radicle reached 1 mm. The germinated seeds were counted daily for each petri dish and then removed after each count. Subsequently, the petri dishes were resealed and incubated until the end of the experiment.

Effects of Temperature and Light on Germination

Type A and type B fruits were used to test the effects of temperature and light on seed germination. Forty fruits of each type were incubated in distilled water at four alternating day/night temperature regimes of 15/5, 20/10, 25/15, and 30/20 C. For each temperature regime, germination was tested under 12-h light/12-h dark and 24-h continuous-dark conditions. The petri dishes were wrapped immediately after the distilled water was added, using aluminum foil (bilayer) to provide the continuous-dark environment. These alternating temperature regimes reflect the environmental variations that *S. collina* might experience in the cropping regions of northern China. The number of germinated seeds under light conditions was examined daily for 14 d. In contrast, the seeds incubated in dark conditions were only counted after 14 d.

Effect of Winged Perianth on Germination

To investigate the effect of the winged perianth on the germination of *S. collina* green seeds, the winged perianths were removed from type

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Figure 1. *Salsola collina*. (A) Positions of type A and type B fruits on the branch. (B) Fruit and seed morphological characteristics at mature stage.

A fruits using a tweezer and not scarifying the seed coat when the wings were removed. Subsequently, the winged seeds (fruits), dewinged seeds (seeds), and "wing + seeds" were incubated at four alternating day/night temperature regimes of 15/5, 20/10, 25/15, and 30/20 C under 12- h photoperiod. Germination percentage was calculated after incubation for 14 d.

Effect of Salt Stress on Seed Germination

To determine the effect of salt stress on the germination of *S. collina* green seeds, 40 green seeds were incubated at 20/10 C with a 12-h photoperiod and moistened using 0, 50, 100, 200, 400, 600, 800, and 1,000 mM NaCl solutions, respectively.

After 7 d of incubation, the nongerminated seeds in all treatment solutions were picked and then rinsed using distilled water for 1 min. Subsequently, these nongerminated seeds were transferred to petri dishes containing 5 ml of distilled water and then incubated for 7 d. The initial germination, recovery germination, and final germination percentages were evaluated using the formula described by Wang et al. (2008).

Effect of Osmotic Potential on Germination

To test the effect of osmotic potential on germination of *S. collina* green seeds, 40 green seeds were germinated at 20/10 C with a 12-h photoperiod and moistened using 0, −0.1, −0.2, −0.3, −0.4, −0.5, −0.6, −0.8, and −1.0 MPa polyethylene glycol (PEG) 6000 solutions, respectively. The nine levels of PEG 6000 solutions were prepared using the method described by Michel and Kaufmann (1973). Germinated seeds were recorded daily for 14 d.

Effect of Burial Depth on Emergence

To evaluate the effect of burial depth on the emergence of *S. collina* green seeds, 20 green seeds were sown in plastic pots (8 cm by 8 cm by 10 cm) filled the soil. The soil was taken from the natural habitat of *S. collina* and sieved using a mesh metal sieve (1 mm) for removing soil impurities. The filtered soil was autoclaved (LDZX-75KBS, Shenan Medical Instrument Factory, Shanghai, P.R. China), cooled at room temperature, and then used to fill the plastic pots. The seeds were either placed on the soil surface (0 cm) or sown at burial depths of 0.5, 1, 2, 4, 6, and 7 cm. All plastic pots

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Table 1. Morphological characteristics of heteromorphic seeds in *Salsola collina*

Type	Wings	Leaf base lignification	Seed characteristics[a]				
			Length	Width	Height	Seed mass	Seed color
			mm			mg	
Type A	Yes	No	1.88 ± 0.22 a	1.58 ± 0.17 a	1.17 ± 0.14 a	1.37 ± 0.09 a	Green
Type B	No	Yes	1.36 ± 0.13 b	1.24 ± 0.12 b	1.12 ± 015 b	1.23 ± 0.05 b	Yellow

[a]Data are shown as mean ± SD. Values followed by different lowercase letters in each column indicate significant difference between heteromorphic seeds of *S. collina* according to Student's *t*-test at P < 0.05.

were immediately subirrigated using tap water after sowing and then incubated at 20/10 C with a 12-h photoperiod. The water was added manually into the plastic pots every week and ensured adequate soil moisture for seedling emergence. The seedlings were considered to have emerged when two cotyledons could be discerned on the soil surface. The number of seedlings was recorded every 2 d, and the experiment lasted for 30 d.

Statistical Analysis

All germination experiments included two experimental runs, and each run contained four biological replications. A completely randomized design was carried out in the germination and emergence experiments. All data presented in two experimental runs were pooled and then used for data analysis. An ANOVA of all experimental data was performed using SPSS software (v. 19.0, IBM, Armonk, NY, USA), and the significant difference of mean values was evaluated using the LSD test at P < 0.05. The significant difference of morphological traits between heteromorphic seeds was identified using Student's *t*-test at P < 0.05. Germination percentage and emergence percentage were arcsine transformed, and seed characteristics were log transformed to ensure the homogeneity of variances before analyses. SigmaPlot software (v. 12.5, Systat Software, Point Richmond, CA, USA) was used to create all graphs.

The effect of osmotic potential or burial depth on seed germination was determined using nonlinear regression analysis. A three-parameter logistic model was fit to the germination percentage or seedling emergence (%) obtained at different osmotic potentials or burial depths. The fitted model (Chauhan et al. 2006) is as follows:

$$G(\%) = Gmax/[1 + (x/x50)^{Grate}] \qquad [1]$$

In Equation 1, G indicates the germination percentage or seedling emergence (%) at osmotic potential or burial depth x; $G_{\max}$ is the maximum germination or seedling emergence (%); x_{50} represents the effective osmotic potential or burial depth required to reduce germination or emergence by 50%; and G_{rate} is the slope.

Results and Discussion

Observations of Seed Characteristics

As shown in Figure 1, two different types of fruits were observed on the same *S. collina* plant. Type A fruits were located at the tops of the branches, while type B fruits were distributed mainly in the middle and lower parts of branches (Figure 1A). Type A fruits exhibited membranous perianth segments with abaxially crested humps, contained a green seed, and then dispersed easily from the mother plant; whereas type B fruits were enveloped tightly by the lignified bracts, contained a yellow seed, and were tightly attached to the mother plant (Figure 1B). In addition, significant differences between the heteromorphic seeds of *S. collina* were also obtained (Table 1) in seed mass (P < 0.001), seed height (P < 0.001), seed length (P < 0.001), and seed width (P < 0.001). Type A seeds were significantly greater in size, compared with type B seeds. These results demonstrate that *S. collina* produces two different types of fruits (seeds) in the same plant that exhibit significant differences in seed color, seed size, external structure, and dispersal ability, consistent with previous observations (Crompton and Bassett 1985; Mosyakin 1996).

Effects of Temperature and Light on Germination

The germination of *S. collina* was significantly affected by seed types (P < 0.001; Table 2). Compared with the low germination rate (≤1.0%) observed in type B seeds of *S. collina*, type A seeds (green seeds) exhibited higher germination percentages (96.67% to 99.17%) across four alternating temperature regimes (Figure 2). Similarly, Zhang et al. (2015) found that the seeds of *S. collina* germinated well at a wide range of temperatures from 5 to 35 C, and germination percentages were >80%. The results indicate that the type A seeds of *S. collina* are nondormant, and their germination is insensitive to temperature regimes, consistent with the temperature effect on the germination of *S. affinis* seeds noted by Wei et al. (2008). In contrast, the temperature regimes significantly influenced the seed germination of *S. ferganica* (Ma et al. 2018) and *Salsola villosa* Schult. (Assaeed 2001). For example, Ma et al. (2018) found that a high-temperature regime (30/20 C) significantly inhibited seed germination of *S. ferganica* compared with low- and moderate-temperature regimes (15/5, 20/10, and 25/15 C).

There was no significant difference in the germination of type A seeds between light/dark and continuous-dark conditions (Figure 2). The result indicates that light irradiation is not a limiting factor for the germination of type A seeds, which was consistent with light effect on seed germination of *Salsola grandis* Freitag Vural & Adigüzel (Çinar et al. 2016), *S. imbricata* (Mehrun-Nisa et al. 2007), and *S. affinis* (Wei et al. 2008). In contrast, Ma et al. (2018) found that light significantly enhanced the germination of *S. ferganica* seeds.

In addition, type B seeds (yellow seeds) exhibited poor germination (≤1%) in light or darkness conditions under four temperature regimes (Figure 2). The result indicates that the type B seeds are dormant. Similarly, the dormancy characteristics of yellow seeds were also present in *S. affinis* (Wei et al. 2007) and *S. volkensii* (Negbi and Tamari 1963). These results indicate that the heteromorphic seeds of *S. collina* exhibit two different germination behaviors: green seeds are nondormant and germinate well under a wide range of temperatures, which favors their occupation of many different spaces; in contrast, the yellow seeds

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Table 2. Three-way ANOVA results for the effects of temperature, light condition, seed type, and their interactions on the germination of heteromorphic seeds in *Salsola collina*

Source of variation	df	P-value
Temperature	3	0.882
Light	1	0.087
Seed type	1	<0.001
Temperature × light	3	0.954
Temperature × seed type	3	0.127
Light × seed type	1	0.087
Temperature × light × seed type	3	0.954
Error	108	

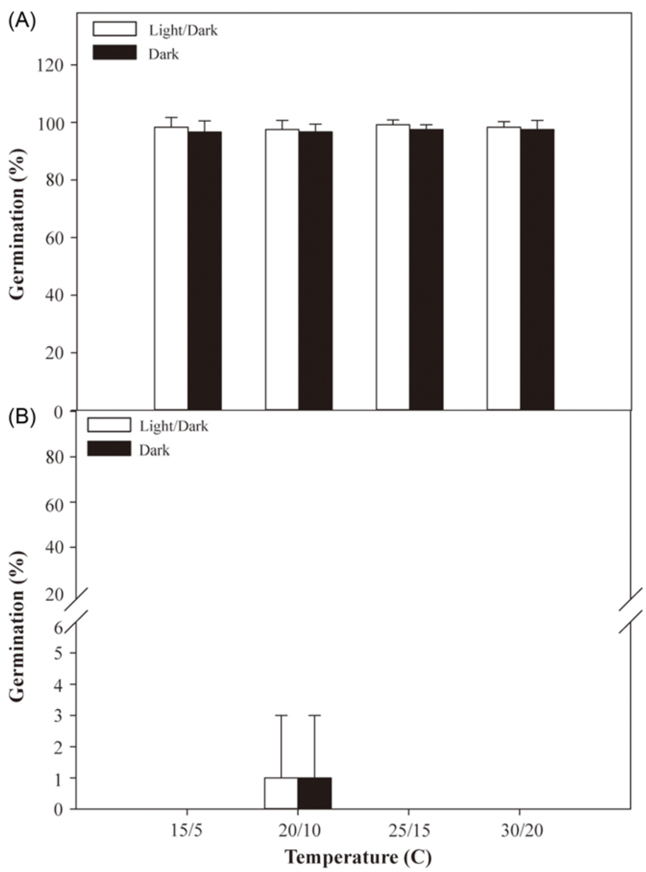

Figure 2. Effects of temperature regimes and light conditions on final germination of *Salsola collina* (A) type A and (B) type B seeds. The vertical bars indicate the standard deviation of the mean.

are dormant, and their dormancy-breaking methods need to be further investigated.

Effect of Winged Perianth on Germination

The two-way ANOVA showed that the germination of type A seeds (green seeds) was not influenced by winged perianth (P = 0.524), temperature (P = 0.128), or the interaction of winged perianth and temperature regimes (P = 0.758). No significant differences were observed in the germination between seeds with winged perianth and seeds for which the winged perianth was removed (Figure 3), and high germination percentages (98.3% to 100%) were present under all temperature regimes. These results

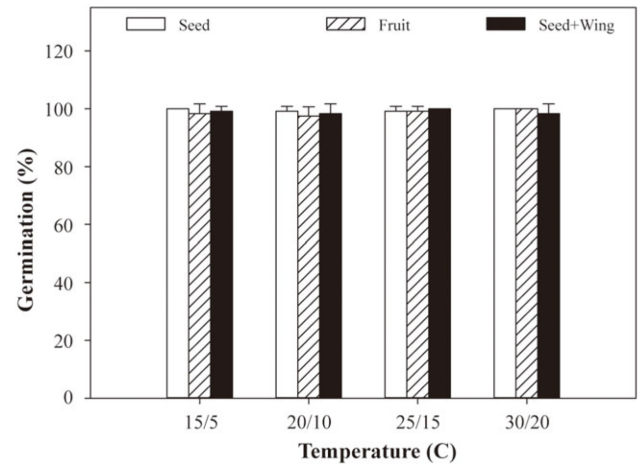

Figure 3. Effects of winged perianth and temperature regimes on final germination of *Salsola collina* green seeds in light/dark photoperiods. The vertical bars indicate the standard deviation of the mean.

Table 3. Effect of NaCl on the initial germination, recovery germination, and final germination of *Salsola collina* green seeds incubated at temperature regime of 20/10 C under light/dark (12/12-h) conditions[a]

Salinity	Initial germination	Recovery percentage	Final germination
mM		%	
0	91.11 ± 5.09 a	16.67 ± 28.87 a	93.33 ± 3.33 a
50	92.22 ± 5.09 a	16.67 ± 28.87 a	94.44 ± 1.92 a
100	90.00 ± 3.33 a	36.11 ± 37.58 a	94.44 ± 1.92 a
200	53.33 ± 10.00 b	87.22 ± 6.29 b	94.44 ± 1.92 a
400	11.11 ± 1.93 c	97.48 ± 2.18 b	97.78 ± 1.92 a
600	2.22 ± 3.85 d	96.59 ± 3.34 b	96.67 ± 3.33 a
800	0.00 ± 0.00 d	72.22 ± 5.09 b	72.22 ± 5.09 b
1,000	0.00 ± 0.00 d	72.22 ± 3.85 b	72.22 ± 3.85 b

[a]Germination data are shown as mean ± SD. Values followed by different lowercase letters in each column indicate significant differences across all NaCl concentrations according to LSD test at P < 0.05.

indicate that the winged perianth does not affect the germination of *S. collina* green seeds, consistent with the effect of winged perianth on the germination of *Salsola ruthenica* Iljin (Chen et al. 2022a). In contrast, El-Keblawy et al. (2014) found that the winged perianth significantly inhibited seed germination of *S. rubescens*. Similarly, the inhibitory effect of winged perianth on seed germination was also observed in *Salsola ikonnikovii* Iljin (Xing et al. 2013), *S. komarovii* (Takeno and Yamaguchi 1991), *S. affinis* (Wei et al. 2008), *S. ferganica* (Ma et al. 2018), *S. brachiata* (Chen et al. 2022b), *Salsola vermiculata* L. (Osman and Ghassali 1997), as well as *Salsola heptapotamica* Iljin, *Salsola nitraria* Pall., and *Salsola rosacea* L. (Chen et al. 2022a).

Effect of NaCl on Germination

The germination of *S. collina* green seeds was significantly influenced by the different NaCl concentrations (P < 0.001) (Table 3). No significant differences were obtained in germination percentages under lower NaCl concentrations (0 to ~100 mM NaCl), and ≥90% seeds germinated (Table 3), which was consistent with the effects of NaCl on seed germination of *S. ferganica* (Ma et al. 2016) and *Salsola turcica* Yıld. (halophytic ecotype and gypsicole ecotype) (Çinar and Tuğ 2021). The germination percentages of *S. collina* green seeds declined rapidly when NaCl concentration was more than 100 mM (Table 3), which differed from the inhibitory effects of NaCl on seed germination of *S. vermiculata* (Guma et al. 2010) and *S. villosa* (Assaeed 2001). Guma et al. (2010) found that the seed germination of *S. vermiculata* decreased significantly when NaCl concentrations was more than 200 mM at 20/10 C. In contrast, Ignaciuk and Lee (1980) found that the seed germination of *S. kali* was reduced at 60 mM NaCl.

Only 2.22% of seeds germinated at 600 mM NaCl, and no germination was observed at 800 mM and 1000 mM NaCl solutions (Table 3). Similarly, only some *S. kali* seeds germinated at 600 mM NaCl (Woodell 1985). However, other species in genus *Salsola* were reported to exhibit higher salt tolerance at the germination stage, including *S. imbricata* (800 mM NaCl) (Mehrun-Nisa et al. 2007), *S. grandis* (800 mM NaCl) (Çinar et al. 2016), *S. villosa* (800 mM NaCl) (Assaeed 2001), *S. nitraria* (1,000 mM NaCl) (Chang et al. 2008), *S. ferganica* (1,000 mM NaCl) (Wang et al. 2013), *S. iberica* (1,000 mM NaCl) (Khan et al. 2002), *Salsola drummondii* Ulbr. *ikonnikovvii* (1,000 mM NaCl) (Rasheed et al. 2015), and *S. affinis* (2,000 mM NaCl) (Wei et al. 2008).

It is well known that halophyte seeds can tolerate high salt solutions by inhibiting seed germination and may have the ability to then recover germinability once the high-salinity conditions are alleviated (Gupta and Huang 2014). Although the germination percentages of *S. collina* green seeds were sharply reduced as NaCl concentration increased (Table 3), the nongerminated seeds incubated in 200 to 1,000 mM NaCl exhibited favorable recovery percentages that ranged from 72.22% to 97.48%. Similarly, Wang et al. (2013) found that the seeds of *S. ferganica* incubated in 200 to 800 mM NaCl also recovered well. In contrast, Mehrun-Nisa et al. (2007) found that *S. imbricata* seeds incubated in high-saline solutions showed poor recovery ability, which varied between 20% and 30%. Although *S. collina* green seeds exhibited high recovery percentages, the final germination percentages were also significantly reduced when the seeds were incubated at >800 mM NaCl (Table 3). Similarly, the lower recovery percentage was also observed in S. affinis, when it's seeds were treated with 1,000 to 4,000 mM NaCl (Wei et al. 2008). These results indicate that *S. collina* green seeds have moderate salt tolerance during the germination stage and retain high seed germinability under high-salt stress. However, a portion of seeds also permanently lost their germinability during high-salinity stress because of ion toxicity resulting from high Na^+ concentrations (Kumari et al. 2015).

Effect of Osmotic Potential on Germination

The germination of *S. collina* green seeds was significantly affected by osmotic potential ($P < 0.001$). The germination percentage decreased significantly with a decline in osmotic potential, and 62.00% germination was achieved at −0.6 MPa (Figure 4). However, only 10.11% and 8.00% germination was obtained at −1.0 MPa and −1.2 MPa, respectively. Similar results were obtained in *S. villosa* (Assaeed 2001), for which a germination rate of 8.33% was observed at −1.2 MPa. In contrast, Yousefi et al. (2020) found that *S. kali* seeds germinated well (>50%) at −1.2 MPa.

The three-parameter logistic model (Equation 1) indicated that the germination of *S. collina* was inhibited by 50% at −0.72 MPa, which was significantly higher than the value of common lambsquarters (*Chenopodium album* L.) (Eslami 2011) and common seepweed [*Suaeda glauca* (Bunge) Bunge] (Wang et al. 2020). Taken together, these results indicate that although *S. collina* shows less drought tolerance than *S. kali* at the seed germination stage, it can germinate under moderate drought-stress conditions and thus exhibits good competitive ability in arid or semiarid environments.

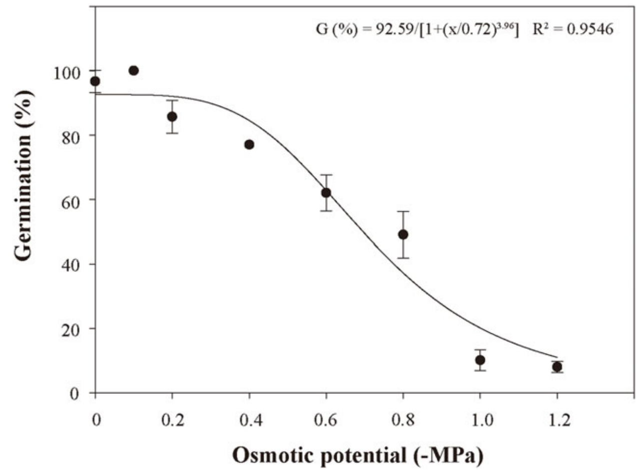

Figure 4. Effect of osmotic potential on the germination of *Salsola collina* green seeds incubated at 20/10 C under light/dark (12/12-h) conditions for 14 d. The vertical bars indicate the standard deviation of the mean, and the line represents the three-parameter logistic model, $G\ (\%) = G_{max}/[1 + (x/x_{50})^{Grate}]$, fit to the data. In the equation, G_{max} represents the maximum germination percentage (%), x_{50} represents the osmotic potential required for 50% inhibition of the maximum germination, and G_{rate} is the slope.

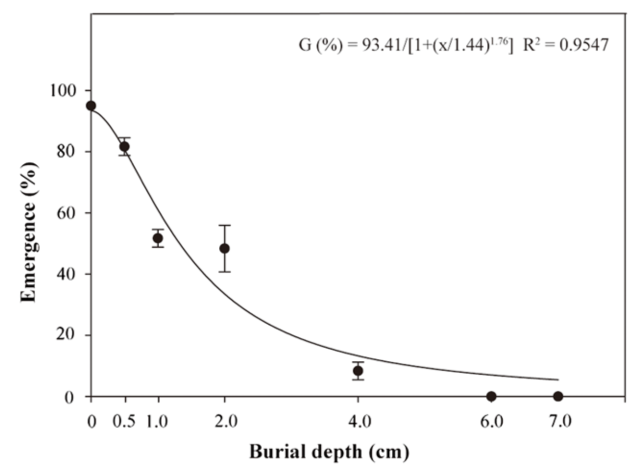

Figure 5. Effect of burial depth on the emergence of *Salsola collina* green seeds incubated at 20/10 C under light/dark (12/12-h) conditions for 30 d. The vertical bars indicate the standard deviation of the mean, and the line represents the three-parameter logistic model, $G\ (\%) = G_{max}/[1 + (x/x_{50})^{Grate}]$, fit to the data. In the equation, G_{max} represents the maximum seedling emergence (%), x_{50} represents the burial depth required for 50% inhibition of the maximum seedling emergence, and G_{rate} is the slope.

Effect of Burial Depth on Germination

Seedling emergence of *S. collina* green seeds was significantly influenced by soil burial depth ($P < 0.001$). The emergence percentage of *S. collina* green seeds decreased significantly with an increase in burial depth. The highest emergence (95.0%) was achieved when the seeds were placed on the soil surface, while seedling emergence declined significantly when the burial depth

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was more than 1.0 cm, and only 8.33% emergence was observed at the 4.0-cm burial depth. No seedling emergence was observed at the 6.0-cm burial depth (Figure 5). A similar result was obtained by Lu et al. (2012), who found that the seedling emergence percentage of saltlover [*Halogeton glomeratus* (M. Bieb.) C.A. Mey] seeds that were sown at burial depths of 1.0 or 2.0 cm decreased markedly compared with those sown on the soil surface. In contrast, Evans and Young (1972) found that the seedling emergence of *Salsola kali* var. *tenuifolia* Tausch was >82% when seeds were sown at burial depths of 1.0, 2.0, and 3.0 cm; and 16% of seedling emergence was obtained at the 6.0 cm burial depth. Wallace et al. (1968) also found that the seedlings of *S. kali* could emerge from a burial depth of 7.5 cm. In the present study, the model (Equation 1) showed that the burial depth of 1.44 cm inhibited seedling emergence of *S. collina* by 50%.

Previous studies showed that the inhibitory effect of burial depth on seedling emergence might be attributed to small seed size, low rates of gaseous diffusion, and oxygen deficiency (Joly et al. 2013; Tobe et al. 2005). In our experiment, the mean mass of *S. collina* green seeds was 1.37 mg (Table 1), indicating it belonged to the small-seeded species based on the criteria described by Thompson (1987). Chancellor (1964) found that small seeds stored less energy and were more sensitive to burial depth compared with large seeds. In addition, the oxygen deficiency in deep burial conditions also adversely affected seed germination (Crawford 1992; Tobe et al. 2005; VanderZee and Kennedy 1981). Taken together, these results indicate that the seedling emergence of *S. collina* green seeds is optimal from burial depths of 0 cm to 0.5 cm and shallow tillage (>2.0 cm) can effectively minimize seedling emergence.

In summary, *S. collina* produces two different types of fruits/seeds on the same plant that exhibit significant differences in seed size, seed color, seed mass, external structure, and germination/dormancy behavior. *Salsola collina* green seeds (type A) are nondormant and achieve a high germination percentage at all incubation conditions; whereas yellow seeds (type B) exhibit dormancy characteristics and exhibit poor germination (≤1%) under all incubation conditions. *Salsola collina* green seeds can germinate well under a wide range of temperatures, which ensures they can occupy different spaces as early as possible in early spring, enhancing their competitive ability; whereas yellow seeds exhibit dormancy characteristics, which benefits their survival in unpredictable environments. The germination of *S. collina* green seeds is insensitive to the presence of winged perianth. In addition, *S. collina* can maintain high seed viability in high salt solutions and also exhibits high germination percentages under high water stress, indicating that it can tolerate arid or semi-arid environments, which may allow it to spread farther in northwest regions of China. It is noteworthy that the seedling emergence of *S. collina* green seeds is very sensitive to soil burial depth; therefore, shallow tillage (>2.0 cm) can effectively restrict the *S. collina* seedling emergence.

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