



CARBOHYDRATE COMPOSITION AT DIFFERENT SALT CONCENTRATIONS OF HALOPHYTES OF THE CHENOPODIACEAE FAMILY

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Annotation

Our study is aimed at studying the content of soluble sugars in plants in a comparative aspect (under Aralkum and in vitro conditions), indicating their contribution to the osmotic pressure of organ cells. Thus, to demonstrate the participation of soluble carbohydrates in reactions that provide stability in stressful situations. A protective mechanism that allows maintaining the water status of halophyte cells under conditions of high salinity is the accumulation of low molecular weight compounds: amino acids (proline, alanine, etc.), carbohydrates, etc. So, the obtained data of 3 species of wild-growing halophytes, differing in the type of regulation of salt metabolism: salt-accumulating - salt-releasing, indicate that the accumulation of sugars in plant organs depends both on the genetic characteristics of the studied species and the level of soil salinity. The division of plants according to the halotolerant trait has a clear biochemical basis. Thus, a higher total sugar content is characteristic of *Climacoptera intricata*, *Suaeda altissima* (hyperhalophytes), compared to *Atriplex aucheri* (crinohalophyte). Our results confirm the data on the formation of a community with the participation of euhalophytes on soils with higher salinity (3–4%) than the crynohalophyte (*Atriplex aucheri*). The study makes it possible to identify the functional groups of plants and predict their response to global and local environmental changes.

Keywords: halophytes, drained bottom of the Aral Sea, carbohydrate composition, salt concentrations, Chenopodiaceae, *Climacoptera intricata* (Iljin) Botsch., *Suaeda altissima* (L.) Pall., *Atriplex aucheri* Moq.

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1. Introduction

To obtain valuable medicinal and competitive salt-tolerant plants, it is necessary to take into account the structural and physiological-biochemical features of halophytes.

The aim of this study was to study biochemical changes in plants (in particular, the accumulation of soluble carbohydrates), in a comparative aspect, in clones of regenerants of promising halophyte plants grown on a nutrient medium with different salt content and growing under natural growing conditions (drained bottom of the Aral Sea).), to identify their adaptation strategies, and the level of evolutionary development.

Soluble carbohydrates, being products of photosynthesis, the so-called "depot" for short-term energy storage, carbon sources and components for the synthesis of oligo- and polysaccharides, take part in key physiological, biochemical and molecular genetic processes that ensure growth, development, reproduction and protection from unfavorable biotic and abiotic factors [1-3].

One of the main objectives of this work is to obtain the richest tissue clones of biologically active substances, to study plants for salinity resistance by accumulating sugars, maintaining a high level of hydration of organs under saline conditions.

In this regard, it seemed relevant to us to conduct comparative studies and identify a correlation between an increase in the concentration of salts in the environment and an increase in the content of the production of primary metabolites, indicating their participation in the protective processes of the plant organism, for example, in the formation of proline, which affects the functioning of the antioxidant system in plants. plants, protecting from salt stresses and in cells cultivated in vitro.

According to recent studies, the salinity of the Aral Sea has reached >200 g/l. According to the data, these waters correspond to the cationic (Ca^{2+} , Mg^{2+} , Na^+ , K^+ , NH_4^+ , Fe^{3+} , and Fe^{2+}) and anionic (Cl^- , SO_4^{2-} , HCO_3^-) composition [4]. Moreover, according to the anionic composition, they mainly belong to the chloride-sulfate and sulfate-chloride types of salinity. (SO_4^{2-} to 1572 mg/l, Cl^- to 1326 mg/l), cation content Na + K (209–710 mg/l), Ca to 410 mg/l, Mg to 210 mg/l [5].

Halophytes are plant species that can successfully survive, grow and reproduce in soils with a salt concentration of more than 200 mM. NaCl. Some halophytes can even grow well at higher salt concentrations. (> 500 mM NaCl) [6,7].

Currently, various aspects of plant response to salt stress and the prospects for the use of representatives of halophytes at the functional level are being studied. Most of the salt-accumulating halophytes have the property of halophilicity. The process of maintaining low ion concentrations Na^+ и Cl^- in the cytosol at high concentrations NaCl in the environment is one of the mechanisms underlying the salt tolerance of plants. To avoid the toxic effect of ions Na^+ and Cl^- , cells export them from the cytosol to the extracellular environment or to the vacuole [8].

The adaptation of halophytes to salinity was formed in the process of phylogenesis and affects different levels of organization: molecular, cellular, population, phytocenotic. Our study is aimed at studying the content of soluble sugars in plants in a comparative aspect (under Aralkum and in vitro conditions), indicating their contribution to the osmotic pressure of organ cells. Thus, to demonstrate the participation of soluble carbohydrates in reactions that provide stability in stressful situations. A protective mechanism that allows maintaining the water status of halophyte cells under conditions of high salinity is the accumulation of low molecular weight compounds: amino acids (proline, alanine, etc.), carbohydrates, etc. A high osmotic concentration in plant cells is created due to the high intensity of activation and biosynthesis, inhibition of the breakdown or degradation of macromolecules, and the accumulation of soluble carbohydrates [9].

There is an opinion that an increased level of sucrose in parallel with an increase in salinity may not be a primary response to salt stress, but rather the result of reactivation of photosynthesis caused by the activation of other defense mechanisms [1]. Thus, soluble carbohydrates play a key role as metabolites for the growth and synthesis of basic compounds, osmolytes, and also as signals for the regulation of gene expression [2].

Simple sugars that accumulate under the action of salinity, drought, and other adverse environmental factors on plants are widespread and universal osmotic agents that have a protective effect, protecting the protein-lipid components of membranes from denaturation during dehydration. Compatible osmolytes not only lower the water potential of cells, thereby restoring water supply, but also protect hydrolytic enzymes from inactivation, ensure the integrity of structural proteins, and preserve the functional activity of cell membranes [2].

The results of numerous experiments indicate that shrubs, semi-shrubs and annuals from the

Chenopodiaceae family are extremely promising for use not only in the ecological restoration of saline areas, but also as a source of biologically active substances rich in protein, fat, carotene, fiber, ash, vitamins and macroelements. [10,11]. The center of diversity of Chenopodiaceae is the desert belt of the Old World from the Canary Islands to Central Asia. It includes about 100 genera, including 1600 species, which are mainly distributed in the desert and steppe regions of the world [12].

However, for the industrial introduction of “profitable” halophytes in the Republic, basic research is needed, using the technical base available in the area in Muynak (Karakalpakstan), which is the purpose of this study.

2. Material and methods

The studies were carried out in 3 repetitions, during the period of intensive plant growth (July, 2022). For clonal micropropagation, nutrient media were prepared according to the Murashige-Skoog recipe, with the addition of: 1.0 μM BAP (6-benzylaminopurine), 0.5 NLA (α - naphthylacetic acid) and 0.5 μM kinetin (6-furfurylaminopurine). The explants were cultured under conditions of a photoperiod of 16/8 h, light/dark, at 24°C. The salt content in the medium was 0, 200, 500, 700 mM NaCl, which corresponds to medium and high salinity.

Free proline was determined by the method of Bates et al. [15], mono- and disaccharides were analyzed by HPLC. Carbohydrate content in plants was measured by an Agilent 1260 HPLC system with a RIDG1362A refractometric detector. The objects of study we have chosen belong to the group of “salt-accumulating” and “salt-releasing” plants differing in salt tolerance of halophytes, which are an important biochemical resource as a source material for growing ecologically differentiated salt-tolerant species [9]. Material for research, collected in places of natural growth: *Climacoptera intricata* (Iljin) Botsch., *Suaeda altissima* (L.) Pall., *Atriplex aucheri* Moq. on saline soil. *Suaeda altissima* is a tall, highly salt-tolerant plant, salt-accumulating, annual halophyte, 25–200 cm high. *Climacoptera intricata* - woolly climacoptera, grows on salt marshes, endemic to

Central Asia. An annual, long-term vegetative fodder halophyte 10–60 cm high, with branched roots covering shallow soil layers (40–60 cm). *Atriplex aucheri* is an annual, the stem is tetrahedral, flattened in places of branching, often winding. The material of the study was the leaves of plants in the vegetation phase.

The studies were carried out in 3 experiments in 3 biological replicates. For statistical processing of experimental data, the standard method of dispersion (ANOVA) analysis of a one-factor complex was used in the Statistica 6.1 program. The graphs show the arithmetic mean values. Differences in each pair of compared values were considered statistically significant at $p \leq 0.05$.

3. Results and discussion

Representatives of the genera *Climacoptera*, *Suaeda*, and *Atriplex* attract the attention of scientists as models for studying the mechanisms of salt tolerance, in particular, osmotic regulation, regulation of antioxidant capacity, an example of a transition to C4 photosynthetic metabolism, etc. [16–19]. The range of mineralization of the soil solution, in which the halophyte can normally grow and renew itself, is not the same for different species. So, according to the degree of halotolerance - a reaction to the degree of soil salinity, halophytes are classified into:

- 1) hyperhalophytes - capable of self-renewal and cenosis formation on excessively saline soils with a dry residue content of 2.3–3.0% (3.5), $\text{Cl}^- > 0.23$ with chloride-sulfate and sulfate salinity or dry residue 1.8 –2.3%, $\text{Cl}^- > 0.23$ with sulfate-chloride and chloride salinity.
- 2) euhalophytes - characterized by a wide range of halotolerance to the mineralization of the soil solution. They dominate on soils with a dry residue of 1.8–2.3% (2.5).
- 3) hemihalophytes - develop normally with soil salinity corresponding to a dry residue of 1.0–1.8% (2.0).
- 4) haloglycophytes - plants with low salt tolerance, develop normally and renew at a dry residue content of 0.3–0.8%. They have developed an adaptive reaction to weakly saline soils [20, 21].

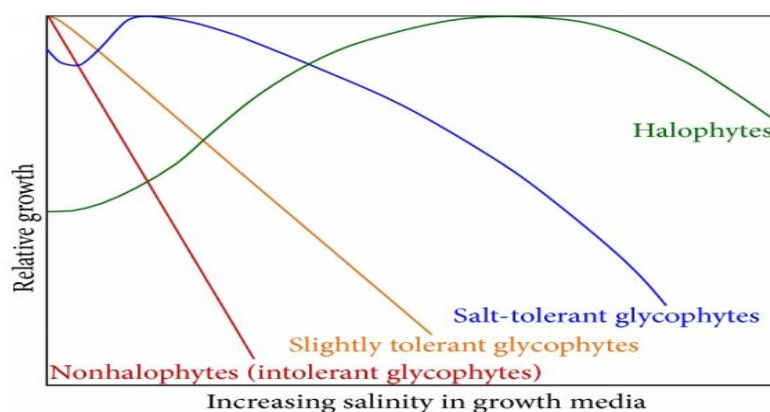


Figure 1. Schematic representation of the growth of various plant species in saline conditions.

Moreover, the species composition in natural ecosystems varies depending on the salinity factor of the substrate from the largest to the smallest: euhalophytes → cynohalophytes → glycohalophytes [9, 22].

According to the method of salt tolerance mechanisms by salt accumulation and salt release and their effectiveness, halophytes are distinguished:

- “salt-accumulating” (euhalophytes) plants, characterized by succulent leaves with large photosynthetic cells, are able to maintain high osmotic pressure inside the cell by selective accumulation of mineral salt ions (Na^+ and Cl^-), which are transported in large quantities from the roots to above-ground organs, where accumulate mainly in vacuoles, differ in the organization of long-range transport of ions.
- “salt-producing” (crinohalophytes) are characterized by xerophytic leaf structure with small chlorenchyma cells, have specialized salt glands (salt glands) that secrete salt on the leaf surface, low molecular weight osmolytes, such

as proline, sugars, etc., play an osmoregulatory role.

- “salt-resistant” (glycohalophytes) plants with xerophytic leaf structure, limit the flow of salts into the aboveground organs. They create a high osmotic pressure by synthesizing carbohydrates or other low molecular weight organic compounds; preventing the entry of salts into the root cells [23,24].

From a physiological point of view, a distinction is made between true (obligate) halophytes, whose existence (seed germination, biomass growth) requires increased mineralization, and salt-tolerant (facultative) species that can exist both in the presence and in the absence of salts [9]. Thus, species of *Climacoptera*, *Suaeda* are obligate halophytes, which are highly salt-tolerant salt-accumulating euhalophytes with a highly organized adaptation mechanism, are able to increase their drought resistance under salinity conditions (up to 700 mM NaCl) [25,26,27], and have mesostructural characteristics [28].

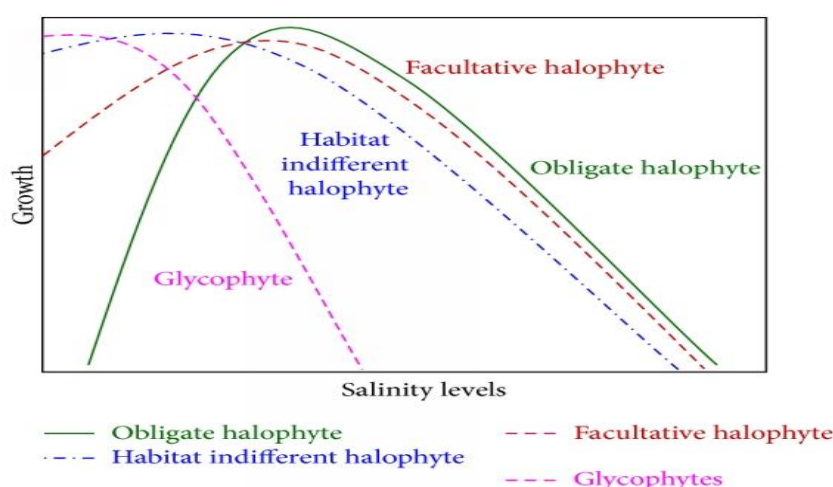


Figure 2. The nature of the growth of halophytes in saline conditions.

These plants have an active transport system - carriers and ion channels. The accumulation of Na^+ in vacuoles leads to the formation of a water potential gradient between the solution surrounding the cell and the cell (the water potential of the cell decreases), and the water flow is directed into the cell, maintaining redox homeostasis [29]. In the cytoplasm, the water potential decreases due to the biosynthesis of osmolytes, low molecular weight organic compounds that also have a protective effect in relation to cytoplasmic biopolymers [30]. *Suaeda altissima* (L.) Pall. (high sveda) is one of the most salt-tolerant representatives; it functions in conditions of high soil salinity and can grow on media with NaCl concentration up to 1 M [25]. It is known that in the membranes of the Golgi complex isolated from the cells of the roots of *S. altissima*, Cl^-/H^+ - antiporter, which plays an important role in halophytes, where it is involved in the regulation of concentrations Cl^- in the cytoplasm under saline conditions. The supposed role of this antiporter is to export ions Cl^- from the cytoplasm to the vacuole, which provides plants with salt tolerance [31]. It has been established that the content of ions in organs is the greater, the higher the concentration Na^+Cl^- in nutrient solution. Ions Na^+ in the cells of the leaves of this plant, they reach 800 mmol/kg wet weight [32]. The increasing distribution of ions (soil-roots-leaves) ensures the maintenance of the water potential gradient in the system of the whole plant [33,34]. *Climacoptera intricata* (Iljin) Botsch. (woolly climacoptera) - in terms of halotolerance, the species belongs to the group of highly salt-resistant salt-accumulating euhalophytes, adapted to significantly saline soils [35]. Species of *Climacoptera* are obligate halophytes, capable of developing only in a salty environment. The leaves of *C. intricata* are typical succulent, pubescent with numerous long thin filamentous trichomes of the same type, the

hemiparacytic type of stomata predominates, the mesophyll is Kranz-centric, without hypodermis. The adaptive features of the group of succulents is the presence of a specialized water-storing leaf tissue. Thus, one of the haloindicative features of *Climacoptera* species, as a result of halophytosis, in addition to the protective function, the epidermis of the leaf acquired a specific function of water and salt accumulation. Characteristic features for this species are a high palisade index, epidermal cells with thickened outer walls [36]. Resistance to xero- and halofactors is determined by the genome of species with the Kranz structure of vegetative organs, which provides them with greater marginal halotolerance. *Atriplex* species belong to the group of salt-producing halophytes (crinohalophytes), a long-term vegetative fodder halophyte 10–60 cm high, with branched roots covering shallow soil layers (60–120 cm). Representatives of this genus with xeromesophytic characteristics are less resistant to salinity (up to 200 mM NaCl) [37]. *Atriplex aucheri* Moq. semishrub, late summer annual, tetrahedral stem, flattened in places of branching, often winding. *Atriplex* species are true xerophytes. A special type of anatomical and morphological adaptations is characterized by the presence of a typical Kranz anatomy with a layer of bundle sheath cells, radially arranged palisade cells [38]. Crinohalophyte plants are covered with vesicular hairs - salt vesicles (have a unicellular structure) or special glandular trichomes - salt glands (with a two- or multicellular structure) that accumulate salt. From the cells of the mesophyll, salt enters the gland through the collecting cells, and moves along the plasmodesmata. It accumulates in vesicles, which then merge with the plasmalemma. As a result, the salt comes out. In dry weather, the plant is covered with a continuous layer of salts released from their cells, some of which is blown away by the wind [38].

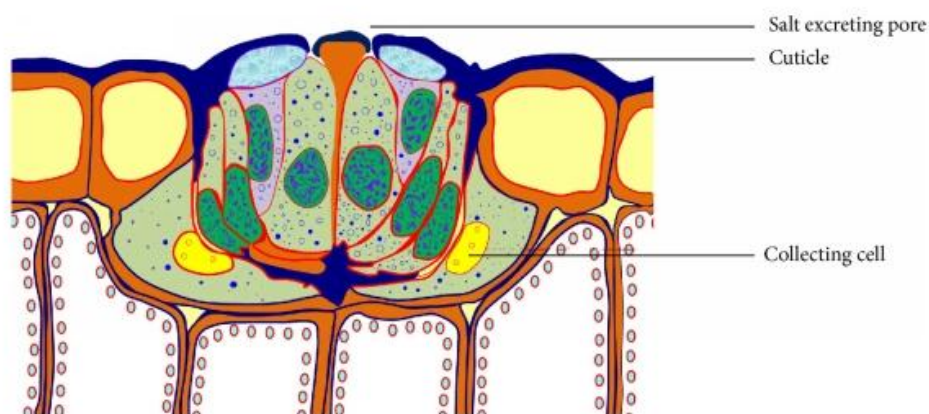


Figure 3. Excretory system of crinohalophyte plants

Atriplex aucheri has specialized excretory structures - vesicular hairs that accumulate NaCl solution, which cover the upper and lower sides of the leaves with a continuous whitish coating. Vesicular hairs are modified formations of the epidermis that transport ions from the stalk to the vesicle (atriplicoid type of leaves) [39,40]. The center of education and diversification of the genus is Central Asia (Old World), resettlement around the world occurred from the Aral-Caspian region during the Miocene. According to studies, the formation of the ancestral group of the genus *Atriplex* dates back to the Upper Cretaceous in climatically arid areas [41]. Morphological and anatomical features: fender structure of the leaf, C4-type of photosynthetic metabolism, abundant amount of salt-excreting blister-like hairs indicate the formation of the genus along the solonchak plains. The evolutionary development of the C4 lines took place over 30 Ma [42]. It should be noted that obligate halophytes (*Suaeda*, *Climacoptera*) in the evolutionary aspect have taken the path of greater ecological specialization, which allows them to grow on highly saline soils and effectively use moisture and mineral nutrients (and, at the same time, enrich the soil with organic matter when dying plants). So, in the process of evolution, they formed mechanisms that effectively maintain concentrations Na^+ and Cl^- in the cytoplasm at a lower level than in the soil solution and reduce the water potential in the cells to lower values than in the soil. It is known that a group of obligate halophytes, in response to an increase in salinity up to certain concentration limits (700 mM NaCl), increases the level of succulence, maintaining ionic and water homeostasis of the cytoplasm [30]. The group of facultative halophytes has taken the path

of ecological plasticity, the main strategy of which is to limit the entry of ions through the roots, which allows these plants to grow on soils with a wider range of salinity (but not with extreme salinity) and good ability to compete [10] (Figure 3). Soluble sugars function as metabolic resources and structural building blocks, and also act as signals regulating various processes associated with plant growth and development. Such signaling can modulate stress pathways into a complex network for further organization of plant metabolic reactions and is important for halophyte osmoregulation. Exposure to high NaCl reveals the presence of an increased amount of soluble sugars, which simultaneously act as compatible osmolytes and antioxidants. The results showed that proline was found in significant amounts in salinity-sensitive plants experiencing salt stress and water deficiency in natural conditions. Thus, the lowest content of proline in the “moderately salt-tolerant” *Atriplex aucheri* was observed in control samples, and the highest at NaCl= 700mM (by 50%) (Graph 1.). Thus, the C4 species exhibits weak resistance to osmotic stress and significantly accumulates proline in the presence of an excess of sodium ions; under saline conditions [43]. Also, an increase in salt concentration was reflected in *Suaeda altissima*, which is a “highly salt-tolerant” species, the level of proline in samples exposed to extreme salinity (NaCl 700mM) increased significantly, almost 2 times compared to the control. The highest proline values in *Climacoptera intricata* were found in samples exposed to NaCl 700mM, compared to control plants, the values increased by 30% [30].

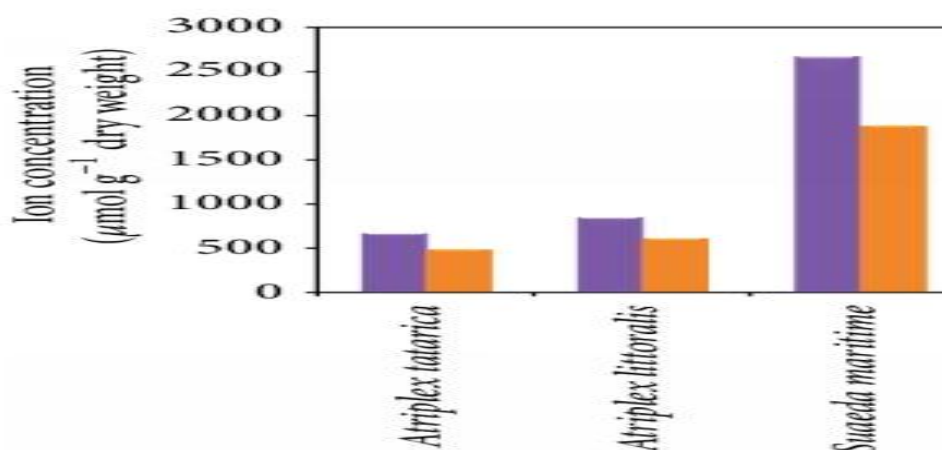
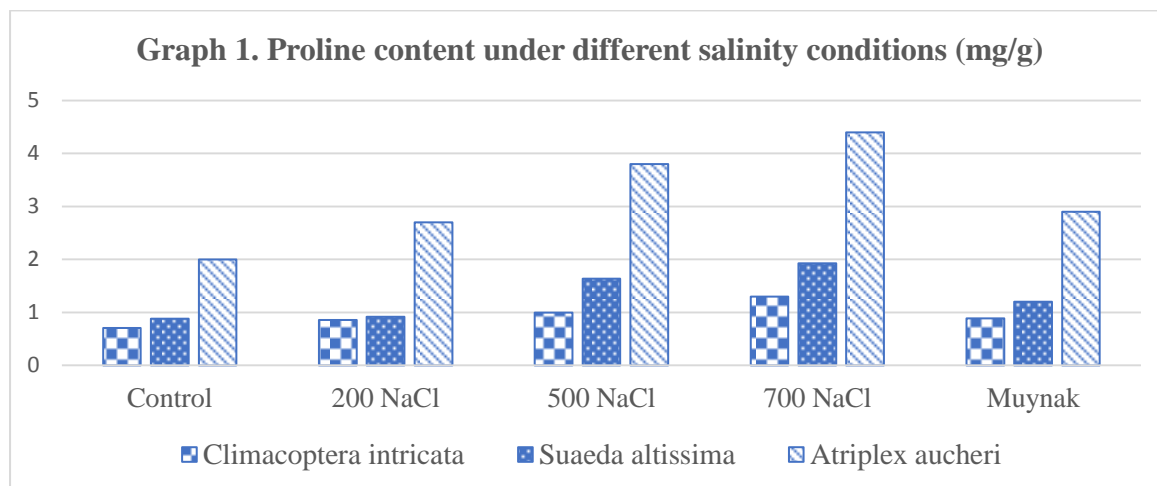


Figure 3. The content of Na^+ and Cl^- ions in plants of obligate (*Suaeda*) and facultative (*Atriplex*) halophytes under growing conditions



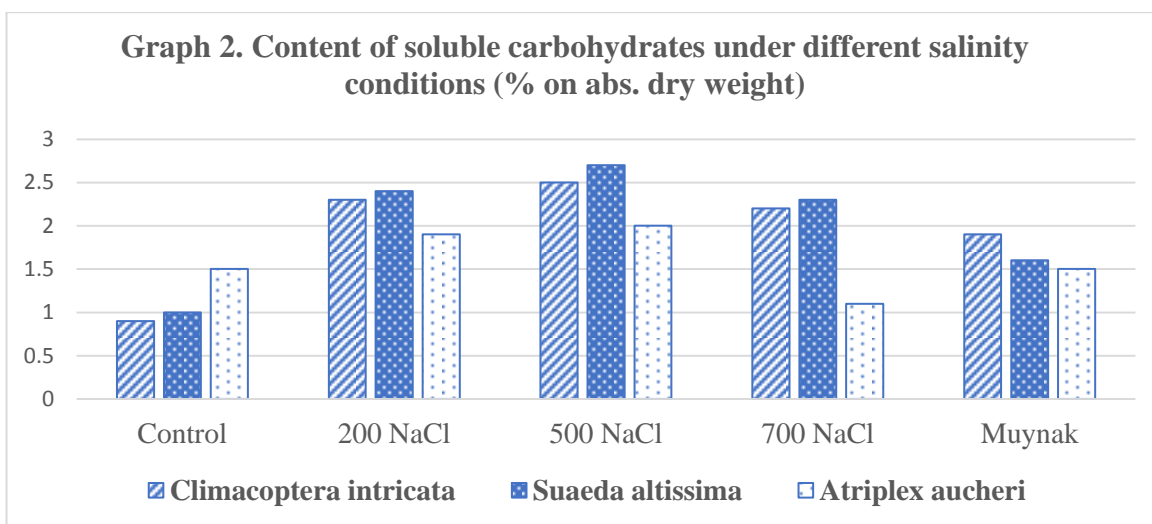
Apparently, these data confirm the point of view that proline (stress amino acid) is synthesized as a result of osmotic stress, which is characterized by a protective rather than osmoregulatory function [44].

It affects the intracellular regulation between the cytoplasm and vacuoles, regulates the pH of the cytosol, protects enzymes and intracellular structures, inactivates free radicals, and is a source of carbon and nitrogen for recovery after stress [45,46,2]. As is known, simple sugars accumulate under the action of salinity and other factors on plants [46, 47]. In our study, plants differ in the content of various forms of sugars in different growing conditions (Graph 2). Thus, as a result of the analyzes, a positive correlation was revealed between an increase in the concentration of salts in the nutrient medium and an increase in the concentration of soluble sugars. For true (obligate) halophytes, salt has a beneficial effect. This is evidenced by the high level of biomass of seedlings of *Climacoptera* and *Suaeda* at NaCl=200mM-500mM, and the content of total carbohydrates (Figure 2.3). Thus, sodium chloride introduced into the medium caused an increase in carbohydrates at a concentration of 200–500 mM, while the content of carbohydrates in the control turned out to be reduced. This is explained by the fact that euhalophytes effectively use the mechanisms of Na⁺ exclusion from the cytosol to achieve a high level of antioxidant protection developed during evolution. Therefore, the carbohydrate metabolism of plants remains consistently high under the influence of salts. At the same time, the development of mechanisms that ensure salt tolerance weakened the ability of obligate (true) halophytes to interspecific competition and limited their distribution in less mineralized areas. Thus, the absence of NaCl in the nutrient medium (control) led to a clear decrease in growth in control samples (Figure 1) and a reduced content of carbohydrates (Figure 2.3), which confirms the

need of plants of this group for the presence of salts in the habitat for normal development. Accessions of *Atriplex aucheri*, which are facultative halophytes, were found to be sensitive to salt. Thus, when the salinity of the medium exceeds the threshold level (NaCl 500-700mM), the growth of *Atriplex* decreases, indicating a negative effect of high salt concentrations. The range of variability in carbohydrate content is similar to the range of variability in proline, which is probably due to species genetic characteristics (Graph 2). Thus, it was found that the sugar content depends on the level of salinity of the medium. Comparative analysis (the results are shown in the graph) showed that chloride-sulphate salinization of the soil in the territory of Muynak and in vitro experiments (200 mM NaCl) in *Atriplex*, contribute to an increase in carbohydrates, compared with the control and exceeding the threshold level of samples. The high content of carbohydrates in species growing on soil with chloride-sulfate salinity shows that one of the effective mechanisms of physiological adaptation to salinity is the accumulation of water-soluble carbohydrates in cells [1]. It is believed that active accumulation during salt stress and drought of compatible substances such as amino acids, polyamines and carbohydrates is an effective mechanism of salt tolerance [46,47]. Sugars accumulated under the influence of salinity, drought and other unfavorable environmental factors on plants are widespread and universal osmotic agents that have a protective effect, protecting the protein-lipid components of membranes from denaturation during dehydration. According to the authors [1-3,46], sugars bind the excess amount of harmful ions entering the plant and regulate the ionic balance of plants. Organic acids formed with the participation of sugars can bind an excess amount of harmful ions entering the plant, regulate the ionic balance of plants, maintain electrical neutrality in cells and neutralize basic compounds. In fact, soluble sugars are involved in

a variety of basic cellular functions as a source of metabolism, structural compounds, and signaling molecules in plants [1,2]. Thus, in highly salt-tolerant species of *Climacoptera intricata*, *Suaeda altissima*, the constancy of sugar content was noted under various salinity conditions (Muynak and 200-700NaCl), and no statistically significant differences were observed (Table 1.). Whereas *Atriplex aucheri* showed lability in carbohydrate

metabolism. As can be seen from our results, a higher level of accumulation of mono- and oligosaccharides was noted in *Climacoptera intricata* (), *Suaeda altissima* (), euhalophytes - ecologically specialized in the evolutionary aspect, they exhibit "salt tolerance", which allows them to grow on highly saline soils and efficiently use moisture and mineral nutrients.



So, the obtained data of 3 species of wild-growing halophytes, differing in the type of regulation of salt metabolism: salt-accumulating - salt-releasing, indicate that the accumulation of sugars in plant organs depends both on the genetic characteristics of the studied species and the level of soil salinity. The division of plants according to the halotolerant trait has a clear biochemical basis. Thus, a higher total sugar content is characteristic of *Climacoptera intricata*, *Suaeda altissima* (hyperhalophytes), compared to *Atriplex aucheri* (crinohalophyte). Our results confirm the data on the formation of a community with the participation of euhalophytes on soils with higher salinity (3–4%) than the crinohalophyte (*Atriplex aucheri*).

The study makes it possible to identify the functional groups of plants and predict their response to global and local environmental changes.

Thus, we can conclude:

- 1) The reaction of halophytes to salt stress is specific with respect to the type of regulation of salt metabolism: salt-accumulating - salt-releasing
- 2) Groups are clearly distinguished: with respect to halotolerance, *Climacoptera intricata*, *Suaeda altissima* (euhalophyte group), *Atriplex aucheri* (crinohalophyte group); in one group, plants grown in the control, and in the second - under saline conditions.

- 3) 3) The high content of carbohydrates of species growing on soil with chloride-sulfate salinity shows that one of the effective mechanisms of physiological adaptation to salinity is the accumulation of proline and water-soluble carbohydrates in cells.

4. References

- Gil R., Boscaiu M., Lull C., Bautista I., Lidón A., Vicente O. Are soluble carbohydrates ecologically relevant for salt tolerance in halophytes? *Functional Plant Biology*. 2013. 40, p. 805-818. <http://dx.doi.org/10.1071/FP12359>
- Gil R., Lull C., Boscaiu M., Bautista I., Lidón A., Vicente O. Soluble carbohydrates as osmolytes in several halophytes from a Mediterranean salt marsh. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*. 2011. 39. p.9–17.
- Flowers T.J., Colmer T.D. Salinity tolerance in halophytes. *New Phytologist*. 2008. V.179, 945–963. doi:10.1111/j.1469-8137.2008.02531.x
- Zihao Duan, Xiaolei Wang, Lin Sun Monitoring and Mapping of Soil Salinity on the Exposed Seabed of the Aral Sea, Central Asia. *Water*. 2022, V.14, 1438. <https://doi.org/10.3390/w14091438>.
- Kawabata Y., Aparin V., Jollibekov B., Watanabe M., Chida T., Kubota J., Aladin N., Jollibekov

- B., Katayama Y. Change in the water quality of the Aral Sea in Uzbekistan, Central Asia. *Journal of Arid Land Studies*, 2018, V.28-S, 151-154.
https://doi.org/10.14976/jals.28.S_151
- Grigore M.-N., Villanueva M., Boscaiu M., Vicente O. Do halophytes really require salt for their growth and development? An experimental approach. *Notulae Scientiae Biologicae*, 2012. V.4(2), pp.23–29.
- Breckle S. W. An Ecological Overview of Halophytes from the Aralkum Area// In book: *Handbook of Halophytes*. Springer. 2021. pp. 393-451.
- Flowers T. J., Galal H. K., Bromham L. Evolution of halophytes: multiple origins of salt tolerance in land plants. *Functional Plant Biology*. 2010. V. 37, p.604–612.
- Розенцвиг О. А., Нестеров В. Н., Богданова Е. С. Структурные и физиолого-биохимические аспекты солеустойчивости галофитов. *Физиология растений*. 2017, Т. 64, № 4, с. 251–265.
- Wang, X.; Shao, X.; Zhang, W.; Sun, T.; Ding, Y.; Lin, Z.; Li, Y. Genus Suaeda: Advances in Phytology, Chemistry, Pharmacology and Clinical Application (1895–2021). *Pharmacol. Res.* 2022, 179, 106203.
- Murshid S.A., Atoum D., Abou-Hussein D.R., Abdallah H.M., Hareeri R.H., Almukadi H., Edrada-Ebel R. Genus Salsola: Chemistry, Biological Activities and Future Prospective-A Review. *Plants*. 2022, V.8;11(6):714. doi: 10.3390/plants11060714.
- Sukhorukov A.P., Liu P.-L., Kushunina M. Taxonomic revision of Chenopodiaceae in Himalaya and Tibet. *PhytoKeys*. 2019. V.116: p.1-141.
<https://doi.org/10.3897/phytokeys.116.27301>
- Бочанцев В. П. Семейство Chenopodiaceae/Флора Узбекистана. Ташкент: изд-во АН УзССР. 1953. Т. II. С. 207-333.
- «Красная книга Республики Узбекистан», Том 2, Ташкент. 2019. 183 с.
- Bates, L.S., Waldren, R.P., Teare, I.D., 1973. Rapid determination of free proline for water-stress studies. *Plant Soil* 39, 205–207.
- Song, J., and Wang, B. (2014). Using euhalophytes to understand salt tolerance and to develop saline agriculture: Suaeda salsa as a promising model. *Ann. Bot.* V. 115, p. 541–553. doi: 10.1093/aob/mcu194
- Tahmasebi A. Molecular, micromorphological and anatomical study of rangeland species of Atriplex (Chenopodiaceae) in Iran. *Acta Biologica Szegediensis*. 2021. V. 65(2):133-143, doi:10.14232/abs.2021.2.133-143
- Samieia L., Pahnehkolayib M. D., Karimianc Z., Nabatid J. Morpho-Physiological Responses of Halophyte Climacoptera crassa to Salinity and Heavy Metal Stresses in In Vitro Condition. *South African Journal of Botany*. 2020, V.131, p.468-474.
- Schütze P., Freitag H., Weising K. An integrated molecular and morphological study of the subfamily Suaedoideae Ulbr. (Chenopodiaceae). *Plant Syst. Evol.* 2003, V. 239, p. 257–286.
- Ажигитова Н.И. Галофильная растительность Средней Азии и её индикационные свойства. Ташкент: Фан, 1982
- Мамедов Э.Ю., Эсенов П.Э., Дуриков М.Х., Зверев Н.Е., Цуканова С.К. Выращивание галофитов на деградированных землях. Проблемы освоения пустынь. 2009. №1-2. с. 33-37.
- Розенцвиг О.А., Нестеров В.Н., Богданова Е.С., Табаленкова Г.Н., Захожий И.Г. Биохимическая обусловленность дифференциация галофитов по типу регуляции солевого обмена. *Сибирский экологический журнал*. 2016. №1, с.117-126.
- Акопян Ж. А. Биолого-морфологические особенности и таксономический состав семейства Маревых (Chenopodiaceae Vent.) в Южном Закавказье. Автореферат дисс. д. б. н. Ереван. 2013.
- Nedelyaeva O.I., Popova L. G., Khramov D. E., Volkov V. S., Balnokin Y. V. Chloride Channel Family in the Euhalophyte Suaeda altissima (L.) Pall: Cloning of Novel Members SaCLCa2 and SaCLCc2, General Characterization of the Family. *Int. J. Mol. Sci.* 2023. 24, 941.
<https://doi.org/10.3390/ijms24020941>
- Song J., Wang B. Using euhalophytes to understand salt tolerance and to develop saline agriculture: Suaeda salsa as a promising model. *Ann. Bot.* 2014. V.115, p. 541–553. doi: 10.1093/aob/mcu194
- Samieia L., Pahnehkolayib M. D., Karimianc Z., Nabatid J. Morpho-Physiological Responses of Halophyte Climacoptera crassa to Salinity and Heavy Metal Stresses in In Vitro Condition. *South African Journal of Botany*. 2020, V.131, p.468-474.
- Бутник А.А., Нигманова Р.Н., Пайзиева С.А., Сатдов Д.К. Экологическая анатомия пустынных растений Средней Азии. Ташкент, 1991. Т.1. 148 с.
- Балнокин Ю.В. 2012. Ионный гомеостаз и солеустойчивость растений. М.: Наука. 99 с.
- Воронин П. Ю., Иванова Л. А., Ронжина Д. А., Мясоедов Н. А., Балнокин Ю. В. Морфометрическая характеристика хлоропластов растений-галофитов.

- Физиология растений. 2019, том 66, № 5, с. 354–359
- Шувалов А. В. Функциональная идентификация и транспортные свойства Cl^-/H^+ -антипортера мембран аппарата Гольджи клеток корня галофита *Suaeda altissima* (L.) Pall. Автореферат дисс. на с. уч. с. к. б. н., Москва. 2013, 25 с.
- Воронин П. Ю., Мясоедов Н. А., Халилова Л. А., Балнокин Ю. В. Водный потенциал апопласта подустьичной полости листа *Suaeda altissima* (L.) Pall. при солевом стрессе. Физиология растений, 2021, том 68, № 3, с. 308–314.
- Халилова Л. А. Пути транспорта Cl^- в системе целого растения у галофита *Suaeda altissima* (L.) Pall. Автореферат дисс. на с. уч. с. к. б. н., Москва- 2008, 26 с.
- Shuvalov A.V., Yurchenko A.A., Nedelyaeva O.I., Myasoedov N.A., Karpicheva I.V., Khalilova L.A., Popova L.G., Balnokina Y.V. Identification of Some Anion Transporter Genes in the Halophyte *Suaeda altissima* (L.) Pall. and their expression under Nitrate Deficiency and Salinity. Russian Journal of Plant Physiology. 2021, Vol.68, No.5, p. 873–882.
- Butnik A., Matyunina T., Duschanova G., Yusupova D. Biological diversity of different ecological types of halophytes. Journal of Arid Land Studies, 2015. V.25-3, p.221-224.
- Duschanova G. M. Structural adaptation of the leaf to xero- and halofactors in some species of the genus *Climacoptera* Botsch. Acta Botanica Hungarica. 2015. V.57(1–2), pp. 29–39. DOI: 10.1556/ABot.57.2015.1–2.6
- Tahmasebi A. Molecular, micromorphological and anatomical study of rangeland species of *Atriplex* (Chenopodiaceae) in Iran. Acta Biologica Szegediensis. 2021. V. 65(2):133-143. DOI:10.14232/abs.2021.2.133-143
- Yuan F., Leng B., Wang B. Progress in Studying Salt Secretion from the Salt Glands in Recrethohalophytes: How Do Plants Secrete Salt? Front. Plant Sci., 2016, V. 7.
- Kadereit G., Mavrodiev E. V., Zacharias E. H., Sukhorukov A.P. Molecular phylogeny of *Atripliceae* (Chenopodioideae, Chenopodiaceae): implications for systematics, biogeography, flower and fruit evolution, and the origin of C4 photosynthesis. American Journal of Botany. 2010. V.97(10): 1664–1687.
- Розенцвет О.А., Нестеров В.Н., Богданова Е.С. Структурные и физиолого-биохимические аспекты солеустойчивости галофитов. Физиология растений, 2017, том 64, № 4, с. 251–265.
- Žerdoner Čalasan, S. Hammen, A.P. Sukhorukov, J.T. McDonald, N.F. Brignone, T. Böhnert, G. Kadereit From continental Asia into the world: Global historical biogeography of the saltbush genus *Atriplex* (Chenopodiaceae, Amaranthaceae). Perspectives in Plant Ecology, Evolution and Systematics, Volume 54. 2022. <https://doi.org/10.1016/j.ppees.2022.125660>.
- Рахманкулова З.Ф., Шуйская Е.В., Воронин П.Ю., Усманов И.Ю. Сравнительное изучение устойчивости С3 и С4 ксеро-галофитов рода *Atriplex* в условиях водного дефицита и засоления// Физиология растений. 2019. Т. 66. С. 112.
- Rakhmankulova Z. F., Shuyskaya E. V., Voronina P. Yu., Usmanov I. Yu. Comparative Study on Resistance of C3 and C4 Xerohalophytes of the Genus *Atriplex* to Water Deficit and Salinity. Russian Journal of Plant Physiology, 2019, Vol. 66, No. 2, pp. 250–258.
- Guan B., Yu J., Chen X., Xie W., Lu Z. Effects of salt stress and nitrogen application on growth and ion accumulation of *Suaeda salsa* plants. Intl. Conf. Remote Sens. Environ. Transport Engin. 2011, pp. 8268-8272.
- Al-Shamsi Naeema, Iftikhar H. M., El-Keblawy A. Physiological responses of the xerohalophyte *Suaeda vermiculata* to salinity in its hyper-arid environment. Flora. 2020. V.273, I.151705. <https://doi.org/10.1016/j.flora.2020.151705>
- Zhu J-K. Salt and drought stress signal transduction in plants. Annual Review of Plant Biology. 2002. V.53, 247–273. doi:10.1146/annurev.arplant.53.091401.143329
- Parida A.K., Das A.B. Salt tolerance and salinity effects on plants: a review. Ecotoxicology and Environmental Safety. 2005. V.60, 324–349. doi:10.1016/j.ecoenv.2004.06.010
- Alla M.M.N., Khedr A.H.A., Serag M.M., Abu-Alnaga A.Z., Nada R.M. Regulation of metabolomics in *Atriplex halimus* growth under salt and drought stress. Plant Growth Regulation. 2012. V.67, 281–304. doi:10.1007/s10725-012-9687-1