Response of seed germination and seedling emergence of Haloxylon ammodendron to climate change in desert ecosystem

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Research Article

Keywords: Alternating temperature, Constant temperature, Rain frequency, Seed germination, Seedling emergence

Posted Date: April 8th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1527835/v1

Abstract

Climate change will result in the variation of rain frequency and warming in arid zone, which is expected to affect seed germination and seedling emergence in desert ecosystem. However, the effect of unpredictable rainfall and increasing temperature on seed germination and seedling emergence of dominant desert plants remains unclear across different deserts, which is important for population regeneration and community succession in desert ecosystem. Seed germination and seedling emergence of *Haloxylon ammodendron* across four desert in Northwest China was examined at different rain frequencies, and constant and alternating temperatures, to investigate their response to climate change. Rain frequency determined seed germination and seedling emergence of *H. ammodendron* in Tengger Desert, Badain Jaran Desert, Gurbantonggut Desert and Mutthar Desert, which was maximal at rain frequency of 10 times per month and decreased with a decrease of rain frequency. Temperature was not a restricting factor for seed germination of *H. ammodendron* in Tengger Desert, Badain Jaran Desert and Gurbantonggut Desert, varying from 10 °C to 25 °C and from 20/10 °C to 30/15 °C, respectively. However, the highest temperature of 25 °C and 30/15 °C inhibited seed germination of *H. ammodendron* in the Mutthar Desert. *Haloxylon ammodendron* had an opportunistic germination strategy to adapt to the arid climate. Under climate change in the future, seed germination and seedling emergence of *H. ammodendron* would be restricted by the combination of less frequent rainfall and increased temperature in desert ecosystem. The regeneration of *H. ammodendron* community should be promoted by irrigation and seedling transplant.

Introduction

Global climate change has resulted from the greenhouse effect of elevated CO_2, including changing precipitation regimes and warming (IPCC 2013). A desert ecosystem is highly sensitive to climate change because plant species are already struggling in an extreme environment, including drought and high temperature. Since water and temperature are two key factors for plant survival and growth in a desert ecosystem, the changes of hydrothermal availability are expected to have influence on the structure and function of the desert plant community (Bai et al. 2020; Liu et al. 2016).

The regeneration of plant community relies primarily on seed germination of plant species from soil seed bank (Wang et al. 2019). Seed germination is the key stage in the establishment of plant species, which is also the most sensitive stage to environmental change in the life cycle (Baskin and Baskin 2014). Plant species have different seed germination strategies to ensure their survival in desert ecosystem (Gutterman 2002). Some desert plants, especially annuals, adapt to extreme environmental conditions with an opportunistic strategy, which produce plenty of seeds that germinate soon after rain in the growing season (Tobe et al. 2005a). However, other desert plants, especially perennial herbs and shrubs, have a cautious strategy to lower the risk of germination failure (Commander et al. 2017), which produce fewer seeds that germinate only in specific conditions. Seed germination of desert plants are often restricted by many environmental factors, such as moisture, temperature, light and sand burial (Li et al. 2012; Zhu et al. 2014). Germination time of some species is limited to spring, autumn or wet season. In contrast, other species can germinate throughout the growing season (Baskin and Baskin 2014). Therefore, investigating seed germination of desert plants will increase understanding of their adaptive strategy to arid climate, and result in sustainable management practices of desert vegetation.

In desert ecosystems, precipitation is usually low and unpredictable in its spatiotemporal pattern (Gutterman 2002), and mainly occurs as sporadic rainfall during the growing season, restricting seed germination and seedling emergence (Gillespie et al. 2004; Tobe et al. 2006). It was predicted that under global warming, less frequent, higher precipitation events will increase in the future (Allan and Soden 2008; IPCC 2013). The frequency, intensity and spatial pattern of rain have important effects on seed germination and seedling establishment in desert (Gutterman 2002). Desert shrub may need continuous rain events or heavy rainfall to trigger seed germination (Schwinning and Sala 2004). For example, higher seedling emergence of two *Artemisia* semi-shrubs, *Caragana korshinskii* and *Hedysarum fruticosum* occurred at 10 mm, 5 and 7.5 mm and 5 mm rain every 3 days in Mu Us Sandy Land (Zheng et al. 2005). Seedling emergence of three *Artemisia* semi-shrubs was maximal with initial 16 mm and subsequent 3 mm irrigation at 1d intervals in deserts of northwest China (Tobe et al. 2006). Watering level for maximal seedling emergence of *C. korshinskii*, *Hedysarum leave* and *Artemisia ordosica* in Mu Us Sandy Land were 10 mm, 10–20 mm and 15–20 mm, respectively (Zheng et al. 2009). Moreover, with the increase of rain amount, seed germination and seedling emergence generally increased, such as three *Artemisia* semi-shrubs (Tobe et al. 2006) and *Artemisia sphaerocephala* in Mu Us Sandy Land (Yang et al. 2012), and *Reaumuria soongarica* in Badain Jaran Desert (Shan et al. 2018). Rain frequency also influenced seedling emergence. With the decrease of rain frequency, seedling emergence decreased, such as *A. ordosica* (Tobe et al. 2006). However, most studies about seed germination and seedling emergence in different rain patterns were performed for one species or the inter-specific variation in one area. For widely distributed species across different areas, we still do not know the intra-specific variation of seed germination under different rain regime.

Temperature is another environmental factor that determines seed germination (Dürr et al. 2015). Moreover, the seasonal change of temperature primarily regulates germination in the field. Seed of most shrubs in temperate desert ecosystems generally germinate in a wide range of temperatures, varying from 3 °C to 30/15 °C (Baskin and Baskin 2014). Seeds of some desert shrubs germinated well when they were incubated at constant temperature. For example, most seeds of two *Haloxylon* shrubs germinated from 5 °C to 30 °C in Chinese desert (Tobe et al. 2000). Maximal seed germination of *Nitraria tangutorum* and *Nitraria spaerocarpa* occurred from 15 °C to 25 °C and 20 °C and 25 °C, respectively (Wang and Zhang 2009). In Horqin Sandy Land, seeds of two *Artemisia* semi-shrubs germinated from 10 °C to 34 °C (Li et al. 2012); however, seeds of *Caragana micophylla* germinated well from 15 °C to 30 °C (Lai et al. 2019). Seed of other desert shrubs germinated well at alternating temperatures. For example, seeds of *C. korshinskii* germinated from 5/15 °C to 25/35 °C on Ordos Plateau (Lai et al. 2015). Seeds of *Artemisia halodendron*, *C. korshinskii* and *C. microphylla* germinated well from 20/10 °C to 30/20 °C in Horqin Sandy Land (Lai et al. 2016). Seed germination of 11 species increased with temperature increasing from 0/12 °C to 15/27 °C whereas another 9 species germinated well at the lowest temperature of 0/12 °C in a desert steppe of Inner Mongolia (Yi et al. 2019). Moreover, alternating temperature was more favorable than constant temperature for seed germination of some psammophyte, such as *C. korshinskii* (Baskin and Baskin 2014). However, most previous studies about seed germination in different temperatures were carried out for one species or the inter-specific variation in one area. For widely distributed species, there were few studies about the intra-specific variation of seed germination from different areas, e.g. the differentiation in seedling emergence of *Coleogyne ramosissima* in Mojave Desert and Colorado Plateau (Meyer and Pendleton 2005).

Haloxylon ammodendron (C. A. Mey) Bunge. is a dominant shrub or small tree in the desert of Northwest China and central Asia, which widely inhabits sandy desert, Gobi, clay desert and salt desert (Ma 1991). This species not only plays an important role in the ecological function of desert ecosystem, such as sand dune stabilization, carbon sequestration and biodiversity conservation (Gao et al. 2010; Zhu and Jia 2011); but also has important economic value as the host plant for *Cistanche deserticola*, a precious Chinese traditional herb (Ma 1991). It has been widely used in land desertification control in Northwest China. The regeneration of *H. ammodendron* community relies on seed germination and seedling establishment. Previous studies showed that seed germination of *H. ammodendron* was affected by temperature, which was suitable at 10 ºC and lowest at 30 ºC (Huang et al. 2003). Higher seedling emergence of *H. ammodenron* resulted from 8–20 mm irrigation (Tobe et al. 2005b). However, we still don't know the effect of rain frequency and alternating temperature on seed germination of this dominant shrub in desert ecosystem. To obtain a better understanding of the adaptive strategy of dominant desert shrub to a harsh environment, we investigated the effects of rain frequency and temperature change on seed germination of *H. ammodendron* and discussed the possible impact of climate change on its population regeneration. Our research will give theoretical support to the sustainable management of desert vegetation under climate change.

Material And Methods

Seed collection

In late October and early November of 2019, seeds (utricles) of *H. ammodendron* were collected in four desert ecosystems from east to west, e.g. Tengger Desert, Badain Jaran Desert, Gurbantonggut Desert and Mutthar Desert. The location and climate of four seed source are shown in Table 1. There is a typical temperate continental climate in these four areas, which are the main distribution areas for *H. ammodendron* in the arid zone of northwest China. Tengger Desert and Badain Jaran Desert are located on Alxa Plateau of Mongolian Plateau, which has less mean annual precipitation. Gurbantonggut Desert and Mutthar Desert are located in Junggar Basin of central Asia, which has more rainfall. The air temperature in July is highest in Mutthar Desert. The mean daily air temperature is highest in July in Mutthar Desert. Seeds were manually shaken from shoots of *H. ammodendron*, and then stored in a cotton bag at room temperatures varying from 13°C to 22°C.

Table 1
The location and climate of four deserts for seed collection of *Haloxylon ammodendron* in Northwest China

Seed source	Longitude, Latitude	Elevation (m)	MAP (mm)	MAT (ºC)	T_{max} (ºC)	T_{min} (ºC)
Tengger Desert	N 39º34.13', E 105º45.03'	1048	115	8.3	23.5	−9.2
Badain Jaran Desert	N 39º24.53', E 102º46.02'	1236	113	8.4	24.5	−7.8
Gurbantonggut Desert	N 44º11.21', E 89º32.03'	651	150	5.5	22.6	−18.9
Mutthar Desert	N 44º32.75', E 83º23.41'	366	167	7.8	26.3	−19.2

MAP: mean annual precipitation. MAT: mean annual air temperature. T_{max}: mean daily air temperature in July. T_{min}: mean daily air temperature in January.

Before this experiment, the pericarp and wing of *H. ammodendron* seeds were removed manually. Seed mass was measured by an electronic balance (0.01 g) for 1000 seeds with four replicates. The mean mass of 1000 *H. ammodendron* seeds was 3.25 ± 0.05, 2.65 ± 0.03, 3.63 ± 0.05 and 2.73 ± 0.07 g in Tengger Desert, Badain Jaran Desert, Gurbantonggut Desert and Mutthar Desert, respectively.

Experimental design and measurement

Based on the field observation, most seeds of *H. ammodendron* germinated after rain from April to June. Thus, climate data of four seed source was analyzed to determine experiment conditions. There were 2.00 to 3.71 times (0—6) rain of four seed sources in April, 1.71 to 5.00 times (1—6) rain in May, and 4.00 to 5.00 times (1—7) rain in June (Table 2). Thus, four rain frequencies (10, 6, 3, or 2 times per month) were applied in our experiment, considering history rain data and the decrease of rain frequency resulting from climate change in the future.

Table 2
The rain frequency (times per month) (mean ± SE, range) in the germination season of four deserts, Northwest China

Seed source	April	May	June	Mean
Tengger Desert	2.29 ± 1.25 (1—4)	3.14 ± 1.35 (1—5)	4.00 ± 1.63 (1—6)	3.14 ± 1.53
Badain Jaran Desert	2.00 ± 1.53 (0—4)	1.71 ± 0.95 (1—3)	4.29 ± 1.98 (1—6)	2.67 ± 1.88
Gurbantonggut Desert	3.71 ± 1.50 (2—6)	4.29 ± 0.76 (3—5)	4.86 ± 1.07 (4—7)	4.29 ± 1.19
Mutthar Desert	3.71 ± 1.60 (1—6)	5.00 ± 1.41 (2—6)	5.00 ± 1.41 (4—7)	4.57 ± 1.54

Experiments of seed germination and seedling emergence were conducted from April 12 to May 13 in 2020 in a non-heated greenhouse at the Chinese Academy of Forestry. The substrate for seed germination was river sand passed through a sieve with the diameter of 2 mm. Plastic pots (15.6 cm diameter × 13.2 cm height) were filled with sand to within 1 cm of the top, and 25 seeds were planted uniformly with forceps at 1 cm depth in each pot because the highest seed germination percentage of *H. ammodendron* was obtained at 1 cm depth (Wang and Zhao 2015).There were four pots (replicates) for each treatment, totaling 64 pots in this experiment (4 rain frequencies · 4 seed sources · 4 replicates). A seedling was considered to be emerged when its first foliage leaf was 5 mm above sand surface. Daily air temperatures varied from 14°C to 31°C in the greenhouse during the experiment with the mean minimal value of 20.1°C and the mean maximal value of 28.1°C.

There were four frequencies of watering (10, 6, 3, or 2 times per month) for *H. ammodendron* seeds on four seed sources with the monthly rain amount of 50 mm, which are equivalent to 88, 147, 293, and 440 mL water each time, respectively. Seedling emergence was recorded daily for each pot, and the experiment was terminated after 30 days, at which time no seedlings had emerged for at least 5 consecutive days. All sand in each pot was passed through a sieve with 2 mm diameter to examine germinated but un-emerged seedlings, and then seed germination percentage was calculated for each treatment.

From April to June, the maximal daily temperature of four seed sources varied from 17.62 ºC to 21.01 ºC, from 22.91 ºC to 26.82 ºC, and from 26.90 ºC to 32.44 ºC, respectively; meanwhile, the minimal daily temperature varied from 4.12 ºC to 8.51 ºC, from 9.33 ºC to 14.11 ºC, and from 15.19 ºC to 19.37 ºC, respectively (Table 3). Thus, there were four constant temperatures (10 ºC, 15 ºC, 20 ºC and 25 ºC) and four alternating temperatures (20/10 ºC, 25/10 ºC, 25/15 ºC and 30/15 ºC) in our experiment based on the air temperature data in the germination season.

Table 3

The air temperature (ºC) in the germination season of four deserts, Northwest China

Seed source	T_{max} in Apr.	T_{min} in Apr.	T_{max} in May	T_{min} in May	T_{max} in Jun.	T_{min} in Jun.
Tengger Desert	17.62 ± 1.25	6.22 ± 0.25	22.91 ± 1.11	11.73 ± 1.02	26.90 ± 0.89	16.71 ± 0.84
Badain Jaran Desert	18.57 ± 0.93	5.61 ± 0.41	23.61 ± 1.22	11.03 ± 0.72	28.38 ± 1.17	16.69 ± 0.77
Gurbantonggut Desert	19.33 ± 1.39	4.12 ± 1.18	24.20 ± 1.24	9.33 ± 0.96	28.99 ± 1.11	15.19 ± 1.03
Mutthar Desert	21.01 ± 1.76	8.51 ± 1.66	26.82 ± 1.64	14.11 ± 1.36	32.44 ± 0.71	19.37 ± 0.83

T_{max}: maximal daily temperature; T_{min}, minimal daily temperature.

Seeds of *H. ammodendron* from four seed sources were germinated in the illumination incubator at the Plant Ecophysiology Laboratory in Chinese Academy of Forestry. Experiment on seed germination in four constant temperatures was conducted from April 22 to May 7; and then the experiment on seed germination in four alternating temperatures was conducted from June 11 to June 26 in 2020. The period for high and low temperature was 12 h and 12 h in the alternating temperature treatments, respectively. Twenty five seeds were placed uniformly with forceps in a 9 cm diameter plastic Petri dish with two layers of Whatman No. 1 filter paper and 2 mL distilled water. There were four Petri dishes (replicates) for each treatment and a total of 64 dishes in each experiments (4 temperatures · 4 seed sources · 4 replicates). A seed was considered to be germinated when the radicle appeared (1 mm) from seed coat. Germination was examined daily, distilled water was added when necessary and the germinated seeds were removed from the Petri dish. The seed germination experiment was terminated after 15 days, at which time no seed had germinated for at least 5 consecutive days.

Statistical analysis

A completely randomized design was used in all experiments. Percentages of seed germination and seedling emergence were expressed as mean ± SE (standard error). The percentages were arcsine square root transformed before analysis, but untransformed data are shown in tables and figures. Two-way ANOVA at the 95% probability level was conducted to compare the effects of rain frequency and seed source on the percentage of seedling emergence and seed germination of *H. ammodendron*, and the effects of constant temperature or alternating temperature and seed source on seed germination percentage (Sokal and Rohlf 1995). If ANOVA showed significant effects, Duncan's test was used to determine the difference between treatments. All analysis were conducted by SPSS 19.0 for Windows (SPSS Inc., Chicago, USA).

Results

Effects of rain frequency on seed germination and seedling emergence

Seedling emergence of *H. ammodendron* was delayed with the decreasing rain frequency (Fig. 1). In Tengger Desert, seedling of *H. ammodendron* emerged on the second day at the rain frequency of 6 and 3 times per month but on the fourth day at 2 times per month. In Badain Jaran Desert, seedling of *H. ammodendron* emerged on the third day at the rain frequency of 10 and 6 times per month but on the fifth day at less frequent rain. In Gurbantonggut Desert, seedling of *H. ammodendron* emerged on the third day at the rain frequency of 10 and 6 times per month but on the fourth day at less frequent rain. In Mutthar Desert, seedling of *H. ammodendron* emerged on the seventh day at the rain frequency of 10 times per month but on the eighth day at less frequent rain. In general, seedling emergence of *H. ammodendron* was delayed from east to west, which was fastest in Tengger Desert and slowest in Mutthar Desert.

Seed germination and seedling emergence percentage of *H. ammodendron* were affected significantly by rain frequency ($p < 0.001$), seed source ($p < 0.001$) and their interactions ($p < 0.01$, Table 4). Generally, seedling emergence declined with the decreasing rain frequency (Fig. 1). The percentages of seed germination (91%) and seedling emergence (89%) of *H. ammodendron* in Tengger Desert were higher at the rain frequency of 6 times per month than those at other treatments. The percentages of seed germination and seedling emergence of *H. ammodendron* in Badain Jaran Desert were higher at the rain frequency of 10, 6 and 3 times per month than at 2 times per month. The percentages of seed germination (73% and 72%) and seedling emergence (67% and 63%) of *H. ammodendron* in Gurbantonggut Desert were higher at the rain frequency of 10 and 6 times per month than those at other treatments. The percentages of seed germination (37% and 36%) and seedling emergence (32% and 29%) of *H. ammodendron* in Mutthar Desert were higher at the rain frequency of 10 and 6 times per month than those at other treatments (Fig. 1—2). At the rain frequency of 10 times per month, the percentages of seed germination and seedling emergence of *H. ammodendron* were higher in Badain Jaran Desert and Gurbantonggut Desert. At the rain frequency of 6 times per month, the percentages of seed germination and seedling emergence were highest in Tengger Desert. At the rain frequency of 3 times per month, the percentages of seed germination and seedling emergence were higher in Tengger Desert, Badain Jaran Desert and Gurbantonggut Desert. At the rain frequency of 2 times per month, the percentages of seed germination and seedling emergence were higher in Gurbantonggut Desert and Tengger Desert (Fig. 2).

Different upper case letters mean significant difference between seed sources, different lower case letters mean significant difference between rain frequencies

Table 4
Two-way ANOVA of response of seed germination and seedling emergence of *Haloxylon ammodendron* in different seed source to rain frequency

Source	Seed germination				Seedling emergence			
	SS	MS	F value	*p* value	SS	MS	F value	*p* value
Rain frequency	0.607	0.202	11.749	< 0.001	0.905	0.302	14.168	< 0.001
Seed source	1.690	0.563	32.689	< 0.001	1.907	0.636	29.862	< 0.001
Rain frequency × Seed source	0.493	0.055	3.179	0.004	0.677	0.075	3.532	0.002

Effects of constant temperature and alternating temperature on seed germination

In Tengger Desert, Badain Jaran Desert and Gurbantonggut Desert, all seed of *H. ammodendron* germinated on the second day at four constant temperatures (Fig. 3). However, seed germination of *H. ammodendron* was delayed with the decreasing constant temperature in Mutthar Desert, which started on the second day at 20 ºC and 25 ºC but on the third day at lower constant temperatures.

Seed germination percentage was affected significantly by seed source ($p < 0.001$) and its interactions with constant temperature ($p < 0.05$, Table 5). For *H. ammodendron* in Tengger Desert, Badain Jaran Desert and Gurbantonggut Desert, seed germination percentage was higher than 80% at four temperatures. However, seed germination percentage of *H. ammodendron* in Mutthar Desert was significantly lower (75%) at 25 ºC (Fig. 3—4). At the lower temperatures (10 ºC — 20 ºC), seed germination percentage was similar in the four deserts. However, seed germination percentage was significantly higher in Tengger Desert, Badain Jaran Desert and Gurbantonggut Desert than that in Mutthar Desert at 25 ºC ($p < 0.001$) (Fig. 4).

Table 5
Two-way ANOVA of response of seed germination of *Haloxylon ammodendron* in different seed source to constant or alternating temperature

Source	Constant temperature				Alternating temperature			
	SS	MS	F	*P*	SS	MS	F	*P*
Temperature	0.107	0.036	1.528	0.219	0.194	0.065	12.182	< 0.001
Seed source	0.628	0.209	8.986	< 0.001	0.756	0.252	47.579	< 0.001
Temperature × Seed source	0.462	0.051	2.202	0.038	0.314	0.035	6.577	< 0.001

Different upper case letters mean significant difference between seed sources, different lower case letters mean significant difference between temperatures.

In Tengger Desert, Badain Jaran Desert and Gurbantonggut Desert, seed of *H. ammodendron* germinated on the second day at four alternating temperatures (Fig. 5). However, seed germination of *H. ammodendron* was delayed with the increasing alternating temperature in Mutthar Desert, which started on the second day at 20/10 ºC but on the third day at higher alternating temperatures.

Seed germination percentage of *H. ammodendron* was affected significantly by alternating temperature, seed source and their interactions ($p < 0.001$, Table 5). For *H. ammodendron* in Tengger Desert, Badain Jaran Desert and Gurbantonggut Desert, seed germination percentages were higher than 95%, 80% and 85% at four alternating temperatures, respectively. However, seed germination percentage of *H. ammodendron* in Mutthar Desert was significantly higher (75%) at 20/10 ºC, 25/15 ºC and 25/15 ºC than that at 35/10 ºC (36%) ($p < 0.001$, Fig. 4—5). At 20/10 ºC, seed germination percentage was significantly higher in Tengger Desert and Gurbantonggut Desert than that in Mutthar Desert ($p < 0.05$). At 25/10 ºC, seed germination percentage was significantly higher in Tengger Desert than that in Mutthar Desert ($p < 0.05$). At 25/15 ºC and 30/15 ºC, seed germination percentage was significantly higher in Tengger Desert, Badain Jaran Desert and Gurbantonggut Desert than that in Mutthar Desert ($p < 0.001$) (Fig. 4).

Discussion

The suitable environmental conditions for seed germination are highly unpredictable over space and time in desert ecosystem (Wang et al. 2018). Seeds of most desert plants generally germinate after enough rainfall in the growing season, and have an opportunistic strategy to adapt to the harsh environment (Gutterman 2002). Our experiment results showed that seeds of *H. ammodendron* in four deserts germinated rapidly and well at the rain frequency of 10 times per month totaling 50 mm. Moreover, seed germinated well in a relatively wide range of temperatures varying from 10 °C to 25 °C and from 20/10 °C to 30/15 °C, except in Mutthar Desert where the highest temperature inhibited seed germination of *H. ammodendron*.

Response of seed germination and seedling emergence to rain frequency change

Seed germination and seedling emergence of *H. ammodendron* in the four deserts was higher at the highest rain frequency (10 times per month) and inhibited by the decrease of rain frequency (Fig. 1). Therefore, the best time for seed germination and seedling emergence of this shrub is late spring or early summer after a few days of continuous rain. The responses of *H. ammodendron* to rain frequency may reflect their ecological adaptations to the climate in the germination season. It takes an opportunistic strategy of seed germination to adapt to the arid climate in a desert ecosystem, which is typical in many desert plants. For example, after initial irrigation of 8 mm or 16 mm, subsequent irrigation of 3 mm at 1 d or 2 d intervals resulted in higher seedling emergence in three annuals (*Agriophyllum squarrosum*, *Bassia dasyphylla* and *Aristida asdcensionis*) in Mu Us Sandy Land, while irrigation at 4 d or 6 d intervals only favored seedling emergence of *A. adscensionis* (Tobe et al. 2005a). Seedling emergence of three *Artemisia* species was maximal when they were initially and subsequently treated with 16 mm and 3 mm irrigation at 1-d intervals. However, when they were initially and subsequently treated with 8 mm and 3 mm irrigation at 2-d intervals, seedling emergence was almost completely suppressed due to water deficiency in sand (Tobe et al. 2006). Similarly, seedling emergence of *Leymus secalinus* is adapted to 150 mm of monthly rain with the frequency of 10–30 times per month, and decreased as rain frequency decreased in Mu Us Sandy Land (Zhu et al. 2014). More rains in late spring also enhanced seedling emergence of *Aspidosperma quebracho-blanco*, and the regular rainfall distribution rather than rainfall amount was the most significant factor in the survival of this species in central Argentina (Barchuk et al. 2005). Rain frequency was as important as rain amount to seedling emergence of *R. soongarica* since the highest emergence was obtained with a 30% increase in rain amount and a 50% reduction in rain frequency at southern edge of Badain Jaran Desert (Shan et al. 2018). Therefore, rain frequency plays an important role in seed germination and seedling emergence of desert plants. Less frequent rainfall will restrict seed germination and seedling emergence of desert plants in the future.

In Tengger Desert and Badain Jaran Desert, the mean rain frequency was about 3 times per month during the germination season. In Gurbantonggut Desert and Mutthar Desert, the mean rain frequency was about 4 times per month during the germination season (Table 2). Under future climate change, less frequent and larger precipitation events will increase (IPCC 2013), thus the rain regime in the arid zone would be more unpredictable. Less frequent rain events will inhibit seed germination and seedling emergence of *H. ammodendron*. Moreover, the regeneration of *H. ammodendron* community might be more sensitive to rain change in Tengger Desert and Badain Jaran Desert than in Gurbantonggut Desert and Mutthar Desert, since there is less rain in the two former deserts (about 110 mm) than in the latter areas (about 150 mm) (Table 1).

Response of seed germination to warming

Seed germination of *H. ammodenron* was adapted to a relatively wide range of temperature in desert ecosystems, which was higher both at constant temperature (10°C to 25°C) and alternating temperature (20/10°C, 25/10°C, 25/15°C and 30/15°C) in Tengger Desert, Badain Jaran Desert and Gurbantonggut Desert. Similarly, seeds of *C. korshinskii* germinated well from 5/15°C to 25/35°C on Ordos Plateau (Lai et al. 2015). However, seed germination of *H. ammodendron* was inhibited by high temperatures (25°C or 30/15°C) in Mutthar Desert (Fig. 3–5). Based on field observation, seed germination of *H. ammodendron* generally occurred in spring. The inhibition of seed germination in this area may result also from higher air temperatures in the later germination season, which were 26.82°C and 32.44°C in May and June, respectively (Table 3). Mean temperature for seed germination was 17.8 ± 0.6°C in cold deserts (Baskin and Baskin 2014), which was similar to spring air temperatures. High temperature in summer inhibited seed germination of many desert plants. For example, seeds of *Agropyron cristatum*, *A. halodendron*, *C. korshinskii* and *Melilotus suaveolens* germinated well at 25/15°C and 30/20°C but poorly at 35/25°C in Horqin Sandy Land (Lai et al. 2016). Warming also inhibited seed germination or seedling emergence of four woody *Banksia* species in South Western Australia (Cochrane et al. 2015). Therefore, desert plants may germinate earlier to adapt to global warming in the future.

In deserts of Northwest China, the best time for seed germination of *H. ammodendron* is late spring and early summer, when temperature would be appropriate and sand would be moist after rainfall. It is predicted that seed germination of *H. ammodendron* will occur earlier under global warming. However, considering both warming and less frequent rainfall, seed germination might be more difficult for *H. ammodendron*, especially in Mutthar Desert. Therefore, the regeneration of *H. ammodendron* community should be enhanced in the future by irrigation and seedling transplant.

Conclusions

In temperate desert ecosystems, *H. ammodendron* had an opportunistic seed germination strategy to adapt to the unpredictable environment. Seed germinated and seedling emerged at higher rain frequencies and a wide range of air temperatures in the four deserts of northwest China. However, seed germination of *H. ammodendron* was inhibited by the highest temperature in Mutthar Desert. Therefore, the optimal germination time for *H. ammodendron* is spring and early summer after rainfall. Under future climate change, seed germination and seedling emergence of *H. ammodendron* would be restricted by warming and less frequent rainfall in desert ecosystems. The regeneration of *H. ammodendron* community should be promoted by irrigation and seedling transplant.

Declarations

Acknowledgements We thank Mrs. Anne Nyren from North Dakota State University for improving English. We are thankful to Prof Lei Wang from Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences for reviewing this manuscript.

Author Contributions YZ: Conceptualization, Methodology, Investigation, Formal analysis, Writing; ZJ: Supervision, Funding acquisition, Review; GW: Review & editing.

Funding This study was supported by the National Key Technology R&D Program (2012BAD16B0102) of China and the Science and Technology Plan Project of Nei Mongol (2021GG0306).

Data Availability The data that support the findings of this study are available on request from the corresponding author.

Conflict of interest The authors declare that they have no conflict of interest.

Consent to participate All authors participated in this manuscript.

Consent for publication All authors revised the manuscript critically and approved the final manuscript for publication.

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Figures

Figure 1

The cumulative daily seedling emergence of *Haloxylon ammodendron* in four deserts at different rain frequency. Seedling percentages are expressed as means ± SE of four replicates of 25 seeds

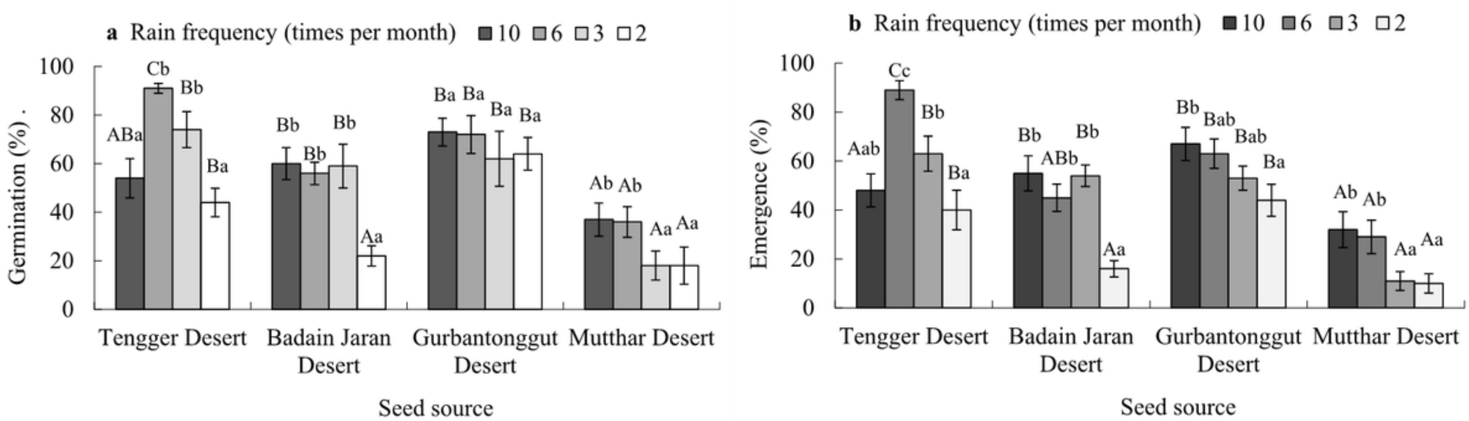

Figure 2

The final percentage of seed germination and seedling emergence of *Haloxylon ammodendron* in four deserts at different rain frequency. Seed germination and seedling emergence percentages are expressed as means ± SE of four replicates of 25 seeds

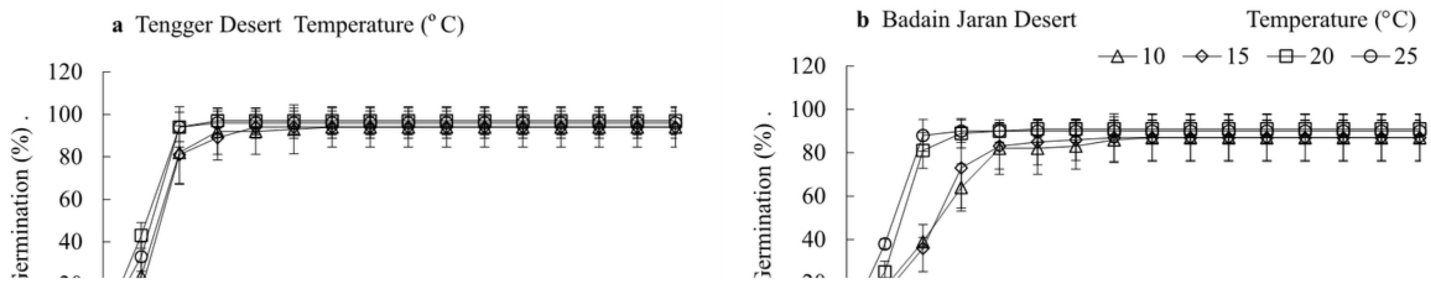

Figure 3

The cumulative daily seed germination of *Haloxylon ammodendron* in four deserts at constant temperature. Seed germination percentages are expressed as means ± SE of four replicates of 25 seeds.

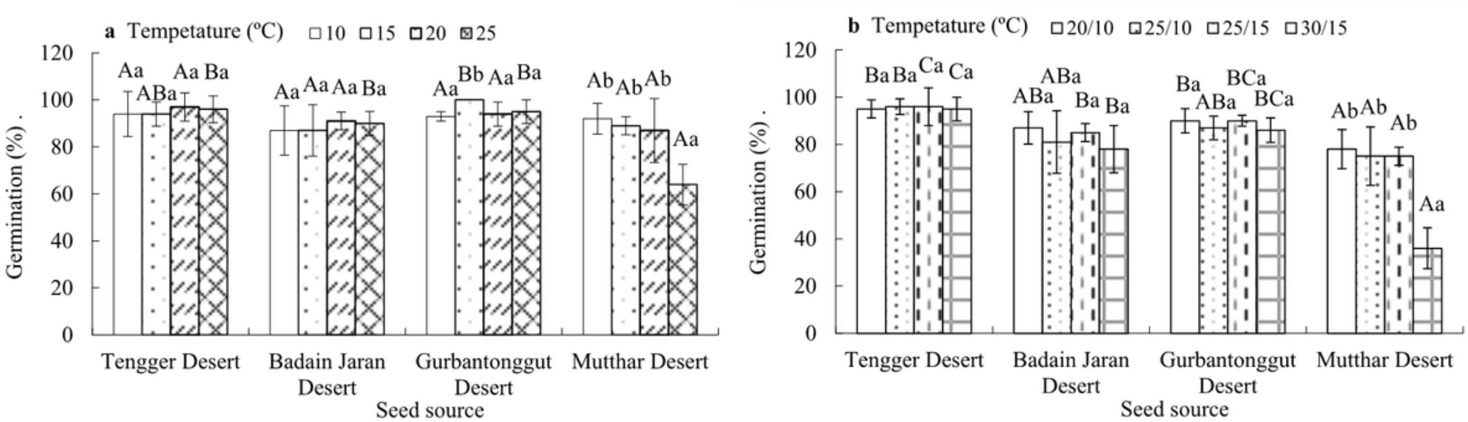

Figure 4

Seed germination of *Haloxylon ammodendron* in four deserts at constant and alternating temperature. Seed germination percentages are expressed as means ± SE of four replicates of 25 seeds.

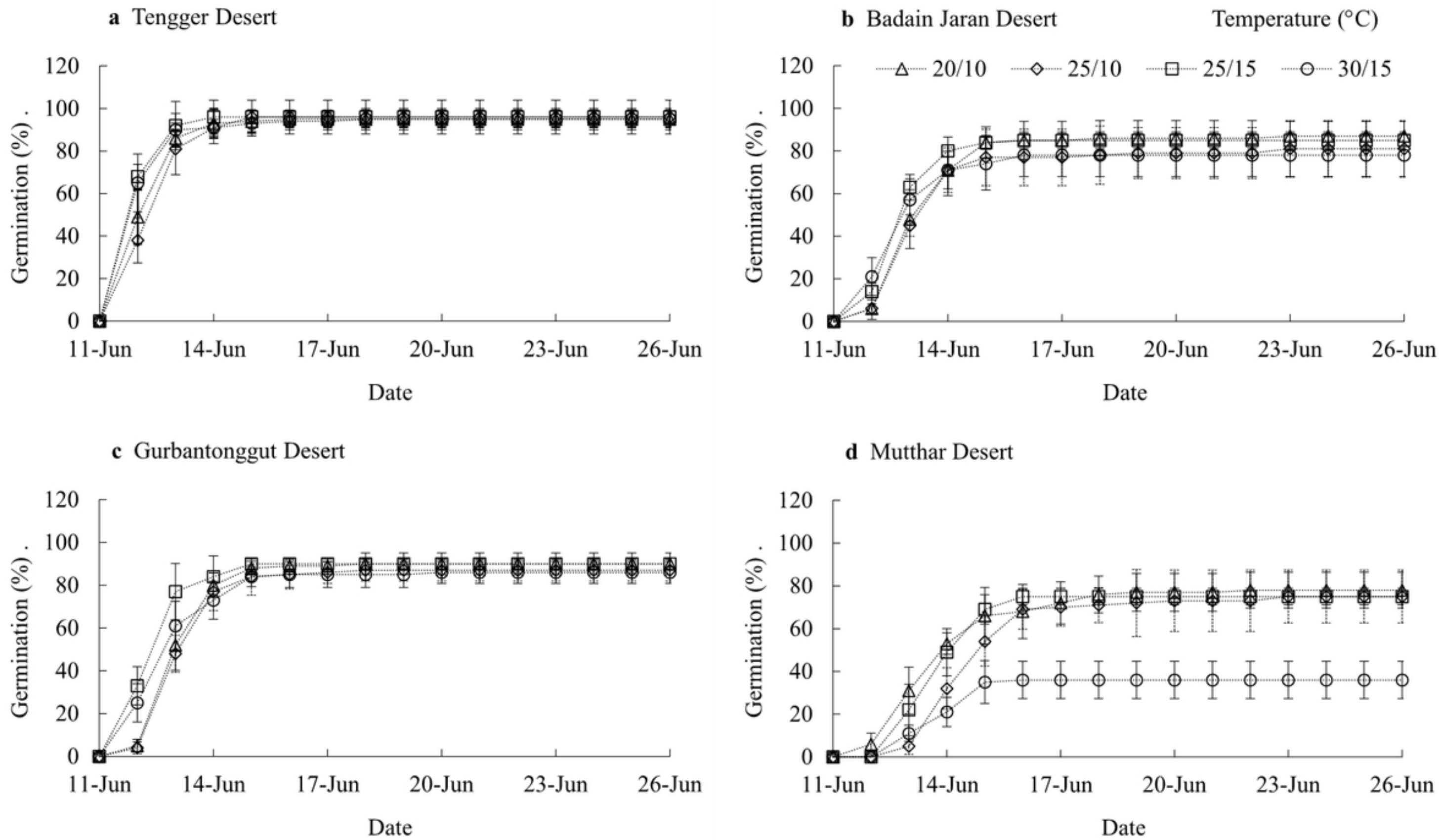

Figure 5

The cumulative daily seed germination of *Haloxylon ammodendron* in four deserts at alternating temperature. Seed germination percentages are expressed as means ± SE of four replicates of 25 seeds