Effects of water stress and NaCl stress on different life cycle stages of the cold desert annual Lachnoloma lehmannii in China Postprint

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Date: 2019-10-26T00:00:00+00:00

Abstract

For a plant species to complete its life cycle in arid and saline environments, each stage of the life cycle must be tolerant to the harsh environmental conditions. The aim of the study was to determine the effects of water stress (water potentials of -0.05, -0.16, -0.33, -0.56, -0.85 and -1.21 MPa) and NaCl stress (50, 100, 200, 300, 400, 500 and 600 mmol/L NaCl) on seed germination percentage, seedling survival and growth, juvenile growth and plant reproduction of Lachnoloma lehmannii Bunge (Brassicaceae), an cold desert annual that grows in the Junggar Basin of Xinjiang, China in 2010. Results indicated that low water stress (-0.05 and -0.16 MPa) had no significant effect on seed germination percentage. With a decrease in water potential, germination percentage decreased, and no seeds germinated at -0.85 and -1.21 MPa water stresses. Germination percentage of seeds was significantly affected by NaCl stress, and higher germination percentages were observed under non-saline than saline conditions. An increase in NaCl concentrations progressively inhibited seed germination percentage, and no seeds germinated at 400 mmol/L NaCl concentration. Non-germinated seeds were transferred from both PEG (polyethylene glycol-6000) and NaCl solutions to distilled water for seed germination recovery. The number of surviving seedlings and their heights and root lengths significantly decreased as NaCl stress increased. About 30% of the plants survived and produced fruits/seeds at 200 mmol/L NaCl concentration. Thus, seed germination, seedling establishment and reproductive stage in the life cycle of L. lehmannii are water- and salt-tolerant, with seedlings being the least tolerant. These tolerances help explain why this species can survive and produce seeds in arid and saline habitats.

Full Text

Preamble

Effects of Water Stress and NaCl Stress on Different Life Cycle Stages of the Cold Desert Annual *Lachnoloma lehmannii* in China

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Abstract: For a plant species to complete its life cycle in arid and saline environments, each stage must tolerate harsh environmental conditions. This study determined the effects of water stress (water potentials of -0.05, -0.16, -0.33, -0.56, -0.85 and -1.21 MPa) and NaCl stress (50, 100, 200, 300, 400, 500 and 600 mmol/L NaCl) on seed germination percentage, seedling survival and growth, juvenile growth, and plant reproduction of *Lachnoloma lehmannii* Bunge (Brassicaceae), a cold desert annual growing in the Junggar Basin of Xinjiang, China in 2010. Results indicated that low water stress (-0.05 and -0.16 MPa) had no significant effect on seed germination percentage. As water potential decreased, germination percentage declined, and no seeds germinated at -0.85 and -1.21 MPa. Germination percentage was significantly affected by NaCl stress, with higher germination observed under non-saline than saline conditions. Increasing NaCl concentrations progressively inhibited germination, and no seeds germinated at 400 mmol/L NaCl. Non-germinated seeds from both PEG (polyethylene glycol-6000) and NaCl solutions were transferred to distilled water for germination recovery. The number of surviving seedlings and their heights and root lengths significantly decreased as NaCl stress increased. About 30% of plants survived and produced fruits/seeds at 200 mmol/L NaCl. Thus, seed germination, seedling establishment, and reproductive stages in the life cycle of *L. lehmannii* are water- and salt-tolerant, with seedlings being the least tolerant. These tolerances help explain how this species survives and produces seeds in arid and saline habitats.

Keywords: drought stress; *Lachnoloma lehmannii*; salinity tolerance; seed germination; seedling growth

Citation: Jannathan MAMUT, TAN Dunyan, Carol C BASKIN, Jerry M BASKIN. 2019. Effects of water stress and NaCl stress on different life cycle stages of the cold desert annual *Lachnoloma lehmannii* in China. *Journal of Arid Land*, 11(5): 774–784. https://doi.org/10.1007/s40333-019-0015-8

1 Introduction

Desert habitats are characterized by harsh environmental conditions, including seasonal and daily temperature extremes, low precipitation, and high evaporation (Gutterman, 2002). Additionally, high groundwater levels and strong physical weathering lead to salinity accumulation in surface soil layers (Xi et al., 2006). In these habitats, substrate drought and salinity are major factors affecting seed germination percentage, seedling establishment (Ma et al., 2016), and plant growth and reproduction (Galle et al., 2007; Li et al., 2013).

Since seed germination and seedling establishment and growth are the most critical stages in plant life cycles, the status and timing of seedling growth determine survival (Kitajima and Fenner, 2000; Baskin and Baskin, 2014; Ludewig et al., 2014; Hu et al., 2015). After dormancy is broken, favorable temperature, soil moisture, and light conditions must overlap with seed germination requirements; otherwise, seeds do not germinate. For desert annuals, understanding how seeds and seedlings respond to drought and high soil salinity is essential for developing knowledge of ecological adaptation to stressful desert habitats (Fenner and Thompson, 2005; Zhang et al., 2010; Hu et al., 2015; Zhang et al., 2015).

Drought, related to water potential of both soil and seed (Evans and Etherington, 1990; Bradford, 2002; Li et al., 2013; Hu et al., 2015), is one of the most important limiting factors restricting germination and successful seedling establishment. Drought affects seed imbibition, germination percentage, and seedling growth (Galle et al., 2007; Ahmad et al., 2009). Salinity also critically influences germination and plant establishment. For example, increasing salinity may inhibit or delay germination, negatively affect seed viability, induce secondary dormancy, and reduce seedling growth (Khan and Gul, 2006; Zehra et al., 2013; Baskin and Baskin, 2014; Santo et al., 2017).

Lachnoloma lehmannii Bunge is a cold desert annual occurring in central and southwestern Asia. In China, this species grows only in rocky or saline sandy soils of deserts in the Junggar Basin of Xinjiang (Zhou et al., 2001; Mamut et al., 2014). Since *L. lehmannii* grows and sets seeds in arid and saline habitats (Mamatriyim et al., 2011), we hypothesized that the seed and seedling stages of its life cycle are tolerant to water stress and NaCl stress—important adaptations to harsh arid and saline habitats. To test this hypothesis, we investigated the effects of water stress and NaCl stress on seed germination percentage and recovery, seedling survival and growth, juvenile growth, and plant reproduction in *L. lehmannii* in the Junggar Basin of Xinjiang, China.

2.1 Seed Collection and Field Site Description

Freshly matured silicles were collected from dry infructescences of *L. lehmannii* plants growing on saline and sandy soils of the Junggar Basin (44°22 25 N, 88°08 30 E; 454 m a.s.l.), Xinjiang, China, on 21 June 2009 and 4 July 2010.

After collection, silicles were stored in paper bags under ambient laboratory conditions (18°C-30°C temperature and 20%-30% relative humidity) until use.

The study area is an inland cold basin with a typical temperate desert climate. Mean monthly precipitation and monthly maximum and minimum temperatures at the Fukang Meteorological Station near the Junggar Basin during 2001-2010 are shown in Figure 1 [Figure 1: see original paper]. Annual mean temperature is 8.3°C, with mean temperatures of -15.6°C in the coldest month (January) and 26.0°C in the hottest month (July). Average annual precipitation (including rainfall and snow) is 222 mm, about two-thirds of which occurs in spring and summer, with snow that falls in winter beginning to melt in March or April. Annual potential evaporation exceeds 2000 mm (Wei et al., 2003).

2.2 Effects of Water Stress on Seed Germination Percentage and Germination Recovery

To determine the effect of water stress on germination percentage, we used distilled water and polyethylene glycol-6000 (PEG-6000) solutions (Michel and Kaufmann, 1973) with water potentials of -0.05, -0.16, -0.33, -0.56, -0.85, and -1.21 MPa. Seeds were incubated in 9-cm-diameter Petri dishes on two sheets of Whatman No. 1 filter paper moistened with distilled water or one of the six PEG concentrations. Petri dishes were sealed with plastic film to retard evaporation, and seeds were incubated under a daily 12 h/12 h light/dark regime (100 mol/(m^2·s), 400-700 nm, cool white fluorescent light; hereafter referred to as light) at 15°C/2°C, the optimum conditions for germination (Mamut et al., 2014). Three replications of 50 seeds (dry-stored for 6 months after ripening) were used for each treatment. Germination percentage in light was monitored daily for 15 d, after which non-germinated seeds were rinsed three times with distilled water and incubated for an additional 15 d in Petri dishes containing 5 mL distilled water to test for germination recovery. Germination recovery was calculated using the formula: (a-b)/(c-b)×100%, where *a* is the total number of seeds that germinated in PEG solution plus those that recovered to germinate in distilled water; *b* is the number of seeds germinated in PEG solution; and *c* is the total number of seeds tested (Gul and Weber, 1999). Final germination percentage was calculated as (a/c)×100%. Seed viability was expressed as (a+d)/c×100%, where seeds were cut open and placed in a 0.1% aqueous solution of 2,3,5-triphenyl-2H-tetrazolium chloride (TTC) at 20°C for 24 h following the germination recovery test. Embryos that stained red or pink were considered viable, and those that did not stain were considered nonviable (Baskin and Baskin, 2014).

2.3 Effects of NaCl Stress on Seed Germination Percentage and Germination Recovery

The effects of 50, 100, 200, 300, 400, 500, and 600 mmol/L NaCl concentrations on seed germination percentage were tested at a daily temperature regime of

15°C/2°C (12 h/12 h) in light; control seeds were incubated in distilled water. Three replicates of 50 seeds were used for each treatment and control. Seeds were incubated in 9-cm-diameter Petri dishes on two sheets of Whatman No. 1 filter paper moistened with distilled water or one of the seven NaCl concentrations. Germination percentage was monitored daily for 15 d, after which all non-germinated seeds were rinsed three times with distilled water and incubated for 15 d in Petri dishes containing 5 mL distilled water. Germination recovery, final germination percentage, and seed viability were determined as described above.

2.4 Effects of Water Stress on Plant Growth and Reproduction

On 28 March 2010, 600 ripened seeds were sown to a depth of 3 cm in 30 plastic pots (18 cm depth and 21 cm diameter with drainage holes at the bottom) filled with soil from natural *L. lehmannii* habitats. The sown seeds were exposed to near-natural temperatures in a non-temperature-controlled metal frame house (top covered with plastic sheeting only when it rained) in the experimental garden of Xinjiang Agricultural University, China. Before treatment began, soil was watered daily to field capacity. To prevent variation in initial seedling size, we kept three seedlings of uniform size in each pot and removed the others. After 20 d, when seedlings had four leaves, three moisture levels were applied: watered to field capacity daily (high water supply), watered every 3 d, and watered every 6 d. There were 10 replicates per treatment (10 pots each with three seedlings; 3 treatments × 10 replicates × 3 seedlings per replicate). The experiment was terminated on 1 July 2010, when plant height, length of the longest roots, number of fruits, and number of seeds were recorded for the 30 plants from each treatment. Each plant was divided into root and shoot (including leaves, stems, and fruits) and oven-dried to constant weight at 80°C for 48 h in paper bags, after which all parts were weighed using an electronic balance (0.0001 g precision).

2.5 Effects of NaCl Stress on Seedling Survival and Growth

Five replicates of 20 seeds were sown on 24 March 2010 in 35 pots (10 cm diameter and 10 cm depth). Pots were watered with tap water and fertilized every 3 d with half-strength Hoagland solution. Twelve days after sowing, seedlings (with two cotyledons each) were thinned to four per pot, and NaCl treatments were initiated. All plants were watered daily either with Hoagland solution or with Hoagland solution plus 50 mmol/L NaCl. Control plants (five pots) received only Hoagland solution. Plants receiving 50, 100, 150, 200, 250, and 300 mmol/L NaCl were watered with Hoagland solution plus NaCl for 1, 2, 3, 4, 5, and 6 d, respectively. After receiving their allotted NaCl, plants were watered only with Hoagland solution. The experiment was terminated after 3 weeks. During the experiment, a seedling was defined as dead when it became yellow and wilted, and the number of dead seedlings was recorded daily. At termination, height of living seedlings and length of the longest root were measured. Seedling biomass was determined after drying at 80°C for 48 h.

2.6 Effects of NaCl Stress on Juvenile Growth and Plant Reproduction

We determined the effect of NaCl on growth and reproduction of plants grown in aerated Hoagland solutions. Twenty 8-month-old (dry-stored) seeds were sown on 24 March 2010 in each of 50 pots (15 cm diameter and 11 cm depth) filled with sand and watered daily with tap water. Seedlings with three rosette leaves were transferred to plastic containers (40 cm × 30 cm × 12 cm) filled with Hoagland solution. There were 10 seedlings per container and three replicates (containers) per treatment. After 7 d, when seedlings had four leaves, NaCl treatments were initiated. Control seedlings received no NaCl, while others received 50 mmol/L NaCl (in Hoagland solution) for 1, 2, 3, and 4 d, resulting in NaCl concentrations of 0, 50, 100, 200, and 300 mmol/L, respectively. During the experiment, Hoagland solution (including NaCl) was changed weekly and aerated in all containers with SP-780 pumps (Zhongshan Risheng Electric Appliance Co., Zhongshan, China). At the end of the life cycle on 30 June 2010, the number of surviving plants, plant height, length of the longest root, number of fruits, and number of seeds per plant were recorded. Plants in each treatment were collected separately, divided into root and shoot (including leaves, stems, and fruits), and oven-dried to constant weight at 80°C for 48 h in paper bags. After drying, all parts were weighed using an electronic balance (0.0001 g precision).

2.7 Data Analyses

Data were log or arcsine transformed as necessary to meet normality and homogeneity of variance assumptions (non-transformed data appear in all tables and figures). If ANOVA assumptions were violated after transformation, treatment differences were assessed using the more conservative Kruskal–Wallis nonparametric test. One-way ANOVA was used to test effects of water stress and NaCl stress on germination percentage and recovery, percentage of seedling survival, seedling growth, plant size, and fruit/seed production. Tukey' s HSD test and paired two-tailed tests were performed for multiple comparisons to determine if differences between individual treatments were significant ($P<0.05$). Values are means±SE (Sokal and Rohlf, 1995). Data were analyzed using SPSS for Windows, Version 16.0 (SPSS Inc., Chicago, IL, USA).

3.1 Effects of Water Stress on Seed Germination Percentage and Germination Recovery

Water stress had a significant effect on germination percentage ($P<0.001$). In general, germination percentage decreased with decreasing water potential during incubation. Germination percentage exceeded 80% at 0.00, -0.05, and -0.16

MPa water potentials; however, no seeds germinated at -0.85 and -1.21 MPa (Fig. 2 [Figure 2: see original paper]). Germination recovery of seeds incubated at -0.85 and -1.21 MPa was higher than that of seeds incubated at 0.00, -0.05, -0.16, and -0.56 MPa. TTC staining showed that all non-germinated seeds were viable.

3.2 Effects of NaCl Stress on Seed Germination Percentage and Germination Recovery

Germination percentage was significantly affected by NaCl stress ($P<0.001$). At 0 and 50 mmol/L NaCl concentrations, approximately 89% and 78% of seeds germinated, respectively, but at 400 mmol/L NaCl, none germinated (Fig. 3 [Figure 3: see original paper]; Table 1). After non-germinated seeds were transferred from NaCl solution to distilled water, they recovered and germinated. As NaCl concentration decreased, germination recovery increased, and for NaCl concentrations ranging from 100 to 600 mmol/L, germination recovery was significantly higher than that of the control ($P<0.001$) (Table 1). TTC staining showed that the percentage of viable non-germinated seeds remaining after the recovery period increased with increasing NaCl concentration.

3.3 Effects of Water Stress on Plant Growth and Reproduction

Water stress significantly inhibited plant height ($P<0.001$), number of fruits ($P<0.001$), number of seeds ($P<0.001$), and shoot mass ($P<0.001$), all of which decreased with reduced watering frequency. However, root length ($P=0.67$), root mass ($P=0.57$), and root/shoot ratio ($P=0.44$) were not significantly affected by water stress (Table 2).

3.4 Effects of NaCl Stress on Seedling Survival and Growth

NaCl stress had significant effects on seedling survival ($P<0.001$), height ($P<0.001$), root length ($P<0.001$), seedling biomass ($P<0.001$), and root/shoot ratio ($P<0.001$; Fig. 4 [Figure 4: see original paper]). Low salinity (50 mmol/L NaCl) had no effect on seedling survival or root/shoot ratio, but 100 and/or 150 mmol/L NaCl significantly inhibited survival, height, and biomass, though not root/shoot ratio. No seedling growth occurred at NaCl concentrations 250 mmol/L.

3.5 Effects of NaCl Stress on Juvenile Growth and Plant Reproduction

Number of surviving plants ($P<0.001$), plant height ($P<0.001$), root length ($P<0.001$), number of fruits ($P<0.001$), number of seeds per plant ($P<0.001$), and seedling biomass ($P<0.001$) significantly decreased with increasing NaCl concentration (Table 3). In this study, 50 mmol/L NaCl had no effect on any of these variables except plant height. However, seedling growth and development were inhibited at 100 mmol/L NaCl, all parameters were significantly inhibited at 200 mmol/L NaCl, and no seedlings survived at 200 mmol/L NaCl concentration.

4 Discussion and Conclusions

Our hypothesis that seed and seedling stages of the *L. lehmannii* life cycle are tolerant to water stress and NaCl stress was supported by data from laboratory germination experiments (Figs. 2 and 3) and from seedling survival, juvenile growth, and plant reproduction studies (Fig. 4; Tables 2 and 3). *Lachnoloma lehmannii* is an annual that germinates and completes its life cycle in saline regions of the cold desert; thus, its seeds and plants are subjected to both water stress and NaCl stress. Not surprisingly, seeds of this species are tolerant to moderate water (-0.05 and -0.16 MPa) and NaCl (50 and 100 mmol/L) stress. However, germination percentage was inhibited at -0.85 MPa water stress and reduced to 10% at 300 mmol/L NaCl concentration. Mamatriyim et al. (2011) reported that germination percentage of *L. lehmannii* seeds was about 22% when incubated in 300 mmol/L NaCl solution at 15°C/5°C.

The ecological implications of these responses are that the most favorable time for germination in the cold desert would be summer when rainfall is relatively high. Summer germination, however, would result in plants of this annual species having a short growing season before autumn frost onset. For maximum fitness (i.e., seed production), early spring germination is better than summer germination because plants from spring-germinating seeds have more time to grow and thus produce more seeds.

Spring germination of *L. lehmannii* seeds is possible due to: (1) moderate tolerance of seeds to water and NaCl stress; (2) snow melt and possibly some rainfall that reduce water and NaCl stress; and (3) ability of seeds to germinate at early spring temperatures (i.e., 5°C/2°C and 15°C/2°C) (Mamut et al., 2014). It has been shown that seeds of halophytes germinate when rainfall (or snow melt) decreases soil salinity (Ungar, 1991; Khan and Ungar, 2001; Huang et al., 2003; Wetson et al., 2008).

The fact that high NaCl did not kill *L. lehmannii* seeds and that they could germinate when moved to fresh water suggests that high NaCl inhibits germination percentage in the field until sufficient soil moisture reduces salinity. However, isolated seeds of *L. lehmannii* germinated to only about 20% at high summer temperatures (e.g., 25°C/15°C and 30°C/15°C), and none of the seeds enclosed by fruits and incubated in light or darkness germinated at these temperatures (Mamut et al., 2014). Thus, due to high summer temperatures in the habitats, rainfall would not result in high germination percentage even if soil salinity decreased. Furthermore, some *L. lehmannii* seeds did not germinate after being transferred from high NaCl concentrations to distilled water, suggesting they had entered secondary dormancy, which further ensures seeds would not germinate following summer rainfall. Consequently, seeds remain non-germinated in soil until spring when temperatures are relatively low and snow melt and rainfall decrease salinity. Spring germination has also been documented in other desert-inhabiting Brassicaceae such as *Alyssum minus* (Sun et al., 2012), *Diplotaxis harra* (Tlig et al., 2008), and *Farsetia aegyptia* (Bhatt et al., 2018).

Seed germination is a key stage in plant life cycles (Tevis, 1958; Mott, 1974; Tang et al., 2009), but unless it occurs when habitat conditions are favorable for seedling establishment and growth, seedlings will die (Ungar, 1995; Khan and Gulzar, 2003; Tlig et al., 2008; Bojović et al., 2010; Gul et al., 2013; Wang et al., 2015). Thus, germination is most likely to occur when seedlings can survive due to long-term natural selection (Grappin et al., 2000; El-Keblawy and Al-Rawai, 2005). In arid and semi-arid regions, soil moisture is one of the most important factors controlling germination (Koller, 1969; Gutterman, 1990; Tang et al., 2009) and limiting seedling survival, growth, and productivity (Raich et al., 1991; Haase et al., 1999). In our study, decreased watering frequency resulted in smaller *L. lehmannii* plants, but even the smallest plants produced seeds. Since *L. lehmannii* plants can produce seeds when water-stressed, some seeds will be produced regardless of unpredictable spring and summer rainfall, ensuring population persistence in local habitats.

Salt tolerance during growth and sexual reproduction stages may differ from that during germination (Kigel, 1995; Gutterman, 2002; Tlig et al., 2008). Some studies suggest the seedling stage has the lowest tolerance to extreme environmental factors (Gutterman, 1993; Khan and Rizivi, 1994; Qu et al., 2008). In *L. lehmannii*, the number of surviving seedlings and their height and root length decreased significantly as NaCl concentration increased. This characteristic is similar to that of the desert species *Suaeda corniculata* (Yang et al., 2017). However, the root/shoot ratio increased with increasing NaCl concentration (Fig. 4d), suggesting root proliferation/growth occurred in young seedlings, which would increase water uptake from saline substrate, thereby helping prevent seedling death.

For *L. lehmannii* plants grown to maturity (Table 3), increased NaCl concentration decreased the number of surviving plants, height, root length, number of fruits/seeds per plant, biomass, and root/shoot ratio. Thus, NaCl stress inhibition of growth and development was lower than in the seedling stage. In this study, 50 mmol/L NaCl had no effect on plant growth and reproduction except for plant height. About 30% of plants survived and produced fruits/seeds at 200 mmol/L NaCl, suggesting *L. lehmannii* plants are more salt-tolerant than other desert species such as *Pachypterygium multicaule*, *Malcolmia africana*, and *Tetracme quadricornis* (Mamatriyim et al., 2011).

Flowers and Colmer (2008) defined halophytes as species that survive and reproduce in environments where salinity is around 200 mmol/L or more. In our study, *L. lehmannii* seeds germinated and plants survived and produced seeds at 200 mmol/L NaCl. Like seeds of other halophytes (Khan and Ungar, 2001; Huang et al., 2003; Tlig et al., 2008), *L. lehmannii* seeds remained viable and most recovered and germinated after exposure to high NaCl concentrations.

During the seed germination stage, the *L. lehmannii* life cycle has the highest resistance to water and NaCl stress, while seedlings are most susceptible. However, tolerance to water and NaCl stress increased with plant growth and reproduction. In the field, newly germinated seedlings can be found in early spring when rainfall is unpredictable but water from snow melt is available. With low rainfall and increasing temperatures, soil salinity concentration increases, causing some seedling mortality. Surviving seedlings become increasingly tolerant, no doubt due in part to development of a good root system. Also, summer rainfall may increase. Nonetheless, plants grow, flower, and produce seeds under high salinity stress. We conclude that high tolerances to water and NaCl stress are important adaptations enabling *L. lehmannii* plants to persist in arid and saline habitats of the cold desert with unpredictable timing and amount of rainfall.

Acknowledgements

This study was supported by the National Basic Research Program of China (2014CB954202) and the National Natural Science Foundation of China (31460128, U1603231, 31760060).

References

Ahmad S, Ahmad R, Ashraf M Y, et al. 2009. Sunflower (*Helianthus annuus* L.) response to drought stress at germination and seedling growth stages. *Pakistan Journal of Botany*, 41(2): 647–654.

Baskin C C, Baskin J M. 2014. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination* (2nd ed.). Elsevier: Academic Press, 1–35.

Bhatt A, Bhat N R, Suleiman M K, et al. 2018. Effects of storage, mucilage presence, photoperiod, thermoperiod and salinity on germination of *Farsetia aegyptia* Turra (Brassicaceae) seeds: implications for restoration and seed banks in Arabian Desert. *Plant Biosystems*, 153(2): 280–287.

Bojović B, Đelić G, Topuzović M. 2010. Effects of NaCl on seed germination in some species from families Brassicaceae and Solanaceae. *Kragujevac Journal of Science*, 32: 83–87.

Bradford K J. 2002. Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Science*, 50: 248–260.

El-Keblawy A, Al-Rawai A. 2005. Effects of salinity, temperature and light on germination of invasive *Prosopis juliflora* (Sw.) D.C. *Journal of Arid Environments*, 61(4): 555–565.

Evans C E, Etherington J R. 1990. The effects of soil water potential on seed germination of some British plants. *New Phytologist*, 115(3): 539–548.

Fenner M, Thompson K. 2005. *The Ecology of Seeds*. Cambridge: Cambridge University Press, 331-359.

Flowers T J, Colmer T D. 2008. Salinity tolerance in halophytes. *New Phytologist*, 179(4): 945-963.

Galle A, Haldimann P, Feller U. 2007. Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery. *New Phytologist*, 174(4): 799-810.

Grappin P, Bouinot D, Sotta B, et al. 2000. Control of seed dormancy in *Nicotiana plumbaginifolia*: post-imbibition abscisic acid synthesis imposes dormancy maintenance. *Planta*, 210(2): 279-285.

Gul B, Weber D J. 1999. Effect of salinity, light, and temperature on germination in *Allenrolfea occidentalis*. *Canadian Journal of Botany*, 77(2): 240-246.

Gul B, Ansari R, Flowers T J, et al. 2013. Germination strategies of halophyte seeds under salinity. *Environmental and Experimental Botany*, 92: 4-18.

Gutterman Y. 1990. Does the germination differ in plants originating in deserts receiving winter or summer rain? *Israel Journal of Botany*, 39: 355-372. (in Hebrew)

Gutterman Y. 1993. *Seed Germination in Desert Plants*. Berlin: Springer-Verlag, 222-230.

Gutterman Y. 2002. *Survival Strategies of Annual Desert Plants*. Berlin: Springer-Verlag, 211-280.

Haase P, Pugnaire F I, Clark S C, et al. 1999. Environmental control of canopy dynamics and photosynthetic rate in the evergreen tussock grass *Stipa tenacissima*. *Plant Ecology*, 145(2): 327-339.

Hu X W, Fan Y, Baskin C C, et al. 2015. Comparison of the effects of temperature and water potential on seed germination of Fabaceae species from desert and subalpine grassland. *American Journal of Botany*, 102(5): 649-660.

Huang Z Y, Zhang X S, Zheng G H, et al. 2003. Influence of light, temperature, salinity and storage on seed germination of *Haloxylon ammodendron*. *Journal of Arid Environments*, 55(3): 453-464.

Khan M A, Rizvi Y. 1994. Effect of salinity, temperature, and growth regulators on the germination and early seedling growth of *Atriplex griffithii* var. *stocksii*. *Canadian Journal of Botany*, 72(4): 475-479.

Khan M A, Ungar I A. 2001. Effect of germination promoting compounds on the release of primary and salt-enforced seed dormancy in the halophyte *Sporobolus arabicus* Bioss. *Seed Science and Technology*, 29: 299-306.

Khan M A, Gulzar S. 2003. Germination responses of *Sporobolus ioclados*: a saline desert grass. *Journal of Arid Environments*, 53: 387-394.

Khan M A, Gul B. 2006. Halophyte seed germination. In: Khan M A, Weber D J. *Ecophysiology of High Salinity Tolerant Plants*. Netherlands: Springer, 11-30.

Kigel J. 1995. Factors affecting germination of arid and semiarid regions. In: Kigel J, Galili G. *Seed Development and Germination*. New York: Marcel Dekker, 645-700.

Kitajima K, Fenner M. 2000. Ecology of seedling regeneration. In: Fenner M. *Seeds: the Ecology of Regeneration in Plant Communities* (2nd ed.). Wallingford: CABI Publishing, 331-359.

Koller D. 1969. The physiology of dormancy and survival of plants in desert environments. *Symposium of the Society of Experimental Biology*, 23: 449-469.

Li H, Li X, Zhang D, et al. 2013. Effects of drought stress on the seed germination and early seedling growth of the endemic desert plant *Eremosparton songoricum* (Fabaceae). *Excli Journal*, 12: 89-101.

Ludewig K, Zelle B, Eckstein R L, et al. 2014. Differential effects of reduced water potential on the germination of floodplain grassland species indicative of wet and dry habitats. *Seed Science Research*, 24(1): 49-61.

Ma Y L, Zhang J H, Li X R, et al. 2016. Effects of environmental stress on seed germination and seedling growth of *Salsola ferganica* (Chenopodiaceae). *Acta Ecologica Sinica*, 36(6): 456-463. (in Chinese)

Mamatriyim N, Yunus Q, Tan D Y. 2011. Seed germination and plant growth of four ephemeral species under salt stress. *Acta Botanica Boreali-Occidentalia Sinica*, 31(8): 1618-1627. (in Chinese)

Mamut J, Tan D Y, Baskin C C, et al. 2014. Role of trichomes and pericarp in the seed biology of the desert annual *Lachnoloma lehmannii* (Brassicaceae). *Ecological Research*, 29(1): 33-44.

Michel B E, Kaufmann M R. 1973. The osmotic potential of polyethylene glycol 6000. *Plant Physiology*, 51(5): 914-916.

Mott J J. 1974. Factors affecting seed germination in three annual species from an arid region of Western Australia. *Journal of Ecology*, 62(3): 699-709.

Qu X X, Huang Z Y, Baskin J M, et al. 2008. Effect of temperature, light and salinity on seed germination and radicle growth of the geographically-widespread halophyte shrub *Halocnemum strobilaceum*. *Annals of Botany*, 101(2): 293-299.

Raich J W, Rastetter E B, Melillo J M, et al. 1991. Potential net primary productivity in South America: application of a global model. *Ecological Applications*, 1(4): 399-429.

Santo A, Mattana E, Frigau L, et al. 2017. Effects of NaCl stress on seed germination and seedling development of *Brassica insularis* Moris (Brassicaceae). *Plant Biology*, 19(3): 368-376.

Sokal R R, Rohlf F J. 1995. *Biometry: the Principles and Practice of Statistics in Biological Research* (3rd ed.). San Francisco: Freeman, 887.

Sun Y, Tan D Y, Baskin C C, et al. 2012. Role of mucilage in seed dispersal and germination of the annual ephemeral *Alyssum minus* (Brassicaceae). *Australian Journal of Botany*, 60(5): 439-449.

Tang A J, Tian M H, Long C L. 2009. Seed dormancy and germination of three herbaceous perennial desert ephemerals from the Junggar Basin, China. *Seed Science Research*, 19(3): 183-189.

Tevis L. 1958. Germination and growth of ephemerals induced by sprinkling a sandy desert. *Ecology*, 39(4): 681-688.

Tlig T, Gorai M, Neffati M. 2008. Germination responses of *Diplotaxis harra* to temperature and salinity. *Flora*, 203(5): 421-428.

Ungar I A. 1991. *Ecophysiology of Vascular Halophytes*. Boca Raton: CRC Press, 209.

Ungar I A. 1995. Seed germination and seed-bank ecology of halophytes. In: Kigel J, Galili G. *Seed Development and Germination*. New York: Marcel Dekker, 599-627.

Wang F X, Xu Y G, Wang S, et al. 2015. Salinity affects production and salt tolerance of dimorphic seeds of *Suaeda salsa*. *Plant Physiology and Biochemistry*, 95: 41-48.

Wei W S, Zhang P, Gao W D, et al. 2003. Climate and desert environment evolution in sandstorm source area of Xinjiang, China. *Journal of Desert Research*, 23(5): 483-487. (in Chinese)

Wetson A M, Cassaniti C, Flowers T J. 2008. Do conditions during dormancy influence germination of *Suaeda maritima*? *Annals of Botany*, 101(9): 1319-1327.

Xi J B, Zhang F S, Tian C Y. 2006. *Halophytes in Xinjiang*. Beijing: Science Press, 235-255. (in Chinese)

Yang F, Baskin J M, Baskin C C, et al. 2017. Divergence in life history traits between two populations of a seed-dimorphic halophyte in response to soil salinity. *Frontiers in Plant Science*, 8: 1028.

Yang H L, Huang Z Y, Baskin C C, et al. 2009. Responses of caryopsis germination, early seedling growth and ramet clonal growth of *Bromus inermis* to soil salinity. *Plant and Soil*, 316(1-2): 265-275.

Zehra A, Gul B, Ansari R, et al. 2013. Interactive effect of salt, light and temperature on seed germination and recovery of a halophytic grass—*Phragmites karka*. *Pakistan Journal of Botany*, 45: 725-736.

Zhang S R, Song J, Wang H, et al. 2010. Effect of salinity on seed germination, ion content and photosynthesis of cotyledons in halophytes or xerophytes growing in central Asia. *Journal of Plant Ecology*, 3(4): 259-267.

Zhang T, Song J, Fan J L, et al. 2015. Effects of saline-waterlogging and dryness/moist alternations on seed germination of halophyte and xerophyte. *Plant Species Biology*, 30(3): 231-236.

Zhou T Y, Lu L L, Yang G, et al. 2001. Brassicaceae. In: Wu Z Y, Raven P H. *Flora of China* 8. Beijing: Science Press, 1-63. (in Chinese)

Note: Figure translations are in progress. See original paper for figures.