Title: The features of main osmolytes, silicon and their coupling effects in improving drought resistance of the typical xerophytes in the desert areas of northwest China

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Running title: The coupling effects of the inorganic ions on the xerophytes

ABSTRACT

Succulent xerophytes (SX) and less succulent xerophytes (LSX) is able to accumulate inorganic ions and synthesize organic solutes (OS) to adapt to drought stress. Silicon (Si) is one of the five beneficial elements for plants and its importance to SX has been confirmed. In the study, the features of main osmolytes and Si were studied in SX, and LSX species, and the coupling effects of inorganic ions were investigated in the SX *H. ammodendron* and LSX *C. korshinskii*t. Results showed that SX and LSX had the common adaptive characteristics by preferentially accumulating inorganic ions rather than OS for drought resistance, and the total amount of osmotica in SX was 2.36 times higher than that in the LSX. The greatest contribution to drought resistance was K^+ (29.7%), the lowest was Na^+ (2.4%) in LSX, while the greatest contribution was Na^+ (41.7%), the total OS was the lowest (2.4%) in SX. The coupling effects of inorganic ions played vital important roles in drought resistance of the SX and LSX. The better coupling ratios of NaCl, NH_4NO_3, $CaCl_2$, $MgCl_2$ and Na_2SiO_3 in *H. ammodendron* were 20: 5: 20: 40: 10 and 40: 10: 60: 10:7.5 (g kg^{-1} dry soil), and the better coupling ratios of KNO_3, $CaCl_2$, $MgCl_2$ and K_2SiO_3 in *C. korshinskii*t were 20: 10: 20: 10: and 40: 20: 60: 5 (g kg^{-1} dry soil). Findings suggested that the rational coupling of inorganic ions can be utilized as mineral compound fertilizers to restore and reconstruct degraded vegetations in arid areas.

KEYWARDS: Coupling effects; drought resistance; feature; succulent and less succulent xerophyte; osmolytes

INTRODUCTION

Xerophytes are one of the special species for plants that can maintain survival and reproduction in arid regions by their excellent morphological or physiological adaptations which are differently adapted to conserve water, and in general also to store large amount of water in their leaves or round stems in periods of drought (Filella *et al*., 1998). Xerophytes, such as succulent xerophytes (SX) *Haloxylon ammodendron*, *Zygophyllum xanthoxylum* and *Nitrarial tangutorum*, and less succulent xerophytes (LSX) *Artemisia sphaerocephala* and *Caragana korshinskii* grown in the arid areas, however, have developed multiple protective strategies that assist them to resist to dry environments (Wang *et al*., 2004;Yue *et al*., 2011). Osmotic adjustment is one of the major adaptative strategies for plants, which is owing to the assimilation and storage of cellular solutes to against with stressful environments (Ma *et al*., 2012). The intracellular osmotica includes inorganic ions Na^+, Ca^{2+}, K^+, Mg^{2+} and Cl^- absorbed from the outside of cells, and organic solutes free proline (FP), soluble sugar (SS) and glycine betaine (GB) synthesized by cells (Wang *et al*., 2004; Cai *et al*., 2011).

Na^+ is considered as the dominant soluble cation in many desertified soils. Nevertheless, many plants, particularly some cultivated crops (glycophytes) are easily affected by Na^+. Whereas, when the Na^+ content of growth medium is in comparatively low, it can be utilized as a requisite nutrient for many halophytes (*Suaeda salsa*) and C_4 plants, especially when K^+ contents is restricted (Wang *et al*., 2001; Kang *et al*., 2013). However, both halophytes and glycophytes have the ability to compartmentalize the cells Na^+ into vacuoles, therefore maintain the cytosolic Na^+ content at low-toxic levels, indicating that the physiological mechanism of compartmentalization allow plants to harness Na^+ as an important physiological osmotica to adapt to environmental stresses (Zeng *et al*., 2009; Wu *et al*., 2011; Ma *et al*., 2012; Kang *et al*., 2016a). It has been demonstrated that Na^+ is considered to be a vital physiological osmotica of SX species to resist to drought stress (Dennis & Andrea, 2012; Yue *et al*, 2012; Ma *et a*l., 2012, 2014). K^+ is a main macronutrient for many higher plants that acts as significant effects related to enzyme activator, photosynthesis, stomatal opening, metabolism, etc. Plants have to assimilate majority of K^+ from the soil to maintain normal growth and reproduction (Elumalai *et al*., 2002; Shahzad *et al*., 2016). Large amount of K^+ contents are also strongly linked to drought tolerance for plants. K^+ could not only enhance the osmotic adjustment ability to improve the water status, but also can improve photosynthetic activity, reduce inhibitory effect of drought on photosynthesis of plants under drought stress (Egilla *et al*., 2001; Farooq *et al*., 2009; Ahanger *et al*., 2017). Ca is the fourth essential element which plays a vital important physiological function for plant growth. Ca^{2+} acts as an intracellular second messenger to transduct the drought signal, and regulates the physiological responses induced by drought stress, particularly, Ca^{2+} and calmodulin (CAM) involved in the perception, transmission, response and expression of stress signals under dry conditions (Monroy *et al*., 1993; Volk *et al*., 2002; Dauer & Perakis, 2014). Additionally, exogenous Ca^{2+} could inhibit the production of active oxygen substances, protect the structure of cell plasma membrane, maintain normal photosynthesis and regulate metabolisms of hormone to improve the drought-resistant capability of plants (Yuan *et al*., 2014; Kang *et al*., 2017). Mg is a main necessary element for plants growth which serves as significant functions involved in chlorophyll and pigment, osmotic adjustment, enzyme activator, protein synthesis, enzymatic reaction and formation of vitamin, etc (Gerendás and Führs., 2013; Rahmawati et al., 2015). Large amount of Mg^{2+} concentrations are also strongly related to drought resistance for plants (Salama *et al*., 2014; Rahmawati *et al*., 2015). Si is classified as one of the five beneficial elements (Na, Si, Al, Co and Se) for plants and its content in plants usually reaches the value of macronutrients (Elizabeth *et al.*, 2009). Although it is not generally requisite by all plants, its absolute importance and necessity to particular taxa such as Gramineae, Baeillariophyta and Equisetaceae species has been widely confirmed (Abdul *et al*., 2013; Marie *et al*., 2017). The beneficial roles of Si to enhance drought resistance of plants have been conclusively proved (Ma & Yamaji, 2006; Elizabeth *et al*., 2009; Li *et al*., 2016). Si not only can reinforce biofilm dependence function of cells and adjust the absorption of various elements, but also can also decrease transpiration rate, reduce water loss to modulate the photosynthesis and transpiration, therefore improve drought resistance of plants under drought stress (Kim *et al*., 2002; Kang *et al*., 2016b; Zhang et al., 2017). The organic solutes FP, SS and GB contents in plant usually have been closely related to osmotic adjustment under drought stress (Ma *et al*., 2012; Silva *et al*., 2015). As small molecule osmolytes, they can not only prevent intracellular macromolecular substances from dehydrating and play important role in the process of hydroxyl radical scavenging during dry period (Yoshiba *et al*., 1997; Wang *et al*., 2012; Zrig *et al*., 2015), but also can decrease the water potential, participate in osmotic adjustment, and maintain the stability of protein under drought stress (Shao *et al*., 2006; Oliveira *et al*., 2011).

The intracellular solutes play vital significant functions for plants to adapt to drought environment. Yet, to date only the accumulation characteristics of Na^+, K^+, and FP and free amino acid in several drought tolerant species have investigated (Wang *et al*., 2004; Zhang *et al*., 2004), very little is known about their contribution to drought resistance, especially the accumulation features of other intracellular solutes (Ca^{2+}, Mg^{2+}), inorganic nutrients Si, N and P, their contribution to drought resistance, coupling roles and application involved in xerophytes are not clear. It is worth mentioning that Wang *et al*. (2007) have successfully invented a Na compound fertilizer (NaCF: Na^+, Si, N and P) (Patent No: 2007100188400), which can positively stimulate growth and enhance drought tolerance of SX, and confirmed that mineral nutrients play important roles in improving drought resistance of SX species (Kang et al. 2013, 2016a). In the study, we comprehensively and systematically investigated the features (accumulation, distribution and contribution to drought resistance) of osmolytes and Si in the typical SX and LSX species exposed to drought stress, and evaluated the coupling roles of the main inorganic nutrients in regulating plant growth and improving drought resistance of the SX (compared with NaCF) and LSX species, respectively. The results indicate that the coupling effects of inorganic ions play vital important roles in improving drought resistance of the SX and LSX and their optimum coupling ratio can be used as fertilizer formulation to cultivate strong drought-resistant seedlings to restore and reconstruct degraded vegetations in many arid and semi-arid areas.

MATERIALS AND METHODS

Accumulation characteristics, distribution regulation and contribution of main osmolytes and Si responding to drought stress

The outdoor investigation and sampling were carried out in late September, 2015, at the Minqin National Studies Station for Desert Steppe Ecosystems (MSDSE) in Gansu province, which was affiliated with the Chinese Ecosystem Research Network (102°59′05″E, 38°34′28″N). The sampling area is a representative desert and oasis region in China which located in the lower reaches of the Shiyang River Basin and surrounded by the Badain Jaran Desert in the west and north, and by the Tengger Desert in the east. The average annual rainfall and temperature are 110 mm and 7.6 C, respectively; the average annual evaporation is 2644 mm (Zhao *et al*., 2011; Kang *et al*., 2013). In order to clarify the accumulation characteristics, distribution regulation and contribution of main osmolytes and Si in the xerophytes exposed to drought stress, two major groups of xerophytes - SX and LSX species that have grown for one year were selected and used for this test. The tested typical SX species *H. ammodendron*, *Z. xanthoxylum*, *N. tangutorum*, and LSX species *A. sphaerocephala* and *C. korshinskii* were the predominant plants for sand fixation, and soil and water conservation, and they were collected from wild plants which were naturally distributed in the MSDSE of Northwest China. These SX species are characterized by a few of big stomata, thickness cuticle and developed water storage tissue and LSX species are characterized by a lot of small stomata, a large number of epidermal hair and developed conducting tissue. The LSX *A. sphaerocephala* and *C. korshinskii* were collected with the height of 25 cm and 40 cm, and their main roots were 30 cm and 100 cm deep, respectively. The SX *Z. xanthoxylum* and *N. tangutorum* were 25 cm and 35 cm in height with the main roots of 50 cm and 60 cm deep, respectively. The four plants were collected and then divided into roots, stems and leaves. Plants of *H. ammodendron* were 40 cm in height with main roots that reached 90 cm deep, and plants were divided into roots, perennial stems and photosynthesizing branches (PB). All plant tissues were washed 4 times with distilled water and oven-dried (80℃ for 3d). All evenly mixed soil samples were collected from the root zones of each plant at all sites, air-dried and passed through a 2 mm sieve for chemical analyses. All collected soil samples were no less than 15 plants for each species.

The coupling effects of inorganic nutrients by using orthogonal experimental design

The pot experiment in field environment was conducted at the Linze Inland River Basin Research Station (100°07′E, 39°21′N) of the Chinese Academy of Sciences (IRBRS-CAS) in 2016 and 2017, which belongs to the Chinese Ecosystem Research Network. The station is located in Linze County, Gansu Province, China, an area positioned at the Badain Jaran desert in northwestern China. The mean annual precipitation and temperature are 117 mm and 7.6 °C, respectively, the mean annual evaporation is 1830.4 mm. Mature seeds of *H. ammodendron* and *C. korshinskii*t were collected in the IRBRS-CAS in November and June, 2015, respectively. The tested soil samples were collected from the IRBRS-CAS where the SX *H. ammodendron* and LSX *C. korshinskii*t were naturally distributed. The compositions of tested fertilizer (specification: analytical reagent) of *H. ammodendron* ($NaCl$, NH_4NO_3, $CaCl_2$, $MgCl_2$ and Na_2SiO_3 .$9H_2O$) and *C. korshinskii*t (KNO_3, $CaCl_2$, $MgCl_2$ and K_2SiO_3) respectively, were produced by Damao chemical reagent factory, Tianjin, China. To maximally decrease the effects of possible environmental factors in the desert, all treatments in plant cultivation of *H. ammodendron* and *C. korshinskii*t were stochastically allocated to new positions every two weeks.

The coupling effects of the inorganic nutrients in *H. ammodendron*: The Na compound fertilizer (NaCF) and combinations of inorganic nutrients were used for *H. ammodendron* to confirm that the combination of inorganic nutrients was more beneficial to the growth of *H.*

ammodendron compared with NaCF in drought stress, and then screen out the optimal combination of inorganic nutrients for *H. ammodendron* (April to September, 2016). The basis of setting the composition of NaCF came from the Chinese invention patent (Patent No: 2007100188400) that we have applied in 2007, and the basis of setting the composition of inorganic nutrients consulted to the published references of Kang et al (2014, 2015, 2016, 2017). The composition of the NaCF (N, P, Na and Si) is as follows: $NaNO_3$ (0.14 g kg^{-1} dry soil), $NaH_2PO_4 .2H_2O$ (0.121 g kg^{-1} dry soil) and $Na_2SiO_3 .9H_2O$ (0.65 g kg^{-1} dry soil); the combination of inorganic nutrients is consisted of the following components: NaCl, NH_4NO_3, $CaCl_2$, $MgCl_2$ and $Na_2SiO_3 .9H_2O$, and the specific combinations are described in Table 1. The experiment was conducted using a randomized complete block design with five replications. The soil used was firstly dried out in a dry place, then crushed, and finally screened with a 2 mm sieve. Fifteen germinated seeds were evenly transplanted in each pre-made thickened plastic bucket (30 cm diameter × 65 cm height) filled with 40 kg dried soil and fully irrigated with water (the maximum field water capacity is 8 kg), and then all buckets were covered by a white plastic film (10 d) to decrease water loss and promote rapid growth of seedlings. Soil water content (SWC) was maintained at 70 % of field water capacity (FWC) by weighting. After eight weeks, plants were thinned out when they grown to15 cm in height and then retained 4 uniform plants that grow at the same rate in each bucket, and then plants were divided into 4 big groups: control (C), drought with control (D + C), drought with additional NaCF treatment (D + NaCF) and drought with additional inorganic nutrients treatment (D + IN). The D + IN treatment was divided into 25 subgroups, and the detailed subgroups are described in Supplemental Table S1. The amount of fertilizer in each bucket culture treatment was calculated with the following formula: $T\text{s} = 40 \times T_f$

Where T_s refers to the total amount of fertilizer applying in each bucket; T_f is the amount of fertilizer used in 1 kg dried soil. The SWC in the C, D + C, D + NaCF and D + IN groups was maintained at 70 % of FWC for 15 d by irrigating with water; then water in D + C, D + NaCF and D + IN groups was withheld 20d to induce drought stress gradually. When the SWC has decreased to 30 % of the FWC, this value was maintained by irrigating with the corresponding water. After the plants were harvested, 3 buckets (survived and uniform plants) of each treatment were dug out and separated into roots and aboveground parts (washed three times with water and dried) for morphological and physiological analysis.

The coupling effects of the main inorganic nutrients in *C. korshinskii*t: The combinations of inorganic nutrients were used for *C. korshinskii*t to confirm that the combination of inorganic nutrients also play important roles in improving drought resistance of *C. korshinskii*t in drought stress, and screen out the optimal combination of inorganic nutrients for *C. korshinskii*t (April to September, 2017). The combination is consisted of the following components: KNO_3, $CaCl_2$, $MgCl_2$ and K_2SiO_3, and the specific combinations are described in Table 1. The plant cultivating of *C. korshinskii*t were the similar to that in *H. ammodendron*. After eight weeks, the plants were thinned out (8-10 cm in height) and retained 6 uniform plants in each bucket, and then plants were divided into control (C), drought with control (D + C) and drought with additional inorganic nutrients treatment (D + IN). The D + IN treatment was divided into 20 subgroups which are described in Supplemental Table S2. The calculation of fertilizer, water control treatment and sample collection were the same as that in experimental design of *H. ammodendron*.

Determination of samples

Determination indexes related to plant growth

Plant height (PH), crown diameter (CD), main root length (MRL) were measured using the steel tape (3 m); the fresh weight (FW) and dry weight (DW) (80 ℃ for 4 d to constant weight) were weighted using an electronic scale (0.001 g precision).

Determination indexes related to inorganic ions (organic solutes) in plants and soil

Soluble Na^+ and K^+ in soils were obtained from the soaked soil with deionized water (water: soil, 5: 1). Exchangeable and available non-exchangeable Na^+ and K^+ in soils were obtained with 2 mol.L^{-1} cold HNO_3. Available Na^+ and K^+ in soils included the sum of soluble, exchangeable and available non-exchangeable Na^+ and K^+. The lanthanum or strontium salt were used as a released agent to extract the Ca^{2+} and Mg^{2+} in soils. Available N and P in soils were measured by using the method of alkali-hydrolyzable diffusion and the Bray method, respectively; available Si in soils was measured by using the method of citric acid extract (Zhou et al. 2006). Soil water content was calculated by the gravimetric method. The more detailed methods of soil indexes refer to reference (Bao, 2000). The oven-dried plant samples were sieved (0.5 mm). Na^+ and K^+ contents were obtained from the dried plant tissues in 100 mM acetic acid at 90 °C for 2 h (Kang *et al*., 2013, 2014, 2015). Plant samples were digested by nitric acid and perchloric acid (nitric acid: perchloric acid, 4:1), then Ca^{2+} and Mg^{2+} content were measured (Tao *et al*., 2006). The Na^+, K^+, Ca^{2+} and Mg^{2+} in plant tissues and soils were determined by an atomic absorption spectrophotometer (2655-00, Cole-Parmer Instrument Co., Vernon Hills, IL, USA). The Si content in plants tissues was analyzed by the method of the colorimetry (Dakora & Nelwamondo, 1992). The FP contents were analyzed using the method of acidic indene three ketone and determined with an atomic absorption spectrophotometer. The SS contents in plants included the sum of sucrose, fructose and glucose which was analyzed by the method of HCl transformation -copper reduction- iodimetry, and RS was analyzed by the method of copper reduction- iodimetry.

Data analysis

All experimental data was analyzed using the SPSS program for Windows Version 13.0 (SPSS Inc., Chicago, Illinois, 1975). Duncan's multiple range tests and one-way analysis of variance (ANOVA) for a completely randomized design were used to compare the difference of contents of ions (K, Na, Ca Mg and Si) and organic solutes (FP, SS and RS) of different parts of the SX and LSX species, and the the positive coupling effects of inorganic nutrients on the growth-related (PH, FW, BN and MRL) and physiological (Na^+, K^+, Ca^{2+}, Mg^{2+} and Si contents) indexes of *H. ammodendron* and *C. korshinskii*t. Data reported for soil nutrients (N, P, K, Na, Ca Mg and Si) were also analyzed by the ANOVA. The least significant difference (LSD) tests were performed to detect the obvious significances of the determined data between means at a significance level of $P < 0.05$.

RESULTS

Accumulation features of inorganic nutrients and organic solutes in soil and plants

Status of inorganic nutrients and water content (SWC) in soil

SWC in the root region soil of the tested plants changed from 0.71% to 2.19%, therefore all tested species encountered severe drought stress (Table 2), and the most serious drought stress appeared in the rhizosphere soil of *H. ammodendron*. The contents of available Na^+ in the root region soils of SX species were significant higher, while the K^+ contents were lower than that of LSX species. The Na^+/ K^+ in root region soils of SX were average of 2.7 times higher than those of the LSX species. The contents of Ca^{2+}, Mg^{2+}, N, P and Si in the root region soils have no significant difference between SX and LSX species (Table 2).

Accumulation features of inorganic nutrients and organic solutes plants

The roots, stems and leaves of LSX accumulated lower content of Na^+, while the leaves accumulated much higher levels of K^+, Ca^{2+} and Mg^{2+} (Table 4). Although the content of Na^+ was the lowest in whole plant of LSX, the contents of Na^+ in the roots of *A. sphaerocephala* and *C. korshinskii* were much higher than in the other plant parts. The contents of Na^+ in roots of *A. sphaerocephala* and *C. korshinskii* reached 2.89 and 2.67 mmol.100g^{-1}DW, respectively, which were 14.42% and 58.8, 169.9% and 148.0% higher, respectively, than in the leave and shoot. Mg^{2+} was the most abundant ion after K^+, Ca^{2+} in LSX, especially the Mg^{2+} contents in leaves of LSX were much higher than in other tissues, while the Mg^{2+} content were lowest in their shoots The contents of Mg^{2+} in leaves of *A. sphaerocephala* and *C. korshinskii* were as high as 22.3 and 26.4 mmol.100g^{-1}DW, respectively, which were

253.4% and 117.6, 263.6% and 133.0% higher, respectively, than in the stem and root. The Si content in stems of LSX were much higher than in other tissues, and the N content in the whole plant was much higher than P in LSX (N accumulation is 30-40 times that of P) (Table 3, 4). The FP, RS in leaves, and SS in roots of LSX were much higher than in other tissues. Especially the FP contents increased by 23.1% and 52.2% from roots to stems, and 51.5% and 63.4% from stems to leaves, respectively in *A. sphaerocephala* and *C. korshinskii* (Table 4).

The PB (leaves) of SX gathered very high contents of Na^+, especially the Na^+ in PB (296.4 mmol.100g^{-1} DW) of *H. ammodendron* was 7.4 and 6.5 times as much as its perennial stems and roots, respectively (Table 3). Contents of Ca^{2+}, K^+ and Mg^{2+} in PB of *H. ammodendron*, leaves of *Z. xanthoxylum* and stem of *N. tangutorum* were much higher than in other plant tissues, showing an increasing tendency from roots to perennial stems, and then to PB as well as leaves (Table 3), while the contents of Si in roots of *H. ammodendron*, stem of *Z. xanthoxylum* and leaves of *N. tangutorum* were much higher than in other tissues. The Na^+/K^+ in PB (leave), stem and root of SX was more than 1 (data not shown). Contents of FP and RS in PB (leaves), stems and roots of SX were higher than in other tissues (Table 4). There is noteworthy that the FP, SS and RS in the different tissues of the SX were significantly lower than that in the LSX species (Table 4). The changes of N and P contents in the SX species were the same as LSX species, both of them showed a typical characteristic of accumulation a large of N and exclusion of P (Table 4).

The distribution rules of inorganic nutrients and organic solutes in plants

The K^+ and Ca^{2+} contents in above-underground parts of LSX were much higher than in other inorganic osmolytes, while the Na^+ and Ca^{2+} contents in above-underground parts of SX were significantly higher than in other inorganic osmotica (Table 5). The contents of SS in above-underground parts of LSX were much higher than in other organic osmolytes, and the changes of FP, SS and RS contents in above-underground parts of SX were similar to the

LSX, but the contents are significantly lower than in the LSX species (Table 5).

The distribution rules of inorganic nutrients and organic solutes in plants can be expressed by a ratio of inorganic, organic nutrients contents in aboveground to underground part or total contents of nutrients in aboveground to underground part. Except for the ratio of Na^+ contents, the main osmotica ratios of above-underground parts are more than 1 in LSX, and the ratios of K^+, Mg^{2+} and FP contents were maximum, which reached to 2.69, 2.88 and 3.56, respectively, and the ratio of Na^+ and SS contents were minimum which reached to 1.14 and 1.27, respectively in LSX (Table 6). The ratios of main osmolytes contents of above-underground parts in SX were more than 1, and the ratios of Na^+ and Mg^{2+} contents were maximum, which reached to 6.94 and 4.92, respectively, and the ratios of Si and SS contents were minimum which reached to 1.99 and 1.36, respectively (Table 6). The basic allocation features of the total amount of osmolytes and Si in SX and LSX species was 3.80 and 2.20 times more than that in underground part, respectively, and the total amount of osmolytes in SX was 2.36 times higher than that in the SX.

The contributions of main osmotica and Si to drought resistance in plants

The contribution of osmolytes and Si to drought resistance in plants can be expressed by a percentage of single ion or organic solute content accounted for the total content of ions and organic solutes. The larger the value, the greater the contribution to drought resistance is. The contributions of K^+ and Ca^{2+} to drought resistance in above-underground parts of LSX were biggest which accounted for 20.25% and 17.75%, and 9.4% and 7.0%. The lowest contribution is Na^+ only accounted for 1.15 % and 1.05 %, respectively (Table 7). The contributions of Na^+ and Ca^{2+} to drought resistance in above-underground parts of SX were biggest which accounted for 36.4% and 16.53%, and 5.3% and 6.73%, respectively. The lowest contributions were K^+ and Mg^{2+}contents in underground parts which accounted for 2.17 % and 2.20 %, respectively. It is worth mentioning that the contribution of Si to the drought resistance accounted for 13.65% and 13.13% in LSX and SX, respectively which is roughly the same as Mg^{2+} (15.9% and 10.17%, respectively).

The contributions of SS to drought resistance in above-underground parts of LSX were biggest which accounted for 4.15% and 3.55%, respectively, and the lowest contribution was FP which accounted for 2.0 % and 0.6 %, respectively (Table 7). The contributions of FP, SS and RS to drought resistance in SX species were similar to the LSX species, but the contributions of FP, SS and RS to drought resistance were significantly lower than in the LSX species (Table 7). The sequence of main osmolytes and Si to drought resistance in LSX was: $K^+ > Ca^{2+} > Mg^{2+} >$ Si > SS > RS > FP > Na^+, and in SX was: $Na^+ > Ca^{2+} > Mg^{2+} >$ Si > $K^+ >$ SS > RS > FP (Table 7).

The coupling effects of inorganic nutrients induced a significant promotion on the growth performance of *H. ammodendron* and *C. korshinskii*t

In order to investigate the coupling function of main inorganic nutrients under drought stress, *H. ammodendron* and *C. korshinskii*t were subjected to different orthogonal experimental treatments of different fertilizers for 3 months under drought stress. We separately screened out two optimal coupling ratios from 25 and 20 coupling treatments for *H. ammodendron* and *C. korshinskii*t, respectively (Table 9, Supplemental Table. S3 and S4), the optimal coupling ratios of NaCl: NH_4NO_3: $CaCl_2$: $MgCl_2$: Na_2SiO_3 in *H. ammodendron* were D+IN_6-*H* (20: 5: 20: 40: 10) and D+IN_{12}-*H* (40: 10: 60: 10:7.5) (g kg^{-1} dry soil) , and the optimal coupling ratios of KNO_3: $CaCl_2$: $MgCl_2$: K_2SiO_3 in *C. korshinskii*t were D+IN_6-*C* (20: 10: 20: 10) and D+IN_{12}-*C* (40: 20: 60: 5) (g kg^{-1} dry soil). Compared with C+D treatment, the application of NaCF significantly promoted the growth of *H. ammodendron*, and increased PH by 25.2 %, FW by 46.1%, BN by 25.4%, MRL by 19.8%. Compared with D+NaCF treatment, the coupling effects of D+IN_6-*H* and D+IN_{12}-*H* on the growth performance of *H. ammodendron* were further promoted which resulted in optimal plant growth and alleviated the deleterious impacts on plant growth under drought stress.

Compared with the D+NaCF treatment, the PH, FW, MRL were significantly higher, by 24.2% and 15.8%, 33.1% and 37.7%, 20.9% and 18.9%, respectively, under the D+IN_6-*H* and D+IN_{12}-*H* treatments (Table 8, Supplemental Table. S3). The positive coupling effects of inorganic nutrients on the growth performance of *C. korshinskii*t were similar to that of *H. ammodendron* (Table 8, Supplemental Table. S2). Compared with C+D treatment, the coupling effects of D+IN_6-*C* and D+IN_{12}-*C* significantly increased the PH by 65.6% and 61.2%, FW by 93.8% and 87.5%, dry weight by 170.2% and 142.5%, MRL by 19.9% and 23.8%, respectively (Table 8, Supplemental Table. S4).

The coupling effects of inorganic nutrients promoted nutrient uptake, accumulation and improved drought resistance of *H. ammodendron* and *C. korshinskii*t

To further understand the physiological role of inorganic nutrients on the drought resistance of *H. ammodendron* and *C. korshinskiit*, the Na^+, K^+, Ca^{2+}, Mg^{2+} and Si concentrations were analyzed under the optimal coupling ratios of fertilizers, respectively. Compared with C and C+D treatments, the K^+ concentrations were significantly decreased by 25.4% and 14.5% when *H. ammodendron* was subjected to water deficit (30% of FWC); however, significant increases in Na^+ concentrations by 79.4% and 50.0%, Si concentrations by 52.1% and 26.5%, were observed in *H. ammodendron* grown in the presence of the NaCF. Compared with D+NaCF treatment, the coupling effects of D+IN_6-*H* and D+IN_{12}-*H* treatments on the ion accumulations (Na^+, Ca^{2+}, Mg^{2+} and Si) of *H. ammodendron* were further improved, and the Na^+, Ca^{2+}, Mg^{2+} and Si concentrations in D+IN_{12}-*H* treatment were significantly increased by 32.5%, 22.3%, 28.2% and 12.6%, respectively (Table 9). The positive coupling effects of inorganic nutrients on the ions concentrations of *C. korshinskii*t were also observed (Table 10). Compared with C+D treatment, the coupling effects of D+IN_6-*C* and D+IN_{12}-*C* significantly increased the K^+ concentrations by 44.7% and 55.3%, Ca^{2+} concentrations by 41.2% and 51.2%, Mg^{2+} concentrations by 46.6% and 76.7%, and Si concentrations by 31.3% and 19.6%, respectively (Table 9).

The coupling effects of inorganic nutrients induced a significant increase on soil fertility

We also investigated the coupling effects of inorganic nutrients on soil fertility. As shown in Table.10, the coupling effects of inorganic nutrients had important significantly influences on soil fertility of nursery soil of *H. ammodendron*. The application of NaCF and the coupling effects of D+IN$_6$-*H* and D+IN$_{12}$-*H* treatments could effectively increased inorganic ions and improved the soil fertility, and the D+IN$_6$-*H* and D+IN$_{12}$-*H* treatments could more effectively induced a significant improvement on soil fertility than the NaCF treatment (Table 10). Compared with C+D and the NaCF treatments, the D+IN$_{12}$-*H* significantly increased the Ca^{2+} concentrations by 111.6% and 245.7%, Mg^{2+} concentrations by 39.9% and 60.4%, and Si concentrations by 66.7% and 31.7%, respectively. The positive coupling effects of inorganic nutrients on soil fertility of nursery soil of *C. korshinskii*t were similar to that of *H. ammodendron* (Table 10). Compared with C+D treatment, the D+IN$_6$-*H* and D+IN$_{12}$-*C* significantly increased the K^+ concentrations by 10.8% and 19.2%, N concentrations by 123.6% and 190.3%, Ca^{2+} concentrations by 68.2% and 163.5%, Mg^{2+} concentrations by 63.0% and 252.3%, and Si concentrations by 50.6% and 19.3%, respectively.

DISCUSSION

The features of organic and inorganic nutrients in LSX and SX species make them well adapted to arid environment

Osmotic adjustment is an important strategy for plants to decline osmotic potential and resist to stressful conditions (Ma *et al*., 2012). Results have showed that SX species can absorb and accumulate large amount of Na^+ from arid soils with very low salinity for osmotic regulation under dry environments (Yue *et al*., 2012; Kang *et al*., 2013, 2014, 2015). Our results indicated that the SX species accumulated very high contents of Na^+ with an average of 304.3 mmol.100g^{-1} DW in whole plant, however, the average Na^+ content (6.9 mmol.100g^{-1} DW) in whole plant of LSX species were no more than 2.3 % of the SX species, indicating that the LSX were salt-excluding species, while SX species exhibited a strong salt accumulating characteristics (Table 3, 5). As report goes the salt accumulating halophyte *Suaeda salsa* grows well in high-salinity medium where the available Na^+ content (272.9 μmol g^{-1} dry soil) is about 66 times more than that of SX plants (4.1 μmol g^{-1} dry soil) growing in low salt environment (Wang *et al*. 2004; Kang *et al*., 2013). But, SX species have the strong ability to obtain large amount of Na^+ and mainly gathered it in PB (leaves) which were equal to *S. salsa*, and even more than that of other halophytes grown in high-salinity conditions (Tobe *et al*., 2000; Kang *et al*., 2013). Those results may be demonstrated that, just like salt-accumulating halophytes, SX species show an obvious salt-diluting trait, and should be considered to be the xero-halophyte species (Wang et al., 2004; Wu et al., 2011).

The average K^+ and Ca^{2+} contents in LSX were much higher than in the other osmolytes, especially the K^+ contents in root of the LSX were more than 41% than that in SX (Table 3). In addition, the LSX gathered moderate organic solutes in aboveground part, and the average FP, SS and RS in whole plant were 4.8, 2.6 and 2.0 times more than that of SX species (Table 4, 5). The physiological functions of organic solutes in LSX are unknown duo to their comparatively low contents compared with K^+ and Ca^{2+}. The FP, SS and RS accumulation may be a symbol of environmental stresses in LSX, but the contribution of FP (2.6%), SS (7.7%) and RS (4.9%) to drought resistance were obviously unimportant in comparation with K^+ (29.7%) and Ca^{2+} (24.8%) (Table 7). In spite of significant increases of organic solutes in their leaves, the salt-excluding plants LSX have a very low ability to gather Na^+ for drought resistance, maybe indicating that the feature of ion exclusion improve the plant resistance to toxic effects of Na^+ on shoots. LSX growing in dry environments, gathering higher contents of K^+ and Ca^{2+}, and moderate amount of organic solutes may act as a significant effect in adapting to water deficit. Why the LSX gathered moderate amount of FP, SS and RS are unclear. Maybe it is because they are unbearable to high Na^+ contents in the growth medium, and organic solutes may act as optional compatible solutes for these LSX to adapt to drought stress (Tobe *et al*., 2001; Wang *et al*., 2004; Zhang *et al*., 2004). Therefore, the physiological mechanisms of organic solutes involved in LSX responses to drought stress need to be further investigated. Moreover, both LSX and SX accumulate high concentrations of N and low concentrations of P (N accumulation is 30-40 times higher than that of P) (Table 4). It is not clear why LSX and SX showed a typical characteristic of accumulation high level of N and exclusion of P, and the reasons need to be further studied. For SX species, although they accumulated lower K^+ and organic solutes, but they gathered the abundant ions especially Na^+ and Ca^{2+} for drought resistance (Table 3, 5). The higher Na^+ and Ca^{2+} accumulation should be a symbol of drought stress in SX, and the contribution of Na^+ (41.7%) and Ca^{2+} (23.3%) to drought resistance were significantly important compared with K^+ (9.4%) and total organic solutes (2.5%) (Table 7). Thus, due to the unique properties of accumulating larger amount of Na^+ and Ca^{2+} than K^+ and organic solutes for drought resistance, the SX species had a strong drought resistance than the LSX, indicating that ion assimilation (Na^+ and Ca^{2+}) instead of exclusion (Na^+) may well be one of the most effective adaptation characteristics for SX to adapt to dry conditions. Interestingly, why SX in saline conditions continues to assimilates and gather large amount of Na^+ without any detectable signs of NaCl toxicity is unclear, maybe it is due to the Na^+ compartmentalization from cells into vacuoles regulated by the vacuolar Na^+/H^+ antiporter (NHX), therefore made cytosolic Na^+ content maintained at low toxic levels (Blumwald *et al*., 2000; Zeng *et al*., 2009; Wu *et al*., 2011; Dennis & Andrea, 2012). In general, it has been approved that Na^+ is stored mainly in vacuoles to maintain a low cellular osmotic potential, while the majority of K^+ and organic solutes are gathered in the cytosol to maintain the osmotic balance between cytoplasm and vacuole (Pitman *et al*., 1981; Binzel *et al*., 1988). Former results also indicated that low content of Na^+ was probably to be toxic in the cytoplasm, and even high contents of Na^+ were not obvious toxic in the vacuole (Blumwald *et al*., 2000; Subbarao *et al*., 2003). However, Chen *et al*. (2002) indicated that many species preferentially store Na^+ in the apoplastic space rather than compartmentalization in the vacuole. All these findings stressed the drought resistant mechanisms primarily conducted at the stem level to maintain effective metabolism and maintain growth by symplastic or apoplastic pathway (Kang et al., 2013). Thus, it is worth investigating deeply to elaborate the intricate physiological mechanisms.

The average total amount of osmolytes in SX (725.5 mmol.100g^{-1} DW) was 2.4 times higher than that in the LSX (307.35 mmol.100g^{-1} DW), and the total amount in SX and LSX was 3.8 and 2.2 times more than that in underground part, respectively (Table 6), indicating that the allocation feature of osmolytes has important significance for the water conduction of xerophytes. The research on water relations and xerophytic structure comparison of main different ecotypes plants showed that the average water potential (-26.09bar) of SX was lowest compared with mesophytes and LSX in the central desert areas of China (Liu *et al*. 1987), while the osmotic adjustment can cause a decrease of water potential in plants which allow plants to have enough water potential difference to absorb water from the low water potential of soil (Wang *et al*., 1991). The total content of main osmolytes in LSX and SX are closely related to water potential, and the relationship between total content of main osmolytes and water potential needs to be further studied. In our study, only one year old plant materials in Minqin of Badain Jaran desert (the average annual rainfall is 110 mm) were randomly selected and studied. How do the distribution characteristics of the main osmolytes and Si, and their contribution to drought resistance change in those xerophytes species with different ages (2, 5, 10, 15, 20, 30 or 40 years) and different rainfall areas (40 mm, 180 mm and 360 mm in Dunhuang of the Kmtag desert, Shapotou of Tengger Desert, and Naiman of Horqin Sandy Land, respectively)? Which factors (genetic, climatic or geographical factors) impact? All these above mentioned questions need further research.

The coupling effects of inorganic nutrients significantly promoted the growth and improved the drought resistance of *H. ammodendron* and *C. korshinskii*t

In soils of arid areas, the mineral nutrients are very deficient. However, the desert plants can well absorb and harness mineral nutrients to enhance their drought resistance (Kang *et al*., 2016a, b; 2017; Zhang *et al.*, 2017). Our latest findings showed that SX *H. ammodendron* and *N. tangutorum*, resistance to water stress are harnessing a large amount of Na^+ as important physiological osmotica, while still assimilating moderate Si to against with water stress, and the coexistence of Na and Si could more significantly mitigated the adverse effects of water deficit on SX than the addition of Na or Si (Kang et al., 2014, 2015). Moreover, K_2SiO_3 at 2.5 mM not only optimized the growth condition of *Z. xanthoxylum* but also improved the drought tolerance under water stress (Kang *et al*., 2016b). Further study demonstrated that $CaCl_2$ at $0.4 g.kg^{-1}$ dry soil both maximized the growth potential of SX *H. ammodendron* and enhanced its resistance to water stress (Kang *et al*., 2017). Our current results have demonstrated that accumulating higher levels ions (especially K^+, Ca^{2+}) and moderate organic solutes is a main adaptive mechanism of drought tolerance for LSX, while the SX assimilate and accumulate abundant Na^+ and Ca^{2+} than K^+ and organic solutes as one of the major adaptation strategies to resist to water deficit (Table 3, 4, 5,7). Results also confirmed that Ca^{2+} is known as the second major osmotica for LSX (after K^+) and SX species (after Na^+) under water stress (Table 7). On the whole, both SX and LSX species showed the common adaptive characteristics by preferentially absorbing and accumulating inorganic ions rather than organic solutes for drought resistance. Interestingly, for the significant roles of Na^+ on the drought resistance of *Z. xanthoxylum*, Wang *et al*. (2007) have successfully invented a Na compound fertilizer (NaCF: Na^+, Si, N and P) (Patent No: 2007100188400), which can positively stimulate growth and enhance drought tolerance of *Z. xanthoxylum*, and large-scale popularizing and applying to restore and reconstruct the degraded vegetation in Minqin and Alxa desert regions of northwest China (Kang *et al*., 2013, 2016a). However, there are still some drawbacks: (1) The SX and LSX species showed a typical characteristic of accumulation large quantities of N and exclusion of P (30-40 times higher than that of P), it is unreasonable to add P in NaCF formulation because it content in soil habitats can meet the needs of plants growth; (2) The NaCF lacks Ca^{2+}, Mg^{2+} and other important nutrients, and the fertilizer efficiency has not been maximized in enhancing drought resistance of plants and soil fertility; (3) At present, the NaCF was mainly applied to desert SX species, there is no report of fertilizer that can significantly enhance drought resistance LSX species. In our study, the above problems have been well solved. Compared with D+NaCF treatment, the coupling effects of D+IN_6-*H* and D+IN_{12}-*H* on the growth performance and drought resistance of *H. ammodendron* were further promoted, and soil fertility was further improved, and the positive coupling effects of inorganic nutrients (D+IN_6-*C* and D+IN_{12}-*C*) on *C. korshinskii*t were also proved (Table 8, 9, 10) . Based on the above scientific discoveries, the China's invention technology patents of mineral compound fertilizer of SX (Patent No: 201811514620.1) and LSX (Patent No: 201811514620.5) species and their application in arid areas have been applied. These above mentioned studies may be indicated that through better coupling of mineral nutrients Na^+, K^+, Ca^{2+}, Mg^{2+}, Si and N, and using them as fertilizers, we can cultivate strong drought-resistant SX and LSX plants, rejuvenate, renew and promote the degraded vegetations, protect, restore and reconstruct the degraded ecological environment in desert areas. Further studies are worthwhile to reveal the detailed coupling mechanisms among inorganic ions in SX and LSX species.

CONCLUSIONS AND ECOLOGICAL HINTS

Our results demonstrate that both SX and LSX have the common adaptive characteristics by preferentially absorbing and accumulating inorganic ions rather than organic solutes for drought resistance, and accumulation of higher levels of ions (especially K^+ and Ca^{2+}) and moderate organic solutes is an important drought resistant mechanism for LSX, while the SX do not depend on the accumulation of K^+ and organic solutes to resist to water deficit, and especially accumulating a large quantity of Na^+ and Ca^{2+}, and maintaining the stability of K^+ concentration was one of the main effective strategies to against with arid environments.

The coupling effects of main inorganic nutrients not only play important roles in improving drought resistance of SX *H. ammodendron* and LSX *C. korshinskii*t, but also have important impacts on improving the fertility of barren soil in desert areas. Two better coupling ratios of main inorganic nutrients for SX were as follows: NaCl, NH_4NO_3, $CaCl_2$, $MgCl_2$ and Na_2SiO_3 are 20: 5: 20: 40: 10 or 40: 10: 60: 10:7.5 (g kg^{-1} dry soil), and for LSX were as follows: KNO_3, $CaCl_2$, $MgCl_2$ and K_2SiO_3 are 20: 10: 20: 10: or 40: 20: 60: 5 (g kg^{-1} dry soil). So the finding that the better coupling ratios of inorganic nutrients in SX and LSX species, respectively can be assisted in developing new fertilizers is inspiring and initiates a new viewpoint for deserts plants to improve biomass production and restore and reconstruct the degraded vegetation in arid regions.

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CONFLICT OF INTEREST STATEMENT

We declare that we do not have any commercial or associative interest that represents a conflict of interest in connection with this work.

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Table 1 The orthogonal experimental design of inorganic nutrients in *H. ammodendron* and *C. korshinskii*t

Plant	Level	Factor ($g.kg^{-1}$ dry soil)				
		NaCl	NH_4NO_3	$CaCl_2$	$MgCl_2$	$Na_2SiO_3 .9H_2O$
H. ammodendron	1	0.1	0.05	0.1	0.1	0.025
	2	0.2	0.1	0.2	0.2	0.05
	3	0.4	0.15	0.4	0.4	0.075
	4	0.6	0.2	0.6	0.6	0.1
	5	0.8	0.25	0.8	0.8	0.125

Plant	Level	Factor ($g.kg^{-1}$ dry soil)			
		KNO_3	$CaCl_2$	$MgCl_2$	K_2SiO_3
*C. korshinskii*t	1	0.1	0.1	0.1	0.05
	2	0.2	0.2	0.2	0.075
	3	0.4	0.4	0.4	0.1
	4	0.6	0.6	0.6	0.125
	5	0.8	0.8	0.8	0.15

Table 2 Available Na^+, K^+ (μmol.g^{-1} dry wt.) contents , water content (%) , available Ca^{2+}, Mg^{2+}, Si, N and P (μmol.g^{-1} dry wt.) contents in the root zone soil.

Species	WS (μmol g^{-1})		CU (μmol g^{-1})		Na^+/ K^+	Water content	Ca^{2+}	Mg^{2+}	Si	N	P
	Na^+	K^+	Na^+	K^+							
A. sphaerocephala	3.3±0.3c	5.8±0.2ab	6.1±0.5c	7.6±0.6ab	0.65	1.23±0.08b	1.20±0.10ab	1.72±0.16a	3.41±0.17ab	0.53±0.03ab	0.08±0.03a
C. korshinskii	3.0±0.2c	6.3±0.3a	5.6±0.3cd	8.2±0.4a	0.59	2.19±0.14a	1.25±0.15ab	1.66±0.13ab	3.20±0.26ab	0.60±0.06a	0.07±0.01ab
H. ammodendron	9.4±0.7a	2.7±0.3d	11.6±1.0a	8.6±0.5a	1.95	0.71±0.11d	1.29±0.12a	1.65±0.17ab	3.63±0.29a	0.59±0.02a	0.09±0.01a
Z. xanthoxylum	8.3±0.6ab	3.6±0.5c	10.1±0.7ab	7.7±0.4ab	1.63	1.16±0.09b	1.34±0.16a	1.76±0.20a	3.51±0.20a	0.61±0.03a	0.10±0.02a
N. tangutorum	8.8±0.8ab	3.9±0.2c	9.3±0.6b	8.0±0.7a	1.52	1.04±0.06bc	1.26±0.11ab	1.56±0.15ab	3.71±0.31a	0.54±0.04ab	0.06±0.03ab

Note: WS: water soluble Na^+, K^+ contents (μmol g^{-1}); CU: changeable and unchangeable Na^+, K^+ contents (μmol g^{-1}); Available Na^+ and K^+ = WS+ CU; Values are means ± SD (n = 6). Columns with different letters indicate significant difference at P < 0.05 (Duncan test).

Table 3 Contents of Na^+, Ca^{2+}, K^+, Mg^{2+} and Si (mmol.100 g^{-1} dry wt.) in different tissues.

Species	Tissues	Na^+	Ca^{2+}	K^+	Mg^{2+}	Si
	L	2.53±0.33i	31.46±1.32b	32.16±2.12e	22.30±2.02de	14.32±0.92e
A. sphaerocephala	S	1.82±0.17j	31.21±2.10b	19.36±2.17g	6.31±0.51ij	23.17±1.76bc
	R	2.89±0.41hi	28.81±0.96c	25.31±1.78f	10.25±0.75g	19.13±2.11cd
	L	1.36±0.22k	25.56±1.27d	46.44±3.10cd	26.38±2.16d	10.71±0.97g
C. korshinskii	S	1.48±0.39jk	20.25±1.12e	26.17±2.66f	7.26±0.96i	17.28±1.68d
	R	3.67±0.69h	14.47±0.83	32.26±2.19e	11.33±1.04g	13.25±0.76ef
	PB	296.41±6.38a	78.92±6.38ab	37.21±1.72a	71.97±5.23a	18.26±1.12d
H. ammodendron	PS	40.21±2.30e	57.34±4.11c	17.19±1.17f	44.27±3.19c	20.53±2.03c
	R	45.52±3.03de	66.93±4.29b	12.43±0.88h	21.61±4.41e	25.12±1.92b
	L	172.27±6.10b	88.38±7.26a	28.43±2.20c	42.61±4.23c	21.78±1.76bc
Z. xanthoxylum	S	46.28±2.71de	21.10±2.17fg	18.89±2.10ef	9.70±0.88gh	26.31±1.45b
	R	38.37±1.19ef	48.73±3.63cd	15.23±1.91fg	11.87±1.22g	19.78±1.70cd
	L	193.12±5.11c	45.98±6.05cd	30.22±2.27bc	62.29±5.18b	31.15±2.40a
N. tangutorum	S	49.43±3.36d	66.26±7.19b	22.81±2.52de	13.31±1.22fg	23.97±2.31bc
	R	31.34±1.76g	32.10±3.55e	18.37±1.77ef	15.24±1.48f	27.60±2.52ab

PB: Photosynthesizing branch; S: stem; R: Root; L: Leaf; S: Stem; the same as below. Values are means ± SD (n = 6). Columns with different letters indicate significant difference at P < 0.05 (Duncan test).

Table 4 Contents of free proline (FP), soluble sugars (SS), reducing sugar (RS), N and P (mmol.100 g^{-1} dry wt.) in different tissues.

Species	Tissues	FP	SS	RS	N	P
	L	3.47±0.36ab	6.73±0.76cd	4.32±0.33ab	76.72±7.7de	2.41±0.20bc
A. sphaerocephala	S	2.29±0.21cd	5.21±0.43e	3.06±0.29cd	70.21±6.0e	2.17±0.22cd
	R	1.86±0.43d	10.33±0.79a	3.41±0.34c	63.41±5.1ef	2.01±0.16cd
	L	4.15±0.53a	7.24±0.54c	4.93±0.41a	103.0±9.4c	2.62±0.24bc
C. korshinskii	S	2.54±0.48c	6.33±0.46cd	3.51±0.34c	79.32±8.9de	2.46±0.21c
	R	1.67±0.31e	9.87±0.87ab	4.21±0.27ab	92.27±8.1d	2.26±0.19cd
	PB	0.45±0.03hi	2.77±0.23hi	2.17±0.20ef	97.79±8.7cd	2.50±0.21bc
H. ammodendron	PS	0.19±0.01k	1.96±0.21jk	1.31±0.16gh	90.43±7.9d	2.21±0.23cd
	R	0.27±0.03j	3.57±0.32fg	1.67±0.19fg	88.51±9.1d	2.09±0.18cd
	L	1.07±0.13f	3.02±0.25h	2.43±0.20de	135.0±11.3b	3.72±0.27a
Z. xanthoxylum	S	0.76±0.07g	2.28±0.18j	1.79±0.17f	96.02±9.1cd	2.89±0.31b
	R	0.51±0.05h	4.13±0.30f	2.05±0.18ef	115.52±10.6bc	2.98±0.28b
	L	0.98±0.11fg	3.25±0.22g	2.74±0.16d	155.21±12.2a	2.94±0.21b
N. tangutorum	S	0.32±0.05j	2.14±0.20j	1.53±0.14g	105.84±9.9c	2.79±0.14bc
	R	0.43±0.03hi	3.66±0.27fg	2.27±0.23e	128.39±11.2b	2.04±0.22cd

Values are means ± SD (n = 6). Columns with different letters indicate significant difference at $P < 0.05$ (Duncan test).

Table 5 Total ion contents of Na^{+}, K^{+}, Ca^{2+}, Mg^{2+} and Si (mmol.100 g^{-1} dry wt.), total solutes contents of free proline (FP), soluble sugars (SS), reducing sugar (RS) (mmol.100 g^{-1} dry wt.), and total content of osmoregulators in above-underground parts.

Species	Na^{+}		K^{+}		Ca^{2+}		Mg^{2+}		Si		FP		SS		RS		Total contents		Total
	AP	UP	AP	UP	AP	UP	AP	UP	AP	UP	AP	UP	AP	UP	AP	UP	AP	UP	
A. sphaerocephala	4.35	2.89	51.52	25.31	63.37	28.81	28.61	10.25	37.49	19.13	5.76	1.86	11.94	10.33	7.38	3.41	210.42	101.99	312.4
C. korshinskii	2.84	3.67	72.61	32.26	45.81	14.47	33.64	11.33	27.99	13.25	6.69	1.67	13.57	9.87	8.44	4.21	211.59	90.73	302.3
Average	3.60	3.28	62.07	28.79	54.59	21.64	31.13	10.79	32.74	16.19	6.23	1.77	12.76	10.1	7.91	3.81	211.01	96.36	307.35
H. ammodendron	336.62	45.52	54.4	12.43	136.26	66.93	116.24	21.61	38.79	25.1	0.64	0.27	4.73	3.57	3.48	1.67	691.16	177.1	868.3
Z. xanthoxylum	218.55	38.37	47.32	15.23	109.48	48.73	52.31	11.87	48.09	19.78	1.83	0.51	5.3	4.13	4.22	2.05	487.1	140.67	627.8
N. tangutorum	242.55	31.34	53.03	18.37	112.24	32.1	75.6	15.24	55.12	27.6	1.30	0.43	5.39	3.66	4.27	2.27	549.5	131.03	680.5
Average	265.91	38.41	51.58	15.34	119.33	49.25	81.38	16.24	47.33	24.16	1.26	0.40	5.14	3.79	3.99	2.00	575.92	149.6	725.53

Note: AP: aboveground part; UP; underground part; the same as below.

Table 6 the allocation of inorganic ions, and organic solutes in drought-tolerant species

	Na^{+}	K^{+}	Ca^{2+}	Mg^{2+}	Si	FP	SS	RS	AP/UP
A. sphaerocephala	1.51	2.20	2.04	2.79	1.96	3.10	1.16	2.16	2.06
C. korshinskii	0.77	3.17	2.25	2.97	2.11	4.01	1.37	2.00	2.33
Average	1.14	2.69	2.15	2.88	2.04	3.56	1.27	2.08	2.20
H. ammodendron	7.39	4.38	2.04	5.38	1.55	2.37	1.32	2.08	3.90
Z. xanthoxylum	5.70	3.11	2.25	4.41	2.43	3.59	1.28	2.06	3.46
N. tangutorum	7.74	2.88	3.50	4.96	2.00	3.02	1.47	1.88	4.19
Average	6.94	3.56	2.60	4.92	1.99	2.99	1.36	2.01	3.85

Table 7 The contributions of main inorganic osmotica and organic solutes to drought resistance in drought-tolerant species

Species	Na^{+}		K^{+}		Ca^{2+}		Mg^{2+}		Si		FP		SS		RS	
	AP	UP	AP	UP	AP	UP	AP	UP	AP	UP	AP	UP	AP	UP	AP	UP
A. sphaerocephala	1.4	0.9	16.5	8.1	20.3	9.2	9.1	3.3	12.0	6.1	1.8	0.6	3.8	3.8	2.4	1.1
C. korshinskii	0.9	1.2	24.0	10.7	15.2	4.8	11.1	3.8	9.3	4.4	2.2	0.6	4.5	3.3	2.8	1.4
Average	1.15	1.05	20.25	9.4	17.75	7	10.65	5.25	10.1	3.55	2	0.6	4.15	3.55	2.6	1.25
H. ammodendron	38.8	5.2	6.3	1.4	15.7	7.7	13.4	2.5	4.5	2.9	0.1	0.03	0.5	0. 4	0.4	0.2
Z. xanthoxylum	34.8	6.1	7.5	2.4	17.4	7.8	8.3	1.9	7.7	3.2	0.3	0.1	0.8	0. 7	0.7	0.3
N. tangutorum	35.6	4.6	7.8	2.7	16.5	4.7	11.1	2.2	8.1	4.1	0.2	0.06	0.8	0. 6	0.6	0.3
Average	36.4	5.3	7.2	2.17	16.53	6.73	10.93	2.2	6.77	3.4	0.2	0.06	0.7	0.57	0.57	0.27

Table 8 Plant height (PH), fresh weight (FW), branch numbers (BN) and main root length (MRL) of *H. ammodendron* and *C. korshinskiit* treated with different orthogonal experimental treatments of fertilizers under drought stress

Plant	Treatments	PH (cm)	FW ($g.plant^{-1}$)	BN ($number.plant^{-1}$)	MRL ($cm. plant^{-1}$)
H. ammodendron	C	37.5±2.7b	14.2±1.0b	21.0±1.9a	28.3±1.8d
	C+D	27.4±1.7d	8.9±0.8d	14.2±1.1d	34.1±2.9c
	D+NaCF	34.3±2.0bc	13.0±1.3bc	17.8±1.4c	40.1±2.0b
	D+IN_6-*H*	42.6±2.8a	17.3±1.7a	22.2±1.9a	48.5±3.3a
	D+IN_{12}-*H*	39.7±2.4ab	17.9±1.2a	20.8±2.1ab	47.7±2.7a
	Treatments	PH (cm)	FW ($g.plant^{-1}$)	DW ($g.plant^{-1}$)	MRL ($cm. plant^{-1}$)
*C. korshinskii*t	C	19.8±1.0ab	2.5±0.2ab	0.99±0.06b	26.3±1.3c
	C+D	13.1±0.9c	1.6±0.3c	0.47±0.04c	31.1±1.6b
	D+IN_6-*C*	21.7±1.5a	3.1±0.3a	1.27±0.08a	37.3±2.0a
	D+IN_{12}-*C*	21.1±1.7a	3.0±0.4a	1.14±0.07a	38.5±1.9a

Values are means ± SD (*n* = 5). Columns with different letters indicate significant difference at $P < 0.05$ (Duncan test).

Table 9 Na^+, K^+, Ca^{2+}, Mg^{2+} and Si concentrations of *H. ammodendron* and *C. korshinskiit* treated with different orthogonal experimental treatments of fertilizers under drought stress

Plant	Treatments	Na^+ ($mg.g^{-1}$)	K^+ ($mg.g^{-1}$)	Ca^{2+} ($mg.g^{-1}$)	Mg^{2+} ($mg.g^{-1}$)	Si ($mg.g^{-1}$)
H. ammodendron	C	24.2±2.9d	28.6±3.1a	17.7±1.4d	13.4±1.5c	9.4±0.6d
	C+D	31.6±3.0c	26.1±2.6ab	24.3±2.5bc	14.7±1.8bc	11.3±1.0c
	D+NaCF	47.4±2.1b	22.8±2.8b	26.5±3.7b	17.0±1.7b	14.3±0.9ab
	D+IN_6-*H*	54.0±3.3ab	22.0±2.2bc	34.6±2.0a	23.3±2.0a	15.6±1.3a
	D+IN_{12}-*H*	62.8±2.8a	19.2±1.9c	32.4±2.3a	21.8±1.6a	16.1±1.1a
	Treatments	Na^+ ($mg.g^{-1}$)	K^+ ($mg.g^{-1}$)	Ca^{2+} ($mg.g^{-1}$)	Mg^{2+} ($mg.g^{-1}$)	Si ($mg.g^{-1}$)
*C. korshinskii*t	C	1.3±0.13c	21.7±2.0d	18.9±1.9c	7.6±0.8d	6.8±0.7c
	C+D	2.4±0.20a	30.2±3.1c	25.2±2.2b	10.3±1.1c	10.2±0.7b
	D+IN_6-*C*	2.1±0.15ab	43.7±2.4ab	35.6±2.8a	15.1±1.1b	13.4±1.0a
	D+IN_{12}-*C*	1.9±0.10b	46.9±3.5a	38.1±3.3a	18.2±1.3a	12.2±0.9a

Values are means ± SD (n = 5). Columns with different letters indicate significant difference at $P < 0.05$ (Duncan test).

Table 10 Changes of available (A) Na^+, K^+ , Ca^{2+}, Mg^{2+} and Si concentrations in root zone soil of *H. ammodendron* and *C. korshinskiit* treated with different orthogonal experimental treatments of fertilizers under drought stress

Plant	Treatments	A- Na^+ ($mg.kg^{-1}$)	A- N ($mg.kg^{-1}$)	A- Ca ($mg.kg^{-1}$)	A-Mg ($mg.kg^{-1}$)	A- Si ($mg.kg^{-1}$)
H. ammodendron	C+D	356.3	8.1	57.4	44.9	94.5
	D+NaCF	468.5	11.4	46.4	38.9	86.8
	D+IN_1-*H*	443.9	10.6	98.2	124.5	144.7
	D+IN_2-*H*	590.1	15.5	160.4	62.8	114.3
	Treatments	A- K^+ ($mg.kg^{-1}$)	A- N ($mg.kg^{-1}$)	A- Ca ($mg.kg^{-1}$)	A-Mg ($mg.kg^{-1}$)	A- Si ($mg.kg^{-1}$)
C. korshinskiit	C+D	549.1	7.2	53.2	47.8	90.6
	D+IN_1-*C*	608.6	16.1	89.5	77.9	136.4
	D+IN_2-*C*	654.7	20.9	140.2	168.4	108.1

Supplemental Table S1 The specific combinations of inorganic nutrients of *H. ammodendron* treated with different orthogonal experimental treatments of fertilizers under drought stress

Treatments	NaCl ($g.kg^{-1}$)	NH_4NO_3 ($g.kg^{-1}$)	$CaCl_2$ ($g.kg^{-1}$)	$MgCl_2$ ($g.kg^{-1}$)	$Na_2SiO_3 .9H_2O$ ($g.kg^{-1}$)
CK-C	0	0	0	0	0
C+D	0	0	0	0	0
D+IN_1-*H*	0.1	0.05	0.1	0.1	0.025
D+IN_2-*H*	0.1	0.1	0.2	0.2	0.05
D+IN_3-*H*	0.1	0.15	0.4	0.4	0.075
D+IN_4-*H*	0.1	0.2	0.6	0.6	0.1
D+IN_5-*H*	0.1	0.25	0.8	0.8	0.125
D+IN_6-*H*	0.2	0.05	0.2	0.4	0.1
D+IN_7-*H*	0.2	0.1	0.4	0.6	0.125
D+IN_8-*H*	0.2	0.15	0.6	0.8	0.025
D+IN_9-*H*	0.2	0.2	0.8	0. 1	0.05
D+IN_{10}-*H*	0.2	0.25	0.1	0.2	0.075
D+IN_{11}-*H*	0.4	0.05	0.2	0.8	0.05
D+IN_{12}-*H*	0.4	0.1	0.4	0.1	0.075
D+IN_{13}-*H*	0.4	0.15	0.6	0.2	0.1
D+IN_{14}-*H*	0.4	0.2	0.1	0.4	0.125
D+IN_{15}-*H*	0.4	0.25	0.2	0.6	0.025
D+IN_{16}-*H*	0.6	0.05	0.6	0.2	0.125
D+IN_{17}-*H*	0.6	0.1	0.8	0.4	0.025
D+IN_{18}-*H*	0.6	0.15	0.1	0.6	0.05
D+IN_{19}-*H*	0.6	0.2	0.2	0.8	0.075
D+IN_{20}-*H*	0.6	0.25	0.4	0.1	0.1
D+IN_{21}-*H*	0.8	0.05	0.8	0.6	0.075
D+IN_{22V}	0.8	0.1	0.1	0.8	0.1
D+IN_{23V}	0.8	0.15	0.2	0.1	0.125
D+IN_{24}-*H*	0.8	0.2	0.4	0.2	0.05
D+IN_{25}-*H*	0.8	0.25	0.6	0.4	0.075

Supplemental Table S2 The specific combinations of inorganic nutrients of *C. korshinskiit* treated with different orthogonal experimental treatments of fertilizers under drought stress

Treatments	KNO_3 ($g.kg^{-1}$)	$CaCl_2$ ($g.kg^{-1}$)	$MgCl_2$ ($g.kg^{-1}$)	Na_2SiO_3 ($g.kg^{-1}$)
CK-C	0	0	0	0
C+D	0	0	0	0
D+IN_1-*C*	0.1	0.1	0.1	0.05
D+IN_2-*C*	0.1	0.2	0.2	0.075
D+IN_3-*C*	0.1	0.4	0.4	0.1
D+IN_4-*C*	0.1	0.6	0.6	0.125
D+IN_5-*C*	0.1	0.8	0.8	0.15
D+IN_6-*C*	0.2	0.1	0.2	0.1
D+IN_7-*C*	0.2	0.2	0.4	0.125
D+IN_8-*C*	0.2	0.4	0.6	0.15
D+IN_9-*C*	0.2	0.6	0.8	0.05
D+IN_{10}-*C*	0.2	0.8	0.1	0.075
D+IN_{11}-*C*	0.4	0.1	0.4	0.15
D+IN_{12}-*C*	0.4	0.2	0.6	0.05
D+IN_{13}-*C*	0.4	0.4	0.8	0.075
D+IN_{14}-*C*	0.4	0.6	0.1	0.1
D+IN_{15}-*C*	0.4	0.8	0.2	0.125
D+IN_{16}-*C*	0.6	0.1	0.6	0.075
D+IN_{17}-*C*	0.6	0.2	0.8	0.1
D+IN_{18}-*C*	0.6	0.4	0.1	0.125
D+IN_{19}-*C*	0.6	0.6	0.2	0.15
D+IN_{20}-*C*	0.6	0.8	0.4	0.05
D+IN_{21}-*C*	0.8	0.1	0.8	0.125
D+IN_{22}-*C*	0.8	0.2	0.1	0.15
D+IN_{23}-*C*	0.8	0.4	0.2	0.05
D+IN_{24}-*C*	0.8	0.6	0.4	0.075
D+IN_{25}-*C*	0.8	0.8	0.6	0.1

Supplemental Table. S3 Plant height (PH), fresh weight (FW), branch numbers (BN) and main root length (MRL) of *H. ammodendron* treated with different orthogonal experimental treatments of fertilizers under drought stress. Values are means ± SD (n = 5). Columns with different letters indicate significant difference at $P < 0.05$ (Duncan test).

Plant	Treatments	PH (cm)	FW (g.plant^{-1})	BN (number.plant^{-1})	MRL (cm. plant^{-1})
H. ammodendron	C	37.5±2.7b	14.2±1.0	21.0±1.9ab	28.3±1.8e
	C+D	27.4±1.7e	8.9±0.8	14.2±1.1c	34.1±2.9cd
	D+NaCF	34.3±2.0c	13.0±1.3c	17.8±1.4b	40.1±2.0b
	D+IN$_{1}$-*H*	36.3±2.3bc	15.3±1.1b	19.5±1.9ab	40.5±3.0b
	D+IN$_{2}$-*H*	36.0±2.1bc	15.1±1.0b	20.0±1.4ab	39.5±2.8b
	D+IN$_{3}$-*H*	34.3±2.0c	13.7±1.3c	17.1±1.4b	34.1±2.1cd
	D+IN$_{4}$-*H*	34.0±2.0c	13.1±1.8c	15.3±1.2bc	33.1±2.1cd
	D+IN$_{5}$-*H*	30.0±1.5d	12.1±1.3cd	13.0±1.5cd	27.1±1.9
	D+IN$_{6}$-*H*	**42.6±2.8a**	**17.3±1.7a**	**22.2±1.9a**	**48.5±3.3a**
	D+IN$_{7}$-*H*	39.1±2.0ab	16.3±1.7ab	19.2±1.9ab	42.5±2.2b
	D+IN$_{8}$-*H*	39.4±1.9b	16.0±1.5ab	19.0±1.8ab	40.5±2.9b
	D+IN$_{9}$-*H*	38.0±1.9b	14.3±1.7bc	16.1±1.3bc	36.7±2.5bc
	D+IN$_{10}$-*H*	36.2±1.8bc	12.1±1.7cd	15.0±1.3bc	35.1±2.0c
	D+IN$_{11}$-*H*	39.0±2.0ab	16.7±1.7ab	19.8±1.8ab	41.0±2.2b
	D+IN$_{12}$-*H*	**39.7±2.4ab**	**17.9±1.2a**	**20.8±2.1ab**	**47.7±2.7a**
	D+IN$_{13}$-*H*	37.0±1.6b	14.5±1.8bc	16.8±1.6b	37.7±2.1bc
	D+IN$_{14}$-*H*	35.4±1.5c	14.0±1.4bc	16.1±1.2b	36.3±2.0bc
	D+IN$_{15}$-*H*	32.1±1.0cd	12.3±1.1cd	13.0±1.6cd	33.3±1.8cd
	D+IN$_{16}$-*H*	35.5±1.5c	14.3±1.6bc	16.6±1.8b	39.7±2.0b
	D+IN$_{17}$-*H*	33.1±1.5c	13.1±1.2c	12.6±1.0d	30.1±1.9de
	D+IN$_{18}$-*H*	31.0±1.1cd	12.1±1.0cd	12.0±1.3d	29.5±1.4de
	D+IN$_{19}$-*H*	28.6±1.3de	11.7±0.9d	10.2±1.0d	28.1±1.1e
	D+IN$_{20}$-*H*	26.7±1.7e	11.0±0.7d	9.6±0.6	28.6±1.0e
	D+IN$_{21}$-*H*	33.4±1.3c	12.3±1.2cd	12.1±1.5d	32.6±2.0cd
	D+IN$_{22V}$	30.2±1.2d	11.0±0.9d	10.8±0.7de	28.1±1.7e
	D+IN$_{23V}$	28.1±1.0de	10.1±0.8de	10.0±1.0de	28.5±1.3e
	D+IN$_{24}$-*H*	26.6±1.2e	9.4±0.6e	9.2±0.5e	27.3±1.0ef
	D+IN$_{25}$-*H*	24.4±1.5ef	8.7±0.6ef	9.0±0.3e	26.5±1.7ef

Supplemental Table. S4 Plant height (PH), fresh weight (FW), dry weight (DW) and main root length (MRL) of *C. korshinskiit* treated with different orthogonal experimental treatments of fertilizers under drought stress. Values are means ± SD (n = 5). Columns with different letters indicate significant difference at P < 0.05 (Duncan test).

	Treatments	PH (cm)	FW ($g.plant^{-1}$)	DW ($g.plant^{-1}$)	MRL ($cm.\ plant^{-1}$)
	C	19.8±1.0ab	2.5±0.2b	0.99±0.06c	26.3±1.3d
	C+D	13.1±0.9de	1.6±0.3c	0.47±0.04f	31.1±1.6bc
	D+IN_1-*C*	18.8±1.1b	2.2±0.2b	0.96±0.04bc	32.1±1.6b
	D+IN_2-*C*	18.9±1.3b	2.0±0.3bc	0.89±0.03cd	31.1±1.3bc
	D+IN_3-*C*	18.7±1.2b	2.1±0.2b	0.86±0.04d	31.0±1.3bc
	D+IN_4-*C*	17.7±1.3bc	2.0±0.2b	0.81±0.03de	30.1±1.5bc
	D+IN_5-*C*	16.4±1.2c	1.9±0.2bc	0.77±0.03e	30.9±1.4bc
	D+IN_6-*C*	**21.7±1.5a**	**3.1±0.3a**	**1.27±0.08a**	**37.3±2.0ab**
	D+IN_7-*C*	20.1±1.2ab	2.6±0.2ab	1.11±0.05b	33.4±1.7b
	D+IN_8-*C*	19.8±1.4ab	2.3±0.3b	1.05±0.06b	32.1±1.4b
	D+IN_9-*C*	18.6±1.3b	2.1±0.2b	0.83±0.03d	31.0±1.3bc
	D+IN_{10}-*C*	16.9±1.2bc	1.9±0.2bc	0.79±0.03de	29.2±1.3c
	D+IN_{11}-*C*	19.0±1.0b	2.3±0.2b	0.91±0.06c	32.6±1.5b
*C. korshinskii*t	**D+IN_{12}-*C***	**21.1±1.7a**	**3.0±0.4a**	**1.14±0.07ab**	**38.5±1.9a**
	D+IN_{13}-*C*	20.9±1.3a	2.6±0.2ab	1.12±0.06b	34.7±1.5b
	D+IN_{14}-*C*	19.1±1.2b	2.2±0.3b	0.91±0.07c	32.0±1.9b
	D+IN_{15}-*C*	16.0±1.3c	1.8±0.2bc	0.78±0.04de	28.6±1.5c
	D+IN_{16}-*C*	18.0±1.2b	2.0±0.3b	0.91±0.06c	32.0±1.5b
	D+IN_{17}-*C*	17.5±1.3bc	1.9±0.3bc	0.89±0.08cd	31.1±1.4bc
	D+IN_{18}-*C*	18.3±1.3b	2.2±0.2b	0.94±0.07c	33.7±1.7b
	D+IN_{19}-*C*	14.6±1.4d	1.50±0.3c	0.52±0.08ef	24.1±1.5bc
	D+IN_{20}-*C*	13.8±1.3de	1.45±0.2c	0.40±0.03g	23.2±1.4e
	D+IN_{21}-*C*	19.0±1.3	2.0±0.3bc	0.90±0.06c	30.0±1.7bc
	D+IN_{22}-*C*	18.7±1.4b	1.9±0.2bc	0.90±0.07c	28.7±1.6c
	D+IN_{23}-*C*	16.7±1.5bc	1.6±0.2c	0.69±0.06e	27.7±1.8cd
	D+IN_{24}-*C*	13.4±0.9de	1.5±0.3c	0.47±0.03f	25.3±1.2d
	D+IN_{25}-*C*	12.2±0.9e	1.3±0.3c	0.39±0.04g	24.3±1.3de