



Research article

The elemental composition of halophytes correlates with key morphological adaptations and taxonomic groups

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ABSTRACT

Halophytes are crucial in the light of increasing soil salinization, yet our understanding of their chemical composition and its relationship to key morphological traits such as succulence or salt excretion is limited. This study targets this issue by exploring the relationship between the elemental composition of 108 plant species from saline environments in Iran and their eco-morphological traits and taxonomy. Leaves and/or photosynthetic shoots of individual species and soils were sampled and analyzed for 20 elements in plant samples and 5 major elements plus % gypsum content, pH, and EC in soil samples. Eu-halophytes and leaf- and stem-succulent and salt-recreting plants showed high concentrations of Na, S, and Mg and low concentrations of Ca and K. In contrast, pseudo-halophytes, facultative-halophytes and eury-hygro-halophytes, which often lack succulent shoots, showed low Na, S, and Mg and high Ca and K concentrations in their leaves. Clear patterns were identified among taxonomic families, with Chenopodiaceae and Plumbaginaceae having high Na and Mg and low Ca and K concentrations, Caryophyllaceae having high K, Poaceae having low Na, and Asteraceae, Boraginaceae, and Brassicaceae showing high foliar Ca concentrations. We conclude that the elemental composition of halophytes and pseudo-halophytes is related to salt-tolerance categories, eco-morphological types and respective taxonomic groups.

1. Introduction

Soil and water salinization are among the most serious problems resulting from agriculture and land degradation in many countries (Chinnusamy et al., 2005; Hariadi et al., 2011; ZuccaRini, 2008). It is estimated by the World Food and Agricultural Organization (FAO) that a total area of 1 billion ha of the world's surface is affected by salinity and sodicity (Pennock et al., 2015). Salinized soils are expanding as a result of irrigation practices, which limit the production of food in an increasingly populated world (Duarte et al., 2015).

Only a small proportion of known vascular plants have the ability to resist high salinity. They are known as halophytes (Duarte et al., 2015), and defined as plants that have the ability to complete their life cycle in salt concentrations of at least 200 mM NaCl (Alhdad et al., 2013; Colmer and Flowers, 2008; Flowers et al., 1986; Naidoo, 1994; Parida and Das, 2005). Contrastingly glycophytes (non-halophytes) are defined as species that cannot survive in a saline environment (Duarte et al., 2015). The crucial impact of saline soils on plant physiology is the

high osmotic pressure, which disturbs net photosynthesis because of the induction of physiological drought, stomatal closure and decreased available turgor for plant growth. In addition, excessive salt in plant tissues enhances ion specific toxicity and disturbing cell homeostasis (Flowers et al., 2014; Hassine et al., 2008; Kudo et al., 2010; Wang et al., 2010). Only c. 1% the world's flora are halophytes (Duarte et al., 2015; Flowers and Colmer, 2008; Flowers et al., 2014). Halophytes show different tolerance mechanisms and regulatory pathways and they can be classified into different functional groups accordingly (Milić et al., 2013; Mori et al., 2010).

Halophytism evolved in multiple lineages of angiosperms as an example of widespread convergence, but it is more prevalent in some lineages, like the order Caryophyllales among dicots and Poales among monocots (Byng et al., 2016). The family Chenopodiaceae is one of the most successful plant group adapted to high salinity and drought conditions (Chenchouni, 2017; Glenn et al., 2012). Some of these species not only tolerate high levels of salinity, but display optimal growth under saline conditions (Barakat et al., 2014). This family includes both

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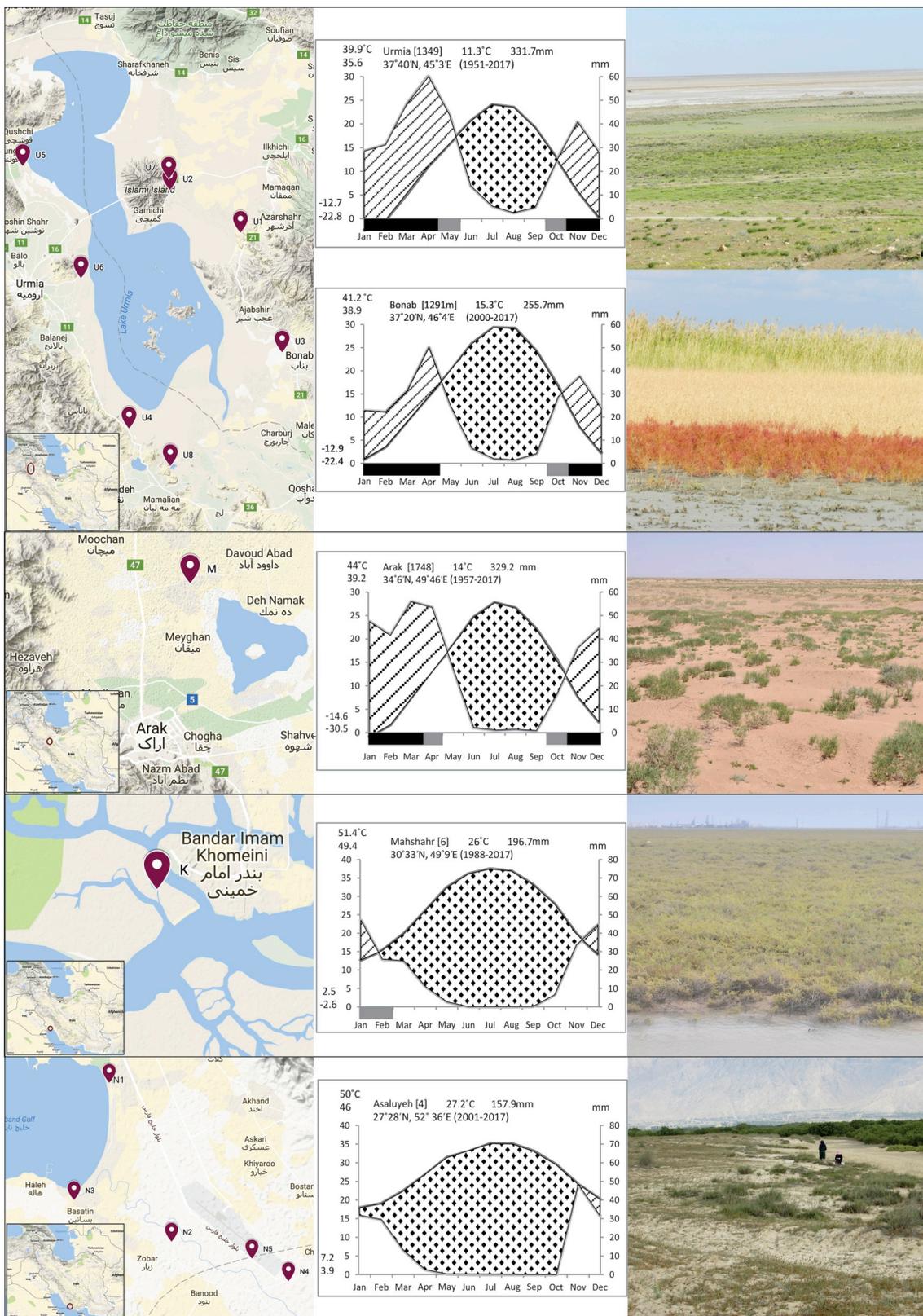


Fig. 1. Location of the studied sites in Iran, climatic diagrams for the studied locations, and pictures of the vegetation in each site. Inserts show the location of each sampling area within Iran.

Table 1
Details of studied sites, their location, geodesic coordinates, altitude (m) and salt marsh names.

Sites	Location	Geodesic coordinates	Altitude	Salt marsh name
U1	East Azerbaijan; Azarshahr	37°42′ 29.4″ N, 45°50′ 34.1″ E	1300	Lake Urmia
U2	East Azerbaijan; Islami Island	37°49′ 51.5″ N, 45°35′ 07.2″ E	1292	Lake Urmia
U3	East Azerbaijan; Akhondgheshlagh	37°21′ 50.8″ N, 45°59′ 36.4″ E	1281	Lake Urmia
U4	West Azerbaijan; Rashakan	37°08′ 37.3″ N, 45°26′ 16.1″ E	1272	Lake Urmia
U5	East Azerbaijan; Gol Tappeh	37°53′ 58.3″ N, 45°03′ 07.4″ E	1281	Lake Urmia
U6	West Azerbaijan; Chi chest	37°34′ 39.5″ N, 45°15′ 49.6″ E	1283	Lake Urmia
U7	East Azerbaijan; Saray	37°51′ 48.6″ N, 45°34′ 45.0″ E	1285	Lake Urmia
U8	West Azerbaijan; Souldouz	37°02′ 08.4″ N, 45°35′ 15.8″ E	1286	Lake Urmia
M	Ostane Markazi; Meyghan	34°16′ 07″ N, 49°45′ 17″ E	1692	Lake Meyghan
K	Khuzestan; Mousa estuary	30°26′ 06″ N, 49°01′ 56.8″ E	1.5	Persian Gulf
N1	Bushehr; Nayband	27°26′ 44.2″ N, 52°40′ 35″ E	7.37	Persian Gulf
N2	Bushehr; Zobar	27°22′ 22.1″ N, 52°42′ 33.1″ E	1.7	Persian Gulf
N3	Bushehr; Basatin	27°23′ 29.3″ N, 52°39′ 29.1″ E	10.2	Persian Gulf
N4	Bushehr; Chah Mobarak	27°21′ 14.8″ N, 52°46′ 09.9″ E	15.1	Persian Gulf
N5	Bushehr; Banood	27°21′ 52.3″ N, 52°45′ 01.4″ E	1.6	Persian Gulf

salt accumulator and salt secretor species (Matinzadeh et al., 2013; Milić et al., 2013; White et al., 2017).

Adaptation to saline soils is the result of several modifications of biophysical, physiological, morphological, and biochemical traits of plants (Wu et al., 2009). Depending on their affinity for saline soils, plants growing in saline environments have been classified as eu-halophytes, facultative-halophytes, eury-hygro-halophytes and pseudo-halophytes (Breckle, 1990). Eu-halophytes exclusively grow on high saline soils, similar to seawater salt concentration (Flowers and Colmer, 2015). Facultative-halophytes are plants that grow both in saline and non-saline conditions by having broader physiological plasticity and including halophytic and glycophytic ecotypes (Parida and Das, 2005). Eury-hygro-halophytes can grow in muddy and subaquatic saline, brackish to fresh water conditions. Most species of this group are monocots (Ogburn and Edwards, 2010). Finally, pseudo-halophytes are non-halophytes or glycophytes which usually occur in saline ecosystems only during favorable seasons and sites where salt concentrations are low. These plants may also show certain mechanisms to avoid salt excess when growing in saline soils, like leaching out salts, root selectivity against Na and Cl or diversion of salt out of the assimilating tissues (Breckle, 1986).

Eu-halophytes are highly specialized in their morphology, being either salt-secreting (salt excreting or salt secreting) or succulent plants. Many of these species have salt bladders and/or salt glands (Lambers et al., 2008). Salt bladders are vesiculated trichomes found in some halophytes like *Atriplex* spp., which can remove toxic salts from the cytosol of epidermal cells on both of the leaf surfaces. Salts accumulated in these trichomes are deposited on the leaf surface when trichomes collapse, and subsequently washed off the plants by rain, wind or gravity (Abdelly et al., 2008; Albert, 1975; Lambers et al., 2008; Schirmer and Breckle, 1982). Salt glands are special appendages within epidermal cell layer that actively secrete salts out of the leaves (Dassanayake and Larkin, 2017; Duarte et al., 2015; Grattan and Grieve, 1992; Lambers et al., 2008; Zedler et al., 2003; Zoerb et al., 2013). Eu-halophytes also include some succulent plants, which accumulate high Na and Cl in their photosynthetic tissues by the absorption of extra water in their vacuoles. This reduces the toxicity of salt either in their leaves, assimilating stems, or both (Breckle, 1986; Milić et al., 2013; Mori et al., 2010; Naz et al., 2013; Zedler et al., 2003). Some plants may have combined strategies, for example some leaf-succulent eu-halophytes have salt trichomes in the early stages of their life cycle (Akhani et al., 2005).

Salt tolerance depends on the ability of plants to exclude Na and maintain nutritional homeostasis (Kudo et al., 2010). Halophytes face multiple challenges in saline environments including toxic ion effects, nutrient limitations, and reduced water potential. The relationship between the chemical composition of plants and saline condition is of

great importance to understand plant adaptation under high salinity. Low leaf K, Ca, and Mg concentrations along with the accumulation of Na were documented in plants growing in high salinity, and have been recorded for some eu-halophytes including many Chenopodiaceae (Albert and Kinzel, 1973; Albert and Popp, 1977; Gulzar et al., 2003; Kachout et al., 2011; Khan et al., 2000a, b; Kudo et al., 2010; Milić et al., 2013; Wiebe and Walter, 1972; Zoerb et al., 2013). Several studies have shown that the accumulation of certain elements in the leaves of some species of eu-halophytes is genetically controlled with poor dependency on the condition of their rhizospheres (Albert, 1982; Breckle, 1986; Krüger and Peinemann, 1996; Matinzadeh et al., 2013). However, to the best of our knowledge, no previous studies have looked at the chemical composition of a broad group of plants growing under natural saline conditions, and the relationship between the chemical composition of different types of halophytes, their morphological adaptations and plant lineages remains mostly unexplored.

This paper includes a comprehensive study of the leaf elemental composition of 108 plant species growing on saline environments from Iran. Our hypothesis was that the salt-tolerant category and the morphological adaptation of halophytes will be related to their chemical composition and phylogeny. In particular, we sought to answer the following questions: (1) is there any relationships between salt-tolerance categories of plants in saline soils and their chemical composition? (2) Are different eco-morphotypes (succulent halophytes, secreting halophytes, semi-succulent halophytes and non-succulent species) related to the plant elemental composition? (3) Up to what point is the elemental composition of halophytes related to their phylogeny?

2. Materials and methods

2.1. Study area, vegetation and climate

Our study area comprises different saline ecosystems in northwest and central of Iran and also the northern coasts of the Persian Gulf. These include eight sites around Lake Urmia (NW Iran, in Provinces of E and W Azerbaijan), one site around Lake Meyghan (Central Iran, Province of Ostane Markazi), one site near Musa estuary on the NW parts of Persian Gulf (Khuzestan Province) and five sites in Nayband Bay coasts in the Persian Gulf (Bushehr Province) and surrounding saline flats (Fig. 1; Table 1). All these areas are good representatives of the different saline environments found in Iran.

Lake Urmia: located within a National Park, is the second largest hypersaline lake in the World and the largest inland lake in Iran. At an elevation of 1274 m, it was highlighted in recent years in national and international media because of its drastic shrinkage reducing its surface area from c. 6000 km² in 1995–2300 km² in July 2018 (Stone, 2015; ULRP, 2018). The drying up of the lake affected the halophytic

vegetation in recent years. In its normal conditions the vegetation profile consisted of a several zones from the coasts (often a belt of *Salicornia*), muddy high saline plains (*Halocnemum strobilaceum*), patches of sedges, C₄ transitional plant formations, *Tamarix* patches or belts and finally *Artemisia* or ruderal plant communities in undulating hills (Asri, 1998; Asri and Ghorbanli, 1997; Djamali et al., 2008). Climate in the area is semi-arid continental with winter rain, being part of the Irano-Turanian Xeric Continental bioclimate (Djamali et al., 2011). The average precipitation varies from 255.7 to 331.7 mm with very cold winters and freezing average minimum temperature for almost half of the year (Fig. 1). The surrounding parts and the coasts of the lake are under extensive grazing pressure. The exposed lake bed in most parts of the lake is too saline for the growth of vascular plants.

Lake Meyghan: Saline depression located c. 10 km north of the city of Arak, in Ostan Markazi Province and at an elevation of 1674 m. This is one of the highest saline areas in Iran. The water body of the lake was c. 112 km² but recently has shrunk due to intensive agricultural and developmental activities (Akhani, 2006). The area has an extremely rich halophytic flora and vegetation consists of hygro-halophytes, muddy salt plants, *Nitraria schoberi* shrub vegetation and *Stipa* steppe (Akhani, 1989 (publ. 1992)). The climate of the area is very similar to that of Lake Urmia, with an Irano-Turanian Xeric Continental bioclimate (Fig. 1). The lake suffers almost the same problem as Lake Urmia regarding reduction of its water inflow. This causes instability of soil with large amount of dust emission in the area. Grazing is largely prohibited in areas under reclamation programs including the site studied here.

Khore Musa (Musa estuary): the vegetation of the study site in the tidal coast of the Musa estuary in southern shores of Khuzestan Province consisted of a *Salicornia sinus-persica* and *Suaeda iranshahrii* C₃ zone followed by C₄ rich plant community of *Bienertia sinuspersici*, *Suaeda khalijefarsica* and *S. fruticosa* (Akhani, 2015; Akhani and Deil, 2012). The area has a mean annual precipitation of 196.7 mm and mean temperature of 26 °C (Fig. 1) with a Tropical Desertic (Trd) bioclimate (Djamali et al., 2011).

Nayband Bay is a National Park located near the industrial zone of Asaluyeh on the Persian Gulf coasts. The tidal vegetation is mostly mangrove forests of *Avicennia marina* followed by *Arthrocnemum macrostachyum* on the high saline shores and end to coastal dunes and xerophytic dry plains. The main disturbing factors in the area are moderate grazing by cow and goat and use of the coasts for recreation. The mean annual precipitation is 157.9 mm and the mean annual temperature is 27.2 °C (Fig. 1). The temperature never drops to freezing point, which is typical of a Tropical Xeric (Trx) bioclimate (Djamali et al., 2011).

2.2. Studied species and nomenclature

Study species included 54 annuals (77 samples; Table 2) and 54 perennials (69 samples; Table 2). Plants were ascribed to different functional groups (eu-halophytes, facultative-halophytes, eury-hygro-halophytes, and pseudo-halophytes) depending on their salinity and moisture preference; and different eco-morphotypes (leaf-succulent, stem-succulent, semi-succulent, salt-secreting, and non-succulent) (Table 2) (Breckle, 1990). Only those functional groups with at least two representatives were included in our analyses. In the case of those species collected from more than one site, (Table 2), average chemical data were calculated across sites prior to statistical analyses.

Nomenclature mostly follows Flora Iranica (Rechinger, 1963-2015). In the case of Chenopodiaceae and several groups which changed in recent years based on new molecular findings, we applied recent generic names (Akhani et al., 2007; Hernández-Iedesma et al., 2015).

2.3. Sampling of plant and soil

Plant and soil samples were collected during 2015 and 2016 from

early March to November depending on the sites and phenology of studied plant species: Lake Urmia (May 2015, July 2015, and April 2016), Lake Meyghan (June 2016), Khore Musa (October 2015) and Nayband (March 2016). Most of our collections for chemical analyses have been done in periods of low phenological activity, owing to the lower chemical variation in plants (Bolukbasi et al., 2016). Leaves and/or photosynthetic shoots of plants were collected from at least 5 individuals for each species and stored in paper bags in cool temperature (using a portable fridge) until transported to the laboratory within the next 48 h. Owing to the low amount of tissue available, leaf material of each species was pooled into one composite sample per plant species and site. In total, we collected 146 samples belonging to 108 plant species for chemical analyses. Also at least 5 soil samples from 5 to 15 cm depth were collected in plastic bags from each site.

2.4. Chemical analyses

Leaves were dried at 75 °C for 72 h (Minden et al., 2012) and then milled in a ball mill (Retsch Mixer MM400) prior to analyses. Plant samples were then dissolved in HNO₃-H₂O₂ (8:2) using Microwave Acid Digestion (speedwave MWS-3⁺, BERGHOF, Eningen, Germany). The filtered extract solution was used for measurement of Al, Ca, Cr, Cu, Fe, K, Li, Mg, Mn, Mo, Na, Ni, P, S, Si, Ti, V and Zn using inductively coupled plasma-optical emission spectrometry (ICP-OES, Varian ICP 720-ES, analytical services of the Estación Experimental del Zaidín, CSIC, Spain). Total nitrogen and carbon (N and C_{total}) concentrations were determined in an elemental analyzer (Elementar N/CN; VarioMax, Hanau, Germany) (Table A1).

Soil samples were air-dried, milled and dissolved in HCl-HNO₃ (9:3) with the same instruments used for plant samples. The extracted solution was used for the determination of Ca, K, Mg, Na, and S content by ICP-OES. Soil pH and conductivity were measured with a pH/conductivity meter (ORION STAR A215) by diluting samples with distilled water to 1:2.5 and 1:5 (g:ml), respectively. The percentage of gypsum content in the soil was determined gravimetrically by comparing the weight of samples sequentially dried at 50 °C and 105 °C (Porta et al., 1986) (Fig. A1, Table A2).

2.5. Statistical analyses

Statistical analyses were performed at three levels: (i) relationships between 20 leaf nutrients in different salt-tolerance categories and eco-morphotypes, using a constrained multivariate approach and PERMANOVA; (ii) differences between the concentrations of selected nutrients (Ca, K, Mg, Na, and S), relevant for saline environments, among salt-tolerance categories and eco-morphotypes using simple linear models and; (iii) relationships between leaf nutrients and plant families using a constrained multivariate approach.

First, differences in the plants elemental composition within salt-tolerance categories and eco-morphotypes were examined with redundancy analyses (RDA). This multivariate technique is an Euclidean-based ordination test using an explanatory matrix (in our case a table with dummy variable representing the 'salt-tolerance categories', i.e. eu-halophytes, facultative-halophytes, eury-hygro-halophytes, and pseudo-halophytes or the 'eco-morphotype', i.e. leaf-succulent, stem-succulent, semi-succulent, salt-secreting, and non-succulent) to explain variation in the dependent matrix (in our case the chemical composition of plants). To estimate the significance of different factors combined, namely the type of life history (annual/perennial), taxonomic family, study sites and eco-morphotypes, we run PERMANOVA analyses where the variability in the elemental composition of plants was explained by 'life history', 'salt-tolerance', 'family', 'site' plus the interaction between 'life history' and 'salt tolerance' as fixed factors, or 'life history', 'eco-morphotype', 'family', 'site' plus the interaction between 'life history' and 'eco-morphotype' as fixed factors (Table 3).

Second, we focused on certain key elements for plants growing on

Table 2

Details of studied taxa, study sites, life cycle, and functional groups. Life cycle included perennials (P) and annuals (A). 'salt-tolerance categories' included Eu-halophytes, Facultative-halophytes, Eury-Hygro-halophytes, and Pseudo-halophytes; and the 'eco-morphotypes', included Leaf-succulent, Stem-succulent, Semi-succulent, Salt-recreting, and Non-succulent.

No.	Taxon	Sites	Life history	Salt-tolerant	Eco-morphotype
Acanthaceae					
1	<i>Avicennia marina</i> (Forssk.) Vierh.	N1	P	Eu-halophyte	Salt-recreting
Apocynaceae					
2	<i>Cynanchum acutum</i> L.	U4	P	Facultative-halophyte	Non-succulent
Asparagaceae					
3	<i>Asparagus verticillatus</i> L.	U1	P	Facultative-halophyte	Non-succulent
Asteraceae					
4	<i>Achillea tenuifolia</i> Lam.	U1	P	Facultative-halophyte	Non-succulent
5	<i>Calendula sancta</i> L.	N2	A	Pseudo-halophyte	Non-succulent
6	<i>Carduus arabicus</i> Murray	U1	A	Pseudo-halophyte	Non-succulent
7	<i>Cirsium alatum</i> (S. G. Gmel.) Bobrov	U1	P	Eu-halophyte	Semi-succulent
8	<i>Grantia aucheri</i> Boiss.	N5	P	Pseudo-halophyte	Semi-succulent
9	<i>Pulicaria arabica</i> (L.) Cass.	N3	P	Pseudo-halophyte	Non-succulent
10	<i>Saussurea salsa</i> (Pall. ex Pall.) Spreng	U1	P	Eu-halophyte	Semi-succulent
11	<i>Scorzonera parviflora</i> Jacq.	U1	P	Pseudo-halophyte	Non-succulent
12	<i>Senecio glaucus</i> L.	U1	A	Facultative-halophyte	Semi-succulent
Boraginaceae					
13	<i>Arnebia decumbens</i> (Vent.) Coss. & Kralik	M	A	Facultative-halophyte	Non-succulent
14	<i>Asperugo procumbens</i> L.	U6, U5	A	Pseudo-halophyte	Non-succulent
15	<i>Heliotropium bacciferum</i> Forssk.	N3	P	Facultative-halophyte	Semi-succulent
16	<i>Lithospermum arvense</i> L.	U2	A	Pseudo-halophyte	Non-succulent
17	<i>Nonnea caspica</i> (Willd.) G. Don	U5	A	Pseudo-halophyte	Non-succulent
Brassicaceae					
18	<i>Brassica tournefortii</i> Gouan	N1	A	Eu-halophyte	Non-succulent
19	<i>Descurainia sophia</i> (L.) Webb ex Prantl	U5	A	Pseudo-halophyte	Non-succulent
20	<i>Erucaria hispanica</i> (L.) Druce	N5	A	Facultative-halophyte	Semi-succulent
21	<i>Erysimum repandum</i> L.	M	A	Facultative-halophyte	Non-succulent
22	<i>Euclidium syriacum</i> (L.) W. T. Aiton	U1, U5	A	Facultative-halophyte	Non-succulent
23	<i>Lepidium cartilagineum</i> (J. C. Mayer) Thell.	U1	P	Eu-halophyte	Semi-succulent
24	<i>Lepidium draba</i> L.	U1, U5	P	Facultative-halophyte	Non-succulent
25	<i>Lepidium perfoliatum</i> L.	U5	A	Facultative-halophyte	Non-succulent
26	<i>Lepidium vesicarium</i> L.	U5	A	Facultative-halophyte	Non-succulent
27	<i>Malcolmia africana</i> (L.) W. T. Aiton	U1, U6	A	Facultative-halophyte	Non-succulent
28	<i>Olimarabidopsis pumila</i> (Stephan) Al-Shehbaz & al.	U1, U5	A	Facultative-halophyte	Non-succulent
29	<i>Sisymbrium septulatum</i> DC.	U1	A	Pseudo-halophyte	Non-succulent
Capparaceae					
30	<i>Capparis spinosa</i> L.	N3	P	Facultative-halophyte	Semi-succulent
Caryophyllaceae					
31	<i>Gypsophila perfoliata</i> L.	U1	P	Eu-halophyte	Semi-succulent
32	<i>Holosteum glutinosum</i> (M. Bieb.) Fisch. & C. A. Mey.	U5	A	Pseudo-halophyte	Semi-succulent
33	<i>Holosteum umbellatum</i> L.	U5	A	Pseudo-halophyte	Semi-succulent
34	<i>Silene conoidea</i> L.	U2	A	Pseudo-halophyte	Non-succulent
35	<i>Spergularia diandra</i> (Guss.) Boiss.	N4	A	Eu-halophyte	Leaf-succulent
Chenopodiaceae					
36	<i>Arthrocnemum macrostachyum</i> (Moric.) K. Koch	N1	P	Eu-halophyte	Stem-succulent
37	<i>Atriplex canescens</i> (Pursh) Nutt.	M	P	Eu-halophyte	Salt-recreting
38	<i>Atriplex leucoclada</i> Boiss.	U1, M	P	Eu-halophyte	Salt-recreting
39	<i>Bienertia cycloptera</i> Bunge ex Boiss.	M	A	Eu-halophyte	Leaf-succulent
40	<i>Bienertia sinuspersici</i> Akhani	N1, K	A	Eu-halophyte	Leaf-succulent
41	<i>Camphorosma monspeliaca</i> L.	U1	P	Facultative-halophyte	Semi-succulent
42	<i>Caroxylon dendroides</i> (Pall.) Tzvel.	U1	P	Eu-halophyte	Leaf-succulent
43	<i>Caroxylon nitrarium</i> (Pall.) Akhani & Roalson	U3, U6	A	Eu-halophyte	Leaf-succulent
44	<i>Chenopodium murale</i> L.	N3	A	Pseudo-halophyte	Non-succulent
45	<i>Climacoptera crassa</i> (M. Bieb.) Botsch.	U3, U1, U6, U5, U2	A	Eu-halophyte	Leaf-succulent
46	<i>Halimione verrucifera</i> (M. Bieb.) Aellen	N2, U3, U1	P	Eu-halophyte	Salt-recreting
47	<i>Halimocnemis rarifolium</i> (K. Koch) Akhani	U3, U1, U6	A	Eu-halophyte	Leaf-succulent
48	<i>Halocharis sulphurea</i> (Moq.) Moq.	N2	A	Eu-halophyte	Leaf-succulent
49	<i>Halocnemum strobilaceum</i> (Pall.) M. Bieb.	N4, K, U3, U1	P	Eu-halophyte	Stem-succulent
50	<i>Petrosimonia brachiata</i> (Pall.) Bunge	U1	A	Eu-halophyte	Leaf-succulent
51	<i>Petrosimonia glauca</i> (Pall.) Bunge	M	A	Eu-halophyte	Leaf-succulent
52	<i>Salicornia iranica</i> Akhani	U3, U6, U4, U8	A	Eu-halophyte	Stem-succulent
53	<i>Salicornia sinus-persica</i> Akhani	K	A	Eu-halophyte	Stem-succulent
54	<i>Salsola drummondii</i> Ulbr.	N5	P	Eu-halophyte	Leaf-succulent
55	<i>Salsola soda</i> L.	U7	A	Eu-halophyte	Leaf-succulent
56	<i>Spinacia tetrandra</i> M. Bieb.	U1	A	Facultative-halophyte	Non-succulent
57	<i>Suaeda gracilis</i> Moq.	U3	A	Eu-halophyte	Leaf-succulent
58	<i>Suaeda aegyptiaca</i> (Hasselq.) Zohary	N4	A	Eu-halophyte	Leaf-succulent
59	<i>Suaeda altissima</i> (L.) Pall.	U3, U1, U2, U6, U5	A	Eu-halophyte	Leaf-succulent
60	<i>Suaeda fruticosa</i> Forssk.	N3, K	P	Eu-halophyte	Leaf-succulent
61	<i>Suaeda heterophylla</i> (Kar. & Kir.) Boiss.	U6	A	Eu-halophyte	Leaf-succulent
Convolvulaceae					
62	<i>Convolvulus lineatus</i> L.	U1	P	Eu-halophyte	Non-succulent
63	<i>Cressa cretica</i> L.	N2	P	Eu-halophyte	Salt-recreting

(continued on next page)

Table 2 (continued)

Cyperaceae						
64	<i>Bolboschoenus affinis</i> (Roth) Drobow	U4	P	Eury-Hygro-halophyte	Non-succulent	
65	<i>Bolboschoenus glaucus</i> (Lam.) S. G. Sm.	N1	P	Eury-Hygro-halophyte	Non-succulent	
Euphorbiaceae						
66	<i>Euphorbia heteradena</i> Jaub. & Spach	U2	P	Pseudo-halophyte	Non-succulent	
Fabaceae						
67	<i>Alhagi maurorum</i> Medik.	U3, U1, U2, U4	P	Facultative-halophyte	Non-succulent	
68	<i>Scorpiurus muricatus</i> L.	N2	A	Facultative-halophyte	Non-succulent	
Frankeniaceae						
69	<i>Frankenia hirsuta</i> L.	U1	P	Eu-halophyte	Salt-recreting	
Juncaceae						
70	<i>Juncus heldreichianus</i> T. Marsson ex Parl.	U1, U4	P	Eury-Hygro-halophyte	Non-succulent	
Malvaceae						
71	<i>Malva parviflora</i> L.	N3	A	Facultative-halophyte	Non-succulent	
Menispermaceae						
72	<i>Cocculus pendulus</i> (J. R. Forst. & G. Forst.) Diels	N3	P	Pseudo-halophyte	Non-succulent	
Nitrariaceae						
73	<i>Nitraria schoberi</i> L.	U1, M	P	Eu-halophyte	Semi-succulent	
74	<i>Peganum harmala</i> L.	U1	P	Facultative-halophyte	Non-succulent	
Papaveraceae						
75	<i>Hypocoum pendulum</i> L.	U5	A	Pseudo-halophyte	Non-succulent	
76	<i>Roemeria hybrida</i> (L.) DC.	U2	A	Pseudo-halophyte	Non-succulent	
Plantaginaceae						
77	<i>Plantago amplexicaulis</i> Cav.	N2	A	Pseudo-halophyte	Non-succulent	
Plumbaginaceae						
78	<i>Limonium axillare</i> (Forssk.) Kuntze	N1	P	Eu-halophyte	Salt-recreting	
79	<i>Limonium failachicum</i> Erben & Mucina	N1, K	P	Eu-halophyte	Salt-recreting	
80	<i>Limonium meyeri</i> (Boiss.) Kuntze	U1	P	Eu-halophyte	Salt-recreting	
81	<i>Psylliostachys spicata</i> (Willd.) Nevski	N4	A	Eu-halophyte	Non-succulent	
Poaceae						
82	<i>Aeluropus lagopoides</i> (L.) Thwaites	N2	P	Eu-halophyte	Salt-recreting	
83	<i>Aeluropus littoralis</i> (Gouan) Parl.	U1, U6	P	Eu-halophyte	Salt-recreting	
84	<i>Bromus tectorum</i> L.	U1, U5	A	Pseudo-halophyte	Non-succulent	
85	<i>Eremopyrum triticeum</i> (Gaertn.) Nevski	U1	A	Facultative-halophyte	Non-succulent	
86	<i>Halopyrum mucronatum</i> Stapf	N1	P	Eu-halophyte	Non-succulent	
87	<i>Hordeum murinum</i> subsp. <i>Glaucum</i> (Steud.) Tzvelev	U1, U6, U5	A	Facultative-halophyte	Non-succulent	
88	<i>Phragmites australis</i> (Cav.) Steud.	U1	P	Eury-Hygro-halophyte	Non-succulent	
89	<i>Poa bulbosa</i> L.	U1	P	Pseudo-halophyte	Non-succulent	
90	<i>Puccinellia bulbosa</i> (Grossh.) Grossh.	U1	P	Eu-halophyte	Non-succulent	
91	<i>Sclerochloa dura</i> (L.) P. Beauv.	U1, U5	A	Facultative-halophyte	Non-succulent	
92	<i>Sporobolus arabicus</i> Boiss.	N1	P	Eu-halophyte	Salt-recreting	
93	<i>Stipa capensis</i> Thunb.	N3	A	Pseudo-halophyte	Non-succulent	
94	<i>Stipa hohenackeriana</i> Trin. & Rupr.	U1	P	Pseudo-halophyte	Non-succulent	
Polygonaceae						
95	<i>Emex spinosa</i> (L.) Campd.	N5	A	Facultative-halophyte	Semi-succulent	
96	<i>Polygonum patulum</i> M. Bieb.	U6	A	Facultative-halophyte	Non-succulent	
Ranunculaceae						
97	<i>Adonis annua</i> L.	U1	A	Pseudo-halophyte	Non-succulent	
98	<i>Ceratocephalus falcatus</i> (L.) Pers.	U5	A	Pseudo-halophyte	Non-succulent	
Resedaceae						
99	<i>Ochradenus baccatus</i> Delile	N3	P	Facultative-halophyte	Semi-succulent	
Rhamnaceae						
100	<i>Ziziphus nummularia</i> (Burm. f.) Wight & Arn.	N3	P	Facultative-halophyte	Non-succulent	
Solanaceae						
101	<i>Lycium ruthenicum</i> Murray	U1	P	Facultative-halophyte	Semi-succulent	
102	<i>Solanum incanum</i> L.	N3	P	Pseudo-halophyte	Non-succulent	
Tamaricaceae						
103	<i>Reaumuria alternifolia</i> (Labill.) Britten	M	P	Eu-halophyte	Salt-recreting	
104	<i>Tamarix meyeri</i> Boiss.	U6	P	Eu-halophyte	Salt-recreting	
105	<i>Tamarix pycnocarpa</i> DC.	N4	P	Eu-halophyte	Salt-recreting	
Typhaceae						
106	<i>Typha grossheimii</i> Pobed.	U4	P	Eury-Hygro-halophyte	Non-succulent	
Zygophyllaceae						
107	<i>Tetradiclis tenella</i> Litv.	U1	A	Eu-halophyte	Leaf-succulent	
108	<i>Zygophyllum fabago</i> L.	U1	P	Facultative-halophyte	Semi-succulent	

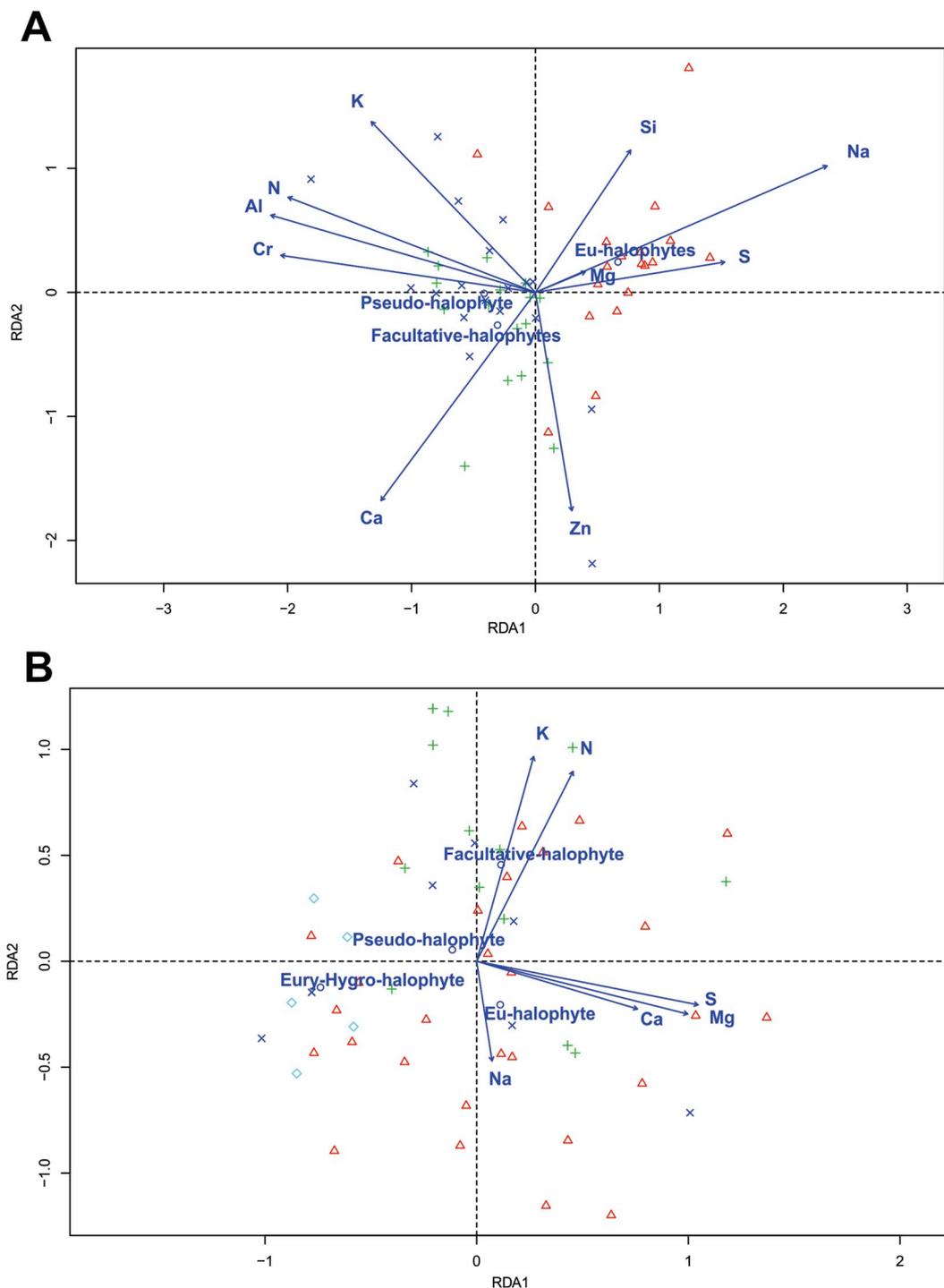


Fig. 2. Triplots of RDA analyses of the chemical composition vs. the salt-tolerance categories in annual (A) and perennial (B) species. Symbols: red triangles Δ = Eu-halophytes, green crosses $+$ = Facultative-halophytes, blue crosses \times = Pseudo-halophytes, blue rhomb \diamond = Eury-Hygro-halophytes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

saline environments (they were selected based on permutation tests and we selected common significant elements among four RDA plots on eco-morphotype and salt-tolerance categories in annual and perennial groups), namely Ca, K, Mg, Na, and S, and explored the differences in the concentrations of these elements among different salt-tolerance categories and eco-morphotypes. To do so, and since we only had one value per species, we used one-way ANOVAs with ‘salt-tolerance categories’ (i.e. eu-halophytes, facultative-halophytes, eury-hygro-

halophyte, and pseudo-halophytes) or ‘eco-morphotype’ (i.e. leaf-succulent, stem-succulent, semi-succulent, salt-recreting, and non-succulent) as factors in the analyses. We ran the analyses separately for annual and perennial species. Differences among eco-morphotypes or salt-tolerance groups after ANOVAs were identified by applying the *post-hoc* Tukey’s test (when variances were homogeneous) or the T3-Dunnnett test (otherwise) (Table 4).

Finally, differences in the chemical composition of the seven most

important taxonomic families in the plant communities studied (with at least four representative species), were examined with RDA. The explanatory matrix was a table with dummy variables representing the ‘family’ (i.e. Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Poaceae, and Plumbaginaceae) while the dependent matrix was the chemical composition of plants for 20 different elements (i.e. the elemental composition of plants) (Fig. 4, Table 5).

Multivariate analyses were done in R i386 3.3.3 (R Core Team, 2017) using the *vegan* package (Borcard et al., 2011). Nutrient data were centered and scaled prior to multivariate analyses by applying the *scale* function. We selected default scaling (scaling 2) in all analyses, and Ezekiel's adjustment was used to obtain adjusted R^2 coefficients (Borcard et al., 2011). The statistical significance of RDA models, individual canonical axes, and individual RDA axes was tested using permutations (Borcard et al., 2011). PERMANOVA analyses were run with the *adonis2* function. Data were checked for normality and homoscedasticity prior to ANOVAs and log-transformed when normality was not met. Univariate simple linear analyses and *post hoc* tests were done in SPSS 15.0 (SPSS Inc., IBM, New York, USA).

3. Results

3.1. Relationship between the elemental composition of plants and their salt-tolerance categories

According to our RDA analysis, annual eu-halophyte species were strongly positively correlated with high Na, S, Si and, to a lower extent, Mg concentrations and negatively correlated with Ca, K, Cr, Al and N contents, which were higher in pseudo-halophytes and facultative-halophytes (Fig. 2A). Pseudo-halophytes and facultative-halophytes showed very similar chemical concentrations, clearly separating from eu-halophytes (Fig. 2A). In annual plants, the ‘salt-tolerant category’ factor explained 16% of total adjusted variance and was highly significant ($P < 0.001$, adjusted $R^2 = 0.16$, $F = 6.21$). In the case of perennial species, the separation among groups was less sharp. Eu-halophytes correlated primarily with high foliar concentrations of Na, S, Mg and, to a lower extent, Ca. Eury-hygro-halophytes, only represented by perennial plants in this study, showed low Ca, Mg, S and Na contents, while facultative-halophytes were related to high N and K concentrations (Fig. 2B). The RDA analysis on perennials was also highly significant ($P < 0.001$, adjusted $R^2 = 0.15$, $F = 4.04$) and explained 13% of the total adjusted variance.

Table 3

Results of PERMANOVA on the effect of the life cycle, taxonomic family, site and salt tolerance categories or eco-morphotypes on the ionic composition of study plants. Model 1 included ‘Salt tolerance’, ‘Life history’, ‘Family’, ‘Site’ plus the interaction between ‘Life history’ and ‘Salt tolerance’ as fixed factors. Model 2 included ‘Eco-morphotype’, ‘Life history’, ‘Family’, and ‘Site’ as fixed factors since the interaction between ‘Life history’ and ‘Eco-morphotype’ was not significant and hence was excluded from the model. The total variance explained (TVE, %), F-ratios and P-values are shown. Significant P-values are highlighted in bold.

Factor	TVE (%)	F-ratio	P-value
Model 1			
Salt tolerance	12.1	8.7	< 0.001
Life history	4.1	8.9	< 0.001
Family	25.1	1.9	< 0.01
Site	12.0	1.8	< 0.01
Life history: Salt tolerance	2.1	2.2	0.012
Model 2			
Eco-morphotype	14.9	7.8	< 0.001
Life history	5.2	10.9	< 0.001
Family	21.7	1.6	< 0.01
Site	12.2	1.84	< 0.01

Results of PERMANOVA showed that all the factors included in the model (model 1) were significant (Table 3). The factor that explained a larger proportion of the total variance was the taxonomic family (25.1%) followed by the salt tolerance categories, site and the life history (perennial vs. Annual). The interaction between the life history and salt tolerance categories was also significant, indicating a different chemical composition of salt tolerance categories in annuals vs. perennial species, as illustrated by the RDA results. According to permutation tests, the first and, in perennials, also the second axis of RDA plots (Fig. 2) were significant ($P < 0.001$ for annuals, and $P < 0.01$, $P < 0.01$ for RDA1 and RDA2, respectively, in perennials). Our analyses indicated that the chemical composition of plants was also affected by the site of collection (Table 3). RDA analyses showed that the effect of sites on leaf chemical composition was mainly driven by site U5, located in Lake Urmia, with high concentrations of metals including Ni, Fe, Cr, Al, Ti and V (Fig. A2). This site demarcated from the rest of sites along the first axis of the RDA plot, which was the only significant axis after permutation tests ($P < 0.001$).

ANOVAs rendered similar results to RDAs, with eu-halophytes showing significantly higher Na concentrations than the rest of salt-tolerance groups both in annual and perennial species (Table 4) and a trend for higher S (only significant in relation to eury-hygro-halophytes in perennials and facultative-halophytes in annuals, Table 4). Annual eu-halophytes showed significantly lower Ca concentrations than the rest of groups and lower K than pseudo-halophytes, while in perennials the lowest Ca concentrations were observed in eury-hygro-halophytes and differences for K was not significant among groups (Table 4).

3.2. Relationship between the elemental composition of plants and their eco-morphotypes

The elemental composition of leaf- and stem-succulent plants was clearly different to that of non-succulent and semi-succulent species, particularly in annual species (Fig. 3). According to the RDA analyses, succulent plants showed high foliar Na concentrations and, to a lower extent, also high S, Mg and Si leaf contents in annual species (Fig. 3A). This analysis was highly significant ($P < 0.001$, adjusted $R^2 = 0.17$, $F = 4.57$) and, in the case of annuals explained 16% of the total adjusted variance. The RDA analysis on perennials explained 17% of the total adjusted variance and was also highly significant ($P < 0.001$, adjusted $R^2 = 0.18$, $F = 3.93$). In perennial species, stem-succulent, salt-secreting plants (a group not represented among annuals in our study) and some leaf-succulent plants, correlated with high foliar Na concentrations, while a second group of leaf-succulents got closer to semi-succulents and displayed high S, Mg and Ca contents (Fig. 3B). Both in annual and perennial species, non-succulent plants showed very similar chemical composition, being related to lower Na, Mg and S, and a tendency for higher N and K (in the case of annuals also higher Ca) contents in their leaves (Fig. 3). In perennials, non-succulent and semi-succulent plants also showed a correlation with higher leaf P and Cu concentrations (Fig. 3B).

According to PERMANOVA, the life history of plants and the eco-morphotypes had a significant effect on the chemical composition of plants, but their interaction was not significant, indicating similar trends among eco-morphotypes both in annual and perennial species (Table 3). This analysis indicated that the effect of the taxonomic family explained 21.7% of the total variance, and this effect was significant (Table 3). Also ‘site’ had a significant effect on the chemical composition of plants, explaining 12.2% of the total variance, an effect that, as indicated above, can be mainly attributed to the atypical chemical composition of site U5 (Fig. A2). RDA axes were also highly significant both in annuals and perennials ($P < 0.001$ for the first axis in annuals, and $P < 0.001$, $P < 0.01$ for RDA 1 and RDA2, respectively in perennials).

In general terms, results from the ANOVAs agreed with multivariate analyses, with succulent plants clearly separating from the rest owing to

Table 4

Average Ca, K, Mg, Na and S (mg g^{-1}) concentrations in the shoots of the different salt-tolerance categories and eco-morphotypes analyzed in this study. Sample sizes (N), F-ratios, P-values and mean values \pm SE are shown. Different letters indicate significant differences after ANOVAs and *post-hoc* tests.

	N	Ca	K	Mg	Na	S
Annuals						
Salt-tolerant		F = 13.571 P < 0.001	F = 3.950 P = 0.025	F = 0.891 P = 0.417	F = 53.311 P < 0.001	F = 8.109 P = 0.001
Eu-halophytes	19	12.7 \pm 2.7 a	19.4 \pm 2.1a	8.8 \pm 1.1	125.7 \pm 12.7b	15.8 \pm 2.9b
Facultative-halophytes	17	33.9 \pm 4.6 b	22.7 \pm 1.7 ab	7.4 \pm 1.1	13.5 \pm 2.1 a	9.9 \pm 1.3 ab
Pseudo-halophytes	18	25.2 \pm 3.1 b	27.6 \pm 3.1b	6.9 \pm 1	9.6 \pm 2.3 a	5.4 \pm 0.6 a
Eco-morphotypes		F = 12.7 P < 0.001	F = 2.535 P = 0.067	F = 3.402 P = 0.025	F = 36.776 P < 0.001	F = 3.504 P = 0.022
Leaf succulent	15	9.7 \pm 0.8 a	20.6 \pm 2.5	8.3 \pm 1.4 ab	132.7 \pm 12.4b	17.5 \pm 3.5b
Stem succulent	2	8.9 \pm 0.6 a	15.5 \pm 0.1	9.3 \pm 0.3 ab	166.6 \pm 11.9b	6.4 \pm 2.4 ab
Semi-succulent	5	30.7 \pm 7.5 ab	34.3 \pm 8.4	12.8 \pm 2.5 b	20.1 \pm 4.4 a	8 \pm 3.3 ab
Non-succulent	32	29.8 \pm 3.1 b	23.1 \pm 1.6	6.5 \pm 0.6 a	11.5 \pm 2 a	7.8 \pm 0.8 a
Perennials						
Salt tolerant		F = 3.881 P = 0.014	F = 2.033 P = 0.121	F = 5.037 P = 0.004	F = 10.279 P < 0.001	F = 3.126 P = 0.034
Eu-halophytes	28	16.2 \pm 1.6 b	14.2 \pm 1.3	8.7 \pm 1 c	44.9 \pm 7.8 b	15.8 \pm 2.4b
Eury-Hygro-halophytes	5	6 \pm 1.8 a	13.7 \pm 2.4	2.2 \pm 0.5a	6.2 \pm 2.2 a	3.6 \pm 0.8 a
Facultative-halophytes	13	19.6 \pm 2.2 b	19.7 \pm 2.2	6.7 \pm 0.9bc	9.6 \pm 2.9 a	12.8 \pm 3.4 ab
Pseudo-halophytes	8	27.1 \pm 8.2 ab	16.9 \pm 2.8	4 \pm 0.8 ab	7.1 \pm 3.6 a	9.3 \pm 4.2 ab
Eco-morphotypes		F = 1.311 P = 0.279	F = 2.059 P = 0.101	F = 7.892 P < 0.001	F = 21.883 P < 0.001	F = 6.623 P < 0.001
Leaf-succulent	3	20.8 \pm 2	16.7 \pm 2.1	12.3 \pm 3.6 ab	112.1 \pm 32.2c	18.2 \pm 12.3 ab
Stem-succulent	2	6.4 \pm 2.9	11.3 \pm 1.2	4.4 \pm 0.4 a	123.6 \pm 19.2c	5.7 \pm 1.5 ab
Salt-recreting	15	18.5 \pm 2.3	12 \pm 1.7	8.4 \pm 1 b	33.9 \pm 4 bc	15.8 \pm 3 b
Semi-succulent	12	22.8 \pm 4.3	18.7 \pm 1.6	10 \pm 1.5 b	22.6 \pm 5.2 b	22.3 \pm 4.1 b
Non-succulent	22	15 \pm 2.8	17.3 \pm 1.8	3.8 \pm 0.6 a	4.9 \pm 1.2 a	5.9 \pm 1.1 a

their higher Na concentrations, followed (in the case of perennials) by salt-recreting species (Table 4). Annual leaf-succulent species also showed higher S and lower Ca concentrations than non-succulent plants (Table 4). Nevertheless, differences among eco-morphotypes were not significant for their K concentrations, neither in annuals nor in perennial species. Also, differences in the Ca concentrations of different eco-morphotypes were not significant in perennial species (Table 4).

3.3. Differences in the elemental composition between taxonomic groups

Our RDA analyses showed clear differences in the chemical composition of the leaves of the seven main taxonomical families analyzed. The 'taxonomic family' explained 21% of the total adjusted variance and was highly significant ($P < 0.001$, adjusted $R^2 = 0.27$, $F = 5.41$). Results of PERMANOVAs confirmed the relevance of the taxonomic family in the elemental composition of plants, with family being the factor explaining a larger percentage of the total variance (Table 3). Based on permutation results the two first axis of RDA plots were highly significant ($P < 0.001$, $P < 0.001$, for the first and second axis, respectively).

Chenopodiaceae, the family with more representatives of eu-halophytes and with large number of succulent species, strongly and positively correlated with Na concentrations. Similarly, Plumbaginaceae, which includes several salt-recreting halophytes, correlated with high Na concentrations, while Poaceae showed the opposite trend, displaying the lowest Na concentrations (Fig. 4, Table 5, Table A1). Both Chenopodiaceae and Plumbaginaceae showed similar positive correlations with Mg and S contents. The highest foliar Na and S concentrations were recorded in the chenopod *Halocharis sulphurea* (192.1 and 49.9 mg g^{-1} for Na and S, respectively), while the lowest values belonged to *Stipa hohenackeriana* (0.3 and 1.1 mg g^{-1} for Na and S, respectively), a member of the Poaceae (Table A1). Members of Caryophyllales showed a tendency for high S concentrations, with 6 species of the order being amongst those with higher S contents. The species with largest Mg concentration was the chenopod *Petrosimonia glauca* (20.5 mg g^{-1}), while *Stipa hohenackeriana* showed the lowest values (0.4 mg g^{-1}). On the other hand Brassicaceae, Boraginaceae and

Caryophyllaceae were correlated with high foliar Ca, N, Fe and P, the latter showing also high K contents (Fig. 4, Table 5, Table A1). Indeed, the Caryophyllaceae *Holosteum umbellatum* was the species with highest foliar K concentrations (67.6 mg g^{-1}), while the lowest K content was found in the salt-recreting member of the Plumbaginaceae *Limonium axillare* (4.2 mg g^{-1}). Other salt-recreting species from the Tamaricaceae and Frankeniaceae showed similarly low K contents (Table 5, Table A1). *Arnebia decumbens*, a member of the Boraginaceae, was the species with the highest foliar Ca contents (69.9 mg g^{-1}), while the lowest value was displayed by *Juncus heldreichianus* (1.9 mg g^{-1}), a member of the Juncaceae, followed by several other Poaceae and Monocots with similarly low foliar Ca concentrations (Table 5, Table A1).

4. Discussion

Results of the present study indicate that the elemental composition of halophytes and pseudo-halophytes is related to salt-tolerance categories, eco-morphological types and their respective taxonomic groups. This relationship is mainly driven by elements directly related to salinity, such as Na, S, Mg, K, and Ca.

Our results also show a significant effect of sampling sites on the chemical composition of plants. Such effects are mainly related to the atypical composition of site U5, located in the eastern side of Lake Urmia, and which showed high concentrations of various metals. Such unusual composition can be explained by the erosion of granite rocks in the north west of this lake, as described in Sharifi et al., (2018).

4.1. Sodium is the main element of succulent and salt-recreting eu-halophytes

Sodium is not an essential element for most plant species, but it is necessary for osmotic adjustment and the maintenance of optimum growth in halophytes (Albert, 1982; Subbarao et al., 2003). Our results indicate that both annual and perennial eu-halophytes have high Na concentrations in their leaves (Fig. 2). Most of these plants are succulents and salt-recreting plants (Table 2). Contrastingly, Na content was

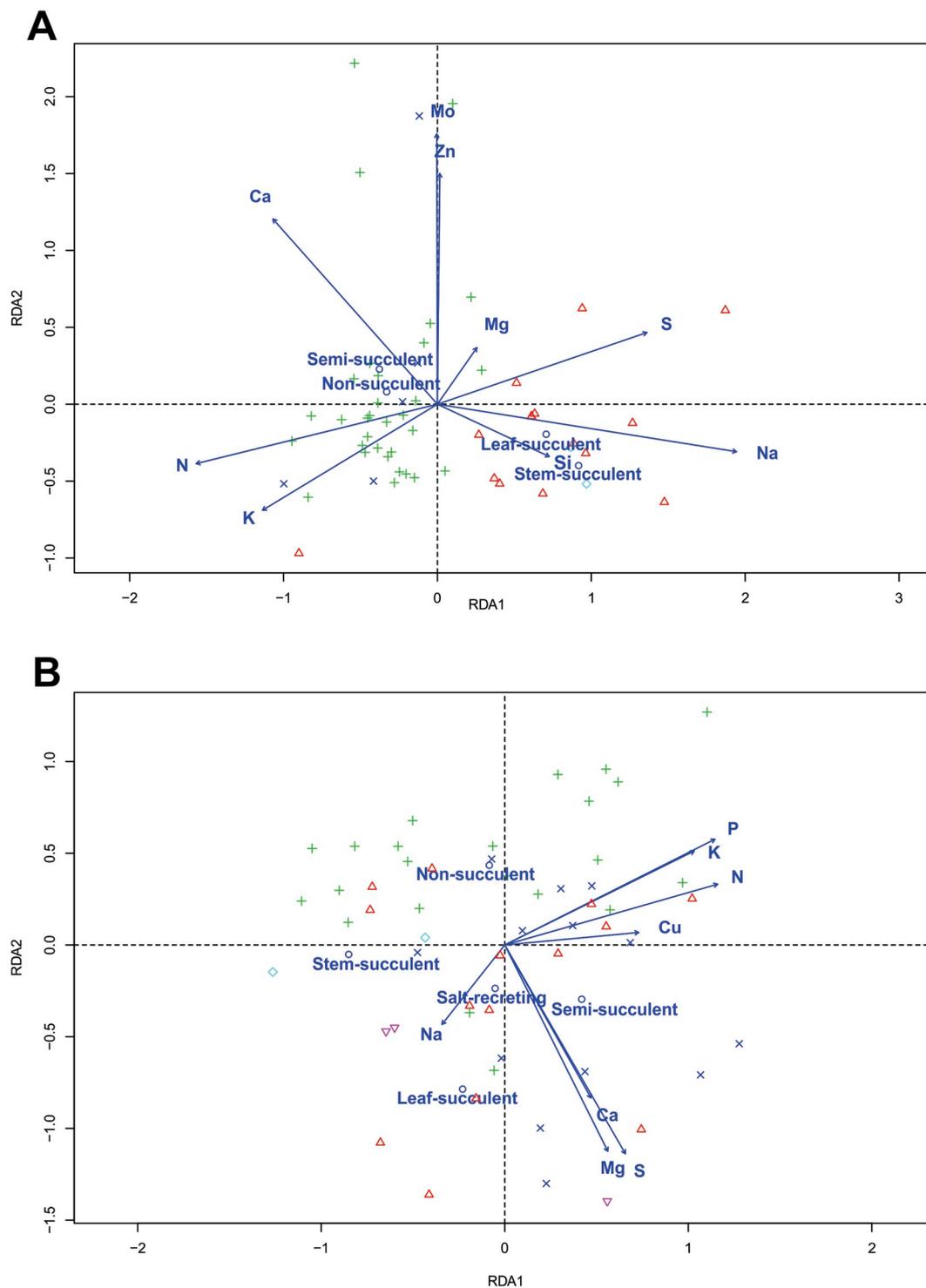


Fig. 3. RDA triplots for the analysis of the chemical composition vs. the eco-morphotypes of annual (A) and perennial (B) species. Symbols: red triangles Δ = leaf succulent, green crosses $+$ = Non-succulent, blue crosses \times = Semi-succulent, blue rhomb \diamond = Stem-succulent, purple triangles ∇ = Salt-secreting. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

clearly less in facultative- and pseudo-halophytes, and also in eury-hydro-halophytic monocots, which include non-succulent or semi-succulent species (Figs. 2 and 3, Table 2). In facultative-halophytes, Na is not an essential element (Al-Ani et al., 1971), and also eury-hydro-halophytes can optimally grow in inundated soils with low salinity (Ogburn and Edwards, 2010). These species are not specialized in using Na for osmoregulation, and excessive Na can disturb their elemental

composition (Kudo et al., 2010). Some eury-hydro-halophytes species, like *Phragmites australis*, can re-circulate Na from the shoots back to the roots, keeping low Na concentrations in the shoots and high Na in the root vacuoles (Fujimaki et al., 2015; Matsushita and Matoh, 1992; Takahashi et al., 2007; Vasquez et al., 2006).

Contrastingly, eu-halophytes have the ability to retain high Na concentrations in the shoots via Na compartmentalization in the leaf

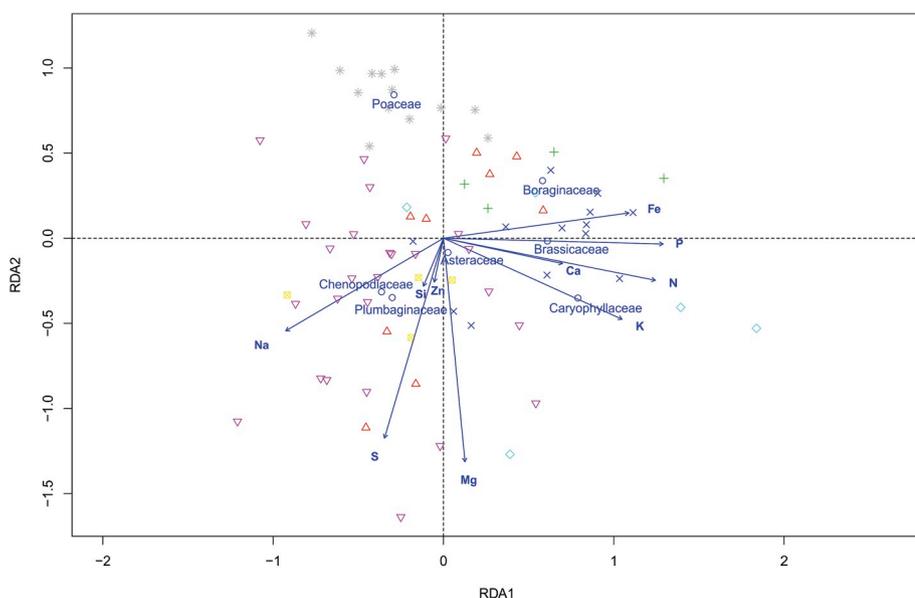


Fig. 4. RDA Triplot of the chemical composition vs. taxonomic family classification of studied species. Symbols: red triangles Δ = Asteraceae, green crosses $+$ = Boraginaceae, blue crosses \times = Brassicaceae, blue rhomb \diamond = Caryophyllaceae, purple triangles ∇ = Chenopodiaceae, grey asterisk $*$ = Poaceae, yellow square \boxtimes = Plumbaginaceae. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

cells vacuoles (such as the succulents *Salicornia* and *Suaeda* species) or by withdrawing it from cells by glands and bladders (in the case of salt-secreting halophytes like *Atriplex* species) (Belkheiri and Mulas, 2013; Flowers and Colmer, 2015; Flowers et al., 1977; Grattan and Grieve, 1992; Khan et al., 2000a, b; Milić et al., 2013; Mozafar and Goodin, 1970; Naidoo, 1994; Parida and Das, 2005; Rozema et al., 1985). Generally, the main metabolic roles of Na in halophytes is still unknown (Kudo et al., 2010), but this element is known to serve as an essential nutrient in halophytes, particularly in C_4 plants (Al-Ani et al., 1971; Gerloff, 1963). For example in the C_4 plant *Atriplex vesicaria*, Na has been found to serve as an essential micronutrient for the regeneration of phosphoenolpyruvate (Al-Ani et al., 1971; Brownell and Crossland,

1972; Mori et al., 2010). It is documented that Na (in the vacuoles) associated with compatible solute (e.g. proline, manitol, sorbitol, etc. in cytoplasm) could contribute to the osmotic adjustment in eu-halophytes (the succulent and re-creting-halophytes), as reported in some mangrove trees; *Aegialitis annulata* and *Avicennia marina* (Popp and Polania, 1989; Zhu et al., 2011). Furthermore the physiological role of Na in succulent eu-halophytes could be related to Na^+/H^+ antiporter activity; which is involved in Na compartmentalization in vacuoles for osmoregulation (Abdelly et al., 2008; Al-Ani et al., 1971; Barakat et al., 2014; Flowers et al., 2014; Hassine et al., 2008; Khan et al., 2000b; Kudo et al., 2010; Mori et al., 2010; Taleahmad et al., 2013). Consequently, in succulent eu-halophytes, water associated with inorganic ions is accumulated in

Table 5

Average Ca, K, Mg, Na and S ($mg\ g^{-1}$) concentrations of the different families with more than two representatives included in the study. Mean values \pm SE and sample size (N) are shown.

Taxon	N	Ca	K	Mg	Na	S
Monocots						
Poales						
Cyperaceae	2	7.3 \pm 1.9	12.9 \pm 4.8	2.4 \pm 0.3	8.1 \pm 4.3	3.3 \pm 1.8
Poaceae	13	8.6 \pm 1.4	14.1 \pm 1.6	2.3 \pm 0.3	7.4 \pm 2.6	3.5 \pm 0.6
Basal Eudicots						
Ranunculales						
Papaveraceae	2	21.6 \pm 2.4	24.3 \pm 8.8	4.6 \pm 0.8	7.7 \pm 5.1	5.8 \pm 1.6
Ranunculaceae	2	23.3 \pm 8.6	28.6 \pm 3	5.9 \pm 1.4	4.2 \pm 1.7	6 \pm 0.2
Asterids						
Asterales						
Asteraceae	9	25.2 \pm 5.3	20.9 \pm 2.1	8.2 \pm 1.8	15.4 \pm 4	14.5 \pm 4.5
Boraginales						
Boraginaceae	5	47.1 \pm 6.6	25 \pm 1.9	5.4 \pm 0.5	7.9 \pm 3.6	5.3 \pm 1.4
Solanales						
Convolvulaceae	2	20.7 \pm 3.5	15.3 \pm 4.9	5.8 \pm 2.7	22 \pm 21.5	5.7 \pm 3.4
Solanaceae	2	33.8 \pm 18	20.2 \pm 5	6 \pm 2.6	7.7 \pm 6.8	6.1 \pm 0.2
Basal Asterids						
Caryophyllales						
Caryophyllaceae	5	14 \pm 2.4	33.9 \pm 8.6	12.2 \pm 2.3	21.4 \pm 9.4	9.4 \pm 5.4
Chenopodiaceae	26	12 \pm 1	20.1 \pm 1.9	9.5 \pm 1	115.9 \pm 11.2	14.2 \pm 2.5
Plumbaginaceae	4	19.6 \pm 3.8	13.8 \pm 5	10.3 \pm 1	32.8 \pm 6.8	22.2 \pm 2.9
Polygonaceae	2	31.2 \pm 16.2	22.9 \pm 3.3	13.6 \pm 6.8	24.4 \pm 7.3	5.6 \pm 0.1
Tamaricaceae	3	26.1 \pm 5.1	7.5 \pm 1.1	10.5 \pm 2.4	28.5 \pm 9	32.4 \pm 3.6
Fabids						
Fabales						
Fabaceae	2	39.8 \pm 11.8	11.4 \pm 4.4	9.7 \pm 2.8	8.5 \pm 5.6	12.4 \pm 6
Zygophyllales						
Zygophyllaceae	2	18.9 \pm 9.3	37.8 \pm 12	5.8 \pm 4.4	51.2 \pm 13.3	26.1 \pm 20.4
Malvids						
Brassicales						
Brassicaceae	12	36 \pm 4.8	21.4 \pm 1.5	7.1 \pm 0.7	11.9 \pm 3.6	15.7 \pm 2
Nitrariaceae	2	11.9 \pm 1.2	20.7 \pm 4.1	5.2 \pm 1.5	31.7 \pm 27	8.3 \pm 2.4

photosynthetic tissues in leaves or assimilating stem leading to succulence (Khan et al., 2005; Naz et al., 2013; Ogburn and Edwards, 2010; Zoerb et al., 2013). In salt-secreting halophytes the salt bladders/glands reduce Na contents by removing it from the tissues to minimize cell toxicity (Dassanayake and Larkin, 2017; Mozafar and Goodin, 1970). Also Na accumulated in salt bladders serves to keep the ionic balance and minimize harmful effects of salt on key metabolic enzyme activities, like the ATPase (Naidoo and Naidoo, 1998). Bladders may collapse with increasing leaf age, being dropped, washed by rain, or remaining on the leaf surface, which may create an additional protection against high radiation (Mozafar and Goodin, 1970; Schirmer and Breckle, 1982). This may explain why we observed slightly lower Na concentration in the leaves of salt secreting halophytes than in succulent species.

4.2. High sulfur and magnesium concentrations are associated with annual and some perennial eu-halophytes

Our results indicate that most annual eu-halophytes and also an important proportion of perennial eu-halophytes, showed high foliar S and Mg concentrations (Fig. 2). In saline environments, evaporitic minerals such as magnesium sulfate or gypsum (di-hydrated calcium sulfate) occur frequently in combination with halite (Pérez-López et al., 2011). Under such circumstances, halophytes may be exposed to high S and Mg concentrations in the soil. Iran has a remarkable extension of gypsum and sodium sulfate-rich soils, and is host to the highest known diversity of gypsophiles in the Old World (Akhani, 2006; Pérez-García et al., 2018). Consequently, it is not surprising that some of the sites studied were S- and Mg-rich (Table A2). Among perennial species, high S concentrations were observed in some leaf-succulents, and also in salt-secreting halophytes (like *Tamarix*) and some semi-succulent species, such as *Grantia aucheri*, *Suaeda salsa* or *Lepidium cartilagineum* (Fig. 3B, Table A1). Similarly, high foliar S concentrations were reported in gypsum endemic plants displaying succulent or semi-succulent leaves (Duvigneaud and Smet, 1968; Merlo et al., 2019). Sulfur is an essential macronutrient occurring in the structure of some key molecules, like amino acids (cystine, cysteine, and methionine), cofactors and vitamins. Sulfur plays also a fundamental role as a signaling molecule in environmental interactions and, therefore, could improve the salinity tolerance by mediating some important physiological and molecular mechanisms (Miura, 2013).

Sulfate accumulation along with other elements (Na and Mg) in leaves of halophytes plays an important role in osmotic regulation and water uptake in saline soils (Duvigneaud and Smet, 1968; Taleahmad et al., 2013). High Mg concentrations have been reported in plants from extreme saline habitats. For example, the Mg concentration in xerophytic monocotyledons and some halophytic chenopods has been shown to reach similar levels to Na concentration (Albert and Popp, 1977; Matinzadeh et al., 2013). Maintaining a high amount of Mg associated with Na in the leaves of perennial eu-halophytes may be essential for their osmotic regulation (Al-Ani et al., 1971). Also high leaf Mg concentrations may be essential under high Na availability, owing to its role in membrane transport, protein translation, and its function in essential enzyme activity such as a cofactor for tonoplast ATPases (Donovan et al., 1997; Flowers and Colmer, 2015). In addition, in high saline condition associated with low Ca concentration in the cytoplasm, Mg could be act as alkali ion in cell stability mechanisms, owing to its strong lyotropic effect on cytoplasm colloids (Albert and Popp, 1977).

4.3. Sodium could replace potassium in metabolic processes of eu-halophytes

According to our results, K concentrations of eu-halophytes were lower than the rest of groups analyzed, particularly in annual species

(Fig. 2, Table 4). Previous studies have shown similarly high Na and reduced K concentrations in halophytes (Grattan and Grieve, 1992; Gulzar et al., 2003; Kachout et al., 2011; Noaman, 2004; Parida and Das, 2005; Taleahmad et al., 2013). Potassium is an essential macronutrient in plant cells, with a key role in many important physiological processes, such as the regulation of stomatal functions, or the adjustment of cell water potential (Noaman, 2004; White and Karley, 2010). Furthermore, this element plays an important role in protein synthesis (Gulzar et al., 2003), Na compartmentalization in vacuoles and in maintaining plasma membrane integrity (Percey et al., 2016; Redondo-Gómez et al., 2007). However, owing to their similar chemical properties, Na and K may compete for their respective membrane transport systems (Bange, 1959; Taleahmad et al., 2013). In saline soils, the high Na concentration can saturate the binding sites leading to a reduced K uptake (Taleahmad et al., 2013). Plants specifically adapted to saline environments such as *Suaeda maritima* (Flowers et al., 1977) and *Sarcobatus vermiculatus* (Donovan et al., 1997) can replace K by Na for the development of some key metabolic functions (Flowers and Colmer, 2008; Noaman, 2004). Also, Na was found to play a strong osmotic regulation role in replacing K in *Atriplex canescens* under high salinity (Glenn et al., 1996; Grattan and Grieve, 1992; Hammou et al., 2014). Indeed, it has been suggested that halophytes tend to keep low cation balances: $([K^+] + [Ca^{2+}] + [Mg^{2+}]) / [Na^+]$, while this ratio may be higher in glycophytes (Kudo et al., 2010).

4.4. Most annual succulent eu-halophytes show low Ca concentrations

Calcium is an essential element in plants. Cytosolic Ca concentration can regulate ion transport across the plasma membrane via its role in the integrity of the cell wall and cellular membranes (White, 2015). Also Ca could play a role in regulating the Na^+/H^+ antiporter to Na compartmentation in vacuoles (Blumwald, 2000). Furthermore Ca is involved in salt toxicity alleviation by controlling Na influx through a voltage-insensitive monovalent channel in the root membrane, which can inhibit Na entry into the roots (Donovan et al., 1997; Grattan and Grieve, 1992; White, 1999). However, we observed low Ca concentrations in most annual succulent eu-halophytes, while Ca concentrations tended to be higher in annual pseudo-halophytes and facultative-halophytes (Fig. 2, Table 4). These trends were not so clearly seen in perennial species, where several succulent and semi-succulent plants showed high Ca concentrations (potentially the same species that showed a tendency to accumulate S and could be growing on gypsum-rich soils). Our findings for annual plants are in agreement with several previous reports on the incompatibility of Ca and Na in plant cells under salt stress (Grattan and Grieve, 1992; Kachout et al., 2011; Krüger and Peinemann, 1996; Naidoo, 1994; Tipirdamaz et al., 2006). Furthermore it may be explained by the lower selectivity for Ca under high Na by transport systems and the ability of pseudo-halophytes and facultative-halophytes to favor Ca and avoid Na uptake when growing in saline environments (Albert and Popp, 1977; Grattan and Grieve, 1992; Kudo et al., 2010).

4.5. The elemental composition of plants is linked to their phylogeny

This study covers 108 species belonging to 80 genera and 30 families of angiosperms growing in salt marshes and surrounding low salinity soils. Although some clear patterns could be identified in relation to the eco-morphotypes and the salt-tolerance categories of plants, independently of their taxonomic origin, our study showed that there is a strong phylogenetic imprint in the chemical composition of plants. Previous studies have reached similar conclusions, pointing at the relevance of phylogenetic relationships for understanding the elemental composition of angiosperms (Neugebauer et al., 2018).

The order Caryophyllales, which includes 38% of the species

studied, shows a high prevalence in saline ecosystems of the Irano-Turanian floristic region. Many species of Caryophyllales are adapted to extreme environments such as high saline soils, and the order represents the most species-rich group of C_4 plants among dicots (Akhani et al., 1997; Hernández-Ledesma et al., 2015; Sage et al., 2011). The present study shows that Na and Mg accumulation is particularly prevalent in certain families of Caryophyllales, namely Chenopodiaceae and Plumbaginaceae (Fig. 4). Such accumulation seems directly related to specific morphological characters among different genera of Caryophyllales which causes the greater accumulation of Mg and Na in their vacuoles (Milić et al., 2013; White et al., 2015). In our study, all succulent chenopods have the highest Na values recorded (Table A1). These results are in agreement with previous studies documenting the ability of Caryophyllales to selectively accumulate higher amounts of Na and Mg, both under controlled (Broadley et al., 2004; Neugebauer et al., 2018; White et al., 2018) and natural conditions (Albert and Popp, 1977; Breckle, 1975; Matinzadeh et al., 2013; Veste et al., 2008) than other angiosperm species (White et al., 2018). The ability to accumulate Na observed in several halophytic and non-halophytic species of Caryophyllales in Aizoaceae, Cactaceae, Portulacaceae, Chenopodiaceae, Tamaricaceae and Polygonaceae seems to have appeared several times throughout evolution (Neugebauer et al., 2018; White et al., 2017) and could be related to the important role of Na in osmotic adjustment instead of K, when K concentrations are low (such as in saline environments). These evolutionary changes may be closely related to several other adaptive traits, such as the formation of succulent tissues (Nyffeler et al., 2008), the acquisition of C_4 or CAM photosynthesis (Akhani and Ghasemkhani, 2007; Akhani et al., 1997; Edwards and Ogburn, 2012; Sage et al., 2011), or the presence of salt trichomes and chalk glands (Dassanayake and Larkin, 2017), which help these families to successfully dominate extreme saline and dry environments. On the other hand, high Mg concentrations occur in almost all Caryophyllales families and are supposed to have evolved from a common old ancestor (Neugebauer et al., 2018; White et al., 2015). Within Caryophyllales, studied members of the Caryophyllaceae showed high foliar K concentrations (Fig. 4), something that was previously reported for this order compared to many other eudicot orders (Broadley et al., 2004), and also for some members of the family, like *Stellaria media* (Chandra and Rewat (2015).

Monocots comprised 16% of our studied species and they characterized by having low Na, K and Ca concentrations (Fig. 4). Comelinid monocots (e.g. Poaceae, Cyperaceae, and Juncaceae) are characterized by lower Mg, Ca and Na concentrations in their leaves than other angiosperm species, and therefore have been classified as Na excluder groups (Albert and Kinzel, 1973; Broadley et al., 2004; Neugebauer et al., 2018; White et al., 2018). The Na/K ratio in these families is commonly less than 1, in contrast to other angiosperm families (Albert and Popp, 1977; White et al., 2017), indicating a clear phylogenetic signal in one of the most widespread angiosperm orders (Edwards et al., 2010; Stromberg, 2011). The low Na accumulation in halophytic grasses is of high practical importance for agriculture in saline arid lands. For example, field observations in many saline habitats in Iran showed that *Puccinellia bulbosa* and *P. distans* might be very good candidates for saline agriculture in many salinized soils (Dashtebani et al., 2014; Liu et al., 2012), an assertion that is supported by our results of low Na concentrations in this species (Table A1). Similarly, salt-tolerant species of *Eremopyrum* and *Hordeum* studied (Table A1) are of high importance, as they are related to the global crops barley and wheat (Soreng et al., 2015).

All Malvid families in this study (Brassicaceae, Capparaceae, Malvaceae, Nitrariaceae, and Resedaceae) are representatives of the vegetation in the early growing season on moderate saline soils. The order Brassicales, which includes 13% of the species in this study, is

characterized by high Ca, N and S concentrations (Fig. 4, Table 5); the latter is considered a phylogenetic signal in this order (Albert and Kinzel, 1973; Neugebauer et al., 2018). The high S in the Brassicales genera and some Malvales species seems to have evolved separately to the other orders in Malvids (Neugebauer et al., 2018). In addition, Brassicales, differently to Malvales and Sapindales, not only accumulate S as glucosinolates in their cells (Neugebauer et al., 2018) but also a high concentration of S as SO_4^{2-} was reported in their cells (Albert and Kinzel, 1973). Our study encompassed several salt-tolerant Malvids, including species of *Capparis*, *Malva*, *Nitraria*, *Peganum* and *Ochradenus* (Table A1). With the exception of *Nitraria schoberi*, an eu-halophytic plant that showed high Na concentrations, all the studied Malvid species were not Na accumulators (Table A1).

Regarding Asterids, our results indicated that the monotypic order Boraginales, with 5 species included in this study, showed a remarkable ability to accumulate Ca (Fig. 4, Table A1). This order is well known for having a dense indumentum of hairs with a basal cystolith and often calcified or silicified walls (Gal et al., 2012; Judd et al., 2015). Silica, calcium carbonate and, more recently, also calcium phosphate, have been described as common mineral deposits in the trichomes of these species (Mustafa et al., 2018). This order is also known to produce abundant Ca deposits in the cell wall (Kinzel, 1989). In the remaining Asterid families the results obtained are inconclusive, mainly because they are based on fewer species, sometimes distinctly related (such as in Asteraceae) (Table A1). Additional sampling is required to better understand the elemental composition of these lineages.

5. Conclusion

There is a strong relationship between the elemental composition of plants growing on saline soils and the categories of salt-tolerance and eco-morphotypes analyzed. Two distinct groups can be identified after our analysis: the eu-halophytes, with succulent assimilating organs or salt-secreting glands; and the pseudo-halophytes, facultative-halophytes, and eury-hydro-halophytes with non-succulent or semi-succulent leaves. The first group is characterized by high Na, S, and Mg and low K concentrations in their leaves; while the second relates to low Na, S, and Mg along with high concentrations of K in their leaves. The high accumulation of Na, S, and Mg in eu-halophytes may be related to the role in osmotic adjustment played by these cations, while the low concentration of K (and, in the case of annual succulents also Ca) could be related to preventing incompatible effects of these elements with Na in the cytoplasm. The low concentration of Na in the leaves of the second group may be related to the inability of these plants to compartmentalize Na in their vacuoles and prevent Na toxicity in the cytoplasm. In addition, their high K concentrations may be due to the very important roles of this element as an essential macronutrient in these less salt-tolerant plants. Our study has shown that the plant elemental composition is strongly constrained phylogenetically, and similar patterns are observed in closely related plants, even when grown in different environments.

Contribution

Zeinab Matinzadeh did the field and laboratory work, made the analysis and provided the first draft.

Hossein Akhiani supervised the project, joined in most of the field works and contributed to the structure and revision of the paper.

Mehdi Abedi contributed to the planning of the project, guided analysis and revised the paper.

Sara Palacio supervised the chemical and statistical analysis and revised the paper.

All four authors discussed the results and wrote the manuscript.

Table A.1
Average elemental composition (mg g⁻¹) of the species included in this study.

No.	Taxon	Al	Ca	Cr	Cu	Fe	K	Mg	Mn	Mo	Na	Ni	P	S	Si	Ti	V	Zn	N	C _{total}	
Acanthaceae																					
1	<i>Avicennia marina</i> (Forssk.) Vierh.	0.18	5.11	0.002	0.007	0.25	10.43	4.50	0.01	0.000	47.83	0.001	1.22	4.56	0.51	0.007	0.000	0.02	0.002	0.04	
Apocynaceae																					
2	<i>Cynanchum actutum</i> L.	0.38	17.05	0.003	0.017	0.43	26.17	6.13	0.12	0.000	10.65	0.001	1.30	8.92	0.80	0.014	0.001	0.03	0.003	0.05	
Asparagaceae																					
3	<i>Asparagus verticillatus</i> L.	0.22	8.61	0.002	0.012	0.25	30.74	4.23	0.07	0.001	3.04	0.008	5.34	4.61	0.75	0.008	0.000	0.08	0.004	0.05	
Asteraceae																					
4	<i>Achillea tenuifolia</i> Lam.	1.41	14.66	0.006	0.016	1.18	27.33	3.51	0.10	0.001	4.81	0.005	2.26	3.48	0.71	0.031	0.003	0.04	0.004	0.05	
5	<i>Calendula sancta</i> L.	0.33	25.37	0.002	0.016	0.37	11.45	5.40	0.05	0.007	14.69	0.003	3.81	6.53	0.68	0.010	0.001	0.21	0.002	0.04	
6	<i>Carduus arvensis</i> Murray	0.97	23.14	0.009	0.012	0.80	24.91	4.56	0.05	0.001	1.36	0.003	2.11	2.88	0.76	0.027	0.002	0.03	0.003	0.04	
7	<i>Cirsium alatum</i> (S. G. Gmel.) Bobrov	0.34	20.08	0.002	0.015	0.33	22.70	2.369	0.08	0.003	12.30	0.003	1.22	27.91	0.87	0.010	0.001	0.03	0.003	0.04	
8	<i>Grantia aucteri</i> Boiss.	0.21	63.14	0.002	0.017	0.23	13.14	6.13	0.03	0.001	22.92	0.001	1.24	37.88	0.58	0.006	0.000	0.06	0.002	0.03	
9	<i>Pulicaria arabica</i> (L.) Cass.	0.53	28.04	0.004	0.015	0.59	25.02	3.64	0.35	0.000	2.31	0.004	2.98	9.14	0.85	0.019	0.001	0.03	0.003	0.04	
10	<i>Saussurea salsa</i> (Pall. ex Pall.) Spreng	0.28	12.40	0.002	0.014	0.35	14.97	19.15	0.04	0.002	37.70	0.002	1.87	29.81	0.70	0.007	0.000	0.04	0.002	0.03	
11	<i>Scorzonera parviflora</i> Jacq.	0.30	9.82	0.003	0.009	0.29	27.22	0.038	0.07	0.000	24.04	0.002	2.07	6.38	0.82	0.008	0.000	0.07	0.002	0.04	
12	<i>Senecio glaucus</i> L.	2.53	30.39	0.009	0.017	2.27	21.82	8.65	0.19	0.002	18.22	0.006	3.10	6.77	1.37	0.065	0.005	0.03	0.003	0.04	
Boraginaceae																					
13	<i>Arnebia decumbens</i> (Vent.) Coss. & Kralkil	0.39	69.62	0.005	0.019	0.41	25.04	0.071	0.15	0.001	21.29	0.001	1.55	10.55	0.69	0.008	0.000	0.01	0.003	0.04	
14	<i>Asperugo procumbens</i> L.	1.87	34.27	0.006	0.019	1.81	29.19	0.009	5.36	0.19	0.001	7.75	0.007	2.93	3.82	0.86	0.055	0.003	0.02	0.003	0.04
15	<i>Heliotropium bacciferum</i> Forsk.	0.17	35.95	0.002	0.017	0.23	18.52	0.004	6.85	0.03	0.000	1.47	0.001	2.54	5.14	0.79	0.005	0.000	0.03	0.003	0.04
16	<i>Lithospermum arvense</i> L.	2.37	41.91	0.013	0.018	1.92	28.45	0.001	4.01	0.11	0.001	1.14	0.004	4.84	3.76	0.80	0.111	0.006	0.03	0.005	0.04
17	<i>Nonnea caspica</i> (Willd.) G. Don	2.63	53.73	0.010	0.013	2.97	23.66	0.011	6.11	0.27	0.000	8.06	0.008	2.29	3.01	1.29	0.145	0.006	0.02	0.002	0.04
Brassicaceae																					
18	<i>Brassica tournefortii</i> Gouan	0.62	59.66	0.006	0.006	0.73	7.13	0.005	12.96	0.03	0.001	13.15	0.002	1.10	8.07	0.92	0.024	0.002	0.02	0.002	0.04
19	<i>Descurainia sophia</i> (L.) Webb ex Prantl	2.32	27.70	0.013	0.012	2.21	20.42	0.009	5.71	0.11	0.005	1.92	0.006	4.52	10.81	0.90	0.118	0.005	0.03	0.004	0.04
20	<i>Erucaria hispanica</i> (L.) Druce	0.57	47.85	0.004	0.017	0.61	23.88	0.020	6.84	0.09	0.011	24.34	0.005	1.43	20.96	0.85	0.018	0.002	0.12	0.003	0.04
21	<i>Erysimum repandum</i> L.	0.41	62.13	0.002	0.015	0.37	22.65	0.027	7.41	0.09	0.015	3.72	0.003	5.05	10.27	0.88	0.007	0.000	0.01	0.003	0.04
22	<i>Euclettium syriacum</i> (L.) W. T. Aiton	3.22	31.97	0.020	0.012	2.83	26.05	0.031	9.97	0.11	0.001	7.27	0.009	3.89	16.76	0.97	0.112	0.006	0.03	0.004	0.04
23	<i>Lepidium cartilagineum</i> (J. C. Mayer) Thell.	0.47	8.06	0.003	0.012	0.48	20.97	0.105	6.83	0.04	0.002	43.79	0.003	2.44	31.87	0.84	0.011	0.001	0.01	0.005	0.04
24	<i>Lepidium draba</i> L.	0.84	23.12	0.005	0.010	0.83	25.10	0.025	5.11	0.08	0.002	2.80	0.005	3.25	22.74	0.86	0.031	0.001	0.04	0.005	0.04
25	<i>Lepidium perfoliatum</i> L.	1.13	18.76	0.006	0.012	1.14	18.67	0.023	7.11	0.06	0.002	21.32	0.005	3.05	12.24	2.03	0.049	0.002	0.03	0.004	0.04
26	<i>Lepidium vesicarium</i> L.	2.08	23.12	0.007	0.013	2.01	19.71	0.004	4.95	0.08	0.002	6.10	0.005	5.03	16.13	1.12	0.106	0.004	0.03	0.004	0.04
27	<i>Malcolmia africana</i> (L.) W. T. Aiton	2.91	39.18	0.016	0.011	2.52	25.75	0.016	5.36	0.10	0.001	7.87	0.007	2.71	15.54	0.85	0.083	0.006	0.03	0.004	0.04
28	<i>Olinarabidopsis pumila</i> (Stephan) Al-Shehbaz & al.	3.72	42.06	0.010	0.012	2.95	21.06	0.010	5.85	0.12	0.003	7.68	0.009	4.40	13.02	1.20	0.094	0.007	0.04	0.004	0.04
29	<i>Sisymbrium sepultatum</i> DC.	1.27	48.53	0.006	0.011	1.09	25.16	0.007	6.65	0.09	0.001	2.32	0.003	2.86	9.45	0.91	0.034	0.002	0.03	0.005	0.04
Capparidaceae																					
30	<i>Capparis spinosa</i> L.	0.21	25.34	0.003	0.005	0.28	8.54	0.013	12.63	0.04	0.000	17.49	0.001	1.88	18.72	0.61	0.007	0.000	0.02	0.003	0.04
Caryophyllaceae																					
31	<i>Gypsophila perfoliata</i> L.	0.53	22.57	0.005	0.020	0.52	27.98	0.034	18.06	0.04	0.003	3.92	0.002	2.97	31.03	0.78	0.014	0.001	0.03	0.004	0.04
32	<i>Holosteum glutinosum</i> (M. Bieb.) Fisch. & C. A. Mey.	2.92	12.50	0.011	0.012	2.84	32.48	0.005	16.64	0.09	0.001	21.40	0.007	6.31	3.29	1.01	0.190	0.006	0.02	0.004	0.03
33	<i>Holosteum umbellatum</i> L.	1.88	15.30	0.007	0.011	1.96	67.06	0.003	11.67	0.13	0.005	4.99	0.005	6.87	3.40	2.14	0.123	0.004	0.03	0.004	0.04
34	<i>Silene conoidea</i> L.	0.71	11.30	0.002	0.010	0.62	21.81	0.001	6.61	0.06	0.002	20.89	0.002	4.82	4.01	0.79	0.038	0.002	0.03	0.004	0.04
35	<i>Spergularia diandra</i> (Guss.) Boiss.	0.31	8.35	0.004	0.009	0.56	19.94	0.028	8.08	0.07	0.001	55.91	0.003	2.77	5.23	0.81	0.017	0.000	0.05	0.002	0.04

(continued on next page)

Table A.1 (continued)

Chenopodiaceae	
36	<i>Arthrocnemum macrostachyum</i> (Moric.) K. Koch
37	<i>Atriplex canescens</i> (Pursh) Nutt.
38	<i>Atriplex leucoclada</i> Boiss.
39	<i>Bienertia cycloptera</i> Bunge ex Boiss.
40	<i>Bienertia sinuspersici</i> Akhani
41	<i>Camphorosma monspeliaca</i> L.
42	<i>Caroxylon dendroides</i> (Pall.) Tzvel.
43	<i>Caroxylon nitrarium</i> (Pall.) Akhani & Roalson
44	<i>Chenopodium murale</i> L.
45	<i>Climacoptera crassa</i> (M. Bieb.) Botsch.
46	<i>Halimione verrucifera</i> (M. Bieb.) Aellen
47	<i>Halimocnemis rarifolium</i> (K. Koch) Akhani
48	<i>Halocharis sulphurea</i> (Moq.) Moq.
49	<i>Halocnemum srobilaceum</i> (Pall.) M. Bieb.
50	<i>Petrosimonia brachiata</i> (Pall.) Bunge
51	<i>Petrosimonia glauca</i> (Pall.) Bunge
52	<i>Salicornia iranica</i> Akhani
53	<i>Salicornia sinu-persica</i> Akhani
54	<i>Salsola drummondii</i> Ulbr.
55	<i>Salsola soda</i> L.
56	<i>Spinacia tetrandra</i> M. Bieb.
57	<i>Suaeda gracilis</i> Moq.
58	<i>Suaeda aegyptiaca</i> (Hasselq.) Zohary
59	<i>Suaeda altissima</i> (L.) Pall.
60	<i>Suaeda fruticosa</i> Forssk.
61	<i>Suaeda heterophylla</i> (Kar. & Kir.) Boiss.
Convulvaceae	
62	<i>Convolvulus lineatus</i> L.
63	<i>Cressa cretica</i> L.
Cyperaceae	
64	<i>Bolboschoenus affinis</i> (Roth) Drobow
65	<i>Bolboschoenus glaucus</i> (Lam.) S. G. Sm.
Euphorbiaceae	
66	<i>Euphorbia heteradena</i> Jaub. & Spach
Fabaceae	
67	<i>Alhagi maurorum</i> Medik.
68	<i>Scorpiurus muricatus</i> L.

(continued on next page)

Table A.1 (continued)

Frankeniaceae																						
69	<i>Frankenia hirsuta</i> L.	2.02	27.67	0.006	0.010	1.77	6.62	0.012	0.012	9.60	0.13	0.000	26.71	0.013	2.11	10.79	0.88	0.051	0.004	0.02	0.003	0.03
Juncaceae																						
70	<i>Juncus hedreichianus</i> T. Marsson ex Parl.	0.10	1.88	0.002	0.007	0.11	8.46	0.003	0.003	1.39	0.12	0.002	4.35	0.002	1.20	2.29	0.73	0.003	0.000	0.02	0.002	0.05
Malvaceae																						
71	<i>Malva parviflora</i> L.	0.58	49.25	0.005	0.008	0.69	23.45	0.012	0.012	10.96	0.08	0.003	16.45	0.002	1.57	13.33	1.01	0.017	0.002	0.02	0.002	0.04
Menispermaceae																						
72	<i>Cocculus pendulus</i> (J. R. Forst. & G. Forst.) Diels	0.18	43.82	0.002	0.009	0.22	8.11	0.011	0.011	6.38	0.07	0.000	2.30	0.001	1.25	7.00	0.59	0.006	0.000	0.02	0.003	0.04
Nitriaceae																						
73	<i>Nitraria schoberi</i> L.	0.26	13.05	0.002	0.016	0.25	16.60	0.058	0.058	6.72	0.08	0.001	58.69	0.004	1.57	10.66	0.83	0.007	0.000	0.01	0.004	0.04
74	<i>Peganum harmala</i> L.	0.38	10.71	0.002	0.009	0.34	24.81	0.018	0.018	3.68	0.11	0.000	4.62	0.003	2.94	5.87	0.89	0.012	0.001	0.04	0.005	0.05
Papaveraceae																						
75	<i>Hypeocum pendulum</i> L.	6.23	23.93	0.026	0.018	5.54	33.11	0.005	0.005	5.41	0.24	0.000	2.60	0.018	3.66	4.18	0.83	0.215	0.012	0.03	0.005	0.04
76	<i>Roemeria hybrida</i> (L.) DC.	1.02	19.20	0.003	0.012	0.83	15.44	0.003	0.003	3.73	0.05	0.002	12.88	0.002	4.17	7.45	0.76	0.045	0.002	0.03	0.005	0.04
Plantaginaceae																						
77	<i>Plantago amplexicaulis</i> Cav.	0.51	32.95	0.003	0.007	0.53	16.43	0.019	0.019	4.44	0.04	0.000	26.16	0.003	1.50	11.72	0.96	0.019	0.001	0.06	0.001	0.04
Plumbaginaceae																						
78	<i>Limonium axillare</i> (Forssk.) Kuntze	0.07	20.09	0.001	0.004	0.11	4.21	0.001	0.001	11.94	0.01	0.000	22.50	0.004	0.76	29.18	0.19	0.003	0.000	0.01	0.001	0.04
79	<i>Limonium failachicum</i> Erben & Mucina	2.04	29.18	0.009	0.011	1.97	6.23	0.003	0.003	11.00	0.05	0.000	28.93	0.011	1.83	24.32	0.76	0.042	0.005	0.04	0.002	0.04
80	<i>Limonium meyeri</i> (Boiss.) Kuntze	0.26	10.92	0.003	0.055	0.26	23.66	0.019	0.019	7.44	0.03	0.000	27.20	0.012	2.15	18.58	0.68	0.007	0.000	0.05	0.004	0.04
81	<i>Psylliostachys spicata</i> (Willd.) Nevski	0.34	18.08	0.002	0.009	0.34	21.15	0.010	0.010	10.96	0.03	0.002	52.75	0.004	1.84	16.54	0.85	0.010	0.001	0.13	0.003	0.04
Poaceae																						
82	<i>Aeluropus lagopoides</i> (L.) Thwaites	0.25	9.67	0.004	0.010	0.28	8.12	0.012	0.012	2.82	0.10	0.000	21.40	0.001	1.91	3.87	0.66	0.009	0.000	0.03	0.003	0.04
83	<i>Aeluropus litoralis</i> (Gouan) Parl.	0.76	8.16	0.014	0.009	0.72	11.11	0.012	0.012	2.22	0.09	0.002	24.73	0.003	1.00	4.63	0.58	0.025	0.001	0.03	0.002	0.04
84	<i>Bromus tectorum</i> L.	0.74	8.78	0.005	0.012	0.71	26.20	0.009	0.009	3.01	0.12	0.001	1.11	0.004	3.31	3.68	1.34	0.026	0.001	0.03	0.003	0.04
85	<i>Eremopyrum triticum</i> (Gaertn.) Nevski	0.93	9.28	0.013	0.009	0.84	12.39	0.005	0.005	1.88	0.13	0.000	0.96	0.004	1.24	1.93	1.37	0.036	0.001	0.03	0.002	0.05
86	<i>Falopyrum mucronatum</i> Stapf	0.41	5.79	0.019	0.007	0.54	4.39	0.001	0.001	2.65	0.01	0.000	7.50	0.002	1.00	3.21	0.74	0.014	0.001	0.02	0.002	0.05
87	<i>Hordeum murinum</i> subsp. <i>Glaucum</i> (Steud.) Tzvelev	1.33	10.21	0.030	0.013	1.42	19.79	0.005	0.005	2.47	0.11	0.001	4.32	0.005	2.38	2.95	1.70	0.037	0.002	0.03	0.003	0.04
88	<i>Phragmites australis</i> (Cav.) Steud.	0.06	2.68	0.003	0.052	0.11	19.49	0.022	0.022	1.07	0.05	0.001	0.43	0.010	2.94	3.03	0.83	0.003	0.000	0.04	0.002	0.04
89	<i>Poa bulbosa</i> L.	1.17	8.34	0.005	0.008	1.01	10.63	0.002	0.002	1.96	0.14	0.000	0.34	0.005	1.76	1.94	0.64	0.029	0.002	0.03	0.002	0.05
90	<i>Puccinellia bulbosa</i> (Grossh.) Grossh.	0.25	3.74	0.007	0.011	0.25	15.70	0.008	0.008	1.64	0.03	0.001	1.33	0.002	1.55	1.82	0.75	0.009	0.000	0.02	0.002	0.05
91	<i>Sclerochloa dura</i> (L.) P. Beauv.	0.80	6.50	0.004	0.009	0.71	18.56	0.006	0.006	1.94	0.08	0.001	7.45	0.003	2.33	3.43	0.91	0.026	0.001	0.03	0.003	0.05
92	<i>Sporobolus arabicus</i> Boiss.	0.26	22.41	0.009	0.007	0.39	13.33	0.002	0.002	3.91	0.02	0.002	23.48	0.001	1.19	10.34	0.80	0.010	0.001	0.01	0.002	0.04
93	<i>Stipa capensis</i> Thunb.	0.28	13.47	0.008	0.011	0.37	13.72	0.005	0.005	3.71	0.07	0.005	3.42	0.002	1.57	3.77	0.63	0.010	0.001	0.02	0.003	0.05
94	<i>Stipa hohentackertana</i> Trin. & Rupr.	0.21	2.71	0.002	0.006	0.23	9.71	0.000	0.000	0.47	0.04	0.000	0.28	0.002	0.92	1.10	0.76	0.008	0.000	0.02	0.001	0.05
Polygonaceae																						
95	<i>Emex spinosa</i> (L.) Campd.	0.74	47.38	0.013	0.007	0.74	26.22	0.028	0.028	20.39	0.08	0.002	31.68	0.003	0.59	5.78	0.94	0.025	0.002	0.02	0.002	0.03
96	<i>Polygonum patulum</i> M. Bieb.	0.81	15.01	0.003	0.010	0.81	19.59	0.018	0.018	6.81	0.04	0.001	17.15	0.004	2.96	5.52	1.23	0.027	0.001	0.04	0.004	0.04
Ranunculaceae																						
97	<i>Adonis annua</i> L.	4.34	31.85	0.010	0.015	3.30	31.66	0.055	0.055	7.30	0.13	0.000	2.46	0.009	3.69	5.79	2.03	0.088	0.007	0.06	0.003	0.04
98	<i>Ceratocephalus falcatus</i> (L.) Pers.	2.41	14.67	0.008	0.012	2.37	25.60	0.005	0.005	4.50	0.14	0.002	5.88	0.009	1.72	6.14	1.11	0.145	0.005	0.01	0.003	0.04
Resedaceae																						
99	<i>Ochradenus baccatus</i> Delile	0.18	15.70	0.003	0.010	0.24	18.41	0.004	0.004	4.94	0.08	0.000	2.96	0.005	2.90	18.95	0.55	0.005	0.000	0.03	0.004	0.04
Solanaceae																						
101	<i>Lycium ruthenicum</i> Murray	0.35	15.80	0.003	0.011	0.32	15.28	1.130	1.130	8.60	0.05	0.000	14.54	0.002	2.74	5.89	0.80	0.010	0.000	0.04	0.004	0.05
102	<i>Solanum incanum</i> L.	0.83	51.78	0.016	0.015	0.93	25.22	0.019	0.019	3.43	0.05	0.000	0.94	0.004	3.53	6.32	1.04	0.035	0.002	0.04	0.002	0.04
Tamaricaceae																						
103	<i>Reaumuria alternifolia</i> (Labill.) Britten	0.47	15.97	0.004	0.010	0.46	7.62	0.012	0.012	5.69	0.06	0.000	46.43	0.001	1.75	25.58	0.73	0.013	0.001	0.02	0.003	0.04
104	<i>Tamarix meyeri</i> Boiss.	0.37	29.88	0.003	0.033	0.40	9.47	0.002	0.002	13.23	0.03	0.000	18.18	0.002	1.78	37.93	0.79	0.014	0.001	0.03	0.004	0.04
105	<i>Tamarix pycnocarpa</i> DC.	0.81	32.39	0.004	0.013	0.78	5.52	0.009	0.009	12.49	0.03	0.000	20.87	0.003	0.64	33.79	1.06	0.028	0.002	0.05	0.001	0.04
Typhaceae																						
106	<i>Typha grossheimii</i> Pobed.	0.14	10.90	0.003	0.008	0.16	15.01	0.002	0.002	3.75	0.32	0.004	9.76	0.001	0.40	5.97	0.34	0.004	0.000	0.02	0.001	0.04
Zygophyllaceae																						
107	<i>Tetradiclis tenella</i> Litv.	0.38	9.58	0.004	0.008	0.40	49.79	0.009	0.009	1.44	0.05	0.002	64.42	0.005	2.91	5.61	0.77	0.014	0.001	0.03	0.006	0.03
108	<i>Zygophyllum fabago</i> L.	0.15	28.14	0.002	0.016	0.17	25.72	0.098	0.098	10.24	0.03	0.000	37.90	0.004	2.65	46.50	0.62	0.006	0.000	0.02	0.004	0.04

Table A.2

Details of soil chemical composition for every studied site. Average pH, Electrical Conductivity (EC mS/cm), and concentrations of Calcium (Ca mg g⁻¹), Potassium (K mg g⁻¹), Magnesium (Mg mg g⁻¹), Sodium (Na mg g⁻¹), Sulfur (S mg g⁻¹), and Gypsum (Gyp %) of soil samples from every site ± SE are shown.

Sites	pH	EC	Ca	K	Mg	Na	S	Gyp
U1	8.7 ± 0.1	5.3 ± 3.1	178.2 ± 23.7	6.6 ± 0.9	37.1 ± 5.1	9.1 ± 5	3.7 ± 1.8	59.2 ± 2.7
U2	8.6 ± 0.1	8 ± 1.3	60.5 ± 9.2	26 ± 1.4	29.3 ± 4.3	15.3 ± 3.4	8.1 ± 1	68.1 ± 4
U3	8.6 ± 0.1	11.3 ± 3.8	19.4 ± 3.8	11.3 ± 2.5	23.2 ± 5.1	17.4 ± 5.7	4.2 ± 1.8	46.5 ± 5.1
U4	8.5 ± 0.1	13.6 ± 9.3	135.2 ± 5.2	8.1 ± 0.02	16.3 ± 1.6	14.9 ± 10.4	5.9 ± 0.3	44.5 ± 3.3
U5	8.9 ± 0.1	0.9 ± 0.4	276.1 ± 62.3	3.6 ± 4.4	10.5 ± 3	3 ± 0.7	5.1 ± 2.9	20.7 ± 2.7
U6	9 ± 0.1	1 ± 0.6	120.6 ± 12.4	6.6 ± 1.3	12.1 ± 2.6	8.1 ± 5.8	1.4 ± 0.5	13.4 ± 5.7
U7	8.3 ± 0.04	4.9 ± 5	59.4 ± 1.3	25.2 ± 0.5	37.2 ± 1.4	8.6 ± 0.4	2.9 ± 0.6	73.7 ± 2.7
U8	8.8 ± 0.03	14.9 ± 2	49.2 ± 1.9	10 ± 0.5	34 ± 0.9	21.5 ± 3.2	3 ± 0.6	31 ± 1.8
M	8.2 ± 0.1	2.9 ± 0.3	74.4 ± 4.1	13.6 ± 1.5	56 ± 5.2	2.5 ± 0.6	37.1 ± 3.5	65.4 ± 1.9
K	8.6 ± 0.02	10.5 ± 0.3	178.7 ± 3.2	8 ± 0.2	50.2 ± 0.7	12.8 ± 0.4	1.7 ± 0.02	45.4 ± 0.3
N1	9.5 ± 0.1	1.8 ± 0.9	375.5 ± 2.1	0.4 ± 0.04	15 ± 0.5	3 ± 0.8	1.5 ± 0.2	2.4 ± 0.1
N2	8.1 ± 0.02	1.5 ± 0.4	177.8 ± 6.1	7.6 ± 0.1	37.5 ± 0.3	1.4 ± 0.3	1 ± 0.4	27.2 ± 1.7
N3	8.4 ± 0.2	6.1 ± 1.5	252.9 ± 11	2.7 ± 0.5	17.8 ± 1.8	4.7 ± 1.4	52.1 ± 21.6	46 ± 7.9
N4	8.3 ± 0.1	3.4 ± 0.7	276.4 ± 5.3	3.3 ± 0.1	22.8 ± 0.2	2.4 ± 0.5	5.1 ± 1.4	29.6 ± 2.8
N5	8.4 ± 0.1	3.5 ± 1.5	242.3 ± 2	3.1 ± 0.2	32.8 ± 0.5	2.7 ± 1.1	1.9 ± 0.7	21.5 ± 1.8

Soil salinity varies from site to site due to existing hydrological conditions and the time of sampling. The sites around Lake Urmia (U1 to U8) are moderate to high saline with EC between 0.88 (U5) and 14.86 (U8) mS/cm, depending on sampling time, leaching and distance from the lake. The highest measured EC was observed near Soulduz wetland (U8). Soil samples from Khore Musa (K) are inundated by saline water of Persian Gulf tides, leading to high EC above 10.4 mS/cm. Nayband (N1 to N5) soil samples are saline with EC between 1.49 and 6.06 mS/cm. The low EC of the uppermost soil surface in this area is largely affected by the presence of a high amount of sand on the shoreline and probably leaching of sands during winter.

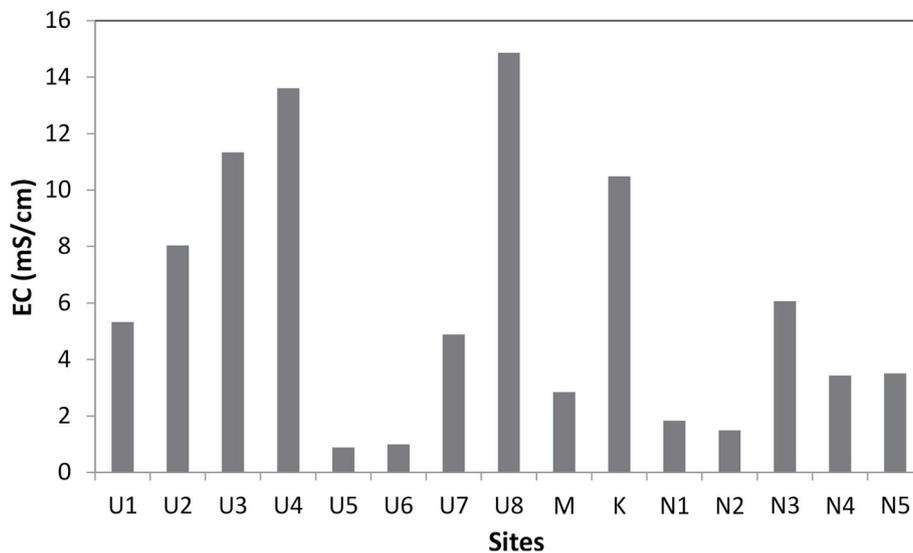


Fig. A.1. Average the soil samples EC (Electric Conductivity) in every site.

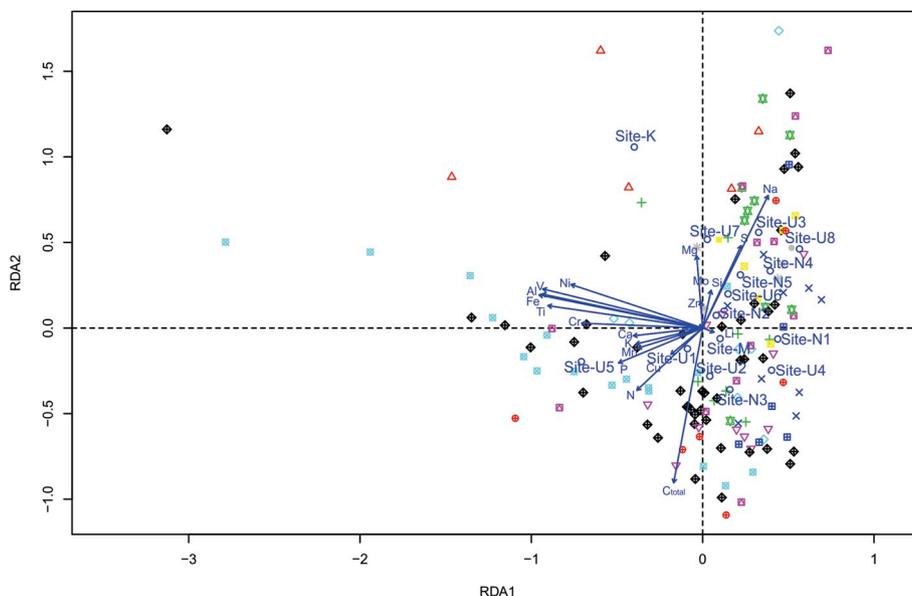


Fig. A.2 RDA Triplot of the chemical composition vs. studied sites. Symbols: ◆ = Site U1, ⊕ = Site U2, ☆ = Site U3, ⊞ = Site U4, ⊠ = Site U5, ▽ = Site U6, ■ = Site U7, ● = Site U8, ◇ = Site M, △ = Site K, × = Site N1, + = Site N2, ▽ = Site N3, * = Site N4, ⊠ = Site N52

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References

- Abdely, C., Öztürk, M., Ashraf, M., Grignon, C., 2008. Biosaline Agriculture and High Salinity Tolerance. Springer Science & Business Media.
- Akhani, H., 1992. A contribution to the vegetation and flora of Kavire-Meyghan (NE, Arak), Iran. *J. Sci. Univ. Tehran (Int. ed.)* 18, 75–84 1989 (publ).
- Akhani, H., 2006. Biodiversity of halophytic and sabkha ecosystems in Iran. In: Ajmal Khan, M. (Ed.), *Sabkha Ecosystems Volume II: West and Central Asia*. Springer, pp. 71–88. https://doi.org/10.1007/978-1-4020-5072-5_6.
- Akhani, H., 2015. *Plants and Vegetation of North-West Persian Gulf: the Coasts and Islands of Khore Musa, Mahshahr and Adjacent Areas*. University of Tehran Press, Tehran.
- Akhani, H., Barroca, J., Koteeva, N., Voznesenskaya, E., Franceschi, V., Edwards, G., Ghaffari, S.M., Ziegler, H., 2005. *Bienertia sinuspersici* (Chenopodiaceae): a new species from southwest Asia and discovery of a third terrestrial C₄ plant without Kranz anatomy. *Syst. Bot.* 30, 290–301. <https://doi.org/10.1600/0363644054223684>.
- Akhani, H., Deil, U., 2012. First observations of the flora and vegetation of three Islands in the NW Persian Gulf (Iran). *Phyton-Ann Rei Bot A* 52, 73–99.
- Akhani, H., Edwards, G., Roalson, E.H., 2007. Diversification of the Old World salsoleae s.l. (Chenopodiaceae): molecular phylogenetic analysis of nuclear and chloroplast data sets and a revised classification. *Int. J. Plant Sci.* 168, 931–956. <https://doi.org/10.1086/518263>.
- Akhani, H., Ghasemkhani, M., 2007. Diversity of photosynthetic organs in Chenopodiaceae from Golestan National Park (NE Iran) based on carbon isotope composition and anatomy of leaves and cotyledons. *Nova Hedwigia Supplement* 131, 265–277.
- Akhani, H., Trimborn, P., Ziegler, H., 1997. Photosynthetic pathways in Chenopodiaceae from Africa, Asia and Europe with their ecological, phytogeographical and taxonomical importance. *Plant Systemat. Evol.* 206, 187–221. <https://doi.org/10.1007/BF00987948>.
- Al-Ani, T., Habib, I., Abdulaziz, A., Ouda, N., 1971. Plant indicators in Iraq. *Plant Soil* 35, 29–36. <https://doi.org/10.1007/BF01372629>.
- Albert, R., 1975. Salt regulation in halophytes. *Oecologia* 21, 57–71. <https://doi.org/10.1007/BF00345893>.
- Albert, R., 1982. Halophyten. In: Kinzel, H. (Ed.), *Pflanzenökologie und Mineralstoffwechsel*. Ulmer, Stuttgart, pp. 33–204.
- Albert, R., Kinzel, H., 1973. Unterscheidung von Physiotypen bei Halophyten des Neusiedlerseegebietes (Österreich). *Z. Pflanzenphysiol.* 70, 138–157. [https://doi.org/10.1016/S0044-328X\(73\)80057-1](https://doi.org/10.1016/S0044-328X(73)80057-1).
- Albert, R., Popp, M., 1977. Chemical composition of halophytes from the Neusiedler Lake region in Austria. *Oecologia* 27, 157–170. <https://doi.org/10.1007/BF00345820>.
- Alhdad, G.M., Seal, C.E., Al-Azzawi, M.J., Flowers, T.J., 2013. The effect of combined salinity and waterlogging on the halophyte *Suaeda maritima*: the role of antioxidants. *Environ. Exp. Bot.* 87, 120–125. <https://doi.org/10.1016/j.envexpbot.2012.10.010>.
- Asri, Y., 1998. [Vegetation of the Orumieh Lake Salt Marshes]. Research Institute of Forests and Rangelands, Tehran Technical Publication No. 191-1998. (In Persian).
- Asri, Y., Ghorbanli, M., 1997. The halophilous vegetation of the Orumieh lake salt marshes, NW. Iran. *Plant Ecol.* 132, 155–170. <https://doi.org/10.1023/A:1009790901167>.
- Bange, G., 1959. Interactions in the potassium and sodium absorption by intact maize seedlings. *Plant Soil* 11, 17–29. <https://doi.org/10.1007/BF01394750>.
- Barakat, N.A., Cazzato, E., Nedjimi, B., Kabieli, H.F., Laudadio, V., Tufarelli, V., 2014. Ecophysiological and species-specific responses to seasonal variations in halophytic species of the Chenopodiaceae in a Mediterranean salt marsh. *Afr. J. Ecol.* 52, 163–172. <https://doi.org/10.1111/aje.12100>.
- Belkheiri, O., Mulas, M., 2013. The effects of salt stress on growth, water relations and ion accumulation in two halophyte *Atriplex* species. *Environ. Exp. Bot.* 86, 17–28. <https://doi.org/10.1016/j.envexpbot.2011.07.001>.
- Blumwald, E., 2000. Sodium transport and salt tolerance in plants. *Curr. Opin. Cell Biol.* 12, 431–434. [https://doi.org/10.1016/S0955-0674\(00\)00112-5](https://doi.org/10.1016/S0955-0674(00)00112-5).
- Bolukbasi, A., Kurt, L., Palacio, S., 2016. Unravelling the mechanisms for plant survival on gypsum soils: an analysis of the chemical composition of gypsum plants from Turkey. *Plant Biol.* 18, 271–279. <https://doi.org/10.1111/plb.12401>.
- Borcard, D., Gillet, F., Legendre, P., 2011. *Numerical Ecology with R*. Springer, pp. 227–292. <http://doi.org/10.1007/978-1-4419-7976-6>.
- Breckle, S.-W., 1975. Ion engehalte halophiler Pflanzen spaniens. *Decheniana* 127, 221–228.
- Breckle, S.-W., 1986. Studies on halophytes from Iran and Afghanistan .2. Ecology of halophytes along salt gradients. *P Roy Soc Edinb B* 89, 203–215. <https://doi.org/10.1017/S026972700009039>.
- Breckle, S.-W., 1990. Salinity tolerance of different halophyte types. In: Bassam, N.E., Dawbtdt, M., Loughwau, J.C. (Eds.), *Genetic Aspects of Plant Mineral Nutrition*. Kluwer Academic Publishers, Dordrecht, pp. 167–175. https://doi.org/10.1007/978-94-009-2053-8_26.
- Broadley, M.R., Bowen, H.C., Cotterill, H.L., Hammond, J.P., Meacham, M.C., Mead, A., White, P.J., 2004. Phylogenetic variation in the shoot mineral concentration of angiosperms. *J. Exp. Bot.* 55, 321–336. <https://doi.org/10.1093/jxb/erh002>.
- Brownell, P., Crossland, C., 1972. The requirement for sodium as a micronutrient by species having the C₄ dicarboxylic photosynthetic pathway. *Plant Physiol.* 49,

- 794–797. <https://doi.org/10.1104/pp.49.5.794>.
- Byng, J.W., Chase, M.W., Christenhusz, M.J.M., Fay, M.F., Judd, W.S., Mabberley, D.J., Sennikov, A.N., Soltis, D.E., Soltis, P.S., Stevens, P.F., Briggs, B., Brockington, S., Chautems, A., Clark, J.C., Conran, J., Haston, E., Moller, M., Moore, M., Olmstead, R., Perret, M., Skog, L., Smith, J., Tank, D., Vorontsova, M., Weber, A., Angiosperm Phylogeny, G., 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181, 1–20. <https://doi.org/10.1111/boj.12385>.
- Chandra, S., Rawat, D.S., 2015. Medicinal plants of the family Caryophyllaceae: a review of ethno-medicinal uses and pharmacological properties. *Integr Med Res* 4, 123–131. <https://doi.org/10.1016/j.imr.2015.06.004>.
- Chenchouni, H., 2017. Edaphic factors controlling the distribution of inland halophytes in an ephemeral salt lake “Sabkha ecosystem” at North African semi-arid lands. *Sci. Total Environ.* 575, 660–671. <https://doi.org/10.1016/j.scitotenv.2016.09.071>.
- Chinnusamy, V., Jagendorf, A., Zhu, J.-K., 2005. Understanding and improving salt tolerance in plants. *Crop Sci.* 45, 437–448. <https://doi.org/10.2135/cropsci2005.0437>.
- Colmer, T.D., Flowers, T.J., 2008. Flooding tolerance in halophytes. *New Phytol.* 179, 964–974. <https://doi.org/10.1111/j.1469-8137.2008.02483.x>.
- Dashtebani, F., Hajiboland, R., Aliasgharzad, N., 2014. Characterization of salt-tolerance mechanisms in mycorrhizal (*Claroideoglossum etunicatum*) halophytic grass, *Puccinellia distans*. *Acta Physiol. Plant.* 36, 1713–1726. <https://doi.org/10.1007/s11738-014-1546-4>.
- Dassanayake, M., Larkin, J.C., 2017. Making plants break a sweat: the structure, function, and evolution of plant salt glands. *Front. Plant Sci.* 8, 1–20. <https://doi.org/10.3389/fpls.2017.00406>.
- Djamali, M., Akhiani, H., Khoshnavesh, R., Andrieu-Ponel, V., Ponel, P., Brewer, S., 2011. Application of the Global Bioclimatic Classification to Iran: implications for understanding the modern vegetation and biogeography. *Ecol. Mediterr.* 37, 91–114.
- Djamali, M., Kürschner, H., Akhiani, H., de Beaulieu, J.L., Amini, A., Andrieu-Ponel, V., Ponel, P., Stevens, L., 2008. Palaeoecological significance of the spores of the liverwort *Riella* (Riellaceae) in a late Pleistocene long pollen record from the hypersaline Lake Urmia, NW Iran. *Rev. Palaeobot. Palynol.* 152, 66–73. <https://doi.org/10.1016/j.revpalbo.2008.04.004>.
- Donovan, L.A., Richards, J.H., Schaber, E.J., 1997. Nutrient relations of the halophytic shrub, *Sarcobatus vermiculatus*, along a soil salinity gradient. *Plant Soil* 190, 105–117. <https://doi.org/10.1023/A:1004211207079>.
- Duarte, B., Santos, D., Marques, J., Caçador, I., 2015. Ecophysiological constraints of two invasive plant species under a saline gradient: halophytes versus glycophytes. *Estuar. Coast Shelf Sci.* 167, 154–165. <https://doi.org/10.1016/j.ecss.2015.04.007>.
- Duvigneaud, P., Smet, S.D.-D., 1968. *Essai de classification chimique (éléments minéraux) des plantes gypsiques du bassin de l'Ébre*. *Bull. Soc. Roy. Bot. Belg.* 101, 279–291.
- Edwards, E.J., Ogburn, R.M., 2012. Angiosperm responses to a low CO₂ world: CAM and C₄ photosynthesis as parallel evolutionary trajectories. *Int. J. Plant Sci.* 173, 724–733. <https://doi.org/10.1086/666098>.
- Edwards, E.J., Osborne, C.P., Stromberg, C.A.E., Smith, S.A., Bond, W.J., Christin, P.A., Cousins, A.B., Duvall, M.R., Fox, D.L., Freckleton, R.P., Ghannoum, O., Hartwell, J., Huang, Y.S., Janis, C.M., Keeley, J.E., Kellogg, E.A., Knapp, A.K., Leakey, A.D.B., Nelson, D.M., Saarela, J.M., Sage, R.F., Sala, O.E., Salamin, N., Still, C.J., Tiplle, B., Consortium, C.G., 2010. The origins of C₄ grasslands: integrating evolutionary and ecosystem science. *Science* 328, 587–591. <https://doi.org/10.1126/science.1177216>.
- Flowers, T., Hajibagheri, M., Clipson, N., 1986. Halophytes. *Q. Rev. Biol.* 61, 313–337. <https://doi.org/10.1086/415032>.
- Flowers, T., Troke, P., Yeo, A., 1977. The mechanism of salt tolerance in halophytes. *Annu. Rev. Plant Physiol.* 28, 89–121. <https://doi.org/10.1146/annurev.1977.28.1>.
- Flowers, T.J., Colmer, T.D., 2008. Salinity tolerance in halophytes. *New Phytol.* 179, 945–963. <https://doi.org/10.1111/j.1469-8137.2008.02531.x>.
- Flowers, T.J., Colmer, T.D., 2015. Plant salt tolerance: adaptations in halophytes. *Ann. Bot.* 115, 327–331. <https://doi.org/10.1093/aob/mcu267>.
- Flowers, T.J., Munns, R., Colmer, T.D., 2014. Sodium chloride toxicity and the cellular basis of salt tolerance in halophytes. *Ann. Bot.* 115, 419–431. <https://doi.org/10.1093/aob/mcu217>.
- Fujimaki, S., Maruyama, T., Suzui, N., Kawachi, N., Miwa, E., Higuchi, K., 2015. Base to tip and long-distance transport of sodium in the root of common reed *Phragmites australis* (Cav.) Trin. ex Steud. at steady state under constant high-salt conditions. *Plant Cell Physiol.* 56, 943–950. <https://doi.org/10.1093/pcp/pcv021>.
- Gal, A., Hirsch, A., Siegel, S., Li, C.H., Aichmayer, B., Politi, Y., Fratzi, P., Weiner, S., Addadi, L., 2012. Plant cystoliths: a complex functional biocomposite of four distinct silica and amorphous calcium carbonate phases. *Chem. Eur. J.* 18, 10262–10270. <https://doi.org/10.1002/chem.201201111>.
- Gerloff, G., 1963. Comparative mineral nutrition of plants. *Annu. Rev. Plant Physiol.* 14, 107–124. <https://doi.org/10.1146/annurev.1963.14.1>.
- Glenn, E., Pfister, R., Brown, J.J., Thompson, T.L., O'Leary, J., 1996. Na and K accumulation and salt tolerance of *Atriplex canescens* (Chenopodiaceae) genotypes. *Am. J. Bot.* 997, 1005. <https://doi.org/10.1002/j.1537-2197.1996.tb12796.x>.
- Glenn, E.P., Nelson, S.G., Ambrose, B., Martinez, R., Soliz, D., Pabendinskas, V., Hultine, K., 2012. Comparison of salinity tolerance of three *Atriplex* spp. in well-watered and drying soils. *Environ. Exp. Bot.* 83, 62–72. <https://doi.org/10.1016/j.envexpbot.2012.04.010>.
- Grattan, S., Grieve, C., 1992. Mineral element acquisition and growth response of plants grown in saline environments. *Agric. Ecosyst. Environ.* 38, 275–300. [https://doi.org/10.1016/0167-8809\(92\)90151-Z](https://doi.org/10.1016/0167-8809(92)90151-Z).
- Gulzar, S., Khan, M.A., Ungar, I.A., 2003. Effects of salinity on growth, ionic content, and plant-water status of *Aeluropus lagopoides*. *Commun. Soil Sci. Plant* 34, 1657–1668. <https://doi.org/10.1081/CSS-120021303>.
- Hammou, K.A., Rubio, L., Fernández, J.A., García-Sánchez, M.J., 2014. Potassium uptake in the halophyte *Halimione portulacoides* L. Aellen. *Environ. Exp. Bot.* 107, 15–24. <https://doi.org/10.1016/j.envexpbot.2014.05.001>.
- Hariadi, Y., Marandon, K., Tian, Y., Jacobsen, S.-E., Shabala, S., 2011. Ionic and osmotic relations in quinoa (*Chenopodium quinoa* Willd.) plants grown at various salinity levels. *J. Exp. Bot.* 62, 185–193. <https://doi.org/10.1093/jxb/erq257>.
- Hassine, A.B., Ghanem, M.E., Bouzid, S., Lutts, S., 2008. An inland and a coastal population of the Mediterranean xero-halophyte species *Atriplex halimus* L. differ in their ability to accumulate proline and glycinebetaine in response to salinity and water stress. *J. Exp. Bot.* 59, 1315–1326. <https://doi.org/10.1093/jxb/ern040>.
- Hernández-Ledesma, P., Berendsohn, W.G., Borsch, T., Mering, S.v., Akhiani, H., Arias, S., Castañeda-Noa, I., Egli, U., Eriksson, R., Flores-Olvera, H., Fuentes-Bazán, S., Kadereit, G., Klak, C., Korotkova, N., Nyffeler, R., Ocampo, G., Ochoterena, H., Oxelman, B., Rabeler, R.K., Sanchez, A., Schlumpberger, B.O., Uotila, P., 2015. A taxonomic backbone for the global synthesis of species diversity in the angiosperm order Caryophyllales. *Willdenowia* 45, 281–383. <https://doi.org/10.3372/wi.45.45301>.
- Judd, W.S., Campbell, C.S., Kellogg, E.A., Stevens, P.F., Donoghue, M.J., 2015. *Plant Systematics: A Phylogenetic Approach*, fourth ed. Sinauer Associates, Sunderland, Massachusetts.
- Kachout, S.S., Mansoura, A.B., Hamza, K.J., Leclerc, J., Rejeb, M., Ouergli, Z., 2011. Leaf-water relations and ion concentrations of the halophyte *Atriplex hortensis* in response to salinity and water stress. *Acta Physiol. Plant.* 33, 335–342. <https://doi.org/10.1007/s11738-010-0552-4>.
- Khan, M.A., Ungar, I.A., Showalter, A.M., 2000a. The effect of salinity on the growth, water status, and ion content of a leaf succulent perennial halophyte, *Suaeda frutescens* (L.) Forssk. *J. Arid Environ.* 45, 73–84. <https://doi.org/10.1006/jare.1999.0617>.
- Khan, M.A., Ungar, I.A., Showalter, A.M., 2000b. Effects of salinity on growth, water relations and ion accumulation of the subtropical perennial halophyte, *Atriplex griffithii* var. *stokesii*. *Ann. Bot.* 85, 225–232. <https://doi.org/10.1006/anbo.1999.1022>.
- Khan, M.A., Ungar, I.A., Showalter, A.M., 2005. Salt stimulation and tolerance in an intertidal stem-succulent halophyte. *J. Plant Nutr.* 28, 1365–1374. <https://doi.org/10.1081/PLN-200067462>.
- Kinzel, H., 1989. Calcium in the vacuoles and cell walls of plant tissue. *Flora* 182, 99–125. [https://doi.org/10.1016/S0367-2530\(17\)30398-5](https://doi.org/10.1016/S0367-2530(17)30398-5).
- Krüger, H., Peinemann, N., 1996. Coastal plain halophytes and their relation to soil ionic composition. *Plant Ecol.* 122, 143–150. <https://doi.org/10.1007/BF00044696>.
- Kudo, N., Sugino, T., Oka, M., Fujiyama, H., 2010. Sodium tolerance of plants in relation to ionic balance and the absorption ability of microelements. *Soil Sci. Plant Nutr.* 56, 225–233. <https://doi.org/10.1111/j.1747-0765.2009.00436.x>.
- Lambers, H., Chapin III, F.S., Pons, T.L., 2008. *Plant Physiological Ecology*. Springer Science & Business Media.
- Liu, S., Kang, Y., Wan, S., Wang, Z., Liang, Z., Jiang, S., Wang, R., 2012. Germination and growth of *Puccinellia tenuiflora* in saline-sodic soil under drip irrigation. *Agric. Water Manag.* 109, 127–134. <https://doi.org/10.1016/j.agwat.2012.03.001>.
- Matinzadeh, Z., Breckle, S.-W., Mirmassoumi, M., Akhiani, H., 2013. Ionic relationships in some halophytic Iranian Chenopodiaceae and their rhizospheres. *Plant Soil* 372, 523–539. <https://doi.org/10.1007/s11104-013-1744-7>.
- Matsushita, N., Matoh, T., 1992. Function of the shoot base of salt-tolerant reed (*Phragmites communis* Trinius) plants for Na⁺ exclusion from the shoots. *Soil Sci. Plant Nutr.* 38, 565–571. <https://doi.org/10.1080/00380768.1992.10415088>.
- Merlo, M.E., Garrido-Becerra, J.A., Mota, J.F., Salmerón-Sánchez, E., Martínez-Hernández, F., Mendoza-Fernández, A., Pérez-García, F.J., 2019. Threshold ionic contents for defining the nutritional strategies of gypsumiferous flora. *Ecol. Indic.* 97, 247–259. <https://doi.org/10.1016/j.ecolind.2018.10.001>.
- Milić, D., Luković, J., Zorić, L., Vasin, J., Ninkov, J., Zeremski, T., Milić, S., 2013. Halophytes relations to soil ionic composition. *J. Serb. Chem. Soc.* 78, 1259–1268. <https://doi.org/10.2298/JSCI3013029D>.
- Minden, V., Andratschke, S., Spalke, J., Timmermann, H., Kleyer, M., 2012. Plant trait–environment relationships in salt marshes: deviations from predictions by ecological concepts. *Perspect. Plant Ecol. Evol.* 14, 183–192. <https://doi.org/10.1016/j.ppees.2012.01.002>.
- Miura, K., 2013. Nitrogen and phosphorus nutrition under salinity stress. In: Ahmad, P., Azooz, M.M., Prasad, M.N.V. (Eds.), *Ecophysiology and Responses of Plants under Salt Stress*. Springer, pp. 425–441. https://doi.org/10.1007/978-1-4614-4747-4_16.
- Mori, S., Akiya, M., Yamamura, K., Murano, H., Arai, T., Kawasaki, A., Higuchi, K., Maeda, Y., Yoshida, M., Tadano, T., 2010. Physiological role of sodium in the growth of the halophyte *Suaeda salsa* (L.) pall. under high-sodium conditions. *Crop Sci.* 50, 2492–2498. <https://doi.org/10.2135/cropsci2010.02.0119>.
- Mozfar, A., Goodin, J., 1970. Vesiculated hairs: a mechanism for salt tolerance in *Atriplex halimus* L. *Plant Physiol.* 45, 62–65. <https://doi.org/10.1104/pp.45.1.62>.
- Mustafa, A., Ensikat, H.J., Weigend, M., 2018. Mineralized trichomes in Boraginales: complex microscale heterogeneity and simple phylogenetic patterns. *Ann. Bot.* 121, 741–751. <https://doi.org/10.1093/aob/mcx191>.
- Naidoo, G., 1994. Growth, water and ion relationships in the coastal halophytes *Triglochin bulbosa* and *T. striata*. *Environ. Exp. Bot.* 34, 419–426. [https://doi.org/10.1016/0098-8472\(94\)90024-8](https://doi.org/10.1016/0098-8472(94)90024-8).
- Naidoo, G., Naidoo, Y., 1998. Salt tolerance in *Sporobolus virginicus*: the importance of ion relations and salt secretion. *Flora* 193, 337–344. [https://doi.org/10.1016/S0367-2530\(17\)30859-9](https://doi.org/10.1016/S0367-2530(17)30859-9).
- Naz, N., Hameed, M., Nawaz, T., Aqeel Ahmad, M.S., Ashraf, M., 2013. Soil-plant relationships in the arid saline desert of Cholistan. *Arid Land Res. Manag.* 27, 140–152. <https://doi.org/10.1080/15324982.2012.719576>.
- Neugebauer, K., Broadley, M.R., El-Serehy, H.A., George, T.S., McNicol, J.W., Moraes, M.F., White, P.J., 2018. Variation in the angiosperm ionome. *Physiol. Plantarum* 163,

- 306–322. <https://doi.org/10.1111/ppl.12700>.
- Noaman, M.N., 2004. Effect of potassium and nitrogen fertilizers on the growth and biomass of some halophytes grown under high levels of salinity. *J. Agron.* 3, 25–30. <https://scialert.net/abstract/?doi=ja.2004.25.30>.
- Nyffeler, R., Eggl, U., Ogburn, M., Edwards, E., 2008. Variations on a theme: repeated evolution of succulent life forms in the Portulacaceae (Caryophyllales). *Haseltonia* 26–36. <https://doi.org/10.2985/1070-0048-14.1.26>.
- Ogburn, R., Edwards, E.J., 2010. The ecological water-use strategies of succulent plants. *Adv. Bot. Res.* 55, 179–225. <https://doi.org/10.1016/B978-0-12-380868-4.00004-1>.
- Parida, A.K., Das, A.B., 2005. Salt tolerance and salinity effects on plants: a review. *Ecotoxicol. Environ. Saf.* 60, 324–349. <https://doi.org/10.1016/j.ecoenv.2004.06.010>.
- Pennock, D., McKenzie, N., Montanarella, L., 2015. Status of the World's Soil Resources. Technical Summary FAO, Rome, Italy.
- Percey, W.J., Shabala, L., Wu, Q., Su, N., Breadmore, M.C., Guijt, R.M., Bose, J., Shabala, S., 2016. Potassium retention in leaf mesophyll as an element of salinity tissue tolerance in halophytes. *Plant Physiol. Biochem.* 109, 346–354. <https://doi.org/10.1016/j.plaphy.2016.10.011>.
- Pérez-García, F.J., Akhiani, H., Parsons, R.F., Silcock, J.L., Kurt, L., Özdeniz, E., Spampinato, G., Musarella, C.M., Salmerón-Sánchez, E., Sola, F., 2018. A first inventory of gypsum flora in the Palearctic and Australia. *Med Bot* 39, 35–49. <https://doi.org/10.5209/MBOT.59428>.
- Pérez-López, A., Pérez-Valera, F., Sánchez Gómez, M., 2011. Origen y naturaleza del yeso. In: Mota, J., Sánchez Gómez, P., Guirado Romero, J.S. (Eds.), *Diversidad Vegetal de las Yeseras Ibéricas*. ADIF and Mediterráneo Asesores Consultores, Almería, pp. 17–32.
- Popp, M., Polania, J., 1989. Compatible solutes in different organs of mangrove trees. *Ann. For. Sci.* 842–844. <https://doi.org/10.1051/forest:198905ART0185>.
- Porta, J., López-Acevedo, M., Rodríguez, R., 1986. Técnicas y experimentos en edafología. Col·legi Oficial d'Enginyers Agrònoms de Catalunya.
- R Core Team, 2017. R: A Language and Environment for Statistical Computing. <https://www.R-project.org>.
- Rechinger, K.H., 1963–2015. *Flora Iranica*, 1–181. Akademische Druck- u. Verlagsanstalt und Naturhistorisches Museum Wien, Graz & Wien.
- Redondo-Gómez, S., Mateos-Naranjo, E., Davy, A.J., Fernández-Muñoz, F., Castellanos, E.M., Luque, T., Figueroa, M.E., 2007. Growth and photosynthetic responses to salinity of the salt-marsh shrub *Atriplex portulacoides*. *Ann. Bot.* 100, 555–563. <https://doi.org/10.1093/aob/mcm119>.
- Rozema, J., Bijwaard, P., Prast, G., Broekman, R., 1985. Ecophysiological adaptations of coastal halophytes from foredunes and salt marshes. *Vegetatio* 62, 499–521. <https://doi.org/10.1007/BF00044777>.
- Sage, R.F., Christin, P.A., Edwards, E.J., 2011. The C₄ plant lineages of planet Earth. *J. Exp. Bot.* 62, 3155–3169. <https://doi.org/10.1093/jxb/err048>.
- Schirmer, U., Breckle, S.-W., 1982. The role of bladders for salt removal in some Chenopodiaceae (mainly *Atriplex* species). *Contributions to the Ecology of Halophytes*. Springer, pp. 215–231. https://doi.org/10.1007/978-94-009-8037-2_15.
- Sharifi, A., Shah-Hosseini, M., Pourmand, A., Esfahaninejad, M., Haeri-Ardakani, O., 2018. The vanishing of Urmia lake: a geolimnological perspective on the hydrological imbalance of the world's second largest hypersaline lake. In: Nooran, P.G. (Ed.), *Lake Urmia: A Hypersaline Waterbody in a Drying Climate* [The Handbook of Environmental Chemistry]. Springer, Berlin, Heidelberg, DE. <https://doi.org/10.1007/978-2018-359>.
- Soreng, R.J., Peterson, P.M., Romaschenko, K., Davidse, G., Zuloaga, F.O., Judziewicz, E.J., Filgueiras, T.S., Davis, J.L., Morrone, O., 2015. A worldwide phylogenetic classification of the Poaceae (Gramineae). *J. Syst. Evol.* 53, 117–137. <https://doi.org/10.1111/jse.12150>.
- Stone, R., 2015. Saving Iran's great salt lake. *Science* 349, 1044–1047. <https://doi.org/10.1126/science.349.6252.1044>.
- Stromberg, C.A.E., 2011. Evolution of grasses and grassland ecosystems. *Annu. Rev. Earth Planet Sci.* 39, 517–544. <https://doi.org/10.1146/annurev-earth-040809-152402>.
- Subbarao, G.V., Ito, O., Berry, W.L., Wheeler, R.M., 2003. Sodium - a functional plant nutrient. *Crit. Rev. Plant Sci.* 22, 391–416. <https://doi.org/10.1080/07352680390243495>.
- Takahashi, R., Liu, S., Takano, T., 2007. Cloning and functional comparison of a high-affinity K⁺ transporter gene PhaHKT1 of salt-tolerant and salt-sensitive reed plants. *J. Exp. Bot.* 58, 4387–4395. <https://doi.org/10.1093/jxb/erm306>.
- Taleahmad, S., Khosh Kholgh Sima, N.A., Mirzaei, H., 2013. Effects of sodium chloride on physiological aspects of *Salicornia persica* growth. *J. Plant Nutr.* 36, 401–414. <https://doi.org/10.1080/01904167.2012.746366>.
- Tipirdamaz, R., Gagneul, D., Duhazé, C., Ainouche, A., Monnier, C., Özkum, D., Larher, F., 2006. Clustering of halophytes from an inland salt marsh in Turkey according to their ability to accumulate sodium and nitrogenous osmolytes. *Environ. Exp. Bot.* 57, 139–153. <https://doi.org/10.1016/j.envexpbot.2005.05.007>.
- ULRP, 2018. Lake Urmia level report. <http://www.ulrp.ir/fa/>.
- Vasquez, E.A., Glenn, E.P., Guntenspergen, G.R., Brown, J.J., Nelson, S.G., 2006. Salt tolerance and osmotic adjustment of *Spartina alterniflora* (Poaceae) and the invasive *M. haplotype of Phragmites australis* (Poaceae) along a salinity gradient. *Am. J. Bot.* 93, 1784–1790. <https://doi.org/10.3732/ajb.93.12.1784>.
- Veste, M., Sartorius, U., Breckle, S.W., 2008. Ion relations of plants and soil patterns. In: Breckle, S.-W., Yair, A., Veste, M. (Eds.), *Ecological Studies, Arid Dune Ecosystems*. Springer, Berlin Heidelberg, pp. 353–365. https://doi.org/10.1007/978-3-540-75498-5_24.
- Wang, C.H., Lu, M., Yang, B., Yang, Q., Zhang, X.D., Hara, T., Li, B., 2010. Effects of environmental gradients on the performances of four dominant plants in a Chinese saltmarsh: implications for plant zonation. *Ecol. Res.* 25, 347–358. <https://doi.org/10.1007/s11284-009-0662-x>.
- White, P.J., 1999. The molecular mechanism of sodium influx to root cells. *Trends Plant Sci.* 4, 245–246. [https://doi.org/10.1016/S1360-1385\(99\)01435-1](https://doi.org/10.1016/S1360-1385(99)01435-1).
- White, P., 2015. Calcium. In: Barker, A.V., Pilbeam, D.J. (Eds.), *Handbook of Plant Nutrition*, second ed. CRC Press, Boca Raton, FL, USA, pp. 165–198.
- White, P.J., Bowen, H.C., Broadley, M.R., El-Serehy, H.A., Neugebauer, K., Taylor, A., Thompson, J.A., Wright, G., 2017. Evolutionary origins of abnormally large shoot sodium accumulation in nonsaline environments within the Caryophyllales. *New Phytol.* 214, 284–293. <https://doi.org/10.1111/nph.14370>.
- White, P.J., Bowen, H.C., Farley, E., Shaw, E.K., Thompson, J.A., Wright, G., Broadley, M.R., 2015. Phylogenetic effects on shoot magnesium concentration. *Crop Pasture Sci.* 66, 1241–1248. <https://doi.org/10.1071/CP14228>.
- White, P.J., Karley, A.J., 2010. Potassium, Cell Biology of Metals and Nutrients. Springer, pp. 199–224.
- White, P.J., Broadley, M.R., El-Serehy, H.A., George, T.S., Neugebauer, K., 2018. Linear relationships between shoot magnesium and calcium concentrations among angiosperm species are associated with cell wall chemistry. *Ann. Bot.* 122, 221–226. <https://doi.org/10.1093/aob/mcy062>.
- Wiebe, H.H., Walter, H., 1972. Mineral ion composition of halophytic species from Northern Utah. *Am. Midl. Nat.* 241–245. <https://doi.org/10.2307/2423898>.
- Wu, Y., Liu, R., Zhao, Y., Li, P., Liu, C., 2009. Spatial and seasonal variation of salt ions under the influence of halophytes, in a coastal flat in eastern China. *Environ. Geol.* 57, 1501. <https://doi.org/10.1007/s00254-008-1427-5>.
- Zedler, J., Morzarria-Luna, H., Ward, K., 2003. The challenge of restoring vegetation on tidal, hypersaline substrates. *Plant Soil* 253, 259–273. <https://doi.org/10.1023/A:1024599203741>.
- Zhu, Z., Zhang, R., Liu, T., Zheng, H., 2011. Solute accumulation and osmotic adjustment characteristics of the mangrove *Avicennia marina* under NaCl-induced salinity stress. *Bot. Mar.* 54, 335–341. <https://doi.org/10.1515/bot.2011.035>.
- Zoerb, C., Sümer, A., Sungur, A., Flowers, T.J., Özcan, H., 2013. Ranking of 11 coastal halophytes from salt marshes in northwest Turkey according to their salt tolerance. *Turk. J. Bot.* 37, 1125–1133. <https://doi.org/10.3906/bot-1205-29>.
- Zuccarini, P., 2008. Ion uptake by halophytic plants to mitigate saline stress in *Solanum lycopersicon* L., and different effect of soil and water salinity. *Soil Water Res.* 3, 62–73. <https://doi.org/10.17221/25/2008-SWR>.