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# Physiological responses of *Bassia dasyphylla* to drought during seed germination from different provenances

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*Bassia dasyphylla* is a prevalent herbaceous plant that exhibits enhanced resilience to dryness and elevated temperatures. It is frequently found in dispersed or grouped formation on sandy soil within steppe, semi-desert, and desert regions. Herein, we conducted experiments to examine the growth and physiological traits of *B. dasyphylla* seeds originated from various regions in response to water scarcity. The study seeks to investigate the ability of these seeds to germinate under drought conditions and offer valuable insights for the development and breeding of high-quality germplasm resources in Inner Mongolia. The results demonstrated that *B. dasyphylla* originating from desert steppe (DS) exhibited a greater capacity to endure drought conditions in comparison to its counterparts from sandy land (SL). At a water potential of -0.30 MPa, the Seed germination rate from DS was 33.3%, while from SL it was 22.7%. With the increase in drought duration and intensity, germination rate, plumule length, both single-seed weight (SSW) and seed water content (SWC) of *B. dasyphylla* declined. The protective enzyme activity exhibited an initial increase, followed by a subsequent decline as the duration of the drought increased. Notably, we found that the protective enzyme activity from DS was higher than that from SL. During the initial and intermediate stages of dryness, the soluble sugar and protein of the plant from DS effectively inhibited the peroxidation of membrane lipids, whereas the osmoregulatory properties from SL did not have a significant impact. The findings suggest that the ability of *B. dasyphylla* to withstand drought conditions in DS can be attributed to its elevated amounts of protective enzymes and osmoregulatory factors, which serve to safeguard the cell membrane during periods of drought.

## KEYWORDS

Horqin sandy land, Urat desert steppe, drought stress, germination, physiological responses

## 1 Introduction

About 36% of the world's area is arid and semi-arid, while 52% of China's land area is arid and semi-arid. Plants growing in humid and sub-humid regions often encounter atmospheric drought or soil drought during their growth (Chen et al., 2019). Economic development and human activities cause the insufficiency of water resources in these regions to become increasingly severe, and aggravate drought sufficiently that it regulates community composition and species diversity (Li et al., 2022). Under the background of global warming, the frequent occurrence of drought events has an important impact on the ecological adaptation of plants (Sala et al., 2015). There are great differences in the seed germination of different plants and their responses to water deficits, and many plants in arid and semi-arid regions have formed various mechanisms and strategies to adapt to water deficits (Jürgen et al., 2014).

Seeds serve as fundamental prerequisites for the growth and reproduction of plants. The adaptability of seeds to sprout and seedlings to emerge in face of stress plays a crucial role in determining the successful establishment and perpetuation of vegetation in challenging environments. Moreover, this adaptability directly impacts the distribution and diversity of vegetation (Li et al., 2009; Paul et al., 2012). Seed germination is influenced by both the exterior environment and its internal heredity, and its susceptibility to adverse conditions is quite great. Soil moisture is an essential element that influences seed germination. For example, seed germination rate is proportional to the level of soil moisture within specific range (Habtmu et al., 2014; Dasanayaka et al., 2022). Polyethylene glycol (PEG) is frequently employed in the simulation environmental conditions through the regulation of various osmotic potentials inside the culture medium (Wang, 2016). The study revealed that the application of a low concentration of PEG has a positive impact on the germination of *Artemisia halodendron*, *Agriophyllum squarrosum* and *Caragana microphylla*. However, the process of seed germination would be impeded and progressively enhanced as the concentration of PEG increases (Chen et al., 2021b). The radicle length, plumule length, germination potential, germination index, and germination percentage of oat seeds that were stressed by drought were all much lower than those in the control group. This observation suggests a notable inhibitory impact of drought stress on these growth parameters (Xiang et al., 2012). Plants have different physiological adaptation mechanisms to withstand adverse environments, such as an upregulation of antioxidant enzymes (eg., peroxidase, superoxide dismutase and catalase (CAT) and accumulation of osmoregulatory substances (Sala et al., 2015). The research conducted on the artificial regulation of soil water in the presence of simulated drought stress demonstrates that moderate drought conditions can lead to an augmentation in the activity of antioxidant enzymes in psammophytes. Conversely, severe drought conditions can result in the impairment of the antioxidant enzyme system and a reduction in such activity (Su et al., 2005; Chen et al., 2021a). In addition, the activity of antioxidant enzyme and malondialdehyde (MDA) content exhibited an upward trend in response to the intensification of drought conditions, while demonstrating a downward trend in response to irrigation when the soil saw repeated arid and rehydrated cycles

(Drazkiewicz et al., 2004; Atkin et al., 2006). Plants exhibit diverse phenotypic traits and undergo genotypic changes in order to adapt to the spatial and temporal variations present in the various habitats. The phenomenon of flexibility can be observed in both morphology and physiology, serving as a crucial factor for plants to thrive in the various environments (Loretta, 2014; Bizet et al., 2015).

*Bassia dasyphylla* is an annual herb with a well-developed root system and increased resilience to adverse environments such as drought, high temperatures, wind-erosion and sand-fixation. The surface layer has a notable abundance of flat pubescence, which functions as a highly effective barrier against the process of water evaporation. In the autumn season, as the plants undergo desiccation, the apical appendages of the five-star fruit tip attach themselves to persons or animals with the purpose of dispersing seeds. The pioneer plant species is commonly observed in desert steppe and sandy terrain and has a regular distribution or clustering pattern in grasslands and semi-arid areas in northern China (Zhuang and Sophia, 2012). The Urat desert steppe is situated in the transition zone that lies between desert and typical steppe, while the Horqin sandy land is positioned in the ecotone that lies between agriculture and husbandry. In recent years, the exacerbation of water scarcity and the heightened challenges with vegetation restoration have been as a result of land degradation in these two places (Kinugasa et al., 2016; Yue et al., 2019). With global warming, the occurrence of frequent drought episodes would significantly affect the community structure and function, as well as the characteristics of plant germination and physiological responses in desert steppe and sandy ecosystems. There existed a limited body of research pertaining to the community structure, spatial distribution pattern analysis and bio-indicator function of *B. dasyphylla*. However, physiological adaptation and regulation mechanism of *B. dasyphylla* inhabiting sandy land and desert steppe remain uncertain (Tobe et al., 2005; Zhou et al., 2015; Xu et al., 2022). Do the physiological and morphological plasticity of *B. dasyphylla* vary significantly depending on the native regions? The primary aims of the study were two folds: (1) to explore the physiological adaptation capabilities of *B. dasyphylla* in desert steppe and sandy land, and (2) to offer guidance for the identification and cultivation of high-quality germplasm resources in Inner Mongolia.

## 2 Materials and methods

### 2.1 Study site

The research area of sandy land was selected in Naiman Banner, Inner Mongolia, with an altitude of 350m, annual average precipitation of 351.7mm, and annual average evaporation of 1900mm. This area belongs to semi-arid continental climate and the main plant species are *Agriophyllum squarrosum*, *Artemisia halodendron*, *Caragana microphylla* and *B. dasyphylla* (Chen et al., 2021b). The other study area of desert steppe was chosen in Wulathou Banner, Inner Mongolia, with an altitude of 1650m, annual average precipitation of 180mm, and annual average evaporation of 1800mm. This area belongs to

typical continental arid climate and the main species are *Stipa capillata*, *Reaumuria songarica*, *A. squarrosus*, *B. dasyphylla* (Yue et al., 2022).

We gathered mature reproductive branches of *B. dasyphylla* with strong plants and high seed setting rate from sand land and desert steppe in late September and brought them back to the laboratory and let it air-dry, and then conserved them in a dry room at 15–25°C. Mean seed weights of *B. dasyphylla* from sand land and desert steppe were  $0.70 \pm 0.01$  g ( $N=1000$ ) and  $0.75 \pm 0.02$  g (mean  $\pm$  SD). Seed moisture contents from sand land and desert steppe were  $6.45 \pm 1.23\%$  and  $7.21 \pm 1.56\%$  before experiments.

One hundred randomly chosen seeds with good kernel plumpness and uniform shape were uniformly placed in a 12 cm diameter Petri dish containing double-layer filter paper humidified with 5 mL of treatment solution. Seeds were cultured in 0, 2.5%, 5%, 7.5%, 10% and 15% solutions ready by dissolving PEG-6000 in distilled water, and the water potential of the above concentration at 25°C at room temperature was 0 MPa, -0.02 MPa, -0.05 MPa, -0.09 MPa, -0.15 MPa, -0.30 MPa, respectively (Chen et al., 2021b). The experiment was made in the incubator at 25°C and the assessment criterion for germination was discernible protrusion of the radical.

Every treatment composed of 30 Petri dishes and seeds were cultivated in succession for 7 days until no seeds germinated. The number of germinated seeds was noted daily and randomly chosen 10 seedlings from each dish were used to determine the radicle and plumule length on days 3, 5, 7. Ten dishes were applied to determine seed weight and water content, while the rest 20 dishes were used to determine the antioxidant enzyme activity and osmotic regulator content. We washed and dried the seeds with clean water after sampling and stored them in liquid nitrogen for the determination of physiological indicators.

## 2.2 Analytical methods

Random 0.1 g fresh samples were extracted with chilled buffer (50 mM phosphate, 1% PVP) and centrifuged at 15,000 g for 20 minutes. The supernatant was applied to measure MDA content and physiological indices. MDA content was determined with thiobarbituric acid method. The activities of antioxidant enzymes (POD, SOD and CAT) were measured spectrophotometrically according to Chen et al. Soluble sugar content was determined spectrophotometrically at 630 nm with anthrone method. Soluble protein content was measured spectrophotometrically at 595 nm using coomassie blue dye combination method and free proline concentration was measured spectrophotometrically at 520 nm with ninhydrin method (An and Liang, 2013; Chen et al., 2021a). The spectrophotometer we used was UV-1601 (Shimadzu Corporation, Japan).

## 2.3 Statistical analysis

All data were presented as the mean  $\pm$  SE and diagnosed for normality of distribution and homogeneity of variance before conducting parameter statistical tests. Data have passed the

normality and equal variance tests, and the analysis of variance (ANOVA) was performed across the plot level using SPSS 20.0. Correlations between seedling growth and physiological characteristics of *B. dasyphylla* from different provenances were analyzed with Origin software.

## 3 Results

### 3.1 Characteristic of germination rate and seedling growth

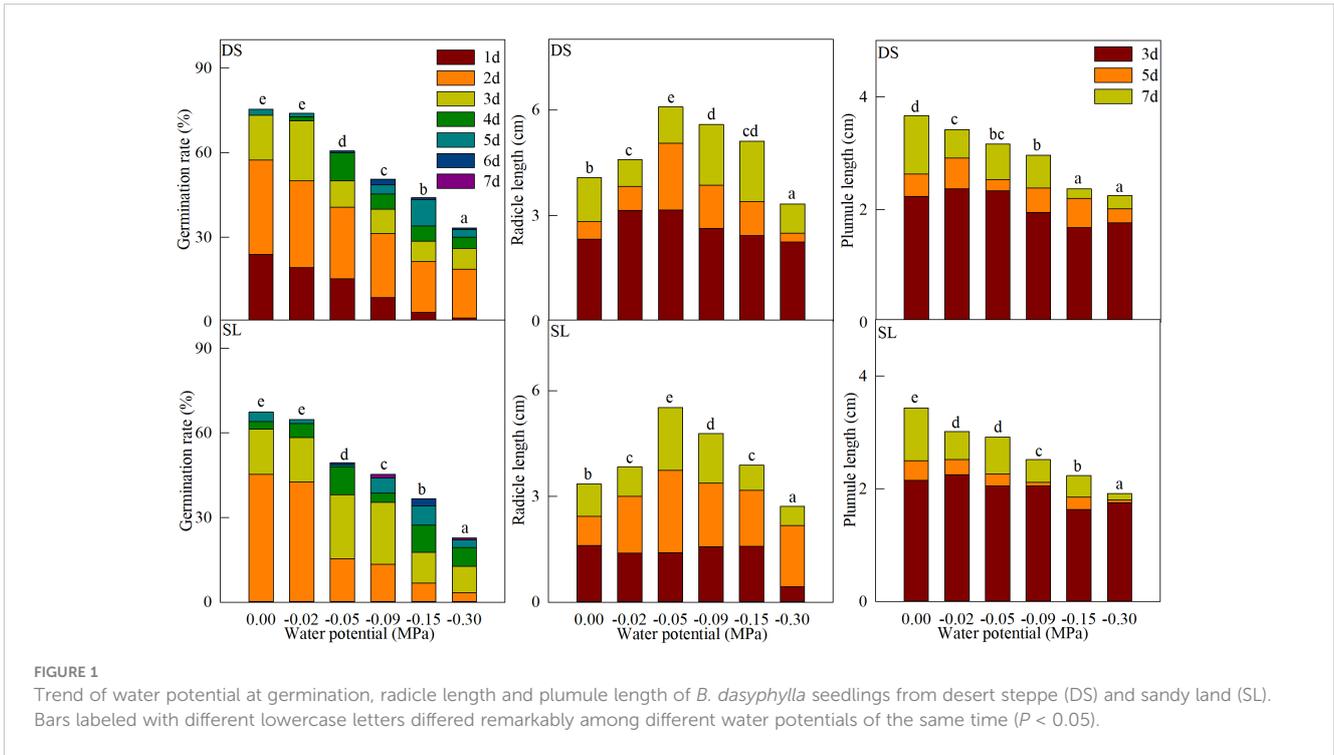
In comparison to the control group, the germination of *B. dasyphylla* was significantly hindered by drought stress (Figure 1) in both habitats. Furthermore, the inhibitory effect on the germination rate became more pronounced as the level of drought stress increased. Numerous DS seeds exhibited germination within a single day of culture, whereas the germination rate of SL seeds was found to be negligible. The majority of seeds from both plants had undergone germination by the sixth day. When the water potential was 0 MPa, the final germination rate of DS seeds was observed to be 76.0%, whereas that of SL seeds was found to be 67.3%. At a drought stress level of -0.30 MPa, germination rate of DS and SL seeds decreased by 33.3% and 22.7% seeds, respectively, compared to the control, which had germination rates of 56.2% and 66.3% lower.

With the aggravation of drought, the radicle length of the two plants first increased and then decreased. On day 3, the radicle length (2.3–3.2 cm) of DS was significantly longer than that of SL (0.4–1.6 cm) ( $P < 0.05$ ). When the water potential was -0.05 MPa, the radicle length of both plants reached the maximum on days 5 and 7; on day 5, the radicle length was 5.1 cm and 3.7 cm of DS and SL seeds, respectively, and were 82.1% and 54.2% higher than in the control; on day 7, the length was 6.1 cm and 5.5 cm of DS and SL seeds, respectively, and were 48.8% and 61.8% higher than in the control, and significantly higher than those of other treatments.

The plumule length of DS exhibited a downward trend with the intensification of water stress. On day 7, the plumule length reached the maximum (3.7 cm) at the potential of 0 MPa. Subsequently, the length experienced a decline of 6.8%, 13.6%, 19.1%, 35.5% and 38.6%, in comparison to the control group, as the water potential decreased from -0.02 MPa to -0.30 MPa. The variation of plumule length for SL was comparable to that of DS. On day 7, the plumule length reached its maximum (3.4 cm) at the potential of 0 MPa and was significantly higher than other potentials ( $P < 0.05$ ). During the drop in water potential from -0.02 MPa to -0.30 MPa, the length reduced by 12.1%, 15.0%, 26.7%, 35.0%, and 44.2% compared to the control.

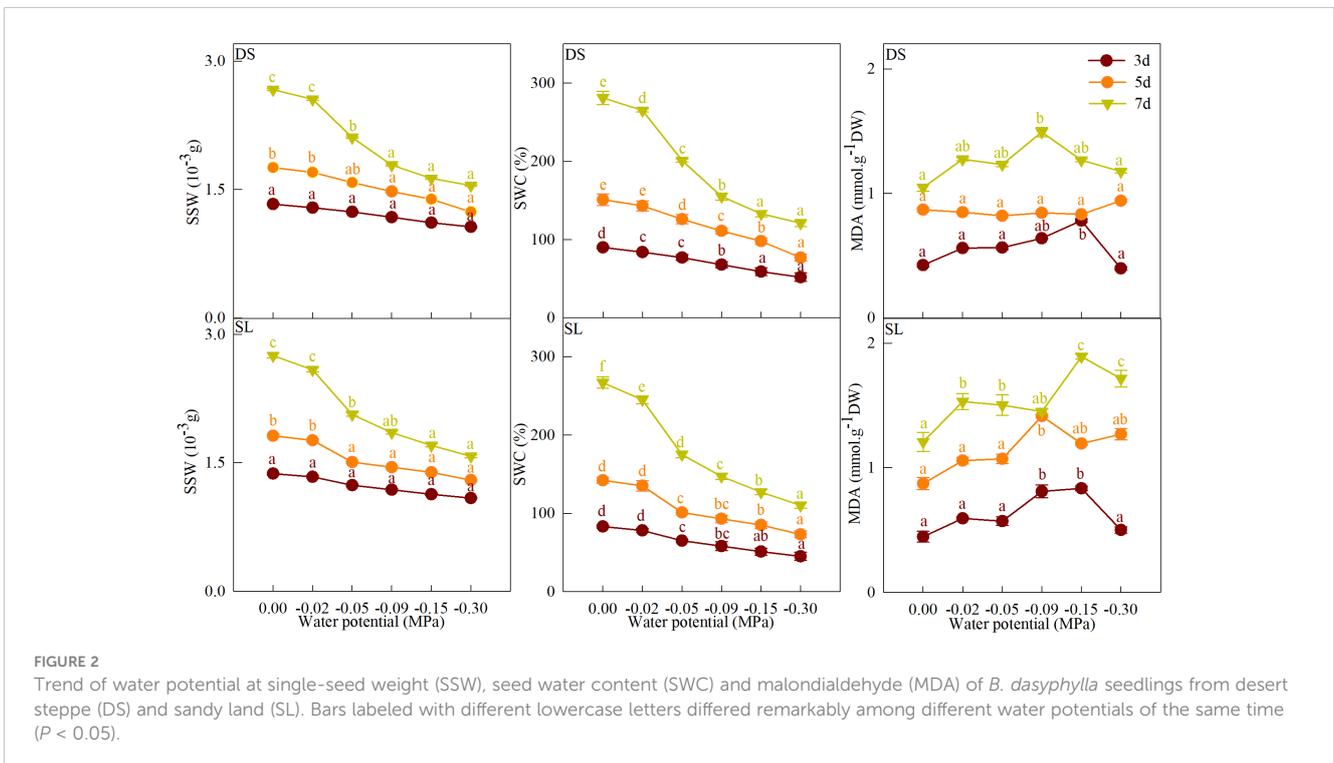
### 3.2 Characteristic of seed fresh weight and water and malondialdehyde contents

The single-seed weight (SSW) of DS and SL (Figure 2) prior to germination was  $0.70 \times 10^{-3}$  g and  $0.75 \times 10^{-3}$  g, respectively. SSW of both plants exhibited a progressive decline as the level of drought stress increased. During the intermediate phase of germination (day



3 to 5), the enhancement of SSW in both plants was comparatively lower than that observed in the initial phase (day 0 to 3) and the advanced phase (day 5 to 7). On day 7, SSW in both plants exhibited a notable drop compared to the control group, as the water potential decreased from -0.05 MPa to -0.30 MPa; SSW of DS and SL at water potential of -0.30 MPa was  $1.55 \times 10^{-3}$ g and  $1.58 \times 10^{-3}$ g. Notably, there was no observed disparity in the water potentials.

The alteration of seed water content (SWC) in both plants exhibited a comparable pattern with SSW. SWC of DS was greater than that of SL under the same water potential. The increase of SWC in both plants in the early stage (day 0 to 3) of germination and the advanced phase (day 5 to 7) was higher than that in the middle stage (day 3 to 5). As the duration of drought extended, the water intake of DS demonstrated a higher level of intensity in



comparison to SL. On day 7, SWC of DS (281.1%) and SL (267.2%) exhibited the highest values in the control.

In both habitats, the malondialdehyde (MDA) content of *B. dasyphylla* was found to be below  $2\text{mmol}\cdot\text{g}^{-1}\text{DW}$ , but the content of DS was less than that of SL. In the case of DS, the levels of MDA exhibited an initial increase followed by a subsequent decline on day 3, coinciding with the escalation of drought stress. The content surpassed that of the control and reached its peak value ( $1.493\text{mmol}\cdot\text{g}^{-1}\text{DW}$ ) at the potential of  $-0.09\text{MPa}$ . For SL, the content fluctuated and was higher than in the control. Its peak value ( $1.892\text{mmol}\cdot\text{g}^{-1}\text{DW}$ ) was seen at a potential of  $-0.15\text{MPa}$  on day 7.

### 3.3 Characteristic of antioxidant enzymes activity

Peroxidase (POD) activity in both habitats (Figure 3) initially rose and subsequently declined as the duration of drought increased. DS exhibited greater activity than SL at all levels, with the exception of  $-0.30\text{MPa}$  on day 3. POD activity of DS on day 5 was significantly higher than those on day 3 and 7, except for  $-0.09\text{MPa}$ . Additionally, the activity on day 7 was significantly higher than that on day 3. The level of SL on day 5 was significantly higher than those on day 3 and 7. However, nonsignificant difference was observed between the levels on day 3 and day 7. On day 5, POD activity of DS reached its maximum ( $91.57\text{Ug}^{-1}\text{DW}$ ) at water potential of  $-0.15\text{MPa}$ , 2.1 times greater than the control ( $43.47\text{Ug}^{-1}\text{DW}$ ). Similarly, the activity of SL reached its maximum ( $32.90\text{Ug}^{-1}\text{DW}$ ) at  $-0.09\text{MPa}$ , 1.6 times higher than the control ( $20.56\text{Ug}^{-1}\text{DW}$ ).

SOD and CAT in both habitats showed the similar patterns with POD. On day 5, SOD activity of DS reached its maximum ( $153.32\text{Ug}^{-1}\text{DW}$ ) at water potential of  $-0.30\text{MPa}$ ; the activity of SL reached

its maximum ( $77.92\text{Ug}^{-1}\text{DW}$ ) at water potential of  $-0.09\text{MPa}$  and decreased with increasing drought duration and intensity. On day 5, CAT activity of DS increased with the increase of stress intensity, and increased by 34.8%, 47.8%, 57.3%, 74.5% and 123.4%, respectively, compared with the control. CAT activity of SL exhibited an increase followed by a subsequent decrease as the stress intensity escalated.

### 3.4 Characteristic of osmoregulatory substances content

As the duration of drought increased, the soluble sugar content of DS (Figure 4) decreased as the level of drought stress increased to  $-0.09\text{MPa}$ . However, when the drought stresses increased from  $-0.09\text{MPa}$  to  $-0.30\text{MPa}$ , the content initially increased and then decreased. On the other hand, the content of SL showed a downward trend. The soluble sugar content in both plants on day 7 exhibited a notable decrease compared to the levels observed on day 3 and 5. At the water potential of  $-0.15\text{MPa}$  and  $-0.30\text{MPa}$ , the content was  $39.061\text{mg}\cdot\text{g}^{-1}\text{DW}$  and  $37.004\text{mg}\cdot\text{g}^{-1}\text{DW}$ , respectively. These values were found to be 2.4 and 2.3 times of the control. When drought stress increased from  $-0.05\text{MPa}$  to  $-0.30\text{MPa}$ , the soluble sugar content of SL was higher than that of the control. When the water potential was  $-0.15\text{MPa}$  and  $-0.30\text{MPa}$ , the contents of DS exhibited a statistically significant increase compared to the other treatments, and a statistically significant increase compared to the SL treatment.

Both plants exhibited a significant decrease in soluble protein contents over time, with the expectation of SL at a water potential of  $-0.05\text{MPa}$ . The content of DS ( $22.91\text{--}95.15\text{mg}\cdot\text{g}^{-1}\text{DW}$ ) was significantly higher than that of SL ( $7.07\text{--}38.78\text{mg}\cdot\text{g}^{-1}\text{DW}$ ) ( $P <$

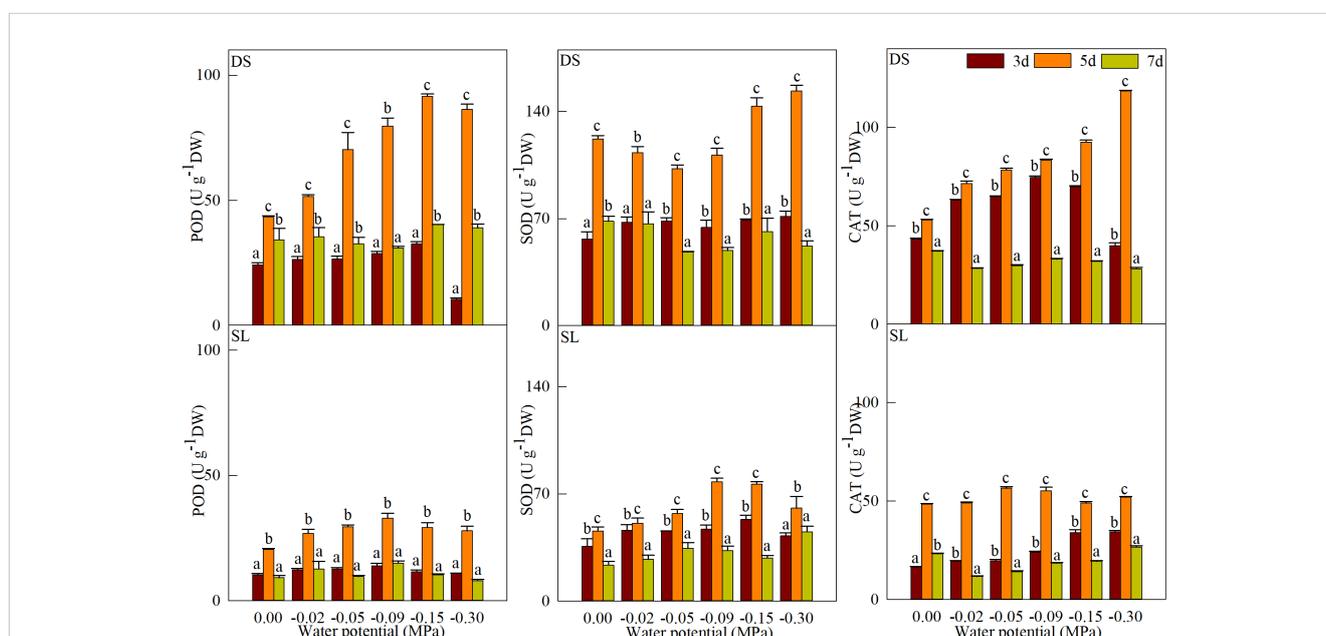


FIGURE 3

Trend of water potential at peroxidase (POD), superoxide dismutase (SOD) and catalase (CAT) of *B. dasyphylla* seedlings from desert steppe (DS) and sandy land (SL). Bars labeled with different lowercase letters differed remarkably among different water potentials of the same time ( $P < 0.05$ ).

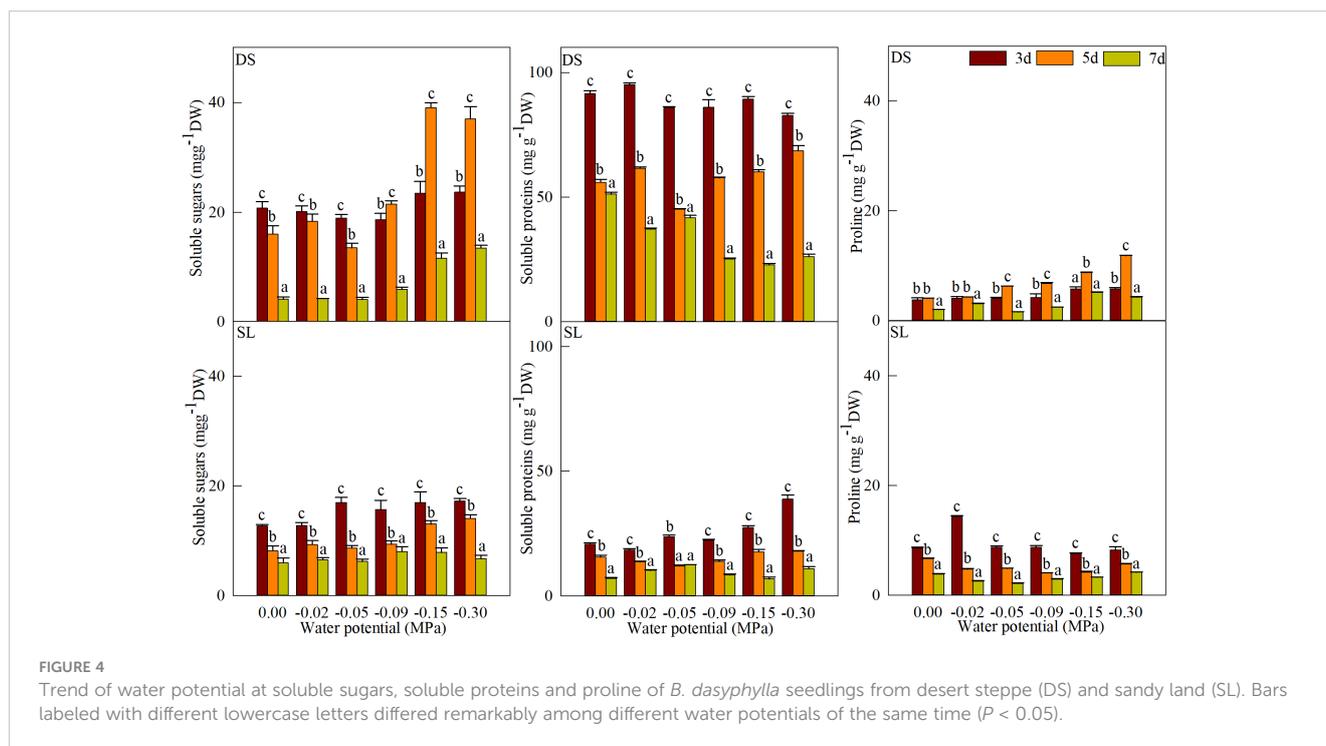


FIGURE 4

Trend of water potential at soluble sugars, soluble proteins and proline of *B. dasyphylla* seedlings from desert steppe (DS) and sandy land (SL). Bars labeled with different lowercase letters differed remarkably among different water potentials of the same time ( $P < 0.05$ ).

0.05). On day 3, the soluble protein content reached its highest point ( $39.06 \text{ mg} \cdot \text{g}^{-1} \text{ DW}$ ) at the water potential of  $-0.30 \text{ MPa}$  and was 1.9 times higher than the control. On day 7, the content of DS was lower compared to the control, but significantly higher than that of SL.

The proline content of DS exhibited an initial increase followed by a subsequent decrease as the duration of drought increased, whereas the content of SL demonstrated a gradual decrease. The proline content of DS exhibited an increase on day 3 and 5 in response to the escalating drought stress, while displaying fluctuations on day 7. When the water potential was  $-0.30 \text{ MPa}$ , the maximum content was observed on day 3 and 5, 1.5 times and 2.9 times as much as the control and was significantly higher than those of other treatments. On day 3, the proline content of SL reached its maximum ( $14.31 \text{ mg} \cdot \text{g}^{-1} \text{ DW}$ ) at  $-0.02 \text{ MPa}$ , which was significantly different from the control and other treatments.

### 3.5 Correlation analysis

Based on the correlations observed between seedling growth and physiological characteristics of *B. dasyphylla* from different provenances (Figure 5), the findings indicated a significant positive correlation between MDA and the factors, such as radicle length, SSW, and SWC. Conversely, soluble sugar and protein exhibited a significant negative correlation with plumule length, SSW, and SWC. However, a significant positive correlation was seen between plumule length and MDA. In addition, strong negative correlations were observed between germination and soluble sugar from SL. Additionally, there was a strong negative association between free proline and radicle length, as well as SSW and SWC.

## 4 Discussion

Seed germination and seedling establishment play a critical role in the natural renewal of plant life history. Plants are very sensitive to changes in the external environment during this stage and are more susceptible to adverse circumstances (Asri et al., 2003; Javid et al., 2018). Due to the high environmental adaptability of plant seeds in this period, the seeds continue to live and the population continues to perpetuate (Benard and Toft, 2008). So the germination characteristics and seedling growth status are often used to evaluate the stress resistance of plants (Delgado et al., 2008). However, global climate change has led to frequent droughts in some regions, exerting a substantial influence on the process of seed germination and seedling growth. Research has verified that in arid environments, the germination of xerophytes is influenced to some degree by their varying resistance to drought and the resistance drive plant population decrease (Fernández et al., 2018). We revealed a negative correlation between drought stress and both seed germination and plumule length of *B. dasyphylla*, which aligns with findings from prior research (Zhang et al., 2011; Chen et al., 2021b). The germination rate and plumule length of DS were higher than those of SL at the water potential of  $-0.30 \text{ MPa}$ , and the germination days at each treatment were shorter than those of SL. Our findings suggest that the seeds obtained from DS exhibited robust drought resistance and rapid seedling emergence, demonstrating their ability to effectively utilize the surrounding environment for optimal growth and development (Anjum et al., 2017; Luo et al., 2022). The radicle length of *B. dasyphylla* exhibited an initial increase followed by a subsequent decrease as the drought stress intensified, ultimately reaching its peak at a pressure of  $-0.05 \text{ MPa}$ . Rapidly growing radicle under mild stress facilitated

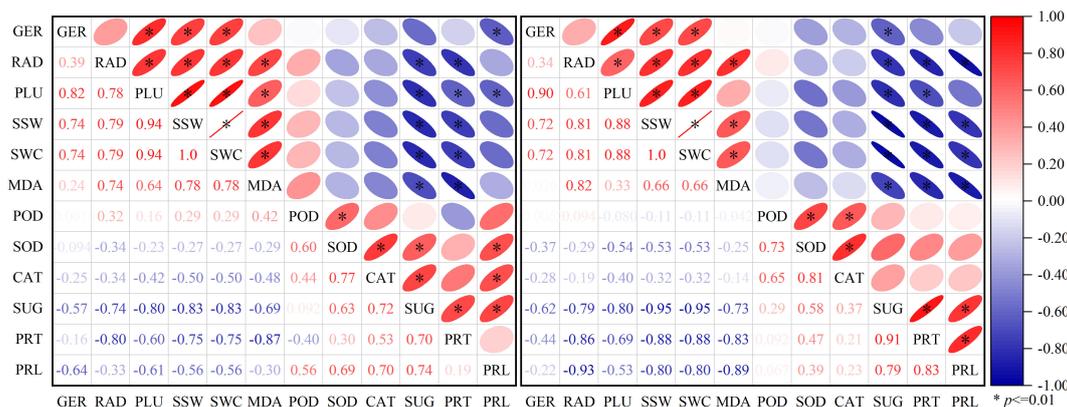


FIGURE 5

Correlations between seedling growth parameters and physiological indices of *B. dasyphylla* from desert steppe (Left) and sandy land (Right). \* indicates a highly significant correlation between two indexes (at 99% confidence level,  $P \leq 0.01$ ); GER represents germination; RAD represents radicle length; PLU represents plumule length; SUG represents soluble sugar; PRT represents soluble protein; PRL represents free proline.

enhanced water and nutrients absorption in seedlings, thereby mitigating the adverse impacts of drought stress on plant growth (Liu et al., 2006; An and Liang, 2013). However, the suppression of plumule development can be attributed to the initial detection of reduced soil moisture by plant roots, which subsequently generated signal substances and conveyed them to the aboveground tissues. In order to survive, plants adapted the allocation of assimilates between the root and plumule, and suppressed the growth of the plumule (Zheng et al., 2004; Ayumi et al., 2018). The growth of radicle and plumule was gradually inhibited due to the escalation of drought stress (Rabiei et al., 2014). This occurred due to the scarcity of water in the environment caused by severe drought stress, which hindered the roots' ability to absorb water. As a result, their growth and reproduction were hindered, leading to a deceleration or cessation of seedling development (Keshtiban et al., 2015). Plants possess the ability to regulate the equilibrium between aboveground and underground organs with drought stress, this enables plants to effectively allocate limited nutrients and prioritize the growth and development of the most crucial organs necessary for their survival (Golzardi, 2016).

Seed germination initiates with water absorption, which can be categorized into three distinct phases, such as initially rapid water absorption is speedy, slow-augment, and eventually a rapid enhancement (Gao et al., 2007; Fernandez et al., 2021). The process of water absorption in *B. dasyphylla* exhibited similarities to this characteristic. However, it was observed that the values of SSW and SWC decreased as the degree of drought increased. This suggests that drought had a suppressive effect on the water absorption of seeds. The water absorption capacity of *B. dasyphylla* from SL exhibited a lower magnitude compared to that from DS as the duration of drought increased. The reason is that *B. dasyphylla* from DS thrived in the exceedingly dry desert environment, characterized by extremely low soil moisture levels. The elevated seed moisture content facilitated earlier germination compared to other plants, thereby enhancing its competitive adaptability. The water sensitivity of *B. dasyphylla* from DS was found to be high, resulting in efficient water utilization and

enhanced seed germination (Gao et al., 2007; Zhang et al., 2023). This is an additional factor contributing to the greater drought tolerance of *B. dasyphylla* from DS compared to SL.

The balance of reactive oxygen species (ROS) metabolism is destroyed under stress, leading to the production of a significant amount of reactive oxygen species and an increase in the lipid peroxidation. MDA is a byproduct that exhibits the capacity to engage with various cellular constituents, leading to substantial detrimental effects. The concentration of this substance can be used as a measure of the harm caused to plant cells during times of stress (Shan and Zhao, 2015; Samal et al., 2021). The findings of the study indicate that the levels of MDA in *B. dasyphylla* were less than  $2\text{mmol}\cdot\text{g}^{-1}\text{DW}$ , suggesting that the maintenance of a reduced level of membrane lipid peroxidation may play a role in the plant's capacity to endure drought conditions. MDA content of *B. dasyphylla* increased with the extension of drought time, but the increase of *B. dasyphylla* from DS was relatively slow, indicating that *B. dasyphylla* from SL had poor drought-resistance ability.

The accumulation of ROS in plants was induced by adversity, leading to their activation as free radicals. At the same time, the accumulated ROS can trigger the activation of the antioxidant enzyme protection system, which hinders the accumulation of ROS. It decreased the membrane lipid peroxidation and preserved the balance of oxygen free radical metabolism. The antioxidant enzyme system has been recognized as a significant defense system for plants in face of adverse environment conditions (Hu et al., 2005; Ma and Zhao, 2019). Our results showed that antioxidant enzyme activity of *B. dasyphylla* first increased and then decreased with the extension of drought time. This indicated that superoxide free radical ( $\text{O}_2^-$ ) in plants increased in the initial stage of drought, which activated the activity of protective enzymes and played a role in removing ROS. However, the effect diminished as the drought intensified, particularly during the advanced phase of drought, resulting in a weakened ability to scavenge ROS (Qu et al., 2008). In general, the antioxidant enzyme activity of *B. dasyphylla* from DS exhibited greater levels compared to SL, potentially attributable to the specific conditions in which they were cultivated. Desert steppe belongs to arid region, while sandy land belongs to semi-

arid region (Ghassemi et al., 2016; Challabathula et al., 2022). The advantage of drought resistance is attributed to the ability of plants to adapt to changes in their habitat. This adaptation serves as a scientific basis for the selection of plants and reconstruction of vegetation.

One of the mechanisms employed by plants to manage stress is the synthesis and accumulation of osmoregulation substances. Plants can actively accumulate solutes in cells to reduce osmotic potential, enhance water absorption capacity, maintain turgor pressure, and avoid further damage to membrane system (Lu et al., 2008; Khan et al., 2021). The soluble sugar and protein of *B. dasyphylla* from DS remained consistently high throughout the initial and intermediate stages of drought, suggesting that the soluble sugar and protein played the regulatory function. During the subsequent phase of drought, there was a decrease in the osmoregulation substances of *B. dasyphylla* derived from DS, potentially attributed to an elevated respiratory consumption. In order to maintain the energy for normal survival, plants have to rely on the decomposition of proteins and other substances for their growth, resulting in lower levels of osmoregulation substances (Ma and Wang, 2021). The osmoregulation substances of *B. dasyphylla* from SL exhibited a negative correlation with the duration of drought. This could be attributed to the diminished humidity of sandy terrain during periods of drought, as well as the inadequate capacity for osmotic regulation and energy metabolism following drought-induced stress. Hence, it is evident that there are notable disparities in the osmotic regulation of *B. dasyphylla* originating from various sources, suggesting that plants from DS exhibited robust physiological adaptability in water.

## 5 Conclusion

The current investigation determined that *B. dasyphylla* from various origins exhibits robust resistance to drought. However, the drought tolerance of *B. dasyphylla* from DS was more pronounced compared to SL. This adaptation to desert and arid environments is a survival mechanism that has developed over an extended period of time. The elongation of radicle length was facilitated by mild drought, while growth was hindered when the drought surpassed a specific threshold. *Bassia dasyphylla* exhibits the capacity for physiological regulation and plasticity, enabling it to effectively maintain water metabolism equilibrium through the utilization of diverse osmotic regulators within specific ecological niches. The wide ecological range of a species may be attributed to the physiological plasticity demonstrated by its diverse surroundings. The examination of the biological characteristics and stress resistance physiology of plants in diverse environments can provide insights into the plasticity of their phenotypic and physiological traits.

## References

An, Y. Y., and Liang, Z. S. (2013). Drought tolerance of *Periploca sepium* during seed germination: antioxidant defense and compatible solutes accumulation. *Acta Physiologiae Plantarum* 35, 959–967. doi: 10.1007/s11738-012-1139-z

## Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

## Author contributions

JC: Data curation, Investigation, Writing – original draft. YQL: Investigation, Software, Writing – review & editing. XZ: Conceptualization, Data curation, Methodology, Supervision, Writing – review & editing. YL: Data curation, Investigation, Project administration, Writing – review & editing. BG: Data curation, Formal analysis, Software, Writing – original draft. RW: Data curation, Investigation, Software, Writing – review & editing. YL: Investigation, Methodology, Writing – review & editing. JM: Conceptualization, Funding acquisition, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Anjum, S. A., Ashraf, U., Zohaib, A., Tanveer, M., and Nazir, U. (2017). Growth and developmental responses of crop plants under drought stress: a review. *Zemdirbyste* 104, 267–276. doi: 10.13080/z-a.2017.104.034

- Asri, Y., Hamzeh'Ee, B., Shirvany, A., Jalili, A., Yazdani, S., and Khoshnevis, M. (2003). Soil seed banks in the Arasbaran protected Area of Iran and their significance for conservation management. *Biol. Conserv.* 3, 425–431. doi: 10.1016/S0006-3207(02)00170-2
- Atkin, O. K., Loveys, B. R., Atkinson, L. J., and Pons, T. L. (2006). Phenotypic plasticity and growth temperature: understanding interspecific variability. *J. Exp. Bot.* 57, 267–281. doi: 10.1093/jxb/erj029
- Ayumi, T. O., Iuki, E., Nobuhito, O., Deni, E., Norikazu, Y., Muneto, H., et al. (2018). A water acquisition strategy may regulate the biomass and distribution of winter forage species in cold Asian rangeland. *Ecosphere* 9, 1–13. doi: 10.1002/ecs2.2511
- Benard, R. B., and Toft, C. A. (2008). Fine-scale spatial heterogeneity and seed size determine early seedling survival in a desert perennial shrub (*Ericameria nauseosa*: Asteraceae). *Plant Ecol.* 194, 195–205. doi: 10.1007/s11258-007-9284-y
- Bizet, F., Bogeat, M. B., Montpied, P., Christophe, A., Ningre, N., Cohen, D., et al. (2015). Phenotypic plasticity toward water regime: response of leaf growth and underlying candidate genes in *Populus*. *Physiologia plantarum* 154, 39–53. doi: 10.1111/ppl.12271
- Challabathula, D., Analin, B., Mohanan, A., and Bakka, K. (2022). Differential modulation of photosynthesis, ROS and antioxidant enzyme activities in stress-sensitive and -tolerant rice cultivars during salinity and drought upon restriction of COX and AOX pathways of mitochondrial oxidative electron transport. *J. Plant Physiol.* 268, 153583. doi: 10.1016/j.jplph.2021.153583
- Chen, J. L., Zhao, X. Y., Li, Y. Q., Luo, Y. Q., Zhang, Y. Q., Liu, M., et al. (2021a). Physiological responses of *Agriophyllum squarrosum* and *Setaria Viridis* to drought and re-watering. *Sci. Rep.* 11, 18663. doi: 10.1038/s41598-021-98246-8
- Chen, J. L., Zhao, X. Y., Zhang, Y. Q., Li, Y. Q., Luo, Y. Q., Wang, P. Y., et al. (2019). Effects of drought and rehydration on the physiological responses of *Artemisia halodendron*. *Water* 11, 793. doi: 10.3390/w11040793
- Chen, J. L., Zhao, X. Y., Zhang, Y. Q., Luo, Y. Q., He, Z. Q., Zhang, R., et al. (2021b). Responses to drought stress in germinating seeds of *Agriophyllum squarrosum* (L.) Moq and *Setaria viridis* (L.) Beauv. *Fresenius Environ. Bull.* 30, 4730–4741.
- Dasanayaka, B., Jinadasa, R. N., Jayasuriya, K. M., and Phartyal, S. S. (2022). Seed ecophysiology of elephant apple (*Dillenia indica*)-an important tree species of the Indomalayan realm. *Ecol. Res.* 37, 532–543. doi: 10.1111/1440-1703.12312
- Delgado, J. A., José, M. S., Francisco, L., and Acosta, F. (2008). Seed size and seed germination in the Mediterranean fire-prone shrub *Cistus ladanifer*. *Plant Ecol.* 197, 269–276. doi: 10.1007/s11258-007-9376-8
- Drazkiewicz, M., SKórzyńska, P. E., and Krupa, Z. (2004). Copper-induced oxidative stress and antioxidant defence in *Arabidopsis thaliana*. *Biol. Metals* 17, 379–387. doi: 10.1023/B:BIOM.0000029417.18154.22
- Fernandez, P., Eduardo, C., Angelino, M., Andrea, C., Lohengrin, A. R., Sergey, V., et al. (2021). The seed germination spectrum of alpine plants: a global meta-analysis. *New Phytol.* 229, 3573–3586. doi: 10.1111/NPH.17086
- Fernández, P., Eduardo, E., Mattana, P., and Hugh, W. (2018). Seeds of future past: climate change and the thermal memory of plant reproductive traits. *Biol. Rev.* 94, 439–456. doi: 10.1111/brv.12461
- Gao, H. J., Yun, J. F., and Liu, D. F. (2007). Study on seed germination of three wheatgrass species in desert steppe. *Pratacultural Sci.* 24, 64–68.
- Ghassemi, G., Kazem, R. L., and Alizadeh, S. S. (2016). Effects of water stress on seed yield and essential oil content of dill genotypes. *J. Biodiversity Environ. Sci.* 9, 420–425.
- Golzardi, F. (2016). Effect of flooding, acidity and high temperatures on seed germination and durability of common purslane. *Seed Sci. Res.* 2, 15–27. doi: 10.29252/yujs.2.2.15
- Habtamu, A., Zelek, M., Mesfin, M., and Ermias, E. (2014). Evaluation of highland maize (*Zea mays* L.) cultivars for polyethylene glycol (PEG) induced moisture stress tolerance at germination and seedling growth stages. *J. Plant Breed. Crop Sci.* 6, 77–83. doi: 10.5897/JPBSC
- Hu, Z. Q., Liu, Y. D., Li, D. H., and Dauta, A. (2005). Growth and antioxidant system of the cyanobacterium *Synechococcus elongatus* in response to microcystin-RR. *Hydrobiologia* 534, 23–29. doi: 10.1007/s10750-004-1319-y
- Javadi, M. M., Florentine, S. K., Knapp, A. A., and Hafiz, C. B. (2018). Environmental factors affecting the germination and emergence of white horehound (*Marrubium vulgare* L.): a weed of arid-zone areas. *Rangeland J.* 40, 47–54. doi: 10.1071/RJ17121
- Jürgen, V., Carrao, H., Spinoni, J., Barbosa, P., and Naumann, G. (2014). World drought frequency, duration, and severity for 1951–2010. *Int. J. Climatology: A J. R. Meteorological Soc.* 34, 2792–2804. doi: 10.1002/joc.3875
- Keshtiban, R. K., Carvani, V., and Imandar, M. (2015). Effects of salinity stress and drought due to different concentrations of sodium chloride and polyethylene glycol 6000 on germination and seedling growth characteristics of lentil (*Lens culinaris* Medik). *Adv. Environ. Biol.* 9, 445–450.
- Khan, R. Y., Ma, X. H., Zhang, J., Wu, X. Y., Lqbal, A., Wu, Y. H., et al. (2021). Circular drought-hardening confers drought tolerance via modulation of the antioxidant defense system, osmoregulation, and gene expression in tobacco. *Physiologia plantarum* 172, 1073–1088. doi: 10.1111/ppl.13402
- Kinugasa, T., Hozumi, Y., Nishizima, H., Ishitobi, A., and Miyawaki, M. (2016). Germination characteristics of early successional annual species after severe drought in the Mongolian steppe. *J. Arid Environments* 130, 49–53. doi: 10.1016/j.jaridenv.2016.03.010
- Li, X. M., Zhao, X. Y., Zhao, F., and Guo, M. J. (2009). Response of seed germination of three Caragana species to temperature and soil moisture. *Pratacultural Sci.* 26, 140–145. doi: 10.1016/j.jelecom.2008.10.019
- Li, X. Y., Zuo, X. A., Zhao, X. Y., Wang, S. K., Yue, P., Xu, C., et al. (2022). Extreme drought does not alter the stability of aboveground net primary productivity but decreases the stability of belowground net primary productivity in a desert steppe of northern China. *Environ. Sci. Pollut. Res.* 30, 24319–24328. doi: 10.1007/s11356-022-23938-1
- Liu, C. L., Wang, W. Q., Cui, J. R., and Li, S. Y. (2006). Effects of drought stress on photosynthesis characteristics and biomass allocation of *Glycyrrhiza uralensis*. *J. Desert Res.* 26, 142–145.
- Loretta, G. (2014). Plant phenotypic plasticity in response to environmental factors. *Adv. Bot.* 4, 1–17. doi: 10.1155/2014/208747
- Lu, S. Y., Su, W., Li, H. H., and Guo, Z. F. (2008). Abscisic acid improves drought tolerance of triploid Bermudagrass and involves H<sub>2</sub>O<sub>2</sub><sup>-</sup> and NO<sup>-</sup> induced antioxidant enzyme activities. *Plant Physiol. Biochem.* 47, 132–138. doi: 10.1016/j.plaphy.2008.10.006
- Luo, W., Robert, J., Griffin, N., Felton, A. J., Yu, Q., Wang, H. Y., et al. (2022). Drought has inconsistent effects on seed trait composition despite their strong association with ecosystem drought sensitivity. *Funct. Ecol.* 36, 2690–2700. doi: 10.1111/1365-2435.14165
- Ma, W., and Zhao, B. (2019). Effect of relative air humidity and high temperature on the physiological and anatomical responses of two rhododendron cultivars. *Hort Sci.* 54, 1115–1123. doi: 10.21273/HORTSCI13974-19
- Ma, X. Z., and Wang, X. P. (2021). Aboveground and belowground biomass and its allometry for *Salsola passerina* shrub in degraded steppe desert in Northwestern China. *Land Degradation Dev.* 32, 714–722. doi: 10.1002/ldr.3772
- Paul, J. R., Andrew, S. M., and Douglas, W. L. (2012). Fine-scale spatial heterogeneity and incoming seed diversity additively determine plant establishment. *J. Ecol.* 100, 939–949. doi: 10.1111/j.1365-2745.2011.01948.x
- Qu, X. X., Huang, Z. Y., Baskin, J. M., and Carol, C. (2008). Effect of temperature, light and salinity on seed germination and radicle growth of the geographically widespread halophyte shrub *Halocnemum strobilaceum*. *Ann. Bot.* 101, 293–299. doi: 10.1093/aob/mcm047
- Rabiei, B., Mardani, Z., Ghomi, K., Sabouri, H., and Sabouri, A. (2014). The effect of rice chromosome on traits associated with drought and salinity tolerance at germination and seedling stages. *Seed Plant Improvement J.* 36, 2690–2700. doi: 10.22092/SPIJ.2017.111197
- Sala, O. E., Gherardi, L. A., and Peters, D. P. (2015). Enhanced precipitation variability effects on water losses and ecosystem functioning: differential response of arid and mesic regions. *Climatic Change* 131, 213–227. doi: 10.1007/s10584-015-1389-z
- Samal, R. R., Kumari, K., Sahoo, Y., Mishra, S. K., and Subudhi, U. (2021). Interaction of artemisinin protects the activity of antioxidant enzyme catalase: A biophysical study. *Int. J. Biol. Macromolecules.* 172, 418–428. doi: 10.1016/j.ijbiomac.2021.01.072
- Shan, C. J., and Zhao, X. L. (2015). Lanthanum delays the senescence of *Lilium longiflorum* cut flowers by improving antioxidant defense system and water retaining capacity. *Scientia Hort.* 197, 516–520. doi: 10.1016/j.scienta.2015.10.012
- Su, Y. Z., Zhang, T. H., Li, Y. L., and Wang, F. (2005). Changes in soil properties after establishment of *Artemisia halodendron* and *Caragana microphylla* on shifting sand dunes in semiarid Horqin sandy land, Northern China. *Environ. Manage.* 2, 36. doi: 10.1007/s00267-004-4083-x
- Tobe, K., Zhang, L. P., and Omasa, K. (2005). Seed germination and seedling emergence of three annuals growing on desert sand dunes in China. *Ann. Bot.* 4, 649–659. doi: 10.1093/aob/mci060
- Wang, D. T. (2016). Vertical distribution of *Artemisia halodendron* root system in relation to soil properties in Horqin Sandy Land, NE China. *Sci. Cold Arid Regions* 8, 411–418. doi: 10.3724/SP.J.1226.2016.00411
- Xiang, J., Jiang, A. N., Fang, Y. P., Huang, L. B., and Zhang, H. (2012). Effects of soil water gradient on stress-resistant enzyme activities in phragmites australis from yellow river delta. *Proc. Environ.* 13, 2464–2468. doi: 10.1016/j.proenv.2012.01.236
- Xu, Z. L., Yan, D. J., Tan, X. M., Niu, S. B., Yu, M., Sun, B. D., et al. (2022). Phaeosphiprone (1/1'), a pair of unique polyketide enantiomers with an unusual 6/5/5/6 tetracyclic ring from the desert plant endophytic fungus Phaeosphaeriaceae sp. *Phytochemistry* 194, 112969–112975. doi: 10.1016/j.phytochem.2021.112969
- Yue, P., Zuo, X. A., Li, K. H., Li, X. Y., Wang, S. K., and Misselbrook, T. (2022). No significant change noted in annual nitrous oxide flux under precipitation changes in a temperate desert steppe. *Land Degradation Dev.* 33, 94–103. doi: 10.1002/ldr.4131
- Yue, X. Y., Zuo, X. A., Yu, Q., Xu, C., Lv, P., Zhang, J., et al. (2019). Response of plant functional traits of *Leymus chinensis* to extreme drought in Inner Mongolia grasslands. *Plant Ecol.* 220, 141–149. doi: 10.1007/s11258-018-0887-2
- Zhang, Y., Liang, Z. S., and An, Y. Y. (2011). Seed germination responses of *Periploca sepium* Bunge, a dominant shrub in the Loess hilly regions of China. *J. Arid Environments* 75, 504–508. doi: 10.1016/j.jaridenv.2010.12.020
- Zhang, H., Shan, T. T., Chen, Y., Lin, M. S., Chen, Y. Z., Lin, L. J., et al. (2023). Salicylic acid treatment delayed the browning development in the pericarp of fresh

longan by regulating the metabolisms of ROS and membrane lipid. *Scientia Hort.* 318, 112073–112086. doi: 10.1016/j.scienta.2023.112073

Zheng, D., Rademacher, J., Chen, J., Crow, T., Bresee, M., and Moine, J. L. (2004). Estimating aboveground biomass using Landsat 7 ETM<sup>+</sup> data across a managed landscape in northern Wisconsin, USA. *Remote Sens. Environ.* 94, 402–411. doi: 10.1016/j.rse.2004.08.008

Zhou, H., Zhao, W. Z., Luo, W., and Liu, B. (2015). Species diversity and vegetation distribution in nekhas of *Nitraria tangutorum* in the Desert Steppes of China. *Ecol. Res.* 81, 301–311. doi: 10.1007/s11284-015-1277-z

Zhuang, Y. L., and Sophia, R. (2012). Relationship between dew presence and *Bassia dasyphylla* plant growth. *J. Arid Land* 4, 11–18. doi: 10.3724/SP.J.1227.2012.00011