Trade-off strategy of leaf functional traits of desert halophyte Lycium ruthenicum in the lower reaches of Heihe River, Northwest China: response to soil moisture and salinity

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Abstract

Abstract Background: Understanding salinity resistance and water utilization on shrub species is a challenge to the management and conservation of desert halophytes. Lycium ruthenicum Murr.with a significant soil and water conservation capacity, is one of the dominant shrubs and halophytes in the lower reaches of the Heihe River, Northwest China. In this paper, the effects of two depths (0-40 and 40-80 cm) of soil salinities and water contents on the leaf functional traits of eight L. ruthenicum communities in different distances from the main channel were studied. Fourteen leaf water physiological and ecological stoichiometric traits were investigated, linking with soil factors to explain desert plant trade-off strategies. Results: Specific leaf volume (SLV), specific leaf area (SLA), leaf thickness (LT), nitrogen (N), C:N, C:P could serve as good indicators of drought and saline resistance. Low N, specific leaf area (SLA) indicated that the plant was located at the slow investment-return axis of the species resource utilization. Low C:N, C:P showed that L. ruthenicum had a defensive life history strategy at drought and salinity areas. The RDA results showed that 0-40 and 40-80 cm soil properties respectively explained 93.45% and 99.96% leaf traits variation. Soil water contents, HCO3- had extremely positive correlation (P<0.01) with leaf functional traits. Shallow soil water contents significantly affects P, and deeper soil water contents significantly responds C and N; shallow soil salinity significantly affected LT, C and N contents, whereas deeper soil salinity significantly affected N and SLV. Conclusions: L. ruthenicum had a foliar resource acquisition and resource conservation trade-off with a defensive life history strategy in the area of drought and salinity. This finding provides baseline information to facilitate the management and restoration of arid-saline desert ecosystem.

Background

Green leaves collect and store nutrients to become the basis of terrestrial ecosystem function. Through many people's discussion, functional traits are defined as measurable morphological, physiological, and phenological properties that are related to individual adaptation [1], these three classification traits accordingly include specific leaf area (SLA), specific leaf volume (SLV), photosynthetic rate, plant height, seed mass, etc. Plant functional traits are a hot topic in current ecological research, aiming to clearly link the phenotypes and physiological changes of individual plants to ecosystem processes and services [2-3]. In the analysis of functional features that are easy to measure, two major trade-offs are immediately identified [4-5]. One of the trade-offs is explained by the fact that leaves with contrasting features promote rapid access to nutrients in fertile habitats while protecting resources in non-productive habitats [4]. The well-known "leaf economics spectrum" described trade-offs based on carbon, nutrients and discovered a trade-off between the quick and slow return of investments of nutrients and dry mass operating independently of biome, growth form or plant functional type [6]. Wherein leaves with higher nitrogen content tend to be lower leaf mass per unit area and short leaf life span, larger A_{max} (the maximum rate of photosynthesis per unit of leaf mass) tends to be shorter leaf life span [6], other suites of related traits have been recognized that may indicate physical or physiological trade-offs [3]. Ecological stoichiometry is a comprehensive method for managing quality balances and provides a new perspective for understanding ecosystem process from the individual organism to the ecosystem level [7-9]. The key chemical components required for organisms, especially those structure and nutrients element: carbon (C), nitrogen (N) and phosphorus (P). Gven the importance of understanding the elemental components and biogeochemical cycles coupled with phenotypic plasticity driven by component patterns found in terrestrial ecosystems, analyses of C:N:P ratios are increasing [10-14]. Previous studies showed that $C:N$ ratios were constrained by variation among different functional groups and scaled N with respect to C content in foliage [11,13]. In addition, the ratio of C:N and C:P indicates the ability of plants to assimilate C while simultaneously absorbing N and P. Comparatively, the ratio of $N:P$ can reflect a dynamic balance between soil nutrients and plant nutrition demands [10,15]. Over the past decade, distribution patterns of C, N, and P in plant leaves at global or regional scales as well as environmental factor relationship research has received widespread attention [12,13,16]. Recent studies tend to explain the temporal and spatial variability of plant functional traits under adverse (salinity, drought and frost stress) conditions [17-21].

Among many soil characteristics, salinity and moisture are important conditions affecting plant growth [22]. In arid environments, drought exerts a strongly selective pressure on morphological-chemical traits and plant life histories [1,4,23]. Salinity is one of the major environmental factors limiting plant growth, development, productivity and distribution pattern [24-26]. Excessive accumulation of salt in the soil imposes physiological limitations on plants, including osmotic stress, ion imbalance, oxidative stress and photosynthesis, thereby affecting plant growth [27-29]. This situation is exacerbated by the impact of human over-exploitation on land and the initial lack of water in the desert-oasis eco-interlaced zone in arid and semi-arid regions [30]. Severe water and salinity stress decreases a plant growth rate, leaf area, biomass accumulation [31]. However previous studies have suggested that appropriate saline conditions can enhance biological C fixation of halophytes [32]. Another stoichiometrical research in an oasis-desert also indicated that soil conductivity was highly positively correlated with leaf C, N contents [20]. But there was a significant negative correlation between leaf P content and soil salt, conversely, a positive correlation was found between the ratios of leaf $C:P$, $N:P$ and soil salt [33]. The regression analyses for three functional groups along salinity gradients indicated that the salinity decreases leaf $C:N$, and increases $N:P$, but salinity was not the driver of leaf C:N:P stoichiometry in halophytes [24]. In summary, plants responses to stress have attracted much attention possibly due to the ecosystem degradation over the past decades. However, the adaptive strategy and tolerance of *L.ruthenicum* to drought and salinity stresses is not well understood.

Many studies have shown that *L. ruthenicum* is an important medicinal desert halophyte in the arid and saline land [34]. In addition to their nutritive values, *L. ruthenicum* can adapt to high salinity and drought through morphology adjustments in both carbon assimilation and metabolism, and can be a colony species with defensive functions on desert saline-alkali land [35]. It can prevent soil desertification and reduce the salinity and alkalinity through the special physiological characteristics of stress environment [36]. Therefore, it is of great significance to study the functional traits of *L. ruthenicum* in the desert saline-alkali region where plant species diversity is lacking. In this paper, we measured the leaf water physiological and ecological stoichiometry traits of *L. ruthenicum* and different depths of soil salinity and water contents, selected an approximately 17 km long north-south transect of eight *L. ruthenicum* communities living under different salinity and moisture regimes from the lower reaches of the Heihe River of China. The objective of the present study was to explore: (1) Trade-off strategies between leaf functional traits under salinity and drought stress habitats; (2) What are the relationships between leaf functional traits and soil factors? ; And (3) Find major environmental factors that affect plant traits.

Methods

Study site

The Heihe River is an inland river located in an extremely arid and fragile ecological environment in northwestern China. The desert ecosystem extends from the upstream to the downstream, with unique ecological structures and plant communities, dominated by shrubs [37]. The Ejina desert area is located in the lower reaches of the Heihe River Basin. According to the data of Ejinaqi Weather Station from 1957 to 2011, the annual average temperature is 8.77°C, the relative humidity is 33.9%, the annual precipitation is 37.40 mm, and the annual evaporation is 3390. 26 mm. In the environment with rare precipitation, the water supply in the Ejina desert area mainly comes from the Heihe River Basin, and the riverside vegetation is mainly assembled by shrubs and grasses. Shrubs are mainly *Tamarix chinensis* followed by *Lycium ruthenicum*, *Nitraria tangutorum* and *Alhagi sparsifolia* [38]. In Ejina desert, the plant species are poor, and the vegetation types are mainly dry and salt-tolerant desert plants, mainly distributed in the Heihe River and the lake plains of Ejina Banner. The soil types of the entire Heihe River series include brown calcium, desert calcium, meadows, salt and sand [37].

Sampling protocol and community characteristics

This study was conducted in early August 2017 within a 17 km long north−south transect in the lower reaches of the Heihe River Basin. Study area was flat and far from the village. We Selected 8 different communities of moisture and salinity conditions from the near to the far from the main river channel. Main distribution areas of plots and different plant habitat types were shown in Table 1. Three quadrats (5×5 m) were established within each selected community and their geographic information (latitude, longitude), desert types and plant community structure were investigated by GPS eXplorist 510 (Magellan, USA). Sunny side and fully expanded mature leaves (n>30) were collected from 15 individuals of each *L. ruthenicum* communities, and all foliage sampled from 3 squares were combined into a mixed sample.

Determination of leaf water physiological and stoichiometric traits

The caliper with an accuracy of 0.02 mm was used to measure the thickness of the upper, middle and lower sides of the leaf (*LT*, mm). The leaf area was determined by a combination of a scanner (EPSON DS-1610) and ImageJ software [39]. The specific leaf area (*SLA*, leaf area per unit dry mass), the specific leaf volume (*SLV*, leaf volume per unit dry mass) was determined by a drainage method using a 10 mL cylinder, leaf dry matter content (*LDMC*, leaf dry mass per unit fresh mass), relative water content (*RWC*, %). Total leaf water content (*TWC*, %), degree of the leaf succulence measured by saturation fresh weight minus dry weight divided by surface area (*Suc*, g·cm^{-2}), leaf tissue density (the ratio of leaf dry weight to volume, *LD*, g·cm^{-3}). Since the leaves dehydrate after leaving the branches, the *LT*, *SLA*, and *SLV* properties were all completed in the field, and then samples were taken back to the laboratory dried at 80 °C for 48h to constant weight as well as other traits. Dried leaves were ground to a 0.15 mm powder using a sample pulverizer to measure the carbon (*C*), nitrogen (*N*) and phosphorus (*P*) contents, and calculate the stoichiometric ratio. *C* content was determined using the $K_2Cr_2O_7$-H_2SO_4 external heating method in oil bath, *N* content was determined by the Semi-automatic Kjeldahl procedure, which involves digestion with concentrated H_2SO_4 followed by measurement of NH_3 on an auto analyzer (Hanon K9840, Jinan, China), and leaf *P* was digested by H_2SO_4-H_2O_2 and then measured by the molybdenum antimony method.

Measurement of soil moisture, salinity and ion contents

Soil was collected at 0-40 and 40-80 cm depths of 8 plant communities. We collected soil samples without rain within 7-10 days. The samples were first passed through a 2 mm screen to remove roots and other impurities, and then dried at 80 °C for moisture content analysis. Electrical conductivity (EC) measured using a DDS-307a portable conductivity meter (Leici Instrument, Shanghai, China). We have previously established a standard curve between the soil salinity and electrical conductivity of saline-alkaline soil in the study area as y = 217.73 x - 22.723, R^2 = 0.994, and the unit of soil salinity is g·kg^{-1}. Soil samples were analyzed within 20 days of collection for carbonate (CO_3^{2-}), bicarbonate (HCO_3^-), chloride (Cl^-), sulfate (SO_4^{2-}), sodium (Na^+), potassium (K^+), calcium (Ca^{2+}) and magnesium (Mg^{2+}) following methods described by the US Salinity Laboratory Staff [40].

Statistical analysis

All one-way analysis of variance (ANOVA) used by the SPSS 19.0 software. In order to distinguish the effects of different *L. ruthenicum* habitats on functional traits, tukey-HSD multiple range tests were performed at a significant level of $P \leq 0.05$. The Shapiro-Wilk test was performed to check for normality. CANOCO (version 4.5) was used for redundancy analysis to determine the effect of environmental gradients on plant functional traits. The Monte Carlo tests based on random permutations were conducted to test the significance of the Eigen values of the first canonical axis and all axes. Monte Carlo permutation test was used in each step and the significant difference level was 0.05. Relationships between different plant functional traits were performed, using the Performance Analytics package of R statistical software [41].

Results

Characteristic of the leaf functional traits in different communities of *L. ruthenicum*

In this study, we measured 14 leaf functional traits (Table 2). Among them, leaf water physiology traits *TWC*, *RWC*, *SLA*, *SLV*, *LT*, *LDMC*, *Suc*, *LD* were 79.35-88.37%, 70.41-137.35%, 0.005-0.008 cm^2▪mg^{-1}, 5.36-12.80 cm^3▪g^{-1}, 1.02-1.62 mm, 125.0-197.9 mg▪g^{-1}, 0.80-1.38 g▪cm^{-2}, 0.08-0.19 g▪cm^{-3}, respectively. Leaf ecological stoichiometry traits *C*, *N*, *P* were 307.39-351.78, 8.09-17.82, 0.62-5.77 mg▪g^{-1}, and *C:N*, *C:P* and *N:P* ratios were 20.28-37.97, 56.85-415.44, 2.79-17.70, respectively.

In eight different moisture and salinity environment sites (Table 1), we compared the differences between *L. ruthenicum* functional traits and found that larger leaf thickness appeared in severe saline site Ⅷ, significantly different from moderately saline Gobi siteⅦand low saline site Ⅰ with lower leaf thickness (Table 2).

In addition, the largest *SLV*, *Suc*, *TWC* and *RWC* were also observed to appear in severe saline sites (Site Ⅰ and Ⅴ). Conversely, *LDMC*, *LD*, and *N* contents had the lowest values in heavy saline areas. Leaf *N* concentration was the least variable in different regions, but it still showed the effect of heavy saline on *L. ruthenicum* stress, and leaf *C* content was significantly lower. Different degrees of drought stress (eight different soil moisture sites) had significant effects on leaf *P* content (Fig.2), statistical analysis showed that the ratio of *N:P* was more stable than *C:N* and *C:P* adaptation to drought-salt stress. Moreover, we found that there was no significant difference in the *SLA* trait values between eight different habitats, meaning that intra-specific variation in *SLA* at our finer ecological scale was minimal or non-existent.

Correlation between leaf functional traits of *L. ruthenicum* in different habitats

Correlation coefficient between 14 leaf traits of *L. ruthenicum* and significant different results showed (Fig.1) that *LT* was significantly positively correlated with *Suc* (r=0.58, *P*<0.05), on the contrary, extremely significantly negatively correlated with *C* (r=-0.81, *P*<0.001). *SLV* was highly positively correlated with *SLA* (r=0.74, *P*<0.01), both are significantly negatively(r=-0.95, *P*<0.001 and r=-0.68, *P*<0.01 respectively) correlated with *LD* and significantly positively correlated with *TWC* (r=0.81, *P*<0.001 and r=0.57, *P*<0.05 respectively). *LDMC* was significantly positively correlated with *LD* (r=0.89, *P*<0.001), both of which were significantly negatively correlated with *TWC* (r=-0.95, *P*<0.001 and r=-0.84, *P*<0.001 respectively). *Suc* was significantly positively correlated with *TWC*, *RWC*, *P*, respectively (Fig.1), but it was significantly negatively correlated with *C* (r=-0.85, *P*<0.001). *TWC* was significantly positively correlated with *P* contents (r=0.53, *P*<0.05), the latter with *N:P* and *C:P* were significantly negatively correlated (r=-0.76, r=-0.86, *P*<0.001), and *N:P*, *C:P* was significantly positively correlated (r=0.94, *P*<0.001). *RWC* was highly negatively correlated with *N:P* and *C:P* (r=-0.56, r=-0.62, *P*<0.05).

RDA restriction ordering of functional traits in soil water and salinity

In view of the significant effect of salinity on plant growth, we were not only interested in the effects of total soil salinity on leaf functional traits, but also on the exploration of which salt ions mainly affect plant functional trait formation and variation. The RDA results showed that soil water contents and HCO_3^- had an extremely correlation with leaf functional traits, 0－40 cm (Fig.2a) and 40-80 cm soil properties (Fig.2b) respectively explained 93.45% and 99.96% leaf traits variation (the sum of the first two axes explained). Permutation tests for all canonical axes were significant (*P*<0.01, Table 3). This suggested that models using these environmental factors can explain well the functional trait variation. In general, in the 0-40 cm soil layer, soil water contents significantly affected leaf *N:P*, *C:P*, *P* contents and *RWC* (Table 3, *P*=0.002, Fig.2a). Leaf *N:P* and *C:P* ratios are positively correlated with 0－40 cm soil water contents, while leaf *P* contents and *RWC* was negatively correlated with soil water contents. However, soil salinity significantly affected leaf *LT*, *C*, *N* contents and *C:N* ratio, and positively with *LT*, *C:N*, negatively with leaf *C* and *N* contents. In 40-80 cm soil layer, HCO_3^- significantly influenced leaf functional traits (Table 3), soil water contents significantly reduced leaf *C* and *N* contents, but highly positively with *C:N* (Fig.2b), while soil salinity only significantly reduced the leaf *N* contents and highly positively with *C:N,* leaf morphological trait *SLV*. The spatial distribution of the eight community types may be driven by variation in soil chemical characteristics. Communities I, II and VII are close to each other due to their similar soil chemistry, as are VI and III, IV communities being close to each other. However, the V and VIII communities are located away from other communities, so their soil properties may differ from other locations. The Eigen values and total cumulative variance of RDA axes 1 and 2 are also high, indicating that species data are strongly correlated with measured environmental variables (Table 3).

Discussion

Variations of *L. ruthenicum* leaf functional traits in the lower reaches of *Heihe River*

In the long process of evolution, plants interact with the environment and gradually form adaptation strategies for internal physiology and external morphology to minimize the adverse effects of the environment. For example, leaf succulent, the so-called succulent plant refers to the proliferation of parenchyma cells in organs such as leaves and stems, the increase in the number of cells, the increase in volume, and the absorption and storage of large amounts of water, resulting in a significant increase in water content per unit weight or volume of tissue. These adapting plants to a phenomenon of poor environment and intra-plant traits vary with the environment, makes the plant can survive in a new environment [42]. This study showed that the desert halophyte *L. ruthenicum* was characterized by low leaf *SLA*, *LDMC*, *C*, *N* and *N:P* levels, high *LT*, *Suc*, *P content* and *C:N* performance. *SLA* is one of the key leaf traits of plant carbon uptake strategy [43], it can reflect the distribution of plants and their adaptation to habitats [44]. *LDMC* mainly reflects the ability of plants to retain nutrients [45]. In addition, *SLA* and *LDMC* are the best variables for classifying plant species on the plant resource utilization classification axis [6]. This paper showed that *L. ruthenicum* was a resource reservation species for its low *SLA*, *N* content yet high *C:N*, this also indicated that *L. ruthenicum* is in "slow-return" end of the spectrum: Plants that invest in high LMA have a slower photosynthetic rate, but the leaf life is longer, so their slower income (carbon absorption) rate can be compensated by a longer income stream [6,46]. Furthermore, *SLA* and *LDMC* are two important soil-fertility predictors as well as leaf *N*, *P* nutrient contents and *N:P* [15,47-49]. The combination of these predictors indicates that soil fertility is lacking in the Ejina desert area in the lower reaches of Heihe River and the growth of *L. ruthenicum* is mainly restricted by *N*. Prior studies that have noted the importance of *C:N* and *C:P* ratios can effectively reflect the balance between competitive and defensive strategies [33]. When *N* and *P* contents were high, *C:N* and *C:P* ratios were comparatively low. Plants will apply competitive strategies at high photosynthetic rates. Conversely, when *C* content was high, *C:N* and *C:P* ratios were high. This moment plants adopted a strong defensive strategy under low photosynthetic rates [50-51], The results of this study indicated that *L. ruthenicum* had a defensive strategy under desert saline habitats. Leaf thickness (*LT*) is generally considered to be a very important leaf trait characteristic, which may be related to leaf life span, stress tolerance, and litter decomposition rate [52-53]. Osmond et al [54] found that plant leaves are thicker in nutrient-poor environments. This article *LT* pattern was consistent with previous researches. In order to adapt to the poor environment, the succulent plants proliferate in a large number of parenchyma cells, such as leaves and stems. In eight different habitats, *L. ruthenicum* showed a significant succulence (*Suc*) used to store moisture in arid less rainfall environments of Ejina desert areas. Eight *L. ruthenicum* communities had higher *P* content, may suggest that local minerals decompose faster meanwhile ensure that enough young leaves

are produced to reduce the persecution of salt toxic ions in the soil. The leaves of *L. ruthenicum* belong to succulent foliage, and the higher the water content (*TWC*) of the succulent plant, the stronger the degree of tolerance to water stress and the more drought-tolerant [55]. *SLV* is an important leaf trait introduced according to the leaf characteristics of desert plants. *RWC* reflects the resistance of plants to dehydration. The higher *RWC* leads to stronger resistance to dehydration and leaves have higher osmotic adjustment function.

Trade-off strategies among functional traits of *L. ruthenicum*

The existence of a fundamental trade-off between the rapid acquisition and the efficient conservation of resources has been discussed in the ecological literature for more than forty years [56]. However, it is only over the course of the last two decades that the availability of large data sets has allowed for its precise quantification and for the identification of the trait syndromes that can be used to characterize trade-offs for a wide variety of plants [4,6,57]. Those strategies that have been proven include: Species with small SLA have thicker leaves or denser tissues [58], have been explained to allow maintenance of leaf function or delayed leaf death under very dry conditions [6]. Some fundamental relationships found in leaf economics spectrum work: A significantly positive correlation was found between *LT* and *Suc*, which confirmed that succulent plant water conservation strategy[52]. While a significantly negative correlation was found between *LT* and *C* content, this is related to the thicker *LT* causing a decrease in the specific leaf area and thus affecting carbon acquisition [59]. *SLA* is a combination of leaf tissue density (*LD*) and leaf thickness (*LT*): leaf tissue density is significantly positively correlated with leaf dry matter content (*LDMC*), leading to the equation: $SLA = 1/(LD \times LT) \approx 1/(LDMC \times LT)$ [59]. This paper did not show a significant relationship between *SLA* and *LT*, but proved that *SLA* has a strongly negative correlation with *LDMC* and *LD*, the significantly negative correlation of *LT and C* as well as *SLA* (*SLV*) *and LD* (*LDMC*) indicated a trade-off between resource acquisition and resource conservation under drought and saline environment. *LDMC* and *LD* are positively correlated, both of which were significantly negatively correlated with *TWC*. Negative correlation of *TWC*, *RWC* and *LDMC* expressed as another trade-off between the intracellular water content and nutrient accumulation due to photosynthesis. Leaf water content is a useful indicator of plant water balance, *Suc* was significantly positively correlated with *TWC*, *RWC* and *P* content, but strongly negatively correlated with *C*. This study confirms that leaf succulence can improve the energy returns from leaf investment by replacing expensive *C* structures with water [60].

Does soil moisture and salinity affect plant functional traits?

In contrast to significant trait correlation patterns, there were only a few significant changes in the leaf morphological traits and *C:N:P* stoichiometry of desert halophytes with different salinity and moisture habitats. The distribution of salt in different soil layers might explain these results. In this paper, shallow soil layer (0-40 cm) water content significantly affected leaf *P* content but not *C* and *N* contents, also significantly affected leaf *N:P*, *C:P* because of higher leaf *P* content, this result supports evidence from previous observations[61], the effect of shallow soil moisture on leaf stoichiometry may be interpreted as rich applicability of soil *N*, while *P* nutrient element is unstable. In addition, shallow soil layer water content significantly affected the leaf *RWC* trait at the negative direction, and shallow soil water significantly promoted the leaf *C:P* ratio showed *L. ruthenicum* had a defensive life strategy. However, soil salinity significantly affected leaf *LT*, *C*, *N* contents and *C:N* ratio, positively with *LT*, *C:N*, negatively with leaf *C* and *N* contents. This may be a morphological and physiological evolutionary strategy for plants to cope with salt stress. In the deeper soil layer (40-80 cm), HCO_3^- significantly influenced leaf functional traits, deeper soil layer water contents significantly reduced leaf *C* and *N* contents, highly positively with *C:N*, but not obviously influenced leaf *P* content and other functional traits, while soil salinity only significantly reduced leaf *N* contents and highly positively with *C:N* and leaf morphological trait *SLV*. Thus, the hydraulic properties required for plant safety at high salinity are at the expense of lower growth rates [62]. In general, salt stress causes the normal growth of plants to be inhibited to varying degrees, mainly because salt stress inhibits plant photosynthesis by reducing soil water potential and reducing leaf stomatal conductance [63-64]. Therefore, the fixed *C* ability of the blade will also be reduced significant, this was consistent with the low leaf *C* phenomenon in this study. Many studies have confirmed that under salt stress, especially the higher Cl^- content in the soil will inhibit the plant's absorption of NO_3^-, so the NO_3^- content in the leaves of the plants will decrease [65-66], from this point of view, the *N* content of halophytes decreases as well as the *C* content. However, some other studies have shown that the *N* content of succulent plants becomes larger as the salinity increases [24], this controversy will require more research in the future to prove.

Salt stress limits the growth of halophytes through adverse effects on various physiological and biochemical processes. Conversely, halophytes shows a response to increased salinity by diversity growth [28]. Salinisation consists of an accumulation of water soluble salts in the soil that include the ions of K^+, Mg^{2+}, Ca^{2+}, Cl^-, SO_4^{2-}, CO_3^{2-}, HCO_3^- and Na^+. We tried to analysis this process with salt ions of different depths of soil. The RDA results showed that SWC, HCO_3^-, Cl^{-1} and CO_3^{2-} can explain the variation of functional traits well. Surprisingly, Na^+ was not in this rank. Because the importance of Cl^- and Na^+ has been mentioned in much salinity stress studies[67-69]. It was found that Na^+ is more effective than K^+ and Cl^- in cell swelling, leaf succulence and shoot development[70]. According to our knowledge, the soluble salt in the lower reaches of the *Heihe River Basin* dominated by Na^+, HCO_3^-, SO_4^{2-} and Ca^{2+} [71], the above study may explain the results of our soil ion effects on functional traits.

Conclusion

This study found that the patterns of leaf functional traits in arid desert halophyte *L. ruthenicum* in arid and saline environments have a tendency of low leaf *SLA*, *LDMC*, *C*, *N* and *N:P* levels, but high *LT*, *Suc*, *P content* and *C:N* performance, and leaf average *N:P*<14. Our findings are as follows: (1) The ratio of leaf *N:P* was more stable than *C:N* and *C:P* adaptation to drought-salt stress. There was no significant difference in average *SLA* trait values between eight different habitats, indicating that intra-specific variation in *SLA* at a finer ecological scale was minimal or non-existent. (2) Resource acquisition and resource conservation trade-off; (3) Shallow soil moisture significantly affects leaf *P*, and deep soil moisture significantly responds leaf *C* and *N*; Shallow soil salinity significantly affected *LT*, *C* and *N* contents, whereas deep soil salinity significantly affected leaf *N* and *SLV*. HCO_3^- and soil water contents have significant effects on leaf functional traits. (4) Given that these remarkable features we recommend *L. ruthenicum* had a defensive life history strategy at drought and

salinity areas. Although this paper proved to some extent the effect of soil water and salt on functional traits, however, other larger scale studies are needed to determine the drivers of functional characteristics.

Abbreviations

LT: leaf thickness (mm); *SLA*: specific leaf area (cm^2■ mg^{-1}); *SLV*: specific of leaf volume(cm^3■ g^{-1}); *LDMC*: leaf dry matter content (mg■g^{-1}); *Suc*: leaaf Sucuulent (g■cm^{-2}); *LD*: leaf tissue density (g■cm^{-3}); *TWC*: Total water content(%); *RWC*: relative water content(%); *C*: leaf carbon content(mg■g^{-1}); *N*: leaf nitrogen content(mg■g^{-1}); *P*: leaf phosphrous content(mg■g^{-1}); *N:P, C:N, C:P*: the ratios of *C, N* and *P*.

Declarations

Authors' contributions

SJL conceived and designed the experiments, revised the first draft; WG analyzed the data and wrote draft; HW and WG performed experiments; GQW and PXS guided writing and participated in the survey. All authors read and approved the final manuscript.

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Availability of data and materials

The data sets supporting the results are included within the article and additional file 1.

Competing interests

The authors declare that they have no competing interests.

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Ethics approval and consent to participate

There was no requirement to seek ethical approval to carry out the work described above.

Consent for publication

Not applicable.

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Tables

Table 1 Distribution of sampling points of different moisture and salinity habitats of *Lycium ruthenicum* communities in the lower reaches of the Heihe River

No.	Desert types of plots	Longitude	Latitude	Dominance index	Evenness index	0-40 cm Soil Moisture (%)	0-40 cm Soil Salinity(g·kg⁻¹)	40-80 cm Soil Moisture (%)	40-80cm Soil Salinity (g·kg⁻¹)
⬜	Moderately saline Gobi	101°01′0.6″	42°02′9.4″	0.70±0.18bc	0.54±0.28ab	1.60±0.37b	3.09±0.44bc	1.77±0.24d	0.83±0.37c
⬜	Extremely heavy saline Gobi	101°01′42.4″	42°02′7.8″	0.66±0.24bcd	0.55±0.36ab	4.33±1.61ab	12.29±1.69abc	8.99±7.12bcd	2.67±1.64c
⬜	Extremely heavy saline desert	101°03′13.9″	42°01′28.3″	0.51±0.13d	0.66±0.13ab	10.21±3.94a	13.84±2.87abc	4.45±1.34cd	1.93±0.67c
⬜	Extremely heavy saline desert	101°02′42.0″	42°03′11.8″	0.86±0.21a	0.27±0.37cd	14.60±3.20a	11.34±1.49abc	14.15±1.98ab	1.28±0.26c
⬜	Extremely heavy saline desert	101°02′27.5″	42°03′8.0″	0.66±0.14bcd	0.69±0.20ab	16.68±11.4a	34.12±0.76a	11.04±4.67abc	7.15±1.16b
⬜	Slightly saline desert	101°16′59.3″	42°02′17.8″	0.80±0.09ab	0.51±0.17bc	15.51±3.85a	1.94±0.35c	3.49±0.14cd	0.69±0.01c
⬜	Extremely heavy saline desert	101°00′52.5″	42°06′56.8″	0.94±0.11a	0.16±0.26d	4.67±2.23ab	27.39±4.41ab	6.46±3.86bcd	2.67±0.33c
⬜	Extremely heavy saline desert	101°00′3.7″	42°06′52.0″	0.63±0.09cd	0.80±0.15a	7.96±4.26ab	42.24±1.01a	19±0.39a	15.6±0.80a

Soil moisture and salinity are divided into (0-40 cm) and (40-80 cm) data. Comparison of habitat characteristics of different *L. ruthenicum* communities by one-way analysis of variance. Different lowercase letters represent significant differences ($P<0.05$). According to the literature (USSL Staff 1954), the degree of soil salinization was divided into three categories (slightly, moderately, extremely heavy saline).

Table 2 Leaf functional traits of different *L. ruthenicum* communities (Mean ±SD, n=3)

No.	LT	SLV	SLA	LDMC	Suc	LD	TWC	RWC	C	N	P	N:P	C:N	C:P
⬜	1.03±0.01c	6.69±0.47bc	0.007±0.43ns	141.5±13.4ab	0.83±0.03b	0.15±0.01ab	83.15±0.01cd	81.32±0.01b	347.5±0.42a	13.57±0.06c	3.98±0.16b	3.42±0.16b	25.79±0.42c	84.97±4.05
⬜	1.14±0.10bc	7.00±0.67bc	0.006±0.47ns	147.5±5.1ab	0.99±0.04ab	0.14±0.01ab	82.0±0.01cd	78.85±0.03c	337.8±0.29a	14.84±0.43b	3.09±0.00b	4.80±0.14ab	23.34±0.89d	107.48±2.5
⬜	1.26±0.00abc	8.40±1.40abc	0.006±1.11ns	144.7±11.3ab	0.89±0.07b	0.12±0.02bc	82.26±0.01cd	78.46±0.02c	342.4±0.29a	16.92±0.89a	1.53±0.91c	17.70±11.13a	20.28±0.74e	435.75±25
⬜	1.36±0.01ab	7.81±0.19abc	0.005±0.10ns	125.0±1.7abc	1.03±0.03ab	0.13±0.00bc	83.13±0.00cd	70.41±0.00c	324.1±0.12b	13.04±0.04c	1.01±0.14c	13.16±1.76ab	26.16±1.85c	335.3±11.2
⬜	1.26±0.23abc	5.74±0.38c	0.005±0.54ns	197.9±21.0a	0.90±0.04b	0.17±0.01a	79.35±0.02d	94.81±0.00c	337.6±0.16a	9.93±0.04d	0.81±0.00c	12.22±0.00ab	34.34±0.48b	414.1±1.8a
⬜	1.24±0.02bc	7.38±0.13bc	0.007±0.12ns	137.9±2.2abc	0.87±0.03b	0.14±0.00abc	84.91±0.00bc	90.0±0.00c	341.3±0.04a	15.07±0.27b	1.54±0.11c	9.87±0.90ab	22.66±0.35d	223.3±13.1
⬜	1.58±0.05a	9.14±0.64ab	0.006±0.24ns	153.1±7.5bc	1.24±0.14a	0.11±0.01bc	88.37±0.01ab	137.35±0.02a	308.6±0.12c	15.15±0.17b	5.45±0.32a	2.79 ±0.20b	20.56±0.30e	58.05±1.1c
⬜	1.37±0.01ab	10.90±1.90a	0.008±1.48ns	151.5±8.5c	1.03±0.10ab	0.09±0.02c	87.95±0.01a	130.36±0.01b	319.9±0.54b	8.43±0.34e	2.87±0.00b	2.94 ±0.12b	38.54±1.07a	112.3±0.7c

Multiple comparisons of traits between different communities using the tukey-HSD method, Different letters represent significant differences($P<0.05$), ns means no difference. *LT*: leaf thickness (mm), *SLA*: specific leaf area (cm²· mg⁻¹), *SLV*: specific of leaf volume(cm³· g⁻¹), *LDMC*: leaf dry matter content (mg·g⁻¹); *Suc*: leaaf Sucuulent (g·cm⁻²), *LD*: leaf tissue density (g·cm⁻³), *TWC*: Total water content(%), *RWC*: relative water content(%), *C*: leaf carbon content(mg·g⁻¹), *N*: leaf nitrogen content(mg·g⁻¹), *P*: leaf phosphrous content(mg·g⁻¹), *N:P, C:N, C:P*: the ratios of *C, N* and *P*

Table 3 Ordination of the 14 functional traits, according to two depths of soil moistures, salinity and eight ions, along the first two axes of a redundancy analysis

Parameters	Explanation %				F	P
	Axis1	Axis2	Axis3	Axis4		
0-40cm soil ions, salinity and water content						
SO_4^{2-}		5.7			0.84	0.40
Cl^{-1}		14.8			2.43	0.14
CO_3^{2-}		16.0			2.7	0.13
HCO_3^-		16.4			2.76	0.11
Ca^{2+}		3.6			0.53	0.50
Mg^{2+}		4.8			0.70	0.43
Na^+		6.6			0.99	0.35
K^+		19.1			3.30	0.082
Salinity		6.8			1.03	0.276
Soil water content		**62.5**			23.35	**0.002****
Eigen	0.86	0.10	0.03	0.01		
Explained variation (cumulative)	93.27	93.45	93.47	93.48		
Pseudo-canonical correlation	1	1	1	1		
Permutation Test Results: First Axis					6.9	**0.002****
All Axes					11429	**0.002****
40-80cm soil ions, salinity and water content						
SO_4^{2-}		12.5			2.00	0.2
Cl^{-1}		13.6			2.21	0.17
CO_3^{2-}		5.4			0.79	0.38
HCO_3^-		**40**			9.35	**0.004****
Ca^{2+}		8.9			1.37	0.25
Mg^{2+}		9.5			1.48	0.25
Na^+		11			1.74	0.21
K^+		3.8			0.56	0.49
Salinity		10.1			1.57	0.23
soil water content		6.4			0.96	0.36
Eigen	0.99	0.00	0.00	0.00		
Explained variation (cumulative)	99.69	99.96	99.98	100		
Pseudo-canonical correlation	1	1	1	1		
Permutation Test Results: First Axis					365	**0.002****
All Axes					11429	**0.002****

'***' indicates $p < 0.001$, '**' $p < 0.01$ and '*' $p < 0.05$

Additional File

Additional file 1. Raw data of environmental variables included 0-40 cm and 40-80 cm soil ions (Na^+, K^+, Ca^{2+}, Mg^{2+} and SO_4^{2-}, CO_3^{2-}, HCO_3^-, Cl^-) in the lower reaches of Heihe River, Northwest China.
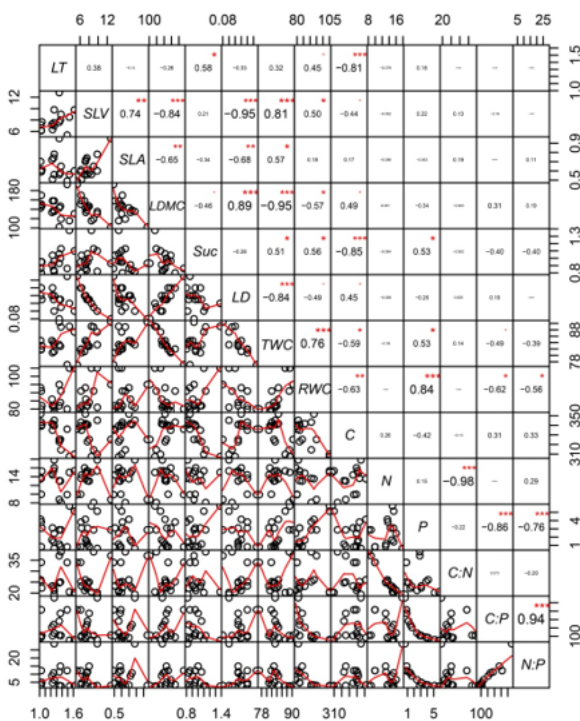
Figures

Figure 1

Correlation analysis among leaf functional traits. Drawing using R software 'PerformanceAnalytics' package, the numbers in the upper triangular region of the graph indicate correlation coefficients, and the asterisks indicate significance, the lower triangle is a linear regression between the two traits. LT: leaf thickness (mm), SLA: specific leaf area (cm2▪ mg-1), SLV: specific of leaf volume (cm3▪ g-1), LDMC: leaf dry matter content (mg▪g-1); Suc: leaaf Sucuulent (g▪cm-2), LD: leaf tissue density (g▪cm-3), TWC: Total water content (%), RWC: relative water content (%), C: leaf carbon content (mg▪g-1), N: leaf nitrogen content (mg▪g-1), P: leaf phosphrous content (mg▪g-1), N:P, C:N, C:P: the ratios of C, N and P. '***' indicates p < 0.001, '**' p < 0.01 and '*' p < 0.05

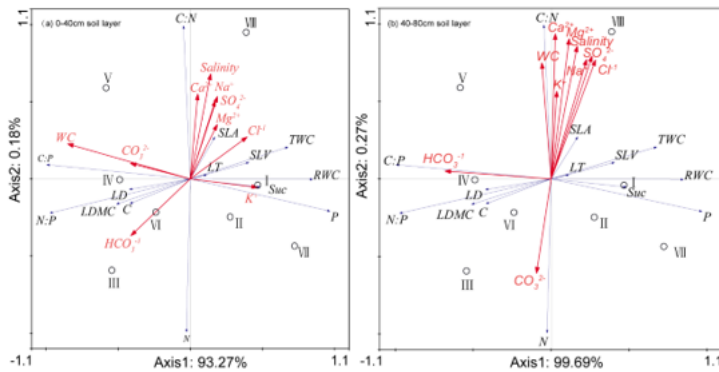## Figure 2

RDA ordination graph of leaf functional traits and environmental variables of the L. ruthenicum communities in the lower reaches of the Heihe River. The direction of the arrow indicating a positive or negative correlation among the environmental factors with the ordination axes. The angle of the arrow reflects the strength of correlation between the environmental factors and functional traits, with small angles indicating strong correlations, large angle opposite. Environmental variables included 0-40 cm and 40-80 cm soil salinity, soil water content (WC) and eight soil ions (Na+, K+, Ca2+, Mg2+ and SO42−, CO32-, HCO3-,Cl-)

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- supplement1.xlsx