

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

Background: Soil salinization affects plant growth and causes changes in leaf traits. *Lycium ruthenicum* Murr., a shrub with significant soil and water conservation capacities. In this paper, we analyze the trade-offs of leaf functional traits of eight *L. ruthenicum* populations growing at varying distances from the Heihe river by dividing the eight sites into three groups according to the average soil salinity and discussing the effects of soil factors at 0-40cm and 40-80cm on leaf trait patterns. We also attempt to explain desert *L. ruthenicum* trade-off strategies by choosing fourteen leaf traits to link with soil factors.

Results: Low 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 C:N. The redundancy analysis "RDA" results showed that 0-40cm and 40-80cm soil properties explained 70.99% and 71.09% of leaf trait variation, respectively. As soil salinity gradients increased, leaf C:N increased and N content decreased, and the difference was significant. Populations in non-saline and very slightly saline habitats tended to have higher leaf C content, while populations in slightly saline habitats tended to have lower leaf C content, and the discrepancy was evident. Relative importance analysis found that in the 0-40cm layer, leaf traits variations were mainly influenced by soil water content (SWC), HCO₃⁻ and CO₃²⁻, while leaf trait variations in the 40-80cm layer were mainly influenced by HCO₃⁻ and SO₄²⁻ ions.

Conclusions: The growth of *L. ruthenicum* in the Ejina desert is mainly restricted by N content, which determines soil fertility. *L. ruthenicum* has a foliar resource acquisition method and a resource conservation trade-off with a flexible life history strategy. Leaf traits can vary significantly due to different environments in a given habitat. As the environmental gradient changes from mild to severe, the populations present a pattern of increased C:N, increased C content, reduced N:P, and reduced N content. In the shallow soil layers of saline-stressed arid environments, water has a greater effect than salt on leaf trait variation. In both shallow and deep soil layers, HCO₃⁻ ions have a relatively large effect on leaf properties.

Background

Green leaves collect and store nutrients, which is the basis of terrestrial ecosystem function. According to Violle et al., functional traits are defined as measurable morphological, physiological, and phenological properties that are related to individual adaptations [1]. These functional traits include specific leaf area (SLA), specific leaf volume (SLV), photosynthetic rate, plant height, and seed mass, among others. Plant functional traits are a hot topic in current ecological research, aiming to clearly link the phenotypical and physiological 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" describes trade-offs based on carbon and other nutrients and 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-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 level to the ecosystem level [7-9]. The key chemical components required for living organisms are the elements carbon (C), nitrogen (N) and phosphorus (P). 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, salinity and moisture are important conditions that affect plant growth [22]. In arid environments, drought exerts a strong 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 patterns [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]. 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 water 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 stoichiometrical 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 salt, and conversely, a positive correlation between the ratios of leaf C:P ratios, leaf N:P ratios, and soil salt [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 has attracted much attention, possibly due to ecosystem degradation over past decades, but the adaptive strategies of *L. ruthenicum* and its tolerance of drought and salinity stresses is not well understood.

Many studies have shown that *L. ruthenicum* is an important medicinal desert halophyte in arid and saline lands [34]. In addition to its nutritive value, *L. ruthenicum* can adapt to high salinity and drought conditions through morphological adjustments in both carbon assimilation and metabolism, allowing it to be a colonial species with defensive functions on 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 lacking. In this study, we measure the leaf water physiological and ecological stoichiometry traits of eight different *L. ruthenicum* populations, as well as the soil salinity and soil moisture 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 salinity and drought stress conditions; (2) the relationships between leaf functional traits and soil factors; and (3) the major environmental factors that affect plant traits.

Results

Characteristic of the leaf functional traits in different populations 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%, $5-8\text{cm}^2\text{mg}^{-1}$, $5.36-12.80\text{cm}^3\text{mg}^{-1}$, 1.02-1.62 mm, 125.0-197.9 $\text{mg}\cdot\text{g}^{-1}$, 0.80-1.38 $\text{g}\cdot\text{cm}^{-2}$, 0.08-0.19 $\text{g}\cdot\text{cm}^{-3}$, respectively. Leaf ecological stoichiometry traits, namely C, N, and P contents were 307.39-351.78, 8.09-17.82, 0.62-5.77 $\text{mg}\cdot\text{g}^{-1}$, respectively, and C:N, C:P and N:P ratios were 20.28-37.97, 56.85-415.44, 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 slightly saline site VIII which was significantly different from non-saline Gobi sites I and VI (Table 2). In addition, the largest SLV, Suc, TWC and RWC traits were also observed to appear at slightly saline sites VIII. Conversely, LDMC, LD, and N contents had the lowest values in heavy saline sites. Leaf N concentration was the least variable between different regions, but it still showed the effects of heavy saline stress on *L. ruthenicum* via significantly lower leaf C content. Statistical analysis showed that the ratios of N:P were more stable than the ratios of C:N and C:P in adaptation to drought-salt stress. 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 between 14 leaf traits of *L. ruthenicum* showed that LT was significantly positively correlated with Suc ($r=0.60$, $P<0.05$), but significantly negatively correlated with C content ($r=-0.75$, $P<0.001$). SLV was highly positively correlated with SLA ($r=0.74$, $P<0.001$) and both were 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 ($r=0.78$, $P<0.001$ and $r=0.56$, $P<0.05$, respectively). LDMC was significantly positively correlated with LD ($r=0.87$, $P<0.001$), and both were significantly negatively correlated with TWC ($r=-0.94$, $P<0.001$ and $r=-0.81$, $P<0.001$, respectively). Suc was significantly positively correlated with TWC and RWC, but was significantly negatively correlated with C content ($r=-0.86$, $P<0.001$). TWC was significantly positively correlated with P content ($r=0.56$, $P<0.05$), while P content was significantly negatively correlated with N:P and C:P ratios ($r=-0.77$, $r=-0.87$, $P<0.001$). N:P and C:P ratios were significantly positively correlated with each other ($r=0.95$, $P<0.001$), while RWC was highly negatively correlated with N:P and C:P ratios ($r=-0.65$, $r=-0.67$, $P<0.01$).

RDA restriction ordering of functional traits in soil water 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). In the horizontal axis, populations growing in high salinity soils had lower C content 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. 0-40cm and 40-80cm 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 (0-40cm RDA, Df=10, F=1.53, Pr(>F)=0.31; 40-80cm RDA, Df=10, F=1.56, Pr(>F)=0.29, Fig.2). In general, the spatial distribution of the eight community types might be driven by variation in soil chemical characteristics. Populations I, II, III, IV, and VI 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 trait 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 0-40cm soil layer, leaf traits patterns were mainly influenced by SWC, HCO_3^- and CO_3^{2-} , and their relative importance values for the fourteen leaf traits are shown in Fig.3. The relative contribution of 0-40cm layer SWC to all but the LT trait was more than 17%, which might be because soil moisture had no direct effect on leaf thickness. SWC had a significant effect on C:P ratios, with an importance of 34%. HCO_3^- was more than 13% important for all traits except SLV and N content. CO_3^{2-} was less important for traits than SWC and HCO_3^- . Soil salinity and other ions contributed relatively little to leaf properties. In the 40-80cm layer, HCO_3^- and SO_4^{2-} were two main drivers for trait differentiation. The relative importance of HCO_3^- for all trait patterns was higher than 20%, and its influence on P content was up to 52%. The influence of SO_4^{2-} on traits was above 12%, except for LDMC, LD, and N content, which were below 10% (values below 10 are not shown in the Fig.3).

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 low SLA, low N content, and high C:N ratio. This also indicates that *L. ruthenicum* is in the "slow-return" end of the spectrum. Plants that invest in high LMA 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 nutrient contents and N:P ratios[15,41-43]. The combination of these predictors indicates that soil fertility is lacking 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 high, C:N and C:P ratios are comparatively low. Plants will apply competitive strategies at high photosynthetic rates. Conversely, when C content is high, C:N and C:P ratios are also high, 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 under different desert saline habitats: when soil salinity is high, foliar N is small, and the C:N ratio is large, a defensive strategy is adopted; when N contents are high and the C:N ratio is low, 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. [48] found that plant leaves are thicker in nutrient-poor environments. The LT pattern presented by Osmond et al. is consistent with previous research. In order to adapt to poor environments, succulent plants produce a large number of parenchyma cells, in areas 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, suggesting that local minerals decompose faster to ensure that enough young leaves are produced to reduce the persecution of toxic salt ions in the soil. The leaves of *L. ruthenicum* belong to the succulent foliage group, and the higher the water content (TWC) of a succulent, the more drought-tolerant and water-stress-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-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. 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 LT causing a decrease in the specific leaf area 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 positively correlated with leaf dry matter content (LDMC), leading to the equation: $SLA = 1/(LD \times LT) \approx 1/(LDMC \times LT)$ [50]. This paper does not show a significant relationship between SLA and LT, but proves that SLA has 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 negatively correlated with TWC. Negative correlation of TWC, RWC and LDMC expresses another trade-off between the intracellular water content and nutrient accumulation due to photosynthesis, showing that leaf water content is a useful indicator of plant water balance. Suc is significantly positively 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 changes 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 HCO_3^- 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 HCO_3^- has the greatest impact on LDMC, these can be inferred from previous research: In desert ecosystems, low soil moisture coupled with high soil alkalinity acts to decrease both soil N and P availability[52], Due to this, here SWC has a great impact on the levels of leaf P and N:P, and HCO_3^- affects the production of dry matter content. Results which are partially supported by evidence from other observations[53]. Changing C:P pattern along environmental gradients suggests that *L. ruthenicum* has a flexible life strategy under a changing environment. In the deeper soil layer, HCO_3^- , followed by SO_4^{2-} , 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. Thus, the hydraulic properties required for plant safety at high 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 a plant's NO_3^- absorption, so the NO_3^- 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^+ , Mg^{2+} , Ca^{2+} , Cl^- , SO_4^{2-} , CO_3^{2-} , HCO_3^- and Na^+ . We tried to analyze this process using salt ions at of different depths of soil. The RDA results show that SWC, HCO_3^- , CO_3^{2-} ,

SO_4^{2-} 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. Leaf traits of *L. ruthenicum* populations vary significantly due to different soil environments in the different habitats. As the environmental gradients change from mild to severe, the populations present a pattern of increased C:N ratios, increased C content, reduced N:P content, and reduced N content. 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 low leaf SLA, LDMC, C content, N content and N:P ratios, but high 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 site

The Heihe River is an inland river located in an extremely arid and fragile ecological environment in northwestern China. The desert ecosystem, which extends from the upstream area to the downstream area and contains unique ecological structures and plant populations, is dominated by shrubs [62]. The Ejina desert area is located in the lower reaches of the Heihe River Basin. According to the data of the Ejinaqi 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 riverside vegetation is mainly composed of shrubs and grasses. The main shrub species are: *Tamarix chinensis*, *Lycium ruthenicum*, *Nitraria tangutorum* and *Alhagi sparsifolia* [63]. In the Ejina desert, the plant species diversity is poor, and are composed mainly of drought and salt-tolerant desert plants that are distributed throughout the Heihe River and the lake plains of Ejina Banner. 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 2017 within a 17 km long north-south transect in the lower reaches of the Heihe River Basin. 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 far away from and close to the main river channel. The main distribution areas and different plant habitat types are shown in Table 1. Three quadrants (5×5 m) were established within each selected community and their geographic information (latitude, longitude) was recorded with the eXplorist 510 GPS device (Magellan, USA). Leaves that were mature, fully expanded, and facing the sun ($n > 30$) were collected from 15 individuals of each *L. ruthenicum* population. All leaves sampled from the three quads were combined into a mixed sample.

Determination of leaf water physiological and stoichiometric traits

Calipers with an accuracy of 0.02 mm were used to measure the thickness of the upper, middle and lower sides of the leaf (LT, mm). Leaf area was determined via a combination of an EPSON DS-1610 scanner and the ImageJ software [64]. The specific leaf area (SLA, leaf area per unit dry mass) and the specific leaf volume (SLV, leaf volume per unit dry mass) were determined by a drainage method using a 10mL cylinder and dry leaf content (LDMC, leaf dry mass per unit fresh mass). The degree of leaf succulence was measured by subtracting the dry weight from the 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 leaf water content (TWC, %) were determined by drying. Since the leaves dehydrate after being detached from the branches, the LT, SLA, and SLV data were all completed in the field. The other 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

Soil was collected at 0-40cm and 40-80 cm depths from where the eight *L. ruthenicum* populations grew. 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, then dried at 80°C for moisture content 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].

Statistical analysis

All one-way analysis of variance (Table 1, 2) were conducted using 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 data normality. R3.5.2 was used for redundancy analysis to check the distribution pattern of plant functional traits in the environmental gradients of different soil layers. Relationships between different plant functional traits were performed using the PerformanceAnalytics package of the R statistical software [66]. "Relative importance analysis" refers to the quantification of an individual regressor'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 of leaf volume ($\text{cm}^3\cdot\text{g}^{-1}$); LDMC: leaf dry matter content ($\text{mg}\cdot\text{g}^{-1}$); Suc: leaf 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

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	0-40cm Soil Moisture (%)	0-40cm Soil Salinity(g*kg ⁻¹)	40-80cm Soil Moisture (%)	40-80cm 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±0.39a	15.61±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* populations processed by one-way analysis of variance. Different lowercase letters represent significant differences ($P<0.05$). According to the literature (USSS Staff 1954), the degree of soil salinization was divided into three categories (Non-saline; Very slightly saline; Slightly saline).

Table 2 Leaf functional traits of different *L. ruthenicum* populations (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±4.0f
□	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±2.5f
□	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±11.7
□	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±1.8e
□	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 populations 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 ($\text{cm}^2 \cdot \text{g}^{-1}$), SLV: specific of leaf volume ($\text{cm}^3 \cdot \text{g}^{-1}$), LDMC: leaf dry matter content ($\text{mg} \cdot \text{g}^{-1}$), Suc: leaf Succulent ($\text{g} \cdot \text{cm}^{-2}$), 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 phosphorous 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-} , HCO_3^- , Cl^-) and soil conductivity in the 0-40cm and 40-80cm soil layers in the lower reaches of Heihe River, Northwest China.

Figures

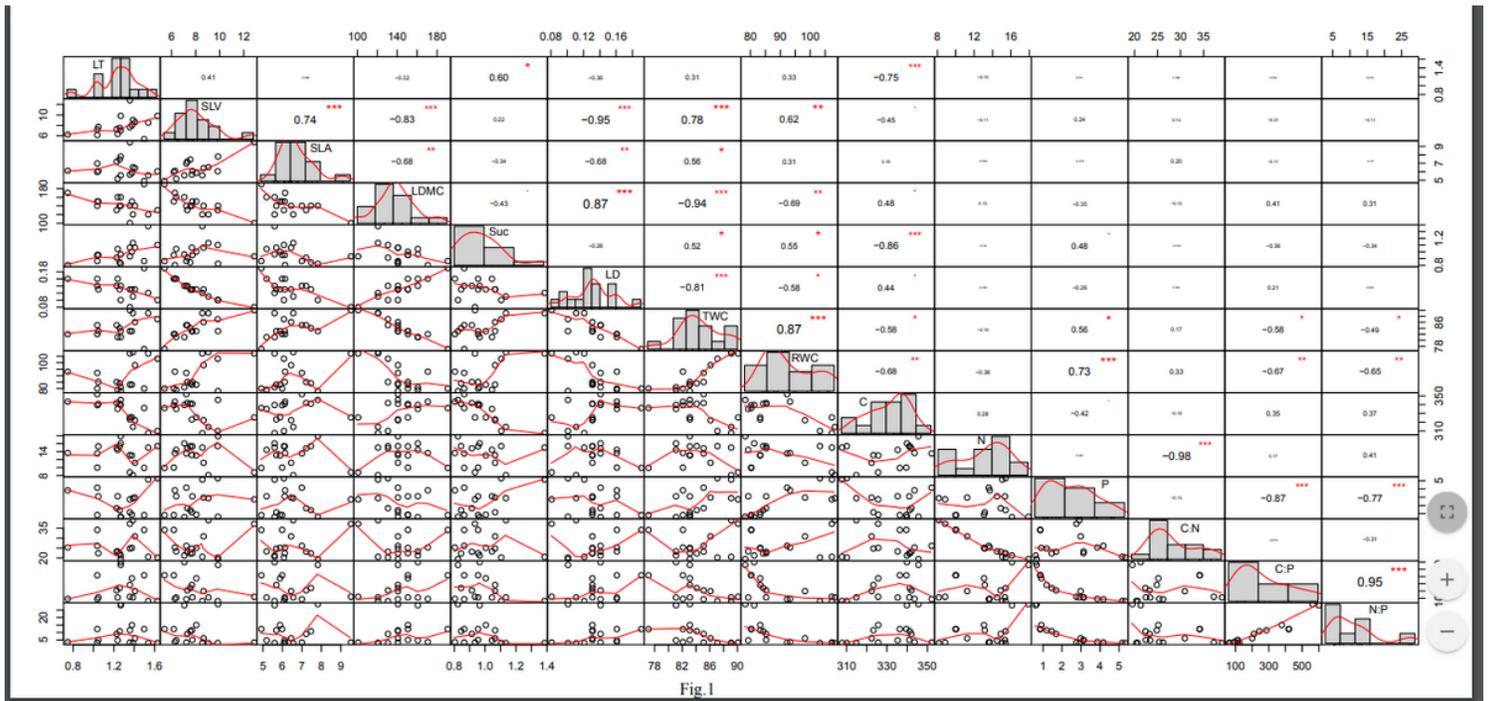


Figure 1

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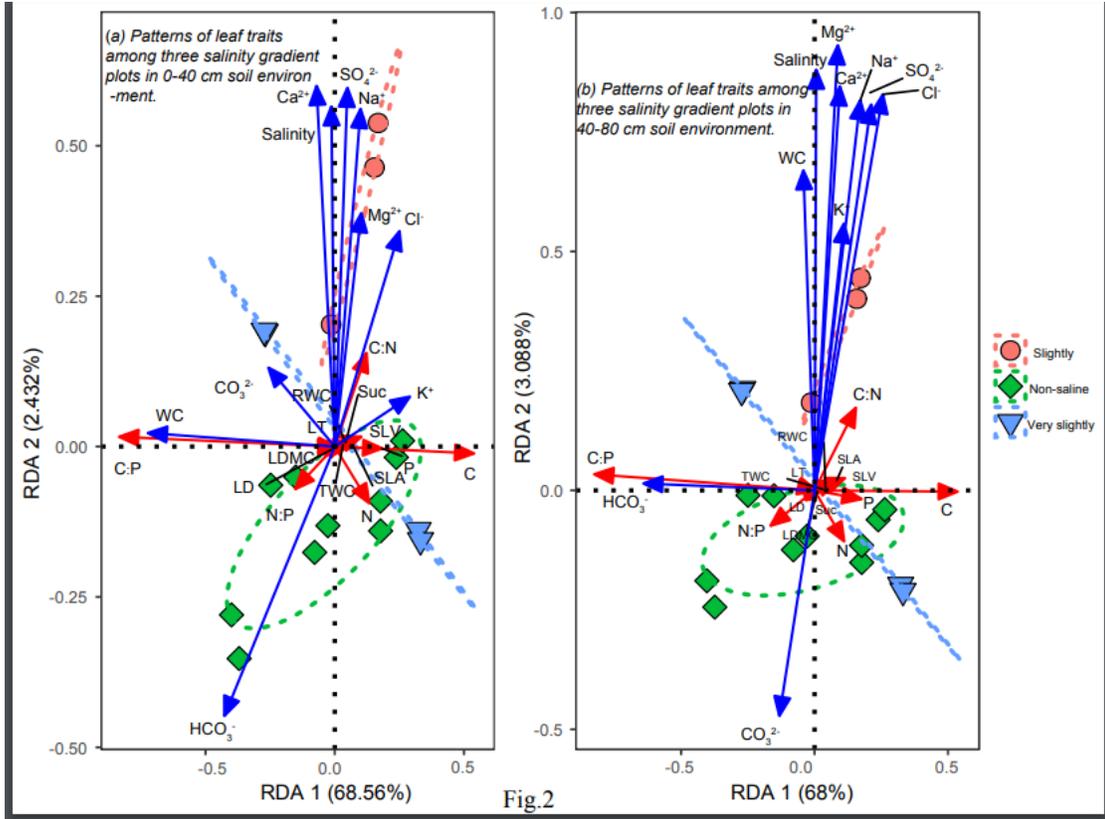


Figure 2

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). In the horizontal axis, populations growing in high salinity soils had lower C content than populations growing in lower salinity soils

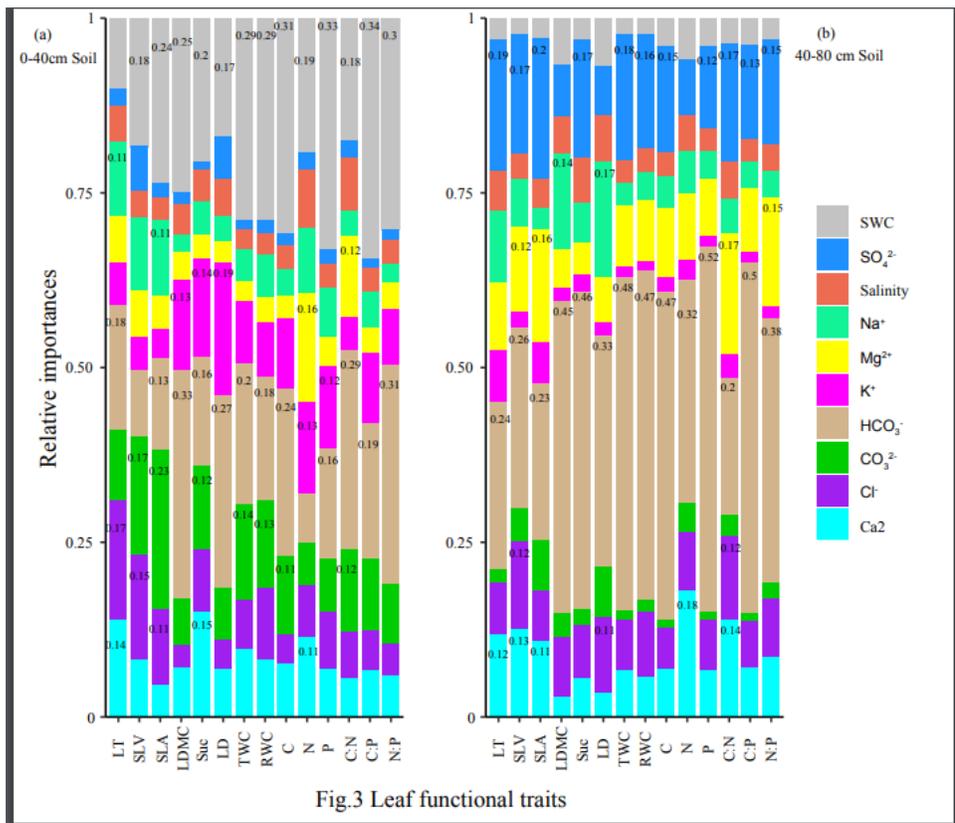


Fig.3 Leaf functional traits

Figure 3

In general, moisture, salinity, and eight major ions corresponded to leaf character variation in different amplitudes. In the 0-40cm soil layer, leaf traits patterns were mainly influenced by SWC, HCO₃⁻ and CO₃²⁻, and their relative importance values for the fourteen leaf traits

Supplementary Files

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