

The Element Composition Strategies in Chenopodiaceae Halophytes Reveal Complex Plant-Soil Interactions in Saline-Alkali Grassland

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Abstract

With the continuous increase of saline-alkali land, sustainable development of the global environment and ecology has been seriously affected. Chenopodiaceae is a pioneer plant family living in saline-alkali land, which plays a crucial role in sustaining the stability, composition and function of saline-alkali arid ecosystems. In this study, 11 elements were analyzed in different plant organs and rhizosphere soil of eight Chenopodiaceae species. Descriptive statistics of the leaf, stem and root element concentrations in eight halophyte species of contrasting salt tolerance types (salt-dilution halophytes and recretahalophytes) were calculated. Spearman's rank correlation coefficients were used to compare the correlations of elements among the leaf, stem, root and soil property, as well as between the plant and soil. General linear model was employed to explore how the variance of element concentrations in leaves, stems and roots depends on salt tolerance type, soil salinity property and soil mineral elements. The results showed that salt tolerance type and soil mineral element concentrations explained most of the variation observed in element concentrations in Chenopodiaceae plants; the soil salinity property played only a minor role. It was concluded that the genetic factors are the prerequisite in the composition pattern of leaf elements in Chenopodiaceae, and soil factors are the key to determine element accumulation. These conclusions provide an effective reference for evaluating plant breeding and its response to environmental change in saline-alkali arid areas in Hulunbuir grassland and other parts of the world.

1 Introduction

Soil salinization is a worldwide problem in terms of resources and ecology (Lobell et al. 2010). Up to now, there is approximately 20% of the irrigated soil in the world affected by salinity (Zhang et al. 2016), which continues to deteriorate (Qian et al. 2019). It is estimated that by 2050, more than 50% of cultivated land will be salinized (Rozema and Flowers 2008; Wang 2003), which will be a severe threat to land utilization rate and crop yield (Singh 2015). Soil salinity induces osmotic stress and ionic toxicity to plants (Hariadi et al. 2011), Osmotic stress can advance leaf senescence, thus reducing nutrient resorption. Simultaneously, ionic toxicity, primarily induced by sodium (Na), disrupts the potassium (K) homeostasis of the whole plant, and further hinders growth and nutrient resorption of the plant (Flowers and Colmer 2015). Halophytes exhibit various adaptive strategies to salinity and nutrient conditions (Hu and Schmidhalter 2005). These types of plants usually require abundant nutrient absorption so as to sustain high levels of photosynthesis and rapid growth in highly saline environments (Caldwell 1974). Therefore, nutrient supply and nutrients uptake during seasonal salt accumulation fluctuation affect the concentrations of nutrients in tissues and the allocation among different organs of halophytes. Several previous studies have focused on the survival of halophytes (Gutterman 2002), whereas plants growing in saline-alkali environments have received limited attention in terms of nutrient resorption. A better understanding of nutrient uptake and allocation in halophytes, as well as their relationships with environmental conditions, is crucial for predicting how saline-alkali ecosystems respond to seasonal salt accumulation change.

Mineral nutrients are indispensable to all plants on our planet (Güsewell 2005; Lü et al. 2015). All essential nutrient elements maintain plant health and thus the functions of ecosystems. Therefore, in order to develop a detailed framework for better comprehension of current biogeochemical cycles and the tendency of future development, an improved understanding of these essential elements (Han et al. 2011) and their interactions is required (Tian et al. 2018). Previous studies on nutrient allocation among different structural organs (Minden and Kleyer 2014) have largely focused on nitrogen (N) and phosphorus (P) stoichiometry (Yan et al. 2016). However, in specific contexts or regions, many other elements are also of considerable significance (Watanabe et al. 2007), by being either limited in supply or toxic to the plant (Du et al. 2017). Realizing the essential roles that other elements apart from N and P play in plant physiological functions (Pilon-Smits et al. 2009) is in no doubt necessary. For example, Na is one of the essential elements for the growth of halophytes (Almeida et al. 2017). Without Na, the health and development of halophytes cannot be guaranteed (Flowers and Colmer 2008). Na can regulate the osmotic pressure in plants, affecting their water balance and cell expansion (Wang et al. 2020; Huang et al. 2012). Another essential nutrient element is K (Zakery-Asl et al. 2014). Under salt stress, K in plants not only helps to reduce the intracellular water potential, but also alleviates the damage of high Na concentrations (Gupta and Huang 2014). Calcium (Ca) plays a key regulatory role in plant cells, which functions as an osmotic regulator to participate in the plant responses to salt stress and improved stress resistance (Luo et al. 2015). Magnesium (Mg) is an important component of chlorophyll molecules in plants (Dong et al. 2014). Under salt stress, the concentration of Na in plants increases while the concentration of Mg decreases due to the antagonism between the two ions (Zhang et al. 2017b), which leads to a decrease in photosynthetic efficiency. Additionally, iron (Fe), manganese (Mn), zinc (Zn) and copper (Cu) are all essential for the enzyme activity (He et al. 2016a). The availability of these nutrients is related to soil pH and cation exchange capacity (Han et al. 2012). Saline-alkali stress depresses soil nutrient availability (Li et al. 2018), hence leading to an increase of K^+ and Na^+ uptake in order to improve salt tolerance (Orsini et al. 2011).

In general, halophytes require maintenance of mineral element concentrations within specific ranges for optimum growth and functioning (Sardans et al. 2012). They also exhibit a certain degree of stoichiometric flexibility in response to fluctuation of soil nutrient availability. Responses to these environmental changes potentially affects plant element composition and stoichiometry against the optima of growth and functioning (Sun et al. 2017). Chenopodiaceae, as pioneer species in saline-alkali arid land, show remarkable adaptation in response to environmental stress. Not only can they survive to reproduce under around 200 mM NaCl or more salt concentration, but they also exploit Na as an osmoticum to cope with water stress (Flowers and Colmer 2015). The halophytes have evolved three tight leaf Na regulation strategies: compartmentation, secretion and rejection (Breckle 2004). Nutrient concentrations may vary according to salt tolerance types of Halophytes. At present, the patterns of chemical composition of Chenopodiaceae in different salt-tolerant types remain unclear. Since the growth characteristics of most Chenopodiaceae halophytes are similar to crops, adopting them as model plants to study plant nutrition regulation in saline soil will provide a valuable insight for plant nutrition studies in saline-alkali agriculture.

As soil salinization increasingly spreads with each passing day, the area of saline-alkali soil never stops growing. Saline-alkali ecosystems are vulnerable to this ever-growing global change. Soil salinization changes soil nutrient cycling and affects the mineral element composition of Chenopodiaceae. Therefore, a better understanding of these processes is necessary for modeling the nutrient cycling of saline-alkali ecosystems. In this study, we analyzed 11 elements in different plant organs and rhizosphere soil of eight Chenopodiaceae species in the Hulunbuir grassland, China. The following issues were scrutinized and

explored through this study: it was hypothesized that the element concentrations of halophytes are primarily affected by genes (according to different salt tolerance types) and soil mineral elements in salt environments, whereas less affected by salt and remains relatively stable under the change of salt concentration. Verification: (1) The connection between salt concentration and plant element concentration is weak. (2) Salt tolerance types are related to the concentration of plant elements. (3) Soil mineral elements have a significant influence on the concentration of plant elements.

2 Materials And Methods

2.1 Study area and species

The Hulunbuir grassland is located in northeast Inner Mongolia, China (115°31'00"~121°34'30", 47°20'00"~50°50'30"). The terrain is a vast, undulating plain at an altitude of 600–750 m. The salt content in its soil is decreasing, which is more severe in winter and early spring due to the increase of rainfall. This area has a temperate continental monsoon climate, with mild short summers and long cold winters. The average annual temperature is approximately between -3 and 0°C. The average annual duration of daylight is approximately 2800–3100 h. The precipitation period is concentrated in June to September and the annual precipitation is approximately 250–350 mm. The annual evaporation is 3–6 times of the precipitation. The total area of the grassland is 25,400,374 hectares, and the saline-alkali land accounts for 2%. There are 24 families, 64 genera and 104 species of halophyte living in this area altogether. Within these species, 19 species of Chenopodiaceae plants were collected for research. Out of the collected samples, only 8 species were known to be salt-tolerant types, of which five were salt-dilution halophytes and three were recretohalophytes (Table 1).

Table 1
Salt tolerance types of eight halophytic Chenopodiaceae.

Salt tolerance type	Species (Chenopodiaceae, taxonomy from Flora of China)	Species (Amaranthaceae, taxonomy from The Plant List)	Family	Organ of salt concentration	Salt gland type
Salt-dilution halophyte	<i>Suaeda salsa</i> (L.) Pall.	<i>Suaeda maritima</i> subsp. <i>salsa</i> (L.) Soó	Suaeda	Vacuole	None
	<i>Suaeda glauca</i> (Bunge) Bunge	<i>Suaeda glauca</i> (Bunge) Bunge	Suaeda		
	<i>Kalidium foliatum</i> (Pall.) Moq.	<i>Kalidium foliatum</i> (Pall.) Moq.	Kalidium		
	<i>Kochia scoparia</i> (L.) Schrad. var. <i>sieversiana</i> (Pall.) Ulbr. ex Asch. & Graebn.	<i>Bassia scoparia</i> (L.) A. J. Scott	Kochia		
	<i>Salsola collina</i> Pall.	<i>Salsola collina</i> Pall.	Salsola		
Recretohalophyte	<i>Atriplex patens</i> (Litv.) Iljin	<i>Atriplex laevis</i> Ledeb.	Atriplex	Salt gland	Having salt vesicle
	<i>Atriplex sibirica</i> L.	<i>Atriplex sibirica</i> L.	Atriplex		
	<i>Chenopodium glaucum</i> L.	<i>Chenopodium glaucum</i> L.	Chenopodium		Having two cell salt gland

In this study, plant samples (taken in the early stage of plant growth) and rhizosphere soil were collected from between the 25th to the 27th of June, 2018. In order to ensure the sample selection was prominent and representative, the sampling process took the convenience of transportation and uniform distribution of sampling points into consideration. The soil samples (rhizosphere) and plant samples were collected from a large area, and each sampling point was accurately positioned through Global Positioning System. Soil and plant samples were paired in correspondence to the original location collected. A total of 32 samples of soil and plants were collected. Four sampling quadrats were randomly selected within 50 m of each sampling point; each quadrat was 0.5 m × 0.5 m. For the sample plants, the uniform soil at 0–20 cm underground was collected using the diagonal method, then mixed and reduced to approximately 500 g using the quarter method.

2.2 Soil and plant sampling and chemical analysis

Aboveground and belowground parts of the plants were kept intact during sample collection. The collected plants were stored in a fresh-keeping box and taken back to the laboratory. The leaf, stem and root samples were rinsed twice with deionized water to remove dust and soil. They were then oven-dried at 120°C for 20 min, cooled to 60°C and desiccated for 48 h. Soil samples were air-dried, crushed, mixed and sieved through a 2-mm sieve before use.

For each plant sample, 0.2 g portion of prepared product was weighed and added into a PTFE beaker along with 5 ml nitric acid as well as 1 ml perchloric acid. The sample was digested using microwave digestion apparatus (MARS Xpress, CEM, USA). The digestion temperature was 160°C for 120 min and 200°C until nearly dry. The sample was processed until turning white and transparent, and the liquid in the tube was clear, with approximately 0.5 ml of liquid remaining. After the digestion was complete, and the digestion tube had been cooled, the volume of the plant sample was fixed with 2% nitric acid to 25 ml.

The soil digestion procedure was the same as the plant digestion procedure, except for the volume of acid added. A 0.2 g soil sample was added in 5 ml nitric acid, 5 ml hydrofluoric acid and 2 ml perchloric acid for digestion; the sample was fixed with 2% nitric acid to 50 ml.

Blank solutions (acid mixture without samples) were measured in duplicate during each group of sample digestions. The concentrations in the plant and soil samples of the elements K, Ca, Na, Mg, Mn, Cu, Zn and Fe were determined using Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES, Optima 8300, Perkin Elmer).

The electrical conductivity of the soil saturated extract (ECe) was chosen as the soil salinity index. The leaching solution of 1:5 soil-water ratio was prepared according to the method described by the American Saline Soil Laboratory (Richards 1954). The electrical conductivity of the saturated extract was obtained through the conversion relationship between ECe and the electrical conductivity of leaching solution extract of 1:5 soil-water ratio (EC_{1:5}) in saline soil of the Songnen Plain. The conversion was made by Eq. 1.

$$EC_e \approx 10EC_{1:5} \quad (1)$$

Here, ECe is the soil saturated extract electrical conductivity (dS m⁻¹) and EC_{1:5} is the 1:5 soil: water extract electrical conductivity (dS m⁻¹).

The soil pH was used to judge the acidity and alkalinity of the soil, and the ratio of soil to water was 1:5. The pH of the extract was determined using a PHS-3F pH meter (Shanghai Lei Magnetic Science Instrument Factory). Organic carbon concentrations in plants and soil were measured with a Walkley-Black method. Total nitrogen concentrations in plants and in soil were measured with the semi-micro Kjeldahl method. Molybdenum antimony colorimetry was used to measure total phosphorus in plants and in soil (Table 2).

Table 2
The physical, chemical and biological properties of these eight plants species (i.e, soil texture, ECe, pH, total organic matter, total nitrogen and total phosphorus).

Salt tolerance type	Species (Chenopodiaceae, taxonomy from Flora of China)	Species (Amaranthaceae, taxonomy from The Plant List)	soil texture	ECe	pH	total organic matter	total nitrogen	total phosphorus
Salt-dilution halophyte	<i>Suaeda salsa</i> (L.) Pall.	<i>Suaeda maritima</i> subsp. <i>salsa</i> (L.) Soó	Calcareous chernozem	1.04	7.71	11.60	0.29	0.65
	<i>Suaeda glauca</i> (Bunge) Bunge	<i>Suaeda glauca</i> (Bunge) Bunge		1.47	8.3	14.38	0.37	0.32
	<i>Kalidium foliatum</i> (Pall.) Moq.	<i>Kalidium foliatum</i> (Pall.) Moq.		1.67	7.84	12.91	0.43	0.41
	<i>Kochia scoparia</i> (L.) Schrad. var. <i>sieversiana</i> (Pall.) Ulbr. ex Asch. & Graebn.	<i>Bassia scoparia</i> (L.) A. J. Scott		1.42	7.84	15.52	0.54	0.40
	<i>Salsola collina</i> Pall.	<i>Salsola collina</i> Pall.		1.69	7.71	9.48	0.22	0.26
Recretohalophyte	<i>Atriplex patens</i> (Litv.) Iljin	<i>Atriplex laevis</i> Ledeb.	Calcareous chernozem	1.3	7.73	18.62	0.48	0.25
	<i>Atriplex sibirica</i> L.	<i>Atriplex sibirica</i> L.		1.40	8.01	11.44	0.40	0.41
	<i>Chenopodium glaucum</i> L.	<i>Chenopodium glaucum</i> L.		1.25	7.74	17.97	0.58	0.59

2.3 Data analysis

We calculated the descriptive statistics (mean, standard error and coefficient of variation) of the leaf, stem and root element concentrations in eight halophyte species of contrasting salt tolerance types (salt-dilution halophytes and recretohalophytes). A two-way ANOVA was performed to assess the effects of salt tolerance type, plant organ and their connection to element concentrations. ANOVA was adopted to analyze the effect of different species on element concentrations. When species effects were significant ($P < 0.05$), we used a Tukey's HSD Post Hoc test to compare the means of the species. Spearman's rank correlation coefficients were used to compare the correlations of elements among the leaf, stem, root and soil property, as well as between the plant and soil.

A general linear model (GLM) was employed to explore the variance in element concentrations in the leaves, stems and roots depending on salt tolerance type, soil salinity property and soil mineral elements. The total variance for each element was separated into salt tolerance type (species), soil salinity (pH and ECe) and soil mineral element factors. All factors included in the linear model were assigned as independent factors. All data was log-transformed to normalize the distribution of element concentrations among leaves, stems and roots. All analyses were conducted using the statistical software SPSS 19.0, JMP (v.10.0.0; SAS Institute, Cary, NC, USA).

3 Results

3.1 Patterns of element concentrations in the leaf, stem and root

Element concentrations showed considerable variation among plant organs (leaves, stems and roots) salt tolerance types (Tables 3). The results of ANOVA showed various effects of plant parts, salt tolerance type and their relationship with element concentrations (Table 3). Salt tolerance type had significant effects on P, N, C, Mg, Fe, Cu and Mn concentrations in plants, wherein these elements (P, N, C, Mg and Fe) were accumulated more in recretohalophytes than in salt-dilution halophytes. The plant organs also had a significant effect on the concentrations of P, K, Na and Na/K. These elements accumulated more in leaves than in stems and roots. Interestingly, it was discovered that in terms of different salt tolerance types and plant organs, there were no significant

differences in element concentrations in plant other than K. The results showed that the photosynthesis related elements (i.e., N, P, Mg and K) revealed higher concentrations in recretohalophytes than in salt-dilution halophytes. However, Na showed the highest concentrations in leaves, stems and roots of salt-dilution halophytes, so did Na/K (Table 3).

Table 3
Concentrations of elements in leaves, stems and roots of halophytes by salt tolerance type.

			Elements(mg·g ⁻¹)													
Salt tolerance type	Part	Statistic	P	N	C	K	Ca	Mg	Na	Fe	Cu	Zn	Mn	Na/K		
Salt-dilution halophyte	Leaf	Mean	1.07	1.89	34.4	21.4	5.83	7.41a	72.26a	1.15	0.01a	0.02	0.09	5.02a		
		N = 20	SE	0.29	0.29	0.21	0.76	0.96	0.3	0.52	0.96	0.28	0.57	0.4	0.71	
		CV	0.07	0.12	1.63	3.65	1.25	0.5	8.47	0.25	0	0	0.01	0.8		
	Stem	Mean	1.07	1.17	41.87	18.19	4.59	4.55	40.57a	0.98	0.01	0.02	0.06a	4.41		
		N = 20	SE	0.34	0.25	0.17	1.08	1.43	0.39	0.66	0.83	0.48	0.53	0.39	1.53	
		CV	0.08	0.06	1.55	4.38	1.47	0.4	5.94	0.18	0	0	0.01	1.51		
	Root	Mean	0.89	0.8	48.56	15.88	2.64a	3.1	24.08	1.33	0.07	0.01	0.05	2.16a		
		N = 20	SE	0.65	0.35	0.13	0.91	0.29	0.52	1.09	1.02	3.7	0.46	0.58	1.01	
		CV	0.13	0.06	1.39	3.22	0.17	0.36	5.85	0.3	0.06	0	0.01	0.49		
	Recretohalophyte	Leaf	Mean	1.26	1.91	37.19	29.12	9.35	9.75b	38.64b	1.13	0.01b	0.02	0.07	2.29b	
			N = 12	SE	0.39	0.19	0.14	0.57	0.6	0.4	0.92	1	0.18	0.37	0.46	1.08
			CV	0.14	0.1	1.49	4.82	1.61	1.13	10.23	0.32	0	0	0.01	0.71	
Stem		Mean	1.19	1.36	43.67	26.1	8.79	4.81	18.27b	0.73	0.01	0.02	0.03b	1.11		
		N = 12	SE	0.33	0.19	0.24	0.64	1.02	0.39	1.01	0.83	0.37	0.42	0.41	1.14	
		CV	0.11	0.08	2.98	4.83	2.58	0.55	5.33	0.18	0	0	0	0.36		
Root		Mean	0.91	0.98	50.18	23.62	5.73b	5.95	10.81	1.25	0.01	0.01	0.06	0.52b		
		N = 12	SE	0.4	0.25	0.28	0.66	0.43	0.79	0.95	0.65	0.19	0.28	0.41	0.87	
		CV	0.1	0.07	4.06	4.47	0.72	1.36	2.96	0.24	0	0	0.01	0.13		
ANOVA results																
Salt tolerance type		F		6.669	14.865	40.466	3.167	1.693	11.130	2.437	9.980	7.346	0.051	8.711	1.273	
		P		0.012	0.000	0.000	0.079	0.197	0.001	0.122	0.002	0.008	0.822	0.004	0.262	
Part	F		3.697	0.880	0.827	4.335	0.153	2.527	3.206	0.380	0.058	0.130	1.248	3.279		
	P		0.029	0.418	0.441	0.016	0.858	0.086	0.045	0.685	0.943	0.878	0.292	0.042		
Salt tolerance type*Part	F		2.653	0.081	0.259	3.149	0.586	3.067	2.496	0.432	0.060	0.157	2.081	1.403		
	P		0.076	0.922	0.772	0.048	0.559	0.052	0.088	0.651	0.942	0.855	0.131	0.251		
Different letters (a, b) indicate significant statistical differences between organs (Turkey's HSD test, ANOVA, $P < 0.05$). P-values are in bold when $P < 0.05$ and in italic when $P < 0.1$. SE, standard error; CV, coefficient of variation; N, sample size																

3.2 Relationships between element concentrations of halophytes and soil salinity

The results show that there was significant correlation between Fe, Zn concentrations in leaf and the ECe (Fig. 1h, j). In conclusion, pH value has a remarkable influence on the concentration of Zn in plant stems (Fig. 2j).

3.3 Correlations between element concentrations of halophytes and soil mineral elements

Element concentrations in leaves, stems and roots showed different correlations with soil element concentrations (Table 4). The Spearman's rank correlation coefficients showed that leaf P was positively correlated with soil P, leaf Fe was positively correlated with soil Fe, stem Fe was positively correlated with soil Fe, and root K was positively correlated with soil K.

Table 4
Spearman's rank correlations (ρ) and P-values (P) between leaf, stem and root minerals and soil nutrients. Leaf, stem and root minerals (mg g^{-1}) were \log_{10} -transformed before analysis. Soil elements are content based (mg g^{-1}). ρ are in bold when $P < 0.05$.

leaves vs soil	ρ	P	stems vs soil	ρ	P	roots vs soil	ρ	P
P	0.41	0.02	P	0.14	0.44	P	-0.15	0.42
N	0.08	0.67	N	0.22	0.23	N	-0.05	0.78
C	-0.02	0.91	C	-0.02	0.91	C	-0.16	0.38
K	0.33	0.07	K	0.13	0.47	K	0.35	0.05
Ca	-0.14	0.45	Ca	0.27	0.14	Ca	-0.30	0.09
Mg	-0.06	0.74	Mg	0.23	0.20	Mg	-0.12	0.51
Na	-0.07	0.71	Na	-0.09	0.63	Na	0.04	0.83
Fe	0.43	0.01	Fe	0.38	0.03	Fe	0.11	0.55
Cu	0.12	0.50	Cu	0.03	0.88	Cu	0.04	0.82
Zn	0.18	0.34	Zn	0.01	0.96	Zn	0.19	0.29

3.4 Differences in element concentrations across plant parts

The factor loading of 11 elements using Principal Component Analysis (PCA) varied among leaves, stems and roots (Table 5). Leaf K, Ca, Mg and Na load mainly on the first PCA axis, explaining 26.5% of the total variability; leaf Fe, Zn and Mn load on the second axis, explaining 18.9% of the total variability; leaf P, C and Cu load on the third axis, explaining 12.3% of the total variability; and leaf N loads on the fourth axis, which explains 10.7% of the total variability. Among the elements in stem, Ca, Fe, Cu and Mn load on the first PCA axis, which explains 24.1% of the total variability; the second axis was loaded with K and Na explaining 15.4% of the total variability; the third axis is loaded with N and Mg, explaining 13.5% of the total variability; and stem P, C and Zn loaded on the fourth axis, which explained 11.6% of the total variability. For root elements, Mg, Na and Mn load on the first PCA axis explains 23.4% of the total variability; the second axis is loaded by P, K, Ca and Cu, explaining 19.2% of the total variability; the third axis is loaded by N, C and Zn, explaining 15.1% of the total variability; and root Fe is loaded on the fourth axis, which explains 13.7% of the total variability (Table 5).

Table 5
The factor loading of 10 elements in the leaf, stem and root of halophytes on the principal components analysis (PCA) axes at species level (N = 32).

element	leaf				stem				root			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
P	-0.09	0.33	0.46	-0.34	-0.17	-0.36	0.37	-0.37	0.41	-0.51	0.34	0.27
N	0.41	-0.32	0.24	-0.65	-0.37	0.33	-0.61	0.24	0.22	0.58	-0.60	0.05
C	0.42	-0.37	0.54	0.28	-0.29	-0.07	0.48	0.51	0.14	-0.26	0.51	-0.17
K	0.87	-0.22	0.03	0.15	-0.35	0.70	0.33	0.17	0.30	0.58	0.40	-0.17
Ca	0.80	0.25	-0.28	-0.18	-0.67	-0.18	0.53	0.01	0.46	0.49	0.43	-0.37
Mg	0.47	0.38	0.08	0.42	0.22	0.23	0.46	-0.45	0.82	0.46	0.10	0.01
Na	-0.82	0.04	-0.01	0.32	0.48	0.57	0.01	-0.49	0.55	-0.22	-0.33	0.53
Fe	-0.15	0.78	0.22	-0.23	0.69	-0.39	0.02	0.33	-0.36	0.32	0.39	0.70
Cu	-0.24	-0.34	0.76	0.09	0.58	0.48	0.20	0.22	-0.44	0.58	0.25	0.57
Zn	0.44	0.46	0.18	0.41	0.42	0.24	0.31	0.44	0.34	-0.40	0.43	0.20
Mn	-0.01	0.73	0.25	-0.08	0.75	-0.35	0.12	0.03	0.79	-0.03	-0.25	0.33
Total variation explained (%)	26.52	18.92	12.30	10.66	24.06	15.44	13.49	11.64	23.37	19.17	15.13	13.67

Black bold indicates the main factor of the component.

3.5 Partitioning of the variance in element concentrations of different plant parts

General linear model (GLM) was employed to model the effect of salt tolerance type, soil salinity property and soil mineral elements on halophyte element concentrations. According to the results, it was discovered that the obtained models altogether explain a substantial part of the variance in element concentrations of plant leaves (Table 6), stems (Table S1) and roots (Table S2). For leaf elements, the model accounts for 26–69% of the total variability, where salt tolerance type and soil mineral elements explain 0.01–17% and 19–55% of the total variances, respectively; but salt only explains 0.5–10% of the variances. In addition, there are various conclusions that can be drawn from these three factors. For example, soil mineral elements account the most for the variances among all elements (Table 6). For stem elements, the model accounted for 35–68% of the total variability, wherein salt tolerance type and soil mineral element factors explain 0.01–26% and 22–58% of the total variances, respectively; but salt only explains 0.3–16% of the variances (Table S1). For root elements, the models reveal more significant than that of the leaf and stem, accounting for 35–70% of the total variation. More of the variances are explained by soil mineral element factors (0.03–47.6%) than by salt tolerance type (20–52%). In addition, soil mineral element factors explain more of the total variances of other elements but calcium (Table S2).

Table 6
Summary of the general linear models for the effects of salt tolerance type, soil salinity property and soil mineral element factors on the concentrations of mineral elements in leaves.

Leaf element	Total effects (r^2 , %)			
	Full	Salt tolerance type	Soil mineral element	Soil salinity
P	68.5	5.5	52.7	10.3
N	29.4	0.5	20.6	8.3
C	26.2	4.3	19.5	2.4
K	41.9	5.2	33.9	2.8
Ca	45.5	9.1	35.9	0.5
Mg	56.8	13.5	40.7	2.6
Na	54	17.1	32.9	4
Fe	53.3	0.01	52.2	1.1
Cu	50.7	12.5	30.9	7.3
Zn	58.9	1.4	55.1	2.4
Mn	47.9	9.7	32.4	5.8

Soil salinity variables: pH and electrical conductivity of soil saturated extract (ECe); soil mineral elements: P, N, C, K, Ca, Mg, Na, Fe, Cu, Zn and Mn.

4 Discussion

Some studies have found that the concentration of plant elements in arid environment is affected by the classification of plant and soil mineral elements (Miatto and Batalha 2016; Zhang et al. 2017a). However, the effects of salt tolerance type and salt environment on the concentration of elements in different plant organs have not been resolved. The analysis carried out in this study provides new insights into the relationships between element concentrations in different plant parts and salt tolerance type, salt stress and soil mineral elements.

4.1 The effect of salt tolerance type on element concentrations in different plant parts

Plant organs, salt tolerance type and their interaction had varied effects on element concentrations. The variance components attributable to salt tolerance type differed considerably between elements. This relationship is mainly driven by elements directly related to salinity, such as P, Na, Mg, K, and Ca (Matinzadeh et al. 2019). The results reveal high correlation between the elemental composition of plants growing on saline arid soils and salt-tolerance types.

Na is necessary for osmotic adjustment and the maintenance of optimum growth in halophytes (He et al. 2016b). The study found that both salt-dilution halophytes and recretohalophytes revealed high Na concentrations in leaves, stems and root, whereas salt-dilution halophytes showed higher concentrations of Na than in recretohalophytes. The accumulation of Na is largely restricted to salt-accumulation organs of halophytes. Some halophytes species, like *Phragmites australis*, can recirculate Na from the shoots back to the roots, keeping low Na concentrations in shoot vacuoles and high Na in root vacuoles (Wang et al. 2020; Fujimaki et al. 2015). Salt ions in salt-dilution halophytes accumulate in the vacuoles of succulent leaf tissues and other green tissues, as well as in the succulent column. Contrastingly, recretohalophytes have the ability to secrete salt through specialized leaf structures (salt glands), which is arguably one of the most remarkable features of recretohalophytes (Flowers and Colmer 2015; Yuan et al. 2016). This may explain why we observed slightly lower Na concentration in the leaves of recretohalophytes than in salt-dilution halophytes.

In our work, it was found that the content of K, Ca, and Mg in recretohalophytes is higher than that in salt-diluted halophytes. In saline soils, high concentration of Na in plants saturate the binding sites of ion pumps in the saturating salt-tolerance pathway, resulting in reduced potassium absorption (Taleahmad et al. 2013). In our results, Na accumulation revealed higher in salt-diluted halophytes, as a result the K content is lower compared with

recretohalophytes. Studies have pointed out that halophytes that grow in saline-alkali environments, such as *Suaeda maritima* (Flowers et al. 1977) and *Sarcobatus vermiculatus* (Donovan et al. 1997), can take advantage of Na to develop some key functions instead of K (Flowers and Colmer 2008). This indicates the possibility that Na plays the same or more important role than K in osmotic regulation. Ca regulates Na^+/H^+ reverse transportation in vacuoles as well as inhibiting the entry of Na into roots (Matinzadeh et al. 2019). It was observed in this study that the high concentration of Ca in recretohalophytes is likely to be associated to its increase, leading to the down-regulation of Na absorption. Therefore, the variation of chemical concentration between plants of different salt-tolerant type is not only related to the osmotic adjustment ability of tissues, but also related to the selective absorption of different elements.

4.2 The effects of soil salinity on element concentrations in different plant parts

The ECe is often used to indicate the level of soil salinity (Corwin and Yemoto 2019). The pH value is an important chemical property of the soil. ECe and pH value were used as salt stress factors. The results show that there was significant effect of pH value and ECe on the concentration of Zn in leaf and stem. There was significant correlation between Fe concentrations in leaf and the ECe. It could be argued that the pH value and ECe reveals the same plant element correlation trends. This reflects the plant's physiological and biochemical response to external environment (Elser et al. 2010). The soil type in this studied area is calcareous chernozem, in which the availability of N and P is relatively low. There are reports that the ionome of *Arabidopsis thaliana* plants grown under phosphorus-deficient environment revealed significantly increased concentrations of Fe and Zn (Rouached and Rhee 2017), which further prove the interaction among mineral element homeostasis in plants. As the functions of different plant organs are different, internal stability of different organs tends to vary in the same species (Yu et al. 2011). For example, in the degraded grasslands of Northeast China, the internal stability of N and P in the roots of *Leymus chinensis* (Trin.) Tzvel was higher than that in the leaves (Li et al. 2016). Studies on tree seedlings and shrub plants have also found that the internal stoichiometric stability of plant leaves is higher than that of roots (Schreeg et al. 2014). It can be seen from results that the elemental internal stability of halophytes leaves is also higher than that of roots. Therefore, plants maintain their own growth and development needs by coordinating the nutrient distribution among various organs in a saline-alkali and arid environment.

4.3 Differences in element concentrations across plant parts

Element convergence in different organs of halophytes contributes to their biochemical function and physiological property. For leaf elements (Table 5), it was discovered that the first PC axis represented the major variances for most macronutrient elements (including K, Ca, Mg and Na), which represented the "photosynthesis and osmoregulation" element set (Tuteja 2007). Ca is a key component for cytoderm stabilization, while Mg is found in chlorophyll and actively participates in plant photosynthesis. Na and K are both crucial for osmotic adjustment. The second PC axis represented the "structural and enzymes" element set. Mn helps maintain the structure of the lamellar membrane systems of chloroplasts, and Zn and Fe are activators or components of enzymes (Pilon-Smiths et al. 2009). The third and fourth axis of the PCA of nutrient composition mainly represents variations in leaf N, P, Cu and C, which are associated with the "nucleic acid-protein set" (Zhang et al. 2012). Most elements that constitute a plant are obtained from the soil through roots. These soil-derived elements are required for plant structure, metabolism, protein functioning, signaling and appropriate osmotic and electrochemical potential. Notably, the results are mostly consistent with those of previous studies. In desert shrubs (legumes and non-legumes), Ca, Mg, Mn, Zn, Cu and Fe in leaves, stems, and roots have been shown to mainly load on the first PCA axis. The variations of these element concentrations across desert shrubs are mainly explained by soil characteristics (He et al. 2016a). Leaf element concentrations of terrestrial plants in China were correlated with the environment (Zhang et al. 2012). Thus, the elemental composition of tissues (the "ionome") is a consequence of complex plant processes and plant-environment interactions (Baxter and Dilkes 2012).

4.4 Element composition in the leaf, stem and root and environmental control

The discoveries in this study support our hypothesis that soil mineral elements are more important than salt tolerance type and salt property in explaining the variation of element concentrations across halophytes. According to the results of the partial GLMs, it was found that the percentage of elemental variations explained by three factors combined (salt tolerance type, soil salinity and soil mineral elements) varied among different organs: 26 to 69% of the variation was explained for leaves (Table 6), 35 to 68% for stem (Table S2), and 35 to 70% for roots (Table S3). For leaf, stem and root elements, soil mineral elements had greater explanatory power. The productivity, functioning and biogeochemical cycles of terrestrial ecosystems are strongly affected by leaf element concentrations (Zhang et al. 2012). Soil mineral elements and salt tolerance type explained most of the variation in element concentrations in Chenopodiaceae (Amaranthaceae). Out of the three factors, soil properties explained most of the variances in 11 leaf elements (Table 6). Since the availability of these elements largely depends on soil water conditions, and the soil of the study area is arid and calcareous, where K, Mn, Zn, Cu, and Fe mainly exist in non-exchangeable forms, these elements are largely in limited supply to the halophytes. Similar to leaf element concentrations, salt tolerance type and soil mineral elements explained more of the variance in stem and root elements than soil salinity (Table S2, S3). Several studies have shown that the accumulation of certain elements in the leaves of halophytes is genetically controlled as primarily independent on the condition of their rhizospheres (Kruger and Peinemann 1996; Matinzadeh et al. 2013). However, most mineral elements found in plant tissues come exclusively from the soil, necessitating plants to adapt to highly variable soil compositions to survive and thrive. To adapt to the instability of soil element availability, halophytes must alter the uptake and storage of both nutrients as well as toxic elements. Therefore, it suggests that genetic factors are the prerequisite in the composition pattern of leaf elements in Chenopodiaceae, while soil factors are the key to determine element accumulation.

5 Conclusion

The halophyte has higher element concentrations in leaves than in stems and roots. The higher concentrations of Na in salt-dilution halophytes than in recretohalophytes indicated that Na arguably plays an equal or more important role than K in osmoregulation. The variation of element concentrations within different organs was mainly determined by salt tolerance type and soil mineral elements. In summary, it can be concluded that element composition patterns in these studied Chenopodiaceae plants are the consequence of complex plant-soil interactions. These conclusions can provide an effective

reference for evaluating plant breeding and its response to environmental change in saline-alkali arid areas in Hulunbuir grassland, as well as other parts of the world.

Declarations

Author Contributions: X.-Q.S., Z.-H.Z. and Z.-H.T. conceived and designed the analysis and wrote and reviewed the paper. Y.-H.S. and J.-W.Z. collected the data and performed the experiment. X.-Q.S. and Y.-H.S. carried out analysis the data. Z.-W.L. reviewed the paper.

All authors have read and agreed to the published version of the manuscript.

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Figures

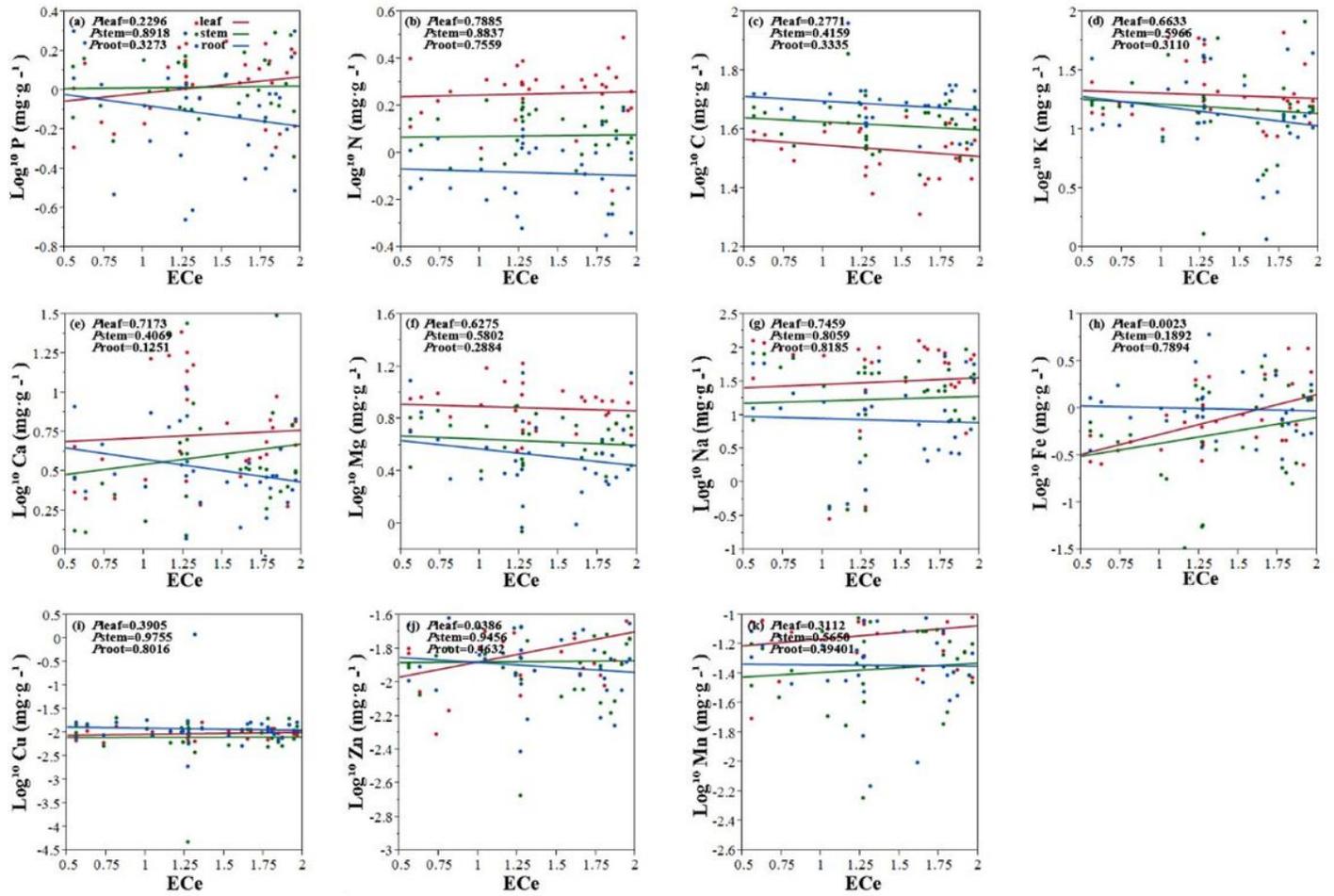


Figure 1

Linear relationships of ECe (dS m⁻¹) with 11 elements concentration among leaves, stems and roots. Colored lines represent significant relationships ($P < 0.05$) for halophytes (red, leaves; blue, stems; green, roots).

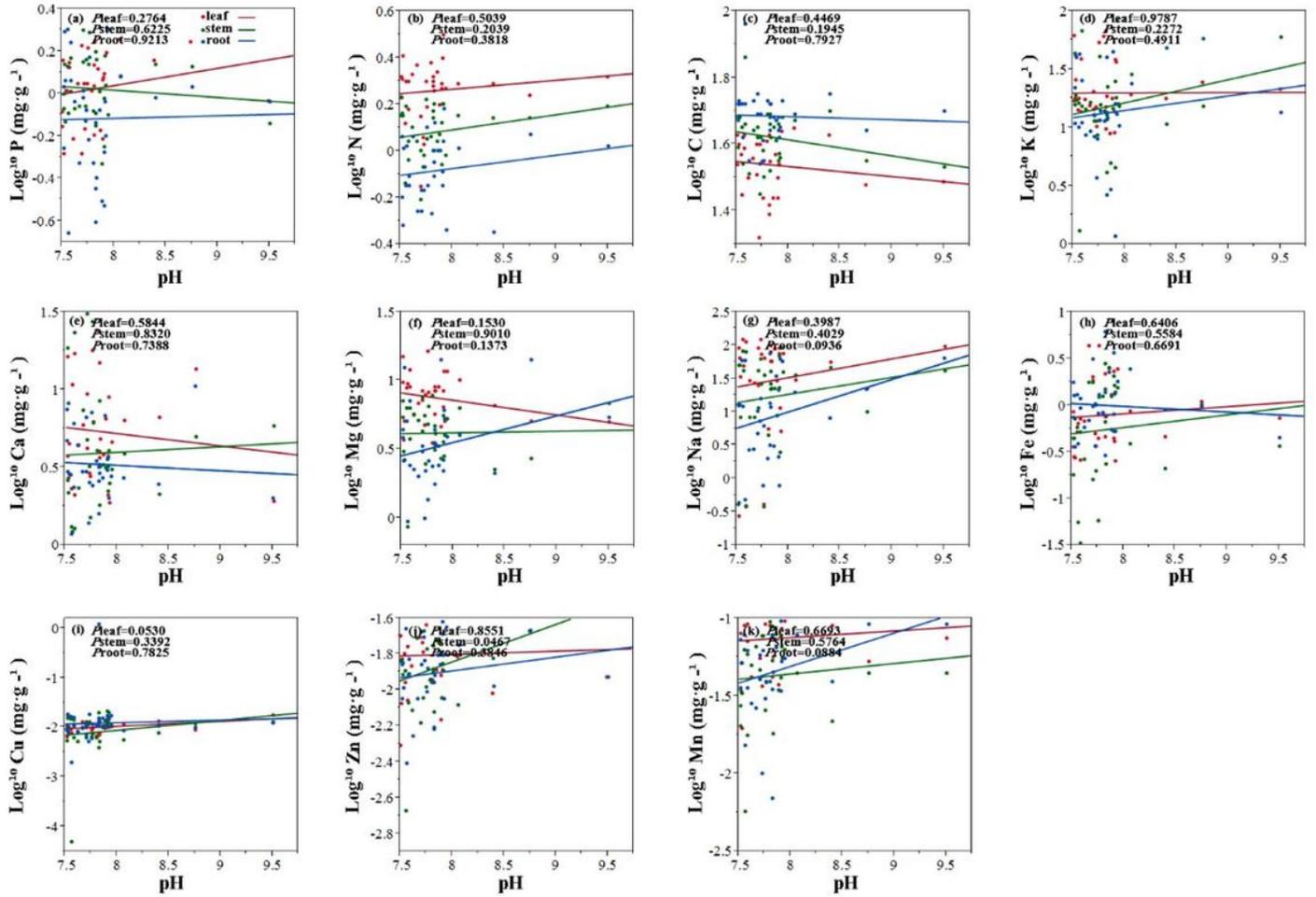


Figure 2

Linear relationships of pH with 11 elements concentration among leaves, stems and roots. Colored lines represent significant relationships ($P < 0.05$) for halophytes (red, leaves; blue, stems; green, roots).

Supplementary Files

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