

Significance of Na⁺ and K⁺ for Sustained Hydration of Organ Tissues in Ecologically Distinct Halophytes of the Family Chenopodiaceae

Yu. V. Balnokin*, N. A. Myasoedov*, Z. Sh. Shamsutdinov**, and N. Z. Shamsutdinov***

*Timiryazev Institute of Plant Physiology, Russian Academy of Sciences,
Botanicheskaya ul. 35, Moscow, 127276 Russia;
fax: 7 (095) 977-8018; e-mail: balnokin@yandex.ru

**Williams All-Russia Fodder Research Institute, Russian Academy of Agricultural Sciences, Moscow, Russia

***Kostyakov All-Russia Research Institute of Hydraulic Engineering and Land Reclamation,
Russian Academy of Agricultural Sciences, Moscow, Russia

Received November 25, 2004

Abstract—The contents of Na⁺, K⁺, water, and dry matter were measured in leaves and roots of euhalophytes *Salicornia europaea* L. and *Climacoptera lanata* (Pall.) Botsch featuring succulent and xeromorphic cell structures, respectively, as well as in saltbush *Atriplex micrantha* C.A. Mey, a halophyte having bladder-like salt glands on their leaves. All three species were able to accumulate Na⁺ in their tissues. The Na⁺ content in organs increased with elevation of NaCl concentration in the substrate, the concentrations of Na⁺ being higher in leaves than in roots. When these halophytes were grown on a NaCl-free substrate, a trend toward K⁺ accumulation was observed and was better pronounced in leaves than in roots. Particularly high K⁺ concentrations were accumulated in *Salicornia* leaves. There were no principal differences in the partitioning of Na⁺ and K⁺ between organs of three halophyte species representing different ecological groups. At all substrate concentrations of NaCl, the total content of Na⁺ and K⁺ in leaves was higher than in roots. This distribution pattern persisted in *Atriplex* possessing salt glands, as well as in euhalophytes *Salicornia* and *Climacoptera*. The physiological significance of such universal pattern of ion accumulation and distribution among organs in halophytes is related to the necessity of water absorption by roots, its transport to shoots, and maintenance of sufficient cell water content in all organs under high soil salinity.

Key words: *Atriplex micrantha* - *Climacoptera lanata* - *Salicornia europaea* - halophytes - different ecological groups - salt resistance - ion accumulation - tissue hydration level

INTRODUCTION

The ability of halophytes to complete their life cycle under high salinity is related to operation of several mechanisms performing essential functions. First, these mechanisms serve to maintain Na⁺ and Cl⁻ concentrations at a much lower level in the cytoplasm than in the soil solution, which protects cytoplasmic biopolymers from toxic effect of ions [1–6]. Second, they reduce cell water potential with respect to water potential of the soil solution, thus ensuring water supply to plants under high salinity [4–8]. At the whole organism level, the “strategy of ionic homeostasis” is realized through the maintenance of low Na⁺ and Cl⁻ concentrations in young plant parts with active metabolism, such as the meristem and generative organs [9, 10]. The “water-supply strategy” is realized in the ability of plants to maintain the upward gradient of water potential in the soil–root–shoot system [8, 11]. The realization of both strategies at the cell level and in the whole organism involves the mechanisms of short-distance and long-distance Na⁺ transport.

Our previous investigations showed that a succulent-type euhalophyte *Suaeda altissima* accumulates Na⁺ ions in leaves to much higher levels than in roots [12] and that the sustained water potential gradient along the plant axis corresponds to the distribution pattern of Na⁺ among the organs [13].

The major part of Na⁺ in mature tissues of halophytes was shown to be sequestered in vacuoles [12]. The Na⁺ loading into this compartment is driven by the tonoplast-located Na⁺/H⁺ antiporter [3, 5, 6, 14, 15]. The other mechanism responsible for compartmentation of Na⁺ in vacuoles of halophytes is apparently related to the formation of pinocytotic invaginations and multivesicular bodies contributing to ion transfer to the vacuole [16].

The key role in the delivery of Na⁺ from roots to shoots belongs to the process of Na⁺ loading into the xylem. Our experiments with *S. altissima* [13, 17] showed that Na⁺ accumulation in the root xylem of euhalophytes is accomplished by the Na⁺/H⁺ antiporter located at the plasma membrane of parenchymal cells adjacent to the xylem.

The diversity of morphological and anatomical traits in halophytes (e.g., the presence or absence of salt glands in leaves, occurrence of xeromorphic or succulent-type tissue structures) raises the question of possible differences in organization of ion transport and water relations in various halophytes. Particularly, the question remains open whether the long-distance Na^+ transport contributes to the maintenance of water potential gradient in halophytes possessing salt glands. Speaking differently, it is yet unknown whether these plants generate the Na^+ concentration gradient along the plant axis.

Our hypothesis is that halophytes with different anatomical structures and morphologies have a unique common property in organization of long-distance ion transport, Na^+ transport in particular. This property originated from the need of absorbing water by root system and transporting water to aboveground organs under conditions of severe soil salinity. It means that plants should cope with the problem of maintaining water potential gradient in the soil–root–shoot system at a very low water potential in soil. According to this hypothesis, *halophytes of all types, including those with salt glands*, accumulate salt in their cells in order to maintain the water potential gradient along the plant axis; furthermore, the extent of ion uptake is much higher in cells of aboveground organs than in the root cells.

The present study aims at verification of the above hypothesis. The immediate task was to measure Na^+ , K^+ , and water contents in leaves and roots of three representative species of Chenopodiaceae (this family comprises the major part of all known halophytes) and to assess biomass accumulation in organs at various salinities of the substrate. Two of three species examined belong to the group of euhalophytes (true halophytes) [18]. One of these—*Salicornia europaea*—is a succulent plant, the other—*Climacoptera lanata*—is characterized by xeromorphic structure of its tissues. The third species, *Atriplex micrantha* is assigned to the group of so-called salt-excreting halophytes [18]; the leaves of such plants contain glands with balloon-like salt containers. The tissue structure of *Atriplex* is similar to those of mesophytes.

MATERIALS AND METHODS

Seeds of halophytes were collected in natural habitats of these plants in Uzbekistan (Kashkadarya oblast) and Turkmenistan (Chardzhou oblast). Experiments were performed with the following plant species: glasswort *Salicornia europaea* L., *Climacoptera lanata* (Pall.) Botsch, and saltbush *Atriplex micrantha* C.A. Mey.

The seeds were germinated in moistened sand. On the 15th day, the seedlings were placed on a mixture of washed quartz sand and podzolic soil (1 : 1, v/v). Seedlings were raised in growth vessels with a volume of 4 l; four seedlings were planted per pot. The growth sub-

strate was supplemented with NaCl at concentrations indicated in the text below and in figure captions. Plants were grown in a greenhouse (in Moscow) in the period from late April to the end of June under natural illumination. Supplementary lighting was provided from DRL-1000 lamps for 12 h per day. The irradiance at the level of upper leaves equaled to 32–43 klx, depending on weather conditions and solar time. Plants were watered every other day to saturate the moisture capacity of the substrate. The soil was fertilized once a week with biogenic elements according to Robinson and Downton [19]. The greenhouse temperature was at least 20°C. Experiments were performed on 60-day-old plants.

The contents of Na^+ and K^+ in organs were determined after preliminary desiccation of plant material at 105°C and subsequent grinding the dry matter to powder. The obtained powder was put in hot water for extraction of Na^+ and K^+ , and the extract was filtered. Concentrations of Na^+ and K^+ in extracts were determined with a flame photometer (Carl Zeiss, Germany). Ion content in organs was calculated on a fresh weight basis.

The weights and water content of organs were determined with a weighing method.

Experiments were performed in three replicates. Data in figures show mean values and their standard errors. Parameter values for each replicate (each point in the graphs) were obtained on specimens representing averaged samples collected from eight plants.

RESULTS AND DISCUSSION

Three halophyte species examined were able to grow at a wide range of NaCl concentrations in the substrate. The plots of dry matter accumulated in leaves and roots at various NaCl concentrations (Figs. 1a, 2a, 3a) contained characteristic maxima corresponding to salt concentrations optimal for growth of each particular species. Generally, we noted that low and moderate NaCl concentrations stimulated organ growth in all three species. The only exception was the case of saltbush roots (Fig. 3a). The highest accumulation of biomass in this halophyte was noticed in the absence of NaCl in the medium, while the addition of even small amounts of salt to the substrate retarded plant growth.

The specific influence of salinity on growth was manifested not only in different positions of maxima on the plots (Figs. 1a, 2a, 3a) but also in different capacities of plants to maintain substantial growth at supraoptimal external concentrations of NaCl. As NaCl concentration was raised, the plant biomass declined with a slope of variable steepness, depending on capability of plants to cope with osmotic and toxic action of salt. If the biomass at optimal NaCl concentration is taken as 100%, the upper concentration corresponding to 50% biomass can be used to quantify the NaCl-sensitivity of growth. This concentration provides a measure of halo-

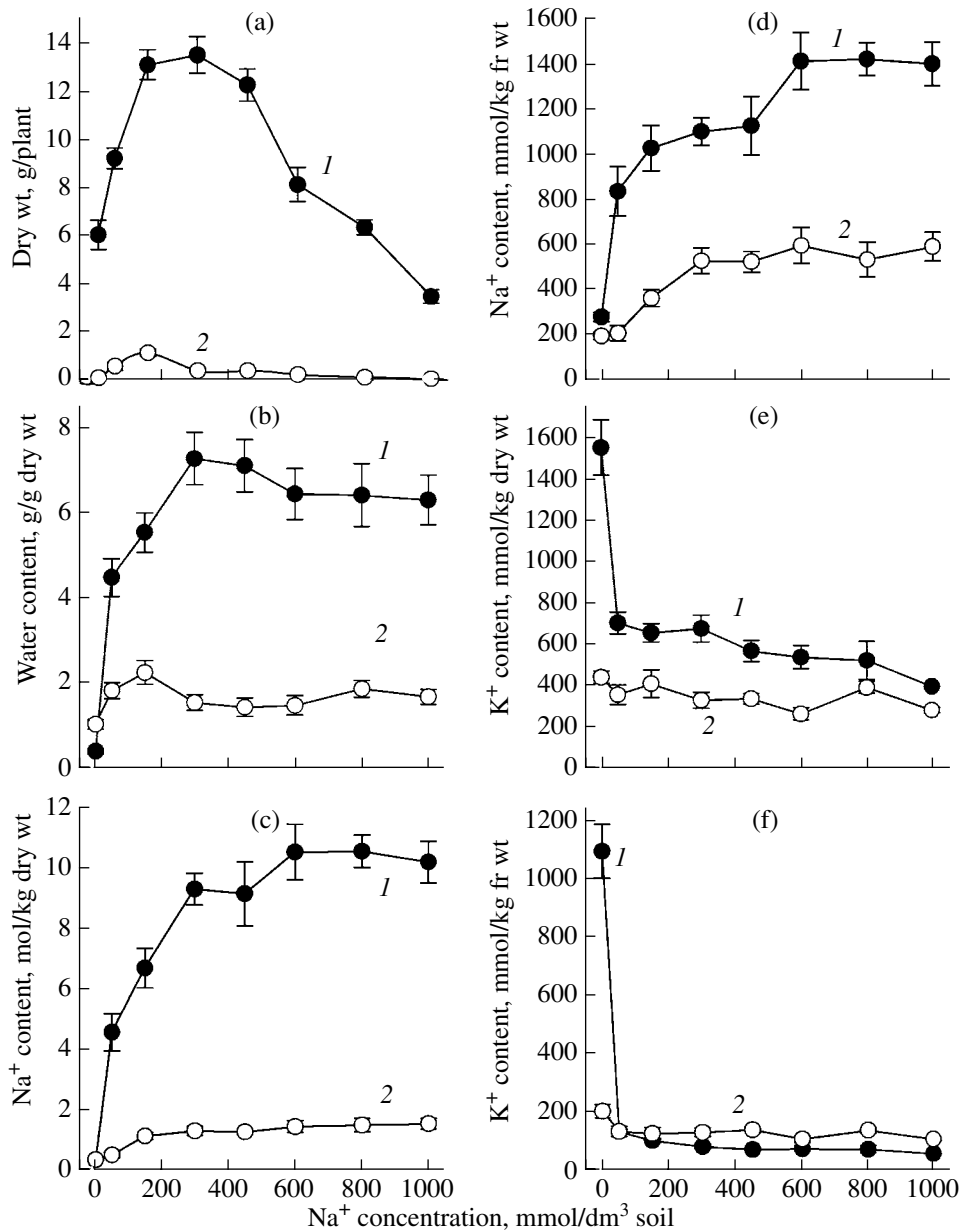


Fig. 1. Dry matter (a), water content (b), and Na⁺ content expressed on a dry matter (c) and fresh weight (d) bases, and K⁺ content expressed on a dry weight (e) and fresh weight (f) bases in organs of *Salicornia europaea* at various concentrations of NaCl in the substrate.

(1) Leaves, (2) roots.

phyte resistance to salinity. These concentration values were estimated for leaves of each species using data shown in Figs. 1a, 2a, and 3a. They equaled to 770, 470, and 300 mM for *Salicornia*, *Climacoptera*, and *Atriplex*, respectively. This row of halophytes reflects their descending resistance to NaCl.

When NaCl was present in the root zone, the water content in plant organs correlated with the capacity of plants to maintain water homeostasis; i.e., to keep water balance under conditions of soil salinity. Figures 1b, 2b, and 3b show water content in leaves and roots of three

species examined as a function of NaCl concentration in the substrate. These curves comprised maxima that were positioned at various points of the concentration scale for various plant species. Only in *Atriplex* (Fig. 1b), the highest hydration level of roots was observed in the absence of NaCl, whereas the addition of even small amounts of NaCl to the substrate resulted in the decrease of root water content.

The hydration level of halophyte leaves was usually higher than the hydration level of roots. Only in *Atriplex* plants grown at 400–600 mmol/dm³ NaCl and in

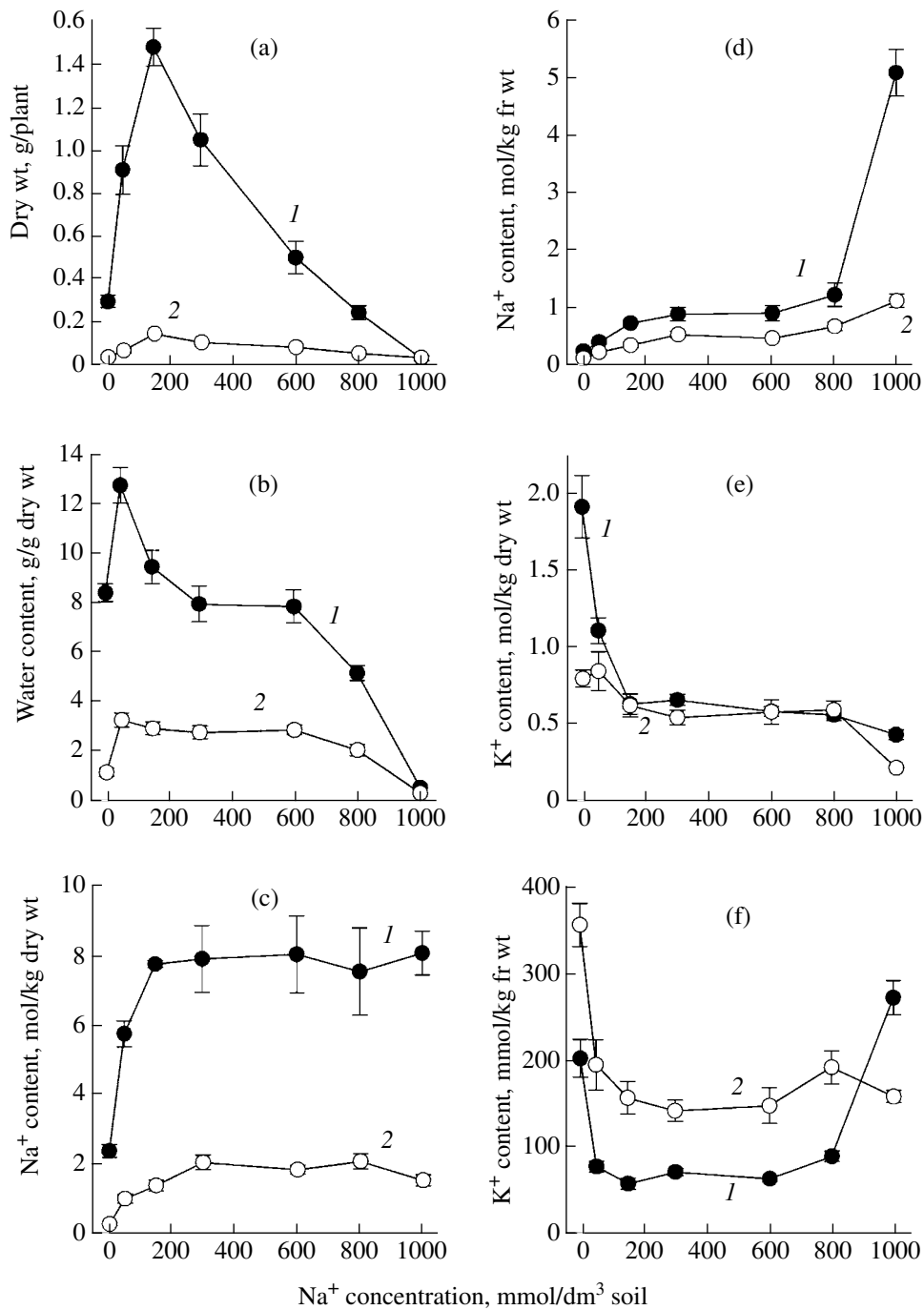


Fig. 2. Dry matter (a), water content (b), and Na⁺ content expressed on dry matter (c) and fresh weight (d) bases, and K⁺ content expressed on a dry weight (e) and fresh weight (f) bases in organs of *Climacoptera lanata* at various concentrations of NaCl in the substrate.

(1) Leaves, (2) roots.

Salicornia grown in the absence of NaCl, the water contents in leaves were lower than in roots (Figs. 1b, 2b).

As external NaCl concentration was increased above optimal levels corresponding to the highest extents of hydration, the water contents in organs

declined in different manners for the three species examined. For example, the water content in leaves and roots of *Salicornia* was hardly affected by NaCl, even at extremely large concentrations (Fig. 1b). The most dramatic drop in water content upon the increase of NaCl concentration in the substrate was observed in

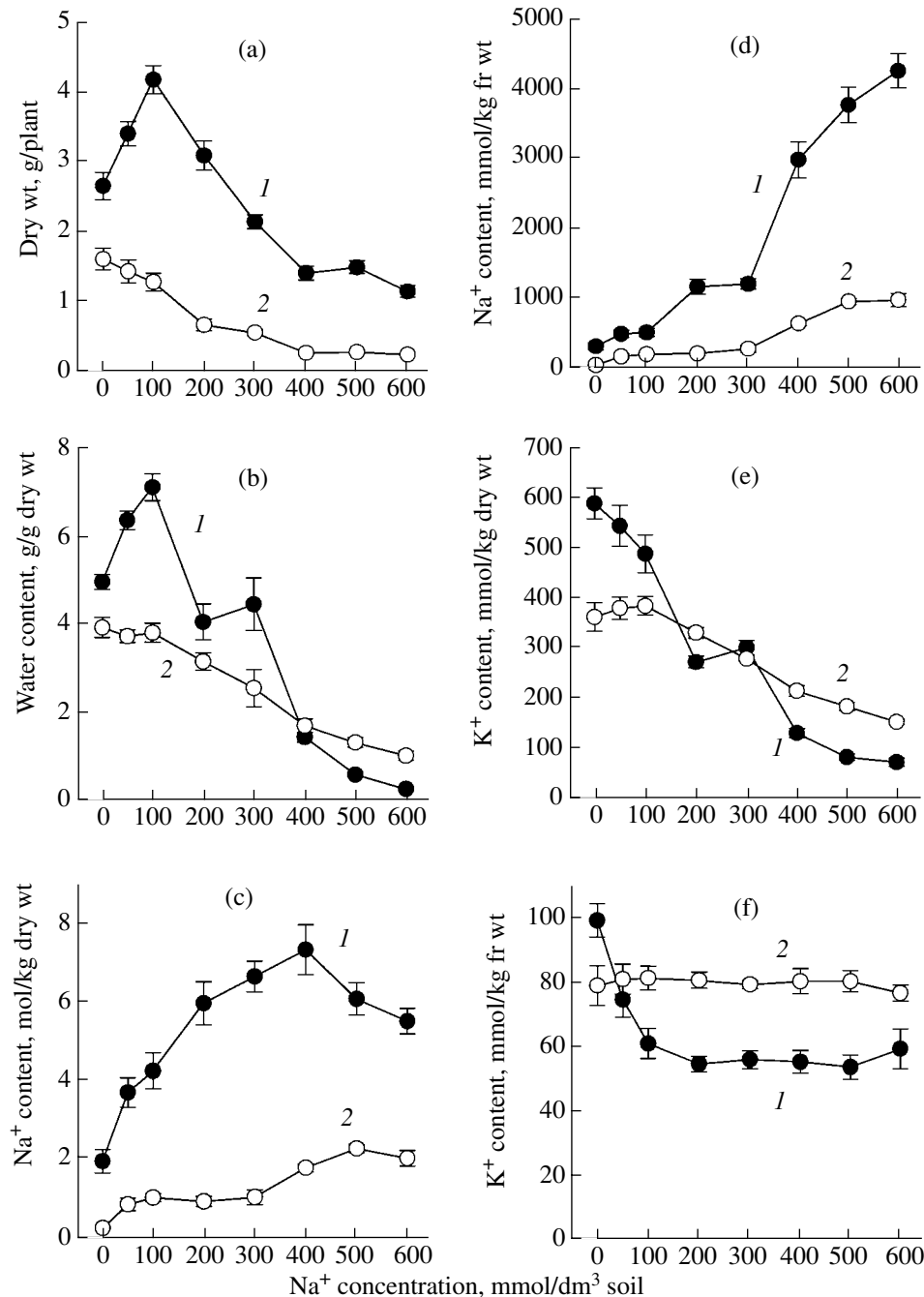


Fig. 3. Dry matter (a), water content (b), and Na⁺ content expressed on dry matter (c) and fresh weight (d) bases, and K⁺ content expressed on a dry weight (e) and fresh weight (f) bases in organs of *Atriplex micrantha* at various concentrations of NaCl in the substrate.

(1) Leaves, (2) roots.

Atriplex organs (Fig. 3b). Data on water content in organs of halophytes at various concentrations of NaCl (Figs. 1b, 2b, 3b) suggest that *Salicornia* exhibits the highest resistance to dehydration, whereas *Atriplex* is the least resistant species. This view is consistent with comparative salt tolerances of these species assessed from the influence of NaCl on organ biomass (see above). External concentrations of NaCl providing the highest water content in halo-

phyte organs were almost identical to salt concentrations that were optimal for plant growth (cf. Figs. 1a, 2a, 3a and Figs. 1b, 2b, 3b). This result nicely illustrates a well-known concept of plant physiology that rapid extension growth would be impossible without massive water uptake.

It should be mentioned that, at extremely high concentrations of NaCl in the substrate, the water content

in roots and leaves of *Climacoptera* and *Atriplex* decreased to its limit equal to or lower than 1.0–1.5 g/g dry wt. However, the plants remained viable under these conditions, which demonstrates their much higher salt tolerance compared to that of glycophytes.

As noticed above, the maintenance of growth under high salinity is ensured by the capacity of plants to absorb water. To cope with this problem, plants should depress the cell water potential below the water potential of soil. One of the main mechanisms contributing to the depression of water potential in cells is ion uptake and ion sequestering in vacuoles. Measurements of Na⁺ content in organs per unit dry weight basis at various concentrations of NaCl in the substrate (Figs. 1c, 2c, 3c) showed that Na⁺ accumulation is common to all halophytes examined, including *Atriplex* whose leaves contain salt glands. In *Salicornia* and *Climacoptera*, the dependences of Na⁺ content per unit dry weight of leaves and roots had the shape of saturation curves (Figs. 1c, 2c). In *Atriplex* these dependences were more complicated (Fig. 3c). As external Na⁺ concentration was raised, the Na⁺ content in *Atriplex* roots increased to a plateau at moderate concentrations of salt (100–300 mM). When the external NaCl concentration was increased in the range 0–300 mM, the Na⁺ content in leaves rose toward a saturation level, but further increase in salinity to 400–600 mM reduced slightly the Na⁺ content in leaves with a concomitant increase of Na⁺ content in roots. The decrease of Na⁺ content in *Atriplex* leaves and the parallel rise of this ion concentration in roots, observed at high NaCl concentrations in the medium, could be related to redistribution of Na⁺ between these organs.

Since vacuoles occupy the major part of the tissue volume, and they retain the overwhelming part of intracellular Na⁺, the Na⁺ contents expressed per unit fresh weight are actually close to vacuolar concentrations of Na⁺. In Figs. 1d, 2d, and 3d, the contents of Na⁺ per 1 kg fr wt are plotted as a function of external NaCl concentration for three species of halophytes. Generally, the Na⁺ content in leaves and roots increased with external Na⁺ concentration for all species examined, including *Atriplex*. Remarkably, the extent of Na⁺ accumulation was much higher in leaves than in roots. Significant differences between Na⁺ contents in leaves and roots were observed at all concentrations of NaCl in the medium for all three species of halophytes. These differences make a substantial contribution to the gradient of osmotic pressure between leaves and roots.

It is worth mentioning that a sharp increase in Na⁺ content (expressed on fresh weight basis) in leaves and roots, which was observed in *Climacoptera* and *Atriplex* at high concentrations of NaCl in the substrate, was related to a drastic dehydration of tissues under these conditions (cf. Figs. 2b, 2d and 3b, 3d). The content of Na⁺ in leaves approached in this case the level of 4–5 mol/kg fr wt, which is close to the solubility limit for sodium chloride. This result is consistent with pub-

lished data that dehydration in some halophytes under extremely high salinities may result in cracking of their leaves [9, 10].

The content of potassium ions in halophyte organs showed a clearly different response to the increase in external NaCl concentration, as compared to Na⁺ content. The amounts of K⁺ per unit dry weight are shown in Figs. 1e, 2e, and 3e as a function of NaCl concentration in the substrate for three halophyte species. If the low-concentration range of external NaCl is excluded from consideration, the conclusion can be drawn that K⁺ content in leaves and roots of halophytes correlates with water content in their tissues (cf. Figs. 1b and 1e, 2b and 2e, 3b and 3e). In other words, the decrease in water content per unit dry weight upon the increase in external NaCl concentration (in the range where salt concentrations exceeded their optima corresponding to the highest water and biomass contents) occurred concurrently with the decrease in K⁺ content. At low concentrations of sodium chloride in the medium and, especially, in its absence, the halophytes showed a trend toward stimulated accumulation of K⁺ in plant organs. This trend was better pronounced in leaves than in roots.

The calculations of K⁺ content in organs per unit fresh weight provide the estimates for average intracellular K⁺ concentrations in organs and, respectively, for the contribution of K⁺ to the osmotic potential gradient between roots and leaves. The dependences of K⁺ content per unit fresh weight on NaCl concentration in the substrate for roots and leaves of three halophyte species are displayed in Figs. 1f, 2f, and 3f. On the whole, the K⁺ content in organs of halophytes grown at various NaCl concentrations in the substrate was substantially lower than the Na⁺ content. This means that the contribution of K⁺ ions to the osmotic pressure of cells was comparatively low (Figs. 1c, 2c, 3c, 4c); hence, these ions were not as important as Na⁺ ions for generation of water potential gradient in the substrate–root–shoot system. At low and moderate NaCl concentrations, the K⁺ content in organs of three halophytes was kept at a relatively constant level, of about 70–220 mmol/kg in root cells and 50–100 mmol/kg in leaf cells, depending on plant species. Substantial deviations from these values were only observed when sodium chloride was either excluded from the substrate or added at extremely high concentrations. As a rule, the K⁺ content in leaves of *Atriplex* and *Salicornia* plants grown on NaCl-free medium was 2–3 and 14 times higher, respectively, than in leaves of plants grown in the presence of Na⁺; moreover, the amount of K⁺ in leaves was higher than that in roots. At high concentrations of NaCl in the substrate, the K⁺ content per unit fresh weight in *Climacoptera* leaves (Fig. 2f) was also higher than the average level observed at moderate NaCl concentrations.

The K⁺ content in *Salicornia* and *Climacoptera* leaves reached in this case the values of 1100 and

370 mmol/kg fr wt, respectively (Figs. 1f, 2f). While measuring K⁺ content in organs of a succulent-type halophyte *Suaeda altissima* grown in water culture at various salinities, we found that this plant, like *Salicornia*, accumulated K⁺ in leaves when the medium was deprived of NaCl [12].

Thus, the present study demonstrates that the three species of halophytes of family Chenopodiaceae are able of growing at various levels of soil salinity, including extremely high concentrations of NaCl and complete absence of NaCl in the substrate. Measurements of water content in roots and leaves of halophytes proved that halophytes effectively control water relations, thereby maintaining comparatively high hydration level of cells at a wide range of external NaCl concentrations (Figs. 1b, 2b, 3b). The obtained dependences of accumulated biomass and water content in organs on NaCl concentration in the outer medium indicate variations in salt resistance for these species.

Water uptake is indispensable for plant growth. Therefore, plants should be able to reduce water potential of their cells and maintain the water potential gradient directed from the soil to root and eventually to shoot. This challenge is particularly pressing in halophytes and xerophytes, i.e. the plants performing their life cycle at low water potentials of soil. In this case, the cells depress their water potential by means of increasing the osmotic pressure of the vacuolar sap.

The osmotic pressure π_i created by solute species i is proportional to solute concentration, as formulated by Boyle–Van't Hoff equation ($\pi_i = RTc_i$, where R is gas constant, T is absolute temperature, and c_i is the solute concentration). Judging from this equation and from ion contents calculated for halophyte organs on a fresh weight basis (Figs. 1d, 2d, 3d and 1f, 2f, 3f), one can conclude that Na⁺ is a main contributor to the intracellular osmotic pressure, whereas the contribution of K⁺ is less significant. When NaCl was excluded from the substrate, the contribution of K⁺ ions to the intracellular osmotic pressure increased and became more significant than the contribution of Na⁺. Apparently, K⁺ ions can partly replace the lacking Na⁺ ions that are required for the increase in intracellular osmotic pressure.

In three halophyte species examined, the total content of Na⁺ and K⁺ in leaves was higher than in roots at all NaCl concentrations in the substrate. This result implies that both cation species contribute to the formation of water potential gradient directed from roots to shoots. Based on the difference in total Na⁺ and K⁺ content for leaves and roots, we applied Boyle–Van't Hoff equation to calculate the osmotic pressure difference between these organs. Figures 4a, 4b, and 4c display the calculated osmotic pressure difference (the contribution of Na⁺ and K⁺ to the water potential gradient between roots and leaves) as a function of NaCl concentration in the substrate for three species of halophytes. Remarkably, this difference was positive for all

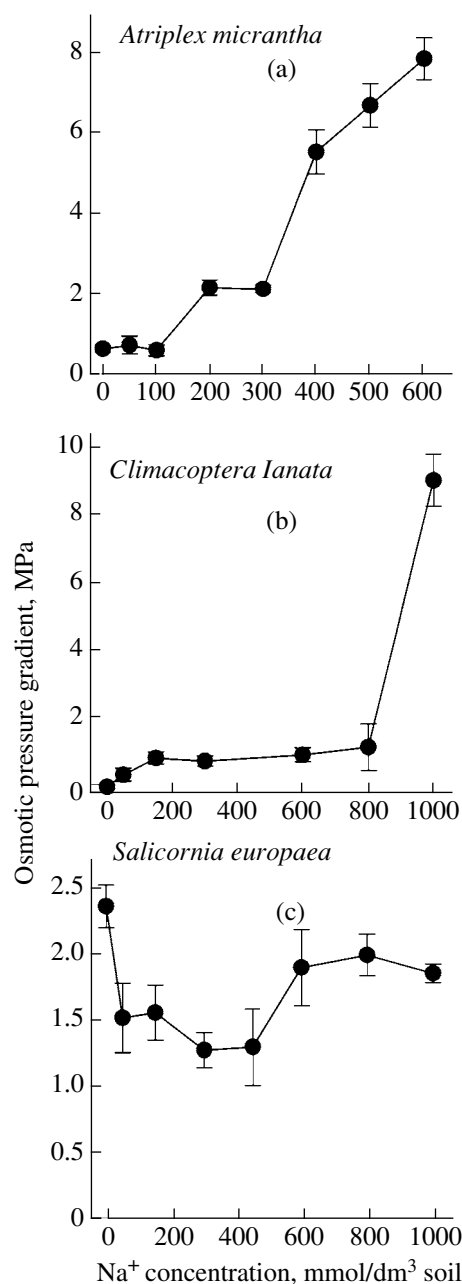


Fig. 4. Total contribution of Na⁺ and K⁺ to the osmotic potential gradient between leaves and roots as a function of external NaCl concentration for (a) *Atriplex micrantha*, (b) *Climacoptera lanata*, and (c) *Salicornia europaea*.

three species (osmotic pressure in leaves is higher than in roots) at all external concentrations of NaCl. In *Atriplex* and *Climacoptera* this difference increased with NaCl concentration in external medium (Figs. 4a, 4b), reflecting a faster rise in Na⁺ content in leaves compared to roots. In *Salicornia* a similar dependence was more complicated; for example, relatively large gradients of osmotic pressure were evident not only at high but also at low concentrations of NaCl (Fig. 4c). Such

pattern resulted, on the one hand, from the gain in leaf Na^+ content at increasing NaCl concentrations in the medium and, on the other hand, from strong accumulation of K^+ by leaves at low salt concentrations. The ability of accumulating high concentrations of K^+ in leaves at low Na^+ content in the substrate is a feature that distinguishes *Salicornia* from two other species examined.

We did not observe any principal other differences in accumulation and partitioning of Na^+ and K^+ as processes contributing to generation of water potential gradient in the whole plant. This was true for euhalophytes of succulent type (*Salicornia europaea*) and xeromorphic type (*Climacoptera lanata*), as well as for the halophyte with salt glands (*Atriplex micrantha*) characterized by the mesophytic type of cell structure. *Atriplex* plants are endowed with glands enabling the excretion of salt to the environment (the excretion is realized through the disruption of the basal cell within the gland and the consequent separation of the bladder cell from the leaf [20]). Nevertheless, *Atriplex* plants accumulate Na^+ ions to nearly the same concentrations as observed in salt-accumulating halophytes (euhalophytes). In halophytes with salt glands, like in salt-accumulating halophytes, much higher concentrations of Na^+ and K^+ were accumulated in leaves than in roots. It should be noted that the volume of specialized salt-accumulating bladder cells of salt glands in various *Atriplex* species constitutes a minor part in the total volume of other leaf cells [1]. Thus, the average Na^+ concentrations in *Atriplex* leaves determined in our experiments should approximately equal to average Na^+ concentrations in vacuoles of mesophyll cells (these vacuoles occupy the predominant part of the leaf volume) rather than to bladder cells of salt glands.

The physiological significance of such universal pattern of accumulation and partitioning of ions between organs in halophytes consists in the necessity for plant to absorb water by roots, transport water to shoots, and maintain the hydration state of cells and organs at a level sufficient for viable functions under high soil salinity. The described results led us to assume that euhalophytes of succulent and xeromorphic types, as well as halophytes whose leaves contain salt glands have common features in organization of long-distance Na^+ transport, as a process contributing to formation of water potential gradient along the plant axis. The root system of halophytes examined is adjusted to enable absorption of large amounts of Na^+ and the transfer of bulk amounts of Na^+ to the aboveground organs.

ACKNOWLEDGMENTS

This work was supported by the Program for Basic Research of the Presidium of Russian Academy of Sciences "Changes in Natural Environment and Climate: Natural Disasters" (contract no. 10002-251/P-13/167-148/250404-157).

REFERENCES

1. Storey, R., Pitman, M.G., Stelzer, R., and Carter, C., X-Ray Micro-Analyses of Cells and Cell Compartments of *Atriplex spongiosa*, *J. Exp. Bot.*, 1983, vol. 34, pp. 778–794.
2. Hajibagheri, M.A. and Flowers, T.J., X-Ray Microanalyses of Ion Distribution within Root Cortical Cells of the Halophyte *Suaeda maritima* (L.) Dum., *Planta*, 1989, vol. 177, pp. 131–134.
3. Niu, X., Bressan, R.A., Hasegawa, P.M., and Pardo, J.M., Ion Homeostasis in NaCl Stress Environments, *Plant Physiol.*, 1995, vol. 109, pp. 735–742.
4. Yeo, A., Molecular Biology of Salt Tolerance in the Context of Whole-Plant Physiology, *J. Exp. Bot.*, 1998, vol. 49, pp. 915–929.
5. Glenn, L.P., Brown, J.J., and Blumwald, E., Salt Tolerance and Crop Potential of Halophytes, *Crit. Rev. Plant Sci.*, 1999, vol. 18, pp. 227–255.
6. Hasegawa, P.M., Bressan, R.A., and Zhu, J.-K., Plant Cellular and Molecular Responses to High Salinity, *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 2000, vol. 51, pp. 463–499.
7. Greenway, H. and Munns, R., Mechanisms of Salt Tolerance in Nonhalophytes, *Annu. Rev. Plant Physiol.*, 1980, vol. 31, pp. 149–190.
8. Adams, P., Thomas, J.C., Vernon, D.M., Bohnert, H.J., and Jensen, R.G., Distinct Cellular and Organismic Responses to Salt Stress, *Plant Cell Physiol.*, 1992, vol. 33, pp. 1215–1223.
9. Flowers, T.J. and Yeo, A.R., *Solute Transport in Plants*, Glasgow: Blackie, 1992.
10. Munns, R., Physiological Processes Limiting Plant Growth in Saline Soils: Some Dogmas and Hypothesis, *Plant, Cell Environ.*, 1993, vol. 16, pp. 15–24.
11. Bressan, R.A., Nelson, D.E., and Iraki, N.M., Reduced Cell Expansion and Changes in Cell Walls of Plants Adapted to NaCl , *Environmental Injury to Plants*, Kattermann, F.R., Ed., San Diego: Academic, 1990, pp. 137–171.
12. Balnokin, Yu.V., Kurkova, E.B., Myasoedov, N.A., Lun'kov, R.V., Shamsutdinov, N.Z., Egorova, E.A., and Bukhov, N.G., Structural and Functional State of Thylakoids in a Halophyte *Suaeda altissima* before and after Disturbance of Salt–Water Balance by Extremely High Concentrations of NaCl , *Fiziol. Rast. (Moscow)*, 2004, vol. 51, pp. 905–912 (*Russ. J. Plant Physiol.*, Engl. Transl., pp. 815–821).
13. Balnokin, Yu.V., Kotov, A.A., Myasoedov, N.A., Khailova, G.F., Kurkova, E.B., Lun'kov, R.V., and Kotova, L.M., Involvement of Long-Distance Na^+ Transport in Maintaining Water Potential Gradient in the Medium–Root–Leaf System of a Halophyte *Suaeda altissima*, *Fiziol. Rast. (Moscow)*, 2005, vol. 52, pp. 549–557 (*Russ. J. Plant Physiol.*, Engl. Transl., pp. 489–496).
14. Serrano, R., Mulet, J.M., Rios, G., Marquez, J.A., de Larrinoa, I.F., Leube, M.P., Mendizabal, I., Pascual-Ahuir, A., Proft, M., Ros, R., and Montesinos, C., A Glimpse of the Mechanisms of Ion Homeostasis during Salt Stress, *J. Exp. Bot.*, 1999, vol. 50, pp. 1023–1036.

15. Blumwald, E., Aharon, G.S., and Apse, M.P., Sodium Transport in Plant Cells, *Biochim. Biophys. Acta*, 2000, vol. 1465, pp. 140–151.
16. Kurkova, E.B. and Balnokin, Yu.V., Pinocytosis and Its Possible Role in Ion Transport in Salt Accumulating Organs of Halophytes, *Fiziol. Rast. (Moscow)*, 1994, vol. 41, pp. 578–582 (*Russ. J. Plant Physiol.*, Engl. Transl., pp. 507–511).
17. Lun'kov, R.V., Andreev, I.M., Myasoedov, N.A., Khailova, G.F., Kurkova, E.B., and Balnokin, Yu.V., Functional Identification of H⁺-ATPase Antipporter in the Plasma Membrane Isolated from the Root Cells of Salt-Accumulating Halophyte *Suaeda altissima*, *Fiziol. Rast. (Moscow)*, 2005, vol. 52, pp. 715–725 (*Russ. J. Plant Physiol.*, Engl. Transl., pp. 635–644).
18. Henkel, P.A., *Fiziologiya zhara- i zasukhoustoichivosti (Physiology of Heat and Drought Resistance)*, Moscow: Nauka, 1982.
19. Robinson, S.P. and Downton, W.J.S., Potassium, Sodium and Chloride Ion Concentrations in Leaves and Isolated Chloroplasts of the Halophyte *Suaeda australis* R. Br., *Aust. J. Plant Physiol.*, 1985, vol. 12, pp. 471–478.
20. Clarkson, D.T., *Ion Transport and Cell Structure in Plants*, London: McGraw-Hill Book, 1974.