

Trade-off strategies 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

Background: Soil salinization affects plant growth and causes changes in leaf traits. *Lycium ruthenicum* Murr. is one of the dominant shrubs and halophytes in the lower reaches of the Heihe River in Northwest China. We analyze the trade-off strategies of fourteen leaf functional traits of eight *L. ruthenicum* populations growing at varying distances from the Heihe River, and discussed the effects soil moisture and salinity on leaf functional traits.

Results: Lower nitrogen (N) contents indicated that *L. ruthenicum* was located at the slow investment-return axis of the species resource utilization graph. Compared to non-saline and very slightly saline sites, populations of slightly saline sites showed higher carbon to nitrogen ratio (C:N). Redundancy analysis (RDA) revealed a relatively strong relationship between leaf functional traits and soil properties, the first RDA axis accounted for 70.99 % and 71.09 % of the variation in 0-40 cm and 40-80 cm of soil moisture and salinity. Populations in non-saline and very slightly saline habitats tended to have higher leaf C content, whereas populations in slightly saline habitats tended to have lower leaf C content, and the discrepancy was evident. Relative importance analysis found that in the 0-40 cm soil layer, leaf traits variations were mainly influenced by soil moisture (SWC), HCO_3^- and CO_3^{2-} ions content, while leaf trait variations in the 40-80 cm soil layer were mainly influenced by HCO_3^- and SO_4^{2-} .

Conclusions: The leaf functional traits of *L. ruthenicum* in this region are mainly restricted by soil N content. The *L. ruthenicum* populations formed a pattern of increased C:N ratios and C content, reduced nitrogen to phosphorus ratio (N:P) and N content from very slightly saline soil to slightly saline. *L. ruthenicum* has a foliar resource acquisition method and a resource conservation trade-off with a flexible life history strategy in habitats with drought and salinity stress. In the shallow soil layers, water has a greater effect than salt on leaf trait variation, in both shallow and deep soil layers, HCO_3^- have a relatively important effect on leaf traits. We believe that these findings will provide some baseline information to facilitate the management and restoration of arid-saline desert ecosystems.

Background

Plant functional traits are defined as measurable morphological, physiological and phenological properties that are related to individual adaptations [1]. The characteristics, relationships and affection factors of plant functional traits are hot topic in current ecological research, aiming to clearly link the phenotypes differences of individual plants to ecosystem processes and services [2-3]. In the analyses of easy-to-measure functional features, two major trade-offs are immediately identified [4-5]. One of the trade-offs can be 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" reveals a trade-off between the quick and slow return of investments of nutrients and dry mass that operates independently of biome, growth form, or plant functional type [6]. For instance, leaves with higher nitrogen content tend to have lower leaf mass per unit area and shorter leaf life span, and leaves with larger A_{max} (the maximum rate of photosynthesis per unit of leaf mass) tend to also have shorter leaf life span [6]. Other suites of related traits have also been recognized that may indicate physical or physiological trade-off strategies [3].

Ecological stoichiometry as an important component of plant functional traits is a comprehensive method for managing quality balances and provides a new perspective for understanding ecosystem process from the individual organism level to the ecosystem level [7]. To study the role of one element in the ecological process, the influence of other elements must be considered at the same time [7-9]. Carbon (C), nitrogen (N), and phosphorus (P) are the core elements in the study of ecological stoichiometry, and they are also particularly important leaf functional traits. Given the importance of understanding the elemental components and the biogeochemical cycles that are coupled with component-pattern-driven phenotypic plasticity found in terrestrial ecosystems, analyses of C:N:P ratios are increasing [10-14]. Previous studies show that C:N ratios are constrained by variations among different functional groups, with N content scaling with respect to C content in foliage [11,13]. In addition, the ratios of C:N and C:P reflect the ability of plants to assimilate C while simultaneously absorbing N and P. Comparatively, the ratios 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 contents in plant leaves at global or regional scales, as well as environmental factor relationship research in general, have received widespread attention [12,13,16]. Recent studies tend to explain the temporal and spatial variability of plant functional traits under adverse conditions (salinity, drought, and frost stress) [17-21].

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

Many studies have shown that *Lycium ruthenicum* Murr. (*Solanaceae*) is an important medicinal desert halophyte in arid and saline region [34]. In addition to its nutritive value, *L. ruthenicum* can regulate carbon assimilation and carbon metabolism through morphological changes to adapt to high salt and drought conditions, allowing the colonization of desert saline-alkali soils [35]. *L. ruthenicum* can prevent soil desertification and reduce soil salinity and alkalinity through special physiological characteristics [36], therefore, it is of great significance to study the functional traits of *L. ruthenicum* in desert saline-alkali

regions where plant species diversity is low. In this study, we measure the leaf water physiological and ecological stoichiometry traits of eight different *L. ruthenicum* populations, as well as the soil moisture and salinity of where they were growing, along an approximately 17 km long north-south transect of the lower reaches of the Heihe River in China. The objective of the study was to explore: (1) the trade-off strategies between leaf functional traits under drought and salinity stress conditions; (2) the relationships between leaf functional traits and soil factors; and (3) Identify the major environmental factors that affecting plant functional traits.

Results

Leaf functional traits in different populations of *L. ruthenicum*

In this study, we measured 14 leaf functional traits (Table 2). Among them, TWC, RWC, SLA, SLV, LT, LDMC, Suc, LD were 79.35-88.37%, 70.41-137.35%, 5-8cm²·g⁻¹, 5.36-12.80 cm³·g⁻¹, 1.02-1.62 mm, 125.0-197.9 mg·g⁻¹, 0.80-1.38 g·cm⁻², and 0.08-0.19 g·cm⁻³, respectively. Leaf ecological stoichiometry traits C, N and P contents were 307.39-351.78, 8.09-17.82, and 0.62-5.77 mg·g⁻¹, respectively. Furthermore, C:N, C:P and N:P ratios were 20.28-37.97, 56.85-415.44, and 2.79-17.70, respectively.

We compared the differences between *L. ruthenicum* functional traits at eight different moisture and salinity sites (Table 1) and found that greater leaf thickness appeared in very slightly saline site VII which was significantly different from non-saline Gobi sites I and VI (Table 2). In addition, the larger SLV, Suc, TWC and RWC traits were also observed to appear at saline sites. Conversely, LDMC, LD, and N contents had the lower values in saline sites. Leaf N concentration was the least variable between different regions, but it still showed the effects of obviously saline stress on *L. ruthenicum*. Statistical analysis shows that the adaptability of *L. ruthenicum* N:P to drought and salt stress was more stable among eight populations than C:N and C:P. Moreover, we found that there was no significant difference in the SLA trait values between the eight different habitats, showing 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 coefficients (see Fig.1) between 14 leaf traits of *L. ruthenicum* showed that LT was significantly positive correlated with Suc, but significantly negative correlated with C content. SLV was highly positive correlated with SLA and both were significantly negative correlated with LD and significantly positive correlated with TWC. LDMC was significantly positive correlated with LD, and both were significantly negative correlated with TWC. Suc was significantly positive correlated with TWC and RWC, but was significantly negative correlated with C content. TWC was significantly positive correlated with P content, while P content was significantly negative correlated with N:P and C:P ratios. N:P and C:P ratios were significantly positive correlated with each other, while RWC was highly negative correlated with N:P and C:P ratios.

RDA of leaf functional traits in soil moisture and salinity gradients

Two RDA maps of different soil layers showed the distribution pattern of traits along the salinity gradients. From non-saline to slightly saline gradients, populations had higher C:N ratios, lower N content, and lower N:P ratios (see RDA vertical axis direction), but the vertical axis (RDA 2) only explained very low proportions of the data. In the horizontal axis, populations growing in high salinity soils had lower C:P than populations growing in lower salinity soils (Fig. 2, Table 2), while the distribution of other leaf traits didn't change much with environmental gradients. 0-40 cm and 40-80 cm soil properties respectively explained 70.99% and 71.09% of leaf traits variation (the sum of the first two axes explained). Permutation tests for all canonical axes were not significant (0-40 cm RDA, Df=10, F=1.53, Pr(>F)=0.31; 40-80 cm RDA, Df=10, F=1.56, Pr(>F)=0.29, Fig. 2). In general, the spatial distribution of the eight populations might be driven by variation in soil chemical characteristics. Populations I, II, III, IV, and VI (see Table1, 2 groups) were close to each other due to their similar soil chemistry, as were populations V and VII. However, population VIII was located away from the other populations, so its soil properties likely differed from the other locations.

Relative importance of soil factors to leaf functional traits variation

We were not only interested in the effects of total soil salinity on leaf functional traits, but also in the exploration of which salt ions affect plant functional trait formation and variation the most. In general, moisture, salinity, and eight major ions corresponded to leaf character variation in different amplitudes. In the 0-40 cm soil layer, leaf traits patterns were mainly influenced by SWC, HCO₃⁻ and CO₃²⁻, and their relative importance values for the fourteen leaf traits are shown in Fig. 3. The relative contribution of 0-40 cm layer SWC to all but the LT trait was more than 17%. SWC had a effect on C:P ratios, with an importance of 34%. HCO₃⁻ was more than 13% important for all traits except SLV and N content. CO₃²⁻ was less important for traits than SWC and HCO₃⁻. Soil salinity and other ions contributed relatively little to leaf properties. In the 40-80 cm layer, HCO₃⁻ and SO₄²⁻ were two main drivers for trait differentiation. The relative importance of HCO₃⁻ for all trait patterns was higher than 20%, and its influence on P content was up to 52%. The influence of SO₄²⁻ on traits was above 12%, except for LDMC, LD, and N content, which were below 10%.

Discussion

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

This study shows that the desert halophyte *L. ruthenicum* is characterized by low leaf SLA, LDMC, C content, N content and N:P ratios, as well as high LT, Suc, P content and C:N ratios. SLA is one of the key leaf traits related to plant carbon uptake strategy [37], it could reflect the distribution of plants and their adaptation to different habitats [38]. LDMC mainly reflects the ability of plants to retain nutrients [39]. 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* is a resource reservation species due to

its lower SLA and N content, and higher C:N ratio. This also indicates that *L. ruthenicum* is in the "slow-return" end of the spectrum. Plants that invest in high LMA (Leaf mass per area) have a slower photosynthetic rate, but longer leaf life, so their slower income (carbon absorption) rate can be compensated by a longer income stream [6,40]. Furthermore, SLA and LDMC are two important soil-fertility predictors in addition to leaf N and P contents and N:P ratios [15,41-43]. The combination of these predictors indicates that soil fertility is lower in the Ejina desert area in the lower reaches of the Heihe River and that the growth of *L. ruthenicum* is mainly restricted by N content. Prior studies that note 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 are higher, C:N and C:P ratios are comparatively lower. Plants will apply competitive strategies at high photosynthetic rates. Conversely, when C content is higher, C:N and C:P ratios are also higher, showing how plants adopt a strong defensive strategy under low photosynthetic rates [44-45]. The results of this study indicate that *L. ruthenicum* has a flexible strategy in different desert saline habitats: when soil salinity is higher, foliar N is lower, and the C:N ratio is large, a defensive strategy is adopted; when N contents are higher and the C:N ratio is lower, a competitive survival strategy is adopted. 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 [46-47]. Osmond et al. found that plant leaves are thicker in nutrient-poor environments, the LT pattern presented by Osmond et al. is consistent with previous research [48]. In order to adapt to harsh environments, succulent plants produce a large number of parenchyma cells, in organs such as the leaves and stems. In eight different habitats, *L. ruthenicum* shows a significant amount of succulence (Suc) used to store moisture in the arid, low-rainfall environments of the Ejina desert. All eight *L. ruthenicum* populations had higher P content compared 753 terrestrial plant species in China [13,24], this shows that local minerals decomposed faster to ensure that enough young leaves were produced to reduce the accumulation of toxic salt ions on each leaf. The leaves of *L. ruthenicum* belong to the succulent foliage group, and the higher water content (TWC) of a succulent, the more drought-tolerant it is [49]. SLV is an important leaf trait according to the leaf characteristics of desert plants. RWC reflects the resistance of plants to dehydration: higher RWC leads to stronger resistance to dehydration, since the leaves have higher osmotic adjustment functions.

Trade-offs between 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. However, it was only over the course of the last two decades that the availability of large data sets has allowed for the precise quantification and identification of the trait syndromes that can be used to characterize trade-offs for a wide variety of plants. For example, species with small SLA have thicker leaves or denser tissues, which allows for the maintenance of leaf function or the delaying leaf death under very dry conditions.

Some fundamental relationships found in leaf economics spectrum research include a significantly positive correlation between LT and Suc, which confirms that succulent plants employ a water conservation strategy [46]. While a significantly negative correlation has been found between LT and C content, this can be related to thicker leaves cause a decrease in the SLA which affects carbon acquisition [50]. Some literature reports that SLA is actually a combination of leaf tissue density (LD) and leaf thickness (LT), since leaf tissue density is significantly positive correlated with leaf dry matter content (LDMC), leading to the equation: $SLA = 1/(LD \times LT) \approx 1/(LDMC \times LT)$ [50]. This paper did not show a significant relationship between SLA and LT, but demonstrated that SLA had a strongly negative correlation with LDMC and LD. The significantly negative correlation between LT and C content, as well as between SLA (SLV) and LD (LDMC), indicates a trade-off between resource acquisition and resource conservation under drought and saline conditions.

LDMC and LD are positively correlated, with both being significantly negative correlated with TWC. Negative correlation of TWC, RWC and LDMC expresses another trade-off between the intracellular water content and nutrient accumulation due to photosynthetic CO₂ assimilation, showing that leaf water content is a useful indicator of plant water balance. Suc is significantly positive correlated with TWC, RWC and P content, but strongly negatively correlated with C content. This confirms that leaf succulence can improve the energy returns from leaf investment by replacing expensive carbon structures with water [51].

To what extent does soil moisture and salinity affect leaf functional traits?

In contrast to significant trait correlation patterns, there are only a few significant differences in the leaf morphological traits and C:N:P stoichiometry of desert halophytes with different salinity and moisture habitats. In this paper, we found that SWC and HCO₃⁻ in shallow soil layers is a good predictor of leaf traits. Between them, SWC has larger contributions to leaf P content, N:P ratios and C:P ratios while HCO₃⁻ has the greatest impact on LDMC, these can be inferred from previous research: in desert ecosystems, lower SWC coupled with higher soil alkalinity acts to decrease both soil N and P availability [52]. Due to this, SWC has a great impact on the levels of leaf P and N:P, and HCO₃⁻ affects the production of leaf dry matter content. The result was supported by other observations [53]. The changing C:P pattern along environmental gradients suggested that *L. ruthenicum* had a flexible life strategy under different environments. In the deeper soil layer, HCO₃⁻, followed by SO₄²⁻, mainly influences leaf functional traits. In the RDA diagram, deep soil SWC have a negative effect on leaf N content and N:P, but had a positive effect on leaf C:N. SWC does not obviously influence other functional traits. At the same time, the effects of soil salinity also converged with SWC. It can be said the hydraulic properties required for plant safety at higher salinity are at the expense of lower growth rates [54]. People already know a lot about the effects of salt stress on plants. The common sense is that salt stress reduces some transaminase activities, reduces plant N content, and damages plant growth [55]. Therefore, the carbon fixation ability of the blade will also be reduced significantly, which is consistent with the low leaf C content phenomenon shown in this paper. Many studies have confirmed that salt stress, especially chloride salt stress, will inhibit plant's NO₃⁻ absorption, so the NO₃⁻ content in a plant's leaves will decrease during salt stress [56-57]. However, some other studies have shown that the N content of succulent plants becomes larger as the salinity increases [24]. This discrepancy will require additional research in the future to resolve.

Salt stress limits the growth of halophytes through adverse effects on various physiological and biochemical processes. Conversely, halophytes respond to increased salinity by expanding in diversity [28]. Salinization consists of an accumulation of water-soluble salts in the soil, including the ions of K⁺, Mg²⁺, Ca²⁺, Cl⁻, SO₄²⁻, CO₃²⁻, HCO₃⁻ and Na⁺. We tried to analyze this process using salt ions at different depths of soil. The RDA results show that SWC, HCO₃⁻, CO₃²⁻, SO₄²⁻ and Cl⁻ can explain the variation of functional traits well. Surprisingly, Na⁺ content could not explain the variation significantly, despite the importance of Cl⁻ and Na⁺ as mentioned in many salt stress studies [58-60]. According to our current knowledge, the soluble salts in the lower reaches of the

Heihe River Basin are mainly Na^+ , HCO_3^- , SO_4^{2-} and Ca^{2+} [61]. However, there are few studies showing how these ions affect leaf functional traits and trade-off strategies, which may be a direction for future research.

Conclusions

L. ruthenicum has a foliar resource acquisition and resource conservation trade-off with a flexible life history strategy in habitats with drought and salinity gradients. In shallow soils in saline-stressed arid environments, water has a greater effect than salt for leaf trait variation. In both shallow and deep soil layers, HCO_3^- ions have a relatively large effect on leaf properties. However, other larger scale studies are needed to determine the drivers of functional characteristics.

We concluded from our findings that: (1) the patterns of leaf functional traits in the desert halophyte *L. ruthenicum* in arid and saline environments have a tendency to display lower leaf SLA, LDMC, C, N content and N:P ratios, but higher LT, Suc, P content and C:N ratios, with leaf average N:P ratios <14, showing that soil fertility in the Ejina Desert is limited by nitrogen; (2) leaf traits of *L. ruthenicum* populations vary significantly according to different soil environments in the habitats; and (3) *L. ruthenicum* has a foliar resource utilization trade-off with a flexible life history strategy in order to survive in environments with drought and salinity gradients.

Methods

Study area

The Heihe River is an inland river located in an extremely arid and fragile ecological environment in northwestern China, this area have extreme arid climate, wind erosion, overgrazing and sand burial, which extends from the upstream area to the downstream area and forms unique desert ecosystem and species composition [62]. The Ejina desert area is located in the lower reaches of the Heihe River Basin. According to the data of the Ejina Weather Station from 1957 to 2011, the annual average temperature is 8.77°C, the relative humidity is 33.9%, annual precipitation is 37.40 mm, and the annual evaporation is 3390.26 mm. In environments with low precipitation in the Ejina desert area, the water supply mainly comes from the Heihe River Basin. The plant communities are characterized by low species diversity, being mainly composed of drought- and salt-tolerant desert plants that are distributed throughout the Heihe River and the lake plains of Ejina Banner, the main shrub species are: *Tamarix chinensis*, *Lycium ruthenicum*, *Nitraria tangutorum* and *Alhagi sparsifolia* [63], among them, the coverage of *Lycium ruthenicum* reaches about 20%. The soil of the entire Heihe River series contains brown calcium, desert calcium, salt and sand [62].

Sampling protocol and community characteristics

This study was conducted in early August 2018 within a 17 km long north to south transect in the lower reaches of the Heihe River Basin. The nearest two of the eight sampling sites were 0.5 km apart, and the farthest straight line distance was 10 km. All collected plant materials were in a unified development stage, that is in August when the biomass was the largest. The study area was flat and far from any villages. We selected eight different populations of *L. ruthenicum* growing in different moisture and salinity conditions from near to far and vertical with the main river channel. The main distribution areas and different plant habitat types are shown in Table 1. Three plots (5×5 m) were established within each selected population and their geographic information (latitude, longitude) was recorded with the eXplorist 510GPS device (Magellan, USA). Fully expanded mature leaves (n>30) at sunny side were randomly collected from 15 individuals for each *L. ruthenicum* population, and all foliage sampled from 3 plots were mixed as one independent sample for further analysis. There were not any signs of herbivory or pathogen infestation on the leaves.

Determination of leaf water physiological and stoichiometric traits

Calipers with an accuracy of 0.02 mm were used to measure leaf thickness (LT, mm). Leaf area was determined via a combination of an EPSON DS-1610 scanner and the ImageJ software [64]. Specific leaf area (SLA) was calculated as leaf area per dry mass, specific leaf volume (SLV, leaf volume per unit dry mass) was determined by a drainage method using a 10 mL cylinder, the specific operation was to inject an appropriate volume of purified water, put in the chopped leaves, and observed the volume of the liquid level rising. Leaf dry matter content (LDMC) calculated by leaf dry mass per unit fresh mass. The degree of leaf succulence was measured by subtracting the dry weight from the 6 h saturated fresh weight, then dividing the resulting number by the surface area (Suc, $\text{g}\cdot\text{cm}^{-2}$). Leaf tissue density (the ratio of leaf dry weight to volume, LD, $\text{g}\cdot\text{cm}^{-3}$), relative water content (RWC, %), and total water content (TWC, %) were determined by drying. Except for the LT measurement performed in the field, the other leaves were divided into two groups. One group was used to measure SLA and SLV, and the other group was used to measure moisture and other properties. Leaf samples were then brought back to the laboratory and dried at 80°C for 48 hours to reach a constant weight in order to measure the other characteristics. Dried leaves were ground to a 0.15 mm powder using a sample pulverizer in order to measure the carbon (C), nitrogen (N) and phosphorus (P) contents and calculate the stoichiometric ratio. C content was determined using the $\text{K}_2\text{Cr}_2\text{O}_7\text{-H}_2\text{SO}_4$ external heating method in an 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). P content was determined by digestion with $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$ followed by measurement with the molybdenum antimony method.

Measurement of soil moisture, salinity and ion contents

Three soil plots were taken near the growth point of each *L. ruthenicum* population, and then mixed 0-40 cm and 40-80 cm soil layer samples respectively. One (pooled) soil sample was taken in each of the plots. These soil samples were taken next to the plant individuals that were used for sampling of leaves and then pooled per plot. Samples were collected from an area after 7-10 rainless days had passed. The samples were first passed through a 2 mm screen to remove roots and other impurities, and then dried at 80°C for soil moisture content (SWC) analysis. Electrical conductivity (EC) was measured using a DDS-307a portable conductivity meter (Leici Instrument, Shanghai China). We had previously established the standard curve between the soil salinity and electrical

conductivity of saline-alkali soil in the study area as $y = 217.73x - 22.723$ ($R^2 = 0.994$), which was used to calculate soil salinity. The unit of soil salinity was $\text{g}\cdot\text{kg}^{-1}$. 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+}) content following the methods described by the US Salinity Laboratory Staff [65]. Specifically, we used this method to measure the total concentration of soil ions rather than the actual concentration available to plants.

Statistical analysis

One-way analyses of variance were conducted using the SPSS 19.0 Software to compare site characteristics between sites as well as leaf functional traits between populations, post hoc Turkey HSD tests and Levene Statistic were used to check for variance homoscedasticity, $\text{sig} > 0.05$. The Shapiro-Wilk test was performed to check for data normality. R3.5.2 was used for RDA to check the distribution pattern of plant functional traits in the environmental gradients of different soil layers. Trait data was processed by Hollinger method, and soil data was logarithmic transformed before computing the RDA. Pearson correlations between different plant functional traits were performed using the Performance Analytics package of the R statistical software [66]. "Relative importance analysis" refers to the quantification of an individual regression's contribution to a multiple regression model [67].

Abbreviations

LT: leaf thickness (mm); SLA: specific leaf area ($\text{cm}^2\cdot\text{g}^{-1}$); SLV: specific leaf volume ($\text{cm}^3\cdot\text{g}^{-1}$); LDMC: leaf dry matter content ($\text{mg}\cdot\text{g}^{-1}$); Suc: succulence ($\text{g}\cdot\text{cm}^{-2}$); LD: leaf tissue density ($\text{g}\cdot\text{cm}^{-3}$); TWC: Total water content (%); RWC: relative water content (%); C content: leaf carbon content ($\text{mg}\cdot\text{g}^{-1}$); N content: leaf nitrogen content ($\text{mg}\cdot\text{g}^{-1}$); P content: leaf phosphorous content ($\text{mg}\cdot\text{g}^{-1}$).

Declarations

Authors' contributions

SJL conceived and designed the experiments and revised the first draft; WG analyzed the data and wrote the 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

All the data were summarized in the manuscript itself. The datasets are available from the corresponding author on reasonable request.

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

Table1:

Site characteristics for different *Lycium ruthenicum* populations in the lower reaches of the Heihe River (Mean \pm SD, n=3)

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 (%)	40-80 cm Soil Salinity (g·kg ⁻¹)
□	Non-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
□	Non-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
□	Non-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
□	Non-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
□	Very slightly 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
□	Non-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
□	Very slightly 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
□	Slightly 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	19.00±0.39a	15.61±0.80a

Simpson dominance index was calculated as $c = \frac{1}{\sum P_i^2}$, Pielou evenness index was calculated as $J_{sw} = \frac{H}{\ln S}$ where P_i is the relative importance value of species i and S is the total number of species in the plot, C is Simpson dominance index, H is Shannon-Wiener diversity index, J_{sw} is Pielou evenness index. Soil moisture and salinity are divided into (0-40 cm) and (40-80 cm) data. Comparison of habitat characteristics of different *L. ruthenicum* populations processed by one-way analyses of variance followed by Tukey-HSD tests. Different lowercase letters represent significant differences ($P < 0.05$). According to the literature (USSL Staff 1954), the soil salinization was divided into three categories (Non-saline; Very slightly saline; Slightly saline).

Table 2: Leaf functional traits of different *Lycium ruthenicum* populations (Mean \pm SD, n=3)

No.	LT	SLV	SLA	LDMC	Suc	LD	TWC	RWC	C	N	P	C:N	C:P	N:P
□	1.03±0.01c	6.69±0.47bc	0.007±0.43a	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	25.79±0.42c	85.0±4.05c	3.42±0.16b
□	1.14±0.10bc	7.00±0.67bc	0.006±0.47a	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	23.34±0.89d	107.5±2.5c	4.80±0.14ab
□	1.26±0.00abc	8.40±1.40abc	0.006±1.11a	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	20.28±0.74e	435.8±25.5a	17.70±11.1c
□	1.36±0.01ab	7.81±0.19abc	0.005±0.10a	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	26.16±1.85c	335.3±11.2ab	13.16±1.76c
□	1.26±0.23abc	5.74±0.38c	0.005±0.54a	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	34.34±0.48b	414.1±1.8a	12.22±0.00c
□	1.24±0.02bc	7.38±0.13bc	0.007±0.12a	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	22.66±0.35d	223.3±13.1bc	9.87±0.90ab
□	1.58±0.05a	9.14±0.64ab	0.006±0.24a	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	20.56±0.30e	58.1±1.1c	2.79±0.20b
□	1.37±0.01ab	10.90±1.90a	0.008±1.48a	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	38.54±1.07a	112.3±0.7c	2.94±0.12b

Multiple comparisons of traits between different populations using one-way analyses of variance followed by Tukey-HSD tests, Different letters represent significant

differences ($P < 0.05$). LT: leaf thickness (mm), SLA: specific leaf area ($\text{cm}^2 \cdot \text{g}^{-1}$), SLV: specific leaf volume ($\text{cm}^3 \cdot \text{g}^{-1}$), LDMC: leaf dry matter content ($\text{mg} \cdot \text{g}^{-1}$); Suc: succulence ($\text{g} \cdot \text{cm}^{-2}$), LD: leaf tissue density ($\text{g} \cdot \text{cm}^{-3}$), TWC: Total water content (%), RWC: relative water content (%), C: leaf carbon content ($\text{mg} \cdot \text{g}^{-1}$), N: leaf nitrogen content ($\text{mg} \cdot \text{g}^{-1}$), P: leaf phosphorus content ($\text{mg} \cdot \text{g}^{-1}$).

Additional File

Additional file 1. Raw data of environmental variables, including soil ions (Na^+ , K^+ , Ca^{2+} , Mg^{2+} and SO_4^{2-} , CO_3^{2-} , $\text{HCO}_3^-/\text{Cl}^-$) and soil conductivity in the 0-40 cm and 40-80 cm soil layers in the lower reaches of Heihe River, Northwest China.

Figures

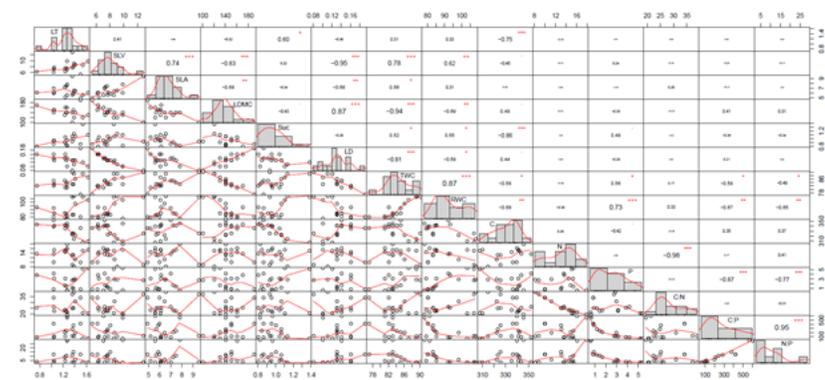


Figure 1 Correlation analysis among leaf functional traits and water-salt response. Drawing using R "PerformanceAnalytics" package. The numbers in the upper triangular region of the graph indicate correlation coefficients, and the asterisks indicate significance. The lower triangle is a linear regression between the two traits. LT: leaf thickness (mm), SLA: specific leaf area (mm^2/mg), SLV: specific leaf volume (cm^3/g), LDMC: leaf dry matter content (mg/g); Suc: succulence (g/cm^2), LD: leaf dry matter concentration (g/cm^3), TWC: Total water content (%), RWC: relative water content (%), C: organic matter content (mg/g), N: nitrogen content (mg/g), P: phosphorus content (mg/g), C:N: the ratio of C and N, C:P: the ratio of C and P, N:P: the ratio of N and P.

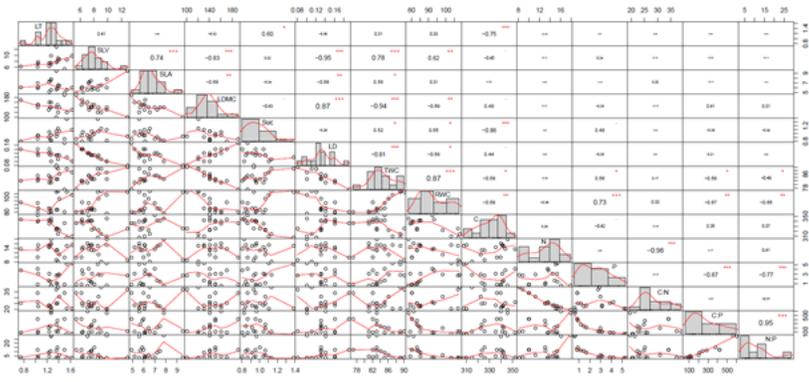


Figure 1
 Correlation analysis among leaf functional traits and water-salt response. Drawing using R "PerformanceAnalytics" package. The numbers in the upper triangular region of the graph indicate correlation coefficients, and the asterisks indicate significance. The lower triangle is a linear regression between the two traits. LT: leaf thickness (mm), SLA: specific leaf area (mm²/mg), SLV: specific leaf volume (cm³·g⁻¹), LDMC: leaf dry matter content (mg·g⁻¹); Suc: succulence (g·cm⁻²); LD: leaf dry matter concentration (g/cm³), TWC: Total water content (%), RWC: relative water content (%), C: organic matter content (mg/g), N: nitrogen content (mg/g), P: phosphorus content (mg/g), C:N: the ratio of C and N, C:P: the ratio of C and P, N:P: the ratio of N and P.

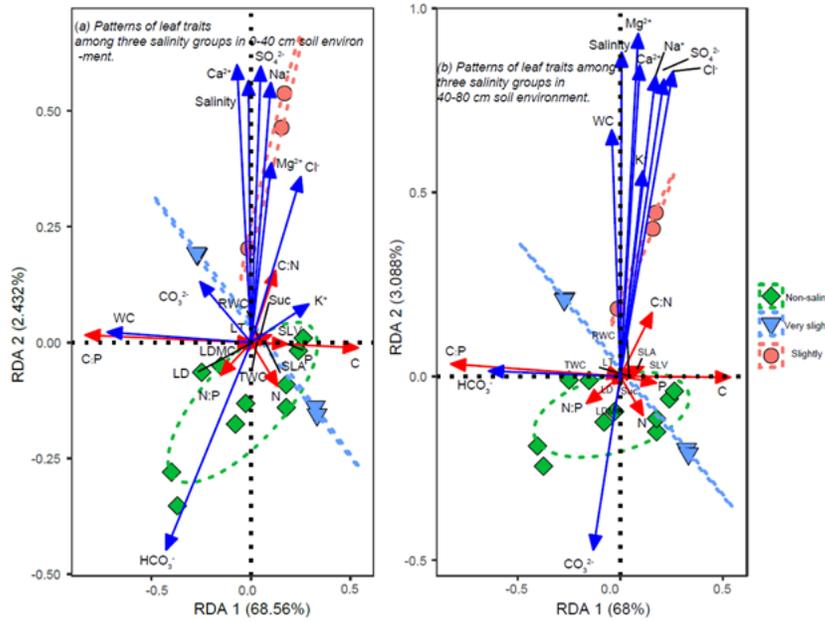


Figure 2
 RDA of leaf functional traits and environmental variables of *Lycium ruthenicum* Murr populations in the lower reaches of the Heihe River. The red arrows are the leaf functional data, the blue arrows represent the soil traits that were included in the models as the underlying environmental factors. 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. Environmental variables include water (WC, 0-40 cm 40-80 cm soil), salinity (0-40 cm 40-80 cm soil) and soil ions (Na⁺, K⁺, Ca²⁺, Mg²⁺, CO₃²⁻, HCO₃⁻, SO₄²⁻, Cl⁻). The dotted green circle represents the non-salt group, the blue circle represents the very mild salt group, and the red circle represents the mild salt group.

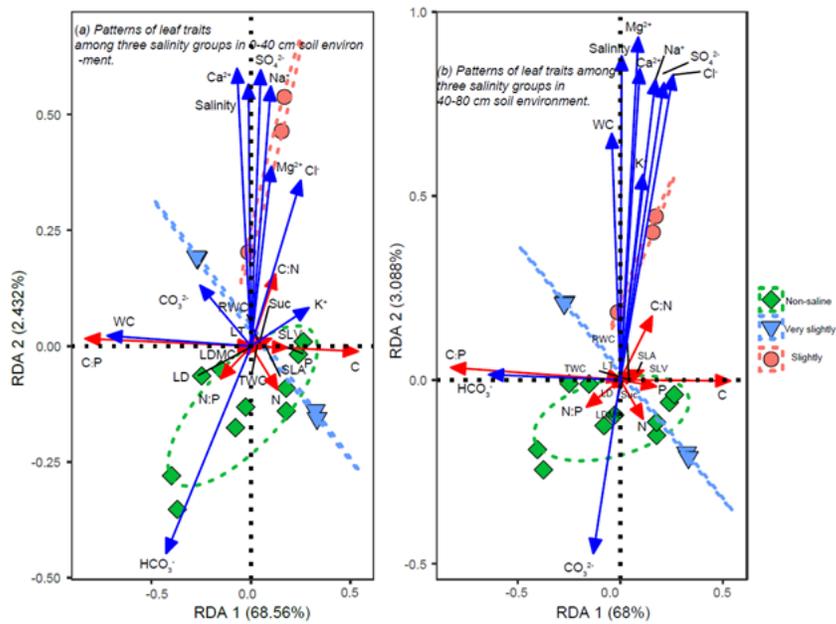


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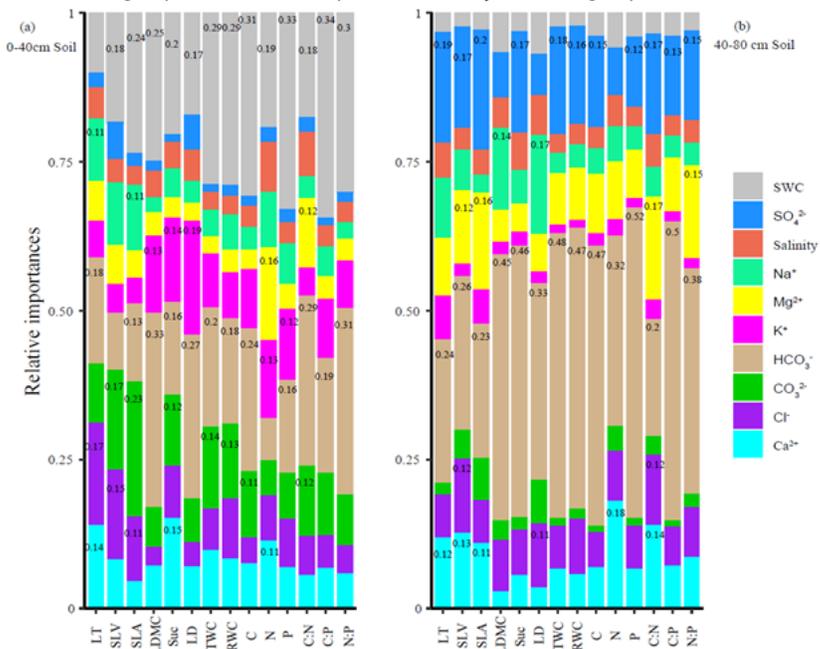


Figure 3

The relative importance of soil factors at different soil depths on leaf functional traits. The horizontal axis is leaf functional traits, and the vertical axis is the relative importance of soil factors. SWC: soil water content. The soil factors from top to bottom on the histogram are SWC, SO₄²⁻, Salinity, Na⁺, Mg²⁺, K⁺, HCO₃⁻, CO₃²⁻, Cl⁻, Ca²⁺. Values below 10% are not shown in the Fig.3.

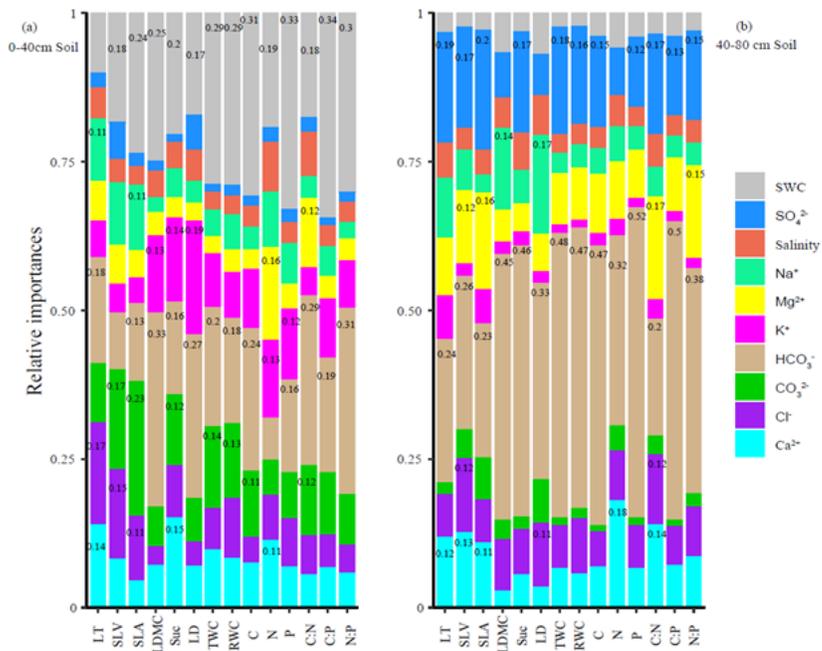


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Supplementary Files

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