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SPECIFICITY OF GERMINATION OF HETEROMORPHIC SEEDS IN FOUR ANNUALS (*SALSOLA* L.) AT DIFFERENT TEMPERATURES IN THE JUNGGAR BASIN

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Abstract

Salsola L. is a large genus of arid desert plants that are primarily distributed in the Junggar Basin, China. We analysed their ability to adapt to arid habitats by comparing differences in germination characteristics of the species and populations of *Salsola affinis* C. A. Mey, *Salsola korshinskyi* Drob., *Salsola brachiata* Pall. and *Salsola nitraria* Pall. We classified the 4 species into four types (A, B, C and D) according to seed wing and seed size, and the heteromorphic seeds were incubated under different temperature regimes (0/10°C, 5/15°C, 10/25°C and 20/35°C). The 4 species had the highest germination rates and germination potential at 0/10°C. Germination rates and potential decreased with increasing temperature. However, the change range of the germination rate among the four species was different. Type A and B seeds of *S. affinis*, *S. nitraria* and *S. korshinskyi* were dominant at all temperatures and decreased with increasing temperature. The germination rate of type C seeds was between that of type A, B and D seeds. D-type seeds had the lowest germination rate and the lowest germination potential under the four temperature regimes among the four species but the differences were not significant. The germination rates of the four types of *S. brachiata* seeds did not significantly change with temperature. These results suggest that *Salsola* spp. can germinate continuously from spring to autumn to adapt to moisture fluctuations in the desert.

Key words: Germination potential, Population, Bet-hedging strategy, Germination characteristics, Polymorphic seeds.

Introduction

Seed germination is an important stage in plants life, particularly the time and number of seeds germinated play an important role in the maintenance and growth of annual populations in arid areas (Venable, 1988; Gutterman, 1993). Seed germination characteristics are based on the combined effects of the external environment and genetics (Baskin & Baskin 1998; Mahmood & Yasin, 2014). Temperature determines the time and seedling numbers of seed germination and promotes seedlings to settle for suitable conditions to increase chances for survival (Venable, 1985; Ungar, 1987; Godínez *et al.,* 1999) and improve competitiveness and reproductive potential (González & Farfán, 2000; Donohue *et al.,* 2010).

Seeds germinate by a bet-hedging strategy to improve chances for survival under a stressful environment in the arid desert (Imbert, 2002; Venable, 1985, 2007; Donohue *et al.*, 2010). Heteromorphic seeds are an important factor in the expression of seed germination characteristics that cannot be ignored. Plants with heteromorphic seeds account for 87% of all plants in arid and semi-arid areas, desertification region, salinization area, as well as strongly disturbed areas (Wang *et al.,* 2010). Differences in heteromorphic seeds are observed to respond to temperature (Khan, 2004; Wei *et al.*, 2007, 2008; Yu *et al.*, 2009; Cao *et al.*, 2012), and they affect distribution, settlement and germination strategy.

A wealth of research results have accumulated regarding germination characteristics of polymorphic seeds. For example, Williams & Harper, 1965 reported that the responses of four types of *Chenopodium album* seeds to 0°C are different. Tanowitz *et al.* (1987) observed that the preferred germination temperature and germination speed for peripheral achenes of *Hemizonia increscents* is lower and faster than that of central achenes. Imbert (1996) found there was no difference in percentages of germination between achene morpha of *Crepis Sancta*. Khan & Ungar (2001) reported that the optimal germination temperature for two types of *Halopyrum mucronatum* seeds is different. Liu & Wei, 2007 showed that germination rates of *Atriplex meranth* brown seeds are significantly higher than that of black seeds at three temperatures (5/15°C, 5/25°C and 15/25°C). Furthermore, Sun *et al.* (2008) observed that germination rates of the central fruit of *Garhadiolus papposus* Boiss. et Buhse are significantly higher than those of transitional and peripheral fruit at 2/15°C and 10/20°C . Wang *et al.* (2008) discovered that germination rates of *Suaeda aralocaspica* brown seeds are higher than those of the black seeds at the same temperature. Yang *et al.* (2012) reported that germination rates of *Suaeda corniculata* brown seeds are considerably higher than those of black seeds under different temperature regimes. We observed several studies on the responses of different seed types to temperature, but few studies that compared germination by polymorphic seeds of different species in the same genus and that also analysed specific temperature requirements for seed germination. Therefore, it is important to comprehensively analyse polymorphic seed germination and understand their adaptation deeply.

Salsola L belongs to the family Chenopodiaceae and is distributed in the arid desert. There are approximately 130 species worldwide and 37 species in China; their distribution is most abundant in Xinjiang, which has 33 species (Mao *et al*., 1994; Huang, 2005). There are 25 *Salsola* annual species that are concentrated in the Junggar Basin, as an indicator species of degraded vegetation and pioneer species of secondary barren areas. These species have a good effect on soil and water conservation, diminish wind- and sand-shifting and have important ecological functions and economic value. We have observed that *S. affinis* C.A. Mey, *S. korshinskyi* Drob, *S. brachiata* Pall and *S. nitraria* Pall are widely distributed and have the ability to germinate at different times in the field investigation in recent years. Their seeds can not only germinate in spring but also in summer and autumn. They can also seed normally before winter snowfall. Thus, seed germination characteristics of these species have evolved to adapt to changes in the desert environment (Liu *et al.*, 2013).

Numerous scholars have studied these 4 species. For example, Wei *et al.* (2007) and Liu *et al.* (2007) studied seed germination of *S. affinis* at constant temperature. Wang *et al.* (2007) studied seed germination of *S. brachiata* Pall, and Li *et al*. (2012) studied seed germination of *S. korshinskyi* under various temperature treatments. However, these studies did not change the temperature in the morning and evening or they did not study the species long enough, and temperature specificity of germination for the polymorphic seeds was different; thus, these factors require further verification.

Therefore, we chose *S. affinis*, *S. korshinskyi*, *S. nitraria* and *S. brachiata*, which are widely distributed in the Junggar Desert, for this study. We compared germination differences among the species under four temperature regimes according to day and night and seasonal temperature changes.

We considered latitude, climate, soil and other available resources that may have an impact on seed germination of the same species in different populations (Winn & Gross 1993; Murray *et al.,* 2004; Vecchio *et al.*, 2012). Therefore, we compared the seed germination characteristics of different populations in the same species and comprehensively analysed the germination specificity of polymorphic seeds to temperature changes to reveal the seed germination characteristics of *Salsola* and how they adapt to precipitation fluctuations in an arid area.

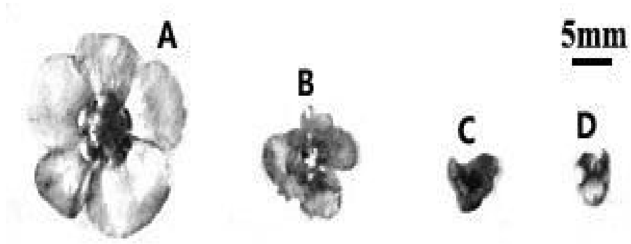
Materials and Methods

Seed sampling method and habitat characteristics of the four *Salsola* species: *S. affinis S. korshinskyi*, *S. brachiata* and *S. nitraria* (bract -enclosed utricles) were collected from natural populations growing in 8 plots at the edge of Junggar Basin in Xinjiang during October–November 2012. We sampled plants that had 80% mature seeds. Each plot was repeat sampled at least three times, and more than 10 plants were sampled in each quadrat. The samples were returned to the laboratory for seed collection and collation. The specific habitat characteristics are shown in Table 1.

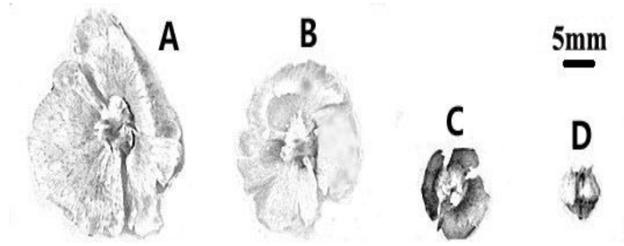
Germination experiments: Seed size and the presence of a bract varied greatly; thus, we classified the seeds into four types such as A, B, C and D (Liu *et al.*, 2013), we collectively referred to the bract appendages as seed wings. Type A seeds had bracts with long wings and were considerably plump with green embryos. Type B seeds had bracts with shorter wings than those of type A seeds and green embryos. Type C seeds had protruding bract appendages and green embryos. Type D seeds had bracts without wings and yellow or green embryos (Fig. 1). This classification was different from that three types of seeds were obtained from *S. Affinis* (Wei *et al*., 2007), four types of seeds from *S. brachiata* (Wang *et al*., 2007) and three types from *S. korshinskyi* (Li *et al*., 2012).

Table 1. The habitat characteristics of the four annual *Salsola* plants.

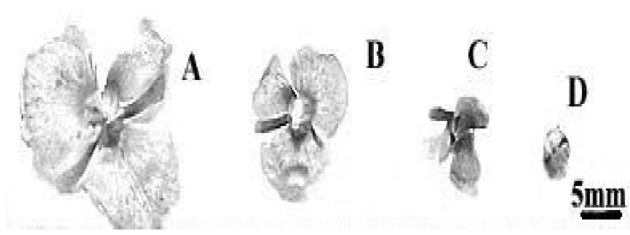
Species	Plots	Altitude /m	Habitat	Accompanying plants	Latitude and longitude
S. nitraria	I	258	Sand of the edge of salt lake	*Artemisia*, *Calligonum*, *Halogeton glomeratus* (Bieb.) C. A. Mey.	N45°28′E85°38′
S. korshinskyi			Saline soil of salt lake beach		
S. nitraria	II	276	Sandy soil between dunes	*Artemisia*, *Ceratoides lateens* (J.F. Gmel.) Reveal et Holmgren, *Haloxylon ammodendron* (C.A. Mey.) Bunge	N45°10′E86°15′
S. affinis	III	276	Gravelly soil of plain desert	*Reaumuria soongonica* (PalL) Maxim., *Haloxylon ammodendron* (C. A. Mey.) Bunge, *Salsola praecox* Litv	N45°14′E84°45′
S. brachiata			Gravelly soil of plain desert		
S. affinis	IV	328	Gravelly soil of gravel desert	*Haloxylon ammodendron* (C.A. Mey.) Bunge, *Halogeton glomeratus* (Bieb.) C.A. Mey., *Artemisia*	N44°54′E82°25′
S. korshinskyi			Saline soil of gravel desert		
S. nitraria			Gravelly soil of gravel desert		
S. affinis	V	489	Gravelly soil of gravel desert	*Salsola praecox* Litv, *Haloxylon ammodendron* (C. A. Mey.) Bunge, Gramineae plants	N44°42′E82°05′
S. korshinskyi			Gravelly soil of gravel desert		
S. affinis	VI	491	Gravelly soil of gravel desert	*Artemisia*, *Calligonum*, *Haloxylon ammodendron* (C. A. Mey.) Bunge	N44°25′E84°00′
S. affinis	VII	514	Sandy soil of desert	*Haloxylon ammodendron* (C. A. Mey.) Bunge	N44°28′E82°54′
S. korshinskyi			Desert saline soil		
S. nitraria			Sandy soil of desert		
S. affinis	VIII	919	Gravelly soil before the mountain	*Atriplex dimorphostegia*, *Halogeton glomeratus* (Bieb.) C. A. Mey., *Salsola praecox* Litv	N44°16′E84°52′
S. brachiata			Gravelly soil before the mountain		



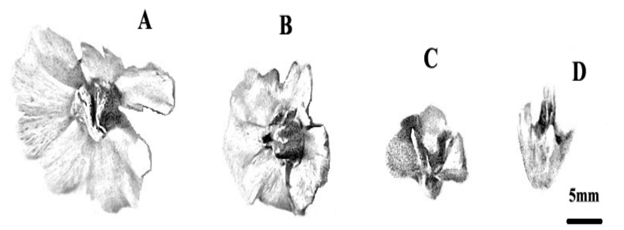
The four fruit types of *S. affinis*



The four fruit types of *S. korshinskyi*



The four fruit types of *S.nitraria*



The four fruit types of *S. brachiata*

Fig. 1. The four fruit types of four *Salsola* annuals.

The bract-enclosed utricles from the eight plots were stored for 6 months in plastic bags in a ventilated room at room temperature before they were used for experiments. The seed experiments were repeated three times, with 30 seeds in each treatment. The seeds were placed in 90-mm-diameter Petri dishes on two layers of filter paper moistened with 10 mL of distilled water to germinate. Seeds that had already germinated were counted at 0/10°C, 5/15°C, 10/25°C and 20/35°C. Radicle protrusion from the utricle was the criterion for germination. Germination was monitored every day during the experiment, and the experiment lasted 21 days.

$$\text{Germination rate} = \frac{\text{Number of normal seeds germinated}}{\text{Total number of seeds}} \text{ x } 100$$

$$\text{Germination potential} = \frac{\text{Number of normal seeds germinated at the peak}}{\text{Total number of seeds}} \times 100 \text{ (Sun, 1992).}$$

Statistical analysis: We used SPSS17.0 software for the statistical analysis (SPSS, Inc., Chicago, IL, USA). Seed germination rates and germination potential of the four annuals under the different temperature gradients were tested using one-way analysis of variance at the 95% confidence interval. Significant differences among treatments were tested by Duncan's multiple range test. The mapping software was Origin 8.6.

Results

Differences in germination characteristics of the four species at 4 different temperatures: The germination rates of *S. affinis, S. korshinskyi* and *S. nitraria* were >50% at 0/10°C. The germination rate of *S. affinis* and *S. brachiata* significantly decreased, but that of *S. nitraria* did not evidently decline with an increase in temperature. The germination rate of *S. korshinskyi* did not significantly change at 0/10°C or 5/15°C; however, it significantly decreased at 10/25°C and 20/35°C. The highest germination rate was 26.21% of *S. nitraria* and the lowest was 0.73% of *S. brachiata* at 20/35°C (Table 2).

Germination potential reflects germination rate and germination uniformity. Vigour of the different types of seed from the four annuals was different under different temperature treatments. The germination potential of the four species gradually decreased from type A to type D (Fig. 2).

Differences in seed germination characteristics of different populations in the same species: Differences in seed germination characteristics of different populations were observed within the same species. Seed germination of different populations of the four species changed consistently and the germination rate of the species decreased from type A to type D seeds at 0/10°C. However, the germination rates of two *S. brachiata* populations were significantly different. The germination rate of sample VIII was significantly higher than that of sample III (Fig. 3).

The germination rate of different populations of *S. affinis* and *S. korshinskyi* decreased with seeds from type A to type D, and the germination rates of *S. affinis* in plots III and IV were lower than those of the other four samples at 5/15°C. The germination rate of *S. brachiata* in sample VIII was significantly higher than that of sample III (Fig. 4).

The germination rates of different populations of the four species decreased with seed types from A to D and type D seeds of *S. korshinskyi* did not germinate, and the germination rates of *S. affinis* C in plots III and IV were lower than those of the other four samples at 10/25°C (Fig. 5).

The germination rates of different populations of *S. affinis* and *S. korshinskyi* were approximately 10%, and the germination rate of *S. nitraria* was significantly higher than that of the other three *Salsola* species at 20/35°C. Type D seeds of *S. korshinskyi* in the four populations and A- and B-type seeds of *S. brachiata* in the two plots did not germinate at the highest temperature (Fig. 6).

Table 2. Germination rates of the four *Salsola* species at four different temperatures.

Species	Temperature gradient	Germination rate (%)	Species	Temperature gradient	Germination rate (%)
S. affinis	0/10℃	63.36 ± 1.15a	*S. nitraria*	0/10℃	60.19 ± 4.57a
	5/15℃	51.90 ± 1.08b		5/15℃	55.08 ± 6.32a
	10/25℃	38.98 ± 2.19c		10/25℃	44.24 ± 3.27a
	20/35℃	8.11 ± 1.33d		20/35℃	26.21 ± 4.35b
S. korshinskyi	0/10℃	50.74 ± 1.54a	*S. brachiata*	0/10℃	40.10 ± 4.60a
	5/15℃	49.56 ± 1.78a		5/15℃	14.57 ± 0.77b
	10/25℃	39.42 ± 1.99b		10/25℃	6.23 ± 1.03c
	20/35℃	5.73 ± 0.75c		20/35℃	0.73 ± 0.16c

Note: Different lowercase letters within the same column indicate significant differences in the germination rates in the same species at the 5% level of significance between temperature regimes

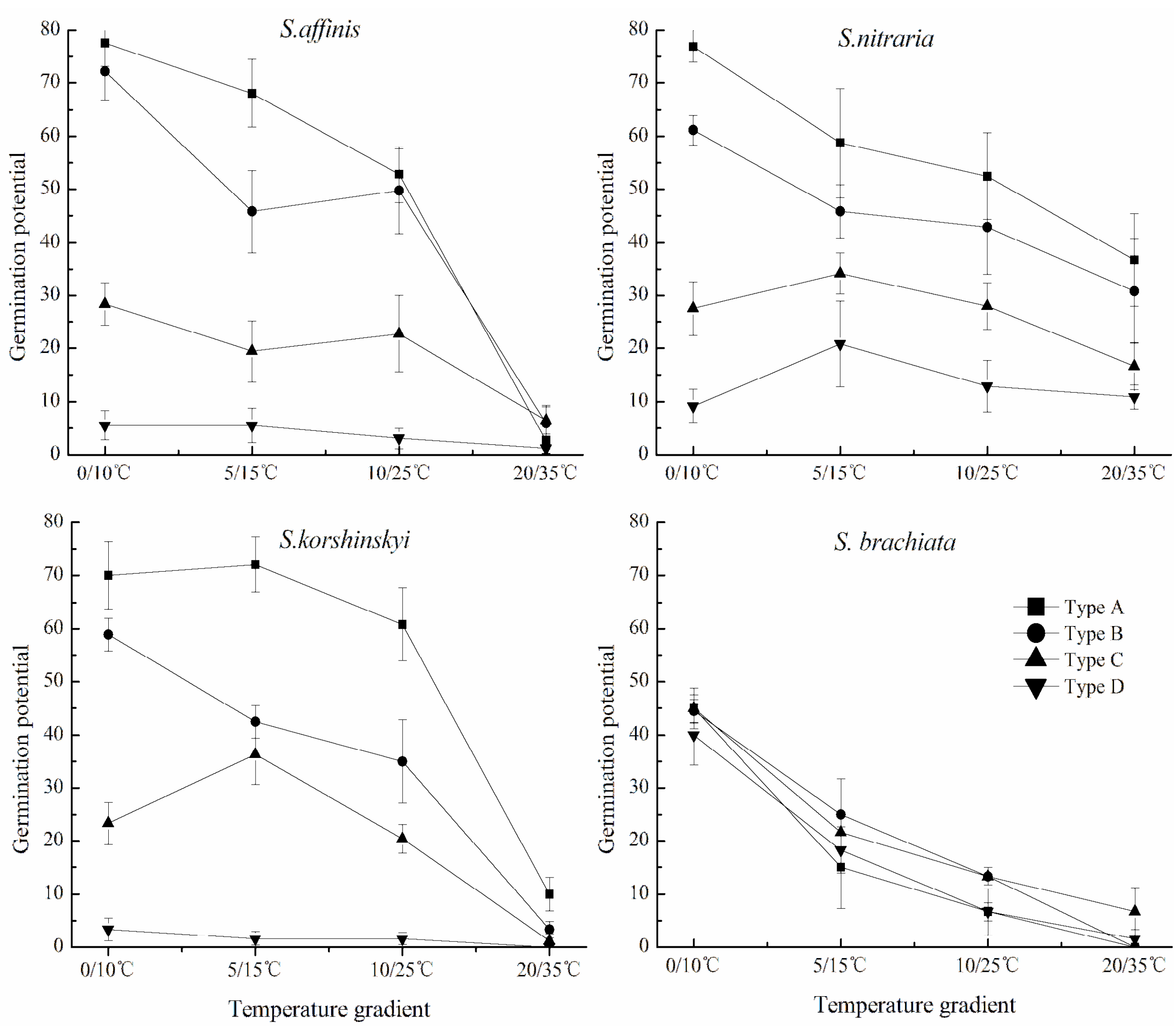


Fig. 2. Differences in germination potential of the four types of seeds from the four species at four different temperatures.

Differences in the germination characteristics of the four seed types under different temperatures: The seed germination characteristics of the different types of seeds to different temperatures were different. The germination rates of type A and B seeds of *S. Affinis*, *S. korshinskyi* and *S. nitraria* were significantly higher than those of type C and D seeds at 0/10°C and 5/15°C. The seed germination rates of type A and B seeds significantly decreased as temperature increased, whereas type A and B seeds had a slower decline. All seed types of *S. brachiata* had their highest germination rates at 0/10°C, and seed germination rates of the four types of seeds declined with increasing temperature (Fig. 7).

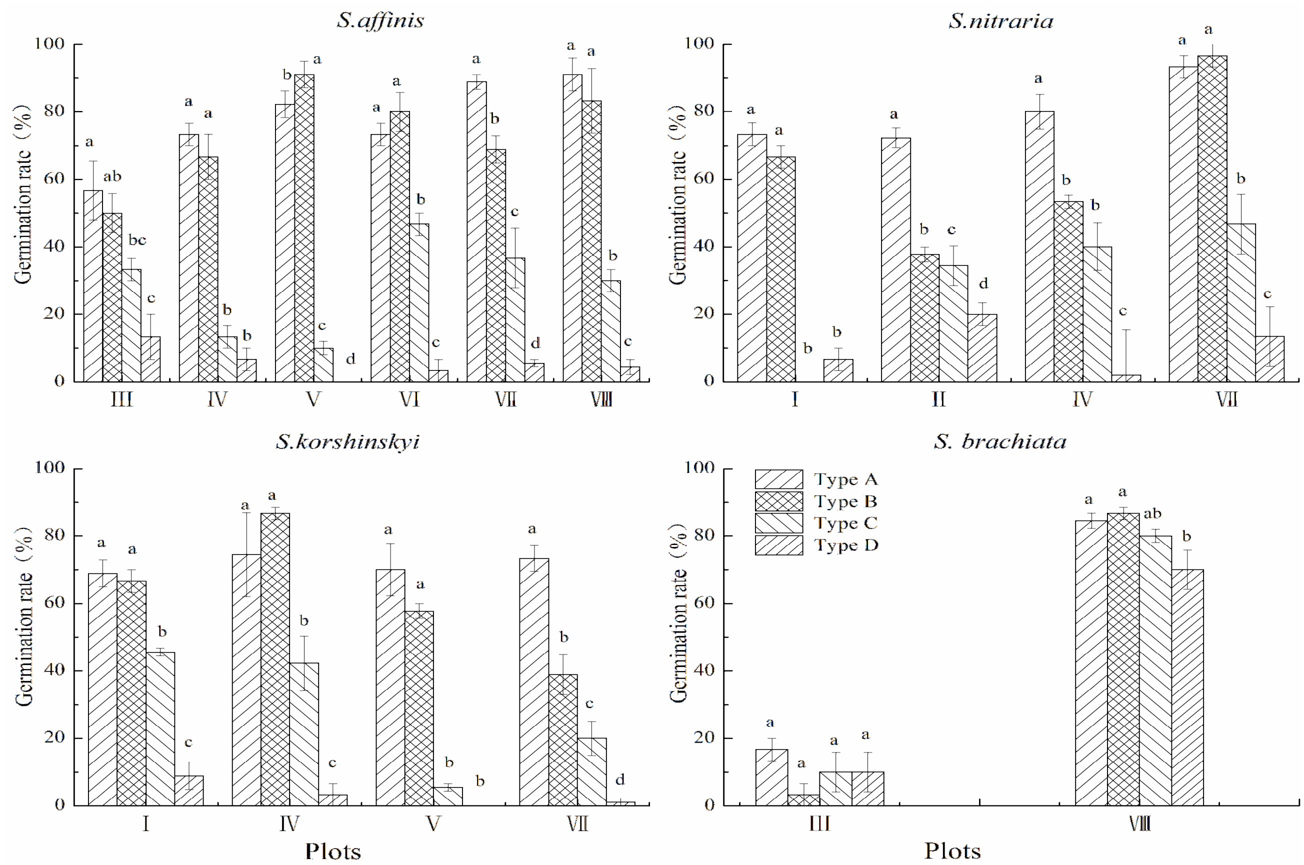


Fig. 3. Differences in the germination rates of the four types of seeds from different populations of the four species at 0/10°C.
Note. Different small letters indicate significance at p = 0.05 among the four seed types inform the different populations.

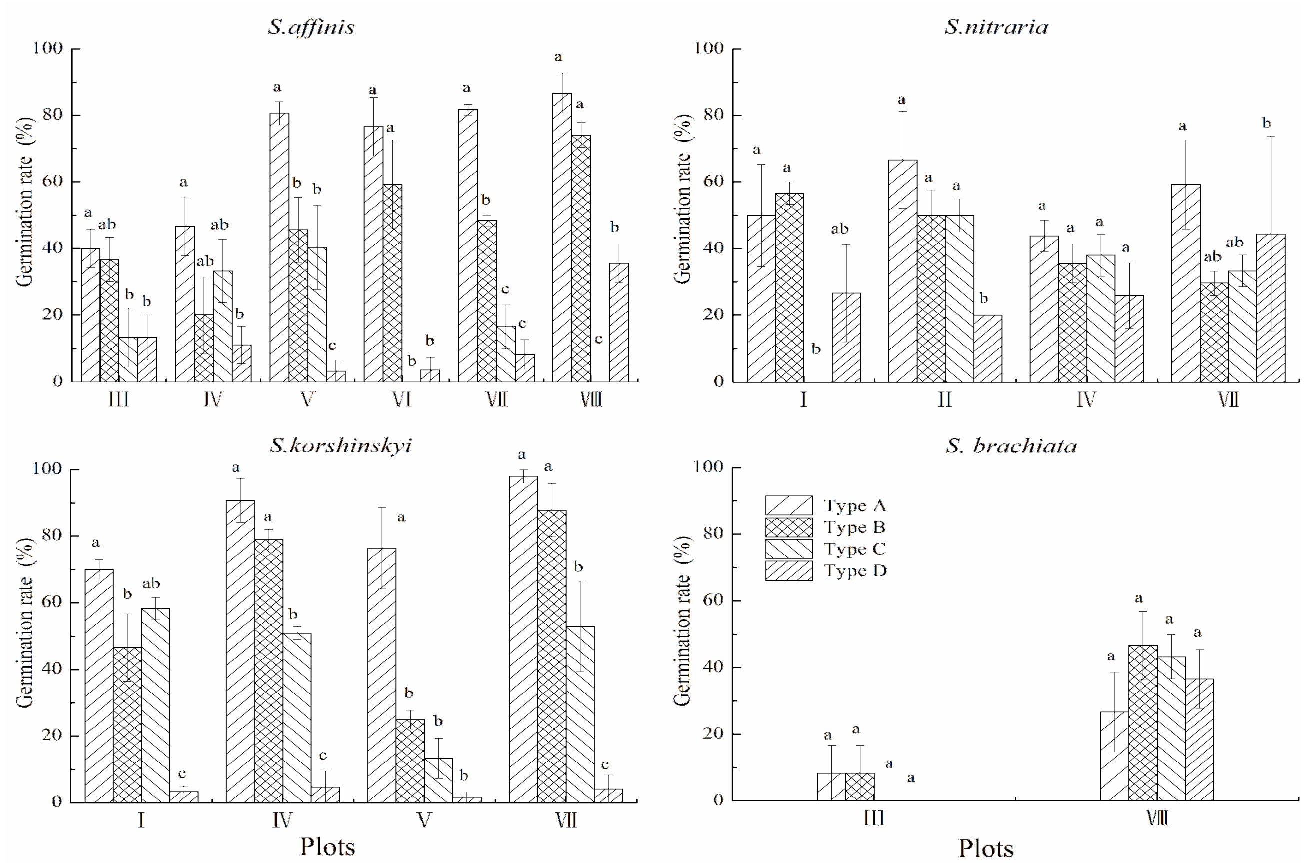


Fig. 4. Differences in the germination rates of the four types of seeds from different populations of the four species at 5/15°C.
Note. Different small letters indicate significance at p = 0.05 among the four seed types inform the different populations.

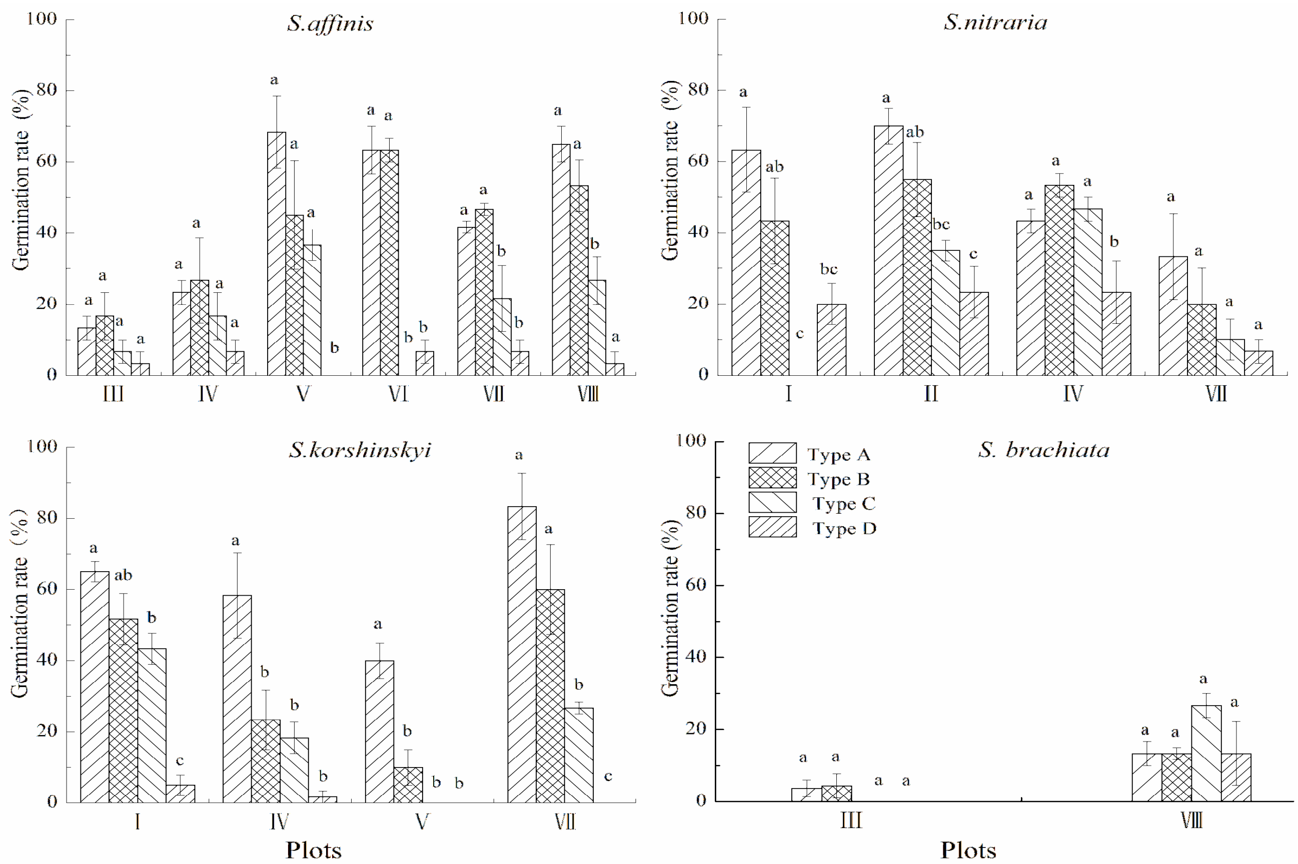


Fig. 5. Differences in the germination rates of the four types of seeds from different populations of the four species at 10/25°C.
Note. Different small letters indicate significance at p = 0.05 among the four seed types inform the different populations.

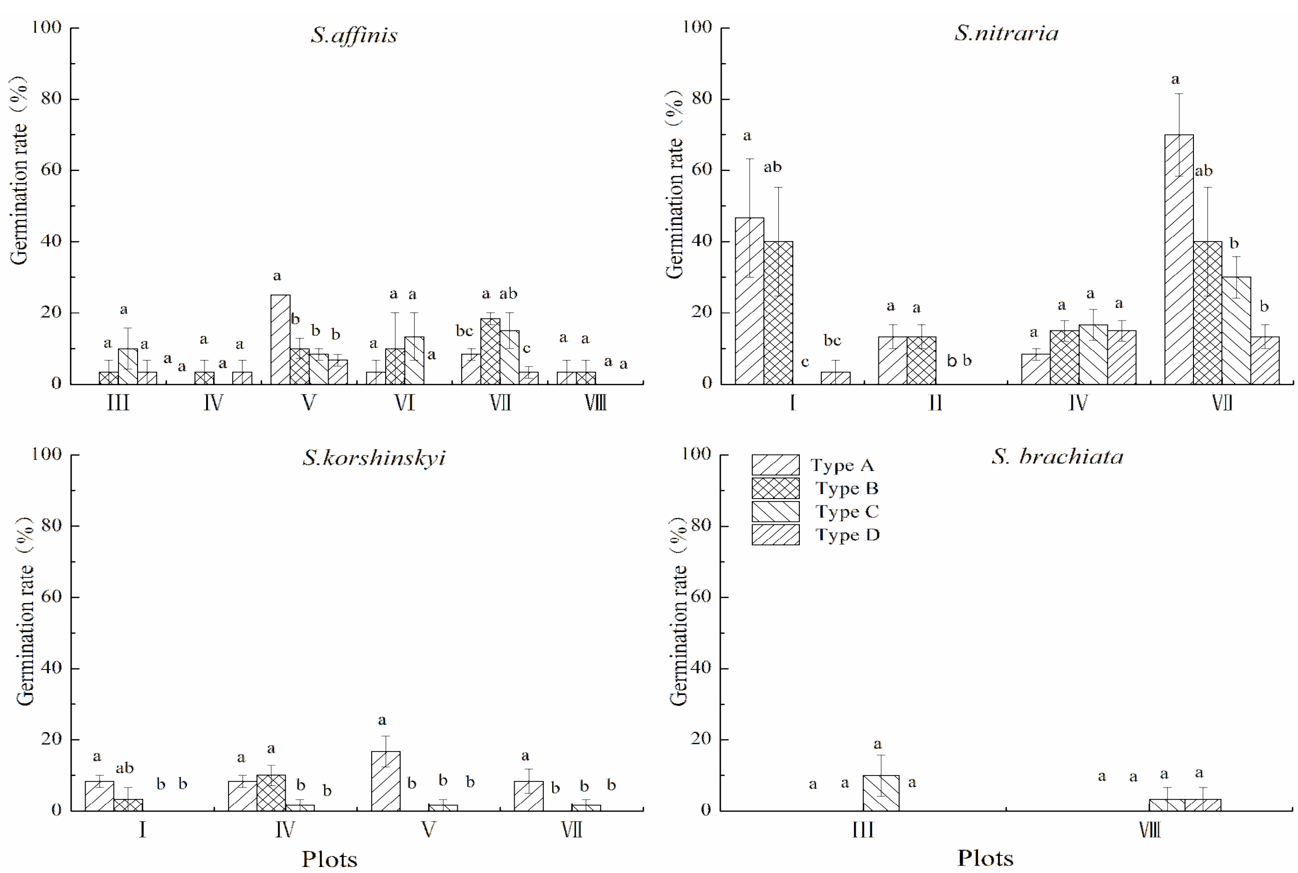


Fig. 6. Differences in the germination rates of the four types of seeds from different populations of the four species at 20/35°C.
Note. Different small letters indicate significance at p = 0.05 among the four seed types inform the different populations.

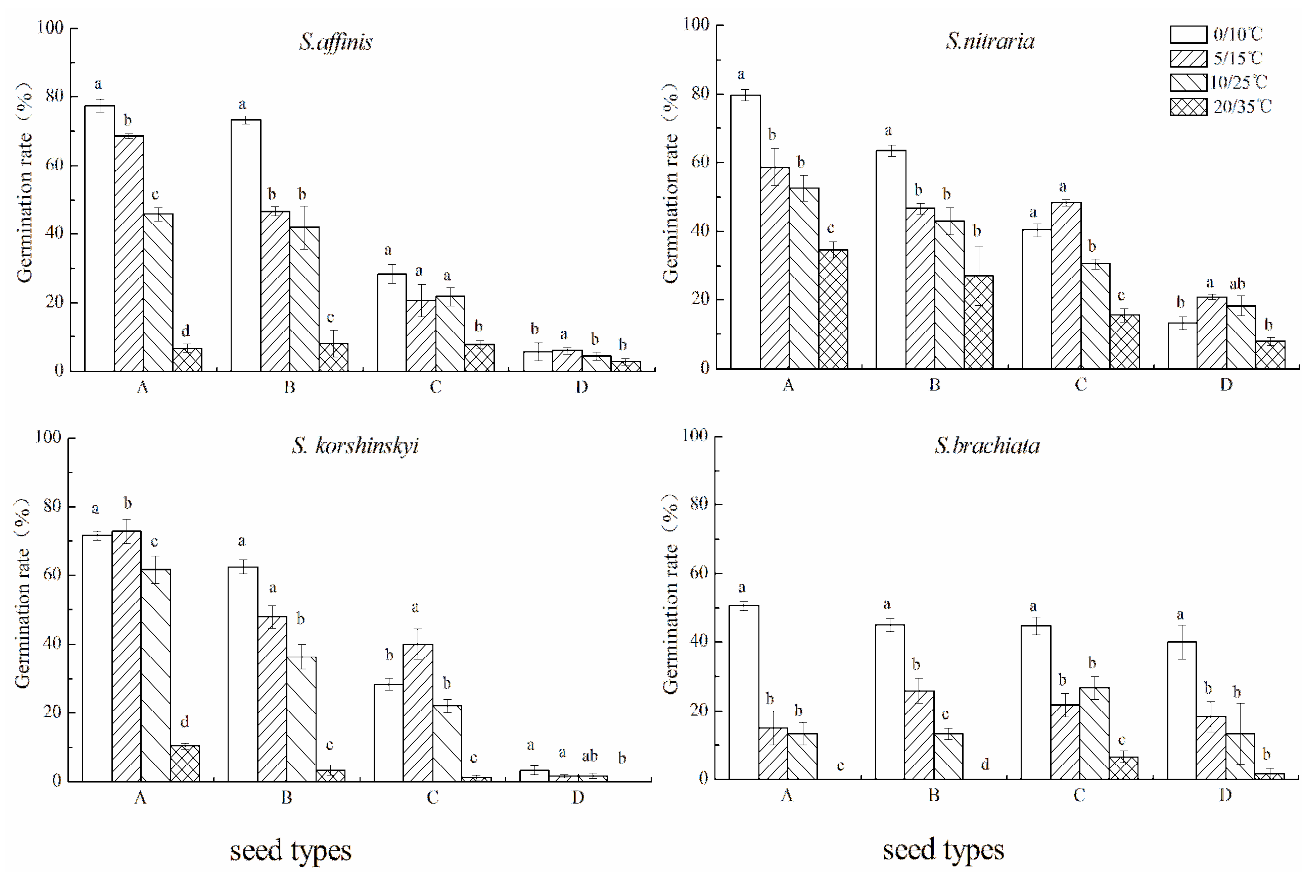


Fig. 7. Differences in the germination rates of the four types of seeds from the four species in different temperature regimes.
Note. Different small letters indicate significance at p = 0.05 among the same type of seed under the different temperature

Discussion

Germination characteristics of the four species at four different temperatures: Seed germination is the beginning of new plant-life activities, and the time and number of germinations determine survival of individuals and maintains the population. The scarcity and fluctuating nature of rainfall in arid areas has a strong impact on the time and seedling numbers of seed germination. Most plants use a bet-hedging strategy to share the risk of seed germination and improve chances for survival (Venable, 2007; Donohue *et al.*, 2010). We observed that the seed germination characteristics of *S. affinis*, *S. korshinskyi*, *S. brachiata* and *S. nitraria* were unique because they could germinate in spring, summer and autumn. It did not matter how late the seeds germinated or how small the plants were, they were all flowering and fruiting normally before snow in the winter. This special ability of flowering and fruiting and their heterochronistic germination were complementary and may be the main countermeasure to adapt to an arid environment.

We observed that the four species of *Salsola* could germinate from 0-35°C, and the range of germination temperatures was wide, verifying the phenomenon observed in nature. Germination ability over a wide temperature range has also been observed in other desert plants such as *Salsola kali* L. (Wallace *et al.*, 1968), *Blepharis persica* (Burm.) Kuntze (Gutterman, 1972), *Cleistogenes songorica* (Yu *et al.*, 2004) and *Suaeda corniculata* (Yang *et al.*, 2012). However, the four annual plants in this study not only delayed seed germination from spring to summer but also to fall, unlike the above species. This germination ability guaranteed that seedlings grew rapidly, flowered and fruited from spring to autumn to maximise seed production when rainfall was available, which could reduce seed losses of animal feeding, decaying and so on because of seeds could not germinate immediately in a year.

We also observed that the germination temperature range of the four species was wide, but the highest germination rate was at the lowest temperature. This result was related to local early snowmelt and precipitation in the spring. Thus, the four annual species seeds used the early spring snowmelt as a suitable low temperature environment to germinate a large number of seedlings, which utilised available resources and completed establishment and growth of the population. As temperatures rose, *S. nitraria* also had a higher germination rate, which was considerably related to the higher temperature of its growth period and distribution in the desert.

Differences in seed germination characteristics of different populations in the same species: Plant germination strategies adapt to the environment to enable the plants to survive and multiply in harsh environments, and different populations of the same species may have different seed germination behaviour because of different habitats (Meyer *et al.*, 1997; Loha *et al.*, 2006; Bognounou *et al.*, 2010). We observed germination differences in different populations of the same species, but not all populations were different. The results showed that germination differences had a stronger relationship with habitat diversity and were particularly related to habitat moisture conditions (Baskin & Baskin 1998; Temel *et al.*, 2011).

The germination rates of *S. affinis* in two plots were lower than those in the other four plots，it may be due to habitat heterogeneity. The germination rate of *S. brachiata* was significantly different in two sampled areas; the front zone of a mountain with more precipitation produced a high germination rate, whereas the plain desert with less rainfall produced a low germination rate. We found that the distribution of *S. brachiata* was narrower than that of the other three species, and *S. brachiata* mostly distributed the front zone of mountains, where ware ample moisture, so moisture should be an important determinant of distribution.

We observed that the germination rates of *S. korshinskyi* and *S. nitraria* were not different in different populations, which was related to their specialised habitats. *S. korshinskyi* prefers alkaline soil, whereas *S. nitraria* prefers sandy soil. Thus, the specialised choice of habitats determined their distribution range and germination differences of the different populations. The result that the four annuals (*Salsola*) had higher germination rates at low temperatures was different from results of Wei *et al.* (2007), who studied *S. affinis*, and Wang *et al.* (2007), who researched *S. korshinskyi* and found no differences under different temperature regimes. These differences may be because of sampling. They only sampled natural populations from the hilly gravel desert on the southern edge of the Junggar Basin in Xinjiang, whereas we sampled natural populations throughout the Junggar Basin and comprehensively selected habitat types of the four species.

Differences in the germination characteristics of the four seed types under different temperature: Seed heteromorphism allows desert plants to adapt to the desert environment and increase temporal and spatial of seed germination (Meyer *et al.*, 1995; Liu *et al.*, 2009; Wang *et al.*, 2012; Wang & Liu, 2013).

We observed that *Salsola* plants have different seed types. Wei *et al*. (2007) reported that *S. affinis* has three seed types. Wang *et al*. (2007) observed that *S. brachiata* has four seed types, and Li *et al.* (2012) reported three seed types in *S. Korshinskyi*. We surveyed a wide range of the four *Salsola* annuals in the Junggar Basin and observed that *S. affinis*, *S. korshinskyi*, *S. brachiata* and *S. nitraria* could be divided into seed types A, B, C and D different from the results of previous studies.

We observed that the four types of seeds of *S. Affinis*, *S. korshinskyi* and *S. nitraria* had the highest germination rates at the lowest temperature and that the A-, B- and C-type seed germination rates decreased with rising temperature. The type A and B seeds were dominant under the four different temperatures, indicating that these two types of seeds were the ones that established the species. This result was considerably different from the study of *S. affinis* (Wei *et al.*, 2007) and *S. Brachiate* (Wang *et al.*, 2007), whose seed germination rates were not different among different temperatures. The germination rate of D type seeds was extremely minimal, with no significant differences at the four temperatures. In addition, they had the lowest germination potential, indicating that the D type seeds could access the persistent seed bank after being scattered. The germination rate of the C type seeds was between that of the A, B and D types seeds, and the germination potential of A, B, C and D type seeds gradually decreased, which made the plants form a continuum of reproductive behaviour (Mandák & Pysek 1999). Because the seed wing sizes of A, B, C and D type seeds were different, they determined the differences in diffusion distance and germination behaviour. Thus, we integrated the seed germination characteristics of the three different types of *Salsola* seeds to reduce the selection effect of density and the competition between conspecific offspring (Imbert, 2002).

We also observed that the four types of *S. brachiata* seeds had the highest germination rates at the lowest temperature, and germination rate decreased with rising temperature, which showed that there was no germination specificity to temperature in the four types of seeds in that species. We discovered that *S. brachiata* was primarily distributed in the front zone of mountain where rainfall was more plentiful and there was a shorter growth period than in the desert plain. The average temperature was considerably lower; therefore, the germination characteristics were closely related to the special habitat.

In conclusion, the 4 annuals (*Salsola*) all had the highest germination rate at the lowest temperature. *S. affinis*, *S. korshinskyi* and *S. nitraria* germinated above 30°C and had continuous germination characteristics, which was an adaptation to scarce precipitation and fluctuations in the desert. All four species had types A, B, C and D seeds, which allowed them to germinate at the same or different times and determined the number seeds germinated, which reduced the siblings competition and increased the chance to settle in a new habitat combining with the diffusion of different type seeds.

The comparative study indicated that within the same species or within a population of the same species, habitat was an important influence on seed germination characteristics, which led to differences among the species and populations. This habitat selection shaped the different adaptation characteristics and also formed different species distribution patterns. Therefore, we determined that this unique germination strategy was an important factor that helped the annuals of *Salsola* adapt to the arid desert.

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