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Full Length Research Paper

Adaptation mechanisms of some desert plants grown in central region of Saudi Arabia

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The distribution characteristics of organic and inorganic materials and the osmotic adjustment were investigated in *Suaeda* fruticosa (halophyte), *Artemisia judaica* (xerophyte), and *Rumex vesicarius* (mesophyte) grown in Qassim desert of Saudi Arabia. Percentage of inorganic solutes was over 90% of total solutes, while the estimated contribution of Na^+ to Ψ_s was over 50% for *S. fruticosa* grown under field condition. In the field grown *A. judaica*, the percentages of inorganic solutes and organic solutes were 66% and 34%, respectively, and the estimated contribution of Na^+ to Ψ_s was less than 18%, while the estimated contribution of soluble sugars to Ψ_s was over 20%. The contribution of proline to Ψ_s was less than 0.2% for all species both in field and under salt stress in a greenhouse experiment. The contribution of NO_3^- to Ψ_s was less than 4% for all species in field condition. In greenhouse experiment, the concentration of NO_3^- was higher under various NaCl treatments than that in control condition for *S. fruticosa*; the estimated contribution of NO_3^- to Ψ_s was over 7% in *S. fruticosa*, and it was higher than that in the other species at various treatments. In conclusion, inorganic ions were more important in osmoregulation for *S. fruticosa* to adapt to saline and arid environment, while organic solutes, especially soluble sugars played more important role in drought adaptation in the xerophyte, *Artemisia judaica*. NO_3^- played an important role in osmoregulation in *S. fruticosa*.

Keywords: Halophytes, osmoregulation, xerophytes, mesophytes, proline.

INTRODUCTION

Saudi Arabia is a vast arid desert covering the major part of the Arabian Peninsula. Accordingly, xerophytic and halophytic vegetations make up the prominent features of the plant life in the kingdom (Chaudhary, 2001). The desert in the central region of the country is characterized by stable sand dunes, stable sand plateau, salty zones and sand valleys with little vegetation. The average annual rainfall in these sandy areas is usually less than 100 mm/day (Chaudhary, 2000).

Several reports have been published on the flora of the Kingdom of Saudi Arabia (Al-Farhan, 2001; Chaudhary, 2000) and illustrated the species dominate in certain parts of the country. Studies on the vegetation environment relationship, indicated that soil water table and salinity cause discontinuities of vegetation in some areas in the country (Abdel-Fattah and Ali, 2005). Therefore, this part of the kingdom, has received intense attention regarding its floristic survey because of the diverse ecosystems comprised this region and the wide variety of plant species grown in it. In this concern, Al-Turki (2002) published a check list on the flora of Qassim region, located in the central part of the country, comprising a total of 450 wild and cultivated species of flowering plants belonging to 257 genera and 62 families.

Plant species found in Qassim were divided into three different categories: xerophytes, such as *Artemisia* spp. *Zygophyllum* spp. and *Atraphaxis* spp. etc. Halophytes, such as *Salsola* spp. and *Suaeda* spp. Ect. and mesophytes, such as *Agriophyllum* spp. and *Rumex* spp. etc (Chaudhary, 2001; Al-Farhan, 2001). Studies on the vegetation of Qassim region was also described by Al-Huquial and Al-Turki (2006) and recorded same species. Among these species, *Suaeda fructicosa*, *Artemisia judaica* and *Rumex vesicarius*, are three

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species common in the saline and/ or drought sandy deserts in Qassim area, which is characterized by a very low precipitation, a very high evaporation, and a very dry region.

Suaeda fructicosa-Forssk, an evergreen plant, belongs to family Chenopodiaceae, and is a halophytic shrub able to grow in salty and sandy soils. Most species are confined to saline or alkaline soil habitats, and have thick, succulent leaves, a characteristic seen in various plant genera that thrive in salty habitats (halophytes) such as coastal salt-flats and tidal wetlands (Ajmal and Ungar, 1998). It is in leaf all year in flower from July to October, and the seeds ripen from August to October. The flowers are hermaphrodite (have both male and female organs) and are pollinated by Wind. The plant is self-fertile. The plant is rich in potassium and is often burnt as a source of potash for making soap and glass, and the leaves are used as a poultice in the treatment of ophthalmia (Chopra , 1986)

Artemisia judaica, family Asteraceae, a xerophytic shrub grow in sandy deserts and drought habitats. Extracts of herbs are used in traditional medicine because it has anti-diabetic effects. Certain fractions of the extract were found to be insulinomemetic while others have glucagon antagonistic properties and have optimum clinical effect **(**Saleh *et al*., 1987).

Rumex vesicarius is an annual herb which belongs to the family Polygonaceae (Sayed, 1998). It spreads throughout desert and semi-desert areas of North Africa, Asia and Australia (Rechinger, 1984). In Saudi Arabia, *R. vesicarius* is widely used as food, as a medicinal herb and as an antidote to scorpion stings (Al-Yahya, *et al*., 1990). Despite its importance, only few studies have been conducted on *R. vesicarius*.

In addition to their medicinal benefits, these species are crucial plants in protecting desert lands against erosion (Tobe *et al*., 2000) and in feeding wild and domestic animals. However, few studies have dealt with adaptation of these species to the harsh conditions under which they grow and live, and little information is available about the ecophysiological characteristics in the three species.

Some studies indicated that desert plants may overcome stress conditions through accumulation of organic solutes such as sugars and amino acids or inorganic solutes such as K+ and Na+ (Taiz and Zeiger, 2002). However, there is a very little information on the distribution of these substances within these species. Furthermore, the functions of these substances in the adaptation of drought and salt resistant plants to the desert environments are not clear. Therefore, it was of interest to use *S. fruticosa* (halophyte), *A. judaica* (xerophyte) and *R. vesicarius* (glycophyte) common in Qassim region, as representative species for different ecosystems, to investigate the distribution and ecological roles of organic and inorganic solutes in these distinct desert adaptive categories, in a trial to understand the adaptation mechanisms and the ecological distribution, of desert species.

MATERIALS AND METHODS

Area of study

Qassim region is located in the central part of Saudi Arabia, and almost in the center of the Arabian Peninsula. It is approximately 400 km northwest of Riyadh the capital of KSA. Qassim is about 600 meters above sea level and comprises diverse ecosystems that provide interesting aspects for studying the eco-physiological characteristics of some species grown in the region.

Topography and geomorphology

Qassim region is characterized by its variation in topography and geomorphology. According to Chapman (1978), the area belongs to the Arabian shield and the great Nafud, a very large depression filled up with masses of sand and covers a very large area. One striking aspect of this great body of sand is the lack of oases and rivers. The mountain chains found in the region are rocks formation and hills characterized by limestone sand.

Climate

The climate of the region under study is generally hot and dry. The weather system in Qassim region is generally arid to extra arid. According to the records of Qassim metrological station for the last 10 years, the study area is characterized by a mean minimum temperature of 10 °C in January and a mean maximum temperature of 45.5 °C in August with an annual mean temperature of about 26.8 °C. The rainfall in the region is erratic and irregular (Chaudhary, 2000); it is mainly winter fall, the high precipitation occurs in November and the average annual rainfall is about 112 mm, however, in summer months no rain has been detected. The relative humidity is extremely low in summer as it reached less than 13.0% in July and relatively high in January (about 43.5%). The average annual wind velocity in the study area is 24 km/h. The ratio of precipitation to evaporation was 42 mm to 3680 mm.

From these facts of weather conditions, it seems that the weather in the area of study is rarely in balance allover the year.

Field condition

S. fruticosa, *A. judaica* and *R. vesicarius* plants, grown in saline and dry sandy deserts, were selected from natural habitats at the region. Four plants of each species were collected randomly. After measuring growth and vegetative parameters, leaves, roots and young branches of each plant were divided into three sub-replicates and were frozen with liquid nitrogen, and deposited in a refrigerator at −15 °C.

Greenhouse

S. fruticosa, *A. judaica* and *R. vesicarius* seedlings, in plastic pots filled with sand, were cultured in the greenhouse at the Agricultural Experimental Station of Qassim University. The temperature in the greenhouse was 27 ± 4 °C day and 20 ± 2 °C night, RH was 60–65%, and light period was 14/10 h day/night, and irrigation and fertilization were practiced as needed. The 3-month-old seedlings of all species were divided into four groups for treatments: (1) 0 mM NaCl (control); (2) 200 mM NaCl; (3) 400 mM NaCl; (4) 600 mM NaCl. Salt concentrations were increased daily in equal increments for 4 days to the final concentration. One week after final concentrations were reached, growth parameters and chemical determination were accomplished. Samples of the fresh plant materials were frozen with liquid nitrogen to measure the osmotic potential. Three replicates were set for each treatment.

Measurements

Soil analysis

Soil samples (40–50 mm under soil surface) around the root environment of each plant were also taken. Soil samples were dried in an oven for 2 days at 105 °C. Soil water contents were determined as WC = (FW − DW)/FW × 100%. Total soluble salt contents (TSS), pH, Na^+ and K^+ were determined in water extracts at a ratio of 1:5 of air-dried soil samples: water. Concentration of Na^+ and K^+ were determined by flame photometer (Lu, 1999). Mean value of three subreplicates of the soils in each plant was used as one replicate.

Growth parameters

The plant material collected both in field and in greenhouse experiment was first cleaned with distilled water, then fresh and dry (on 70°C for 72 h) weights were measured. Water content of leaves and young branches were determined.

Chemical parameters

Frozen plant materials in field experiment were extracted with boiling distilled water, the solution was filtered and the following components were determined: a) the concentration of total organic acid (TOA) was determined by 0.01 mM NaOH titration method, with phenolphthalein as indicator (Wang, 1981), b) NO_3^- concentration was determined by the colorimetric method (Cataldo *et al*., 1975) and c) Cl^- concentration was determined by 0.03 mM $AgNO_3$ titration method, with 5% K_2CrO_4 as indicator. While, total soluble sugars (TSS) was determined in the 80% ethanol extracts of the dry material by the sulphuric acid-phenol colorimetric method [Dubois, 1956]. The frozen plant tissues were also ground in 10% and 5% acetic acid, and the ninhydrin colorimetric methods were used for the determination of amino acids (AA) (Moore and Stein, 1948) and proline concentration (Bates et al., 1973), respectively (using UV-120-02 Spectrophotometer, Shimadzu, Kyoto, Japan). A 15-mg dry sample was put in a muffle stove to be ashed. The ash was dissolved with concentrated nitric acid and then set to a volume of 20 ml with distilled water. The concentrations of Na^+ and K^+ were determined by flame photometer (Model Corning 410, USA). Mean value of three subreplicates in each plant was used as one replicate in field condition. Fresh plant material in greenhouse experiment was used to measure the concentration of NO_3^- and proline, using the methods described above.

Determination of osmotic potential

The frozen plant tissues were put into a syringe to thaw. The liquid squeezed from the plant tissues was put into a freezing point osmometer (Fiske 210, Advanced Instruments INC., Massachusetts, USA) to determine osmotic potential (Zhao *et al*., 2003). Mean value of three sub-replicates in each plant was used as one replicate in field condition.

Statistic analysis

Data were statistically analyzed using the One-way analysis of variance (ANOVA) with the aid of the COSTAT software. Treatment means were compared by LSD at 5%.

RESULTS

Soil characteristics, plant water content and osmotic potential in field condition

The soil total soluble salt content was over 15 g kg^{-1} dry soil in *S. fruticosa* and *A. judaica* growing in saline soils, while it was 4.8 and 0.6 g kg^{-1} dry soil for *A. judaica* and *R. vesicarius* growing in sandy deserts, respectively. Soil water content was much higher in *S. fruticosa* and *A. judaica* growing in saline soils than that in others. A similar trend was observed in concentrations of Na^+. Soil pH and K+ concentration of *A. judaica* growing in sandy desert were higher than that in others (Table 1).

Table 1. Soil parameters, water content (WC, ml g^{-1} dry weight) and osmotic potential (Ψ_s, MPa) of *S. fruticosa* and *A. judaica* and *R. vesicarius* growing in different habitats.

Plant species	**Soil**					**Plant**	
	TSS	WC	pH	Na^+	K^+	WC	Ψ_s
S. fruticosa (saline soil)	16.4 a	14.5 a	7.9 b	7.02 a	1.23 b	4.5 a	-4.2 a
A. judaica (saline soil)	15.3 a	10.4 a	8.1 b	6.32 a	1.86 b	3.2 b	-3.4 b
A. judaica (sandy soil)	4.8 b	5.8 b	8.3 a	2.05 b	2.78 a	3.5 b	-3.2 b
R. vesicarius (sandy soil)	0.6 b	4.7 b	7.6 b	0.34 b	0.62 c	2.1 c	-3.3 b

TSS = total soluble salt, WC = water content (%). Contents of Na^+, K^+ and TSS are indicated as g kg^{-1} dry soil. Means in the same column that have the same letter are not significantly different at $P < 0.05$

Table 2. Concentrations of ions (mol l^{-1} tissue water), estimated contributions of Na^+ (CNa) and NO_3^- (CNO_3) to Ψ_s in *S. fruticosa* and *A. judaica* and *R. vesicarius* growing in different habitats.

Plant species	**Na^+**	**K^+**	**Cl^-**	**NO_3^-**	**CNa (%)**	**CNO_3 (%)**
S. fruticosa (saline soil)	1.55 a	0.45 a	0.27 b	0.07 a	81.8 a	3.9 a
A. judaica (saline soil)	1.21 b	0.41 a	0.34 a	0.02 b	85.9 a	1.6 b
A. judaica (sandy soil)	0.98 c	0.32 c	0.28 b	0.04 b	78.7 b	3.7 a
R. vesicarius (sandy soil)	0.35 d	0.29 b	0.30 b	0.06 a	26.2 c	4.5 a

The Ψ_s of a given solute was calculated as: $\Psi_s = -nRT/V$, where n is the number of solute molecules; R, the universal gas constant; T, temperature in K; and V, volume in l. Osmotic co-efficients of the solutes in tissue water were assumed to equal 1. Means in the same column that have the same letter are not significantly different at $P < 0.05$

Soil water content in the rooting zones of the test plants ranged from 0.47% to 1.45%, thus all of the plants suffered from soil water deficit (Table 1). The most severe water deficit occurred in the rooting zones of *A. judaica* and *R. vesicarius* grown in sandy desert. The concentration of available Na+ in the rooting zones of A. judaica grown in saline soil were about 3 times higher than that grown in sandy desert, while the concentration of available K+ was about 0.75%, respectively.

Leaf water content was 4.5 ml g^{-1} dry weight in S. fruticosa, and it was 1.3- 2.2 times of that in other species. Osmotic potential was -4.2 MPa in S. fruticosa, and it was 1.2-1.3 times of that in other species (table 1)

Ion concentrations and contributions to Ψ_s in field

Data in Table (2) show the ions concentrations and their effect on osmotic potential of plants tissues. Ion concentrations were calculated on a tissue water basis. Concentration of Na^+ in S. fruticosa was 1.3-4.4 times of that in other species, while concentration of K^+ in S. fruticosa was 1.1–1.6 times of that in others, concentration of Cl^- in A. judaica growing in saline soils was almost 1.1–1.2 times of that in others, respectively. NO_3^- concentration was very low in all species since the highest value was 0.07 mol l^{-1} tissue in S. fruticosa. The estimated contribution of Na^+ to Ψ_s was about 25% in R.

Table 3. Concentrations of organic solutes (mmol l^{-1} tissue water), estimated contributions of soluble sugars (C_{ss}) and proline (C_{pro}) to Ψ_s in *S. fruticosa* and *A. judaica* and *R. vesicarius* growing in different habitats.

Plant species	SS	OA	AA	Proline	C_{ss} (%)	C_{pro} (%)
S. fruticosa (saline soil)	22.5 b	32.9 c	6.3 d	3.6 a	1.2 c	0.19 a
A. judaica (saline soil)	46.7 b	50.2 b	12.5 c	1.1 c	3.4 b	0.07 c
A. judaica (sandy soil)	48.2 b	21.7 c	19.7 b	1.2 c	3.9 b	0.09 c
R. vesicarius (sandy soil)	134.7 a	75.4 a	32.6 a	1.9 b	10.2 a	0.14 b

SS, soluble sugars; OA, organic acids; AA, amino acids. The Ψ_s of a given solute was calculated as Table 2. Means in the same column that have the same letter are not significantly different at $P < 0.05$

vesicarius, while it was over 75% for other species. The estimated contribution of NO_3^- to Ψ_s was the lowest in A. judaica (1.6%) in saline soils, while it was less than 5% in all species (Table 2).

Contribution of organic solutes to Ψ_s under field condition

It is clear from Table 3 that the concentration of soluble sugars in R. vesicarius was 2.0-4.4 times of that in other species, the concentration of organic acids was 1.5-3.5 times of that in others, while the concentration of amino acids was 1.6-5.3 times of that in other plant species, respectively. The concentration of proline in S. fruticosa was 1.9-3.3 times of that in other species. The estimated contribution of proline to Ψ_s was the highest in S. fruticosa, but it was less than 0.2% for all species. The estimated contribution of soluble sugars to Ψ_s was over 10% in R. vesicarius, while it was less than 4% for other species (Table 3).

Percentage of inorganic and organic solutes under field condition

It is obvious that, concentration of inorganic solutes in S. fruticosa was 1.0–2.1 times of that in other species, and the concentration of total solutes was 1.0–1.6 times of that in other species, respectively. The concentration of organic solutes in R. vesicarius was 4.3–10.8 times of that in other species. The percentage of inorganic solutes in total solutes was 70% in R. vesicarius, while it was over 90% for other species. The percentage of organic solutes in total solutes was 30% in R. vesicarius, while it was less than 8% for other species (Table 4).

Effects of NaCl in greenhouse experiment

Data recorded in Table 5 show clearly that concentration of NO_3^- was higher at various NaCl levels than that in control for S. fruticosa. In A. judaica , NO_3^- concentration increased at 200 NaCl treatment, while there was no change in NO_3^- concentration for R. vesicarius. Proline concentration was 46% higher at 600 mM NaCl than that in control for S. fruticosa, while it was about 37% higher at 600 mM NaCl than that in control, for A. judaica, and it was 38% higher at 400 mM NaCl than that in control, for R. vesicarius. NaCl treatments decreased the osmotic potential for all species, while S. fruticosa had lower osmotic potential at various NaCl levels compared with that in other species. S. fruticosa had higher water content at various NaCl levels compared with that in other species. The estimated contribution of NO_3^- to Ψ_s was 9% to 15% for S. fruticosa at various treatments, and it was higher than that in other species. The estimated contribution of proline to Ψ_s was less than 0.2% for all species, while it was much lower for R. vesicarius compared with that in the two other species at various treatments (Table 5). It seems that 600 mM NaCl affected negatively the growth of R. vesicarius, therefore it shows the minimal values of measured parameters.

DISCUSSION

Under harsh conditions, plants try to adapt or avoid the deleterious effects that may result from the stress. It is well known that succulence of plant parts (high water content) considers an adaptive response to water stress and drought conditions. Moreover, succulence often contributes to the regulation of internal ion concentration

Table 4. Concentrations of total solutes, inorganic solutes, organic solutes (mol l^{-1} tissue water), percentages of inorganic and organic solutes in total solutes in *S. fruticosa*, *A. judaica* and *R. vesicarius* growing in different habitats.

Plant species	Total solutes	Inorganic solutes	Organic solutes	% of inorganic solutes	% of organic solutes
S. fruticosa (saline soil)	2.15 a	2.11 a	0.04 c	98.1 a	1.9 b
A. judaica (saline soil)	2.11 a	2.03 a	0.08 b	96.2 a	3.8 b
A. judaica (sandy soil)	1.36 b	1.26 b	0.10 b	92.6 a	7.4 b
R. vesicarius (sandy soil)	1.44 b	1.01 c	0.43 a	70.1 b	29.9 a

Means in the same column that have the same letter are not significantly different at $P < 0.05$

Table 5. Effects of NaCl on water content (WC, ml g^{-1} dry weight), osmotic potential (Ψ_s, MPa), concentrations of NO_3^- (mol l^{-1} tissue water) and proline (mmol l^{-1} tissue water), in S. fruticosa, A. judaica and R. vesicarius in a greenhouse experiment

Plant species	NaCl Treatment	WC	Ψ_s	NO_3^-	Proline	CNO_3 (%)	C_{pro} (%)
S. fruticosa)	Control	6.4 a	-4.8 a	0.16 ab	2.8 b	10.4 ab	0.18 a
	200 mM	4.6 a	-5.1 a	0.26 a	3.0 a	15.2 a	0.17 a
	400 mM	4.3 a	-4.4 a	0.21 a	2.9 ab	11.3 a	0.15 a
	600 mM	4.0 a	-5.4 a	0.20 a	4.1 a	9.3 b	0.19 a
A. judaica	Control	2.1 b	-4.3 a	0.11 b	2.7 b	7.5 b	0.19 a
	200 mM	2.0 b	-4.5 a	0.14 b	2.9 ab	9.5 b	0.18 a
	400 mM	2.0 b	-3.5 b	0.11 b	3.1 a	6.8 bc	0.19 a
	600 mM	1.8 b	-4.4 a	0.11 b	3.7 a	5.1 c	0.19 a
R. vesicarius	Control	2.8 b	-3.9 a	0.07 c	0.8 c	5.6 c	0.06 b
	200 mM	2.1 b	-4.1 a	0.08 c	1.0 c	5.4 c	0.08 b
	400 mM	2.4 b	-4.0 a	0.09 c	1.1 c	5.6 c	0.07 b
	600 mM	1.2 c	- 3.5 b	0.05 c	1.4 c	3.7 d	0.05 b

The Ψ_s of a given solute was calculated as Table 2. Means within a species that have the same letter are not significantly different at $P < 0.05$

in many halophytes (Short and Colmer, 1999). In an early studies, it was found that leaf succulence in *Atriplex amnicola* (Aslam et al., 1986), and stem succulence in *Sarcocornia natalensis* (Naidoo and Rughuuanan, 1990) increased when plants were treated with high concentrations of NaCl. The present experiment showed that water content was the highest in leaves of S. fruticosa compared with other species (Table 1) and controlled conditions (Table 5). Therefore, high water content in leaves may be an adaptive feature for S. fruticosa to overcome the effect of high salt condition.

It has been reported that the seedlings of S. fruticosa emerging in high saline environments continued to elongate without any detectable signs of toxic effects of NaCl, reflecting adaptation to high salinity, perhaps through solute compartmentalization at the cellular level (Tobe et al., 2000).

It is well known that halophytes accumulate high concentrations of inorganic ions to lower osmotic potential, thus they can absorb water from saline soils to ensure growth (Glenn and Brown, 1999). In this respect, Wang et al. (2004) found that the halophyte Suaeda salsa grows in saline soils where the concentrations of available Na+ are about 38 and 66 times higher than in the habitats of the xerophyte Haloxylon ammodendron and the mesophyte Zygophyllum xanthoxylum, respectively.

The present study showed that the halophytic S. fructicosa and the xerophytic A. judica in saline soil mainly accumulated inorganic ions (Table 4), especially Na^+ and K^+ to lower osmotic potential (Table 2), even though the Na^+ concentration was low in the soils where A. judaica in sandy desert was growing (Table 1). Whereas, the glycophyte, R. vesicarius accumulated more organic solutes (Table 4), especially soluble sugars and amino acids (Table 3). It is well known that K+ is not only an essential macronutrient for plant growth and development, but also a primary osmoticum in maintaining low water potential of plant tissues (Taiz and Zeiger, 2002).

Furthermore, S. fruticosa showed a greater tendency for Na+ and K+ accumulation in the aerial parts than the xerophyte A. judaica. The high Na+ uptake and transport in S. fruticosa may reflect the growth-dependent ion demand of the shoot, since seedling survival rates in the high salinity treatments were much greater than in the non-saline controls (Tobe et al, 2000).

The halophytic species may compartmentalize these ions, especially Na^+ in the vacuole, and synthesize a relatively small amount of organic solutes to balance the osmotic pressure in the cytoplasm. It has been reported that a positive relationship between biomass accumulation and the excess of cations over anions is found in different plant species, including perennial ryegrass (Sagi *et al*., 1997). Concentrations of Na^+ in S. fruticosa and A. judaica growing in saline lands were much higher than Cl^- (Table 2), while Na^+ may be balanced by inorganic anions, e.g, Cl^-, NO_3^- or SO_4^{2-}, or organic anions (Sagi *et al*., 1997). Ion uptake is a much cheaper source of osmotic solutes because ion uptake and accumulation need less energy compared with synthesizing organic solutes (Greenway and Munns, 1983). Therefore, accumulating ions especially Na^+ rather than synthesizing organic solutes for osmoregulation is an adaptive feature for the halophytic species to adapt to saline and arid environments.

Nitrogen is an essential nutrient element in biosynthesis of nitrogenous organic solutes in higher plants (Sagi et al., 1997). It has been reported that when NO_3^- absorption exceeds reduction, NO_3^- accumulates in the vacuole. When the external source is exhausted, the plants can utilize vacuolar NO_3^- (Stienstra, 1986). In the present study, NO_3^- concentration and the estimated contribution of NO_3^- to Ψ_s were very low for all species in field condition (Table 2). Saline and sandy deserts are practically non fertile, and the nitrogen content is very low (Malik et al., 1991). Therefore, NO_3^- did not play an osmotic role in these species because of the low nitrogen content in field condition in the present experiment. When plants were cultured in full-strength Hoagland's nutrient solution, NO_3^- concentration and the estimated contribution of NO_3^- to Ψ_s in S. fruticosa were much higher than in other species (Table 5). Therefore, more NO_3^- may be accumulated in vacuole of S. fruticosa compared with other species, especially R. vesicarius. It has been shown that NaCl treatment decreased the concentration of NO_3^- severely in shoots of nonhalophytes (Botella *et al*., 1997), and this may be due to antagonism between NO_3^- and Cl^- (Bottacin *et al*., 1985) or the interference of external NaCl with one or more types of transporters at the root plasma membrane (Stienstra, 1986). In the present experiment, leaf NO_3^- concentration increased under various NaCl treatments in S. fruticosa (Table 5), which indicated that NaCl had no adverse effect on NO_3^- uptake or accumulation in S. fruticosa.

Many early studies indicated that the formation of proline in the cytoplasm of plant cells under drought and or salt stress plays an important role in balancing osmotic potential with that in vacuoles or protecting enzymes (Greenway and Munns, 1980). In the present study, the proline concentration and estimated contribution of proline to Ψ_s was higher in S. fruticosa than that in other species in field condition (Table 3), and it was higher in S. fruticosa and A. judaica than in R. vesicarius under salt condition in the greenhouse experiment (Table 5), whereas, the estimated contributions of proline to Ψ_s were less than 0.2% for all species both in field and in greenhouse experiments. Therefore, it can be suggested that proline may not play an important role in osmoregulation under salt condition in the halophytic species used in this study. It has been shown that free proline may be important in drought tolerance of xerophytes (Wang *et al*., 2004). In this concern, Tobe *et al*. (2001) reported that the xerophytes accumulated very high levels of proline perhaps because they are intolerant to high Na+ concentration, and proline serves as an alternative compatible solute for osmotic adjustment. Whereas, the contribution of proline to Ψ_s is less important than other organic solutes, especially soluble sugars, in osmotolerance of R. vesicarius under field condition (Table 3). The physiological role of proline accumulation in R. vesicarius is uncertain due to its relatively small concentration as compared with soluble sugars or organic acids. Therefore, proline may not be correlated with osmoregulation of R. vesicarius in arid environment.

The mechanism for its drought tolerance and high productivity in the desert may lie in its ability to accumulate ions in the seed germination process and in photosynthesizing stems as well as leaves. Thus, the succulent xerophytes can be better established in the desertified or saline lands through seed dispersal. The succulent xerophytes have transpiration-retarding mechanisms to reduce water loss, resulting in higher water use efficiency; while their relatively deep root systems enable them to take up water from greater depths. This combined with the high capacity for osmotic adjustment makes them the most drought tolerant species in the Inner-Mongolian Desert, and desirable species to stabilize sand dunes and to afforest degraded arid lands.

It has been generally accepted that Na+ is accumulated mostly in vacuoles to maintain a low cellular osmotic potential, while most of K+ and free proline are concentrated in the cytosol to maintain the osmotic balance between cytoplasm and vacuole (Wang et al., 2004).

CONCLUSION

Inorganic solutes, especially Na^+, were important in osmoregulation for *S. physophora* (S. fruticosa) and *H. ammodendron* A. judaica in saline and sandy desert, whereas inorganic solutes were less important, but organic solutes, especially soluble sugars were more important in osmoregulation for *H. persicum* (R. vesicarius) to adapt to arid environment. Proline did not play an important role in osmoregulation for all species in saline or sandy desert in the present experiment. Proline accumulation in C. mongolicum leaves may be a symptom of stress in this less drought-tolerant species and its contribution to osmotic adjustment was apparently negligible as compared with K+.

In the xerophytes, proline accumulation in the aerial plant parts may, to some extent, contribute to osmotic adjustment, but the primary osmoticum was K+ (10.5-fold higher than proline concentration in A. sphaerocephala leaves). The succulent xerophytes had lower proline concentration than the xerophytes, but the highest ion concentration and drought tolerance.

NO_3^- played more important role in osmoregulation in *S. physophora* (S. fruticosa) and *H. ammodendron* A. judaica cultured in full-strength Hoagland's nutrient solution under NaCl treatments compared with that growing in saline soils in field condition. NaCl may have no adverse effect on NO_3^- uptake or accumulation in *S. physophora* (S. fruticosa) under controlled condition, and the mechanism remain to be determined.

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