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TOLERANCE



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PREFACE

Salinization of soils used in agriculture is one of the most common degradation processes that leads to their desertification, reduced fertility, and exclusion from intensive use. On an international scale, about 25% of all territories are involved in this process. At the same time, the scale of secondary salinization is increasing, which develops most often with improper irrigation. It is predicted that the salinization process will reduce the amount needed for cultivation by 30% in the next 25 years, and by 50% by 2050.

Soil salinization causes significant damage to agricultural production. In Ukraine, these soils occupy an area of 1.92 million hectares, of which 1.71 million hectares are used for agriculture. In Ukraine, more than 20% of irrigated areas are already saline.

The negative effect of salinity on plants is closely related to the development of water deficit, disruption of ion homeostasis, and the toxic effect of ions. All this leads to a decrease in growth, productivity, and ultimately to a decrease in the productivity of cultivated plants. Salt stress is usually accompanied by water stress, since, unlike soleras, other plants are very poorly adapted to the use of absorbed NaCl as a substance capable of counteracting the high osmotic potential of the soil under salinity conditions. Halophytes are ecologically, physiologically, and biochemically specialized plants capable of functioning and producing normally in saline environments and saline irrigation.

There are different classifications of saline soils, depending on the intensity and quality of salinization. At the same time, the following types of soils are distinguished: salt marshes, highly, medium and slightly saline salt marshes and salt marshes. Depending on the predominant accumulation of individual ions, salinity is divided into sulfate, chloride, sodium or mixed, carbonate-magnesium and chloride-magnesium. All the processes that occur in plants are the result of

PREFACE

their exposure to several salts at once, because there are practically no salts in their pure form in the soil. The most common under salinization is inhibition of plant growth by sodium and chlorine ions.

Primary or physical salinization occurs due to the natural and long-term accumulation of salts in the soil or in surface waters. This process is mainly caused by the weathering of soluble ions Cl^- , Na^+ , Ca^{2+} and Mg^{2+} , and sometimes SO_4^{2-} and CO_3^{2-} from parent rocks. Secondary salinization occurs as a result of improper irrigation. In many irrigated areas, the groundwater level is rising due to excessive use of water with insufficient drainage. In addition, saline groundwater can contribute to salinization. The reasons for soil salinization are different: initial salinization of the parent rock, use of salty water in agricultural production, low rainfall and high evaporation intensity.

Most plants, primarily cultivated, are glycophytes. The resistance mechanisms of halophytes are constitutive, and those of glycophytes are inducible, that is, they are realized only under the influence of factors. There is a significant complex of genes that control plant responses to salinity, but due to the complexity of their regulation, it is quite difficult to increase salt tolerance with the help of classical breeding methods. The following take an active part in the reaction of plants to salinity: 1) genes encoding enzymes that participate in the synthesis of osmotic and other protectors; 2) regulatory genes controlling the development of the stress response; 3) genes regulating the level of phytohormones; 4) genes of response to oxidative stress; 5) genes of molecular chaperones; 6) genes encoding ion transport proteins.

CHAPTER 1. ECOLOGICAL MANAGEMENT OF ASSESSMENT OF SALINE SOILS

The salt state has a noticeable effect on the general ecological condition of the soil, including physical and water properties. Physical properties, processes of moisture, air and heat transfer in saline soils have their own specificity. Which is fundamentally different from the processes in non-saline soils. Taking into account the real spread of saline soils, there is a need for their more objective ecological assessment, which involves properties and features. It was established that with the increase in soil salinity at the landscape level, there is a change in the physical properties of the soil, which determine the productivity of agrocenoses and the ecological functions of the soil, as well as the humus state, in addition, salinity leads to inhibition of growth processes, a decrease in seed germination and germination [Fedotova, Yakovleva, 2012].

Depending on the composition of salts in the soil, there are several main types of salinization: chloride - caused by an excess of sodium chloride and magnesium chloride (NaCl , MgCl_2) in the soil; sulfate - due to the accumulation of sodium sulfate and magnesium sulfate (MgSO_4 , CaSO_4 , Na_2SO_4); sodium (carbonate) - associated with the presence of an increased amount of sodium bicarbonate or other sodium salts (NaHCO_3 , Na_2CO_3) in the soil [Gospodarenko, 2018].

Soil salinization in the south of central Siberia is related to the peculiarities of geology, hydrogeology, climate and topography. The relief of this region is mountain-basin, which determines the structure of the soil cover of the territory. The height of the Tiva basin is 700 meters, and that of Khakassia is 300-500 meters. Saline soils are limited to zones of geochemical flow - intermountain depressions, more often they lie in river valleys, on the first floodplain terraces, around salt lakes, and sometimes at watersheds. As one approaches the center of

the intermountain depressions, the temperature increases and the air and soil humidity decreases, which leads to the development of concentric landscape zoning in the depressions. And this, in turn, determines the ring arrangement of soils - from brown semi-desert-steppe and chestnut in the center of hollows in the semi-desert zone; chestnut and southern chernozems in the steppe zone through ordinary and leached chernozems to gray forest soils in the foothills of the depressions. The southernmost part of the studied territory – the Ubsunur basin is located in the arid region of Central Asia. Despite the arid climate, saline soils are not widespread here [Chernousenko, 2008]. The analysis of soil salinity in the administrative units of the Ural Federal District showed that saline soils are most widespread in the Kurgan region, followed by Tyumen, Chelyabinsk, Sverdlovsk regions and the Yamalo-Nenets Autonomous District [Chernousenko, Kalinina, 2011].

The analysis of the distribution of easily soluble salts in the eastern part of the Volga River delta makes it possible to predict that the investigated soils of the natural landscape are undergoing salt migration processes, which is accompanied by long-term salinization and then desalination, which was manifested in the formation of their salt profile. The intermittency of salinization and desalination revealed by the analysis of the water extraction testifies to the fact that in the studied territory, the lowering of the base of erosion, the beginning of dismemberment and drainage of the area and the subsequent lowering of the groundwater level alternate with its rise. Violation of the natural water regime led to a high content of chloride ions on the surface of the altered deltaic landscape in the southwest of the Astrakhan region. Analysis of topoisopleths showed that the content of chloride ions in the surface layer varies widely from 0.1 to 30.2 mmol/100 g of soil. The supply of these soils with water occurs only due to episodic autumn and summer rains and in the spring when the snow melts, which does not contribute to the movement of this ion to a greater depth. A differentiated distribution of chloride ions is observed with depth. The presence of shallow

drainage channels in this area led to the concentration of soil solutions and the creation of a barrier for the movement of less mobile and less soluble ions, which confirms the relative stability of salinization processes in this landscape [Yakovleva, Fedotova, 2012].

A comparison of the ionic composition of water extracts from soil samples in the Volga delta showed that after 1981 there was a sharp decrease in the content of water-soluble salts by 30%, especially toxic ions of sodium and chlorine. As a result of analyzes carried out from 1979 to 2006 on 126 soil samples, the Cl/SO_4 ratio decreased by a factor of 2, from 0.6 to 0.3. If the decrease in the total amount of salts in the low-level meadows can be attributed to the washing effect of spring-summer floods, then the decrease in salts in the meadows can be explained by the increase in the amount of precipitation [Barmin, Iolin, 2008].

An assessment of changes in salt characteristics of originally automorphic chernozems under the influence of mature forest strips in the Stone Steppe was carried out. The soil cover is represented by a mottling of typical, ordinary, leached, zooturbated chernozems and their arable analogues. Accumulations of salts at a depth of 1.5-2 meters corresponding to a weak degree of salinity were found in chernozems under forest belts. Adjacent arable land has no signs of pulling sodium salts along the entire profile. Accumulations of salts are timed exactly to the territory of the forest belt. There is a sharp decrease in the concentration of salts on the edges of the forests. In other words, the current accumulation of salts in the lower horizons of chernozems is due to the use of groundwater by mature trees for transpiration [Cheverdin et al., 2012].

In the saline soils of the Kura-Araksin lowland in Azerbaijan, with a low content of humic acids, the non-hydrolyzed residue, which reaches 86-97%, prevails quantitatively. The presence of sodium in the absorbing complex contributes to the destruction of humic acids and their transfer into more mobile forms, as a result, humic acids and fulvic acids form soluble salts with alkaline and alkaline earth metals. In addition, the sodium cation reduces the condensation

of the aromatic carbon of humic acids. In order to develop these soils and improve the humus condition, it is necessary to carry out complex land reclamation projects, which also include the creation of cultural coenoses-agrocoenoses under various agricultural crops [Alieva, 2012].

The conducted studies on the gray earth-meadow saline soils of natural coenoses revealed significant changes in the vegetation cover. The prevailing vegetation was holophytic, although some rarefaction was noted in its composition. Herbaceous vegetation (composite, cruciferous, sedges, legumes) is found sporadically, which confirms the gradual change of the meadow soil formation process to the steppe one. The composition of the soil biota, which is represented mainly by desert lichens and some types of insects, also changes significantly. With such a weakly expressed saprophytic complex, phytomass decomposition (990.4 g/m^2 raw, 480 g/m^2 dry) is carried out extremely slowly with an average monthly amount of 0.250 g of above-ground and 0.225 g of root residues. And therefore, when studying the processes of soil salinization, it is necessary to attach great importance to the ecological relationship between plants and saline soil [Alieva, Samedov, 2012].

The leaching of salts from the upper horizons to deeper horizons is accompanied by a change in the salt composition. In the composition of these salts, the share of calcium sulfates increases, which contributes to the suppression of saline properties due to the formation of gypsum. Different features serve to distinguish the gray earth-meadow soils of the Salyan Steppe in Azerbaijan as solonets, such as the compaction and prismatic nature of the soil horizon, the dispersion of the soil mass, which is accompanied by coalescence. Among the chemical features, high alkalinity and the presence of sodium in the absorbing complex are noted. The absorbed bases include calcium and magnesium, and the sodium content can reach 10-17%, and sometimes up to 20%. Groundwater is located at a depth of 1.8-3 meters and, as a result of evaporation, salts enter the upper horizons, causing their salinization [Sadikhova, 2012]. The growth of plants

is quite strongly inhibited by the combination of factors of salinity and acidic pH of the root medium, which can be connected not only with the effect of NaCl and the acidity of the medium, but also with the additional negative effect of toxic soil cations, such as Al^{3+} and Mn^{2+} [Shavrukov, Hirai, 2016].

Modern global climate changes are able to reveal a significant impact on the soil-geochemical processes of sub-arid and arid territories and on their water-salt regime. In the southern regions of Western Siberia, with insufficient precipitation, saline soils, salt marshes and salt marshes, salty and bitter-salty lakes are a fairly common phenomenon. The projected aridization of the climate and the accumulation of salts in the soil are considered as risk factors that can cause qualitative shifts or even transformation of landscape-geochemical combined systems of the most diverse hierarchical level. Integral indicators of soil gas exchange, which also include the rate of carbon dioxide emission, in a known sense characterize the functional state of a rather complex natural system. The conducted observations showed that the release of carbon dioxide by the soils of combined landscape-geochemical systems naturally decreases in the direction from the eluvial position to the transaccumulative and accumulative one. The range of changes of this indicator was characterized by values from 110 to 750 $\text{mg CO}_2/\text{m}^2\cdot\text{h}$. The contribution of the above-ground part of plants to the total flow was 30-50% in steppe and forb-meadow combinations. In areas with sparse vegetation, the measured flows differed by 20-50%. In the coastal zone, among the salt marshes, the release of carbon dioxide was the lowest. It is assumed that the source of carbon dioxide here can be both biological and physicochemical processes [Naumov, 2012].

A significant change in soil and hydrological conditions in the northern Caspian Sea in the 80s of the 20th century, associated with a significant rise in the groundwater level, which amounted to an average of 2 meters, was also revealed. This rise could have been facilitated by an increase in atmospheric moisture by about 20%, compared to the same century. It is quite likely that this phenomenon

has a reverse nature and represents one of the many cycles of the revival of the nature of this territory. In the 80s of the 20th century, quite large-scale irrigation and irrigation projects could also have a certain influence. The rise in the level of groundwater under pristine soils has caused an increase in their mineralization over the past 50 years (on average, 5 times under meadow-chestnut soils and 1.2 times under salt marshes) and equalization of their chemical composition: they become chloride-sulfate-sodium. Over the last 50 years, in virgin salt marshes, there has been a significant increase in chlorine ion reserves in the 50-500 cm layer and a decrease in sulfate ions in the 100-250 cm layer, sodium ions in the 100-200 cm layer, calcium ions in the 150-200 cm layer, and accumulation of magnesium ions in the 0-100 cm layer. From an ecological point of view, the progressive salinization of groundwater under all members of the soil salt complex, the accumulation of the most toxic chlorine in the composition of easily soluble salts, the reduction of the aeration zone by an average of 2 meters, significantly worsen the soil and hydrological situation [Sizemskaya, 2012].

Currently, in the territory of the Republic of Bashkortostan, the process of salinization and salinization can develop in different genetic types of soils when oil industry wastewater and soda ash production effluents get into them. Such soils, while preserving the properties characteristic of their genetic type, acquire the features of saline soils, which is manifested in both morphological and chemical properties. Morphologically, the changes are expressed in the formation of highly compacted solontic horizons with a columnar and straight structure, some lightening of humus-accumulative horizons, and in a wet state, these soils swell, become viscous, sticky, and water permeability decreases [Suleymanov, 2011].

It has also been shown that humates activate the metabolism and reproduction of useful soil microflora, increase the defense mechanism of plants against adverse physical (temperature changes), chemical (salinity, heavy metals,

radionuclides) and biological (fungal, bacterial and viral diseases) factors and contribute to the formation high yield of cultivated plants [Shamardyna, 2006].

It was established that natural and anthropogenic desertification of soil cover in plain Dagestan has identical forms of manifestation, but differs in scale and intensity. Anthropological desertification is much more intense, compared to natural. In the last 50 years of the last century, it doubled in the Tersk-Kum lowland, and in the last 10 years of the current century, a trend of regional dynamics caused by climate warming, pasture overloads and changes in the level of the Caspian Sea is revealed. Climate warming contributes to the aridization of the territory, during the regressive phases of the sea, the scale of degradation decreases in the coastal areas directly affected by the sea, as well as desertification in the areas indirectly affected by the sea. Degradational changes in the soil cover in the Tersk-Kum lowland indicate the need for an immediate reduction in grazing loads; on meadows and typical salt marshes, it is not allowed to lose less than 30% of the projective surface coverage by halophytes; expedient sowing of halophytes and other salt-resistant plants; fixing ravines, shifting sands and limiting the growth of unnecessary dirt roads [Stasiuk et al., 2012].

In laboratory conditions, the hysteresis of the dependence of the full water potential on soil moisture in the range of moisture from the limiting field moisture capacity to the wilting moisture was investigated. The soil of the Volga River delta – a brown semi-desert salt marsh – served as the object of the study. According to the chemistry of salinization, the studied soils belong to the chloride-sulfate type. The content of easily soluble salts in the brown semi-desert soil increases from 0.28% in the surface horizon B to 2.22% in the transition to the BC rock. In the salt marsh, the maximum of salts in the upper part of the profile is 2.28-2.22%. The concentration of salts increases the sorption capacity of the studied soils. These soils have pronounced hysteresis. Its value in brown semi-desert soils ranges from 3.5 to 5.1 cm^3/cm^3 along the profile at a water potential

of 980 j/kg. When the potential of water increases to 31 j/kg, the value of hysteresis changes from 7.2 to 10.3 cm³/cm³ [Koreneva, Shvarov, 2008].

At present, a hydromorphic mode of moistening of these soils has formed in the vast majority of massifs of saline soils in Uzbekistan. At the same time, there were quantitative and qualitative changes in the direction of water-physical, chemical and other processes in the "groundwater - soil" system. Changes in the capacity of the soil-absorbing complex and the resulting chemical and water-physical properties of soils were noted. A slow but steady increase in the number of sodium cations over time is observed. Thus, with the sodium content in the absorbing complex of newly developed meadow soils (Khorezm region) in 12.8-21.8%, in irrigated soils it was 34.9-43.7%, and in swamp-meadow soils it ranged from 20.4- 35.3% of the capacity [Ramazanov, Akhatov, 2008].

Man-made soil salinization is a fairly common phenomenon where oil is extracted. Wear and tear of pipelines occurs during the transportation of oil and highly mineralized reservoir waters. Oil companies are not responsible for man-made salinization. Agricultural enterprises remain unprotected in this respect. Having man-made saline lands, they bear losses and losses, as there is no compensation for losses in connection with the removal of saline areas from the structure of land use and agricultural lands [Abaturova, 2008].

Peculiarities of the humus condition of the soils of the chestnut-saline complexes are quite closely related to their formation in the dry steppe zone. They are characterized by an increased content of humus in the upper horizons and its gradual decrease with depth. It should be noted that meadow-chestnut soils are more humus-rich than chestnut soils, which is due to the formation of these soils in low relief elements, in conditions of increased moisture and during the development of meadow phytocenoses. Thus, the development of salinity in chestnut soils contributes to the formation of the humic-fulvate type of humus, as well as the formation of stable fractions of humic and fulvic acids bound to the

mineral part of the soil in the composition of humus [Ilyina, Nevydomskaya, 2008].

The patterns of distribution and taxonomic structure of complexes of halophilic, alkalophilic and haloalkalophilic actinomycetes in a wide range of saline soils located in the territories of Russia and Mongolia were revealed. The number of actinomycetes in saline soils ranges from hundreds of colony-forming units to tens of thousands of CFU/g of soil, depending on the type of soil, and is 3-4 orders of magnitude lower than the number of mycelial bacteria in sod-podzolic soil and chernozem. Representatives of the genera *Streptomyces* and *Micromonospora* were found among haloalkalophilic actinomycetes. Micromonosporae show less adaptability to existence at high salt concentration than streptomycetes. Haloalkalophilic streptomycetes, identified according to phenotypic and genetic properties as *Streptomyces pluricolorescens*, *Streptomyces prunicolor*, were dominant in the studied soils. The growth of colonies of these cultures was noted at a 5% concentration of sodium chloride and a pH value of 8.0 [Zvyagintsev et al., 2008].

Secondary salt flats in the Volga delta are formed on brown arid soils, which have a specific character and are always carbonate. The type of salinity is sulfate-sodium with SO_4 values of 1.50 mg/eq. per 100 g of soil, HCO_3 1.25 mg/eq. per 100 g of soil. The floristic complex combines features of meadow vegetation with halophytic admixtures: *Petrosimonia brachiata*, *Petrosimonia oppositifolia*, *Eremopyrum orientale*, *Eremopyrum triticeum*, *Suaeda crassa*, *Camphorosma monspeliaca*, *Prangos odontalgica*. Therefore, secondary salt marshes are characterized by a minimum indicator of the total microbial biological mass and a different distribution of the components of the microbial combination in contrast to other soils of the Volga delta [Salnikova, Salnikov, 2008].

Secondary salinization is one of the most urgent problems that is developing quite quickly in agriculture, soil science and soil reclamation. In the

conditions of an arid climate, the spread of the process of secondary salinization is deepened by the specificity of the land use of the region, and more precisely by the use of various means of irrigation, both drip and sprinkler. All this, in combination with the leachate water regime and complete rejection of the use of reclaimed agricultural land, leads to a significant increase in the areas directly exposed to the process of secondary salinization and areas of potential spread of this process. This process involves not only the soils of abandoned agricultural lands, but also the soils of natural ecosystems, due to the dynamically growing anthropogenic load on these territories in recent times [Sorokin et al., 2011].

One of the methods of rational use of saline soils is the cultivation of salt-resistant species and varieties of agricultural crops. To search for salt-resistant genotypes, the researcher needs new methods with a large throughput. For this, the method of extracting elements from a leaf, which is used abroad, was used. The results of the conducted experiment reliably reveal the relationship between the concentration of the soil solution, expressed in its osmotic pressure, the growth indicators of spring wheat in phase 2 of the leaf and the entry of salinizing and nutrient elements into the plant [Kosareva et al., 2008].

The salinity of the gray-brown desert soils of the foothills of the Southern Tien Shan varies quite a lot: the soils can be both weakly and fairly strongly saline. The degree of soil salinity is closely related to the position relative to Lake Ebi-Nur and is maximum in the area of intensive sedimentation of saline eologous material coming from the dried-up bottom of the lake. The chemistry of soil salinization is extremely varied - sulfate, chloride-sulfate, sulfate-chloride, and chloride, but as you move away from the lake, there is a decrease in the proportion of chlorides in the composition of salts in the soil, as well as in the dust. The close dependence of the degree and chemistry of soil salinization on the position relative to the lake allows us to draw conclusions about the determining role of the aeolian factor in soil salinization of the foothill plain of the studied region [Gorbunova et al., 2008].

The only real source for the formation of salt profiles of barrow mounds is the salts of atmospheric precipitation. Mound embankments and grave soils represent a single ion-salt system, the functioning of which is accompanied by the transformation of the ion-salt profile of grave soils regardless of the height of the embankment [Senkov, 2008].

A general analysis of the geography of saline soils showed that the most general regularity between the permafrost and salinity of the soils of Russia from west to east is their mirror ratio, which forms a kind of halocryogenic "Russian cross" in space [Fomynykh, Zolotareva, 2008].

On the example of permafrost fawn soils of central Yakutia and using CuCl_2 reagent as a marker, it was determined that the main amount of trace elements in this type of soil accumulates in the permafrost horizon. As a result of the study of the salinization process, changes in the microelement composition were monitored, and a supra-permafrost horizon of accumulation was detected, as a result of which it is possible to predict with a high degree of probability that in the case of secondary salinization of the investigated soil area, there will be an increase in the pollution of the internal soil runoff, since the permafrost serves as a water barrier [Dyagyleva, Legostaeva, 2015].

The seasonal dynamics and accumulation of salts in the Tersk-Kum lowland illustrates the stable character of the dry period of the year and its dominant position in the formation of the salt regime and processes of salt accumulation. The higher stage of salt accumulation and the strengthening of migration processes contributes to the formation of the halogen-active part of the profile, as a leading factor in the regressive evolution of the soils of the Caspian lowland [Islamgereeva et al., 2008].

It is believed that the silty sulphide muds of the mineral lakes of the lower Volga region can be classified as salt marshes. They are formed under the same conditions, have the same sources of salinity, contain a large amount of salts, and the same chemical processes occur in them [Pshtaeva, 2008].

As the quality of irrigation water deteriorates, even in the presence of a flushing water regime, the degree of danger of the development of processes of general salinization, sodium, and especially magnesium salinization increases with a low degree of initial soil salinity. The washing nature of the water regime in the conditions of the heavy loamy composition of the ordinary chernozems of the High Sirte does not ensure the preservation of a favorable salt regime of the soil and cannot serve as a means of preserving the high fertility of the soil under irrigation. As the mineralization of irrigation water increases and its composition deteriorates, the removal of calcium from the soil-absorbing complex is followed by its replacement by sodium and magnesium, which leads to the development of sodium and magnesium salinization of soils [Bezdina, Ovchinnikova, 2008].

The results of the study showed that during 1 year of cultivation of a perennial herbaceous plant of the legume family of bare licorice (*Glycyrrhiza glabra* L.), depending on the level of moisture, desalination of a meter-long soil horizon occurs by 15-22%. The removal of salts from the soil is related to the level of their content in the oblique mass, the presence of dry matter, the size of the harvest, which is in the range from 13.9 to 74.8 kg/ha. A positive factor is also the fact that licorice plants leave a significant amount of nutrients and root residues in the arable layer of the soil, improve the water-physical, agrochemical properties of the soil, increase its biological activity and humus content [Chaplanova et al., 2008].

The area for growing sorghum crops due to the aridization of the climate is constantly growing, and in agricultural technologies, the possibility of these crops to eliminate the processes of destructive transformation of agricultural landscapes and increase the resource potential of the soil cover should be taken into account [Belousov, Shvets, 2010].

A hypothesis is proposed about the physiological role of Cl^-/H^+ -antiporter in soil salinization. Under these conditions, chlorine ions can enter the cells along the electrochemical potential gradient. It is assumed that Cl^-/H^+ -antiporter exports

chlorine from the cytoplasm. This function is probably most pronounced in halophytes. In addition, the removal of chlorine ions from the cytoplasm into the medium or into the vacuole in exchange for a hydrogen ion leads to membrane depolarization, which reduces the driving force for the entry of sodium ions into the cytoplasm and accelerates the work of H^+ -ATPase. The consequence of this is an increase in $(\Delta)pH$ on the membrane, which stimulates the Na^+/H^+ -antiporter and increases the export of sodium ions from the cytoplasm [Balnokin et al., 2011].

Saline soils are formed on alluvial deposits. According to the morphological structure, meadow soils are characterized by a strong humus horizon, turfiness, lumpy-granular structure, strong moisture and glaciation. In meadow sweetened soils in the lower part of the humus horizon there is a whitish powder. According to the chemical composition, the content of humus is high (5.1-15.0%), the reaction is weakly alkaline ($pH = 7.2$). The dense residue is 0.4-0.7%. The content of calcium and magnesium in the soil-absorbing complex is high, while it decreases in profile [Samoylova, 2014].

In modern conditions, where karyzas fail, insufficient drainage outflow begins, even with excessive irrigation, groundwater rises, which leads to secondary salinization or even waterlogging of the soil. Both of these sharply reduce soil fertility, and lands that have undergone secondary salinization are already in the stage of various salt marshes, especially common on the periphery of irrigated lands, where karyzas used to operate [Guliyev, 2011].

In order to improve lands with an unsatisfactory reclamation state, it is recommended to install a collector-drainage network on lands with an unacceptable depth of the groundwater level to lower the groundwater level and divert excess irrigation water and atmospheric precipitation. On saline lands, it is recommended to carry out salt-regulating chemical land reclamation, consisting in the application of mineral fertilizers and plastering of the soil. It is also recommended to carry out deep loosening in order to reduce the intensity of salt

pulling processes from the lower lithological horizons [Lopatovskaya, Sugachenko, 2011].

Siderates (vegetative mass of agricultural crops – green fertilizers) and phytomeliorants (salt-tolerant agricultural crops) have a positive effect on the physical, physico-chemical, nutritional and biological properties of saline soils. Siderates are an important source of replenishment of organic matter in the soil. They prevent soil erosion and degradation, improve its structural indicators, air and water regimes, are regulators of soil microbiological processes, stimulating the reproduction of soil microorganisms. Among phytomeliorants, burkun tolerates soil salinity much better than other crops. The root system of this plant penetrates deeply into the illuvial horizon of the solonchok soil, loosens it, creating conditions for the leaching of easily soluble salts from the upper horizons. Improvement of the properties of saline soils is also facilitated by deep plowing, application of fertilizers, introduction of up to 20-25% of perennial grasses in crop rotation, rotation of crops in crop rotation, sowing of leguminous crops, etc. [Kisorets, Dychkovska, 2012].

One of the main ways to increase the fertility of saline soils is the use of nitrogen-fixing microorganisms. A salt-tolerant strain of the genus *Rhizobium* grows well on known solid nutrient media. Bacteria of the salt-resistant strain are rod-shaped, motile at a young age, monotrichous, gram-negative, and slow-growing. The size of the cells of a five-day culture on medium No. 79 is 1.5-2.5×0.8-1.0 μm. A stroke on medium No. 79 is abundant, mucous, white. Colonies appear on 5-7 days, small, uniform, 0.8-1.0 mm, round, convex, white, mucous. When inoculated with these drugs from nodule bacteria, changes in some productive signs of plants occur. The use of microbial biotechnology opens up new perspectives for the creation of waste-free and low-waste disposal technologies [Bakahonova, 2012].

In arid areas, specific cyanobacterial communities develop, which are resistant to high temperatures, high salinity, light intensity, drying, ultraviolet

radiation and other negative factors. Cyanobacterial groups are isolated when using the method of mass cultures. As a rule, cyanobacteria of the genera *Phormidium*, *Anabaena*, *Nostoc*, and *Oscillatoria* are the dominant form of structure-formers of these groups [Bataeva, 2012].

CHAPTER 2. ECOLOGICAL MANAGEMENT, ANATOMICAL-MORPHOLOGICAL AND PHYSIOLOGICAL-BIOCHEMICAL MECHANISMS OF PLANT RESISTANCE

Salt stress significantly affects the complex of morphological and physiological-biochemical indicators [Zakharin, 1990; Goncharova, 2011b]. The toxic effect of salinity is associated with the accumulation of excess ions in cells, an increase in osmotic pressure, competition of sodium ions with potassium and calcium ions [Azimov, 1974; Lynch et al., 1988; Vidal et al., 1990]. Salinity causes osmotic stress in plants; the toxic effect associated with the excess content of inorganic ions, especially sodium and chlorine, is revealed; causes ionic imbalance and oxidative stress, reduces the supply of nutrients that stimulate growth and development. All these factors lead to disruption of cellular metabolism [Kostiuk et al., 1994; Chirkova, 2002; Bhaskar and Bingru, 2014]. Plants are able to one degree or another to maintain ion homeostasis, which is one of the factors of their stability [Yasar et al., 2006, Balnokin, 2012, Ivanova et al., 2014]. At the same time, it has been shown that differences in morphological and anatomical features are associated with the presence or absence of salt glands on the leaves, the type of leaf structure – xeromorphic, succulent, or the existence of chlorenchyma cells in certain species of Kranz anatomy [Voznesenskaya et al., 2007].

The main reason that stimulates the inhibition of plant growth under salt stress, in addition to a decrease in water potential, is an excess of sodium ions, which are absolutely not needed by glycophytes for normal growth and development [Greenway, Munns, 1980, Niu et al., 1995].

When the medium is salted with sodium chloride, ultrastructural changes were observed in the cells of the periplasm. The nature and degree of these changes depended on the salt concentration. Changes in the structure of the

nucleus were noted in the experimental variants. Under the influence of 0.2 M NaCl, the expansion of the perinuclear space and the undulation of the contour of the nuclear envelope were observed, in addition, nuclei of a non-typical, disk-like shape were found. In isolated cases, a sharp compression of the nucleoli and isolation of the fibrillar and granular zones was noted, which may indicate macrosegregation of the components of the nucleolus. At the same time, fibrillar oxyphilic zones were located on the periphery of the nucleoli. Under the action of salinization, microstructural changes of mitochondria were observed, which were expressed in a decrease in the electron density of the matrix substance, and the cristae had expanded intracristal spaces [Lutsenko, Galaktionova, 2013].

Adaptation of plants to new conditions of the surrounding environment is achieved due to modification and genotypic variability, that is, by restructuring the entire complex of morphoanatomical and physiological-biochemical features of the plant itself in ontogenesis and the formation of new norms of reactions in phylogeny. If, with the help of modification variability, plants adapt to those environmental conditions that are most significant in the process of their individual development, then the genotypic flexibility of the population and selection ensure adaptation to long-term changes in environmental factors [Zhuchenko, 1988, 2000].

During salt stress, physiological and biochemical processes in plants change, that is, there is a violation of water and ion homeostasis, both at the cellular level and at the level of the whole plant [Volkmar et al., 1998]. As a result, seed germination and growth are inhibited, which in general contributes to a decrease in plant productivity. The negative effect of salinity on seed germination can be manifested in a decrease in the osmotic potential of the environment, which inhibits the ingress of water into the seeds, necessary for the mobilization of nutrients, or in a toxic concentration of salt ions [Said-Al Ahl, Omer, 2011]. These factors lead to the slowing down or stopping of the mobilization of nutrient elements, the inhibition of cell division, and the extension of injury to the

hypocotyl of seedlings [Rahman et al., 2008]. Growth, as a multifactorial process, largely depends on hormones, against the background of salinity is suppressed to a greater extent than the reaction of anabolism. The salt resistance of corn depends strongly on the properties of the genome of individual hybrids and varieties, which is manifested at the initial stages of development [Omelchenko, Kabuzenko, 2013].

Under the influence of salinity, the diameter of the conducting bundles of the leaf blade decreases. The sizes of the conducting bundles directly depend on the diameters of the xylem vessels. And therefore, the reduction in the diameter of the conducting bundles is directly related to the reduction in the area of xylem vessels, which in turn, as conducting elements, quite clearly respond to the conduction of various substances with changes in diameter, that is, a decrease. Accordingly, the concentration of sodium salts in such a volume inhibits the conduction of water with substances dissolved in it [Ortega et al., 2006]. The ratio of the thickness of the exoderm to the thickness of the endoderm is a rather important indicator of plant resistance. The higher this value, the higher the plants' resistance to salinity. The increase in the thickness of the exoderm is an indicator of adaptive plants against this stress [Singh, Prasad, 2009, Gomes et al., 2011].

Wheat varieties were screened for resistance to NaCl based on growth indicators and the anatomical structure of leaves and roots under salinity conditions. For this, plants were grown for 7 days in solutions containing different concentrations of NaCl: control, 50 mM NaCl; 100 mM NaCl. The study of the morphometric indicators of the leaf plate showed that the thickness of the lower and upper epidermis under the influence of NaCl in some species decreases, compared to the control. Under the action of 100 mM NaCl, the thickness of the lower and upper epidermis decreases to the greatest extent in the Melturn variety, and to the least extent – Kazakhstan-3, Chagala and Kaiyr. According to the decrease of these indicators at 100 mM NaCl, the varieties are arranged as follows (in % to the control): according to the thickness of the lower epidermis - Chagala

(96%) > Kazakhstan-3 (94%) > Kazakhstan early (89%) > Kayyr (87%) > Melturn (49%); by the thickness of the upper epidermis - Kazakhstan-3 (96%) > Kayyr (90%) > Chagala (84%) > Kazakhstan early (79%) > Melturn (77%). The diameter of the conducting bundles under the influence of 100 mM NaCl decreased in the following sequence: Kayyr (100%) = Kazakhstan-3 (84%) = Shagala (84%) > Kazakhstan early (80%) > Melturn (53%) [Atabaeva et al. , 2013].

Osmotic stress in plants also causes a deficiency of nutrients as a result of the competition of Na⁺ and Cl⁻ ions with K⁺, Ca²⁺ and NO₃⁻ ions [Luo et al., 2005]. The ratio of K⁺/Na⁺ ions undergoes a strong change in plant tissues during sodium chloride salinization [Volkmar et al., 1998]. Sodium ions also inhibit the work of enzymes of protein and carbohydrate metabolism [Wahid et al., 1999]. The toxic effect of sodium and chlorine ions in plants is manifested in the disintegration of membranes, a decrease in the activity of enzyme systems connected to membranes, which in turn reduces photo- and oxidative phosphorylation and the efficiency of energy processes [Zeid, 2011]. Also, the proliferative activity of the roots decreases [Wang, 2009]. In addition, the processes of absorption, transport and distribution of mineral elements in plant tissues are disturbed [Manivannan et al., 2008]. At the same time, it has been shown that the permeability of cell membranes is an early indicator of changes in the physiological state of cells, and it allows to give a comparative assessment of the resistance of plants against stressors [Aroslankina et al., 2011].

The actin cytoskeleton is a dynamic network consisting of actin microfilaments, both individual and assembled into dense bundles, in which constant processes of synthesis and decomposition of components take place. The putative role of actin cytoskeleton rearrangements in the creation of a plant resistance mechanism against abiotic stresses. It was established that the effect of salt stress during a 12-hour exposure to 150 mM or 250 mM NaCl leads to an increase in the amount of polymeric actin and an increase in the diameter of

filament bundles in epidermal cells of *Arabidopsis* leaves and roots. After 18 hours of 150 mM NaCl, the organization of the actin cytoskeleton was preserved, while at 250 mM NaCl, actin filaments disintegrated and the seedlings died. And the addition of 1.5 μ M phalloidin, a peptide that stabilizes actin filaments, saved seedlings from death under salt stress, and the addition of 1 μ M latrunculin, a substance that prevents actin polymerization, only increased salt stress [Wang et al., 2010]. A hypothetical model was proposed that links the rearrangements of the actin cytoskeleton with other early physiological processes induced by salt stress in plant cells [Pozhvanov et al., 2015].

It was found that the growth of crystal grass plants (*Mesembryanthemum crystallinum* L.) on a medium containing 400 mM NaCl led to a change in the amount of actin in the sediment fractions obtained by centrifugation of the root homogenate at 15,000 and 100,000 g. A noticeable increase in the amount of actin occurred already after 3 hours of salinization, and the highest degree of growth was reached after 6 hours of exposure to NaCl, after 3 days the amount of polymeric actin was already significantly lower than the control [Kulikova, Kuznetsova, 2014]. In the leaves of control plants *Mesembryanthemum crystallinum* L., relatively high concentrations of zeatin, isopentenyladenine and free form of IOC were detected. At the same time, the level of zeatin riboside and ABA was extremely low. Salinity of the medium for 6 hours led to a certain increase in the content of zeatin and bound IOC by approximately 1.5 times. The level of isopentenyladenine and the free form of IOC decreased sharply, ten times, and the level of zeatin riboside and ABA increased sharply [Vedenicheva et al., 2010].

Of all organismic stability mechanisms, unequivocal relationships have been established only for the mass of the root system [Vedrov, 1984; Nikulin, Lyashok, 1990]. This is evidenced by the success achieved in the selection of plants along the length of the root system [Zimnytskyi, 1991].

Salt stress is accompanied by osmotic stress and leads to a loss of cell turgor. Osmoregulation can be carried out thanks to the compartmentalization of sodium, potassium and some other ions during the formation of plants' own organic osmotic agents, which can ensure the appropriate intracellular concentration of osmotically active substances necessary for maintaining water transport in plants [Sidorov, 1990]. Compartmentalization of ions in the vacuole, which leads to a normal osmotic pressure in the cytoplasm, is accepted as a model of the cellular response to salt stress. Salt compartmentation in the vacuole is accompanied by the accumulation of osmotically active organic matter in the cytosol [Babaeva et al., 1968; Kulaeva, 1997; Asimov, 2013].

In the mechanisms of salt resistance, it is necessary to distinguish between the direct effect of an excess of salinizing ions on the plant [Cheeseman, 1988] and a change in the water-physical and mineral regime under the influence of an excess of salts in the soil solution [Gardner, 1967].

It was found that representatives of synanthropic vegetation growing in conditions of man-made chloride-sodium salinization differed significantly in the accumulation of free chlorine and sodium ions. *Triglochium maritima* was characterized by a high concentration of free chlorine and sodium ions in the leaves. *Tussilago farfara* and *Plantago media* concentrated more chlorine ions than sodium ions. The concentration of proline in leaves and roots was many times higher than that of mother-and-stepmother and plantain. However, it was shown that plantain contained the least amount of proline. The studied plants did not differ among themselves in the redox activity of leaves and roots [Botalova, 2014].

Against the background of salinity, the depression of plant growth is caused by a decrease in the content of gibberellin-like growth stimulants in the tissues, which leads to inhibition of the processes of cell division and stretching [Synelnikova et al., 1972; Orton, 1980; Synelnikova, 1981; Kuiper et al., 1988; Lynch et al., 1988]. The phenomenon of increased concentration of sugars in cells

[Gushchyn, 1938], amino acids and ammonia nitrogen [Lapina, 1967], and polypeptides [Prykhodko et al., 1981, Hurkman et al., 1988] can be explained by the anticipation of growth inhibition, compared to inhibition of synthetic processes. The rather important role of glutathione and enzymes that catalyze its synthesis and transformation in various types of plants under salt stress was also shown [Waskiewicz et al., 2014].

In NaCl solution with concentrations of 10, 20 and 30 mM, seeds and seedlings of *Secale cereale* are more sensitive to stress than *Triticum durum*. This was manifested in a decrease in germination, an increase in the average germination time, and a reduction in the average length of the coleoptile [Gordeeva, Tataurov, 2017]. A pronounced decrease in the length of wheat roots and stems was observed in the range of NaCl concentrations of 100-300 mM [Abdullaev et al., 2015]. At the same time, some researchers noted an earlier inhibition of stem growth [Omarova, 2016], others of roots [Veselov et al., 2017].

The mechanisms of resistance of potato plants (*Solanum tuberosum* L.) against chloride salinity were studied using the Luhivska variety as an example. Regenerative plants were obtained from the apical meristem under in vitro conditions and grown on hydroponic equipment on Murashige and Skoog medium with half the content of macro- and microelements under factorostatic conditions. At the age of 6 weeks, the plants were exposed to salt stress (50-150 mM NaCl, 7 days). The reaction of plants to salt stress was evaluated by growth and physiological parameters. It was established that the plants responded to salinity by significantly suppressing growth processes, reducing the content of chlorophyll a, and inhibiting the formation of stolons, which indicates a sufficiently low salt resistance of this variety. At the same time, under mild and moderate salt stress, plants maintained water homeostasis due to effective osmoregulation, actively accumulated proline and practically did not develop oxidative stress. It is assumed that the level of salt resistance of this variety is limited, on the one hand, by the low ability of the root system to retain sodium

ions and provide selective transport of ions to the aerial part, and on the other hand, by the low efficiency of the system of compartmentalization of sodium ions from the cytoplasm of leaf cells to the central vacuole to reduce their toxic effect [Efimova et al., 2018].

Cell membranes are the main targets of many abiotic stresses, but the reasons for the destabilization of these membranes are still not well understood. Despite this, it is clear that a decrease in cell volume leads to an increase in the viscosity of the cytoplasm and thickening of its components. And this, in turn, can lead to protein denaturation and membrane fusion. But the synthesis and accumulation of some substances can prevent cell death. These substances include proline, glutamate, glycine-betaine, carnitine, mannitol, sorbitol, fructans, polyhydric alcohols, trehalose, sucrose, and oligosaccharides [Folkert et al., 2001].

A number of researchers attribute the primary role in the growth of plant resistance and the sequential action of stress factors to the increase in proline content. As is known, proline forms hydrophilic colloids that protect proteins from denaturation under various stresses [Huang, Cavalieri, 1979; Lutts, Guerrier, 1995; Yurkevich, Potopolsky, 1994, Matysik et al., 2002; Kavi et al., 2005; Kaul et al., 2008; Ibrahymova et al., 2010, Maritim et al., 2015]. Glycine betaine, an amphoteric quaternary amine, also performs a rather important function of a compatible soluble osmolyte in plants under various stresses, including salinity and high temperature [Sakamoto, Murata, 2002]. At the same time, the ability to synthesize this substance under stressful conditions depends on the type of plant [Ashraf, Foolad, 2007]. So, for example, a high level of glycine betaine content was found in corn and sugar cane [Quan at al., 2004, Wahid, Close, 2007], and the presence of this osmolyte was not established in rice, mustard, *Arabidopsis* and tobacco [Sakamoto, Murata, 2002; Wahid, Close, 2007]. Mannitol and polyamines also play a rather important role in the adaptation of plants against

osmotic salinity stress [Kuznetsov, Shevyakova, 2007] [Stoop et al., 1996, Shen et al., 1997].

In plants, proline accumulation extends to a relatively small but metabolically significant cytoplasmic fraction of the cell, which is from 5% to 10% of the total cell volume. It has a protective effect on the steric structure of cellular biopolymers and maintains their intact hydration sphere. Proline has a fairly high solubility in water. The hydrophilic behavior of proline is quite unusual, as its molecules have not only hydrophilic, but also hydrophobic properties. Based on the study of the properties of proline by physicochemical methods, it was concluded that the high solubility of this amino acid results from the ability of its molecule to form aggregates due to the presence of hydrophilic and hydrophobic groups. The formed polymers behave as hydrophilic colloids. And that's why proline does not affect proteins. Like detergents, it does not interfere with the intermolecular hydrophobic interactions of proteins, which leads to their denaturation, but binds only to surface hydrophobic residues. The high solubility of this amino acid in combination with its rather low ability to inhibit enzymes can increase the soluble volume of the cell, thereby reducing the concentration of salts in the cytosol. The unusual nature of the interaction of aggregates of molecules in parallel with peptides increases their solubility and protects them from destruction [Shevyakova, 1983; Asimov, 2013].

It is believed that proline regulates the acidity of the cytosol and maintains the NAD^+/NADH ratio, enhances the photochemical activity of photosystem 2 in thylakoid membranes, and reduces membrane lipid peroxidation. Additional synthesis of this amino acid increases the general resistance of plants against abiotic stresses, as proline protects membranes, macromolecules and structural elements of the cell, thus leading to an increase in nonspecific resistance [Kishor et al., 1995, Renard, Guerrier, 1997; Hare et al., 1998, Hong et al., 2000, Sawahel, Hassan, 2002, Gleeson et al., 2005, Soshinkova, Radyukina, 2010, Singh et al., 2014]. It was shown that under normal conditions, NAD^+ -MDG of sorghum is

represented by only two isozymes both in the cells of the mesophyll and in the integument. However, in the mesophyll, salt stress induced the appearance of 6 additional molecular forms of the enzyme, which is probably related to the need to energize cells and accumulate malate. Of the 5 isoforms of NAD⁺.ME, one functions in the mesophyll under control and is induced in Kranz cells under salinity, the other three are inducible for the mesophyll and constitutive for the sheath, and one more is found in the sheath tissue both under normal conditions and under salinity. The spectrum of NADP⁺.ME isoenzymes of the sorghum mesophyll consists of three forms, and only two are found in the cover. Sodium chloride caused the appearance of additional isoforms in both investigated tissues [Fedorina et al., 2009].

It was shown that 150 mM sodium chloride already in the first hours of its action causes changes in the work of four enzymes of the malandehydrogenase system of the corn mesophyll, and NAD⁺-dependent enzymes are activated under salt stress, and NADP⁺-dependent enzymes decrease their activity under salinity. A stress-induced transformation of the isozyme composition was detected for NAD⁺.MDG in mesophyll cells. At the same time, homogeneous products of two constitutive NAD⁺.MDG isoforms were obtained and their kinetic characteristics were studied [Fedorina et al., 2015].

In some plant species, the content of proline under stressful conditions can reach 10% of the dry weight of leaves, but in most cases it is 20-30 mg/g of dry weight. Information on the correlation between the content of proline and resistance to abiotic stresses is quite ambiguous, which to some extent is connected with significant fluctuations in the content of this amino acid in different periods of plant growth, even during one day. Practically all cell lines that were obtained on saline media, as well as regenerants, were characterized by an increased content of proline [Sergeeva, Levenko, 1986]. At the same time, a sharp increase in the level of free proline in rye seedlings and roots was shown when the substrate was salted with seawater salts. For the salt-resistant variety

Slavutych M-1, with increasing salinity, a sharp increase in the stability coefficient was observed – the ratio of the concentration of free proline during salinization to its initial value [Yurkevych, Potopalsky, 1994]. For some cultures, a direct correlation was found between the level of proline supersynthesis and resistance to salinity, drought, and low temperatures [Igarashi et al., 1997, Talanova et al., 1999; Gleeson et al., 2005, Yamada et al., 2005, Koca et al., 2007, Radyukina et al., 2008]. However, no correlation was found between its content and salinity resistance in barley [Chen et al., 2007, Widodo et al., 2009]. It is also known that proline is synthesized from glutamine or ornithine. At the same time, it was shown that the synthesis of proline from glutamine dominates in stressful situations [Delauney, Verma, 1993, Deuschle et al., 2001; Verbruggen, Hermans, 2008; Szabados, Savouré, 2010; Yousfi et al., 2010].

Proline is able to perform the role of a "chemical" chaperone, stabilizing proteins and membrane structures under stressful conditions [Delauney, Verma, 1993; Kuznetsov, Shevyakova, 1999]. At the stage of recovery from stress, proline regulates cell proliferation and cell death [Szabados, Savoure, 2010]. It also performs a protective function, and its role is to maintain water homeostasis in cells [Shevyakova, 1983; Le Rudulier et al., 1984; Shevyakova, Karolevsky, 1994] and stabilization of subcellular structures [Ashraf, Foolad, 2007; Shevyakova et al., 2009]. However, some researchers believe that a high concentration of intracellular proline can be toxic to the cell, and therefore its content should be strictly controlled [Hellmann et al., 2000, Cooper et al., 2008, Verbruggen, Hermans, 2008] .

It was established that proline in pea epicotyls can perform late functions depending on the phase of cell development. In very young epicotyls, when most of the cells have not moved to elongation, proline accumulated in response to stress, and probably performed osmoprotector functions, as well as probably protective functions for cytoplasmic proteins and organelles. In cells that entered the stretching phase, proline accumulated only in the case of severe stress, when

epicotyl growth and protein synthesis were suspended. During the period of cell elongation and epicotyl growth, probably the need for proline as an amino acid used for growing protein synthesis exceeded its need as an osmotic agent accumulating in tissues, and the role of an osmotic agent passed to other compounds. In the conditions of recovery of metabolism after stress, the rapid accumulation of proline in the first hours after water supply could occur due to some imbalance between the processes of recovery of protein synthesis and the production of proline [Generozova, Shugaev, 2011]. The content of proline in leaves, apices, and roots of spring wheat varieties increased with increasing salinity [Kafy et al., 2003].

It is shown that during the cultivation of *Zinnia elegans* Jacq. growth was inhibited on the medium with the addition of 25 mM/l NaCl. Salt stress increased the activity of superoxide dismutase in root and stem tissues. The activity of peroxidases in the root decreased during long-term stress. Based on the obtained results, it can be stated that the plant *Zinnia elegans* Jacq. has a low tolerance against chloride salinity [Plotnikov et al., 2019].

It was established that salt stress had an effect on the formation of the secondary cell wall of tomato and soybean dicot plants. At the same time, there was an increase in the lignification of the cell wall of the root and stem, and as a result, inhibition of plant growth [Ros-Barcelo et al., 2002].

Significant differences between tomato genotypes under salinity conditions were demonstrated in the accumulation of raw and dry biological mass of the roots and stem part of the seedling, the intensity of dark respiration and photosynthesis. In the process of cytological research, significant differences in the size and shape of epidermal and parenchymal cells of the hypocotyl cortex between the two genotypes were revealed. The action of toxic Na⁺ and Cl⁻ ions showed a significant effect on the size and shape of the cells of the examined tissues in both genotypes. It was established that epidermal and parenchymal cells of the hypocotyl of the Recordman variety tomato are less sensitive to the presence of

NaCl in the medium, compared to the YLF line. During histological analysis of cotyledon leaves of tomato line YALF and variety Recordsman, differences in the anatomical structure of epidermal and mesophyll cells of cotyledons were found between the studied genotypes. As the concentration of NaCl in the nutrient medium increased above 50 mM, the thickness of the cotyledon plate decreased in both genotypes. According to ultrastructural analysis data, it was established that during the cultivation of tomato seedlings of the YALF line in conditions of 150 mM NaCl, irreversible damage was observed in the mesophyll cells of cotyledon leaves and a violation of the photosynthetic apparatus – in most chloroplasts, changes in the thylakoid structure of grains and stroma were observed. However, similar changes were not observed in the spongy mesophyll cells of cotyledons of the Recordman variety tomato. Thus, based on the results of the research, it was shown that the studied tomato genotypes have differences in salt tolerance. It was established that according to morphometric, physiological-biochemical and cytological parameters, the Recordman variety tomato is more resistant than the YLF line. Changes in the size and shape of cells of various tissues and organs established during the research can be used as cytological markers for the comparative assessment of tomato genotypes for sensitivity or resistance to salinity [Bogoutdinova, Khaliluev, 2016, Bogoutdinova, Baranova, 2019, Bogoutdinova et al., 2019].

The obtained results directly indicate the presence of Na⁺ in the lumen of endocytotic structures, as well as a certain contribution of endocytosis to the accumulation of Na⁺ and Cl⁻ by cells during salinity. Thus, along with the traditional function of regulating the content of membrane proteins, in particular ion transporters, endocytosis directly participates in the transport of ions and their deposition in vacuoles [Mayorova et al., 2016]. The cells of the water-bearing parenchyma are most likely a depot for chlorine ions entering the leaf with the transpiration flow. It can be predicted that the accumulation of these ions, as well as, probably, sodium ions in the water-bearing parenchyma allows to reduce the

content of these ions in the photosynthesizing cells of the mesophyll and the covering, thus making a certain contribution to the salt tolerance of the halophyte *Suaeda altissima* [Mayorova et al., 2014].

The possibility of involvement of endocytosis in the transfer of sodium ions from the apoplast of the halophyte *Suaeda altissima* and the glycophyte *Arabidopsis thaliana* was clarified. In the halophyte *Suaeda altissima*, the endocytosis process was most active in the cells of the bark and epidermis of the root, and in the leaves – in the cells of the water-bearing parenchyma and chlorenchyma lining; in the root of *Arabidopsis thaliana* – in the cells of the cortex. Endocytotic structures were observed in these experiments. It was also possible to see that the simultaneous entry of the plasmolemma and the tonoplast towards the vacuole occurs. Between the membranes was a thin layer of cytoplasm. Later, the formed intussusception was unlaced in the vacuole and underwent lysis there. The conducted study indicates the formation of endocytosis structures in the cells of *Suaeda altissima* and *Arabidopsis thaliana*, which is accompanied by the capture of sodium ions and their subsequent transfer to the vacuole, which implies the participation of endocytosis in maintaining low concentrations of sodium ions in the cytoplasm under salinity conditions [Mayorova et al. etc., 2015].

Using the method of transmission electron microscopy, the influence on the processes of utilization of protein bodies from storage vacuoles, starch grains from plastids and lipids from oleosomes and the transformation of storage compartments in the cells of the cotyledon mesophyll and root meristem during the germination of *Medicago sativa* seeds in NaCl, Na₂SO₄ and mannitol solutions in various concentrations equalized by osmotic pressure. At the same time, it was shown that salts exhibit both an osmotic and a toxic effect associated with specific reserve mobilization disorders, which was expressed in a change in the shape of the corresponding compartments, the number, sizes, and ultrastructural characteristics of protein bodies, starch grains, and lipid droplets. Utilization of

the main reserves: reserve protein, polysaccharides and lipids is sensitive to the action of salts and osmotic, causing specific disturbances both at low concentrations - low osmotic pressure, and at high isosmotic pressure [Baranova et al., 2007].

A change in the number of starch grains and a slowdown in the development of chloroplasts, depending on the osmotic effect of salt action, are shown. Low concentrations of Na_2SO_4 did not affect the development of the photosynthetic apparatus and utilization of starch inclusions, mannitol caused the preservation of significant reserves of starch without hindering the development of the chloroplast, NaCl did not interfere with the formation of the internal infrastructure of the photosynthetic plastid. When the isoosmotic concentration increased to 607.8 kPa, NaCl also did not affect the transformation of amyloplasts into plastids and the utilization of starch, Na_2SO_4 partially suppressed both the development of chloroplasts and the utilization of starch, and mannitol caused a slowdown in the transformation of amyloplasts with inhibition of the utilization of starch grains. Changes in the transformation of the storage vacuoles into the central vacuole, as well as changes in the number and shape of protein body residues in the middle of the vacuoles depending on the osmotic effect of salt action, were also revealed. At low concentrations corresponding to a pressure of 202.6 kPa, Na_2SO_4 did not affect the transformation of storage vacuoles into the central vacuole and protein utilization; with increasing concentration, both Na_2SO_4 and mannitol caused the preservation of significant protein reserves, and mannitol did not disrupt vacuole transformation processes. NaCl did not have too strong an effect on the conversion of storage vacuoles into the central vacuole and protein utilization in cotyledon cells. The obtained results show different sensitivity to salinity stress factors - important metabolic processes, for example, the utilization of starch grains and the formation of photosynthetic subcompartments of chloroplasts in the mesophyll of cotyledons, the mobilization of reserve protein and the transformation of the vacuolar compartment, and the

mobilization of lipids from the oleosome during seed germination [Baranova et al., 2010].

Fast (in minutes) and slower (in hours) responses of the above-ground part of plants (barley, vetch, wheat, rice, buckwheat) to changes in external conditions were studied: increase and decrease in NaCl concentration in the growing medium, drought and subsequent watering. It is shown that a one-time addition of NaCl to the root zone causes a complex response of plants: a rapid decrease and subsequent increase in the growth rate of the aerial part (fast response phase) and a subsequent slower decrease and increase in its growth rate with reaching a stationary level (slower phase reactions). Recovery of plant growth rate in the process of a biphasic response to the addition of NaCl could be complete (in the case of moderate salinity) or partial (when using increased NaCl concentrations or low salt tolerance of plants). A decrease in the concentration of NaCl (watering, washing of the roots) led the plot to a rapid increase in the growth rate of the above-ground part, and then to a gradual decrease to a stationary level, which is higher than the level at salinity. When NaCl was added in a high concentration, plant growth stopped and a decrease in the linear dimensions (compression) of leaf and stem tissues was noted at first with a high speed, and later with a slower and subsequent attenuation of this process. Similar curves of the rate of compression of tissues of the aerial part of plants were obtained in experiments with simulation of short-term drought conditions. Watering drought-stressed plants caused an increase in the linear dimensions of leaf tissues. The speed of this process first increased, and then decreased. Curves of changes in the linear dimensions of leaf tissues that have finished growing can characterize the dynamics of water exchange in plants when external conditions change (loss of water by tissues and restoration of the water balance) [Budagovskaya, 2007, 2010]. It is believed that water deficiency leads to the development of xeromorphism [Vidal, Pognones, 1984]. And the level of xeromorphism affects a number of physiological processes. At the subcellular level, the main changes

occur in chloroplasts, which leads to a significant change in the process of photosynthesis. These changes are associated with various changes in the structure of the plant's photosynthetic apparatus, carbon metabolism, and the energy of photosynthesis [Downton, 1977; Fedina et al., 1994; Lawlor, Cornic, 2002]. However, it was noted that the xeromorphic structure of the leaves promotes more intense photosynthesis [Gifford, Jenkins, 1987]. The xeromorphic structure of the leaves is more effective from the point of view of assimilation of carbon dioxide, and, quite likely, to some extent compensates for the negative effect of dehydration on the work of the leaves [Schneider, Childers, 1941]. But it is believed that the key mechanism for many plants is the accumulation of organic compounds with low molecular weight, including low molecular weight hydrophilic proteins that bind significant amounts of water [Hare et al., 1998; Sakamoto and Murata, 2002].

Water deficit is a rather important factor in the effect of salinity on plants, and therefore the study of water exchange under salt stress is quite an interesting point. The objects of study were plants of the relatively salt-tolerant barley variety Golf and the more salinity-sensitive durum wheat variety Bezenchukska 139. Long-term (for 3 weeks) action of 100 mM NaCl inhibited the growth of plants of both types, but the effect was more pronounced in plants of durum wheat. wheat (stem mass was 75% and 60% of the mass of control plants in barley and wheat, respectively). These results confirm that the varieties selected for the study showed differences in salt tolerance characteristic of barley and wheat. Suppression of leaf growth appeared immediately after adding salt to the nutrient solution. With the help of a sensitive growth sensor, not only its stoppage was detected, but also the leaf shrinking, which was more pronounced in barley plants (the speed of shrinking was 5 and 20 $\mu\text{m}/\text{min}$ in wheat and barley plants, respectively). The cessation of growth under the action of salinity can be easily explained by a decrease in the inflow of water from the roots and the hydration of tissues, which was evidenced by a decrease in the relative water content by 3.5%

in barley and by 2.5% in wheat. Shrinkage of the leaf indicates a drop in cell turgor as a result of a decrease in hydration, which, judging by the rate of negative growth, was more pronounced in barley plants [Veselov, Sharypova, 2007].

Deficiency of water in a critical period is the cause of sterility of pollen grains and even whole flowers, which negatively affects the productivity of plants as a whole [O'Toole, Moya, 1981; O'Toole, Namuco, 1983; Ekanayake et al., 1990, Altergot et al., 1998].

The studied structures of cucumbers showed different sensitivity to environmental salinity. The reaction of the separated structures is individual and varied depending on the type of culture, the type and degree of salinity, and the complexity of the models themselves. At the same time, the preservation of cotyledons in petioles (hypocotyl with cotyledons, hypocotyl with cotyledons and two true leaves) increased their salt resistance [Hadzhieva, 2007].

It was shown that under the influence of 0.05 M NaCl, the activity of neutral, acidic and alkaline proteases (BAPAases) increases by more than 40% in relation to the control in both cotyledons and embryos on the first day of lupine germination. There is also a significant increase in the activity of trypsin inhibitors (by 50%). The effect of 0.1 M NaCl caused a decrease in the activity of proteases, although the activity of trypsin inhibitor proteins increased almost twofold. Analysis of the activity of the antioxidant enzymes catalase and peroxidase in the leaves of different varieties of lupine and pea under water culture showed a decrease in the level of activity depending on the concentration of sodium chloride. Thus, in the studied varieties of yellow fodder lupine, at 0.05 M NaCl, the decrease in catalase activity was on average 5.5%, at 0.1 M - 17%, and at 0.15 M - 33%. In varieties of narrow-leaved forage lupine, the decrease in activity was 9%, 20% and 43%. Catalase activity in pea leaves decreased by an average of 40% under the influence of salinity. A similar picture was observed in the activity of peroxidase. The total antioxidant activity of the leaves of all studied cultures was quite closely correlated with the decrease in the activity of antioxidant

enzymes. Thus, the stress factor of salinity causes changes in the activity of protein molecules that affect both the components of the proteolysis system and antioxidant enzymes. The obtained experimental information confirms the role of functional proteins in the adaptation of plants against the stress factor [Domash et al., 2007]. It was also shown that disruption of the synthesis of the main photoreceptor of blue spectral light – cryptochrome 1 in the dark leads to a decrease in the resistance of *Arabidopsis thaliana* (L.) Heynh. to the effect of chloride salinization [Manuilova et al., 2013]. It is known that phytochrome changes the sensitivity of plant roots to jasmonic acid, a hormone that determines the response of plants to stress [Costigan, 2011].

The isoenzymatic spectra of four enzymes of the malate dehydrogenase complex of the mesophyll and corn coat were studied – NAD⁺-dependent oxidoreductase MDH and malic enzyme, as well as NAD⁺-dependent malic enzyme and oxidoreductase MDH. NAD⁺-dependent – MDH of corn is represented by a wide range of numerous molecular forms. In the control samples, four isoforms of MDG were recorded in the mesophyll, two of which (with $R_f = 0.36$ and 0.25) were present in the cytoplasm, one was characteristic only of mitochondria ($R_f = 0.28$) and one more was manifested in both fractions ($R_f = 0.4$). Only two bands - mitochondrial ($R_f = 0.4$) and cytoplasmic ($R_f = 0.36$) – were detected in the corn cover. NaCl induced the appearance of an additional MDG isoform both in mitochondria and in the cytoplasm of the mesophyll ($R_f = 0.3$ and 0.28 , respectively). No stress-induced changes were detected in the cover. The synthesis of two additional forms of this enzyme in the cells of the mesophyll under stress provides a quick adaptive response of this tissue to the changed environmental conditions, primarily due to respiratory metabolism. In addition, the cytoplasmic form of MDH is capable of synthesizing malate, which participates in cell osmoregulation. NAD⁺-dependent malic enzyme is represented in corn leaves by two isoforms with $R_f = 0.33$ and 0.26 , and both forms are present in the mesophyll both under normal and stressful conditions, and only the rapidly

mobile one is present in the covering of control plants. A slow-lived form of malic enzyme was detected in the corn husk only after six hours of salinization. It is likely that the functioning of a greater number of enzyme isoforms in the lining than in the control is due to the insufficient lability of NAD⁺-dependent MDH in this tissue during salinity, due to the fact that due to the work of the specified malic enzyme, malate oxidation is bypassed in those conditions when the activity of NAD⁺-dependent MDH is insufficient. It is also shown that the isoenzyme spectrum of NADP⁺-dependent malic enzyme is stable and represented by only one isoform with $R_f = 0.11$. The conservatism of the enzyme is most likely due to the fact that this malic enzyme takes part in the metabolic pathway typical for C4 plants – the Hatch-Slack cycle. Electrophoregrams of NAD⁺-dependent oxidoreductase MDH includes two bands. Both are present in mesophyll cells, both in control and experimental samples. In the cover, the isoform with $R_f = 0.45$ is normally active, and with salinization, a form with $R_f = 0.47$ appears in addition to it. Changes in the isozyme spectrum of the discussed MDH in the lining are probably connected with the need for additional synthesis of malate in this tissue under stressful conditions [Eprintsev et al. 2007]. It was found that under conditions of stress, proteolytic enzymes not only break down defective, denatured and those proteins that have lost their functional value, but also take an active part in nitrogen recycling, processing and activation of synthesized proteins [Callis, 1995].

As a reservoir of information about the abiotic environment of the cell, the apoplast is involved in the generation or reception of stress signals and the subsequent control of growth and protection of plant cells. Studying the relationship between redox processes occurring on the surface of cells and intracellular events is quite important for understanding redox signaling during cell survival or death. The main ROS-synthesizing systems in the apoplast are cell wall-bound oxalate oxidases, peroxidases, and amine oxidases, as well as membrane-bound NAD(F)H-oxidases. The various enzyme systems that

contribute to the oxidative burst may work cooperatively to promote the amplification of the redox signal. Class III peroxidases (EC 1.11.1.7) play a key role among the apoplast proteins induced during the formation of plant immunity. The abundance of plant peroxidase genes is due to their duplication and high conservatism, which ensures the possible reprogramming of these genes and the synthesis of isoforms with different functions. In addition, the involvement of these proteins in numerous physiological processes under stress and in the process of plant development is determined by the versatility of the reactions catalyzed by them. A stress-induced oxidative burst provokes the activation of various signaling pathways localized in the plasma membrane. At the same time, the formation of new signaling platforms can occur, which provide anchoring and enrichment of signaling molecules. Such platforms are formed from lipid microdomains, that is, rafts enriched with sterols and sphingolipids, and the action on one lipid component causes significant changes in another. Thus, the depletion of membrane sterols through their binding by nystatin leads to dramatic changes in the composition of molecular species of sphingolipids, which in turn induces changes in membrane activity. The functioning of ROS as signaling molecules in plant cells and redox-dependent information signal transmission through the activation of protein kinases, guanylate and adenylate cyclases, nucleases, phospholipases and proteases is also ensured as a result of the arrival of divalent calcium ions from the apoplast and its release from intracellular depots, the work of potassium channels and the proton pump of the plasma membrane. Combination in the apoplast of a complex of factors, such as buffer properties and redox activity of the cell wall. The conductivity and sensory properties of the plasma membrane, the concentration of calcium, potassium and proton ions, mediates the regulatory and toxic effects of activated oxygen during stress [Mynybaeva, 2010].

The effect of salt stress on the activity of the peroxidase system in leaves and roots of sweet potato genotypes contrasting in terms of morphological and

physiological indicators was revealed. These genotypes had differences in the shape of the leaf blade, the length of the stems, the number of internodes, root formation, and also had different levels of anthocyanins and β -carotene content in the tubers. To create salt stress, plants were placed in an aqueous medium containing 1% NaCl for 72 hours. At the same time, it was found that the activity of ascorbate peroxidase increased, reaching a maximum value before 24 hours of salt stress in both genotypes, and after 48 hours and further up to 72 hours of exposure to NaCl, its activity decreased slightly, but was higher than the control. The content of this enzyme in the leaves was higher than in the roots of both the anthocyanin-rich and the poor clone. The activity of guaiacol peroxidase also increased, reaching its maximum up to 24 hours of stress, and then decreased in both genotypes. However, the level of activity of this enzyme was higher in the anthocyanin-poor clone. It should also be noted that the increase in enzyme activity was also higher in plant roots than in leaves, i.e., in the leaves of the anthocyanin-rich clone, ascorbate peroxidase activity was lower than in the anthocyanin-rich clone. And in the roots, there was an increase in the activity of guaiacol peroxidase, and in the anthocyanin-rich clone, this indicator was also lower than in the anthocyanin-poor clone. Moreover, it should also be noted that this tendency was maintained both at low (0.5%) and at higher concentrations (1.0%) of salt. Thus, it can be concluded that the response of systems that provide protection against the damaging effect of salt stress differed depending on the localization of antioxidant enzymes in the organs of sweet potato plants. Ascorbate peroxidase activity was significantly higher in leaves than in roots, and guaiacol peroxidase activity in roots was significantly higher than that in leaves in both genotypes. The activity of ascorbate peroxidase and guaiacol peroxidase had different levels of accumulation in sweet potato leaves and roots in all periods of salt stress [Davlyatnazarova et al., 2018].

Clear accumulation of polyamines under the influence of progressive salinity in the extreme halophyte *Thellungiella halophila* Mey. was not observed

in the conducted study. Also, the number of mRNA transcripts of genes encoding enzymes of polyamine biosynthesis changed little. It is likely that the regulation of the content of polyamines was carried out at the translational or posttranslational levels [Ivanov et al., 2007].

The results obtained during the conducted research allow us to consider the response of plants of plantain (*Plantago major* L.) to the action of salinity (100 mM NaCl) as a process consisting, to a lesser extent, of two stages. The first stage (12-18 hours) is short-term, characterized by significant changes in the studied parameters (proline, guaiacol peroxidase, superoxide dismutase, malondialdehyde, proline dehydrogenase), illustrates a classic stress reaction, and the second stage (in the next day) is longer and smooth - the beginning of long-term adaptation. At each of these stages, changing each other, various low molecular weight substances and enzymatic systems play a protective role. It is quite likely that this scheme of protective factors is the plant's transition from a stress reaction to a longer stage of adaptation [Kartashov et al., 2007].

It was determined that the structure of the polymer matrix of cell walls of halophytes and glycophytes contains four types of ionogenic groups capable of participating in exchange reactions with the external environment: these are carboxyl groups of polygalacturonic and oxycornic acids, phenolic and amino groups. It was established that the polymer matrix of cell walls of halophytes and glycophytes does not differ in terms of the qualitative composition of functional groups, as evidenced by the values of dissociation constants. In all variants, the number of cation-exchange groups is significantly greater than anion-exchange groups, that is, it can be stated that the cell walls of halophytes and glycophytes are natural ion exchangers and possess mainly cation-exchange properties. With an increase in NaCl concentration in the environment, both glycophytes and halophytes have an increase in the number of carboxyl groups of polygalacturonic acid, but in the former, their content in the roots increases by 10-30%, while in the latter, it almost doubles. It is assumed that changes in the number of carboxyl

groups of polygalacturonic acid with increasing salt concentration in the environment is one of the responses of halophytes and glycophytes to salinity, and it should be noted that in *Suaeda altissima* (L.) Pall. such changes are more pronounced. With increasing NaCl concentration in glycophytes and halophytes, the ionization constant of the carboxyl groups of polygalacturonic acid sharply decreases or their acidic properties increase, while the pKa of the other two groups have little dependence on the concentration of NaCl in the solution. Thus, in response to salinization, the ion exchange capacity of the polymer matrix of cell walls increases. Evidence of this statement is provided by indicators of the dependence of the ion exchange capacity of isolated cell walls on the concentration of NaCl in the external solution. In all variants of growth in glycophytes and halophytes, the ion exchange capacity of cell walls increases with increasing NaCl concentration. One of the rather important physicochemical parameters that quantitatively characterize the properties of the polymer matrix of cell walls is the weight coefficient - swelling. In halophytes and glycophytes, this parameter increases with a decrease in the ionic strength of the solution and an increase in pH or the degree of dissociation of ionic groups. These results allow us to state that the volume of cell walls of halophytes and glycophytes is not a constant value and depends on the ionic conditions and pH of the external solution and in the apoplast. A comparison of the ability to swell plant cell walls in water shows that halophytes have a higher degree of cross-linking of polymer chains in the matrix compared to glycophytes. In addition, in the former, the share of cell walls from the dry mass of tissues is greater. Thus, the halophyte has a more rigid structure of the polymer matrix, which provides higher mechanical and chemical stability of the cell membranes of *Suaeda altissima* (L.) Pall. in salinity conditions, compared to glycophytes. The obtained results allow us to present the sequence of events that occur with the participation of the root cell walls in response to salt stress. As the concentration of NaCl in the environment in the walls of halophytes and glycophytes decreases, the dissociation constant of

carboxyl groups of polygalacturonic acid decreases, and accordingly, the number of ionogenic groups capable of exchange reactions increases. As a result, the concentration of sodium ions in the water space of the cell walls will be lower than in the external solution. At the same time, due to ion exchange reactions, the concentration of protons and calcium ions in the aqueous phase of the apoplast increases, which will probably lead to a change in the transport functions of the plasma membrane. And on the other hand, as the concentration of sodium ions in the medium increases, the degree of swelling of the cell walls decreases, which leads to a decrease in the hydraulic conductivity of the cell walls and, accordingly, to a decrease in the flow of the sodium ion-concentrated solution in the root. It is likely that these changes in the swelling and ion exchange capacity of the polymer matrix are quite important in the adaptation of plants against salt stress. Thus, ion exchange reactions in cell walls are a rather important specific link in the development of plant resistance reactions against adverse environmental factors [Meychyk et al., 2007].

Until now, it remains unknown which proteins are involved in the active transport of chlorine ions from the cytoplasm of plant cells. The most likely candidate for this role in halophytes is Cl^-/H^+ -antiporter, which belongs to the CLC family of Cl^- -transporting proteins. The study was conducted on the membrane fraction enriched with inverted vesicles of plasmodes. The main approach in the identification of the Cl^-/H^+ -antiporter consisted in the registration of ΔpCl -dependent transport of hydrogen ions through the membrane. The electrogenic properties of the Cl^-/H^+ antiporter were studied by recording the transmembrane electric potential ($\Delta\psi$) on the vesicular membrane based on the change in the differential absorption of the indicators $\Delta\psi$, safranin O, and oxonol VI. The creation of a concentration gradient of chlorine ions on the vesicular membrane, directed from the middle to the middle of the vesicles, led to alkalization of the vesicular lumen, which indicated the transfer of hydrogen ions from the vesicles to the outside. At the same time, an electric potential was

generated on the membrane, negative in the middle of the vesicles. An electric potential with a minus sign in the middle can be the driving force for the transfer of hydrogen ions from the medium to the middle of the vesicles, but not in the opposite direction. ΔpCl -dependent fluxes of hydrogen ions through the vesicular membrane depended on the electric potential applied to the membrane. By hyperosmotic shock, the vesicles were loaded with potassium ions. At higher concentrations of potassium ions in the medium than in the vesicular lumen, in the presence of the K^+ -ionophore valinomycin, a transmembrane diffusion potassium potential with a "plus" sign was generated in the middle of the vesicles, and at lower concentrations of potassium ions from the outside than from the middle, with with a "minus" sign in the middle of the vesicles. ΔpCl -dependent flows of hydrogen ions from vesicles increased at positive values in the middle of the vesicle potential and decreased at negative values. The totality of the obtained information indicates the functioning of the Cl^-/H^+ antiporter in the cell membranes of the root of the halophyte *Suaeda altissima* [Shuvalov et al., 2010].

It was established that the structure of the polymer matrix of all organs of the studied leguminous plants contains four types of ionogenic groups capable of participating in exchange reactions with ions of the external environment under appropriate conditions. At the same time, the level of salinity of the external environment does not affect the qualitative composition of functional groups: amino groups, two types of carboxyl and phenolic groups are present in all variants. The number of carboxyl groups of polygalacturonic acid changes depending on the concentration of NaCl in the growing medium in chickpea cell walls (roots and leaves of the lower tier) and age (stems and leaves of the lower tier). As the concentration of NaCl in the medium increases from 0.5 mM to 80 mM in the polymer matrix of these organs, the content of the latter increases by 10-20%. Changes in the number of polygalacturonic acid groups when the concentration of salt in the medium increases is probably one of the responses of these plants to salinity. The cell walls of the stem and roots of leguminous plants

contain more carboxyl groups of polygalacturonic acid, compared to this indicator in other plants. For example, it has been shown that in the roots of lupine, cucumber, and spinach, the content of carboxyl groups of polygalacturonic acid ranges from 350 to 450, while in the roots of chickpeas of the ILC 482 and age varieties, it reaches 680 and 620 kmol per 1 g of dry mass of cell walls. In leguminous plants, regardless of the concentration of salt in the medium, the largest number of carboxyl groups of polygalacturonic acid is in the polymer matrix of the stem walls, and phenolic groups are in the matrix of the leaves. The walls of different organs differ greatly in the content of amino groups and carboxyl groups of hydroxycinnamic acids: the largest amount of both the former and the latter is found in the polymer matrix of the leaves. The obtained results allow us to state that the composition of structural polymers in the matrix of the extracellular compartment in different organs of the same plant differs significantly. In a whole range of studied plants, the cell membranes of the most salt-sensitive chickpea variety Bivanij have the least number of phenolic OH groups in their composition, which may indicate a comparatively lower degree of lignification and suberinization of the walls of *Cicer arietinum* L. Bivanij, compared to *Cicer arietinum* L. (ILC 482) and *Vicia narbonesis* L. In accordance with the information on the relative salt tolerance, the studied plants are located in the series: *Cicer arietinum* (Bivanij) < *Cicer arietinum* (ILC 482) < *Vicia narbonesis*, and in the same sequence there is an increase in the content of phenol OH groups in the walls of all organs. It can be predicted that a significant share of phenolic polymers in the roots of vetch and chickpea (ILC 482) is one of the factors that determines the greater salt tolerance of *Cicer arietinum* (ILC 482) and *Vicia narbonesis* compared to *Cicer arietinum* (Bivanij). The ionization constant of the carboxyl groups of polygalacturonic acid changes with increasing salt concentration in the nutrient medium in chickpeas and age, while the pKa of the other two groups depend little on this factor. In all cultivation options, the ion exchange capacity of the cell walls increases sharply with an increase in the

concentration of sodium chloride in the studied plants, and for roots, leaves, and stems, the specified dependencies have a similar character. It should be emphasized that, under any conditions, the capacity for ion exchange of cell walls of the stem is higher compared to the rest of the organs [Meychyk et al., 2007a].

A more than 20-fold increase in the concentration of proline in the leaves of crystal grass (*Mesembryanthemum crystallinum* L.) in conditions of prolonged salinity (5-14 days) compared to its values in the leaves of control plants was established. It was also found that salinization simultaneously caused significant activation of one proline degradation enzyme – proline dehydrogenase. The study clarified the relationship between these two indicators at the initial stage of chloride salinization. It was found that the rapid accumulation of proline in the initial period of the stressor occurs in conditions of low activity of proline dehydrogenase, while a strong accumulation of proline probably initiates the activation or stimulates the synthesis of proline dehydrogenase. Finally, during the development of the adaptation syndrome and during the transition to the state of adaptation, there is a significant decrease in the activity of proline dehydrogenase, which in this period eliminates the obstacle to maintaining an increased level of proline in the leaves of the crystal grass plants during salinity [Myronov, Kholodova, 2007].

One of the rather negative consequences of the action of sodium and chlorine ions on cultivated plants is the accumulation of ROS, which cause oxidative stress, which leads to a violation of the functions of structural and enzymatic proteins, and peroxidation of membrane lipids [Menconi et al., 1995]. Therefore, the activation of the antioxidant system plays a rather important role in the adaptation mechanisms of plants under salt stress [Gechev et al., 2002]. The reasons for the increase in the content of ROS in the plant under this stress may be an increase in the activity of ATP-generating enzymes - NADPH oxidase, individual forms of peroxidase and a decrease in the activity of antioxidant enzymes [Doke 1997; Lopez-Delgado et al., 1998; Dat et al., 2000, Almeselmani

et al., 2006; Lee et al., 2006, Shao, et al., 2006, 2007]. For nucleic acids, the most toxic form of ROS is the hydroxyl radical, the increase in which leads to disruption of the purine and pyrimidine bases of the DNA molecule [Halliwell, Gutteridge, 1999].

It is believed that hydrogen peroxide in concentrations of 10^{-2} – 10^{-5} mol/l is a unique, cheap, environmentally friendly anti-stress drug that promotes the survival of plants in extreme conditions of low temperatures, soil salinity, and moisture deficit [Apasheva et al., 2011, Apasheva, Komissarov, 2011, Bilova, Sharova, 2011].

One of the significant, informative and reliable indicators for evaluating salt resistance of plants is the permeability of cell membranes [Gryshenkova, Lukatkin, 2005]. Preserving the integrity of membranes is quite important for maintaining the resistance of plants against stress factors in the external environment. Nonspecific stress reactions largely lead to those changes that are found in cell membrane formations [Chirkova, 1997, 2002; Shakirova, 2001]. A connection has already been found between the resistance of plants against various adverse effects and the state of their membrane components. Plants resistant to stressors show greater structural and functional stability of cell membranes, compared to non-resistant ones [Chirkova, 2002]. A change in the permeability of membranes is observed during various actions, including when the water balance of cells is disturbed during drought, a decrease in temperature, and salinity. Under the influence of metabolic poisons, cooling, increased acidity, hypoxia and anoxia [Shakirova, 2001; Chirkova, 2002; Gryshenkova, Lukatkin, 2005].

The reasons for the increase in membrane permeability are quite diverse. Thus, they are associated with a change in the H^+/Ca^{2+} ratio in membranes. An increase in the concentration of hydrogen ions increased, and the introduction of calcium ions into the solution decreased the permeability of membranes. The increase in permeability may also depend on the level of SH-groups and the

increase of disulfide bonds; also from the formation of defective areas in lipid membranes, which are the result of the accumulation of free fatty acids, products of lipid peroxidation; from the increase in the activity of endogenous phospholipases [Chirkova, 1997; 2002; Koshkin, 2010; Kuznetsov, Dmitrieva, 2011; Medvedev, 2012a]. Membrane permeability can be inhibited with the help of substances that stabilize membranes and prevent their disintegration. These membranotropic compounds include divalent calcium salts and vitamin E-type antioxidants [Medvedev, 2012a].

One of the ways to assess damage to cell membranes is the conductometric method [Gryshenkova, Lukatkin, 2005]. At the same time, the dependence of the output of electrolytes from cuttings of corn leaves on the physiological characteristics of plants (plant age and leaf age and number) and experimental conditions, in particular the size of cuttings, growing and incubation temperature, is shown. A method for determining the relative resistance of wheat varieties to chloride salinization has been developed, which is based on the determination of the electrical conductivity of water extracts from leaves grown under stress and control conditions [Gurova, Berezyna, 2009]. It is shown that the assessment of salt resistance of spring wheat varieties by the conductometric method corresponds to the change of biometric indicators in conditions of salinity [Makarova, Holoshchapova, 2011].

Salinity not only has a negative effect on the permeability of cell membranes, but also leads to their oxidative damage, activates lipid peroxidation, the product of which is malondialdehyde [Hernandez, Almansa, 2002]. The intensity of accumulation of malondialdehyde was studied on different species and varieties of cultivated plants. Numerous studies have noted a high accumulation of malondialdehyde in salinity-sensitive plants [Polesskaya et al., 2006; Hu, Liu, 2008; Yasar et al., 2008; Kiemova et al., 2013; Khabieva, 2016]. It has been shown that lipid peroxidation can lead to disruption of the normal

"packing" of the membrane bilayer, which can, in turn, cause damage to membrane-bound proteins [Richter et al., 1987].

Salinity also has a negative effect on the process of photosynthesis and the photosynthetic apparatus of plants. At the same time, there is information in the literature about the ambiguous influence of salinity on the content of chlorophyll. Some researchers note a decrease in its content [Udovenko, 1977; Alina, Beimukhasheva, 1986; Kahnovich, Doroshevich, 1986; Atoev et al., 2011], and others found its growth [Mukhamedov et al., 1986; Eremchenko et al., 2014; Zhukov et al., 2015].

At the same time, in the course of research, it was established that the content of flavonoids in the stems and roots of triticale under conditions of sulfate salinity (120 mM) increased in the first 12 hours (6.4 mg/g of dry weight and 3.5 mg/g, respectively), which 10% more than control level values. And with further exposure to the salt-containing environment of triticale plants, the content of flavonoids gradually decreased and by the end of this experiment (96 hours) it decreased by 25% from the control level. The increase in the content of phenolic metabolites in triticale organs in the first 12 hours can be explained by the intensification of their synthesis for the detoxification of ROS formed during oxidative stress [Zhukov et al., 2015a].

The negative impact of salinity on the processes of photosynthesis is based on a number of reasons, including a decrease in water potential, loss of turgor by closing cells, as a result of which the access of carbon dioxide decreases [Maser et al., 2002]. Closing the stomata in order to reduce water loss during transpiration affects the functioning of the light-harvesting complex and the energy conversion system, which leads to a change in the activity of chloroplasts [Iyengar, Reddy, 1996].

It was established that the physiological status of the chloroplast affects the expression of nuclear genes that control photosynthesis reactions through a signaling system, one of the main attributes of which, in addition to proteins, are

tetrapyrroles - intermediates of chlorophyll synthesis. The genetic mechanism of light, retrograde, hormonal and metabolic regulation, redox control and apoptosis in a photosynthetic cell are quite closely connected and form a single network, an integral part of which is the process of biosynthesis of tetrapyrroles and carotenoids. In recent years, it has been possible to identify a significant number of factors that take part in these processes, but at the same time, there is still a lot of work ahead [Chekunova, 2019].

Salinity causes significant changes in the transport and accumulation of ions of mono- and divalent metals, as well as anions Cl^- , SO_4^{2-} , which leads to changes in intracellular metabolism [Strogonov et al., 1989; Balnokin, 2012]. The active influx of sodium ions leads to a decrease in the content of potassium, calcium and magnesium [Greenway, Munns, 1980]. The addition of calcium or potassium to the environment prevents the influx of sodium ions, for example, in beans and sunflowers [Cachorro et al., 1994; Delgado, 2007]. Potassium ions play a rather important role in the response of cultivated plants to salinity [Carden et al., 2001; Cuin et al., 2008; Szczerba et al., 2009]. Maintaining a stable level of cytosolic potassium in an environment with a high content of sodium ions may be the main factor in the ability of plants to tolerate salt stress [Maathuis, Amtmann, 1999].

Transport of sodium ions into the cell is regulated by special channels [Garcia et al., 1997; Maser et al., 2002; Yamaguchi et al., 2013]. Sodium ions can also enter the cell with the help of potassium transporters, LCT transporters, HKT transporters, and thanks to the presence of special channels that are activated by glutamate [Rus et al., 2001; Maser et al., 2002; Deinlein et al., 2014]. Some channels through which sodium ions enter can be blocked by calcium ions, and then the flow of sodium ions into the middle of the cell is interrupted [Veselov et al., 2007; Demidchik et al., 2002].

The content of potassium and sodium ions can vary in different organs depending on the type and variety of plants [Strogonov, 1962]. Some researchers

note a correlation between the accumulation of sodium ions in the above-ground part and salt resistance [Mohamed et al., 2006; Ibrahymova et al., 2013]. And other scientists did not observe such a correlation [Komizerko, Strogonov, 1970; Cuin et al., 2008; Arkhipova et al., 2011; Kabuzenko and others. 2013]. The salt-resistant corn hybrid was characterized by a high content of sodium ions in the roots and a more pronounced accumulation of potassium ions in the aerial part [Kazubenko et al. 2013]. Under conditions of chloride salinity (80 mM), salt-tolerant varieties of tomato were characterized by a lower content of sodium ions in leaves and stems than less salinity-resistant varieties [An et al., 2005].

Not only the content of sodium and potassium ions, but also their ratio plays a rather important role in assessing the salt tolerance of plants. Thus, the ratio of potassium to sodium in resistant varieties of rice turned out to be almost constant, while in non-resistant varieties it increased almost 6 times. A decrease in the potassium-to-sodium ratio was associated with increased salt stress, with this ratio being lower in roots than in leaves [El-Ikil et al, 2002].

It was shown that the action of salts (NaCl and Na₂SO₄) causes an increase in the level of ROS in cells, a change in the orderly organization of the microtubule system, and the appearance of atypical elements of the cytoskeleton. These elements of the cytoskeleton are structurally identical to tubulin aggregates, which are formed during experimentally induced imbalance of ROS [Livanos et al., 2012].

In tissue culture cells and leaves of *Arabidopsis thaliana* plants, under osmotic and antioxidant stress, in the first minutes, the stressful formation of ROS occurs, which, as secondary messengers, causes an ROS-induced increase in the activity of peroxiredoxins and thioredoxins – acceptors and transducers of ROS redox signals. In both actions, the detected changes have generally similar patterns in the dynamics of ROS formation and ROS-induced increase in the activity of peroxiredoxins and thioredoxins. However, the molecular mechanisms of the response reaction must have their own stress specificity. Thus, under the action of

the osmotic agent PEG-6000 and the oxidizing agent hydrogen peroxide, different peroxidation substrates in different compartments of the cell and, accordingly, different isoforms of peroxiredoxins and thioredoxins can be involved in the mechanism of stressful oxidant flare [Zhadko, 2011].

On the example of two cotton varieties (Gulistan – salt-resistant and C-4727 - not resistant), a correlation was found between resistance to salinity and the level of activity of antioxidant systems. At the same time, the presence of significant differences in the response to salt stress of sensitive and resistant cotton varieties is shown. Differences in the response to salinity are quite closely related to differences in the activity of enzymes of the antioxidant system and the content of malondialdehyde. The resistance of cotton varieties to fouling is closely related to the high efficiency of the enzymatic system for ROS decontamination, which increases redox homeostasis and the preservation of cell components [Golubenko et al., 2017].

The conducted studies confirmed the existence of processes of endogenous formation of nitrates in cereal plants, their content in seedlings was significantly higher than in the original seed and depended on external factors. In the conditions of the experiments, the maximum increase in the rate of endogenous formation of nitrates in plants under the influence of the tested stressors was noted under the effect of NaCl salinization, while a similar concentration of NH_4Cl increased the rate of nitrogen oxidation in plants to a much lesser extent. Among the studied crops, the most noticeable stimulating effect of salinity on nitrate formation was noted in corn plants [Vernychenko, 2013].

It was established that both at a low and at a high concentration of Fe in salinity conditions, significantly more ferritin was noted, which indirectly indicates a higher absorption of Fe in these variants, compared to the variants without NaCl. This is also indicated by the appearance of phytosiderin in many organelles, a product of the breakdown of the Fe-storing protein ferritin, as a result of more significant formation and destruction of ferritin under these conditions.

Thus, while the level of ferritin has a direct correlation with the total amount of iron received, the level of phytosiderin depends on the amount of ferritin formed. The high accumulation of Fe in cells leads to the accumulation of a significant amount of ferritin, in which metabolically active iron is concentrated, which probably becomes quite dangerous for the cell, and therefore the mechanisms of its removal from active metabolism and the formation of insoluble phytosiderin are included. In salt-resistant plants, which include crystal grass (*Mesembryanthemum crystallinum*), NaCl stimulates iron absorption, accumulation of ferritin and phytosiderin [Paramonova, 2013].

It has been established that in the crystal grass halophyte (*Mesembryanthemum crystallinum*) NaCl activates the development of the plasmolemma and tonoplast, thus increasing their adsorption surface and providing the cells with the main elements of mineral nutrition. It is quite likely that these features explain the information about the low concentration of iron in the environment, only in conditions of salinity, significantly more iron was supplied to the crystal grass plant, and an iron-containing protein - ferritin was detected [Paramonova, 2011].

It was shown that 0.3% soil chloride salinization had a significant inhibitory effect on the main parameters of growth, development and biological weight of several wheat varieties in different phases of vegetation. At the same time, salt stress caused a sufficiently wide range of changes in the formation of growth parameters and the total biological mass of wheat varieties. The results of vegetation experiments showed that soft wheat varieties were relatively more salt-resistant than durum wheat varieties [Atoev et al., 2016].

The possibility of growing grape varieties on saline soils has been studied. The studied varieties differed in the viability of the cuttings when the environment was salinized. Thus, in the Pinot Gris variety, in all variants with salinity, the growth of stems and roots was lower than in the control. In 10^{-2} M NaCl, the growth of stems was 82%, and in 10^{-3} M – 90% compared to the control. In

variants with sulfate salinity, the increase was lower: in 10^{-2} M – 60%, in 10^{-3} M – 73% compared to the control. The root growth of the same variety in variants with a higher degree of salinity differed greatly from the control and amounted to 32% in NaCl and 20% in Na_2SO_4 . In variants with a lower degree of salinity, root growth was slightly higher. Thus, in NaCl, the increase was 78%, and in Na_2SO_4 – 39% compared to the control [Alieva, 2010, 2011].

Accumulation of Cl^- , SO_4^{2-} anions was noted in all structures of grape plants. However, most of all it was manifested in the leaves. Varieties also differed significantly in the level of localization of anions. In some of them, chlorine ions are localized more in the roots, and sulfate ions – in the leaves and stem. Substantial differences in the reaction of seedlings in varieties to the type of salinity of the environment. They turned out to be more sensitive to sodium sulfate than to sodium chloride, which was manifested in the specificity of the terms of the formation of their roots and the growth of stems, the accumulation of the biological mass of neoplasms, the occurrence of salt burns of leaves and apices of stems. At the same time, in cuttings of varieties where the accumulation of anions occurs more in the above-ground part, there is suppression of both the formation of roots and the accumulation of biological mass of roots and stems [Mamedova, 2015].

During the adaptation of plants against man-made salinity (NaCl), there was an accumulation of low molecular weight organic compounds; in the zone of stable salinity, the amount of proline, monosugars, and sucrose in plants increased, compared to the zone of unstable salinity. The content of these osmoprotectants was higher in plants with reduced salt tolerance than in halophytes [Chetyna, 2011].

The change in the content of endogenous hormones in the halophyte plant - crystal grass (*Mesembryanthemum crystallinum* L.) - under the conditions of action of 400 mM NaCl for different durations was studied. Relatively high concentrations of zeatin, isopentenyladenine and free form of IOC were found in

the leaves of control plants of the crystal grass. At the same time, the level of zeatin riboside and ABA were extremely low, at the limit of sensitivity of the method. Salting for 6 hours led to some increase in the content of zeatin and bound IOC, approximately 1.5 times. The level of isopentenyladenine and the free form of IOC decreased sharply, tenfold, and the level of zeatin riboside and ABA also increased sharply [Vedenicheva et al., 2010].

A comparison of changes in the content of phytohormones in plants with different salt tolerance: the glycophyte *Phaseolus vulgaris* L. and the halophyte *Mesembryanthemum crystallinum* L. under the influence of NaCl was carried out. In the roots of *Phaseolus vulgaris* L., in the presence of 100-150 mM NaCl, the content of free ABA significantly increased and the amount of bound ABA decreased. The level of free IOC did not change significantly, while the level of bound IOC decreased by half at a NaCl concentration of 50 mM, and at a concentration of 100 mM, it increased by 3 times. A similar situation was observed in the leaves. Different concentrations of NaCl had the same differential effect on the content of cytokinins. In the roots, NaCl (50 mM) stimulated the growth of the level of zeatin, zeatin riboside, and zeatin glucoside tenfold, and 100 mM NaCl – no more than 3 times. Growing seedlings on a medium with 50 mM NaCl led to a decrease in the concentration of zeatin cytokinins, and with 100 mM – to its tenfold increase in leaves. Changes in the content of isopentenyladenosine in leaves and roots were similar to those for cytokinins of the zeatin series, while the level of isopentenyladenosine did not change significantly. Growing *Mesembryanthemum crystallinum* L. on a medium with 400 mM NaCl for 6 hours led to a 1.5-fold increase in zeatin content. The level of isopentenyladenosine decreased tenfold, while zeatyrbose and isopentenyladenine increased rapidly. Further exposure of the plants to a hypersaline solution caused the accumulation of zeatiriboside, isopentenyladenosine, and isopentenyladenine in the leaves. And the content of zeatin glucoside almost did not change. There was also a sharp drop in the level

of free IOC, and a 1.5-fold increase in the content of bound IOC. The biggest significant difference of the halophyte *Mesembryanthemum crystallinum* L. is a fairly low level of both free and bound ABA in the leaves of control plants and insignificant in absolute terms, but significant in comparison with the control, the accumulation of this hormone under the influence of NaCl salt [Vedenicheva et al., 2011].

The effect of 100 mM sodium chloride on growth, accumulation of biological mass, sodium ion content, ABA, stem/root mass ratio in plants of 4 varieties of barley (*Hordeum vulgare*): Golf, Prairie, Mikhailovsky and Krasnoyarsky-80 was studied. Measurements of the length of the stem and root, the mass of the growing third leaf and the total biological mass of the plants showed that salinity suppressed both the growth of the leaf in length and the accumulation of its biological mass. And also the biological mass of the plant as a whole. The growth rate of plants of the Mikhailovsky and Krasnoyarsk-80 varieties decreased to a greater extent than that of the Golf and Prairie varieties. A stronger decrease in the rate of accumulation of biological mass of roots was observed in plants of Mykhailovsky and Krasnoyarsky-80 varieties compared to plants of Golf and Prairie varieties, which was manifested in a sharp decrease in the ratio of stem and root mass in the first pair of varieties, and the stability of this indicator in the second pair. Maintenance of root growth is an adaptive response to water deficit that optimizes the ability of roots to absorb water, and it was more pronounced in plants of the Golf and Prairie varieties. Exposure of plants for 6 days to a salt solution led to the accumulation of sodium ions in all plant organs. The ion concentration at salinity was maximum in the formed leaves, lower in the roots, and lowest in the growing third leaf. The exceptions were plants of the Mikhailovsky variety, in which the level of accumulation of sodium ions in the roots and in the third leaf was the same. In the growing third leaf, more sodium ions were accumulated in the plants of the Mykhaylovsky and Krasnoyarsk-80 varieties, compared to the Golf and Prairie varieties. The lowest ion concentration

was in the growing third leaf of the Prairie variety, and the highest in the third leaf of the Krasnoyarsky-80 variety. At salinity, the content of ABA increased sharply, by 10 times, compared to the control, in the roots of plants of all studied varieties. In the formed second leaf, salinity led to an increase in the level of ABA, and this process was more pronounced in the plants of the Golf and Prairie varieties than in the Mikhailovsky and Krasnoyarsky-80 varieties. Thus, a higher resistance of growth processes against salinity in the Golf and Prairie varieties was correlated with a greater accumulation of ABA in mature leaves [Veselov et al., 2010].

The protective functions of proline as a chemical chaperone were evaluated when studying the influence of NaCl and copper on the activity of malate dehydrogenase enzyme *in vitro*. The concentration and time dependences of NaCl and CuSO₄ on the activity of malate dehydrogenase were previously studied. It turned out that under the action of 100 mM NaCl for 2 minutes, the activity of this enzyme was inhibited by 20%, at 300 mM – 65%. With a two-minute exposure to 0.1 nM CuSO₄, the activity of malate dehydrogenase decreased by 40%, and exposure to concentrations in the range from 10 nM to 1 μM led to a loss of activity by 60-70%. In the future, the optimal concentrations and the time during which proline restored the activity of the enzyme were selected. With the addition of 500 mM proline, complete recovery of malate dehydrogenase activity was observed after inhibition by 100 mM NaCl and 50% recovery of enzyme activity when inhibited by 300 mM NaCl. Under the action of CuSO₄, 500 mM proline restored the activity of the enzyme inhibited by 0.1 nM CuSO₄ by 20% in 10 minutes and by 30% in 60 minutes. Proline at a concentration above 1 M had a toxic effect on the activity of malate dehydrogenase. Thus, it was established that proline restored the activity of malate dehydrogenase, prionized by the action of NaCl and CuSO₄, acting as a chemical chaperone [Grynin et al., 2010].

Based on the sections of nucleotide sequences of *Arabidopsis* Rab proteins, primers were designed for amplification of the central fragment of the homologous protein and *Thellungiella salsuginea*. Using the selected primers, the

amplification of the central region of cDNA encoding *Rab7* in *Thellungiella salsuginea* was carried out. The resulting sequence was cloned using pGEM-T vector and *Escherichia coli* DH5 α strain and sequenced. The sequences of the untranslated regions of *Rab7* were determined by the RACE-PCR method. Analysis of *Rab7* expression by real-time PCR revealed a trend towards a slight induction in response to salt stress. The increase in the expression of this gene predicts the ability of *Thellungiella salsuginea* cells to adapt to stress conditions through the activation of vesicular transport. An electron microscopic study showed that the cells of *Thellungiella salsuginea* leaves under salinity conditions form microvacuoles in the cytoplasm, unlike control plants. It is quite likely that toxic substances formed under salinity conditions are removed from the cytoplasm of *Thellungiella salsuginea* cells in this way [Zhamaletdinov et al., 2010].

The method of induced chlorophyll fluorescence was used to assess the functional state of the photosynthetic apparatus of cells of the halotolerant monad algae *Dunaliella maritima* (Massjuk.) (department *Chlorophyta*) under conditions of hyperosmotic salt shock of varying intensity. The results of the experiments show that hyperosmotic salt shock leads to a decrease in the functional activity of the photosynthetic apparatus of *Dunaliella maritima* (Massjuk.), which is observed immediately after the shock, as evidenced by a decrease in the values of the indicator $(F_m - F_o)/F_m = F_v/F_m$. However, under conditions of moderate salt shock (1 M NaCl), the photosynthetic apparatus of *Dunaliella maritima* (Massjuk.) retains the ability to effectively carry out the primary separation of charges in 2 FS, because in this variant, all measured fluorescence parameters changed slightly and relaxed quickly enough to the initial level. A completely different situation was observed for cells subjected to a stronger shock effect (1.5 M NaCl and 2.5 M NaCl). In the variant of 1.5 M NaCl, significant disturbances of ionic and osmotic homeostasis in *Dunaliella maritima* (Massjuk.) cells, as well as a longer period of glycerol synthesis, necessary for restoring the

osmotic balance, caused a longer relaxation of chlorophyll fluorescence parameters. In the 2.5 M NaCl variant, irreversible changes in the fluorescence parameters of chlorophyll were observed, which is definitely associated with irreversible disturbances of ionic and osmotic homeostasis in cells of *Dunaliella maritima* (Massjuk.) under these conditions. The dynamics of changes in the rate of photosynthetic oxygen release by cells of *Dunaliella maritima* (Massjuk.) under conditions of hyperosmotic salt shock are similar to the dynamics of changes in the Fv/Fm parameter. In general, the results of the study demonstrate that changes in the parameters of the induced fluorescence of *Dunaliella maritima* (Massjuk.) chlorophyll under stress are dependent on the strength of the stress and correlate with the ability of this organism to restore intracellular ion homeostasis [Zahozhiy et al., 2010].

It has been shown that sodium sulfate inhibits not only cell stretching, but also the process of cell division. Thus, in non-transgenic tobacco, the mitotic index is almost halved, and in transgenic tobacco – by 18-27%, depending on the line. Thus, the action of sodium sulfate leads to the redistribution of interphase cells in the phases of the cell cycle, both in non-transgenic tomato and tobacco, and in transgenic ones. Moreover, in transgenic plants, the duration of the cell cycle is reduced to a lesser extent and there is an effect on the processes of division. A slower decrease in proliferation and delay of cells in the presynthetic phase indicates greater resistance of transgenic plants against these unfavorable growing conditions. In general, transgenic plants were more resistant to sulfate salinity compared to non-transgenic plants. Prolonged action of sodium sulfate showed that according to such parameters as the mitotic index and the distribution of cells by phases of the cell cycle, tomato has greater stability compared to tobacco [Kononenko et al., 2010].

An electron microscopic study showed that the cells of *Suaeda altissima* leaves under salinity conditions intensively form pinocytotic intussusceptions facing the vacuole, which later form multivesicular bodies. The use of a

cytochemical method for determining chlorine ions showed their presence in multivesicular bodies. With the help of multivesicular bodies, chlorine ions are loaded into the vacuole. At the same time, they can be transported into the vacuole both from the cytoplasm and from the apoplast. In *Thellungiella salsuginea*, in contrast to *Suaeda altissima*, the pinocytotic invaginations formed in leaf cells did not unite with the formation of multivesicular bodies, but remained in the cytoplasm. Attempts to detect chlorine ions by the cytochemical method in the cells of *Thellungiella salsuginea* roots and leaves were unsuccessful. It is quite likely that the concentrations of chlorine ions in *Thellungiella salsuginea* cells were below the sensitivity of the cytochemical method of determination [Kurkova et al., 2010].

It was established that the superproduction of proline in the halophyte *Thellungiella halophyla* both at the level of the whole plant and at the cellular level under superoxide stress acts as a "trap" of the superoxide radical, which could compensate for the low activity of superoxide dismutase in this plant in control and under conditions of salt stress [Bakulina et al., 2008].

Accumulation of sodium and proline ions in the cell sap of *Thellungiella salsuginea* (Pall.) OE Schulz. was 2 times higher than similar indicators for cells of *Arabidopsis thaliana* (Heynh.). And at the same time, an increase in the volume of the vacuoles of *Thellungiella salsuginea* (Pall.) OE Schulz cells was noted. and the presence of characteristic ultrastructural signs of a highly energized state of mitochondria. It is likely that *Thellungiella salsuginea* (Pall.) OE Schulz. implements the strategy of several "lines of defense" and resists salinity not only at the level of the whole plant, but also at the level of cells [Nosov et al., 2010].

It was found that moderate osmotic stress, as well as salt stress, causes quite significant accumulations of labeled phosphatidylbutanol in tobacco tissues at the early stages of action. It was also shown that transgenic tobacco plants expressing the *cax1* anti-reporter adapted significantly worse to conditions of moderate stress compared to unmodified tobacco plants. The obtained results indicate that for the

transduction of signals induced by the action of osmotic stress and initiated by the activation of phospholipase D, the participation of calcium ions is necessary. The role of phospholipase D and calcium ions in the processes of plant metabolism regulation under osmotic stress is currently being studied [Pokotylo et al., 2010].

The change in the content of phytohormones and polyamines in bean plants (*Phaseolus vulgaris* L.) grown in water culture under factorostatic conditions was studied. NaCl was added to the nutrient medium once to a concentration of 50, 100, 150, 200 mM and the effect of salinity (4 days) on growth indicators, the content of free and bound polyamines and phytohormones in two-week-old bean seedlings was studied. Raw weight of seedlings, linear dimensions of primary leaves and roots, as well as epicotyl decreased at all NaCl concentrations. In the roots under the action of 50 and 100 mM NaCl, the content of free putrescine decreased by 50-60%, and the level of its derivatives - spermidine and spermine - practically did not change. In leaves, on the contrary, at 50 and 100 mM NaCl salinity, an increase in free putrescine, spermidine, and spermine was noted. At a salt concentration in the medium of 150 mM, the content of cadaverine, spermidine, and spermine in the leaves decreased. Polyamines were not detected in the leaves of bean seedlings under the influence of 200 mM NaCl. The level of free cadaverine increased in leaves in the range of 50-100 mM salt and decreased under the influence of 150 mM NaCl. A concentration of 150 mM NaCl was toxic to the leaves and caused a sharp decrease in the content of all bound conjugates of polyamines, except for spermine. At the same time, in the roots, in the absence of changes in the fraction of free spermidine and spermine, their content in the conjugated form increased slightly, but the most significant accumulation in the bound form was manifested for cadaverine. The most significant changes were observed in the content of free ABA in the roots, and less significant changes in the leaves. In the presence of 100 mM NaCl in the roots, the content of free ABA increases and the amount of bound ABA decreases. The level of free IOC in the roots under salinity conditions did not change significantly, and in the bound form

the level of IOC decreased by half at a NaCl concentration of 50 mM, and at a concentration of 100 mM it increased 3 times. The content of free and bound IOC in the leaves changed in a similar way: in the presence of 50 mM NaCl, the concentration of this hormone decreased, and at 100 mM, it increased by 1.5-1.8 times. A sharp ten-fold increase in the level of zeatin, zeatin riboside, and zeatin glucoside under the influence of 50 mM NaCl was found in the roots, while the content of these cytokinins increased no more than 3 times when salinized with 100 mM NaCl. In leaves, the exposure of seedlings in the presence of 50 mM NaCl led to a decrease in the concentration of zeatin cytokinins, and at 100 mM - to its sharp increase tenfold. Changes in the content of isopentenyladenosine in leaves and roots were similar to those for cytokinins of the zeatin series, while the level of isopentenyladenosine did not change significantly. A positive correlation was also established between the accumulation of ABA and cadaverine during salting of bean seedlings [Stetsenko et al., 2010].

The obtained results on the content of free and conjugated forms of polyamines indicate that bean plants, as a representative of the glycophyte plant group that is not resistant to salinity, are able to adapt to NaCl like halophytes with the participation of polyamines, but within much narrower limits of salinity. At the same time, a distinctive feature of bean plants is the inclusion in the adaptation process of the product of oxidative degradation of high molecular weight polyamines – HClO₄ – insoluble conjugate – 1,3-diaminopropane, which accumulates in leaves exclusively in the form of HClO₄ – insoluble conjugate. It is quite likely that the identified adaptation mechanism is due to the high protein content in leguminous plants and is aimed at protecting protein molecules from oxidative degradation under stressful conditions [Shevyakova, Stetsenko, 2010].

Haematococcus pluviialis strain IBCE H-17 was studied for the induction of accumulation in cells of the keto-carotenoid astaxanthin under conditions of excess salinity of the nutrient medium of 25, 50, 100, 200 and 300 mM NaCl. In parallel with this, the performance of *Haematococcus pluviialis* was evaluated

based on indicators of dry biological mass and protein, the content of photosynthetic pigments and ROS. NaCl in concentrations of 25, 50, and 100 mM stimulated the accumulation of dry biological mass of algae during 12 days of cultivation by an average of 1.3 times, compared to the control. The protein content in terms of dry biological mass decreased and averaged 70% of the control on the 7th day of cultivation when using 50-300 mM salt and 55% on the 12th day for salt concentrations of 100-300 mM. After 7 days of growing in NaCl solutions, the total number of photosynthetic pigments - chlorophyll a and b, as well as carotenoids - neoxanthin, violaxanthin, lutein and β -carotene decreased. Chlorophyll b turned out to be more resistant to salinity, compared to chlorophyll a. The level of β -carotene decreased the most under the influence of NaCl. Stress conditions caused by NaCl led to the generation of ROS. Thus, after 7 days of cultivation, the total ROS content in the "NaCl-100" variant was 1.7 times higher than that in the control and was 3 times higher than the control in the 12-day culture. A significant positive effect of NaCl on astaxanthin content was also noted. The maximum effect was observed when using 100 mM NaCl. After 7 days of cultivation, the content of astaxanthin exceeded the control indicators by 2.8 times, and after 12 days - by 20.5 times. The number of algae cells after 7 days of cultivation in the "NaCl-100" variant decreased by an average of 33%, while the diameter of the cells increased by 29% [Averina et al., 2018]. It is known that the pigment system of plants, in addition to chlorophylls, contains carotenoids that absorb light in the blue spectrum and protect the photosynthetic apparatus from photodestruction, as well as perform other protective functions [Sun et al., 2018]. To study the role of these pigments in ensuring plant resistance to stress, it is proposed to use *hairy roots* model systems overexpressing various genes involved in the biological synthesis of anthocyanins [Mykhaylova et al., 2019].

Carotenoids are natural organic pigments synthesized by bacteria, fungi, algae and plants. Currently, about 600 types of carotenoids have been identified, which are divided into two classes: xanthophylls and carotenes. They are mainly

yellow, orange or red in color, and according to their structure, they are cyclic or acyclic isoprenoids [Blazhey, Shuty, 1977, Britton, 1986]. Isoprenoids are terpenoids, natural compounds from the group of lipids that are formed in living organisms from mevalonic acid. Formally, all isoprenoids are polymers of the hydrocarbon isoprene, which, however, does not participate in isoprenoid metabolism. The construction of the carbon skeleton of isoprenoids occurs in living cells by sequential enzymatic condensation from mevalonic acid. The enormous structural diversity of isoprenoids is due to the ability of the primary condensation products to cyclization, oxidation, reduction, rearrangement reactions, as well as to the inclusion or elimination of one or more one-carbon fragments and to joining other cell metabolites (so-called mixed isoprenoids). According to the structural feature, isoprenoids are divided into subclasses of terpenes (monoterpenes), sesquiterpenes, etc. There are many physiologically active substances among isoprenoids: antibiotics, vitamins A, D, E, K, hormones and hormones, bile acids and alcohols, cardiogenic substances, pheromones, pigments, including those involved in photosynthesis [Britton, 1986].

Under the influence of chloride salinization, the studied wheat varieties show some signs of plants with C₄-type metabolism. It is shown how the adaptive reaction in plants of the experimental variant activates the PEP-carboxylation process, as a result of which a significant amount of labeled carbon is concentrated in C₄ products. In addition, chloride salinization, activating the RBFC/O oxygenation reaction, at the same time inhibits the activity of the carboxylation reaction, as a result of which a significant proportion of the label (¹⁴C) is included in the intermediate products of the glycolate pathway, i.e., the process of photorespiration increases [Atoev et al., 2014] .

In halotolerant marine microalgae of the genus *Dunaliella* growing in environments with a high NaCl content (seawater, salt lakes), ion homeostasis of the cytoplasm is ensured by P-type ATPases functioning in the plasma membrane of these organisms. Specifically, two P-type ATPases, H⁺-ATPase and Na⁺-

ATPase, were functionally identified in the plasma membrane of the marine microalgae *Dunaliella maritima* [Popova et al., 2000, Popova et al., 2005]. A change in the activity of the proton pumps of the tonoplast can be carried out by changing the redox conditions surrounding the enzymes. In addition, the activity of H⁺-ATPase can be regulated by proteolytic enzymes, since an anti-inhibitory domain was found in its structure, the removal of which stimulates the activity of the enzyme. When comparing changes in the physiological activity of proton pumps of the tonoplast under the influence of ions and phytohormones, it was established that ionic regulation for H⁺-pyrophosphatase is more significant than hormonal regulation, and vice versa for H⁺-ATPase. In conditions of ionic stress, phytohormones can support the activity of tonoplast proton pumps [Ozolyina, 2005].

Na⁺-ATPases [IIW1]P-type were found in two species of marine green microalgae: *Tetraselmis viridis* and *Dunaliella maritima*. Enzymes were identified at the functional level in experiments on isolated plasma membrane vesicles. It was demonstrated that plasma membrane vesicles are capable of ATP-dependent accumulation of sodium ions [Popova, Balnokin, 2016]. Since namely Na⁺-ATPases [IIW2] ensure ion homeostasis in marine microalgae, and, accordingly, the survival of these organisms in a salty environment, it is very unlikely that the transcripts in *Dunaliella tertiolecta* Na⁺-ATPase are rare transcripts and because of this were simply lost in the process of instrumental analysis. Based on this, as well as on the basis of a comparative analysis of the primary structure of ATPases, it is believed that one of the putative proteins attributed to H⁺- or Ca²⁺-ATPases is Na⁺-transporting ATPase [Popova et al., 2016].

The latter, as a specialized Na⁺-transporting mechanism, is a rather important determinant of the salt tolerance of this organism, removing excess sodium ions from the cytoplasm into the external environment against the gradient of the electrochemical potential of this ion. The Na⁺-ATPase gene of *Dunaliella*

maritima has not yet been identified, but Na⁺-transporting ATPase genes have been identified in a number of other organisms. However, the hypothesis that of the two H⁺-ATPases whose transcripts were found in *Dunaliella tertiolecta* transcriptome, one enzyme transfers protons, while the other can transfer sodium ions [Garcia-deblas et al., 2010, Uji et al., 2012, Matalyn et al., 2015].

It was demonstrated that an important contribution to the export of Na⁺ and Cl⁻ from the cytoplasm is made by the transport of substances with the help of vesicles. Two branches of vesicular transport (endocytosis and the secretory pathway) are involved in the regulation of the content of ion transporters in membranes, and thus in the maintenance of Na⁺ and Cl⁻ homeostasis of cells. The content of ion transporters in membranes changes in response to external stimuli, specifically, to changes in NaCl concentration in the environment and is regulated by internal factors, for example, Rab5 small GTPases. Along with the regulation of the content of ion-transporting proteins in the membranes, the vesicles carry out the direct transfer of Na⁺ and Cl⁻ to the vacuole, thus lowering their concentrations in the cytoplasm. It is also shown that under conditions of salt shock, due to endocytosis, the internalization of sodium ions that are in the external environment occurs, with the subsequent fusion of Na⁺-containing endosomes with vacuoles. This process is especially common in halophytes [Balnokin et al., 2019].

In the tomato *Solanum lycopersicum* variety Naomi, the concentration of sodium in the xylem of the stem increased to 31 ± 8 mm against 0.5 ± 0.2 mm in the control, which was accompanied by a decrease in the hydraulic conductivity of the leaves to 11.6 ± 2.5 mmol/m² sec⁻¹ versus 22.2 ± 1.6 in the control [Trifilò et al., 2013]. A hypothesis was proposed, according to which the increase in the concentration of cations in the xylem sap affects the water flow in the xylem of plants due to the electrostatic effect in the conducting vessels [Van Doorn et al., 2011]. Weak salinity, regardless of the level of moisture availability, led to a decrease in the mass of stems and roots of soybean plants. As a result of

salinization, the dry density of the stems of soybean plants increased. Deficiency of moisture supply, both on a non-saline background and with salinity, did not have a significant effect on the dry mass of stems and roots, as well as on the dry density of the stems of soybean plants [Kharchuk, Kirillov, 2014].

With moisture deficiency, the relative turgescence of leaves decreases to critical values (~0.6), and the leaf surface decreases, compared to the moisture-provided control, already during the first (flowering phase) of the dry period (35% RH) both on a non-saline background and with salted. Before the phase of seed filling, the leaves of the plants of all variants of the experiment basically completed their growth, and the effect of the second drought is expressed in the acceleration of leaf fall and in a significant decrease in the seed productivity of the plants. Weak salinity, depending on the level of moisture availability, leads to a significant decrease in the leaf surface of plants already at the beginning of the growing season, even before the first drought, and during the second drought, in the phase of seed filling, leaf fall slows down [Kharchuk et al., 2014].

It was shown that, unlike cadmium and zinc, which were more positive for the growth and development of pumpkin plants during salinization at the last two stages of the experiment (14 and 21 days) than each separately, in the case of copper, the plants experienced a synergistic, more intense inhibitory effect from their complex interaction. This was manifested in a decrease in plant turgor, necrotic spots on the leaves and darkening of the roots, in a decrease in growth parameters and a sharp decrease in the accumulation of biological mass by roots and above-ground organs, especially roots. All this indicates a relatively high susceptibility of pumpkin roots to copper-induced toxicity, especially in the presence of NaCl, and, in general, a low species-specific tolerance of *Cucurbita pepo* against copper under salinity conditions [Shirvany et al., 2014].

Since it is believed that plants of the genus *Atriplex* are characterized by higher salt tolerance than the other two studied species, it can be concluded that the increase in the content of sodium ions in the soil does not have an inhibitory

effect on the accumulation of flavonoids by plants of this species. On the contrary, in the closely related and less salinity-resistant plant species *Bassia sedoides* and *Kochia prostrata*, inhibition of the accumulation of flavonoids in response to an increase in the content of sodium ions in the soil was found [Shcherbakov et al., 2014].

According to the results of the research, it was established that heat treatment at a temperature of 41-51 °C of cucumber seeds of Fenix and Palchyki varieties increased the resistance of seedlings to both salts (0.001mM CuSO₄ and 0.01mM ZnSO₄) regardless of the variety. However, the degree of salt tolerance of cucumber plants depended on the temperature regime of seed heating [Hadzhieva, 2011]. As a continuation of these studies, the effect of heat treatment of seeds (51 °C) for one hour on the salt tolerance of seedlings of different genotypes of monocotyledonous and dicotyledonous cultivated plants was studied: tomato (Moskvych, Krakus varieties), cucumber (Feniks, Parad varieties), lentils (Obyknovenny variety), triticale (Magnat, Soyuz varieties), wheat (Rht 1, Rht 9). As a result of the conducted research, it was found that the reaction of the seedlings of monocotyledonous and dicotyledonous cultivated plants to the salinity of the environment is of the same type. Inhibition of growth processes depended more on the concentration and ionic composition of salts (NaCl (150-200 mM) and CuSO₄ (5-10 mM)) than on genotypes. Heat treatment of seeds induced an increase in the level of proline in roots and an increase in salt tolerance of seedlings [Hadzhieva, 2013].

According to the results of a cytological study during in vitro cultivation of tomato seedlings of both genotypes (Recordsman variety, YLF line) in an environment with a high level of chloride salinity (25 mM, 50 mM, 75 mM, 100 mM, 150 mM, 200 mM, 250 mM and 300 mM), the volume of epidermal cells, columnar and spongy mesophyll cotyledons significantly decreased [Bogoutdinova et al., 2013].

According to the results of the histological study, significant differences were established between the investigated tomato genotypes in terms of the size and shape of epidermal and parenchymal cells of the hypocotyl cortex. The effect of toxic Na^+ and Cl^- ions revealed a significant effect on the size and shape of hypocotyl epidermal and parenchymal cells in both genotypes. Genotypes also differed among themselves and in the volume of intercellular spaces in the parenchyma of the hypocotyl bark under salinity conditions. In general, based on the obtained indicators, it can be concluded that epidermal and parenchymal cells of the hypocotyl of the Recordman variety tomato were less sensitive to the presence of toxic ions in the environment. The obtained experimental information is consistent with the previously obtained results, which showed that the reaction of cells of certain types of tissues to chloride salinity varies greatly not only when comparing plants of different species, but also strongly depends on the characteristics of specific analyzed genotypes of the same species [Bogoutdinova et al., 2015].

The effect of hyperosmotic shock on the fatty acid composition of the lipids of the leaves and roots of the salt-accumulating halophyte *Suaeda altissima* was studied. It was shown that hyperosmotic shock caused quite significant changes in the quantitative fatty acid composition of lipids in both leaves and roots, but had practically no effect on their qualitative composition. In the roots, the shock caused some decrease in the amount of lipids, which reached its minimum up to 6 hours after the action, but this decrease was much less pronounced than in the leaves [Ivanova et al., 2011].

In the conducted studies, parameters were used that characterize the dynamics of the passage of cells in the root meristem of seedlings through the cell cycle: cell ploidy, the distribution of cells by interphase periods, the area of nuclei and cells of the root meristem, as well as the morphology of cells of the palisade parenchyma of *Thellungiella* and *Arabidopsis* leaves. It is shown that the area of the nuclei of *Thellungiella salsuginea* cells in the control is approximately two

times greater than the area of the nuclei of *Arabidopsis thaliana* cells, which indirectly indicates a doubling of the chromosomal material in *Thellungiella salsuginea* nuclei. Chloride salinity causes an increase in the area of nuclei, and sulfate salinity – a decrease, compared to the control. Under the influence of salinity, the area of root cells and palisade parenchyma cells in the cotyledon leaves of *Thellungiella salsuginea*, as well as in *Arabidopsis thaliana*, increases with chloride salinity and decreases with sulfate salinity. Cytophotometry showed that in the root system of *Arabidopsis* under the influence of high concentrations of salts, the number of cells in the G1 and S phases decreases, compared to the control, the number of cells increases in the G2 phase, especially significantly in seedlings grown under conditions of sulfate salinity (3 times). In the root meristem of *Thellungiella salsuginea*, a decrease in cells in the G1 and S phases was observed, compared to the control, and the number of cells in the G2 phase increased. In *Thellungiella* plants grown at high concentrations of NaCl and Na₂SO₄, no differences in the distribution of cells by phases were found, compared to the control. However, compared to *Arabidopsis thaliana* and *Thellungiella salsuginea* plants, under conditions of sulfate salinity, the number of cells in the S phase increases by 2.5 and 1.3 times, respectively, and in the G2 phase decreases by 2.4 and 1.8 times [Kononenko et al., 2011].

It was established that plants of both species of the genus *Nigella* (*N. damascena* and *N. sativa*) showed susceptibility to recovery of growth processes after a period of moderate or medium salinity intensity (70 and 150 mM NaCl, respectively) and only *Nigella damascena* plants were not recovered to a large extent after strong salinization (150 mM NaCl). One of the probable reasons for the better ability of *Nigella damascena* plants to recover after strong salinity may be the more intensive use of previously accumulated proline as a source of organic nitrogen during this period [Gogue, Kholodova, 2013].

It was shown that the combined effect of water and salt stress was characterized by the existence of a certain critical level of salt concentration in the

plant growing environment (0.1 M), upon reaching which the positive effect of NaCl changed to a sharply negative one, enhancing the effect of drought [Ivanov, 2013].

It was found that concentrations of 25 and 50 mM/l NaCl have opposite effects on tobacco plants (*Nicotiana tabacum*). A concentration of 25 mM/l activates the antioxidant system and the body's protective reactions. Conversely, 50 mM/l has an inhibitory effect on enzyme activity. as it exceeds the limits of plant resistance. Enzyme activity correlates with cell wall thickness and lignification processes: in plants cultivated at a concentration of 25 mM/l, cell wall thickness and root diameter increase, while growth processes are inhibited at 50 mM/l NaCl [Tugbaeva et al., 2018].

In the *in vitro* culture, the indicators of rhizogenesis and the relative accumulation of the biological mass of tissues had the greatest connection with the object's salt resistance. Using the example of tomato and cucumber, it is shown that the intervarietal differences that are manifested in the reaction of seedlings are less pronounced in cuttings, and even less so in explants *in vitro*, which can be associated with a significant contribution of the organismal level to the regulation of salt tolerance and the intensity of salt accumulation in eorenia The analysis of differences in the threshold sensitivity of structures against stresses is the result of individual differentiation and allows us to judge the rather complex nature of the ecological stability of plants [Alieva, 2015].

The studied wild species of halophytes (*Salicornia perennans* Willd., *Suaeda physophora* Pall. *Anabasis aphylla* L., *Limonium gmelinii* (Willd.) Kuntze, *Limonium caspium* (Willd.) Gams, *Halocnemum strobilaceum* (Pall.) M. Bieb., *Artemisia santonica* L., *Artemisia lerchiana* Weber in Stechm., *Artemisia pauciflora* Weber in Stechm., *Atriplex cana* CA Mey.), growing in the conditions of Prieltonnia, differ not only in their systematic position, salt accumulation strategy, but also in the content of amino acids, including free ones. A characteristic feature of halophytes is a high level of "stress" amino acids, for

glycohalophytes and crinohalophytes it is a high content of proline, and for euhalophytes - alanine and γ -aminobutyric acid [Tabalenkova et al., 2015].

It is likely that chloride salinity, activating the oxygenation reaction of RBFC/O, simultaneously suppresses the activity of the carboxylation reaction, as a result of which a significant proportion of carbon is included in the products of intermediates of the glycolate pathway, i.e., the process of photorespiration increases. In conditions of salinity with a high concentration of NaCl, the intensity of photosynthesis decreases, and the intensity of respiration increases, and at the same time, the carbohydrate orientation of metabolism increases. This is evidenced by the significant inclusion of carbon in sucrose in the chloride salinization variant [Ergashev et al., 2015].

The change in stomatal conductance, leaf growth rate, and ABA content in wheat and barley plants with a sharp decrease in the water potential of the nutrient solution due to the addition of sodium chloride was studied. It was established that the initial reaction of the plants consisted in the rapid transmission, during the first minutes, of a hydraulic signal from the salted roots to the stem, as a result of which the subsequent reactions took place. Since the external signal, that is, the level of salinity, was the same in the case of plants of both varieties, the differences in the level of the hydraulic signal entering the stem of the plants were probably due to the specific features of the hydraulic conductivity of plants [Veselov et al., 2008].

The increase in sensitivity against salt stress of organs and structures and intact cucumber seedlings correlates with the simplification of their organization. Even a decrease in the number of metamers in intact seedlings reduces their resistance to salinity. The reaction of structures and organs to the content of salts varies depending on their status - in an isolated state or as part of a complex system of intact seedlings. Disturbances in the metabolism of leaves under the influence of a stressor with a complication of the level of system organization are expressed less intensively. The increase in interaction between organs during ontogenesis

probably induces protection mechanisms of a different nature, which is realized by higher salt resistance of seedlings with a greater number of metamers [Hadzhieva, Mamaev, 2008].

It has been shown that plants with high peroxidase activity and the ability to intensively accumulate proline can adapt against salt shock caused by a 24-hour stress of 100 mM NaCl, regardless of the level of superoxide dismutase activity [Radyukina, 2008].

The organ specificity of proline accumulation under salt stress has been demonstrated. The significant increase in the amount of this amino acid in the roots can be explained by the fact that they are the first to experience the negative effects of salinity, and they also contain less water than cotyledons and hypocotyls. Thus, it can be predicted that the proline content in the roots better shows the reaction of the plant to the action of the stress factor, as the leaves are additionally affected by the surrounding environment [Kolomeychuk et al., 2016].

The involvement of polyamines in the adaptation of bean seedlings to salinity was expressed in the transient increase in the content of putrescine, spermidine, spermin, and cavaderin in the leaves in free and conjugated form, as well as in the formation of the conjugated form of diaminopropane [Stetsenko, Shevyakova, 2008].

It was established that overexpression of the aquaporin gene increased the ability of tobacco leaf cells to absorb water in the case when osmotic regulation maintained the water potential gradient. And when osmoregulation did not work, and there was a reverse flow of water from the cells, the increase in membrane permeability due to the additional expression of aquaporin negatively affected the hydration of leaf tissues, increasing water loss. Thus, depending on the intensity of stress, membrane permeability increased due to the expression of aquaporins can play both a positive and a negative role [Kuluev et al., 2016].

It was found that acidification of the cytosol in the roots of *Arabidopsis* grown under salinity occurs in the lateral cells of the cap, cells of the rhizoderm,

cortex and endoderm of the absorption zone. In the cells of the columella and the cells of the cap, which cover the zones of division and stretching, no change in pH was noted [Ageeva et al., 2019].

The polymer matrix of the outer compartment of the cell with its ion exchange capacity takes an active part in the formation of the plant resistance mechanism against extreme conditions of mineral nutrition, including in response to salinity [Meychyk et al., 2019].

The ratio of monogalactosyldiacylglycerol to digalactosyldiacylglycerol (MGDH/DGDH) of photosynthetic plant lipids can be used to assess cellular resistance to salt action, specifically, to NaCl. The role of thylakoid lipids is quite closely connected with the functioning of the photosynthetic apparatus - with the maintenance of the oligomeric structure of the FS and the light-harvesting complex. It is believed that these lipids play a rather important role in stabilizing highly curved areas of membranes. The difference in the structure of MGDH and DHDH determines their ability to form lamellar and non-lamellar structures in chloroplast membranes. DHDH molecules are able to form a bilayer, and MGDH form a monolayer in the membrane, and therefore a change in the MGDH/DHGH ratio can affect the structure and microviscosity of membranes, as well as the formation of grains. In the studies, it was established that the salinity of the environment is accompanied by a decrease in the values of the MGDH/DGDH ratio in the membranes of photosynthetic organs, both halophytes and glycophytes. Conversely, plants grown without adding NaCl to the medium have higher values of the MGDH/DGDH ratio: as a rule, 1.4-1.6 times or more [Nesterov et al., 2019].

Autophagy is a necessary component of the cellular stress response and adaptation against adverse factors. The development of autophagy in response to salt stress is preceded by the release of potassium ions from the cells, but the mechanism of this connection is still not fully understood. TOR kinase is one of the most important switches of ana- and catabolic processes in eukaryotes. If the

activity of TOR depends on the supply of potassium ions to the cell, then this may clarify the mechanism of triggering autophagy under stress. The dependence of TOR activity on the concentration of potassium ions in the growing medium was investigated. For this, the *Arabidopsis thaliana* line with overexpression of the TOR kinase substrate S6K was used. The total protein S6K and the relative content of its phosphorylated form were compared. We also compared the intensity of autophagy activation in Col-0 and Ws-0 *Arabidopsis thaliana* ecotypes with different salt tolerance: in the roots of plants exposed to salt stress, the number of autophagosomes was counted and the expression levels of AtATG and AtGORK genes were determined. To reveal the role of GORK potassium channels – the sites of potassium ion release from cells – in salt tolerance of ecotypes, gork knockout mutants of both ecotypes were analyzed under the same conditions [Rabadanova et al., 2019, Tyutereva et al., 2019].

The influence of NaCl on tissue structure and the level of lignification of cell walls of *Zinnia elegans* Jacq was revealed. The plants were grown in soil for 50 days, spraying with NaCl solution at a concentration of 25 (I) and 50 (II) mM/l or with water (control). The height of plants in options (I) and (II) decreased by 11% and 37%, respectively. In (I), there was an increase in the diameter of the root, stem at the level of the hypocotyl and the first internode by 31%, 7.5% and 17.7%, and the thickness of the cell wall did not change. In (II), the thickness of the root did not change, and the diameter of the hypocotyl decreased by 13.9%, the diameter of the first internode – by 27.8%. There was also a reduction in the diameter of the stele in relation to the diameter of the root by 1.18 times. The diameter of the bundle relative to the diameter of the stem (hypocotyl and first internode) decreased by: 1.68 and 1.34 times, respectively. The thickness of the cell wall of the xylem vessels increased. Under the influence of 50 mM/l NaCl, the content of total lignin in stem tissues increased by 38%, Klason lignin – by 57%, and acid-soluble lignin decreased by 25% [Tugbaeva et al., 2019].

Some physiological and biochemical parameters were studied in the leaves of *Avena sativa* L. oat under the separate and combined action of salinity (100mM, 200mM NaCl) and different pH levels of the root medium (pH = 3; pH = 6.5; pH = 10). After 30 minutes, an increase in the content of hydrogen peroxide was noted in all experimental variants. The activity of catalase and peroxidases increased under the separate action of the studied factors of the root environment. Against the background of combined stress, no significant increase in the activity of these antioxidant enzymes was found in plant leaves. The content of proline in the above-ground organs of seeded oats increases with an increase in the NaCl concentration in the root medium under a neutral reaction and decreases in acidic and alkaline medium. It is quite likely that the imbalance between ROS-generating systems and antioxidant defense systems in the combination of unfavorable conditions of the root system is connected with insufficient amount of time for the formation of an adaptive response. The combination of salinity and the acidic reaction of the root medium showed the most negative effect on growth indicators of oats [Chetyna, Akbulyakova, 2019].

The influence of salinity on the level of aquaporins and ABA in barley varieties Prairie and Mykhaylovsky, which are contrasting in terms of salt tolerance, grown in water culture was studied. Salinity was induced by adding sodium chloride to the final concentration of 100 mM. The immunolocation method was used to detect aquaporins and the phytohormone ABA. At the same time, a decrease in the activity of aquaporins in leaves was observed in response to salinity against the background of an increase in the level of ABA. The addition of sodium chloride reduced the level of staining with aquaporins in plants more resistant to salinity of the Prairie variety by almost 3 times and only by 1.5 times in plants of the Mikhailovsky variety, which corresponded to a faster decrease in transpiration in plants of this variety. The results of immunohistological localization showed an increase in the content of ABA in leaves under the influence of salinity, which may be associated with a decrease in water inflow due

to a decrease in the level of aquaporins under these conditions [Sharypova et al., 2019].

Chlorine ions participate in the formation of proton channels in the active center of the water-oxidizing complex. Extraction of chlorine ions is considered to be the main cause of inhibition of PS 2 activity when the pH is increased. Luminal carbonic anhydrase CAH3 can complicate the exchange of chlorine ions between the environment and the active center of the water-oxidizing complex, supporting the functioning of PS 2 [Shukshina, Terentyev, 2019].

A morphometric analysis of regenerated tomato roots under salinity conditions was carried out. A slight decrease in the frequency of root regeneration (up to 93.3%) was found on the nutrient medium with the addition of 250 mM NaCl. High concentrations of sodium chloride (from 150 mM and higher) led to an increase in the period of the start of root organogenesis in the studied genotype. A significant decrease in root length in tomato seedlings of the Recordman variety was observed at 100 mM NaCl, and a decrease in the number of roots compared to the control was recorded only at concentrations of 150-250 mM NaCl. An inverse relationship between the raw biological mass of roots and the degree of salinity was revealed. A decrease in the raw biological mass of regenerated roots occurred only when minimal concentrations of NaCl were added to the nutrient medium, while a significant decrease in the dry biological mass of roots was noted when cultivated on a medium containing 100 mM NaCl. As a result of the cytological study, a decrease in the area of the cover cells was revealed when the nutrient medium contained 75, 100, and 150 mM NaCl. In addition, under the action of 25, 100, and 150 mM sodium chloride, vacuolization of the cytoplasm of the cells of the cap and cortex was noted, and under the action of 75 mM NaCl - vacuolization of the cytoplasm of the cells of the cap. Under the influence of 25, 75 and 150 mm NaCl, a decrease in the thickness of the roots due to a decrease in the size of the cells was established. Under conditions of salt stress, bundles of cortical microtubules of interphase root cells lost their orderliness, were cut

through, and in part of the cells were located at an angle to the axis of division. Long-term exposure to 25, 50, and 75 mM NaCl led to the appearance of short bundles and accumulations of tubulin, and at 150, 200, and 250 mM NaCl, heterogeneous cortical bundles were formed. In the mitotic cells of the root, a violation of the structure of the preprophase ring, a thinning of bundles of microtubules of the division spindle, a violation of the structure of the phlegmoplast and the process of cytokinesis were found. Thus, in the course of the research, changes in the morphometric parameters and structure of the roots, as well as the features of the microtubule systems of the Recordsman variety tomato were shown under the negative effect of salt stress caused by different concentrations of sodium chloride *in vitro* [Bogoutdinova et al., 2017].

Experimental studies showed that the response of plants to the alkalization of the root system is an increase in the total acidity of the plant extract with the accumulation of oxalic acid; in combination with salinity, the change in this indicator increased even more [Botalova et al., 2017].

Analysis of gas exchange showed a high potential for adaptation of the photosynthetic apparatus in *Urochondra setulosa*. The main mechanisms of salt tolerance are the excretion of salt through the salt excretory glands and the accumulation of osmolytes. The inclusion of both NaCl and KCl in the study showed that, most likely, the same mechanisms are involved in the development of stability and excretion of potassium and sodium ions, despite the fact that sodium is toxic to the cell, and the concentration of potassium must be maintained at sufficiently high level [Voznesenskaya et al., 2017].

It was shown that in the range of NaCl concentrations from 50 to 125 mM, potato plants sought to maximally activate defense systems to combat stress. A critical concentration of 150 mM led to irreversible damage at various levels of the organization. At the same time, plants managed to "control" the intensity of oxidative stress at weak and moderate salinity due to the accumulation of proline and antioxidant enzymes [Efimova et al., 2017].

It was found that under the influence of salinity, some structural, physiological and biochemical parameters in species with an intermediate type of photosynthesis shift to the side characteristic of C4 species. This allows us to consider salinization in combination with high insolation as one of the main driving forces in the transition from C3 to C4 in the genus *Salsola* (*Salsola deschaseauxiana*, *Salsola gymnomaschala*, *Salsola verticillata*, *Salsola divaricata*) [Koteeva et al., 2017].

It was shown that despite the differences in the type of photosynthesis (*Spartina anglica* and *Urochondra setulosa* C4 species, and *Oryza coarctata* - C3), all three studied cereal species have high resistance and even induction of photosynthesis when grown with NaCl. At the same time, the expression of the main photosynthetic enzymes (PPDK, PEPC, NAD-ME, PEP-CK, Rubisco) and the enzyme of the photorespiratory cycle, glycine decarboxylase, does not change significantly under salinity. Salt excretory glands are located on both sides of the leaf in *Spartina anglica* and *Urochondra setulosa*, and only on the adaxial side – in *Oryza coarctata*. The studied species differ significantly in the anatomy and ultrastructure of the glands: they are bicellular in *Spartina anglica* and *Urochondra setulosa* and unicellular in *Oryza coarctata*. At the same time, the glands of *Urochondra setulosa* do not have labyrinths of the cell wall in the apical part of the secretory cell, unlike the glands of the other two species. For *Oryza coarctata*, it has been proven that the numerous hairs on the adaxial surface of the leaf are not secretory and do not accumulate salt, which contradicts the generally accepted imagination. It is also shown that the three studied species accumulate osmolytes under salinity conditions, but their composition is markedly different. The main osmolyte of *Oryza coarctata* is proline in the complete absence of glycine-betaine synthesis. *Urochondra setulosa* is characterized by a low content of proline, which increases in salinity conditions, but the main osmolyte is glycine betaine. In *Spartina anglica*, both osmolytes are synthesized with an increase in their content in response to salinity. *Oryza coarctata* lacks expression of betaine

aldehyde dehydrogenase; in *Urochondra setulosa* and *Spartina anglica*, its expression increases under salinity conditions. Thus, all three studied types of cereals are resistant to salinity in maintaining the function of photosynthesis and water balance. The main mechanisms of salt resistance in them are the removal of salt through the salt excretory glands and the accumulation of osmolytes, but these species differ in the structure of the secreting glands and the composition of osmolytes [Koteeva et al., 2017a].

It has been shown that the glycohalophyte *Artemisia santonica* L. is characterized by the localization of sodium ions mainly in the root tissues, while potassium and chlorine ions are localized in the aerial part [Omelchenko, Zhizhina, 2017].

As a result of the conducted observations, it was established that photoreceptors are not only involved in the growth of primary roots and germination of *Arabidopsis thaliana* (L.) Heynh. under the influence of salt stress, but can also affect the salt tolerance of adult plants. Based on the positive trend towards salt tolerance in phototropin and cryptochrome mutants, it can be said that light is indeed a stress factor for plant growth under salinity conditions. At the same time, it should be noted that light is also a signaling factor that helps avoid salt stress, which is clearly visible in the inhibition of germination and growth of the primary root of phytochrome mutants. The determining factor of salt tolerance is most likely the spectral composition and intensity of light received by both the stem and the root [Stryzh, 2017]. At the same time, it was established that if the intensity of light outweighs the need for photosynthesis, it is precisely carotenoids that help dissipate excess energy, protecting the photosystem from damage [Demming-Adams, Adams III, 1996; Croce, van Amerongen, 2014].

Carotenoids are auxiliary photosynthetic pigments that are present in all phototrophic organisms and perform protective and structural functions. According to their structure, carotenoids are terpenoid compounds - tetraterpenes

and tetraterpenoids, which are formed as a result of the condensation of eight isoprenoid units. Formally, they are products of hydrogenation, dehydrogenation, cyclization, oxidation, or their combination of the acyclic precursor Ψ, Ψ -carotene (lycopene) [Britton, 1986]. According to the presence of substituents, they are divided into two groups: simple hydrocarbon compounds – carotenes and their oxidized derivatives – xanthophylls, which contain oxy-, epoxy- and keto groups. All compounds are colored yellow, orange or red. The photoprotective function of carotenoids is based on the ability of these molecules to effectively quench the excited state of chlorophylls and oxygen. At the same time, the mechanism of photoprotection, based on the screening of excess radiation, which functions in a number of algae and higher plants, is also considered, in which forms of carotenoids resistant to photodestruction with extraplastic and extratriloid localization take part [Solovchenko, Merzlyak, 2008].

It was found that salinization and alkalization of the root system was accompanied by the accumulation of ascorbic acid and the growth of its reductive activity in watercress (*Lepidium sativum* L.). Alkalinity had a greater effect on the total content of ascorbic acid compared to salinity. It can be argued that in watercress this reaction has an adaptive nature, since the accumulation of ascorbic acid serves as an indicator of the regenerative and general physiological activity of plants [Chetyna et al., 2017].

The role of potassium ions in salt tolerance of halophytes of the family *Chenopodiaceae* was studied. It was found that the C3 species of *Atriplex verrucifera* is the most resistant to salinity, which is characterized by a positive dependence of the accumulation of dry mass of stems on the content of potassium ions in them. Under stress, proline accumulation is observed in this species, which is negatively correlated with plant growth. Typical C4 plants include *Atriplex tatarica* (with the aspartate NAD-ME subtype), a species that grows in slightly saline areas and is characterized by uncontrolled salt accumulation. The content of proline under stress positively correlates with the intensity of growth. *Atriplex*

tatarica plants are characterized by a relatively low total content of flavonoids, the amount of which correlates positively with the sodium content and negatively with the potassium content in the aerial part of the plants. In species with controlled salt accumulation, *Kochia prostrata* (C4 with malate NADP-ME subtype of photosynthesis) and *Sedobassia sedoides* (with intermediate C3-C4 type of photosynthesis), the antioxidant function is performed to a greater extent by flavonoids, and not by proline. In these species, a positive dependence of the total content of flavonoids on the concentration of potassium ions in the stems is shown. The similarity between the more salt-resistant species *Sedobassia sedoides* (Makan population, C3-C4 with proto-Krantz subtype of photosynthesis) and *Atriplex verrucifera* (C3), in which the high content of potassium ions and flavonoids is an indicator of high productivity and adaptability to germination conditions, was revealed [Shuyskaya, Rakhmankulova, 2017].

It was shown that seedlings of such species as *Triticum dicoccum* Shuebl., *Triticum compactum* Host., *Triticum aestivum* L. under stressful conditions most stably supported the growth of leaf plates. The stable ratio of chlorophylls *a/b*, regardless of changes in the total content of chlorophyll in different types of wheat under conditions of drought and salinity, made it possible to predict that the considered stresses did not cause significant structural changes in the photosynthetic apparatus of seedlings. Studies of photosynthetic carbon dioxide-gas exchange showed a significant decrease in this indicator in all studied wheat species under salt stress. Under salt stress, transpiration significantly decreased in all studied species, except for *Triticum aestivum* L. In all studied species, a change in the speed of electron transport through photosystem 2 under stressors was noted. The species *Triticum aethiopicum*, *Triticum dicoccum*, and *Triticum compactum* were the most resistant to salt stress. It was also noted that species of *Triticum macha* Dek. et. Men., *Triticum dicoccum* and *Triticum aestivum* showed the highest stability of the photosynthetic apparatus under stressful conditions in *in vitro* culture [Terletsckaya et al., 2016].

It has been established that heavy metal ions, acting on the membrane systems of potassium ion transport, prevent its removal from the cell [Lefebvre, 1989, Li et al., 1996, Strang, Macnair, 1999, Nikolaev et al., 2001]. Based on this, a method of obtaining salt-resistant plant cell lines using selective media containing barium ions was developed. The selected tobacco cell clones were resistant not only against the selective stressor, but also against seawater containing 20 g/l of salts or against sodium sulfate. And therefore, based on complex stability, it was possible to expect the establishment of a stable level of potassium ions [Sergeeva, 2002].

Cell lines of tobacco resistant to barium ions were obtained by the method of cell selection. These lines were grown on media containing 20 g/L seawater salts or Na_2SO_4 . When cultivating callus on a medium with Ba^{2+} ions, stable lines accumulated K^+ ions. During cultivation under conditions of any type of salinity, a decrease in the content of K^+ ions and an increase in Na^+ ions were noted in these lines. In cells that grew in the presence of seawater salts, the level of free proline increased; at the same time, when growing callus on media with Ba^{2+} , Na_2SO_4 ions or under normal conditions, this parameter did not differ significantly [Sergeeva et al., 2009]. A correlation between the content of sodium ions and proline was found in other similar studies [Peng et al., 2006, Tani, Sasakawa, 2006]. It was also shown that entering the cell, sodium ions induce the expression of the membrane ATPase gene [Niu et al., 1993].

The effect of cross-adaptation of plants on the viability of seedlings, stem and leaf cuttings of cucumber under the action of NaCl , CuSO_4 or ZnSO_4 was studied. The salinity of the environment contributed to the increase in fluorescence intensity and proline content in leaves, ion imbalance, and decreased survival, growth, and rooting of cuttings. Previous exposure in NaCl solution was accompanied by an increase in the resistance of cucumber seedlings and cuttings under the additional action of sulfuric acid salts of copper and zinc [Hadzhieva et al., 2010].

Chloride salinity of the soil inhibits seed germination, and in conditions of soil contamination with copper or nickel salts, its average salinity (0.3-0.6%) promotes the maximum growth of corn and sunflower. The ability of these crops to extract heavy metals in soils with an average degree of salinity and contamination with copper or nickel 20 MDK compared to non-saline soil increases for copper by 5-13%, and for nickel by 10-20%. But with increasing degree of salinity, phytoextraction activity decreases. With average soil salinity and the content of copper or nickel ions in it up to 500 mg/kg, metals accumulate in the roots of corn. And with concentrations of these metals over 500 mg/kg, saline soils contribute to their more active movement from roots to leaves [Pysarenko, 2009].

It was found that the activity of superoxide dismutase in tolerant potato plants (variety Faizabad, clone-hybrid No. 73) both during salinity and drought increases in all periods of stress, but not in tolerant hybrid clones (clone-hybrid No. 69) the activity of superoxide dismutase decreases. The activity of ascorbate peroxidase in different tolerant genotypes differs significantly in the dynamics of stress. In a resistant genotype, the activity of this enzyme decreases in the first hours of stress, and then stabilizes, both in salt stress and in drought, while in a non-resistant genotype, there is a constant decrease in the activity of ascorbate peroxidase. It has also been shown that the action of stress leads to suppression of catalase activity, but in the resistant genotype it is suppressed to a lesser extent than in the non-resistant genotype in all periods of stress [Norkulov, 2017]. Overexpression of Mn-superoxide dismutase genes in transgenic tobacco plants contributed to their resistance to salt stress [Gao et al., 2003].

It is known that the resistance of halophytes against high concentrations of salts in the soil is closely related to the presence of polyphenolic compounds in them. It is the polyphenolic composition of plants that is one of the factors of the adaptive variability of plants and their adaptation to the conditions of the surrounding environment. Halophytes or soleros include plants of the genus

Limonium Mill., which grow in extreme conditions. Conducted studies of substances obtained in the form of dry extracts based on the plant *Limonium myrianthum* showed a high content of tannins of the condensed type, oxidized forms of flavonoids, as well as fatty acids, amino acids and vitamins. Every organism can be considered as an example of the work of a balanced and well-developed antioxidant system, which consists of many components - these are vitamins C, E and P, and enzymes (glutathione peroxidase, superoxide dismutase), and trace elements (selenium, zinc), and polyphenolic compounds (flavonoids), and sulfur-containing amino acids (cysteine, methionine), as well as the tripeptide glutathione. The synergistic action of the polyphenolic complex isolated by ethanol extraction of the aerial parts and roots of *Limonium myrianthum* determines the manifestation of significant antioxidant activity. It should also be noted that the substance isolated from the roots of *Limonium myrianthum* shows a greater antioxidant effect, compared to the same one from the aerial part of the same plant, which correlates with the quantitative parameters of the content of the main groups of biologically active substances, especially polyphenols, in the studied extracts. Being easily oxidized, phenolic compounds due to the combination of oxidation-reduction reactions contribute to the reduction of other substances in the reaction mixture, or prevent their oxidation. In the presence of phenolic compounds, the intensity of oxidation decreases, and the number of active products slowly increases, or remains at the previous level, and the whole process slows down rapidly [Gadetskaya et al., 2010].

The resistance of rice plants against salinity in different phases of its ontogenesis is not the same. It is relatively resistant to this abiotic stress during germination and active tillering and maturation, but is sensitive during the seedling phase and during flowering. Resistance to salinity in the seedling phase and in the reproductive stages is weakly related, and therefore only samples that show these signs at both stages of their development can be adaptive against stress during the entire growing season. Physiological mechanisms of salt tolerance in

the seedling phase are relatively well studied. These include: allocation of excess salts or their low use; compartmentalization of poisonous ions in the structural formations of the cell or the so-called old tissues (leaves, stems, leaf sheaths and roots); higher resistance of tissues due to compartmentalization of salts in vacuoles. Also, changes in the functioning of stomata (in resistant samples they close faster after the action of salt), which allows to regulate the entry of salts through the rhizosphere, regulation of antioxidant systems, vigorous growth, which allows to reduce the concentration of salt in plant tissues, regulation of osmotic pressure, detoxification of metabolic products at the same time abiotic stress [Kharitonov, Goncharova, 2013]. In the reproductive phase of development, resistant genotypes tend to exclude salt access to leaves close to the panicle, especially to the flag leaf and the developing panicle itself. Early-ripening specimens have an advantage, since the absorption of salts occurs for a shorter period, and also in areas where salinization is associated with drought in the later phases of development. The analysis of the morphophysiological characteristics of varieties - donors of salt resistance showed that in salinity they are characterized by: preservation of high growth rate, biological mass of roots and stems, high relative content of chlorophyll, low accumulation of sodium ions and Na^+/K^+ ratio in stems, compared to non-resistant genotypes [Kharitonov et al., 2011]. The resistance of plants against salinity is largely influenced by the environmental conditions, as it decreases at high or low temperatures, insufficient or unbalanced nutrition. Further growth of the resistance potential is associated with the combination of better alleles that provide tolerance against salinity using different mechanisms. New molecular genetic approaches make it possible to detect and introduce genes of complex adaptive traits to the genotype of samples while simultaneously maintaining a fairly high productivity potential [Kharitonov, Goncharova, 2008, Malyuchenko, Kharitonov, 2017].

The resistance of rice plants to salinity in the seedling phase and the reproductive stages are weakly linked, and therefore only samples that combine

characteristics in both phases can be adaptive against this stress throughout the growing season [Kharitonov, Goncharova, 2010, Goncharova et al., 2015]. The conducted studies showed the absence of reliable differences in the characteristics characterizing the sprout in rice varieties, including when compared to the standard. At the same time, the change of the sign under stress in the samples was reliable and allows to cluster the samples into groups that differ among themselves in terms of salt resistance [Malyuchenko et al., 2016].

The presence of high concentrations of salt in the environment automatically leads to its increased accumulation in the plant, achieving toxic effects at the level of leaves. At the same time, the very mechanism of salt intake and transfer remains largely unknown, since salt can accumulate in the apoplast, causing dehydration, or penetrate into the cytoplasm and chloroplasts, causing disruptions in the work of individual enzymes or even photosynthesis in general [Zhukov et al., 2016].

It was established that leaves with different mesophyll structures accumulate different amounts of salts while growing on chloride-sulfate soil salinity; the highest in Kranz-svedoid (*Suaeda arcuata*) and atroplicoid (*Suaeda microsperma*). They contain a larger amount of water-bearing parenchyma, which accumulates salts. At the same time, it was found that in *Suaeda arcuata* this water-bearing tissue is located in the center of the leaf, and in *Suaeda microsperma* it is a large-celled water-bearing hypodermis [Yusupova, Streltsova, 2009].

It was established that the average chloride salinity (4.7 mS/cm) leads to a significant violation of the water status of rice plants and an increase in the share of bound water, which is necessary under stressful conditions to maintain cellular homeostasis and the passage of physiological processes. This is confirmed by the presence of a close relationship between tissue hydration and the concentration of cell juice under salinity ($r = 0.99$ for leaves and $r = 0.99$ for stems), while on a

fresh background the correlation coefficient between these indicators does not exceed 0.49 for leaves and -0.34 for stems [Doseeva et al., 2011].

It is also necessary to note the release of salt outside the plant organism or its accumulation. Therefore, salt excretion can occur through special cellular structures called salt glands. Through them, salt, especially sodium chloride, is released from the leaves, thanks to which its concentration in the middle of the cells remains at a low level [Marcum, Pessarakli, 2006]. Another similar mechanism consists in the release of salt through the root system, which ensures the maintenance of salt concentration in the middle of the plant at a satisfactory level, which occurs in many halophytes. Selective absorption of ions or substances important for maintaining osmotic pressure, which is ensured through the mass ratio, leads to water retention in the plant organism or the exclusion of sodium ions outside of it [Parida, Das, 2005].

Biochemical mechanisms of salt resistance of plants can be implemented through the following response reactions: 1) selective accumulation or release of ions; 2) control of ion absorption by roots and their transport to leaves; 3) isolation of ions into compartments at the level of a cell or a whole plant; 4) synthesis of some substances to maintain the osmotic pressure of the cytoplasm; 5) changes related to photosynthesis; 6) changes in the structure of membranes; 7) providing signals to start the synthesis of antioxidant enzymes; 8) induction of plant hormones [Torabi, 2014].

Levels of stability created as a result of such changes are divided into mechanisms of low or high complexity. In the first case, such changes affect many biochemical pathways, as a result of which a new balance of rates is formed between them and a new stationary state of the system, while complex mechanisms affect changes in the main metabolic pathways – photosynthesis or respiration, which may be associated with the start of work or changes in the activity of individual genes with corresponding biochemical consequences [Parida, Das, 2005]. To ensure normal metabolism in plant cells, a balance

between the concentrations of ions and substances, as well as a certain amount of osmotic pressure, must be maintained. Therefore, the root system plays a decisive role in this process [Torabi, 2014].

It was shown that the cytological response of cells of primary roots to salt stress was generally similar – the development of the process of plasmolysis, "compression" of the cytoplasm, and cell death. However, genotypic differences of wheat species in terms of their response to stress were also revealed. Thus, in *Triticum aethiopicum* at a NaCl concentration of 6 atm, the beginning of the plasmolysis process was observed in single cells; cells with large vacuoles and even dividing cells were noted. Mass plasmolysis and cell death occurred when stress increased to 9 atm. Cells of *Triticum dicoccum* remained alive even at 9 atm of NaCl. In *Triticum compactum*, with increasing stress, the process of plasmolysis was accompanied by "compression" of the nuclei. In *Triticum sinskaya* already at a NaCl concentration of 6 atm, the beginning of cell membrane lysis was noted, which increased at 9 atm of NaCl. In such forms as *Triticum turgidum*, *Triticum compactum* v. *rufulum*, *Triticum spelta*, *Triticum kiharae*, and the Myronivska 808 variety at a NaCl concentration of 6 atm, the effect of stress was visually manifested not only on hydration, but also on the chromosomal apparatus of cells - in addition to quite strong plasmolysis, fragmentation of the nuclei was noted, which led to their destruction, which increased either quantitatively, becoming massive at a NaCl concentration of 9 atm, or qualitatively – leading to lysis kernels, and in *Triticum compactum* v. *rufulum*, until their complete disappearance and cell death [Terletsckaya, Khaylenko, 2010].

The ability of the membranes of the microsymbiont to ensure salt resistance of leguminous plants was studied. For this purpose, the ion permeability of the membranes of acteria with weak (50 mM NaCl – *Bradyrhizobium lupini*) and relatively high (400 mM NaCl – *Sinorhizobium meliloti*) salt resistance was compared. The sodium ion permeability of the cytoplasmic membranes of free-living and symbiotizing forms of rhizobia, as well as the peribacteroid membrane

of symbiosomes of lupine and alfalfa nodules, was determined. It was shown that the content of sodium ions in the cells of pure cultures of both types of rhizobia increases as the concentration of salt in the nutrient medium increases. Despite the fact that these two species of rhizobia differ in salt tolerance, their cytoplasmic membranes were equally easily permeable to sodium ions. In the fractions of symbiosomes and bacteroids, the content of sodium ions increased with increasing salt concentration in the incubation medium. And therefore, the membranes of microsymbionts of both lupine and alfalfa cannot serve as a reliable barrier for the entry of sodium ions into the cells. The peribacteroid membranes of the symbiosomes of these leguminous plants are also a weak barrier for chlorine ions. The addition of ATP to a suspension of symbiosomes from lupine and alfalfa nodules caused the generation of an electrical potential ($\Delta\phi$) on the peribacteroid membranes. The subsequent introduction of monovalent penetrating nitrate and chlorine ions into the incubation medium led to the dissipation of $\Delta\phi$ on the peribacteroid membranes. The half-life $\Delta\phi$ for nodule symbioses of both legume species was the same. The obtained results allow us to state that the functioning of the nitrogen-fixing symbiotic system of lupine and alfalfa under conditions of salt stress is due to either the low sensitivity to NaCl of the biological polymers of the microsymbiont, or the ability of the host plant to maintain ion homeostasis in the cells of the central tissue of the nodule [Khailova, Andreev, 2010].

The experiment used 4 ecological types of halophytes, which differ in the strategy of adaptation and survival at high concentrations of salt in the environment. *Suaeda altissima* and *Salicornia europaea* were taken as typical salt-accumulating halophytes, which had a similar anatomical structure and ultrastructure of leaf cells and chloroplasts when grown in an optimal salt regime. The effect of salt stress (500-600 mM NaCl) after 24 hours led to a decrease in stem turgor and caused strong changes in the structure of chloroplasts: swelling of thylakoids, both grains and stroma, was noted, especially strongly expressed in the marginal thylakoids of grains. At the same time, the volume of the stroma

decreased, and starch inclusions disappeared or were found quite rarely. However, after 2 days, a complete restoration of the turgor of aerial stems and the ultrastructure of chloroplasts was observed. In *Artemisia lercheana*, which belongs to haloxerophytes, the introduction of high concentrations of salt into the environment (up to 800 mM) caused a slight loss of leaf turgor and small changes in the ultrastructure of chloroplasts. This was expressed in the appearance of small openings between the lamellae running along the entire chloroplast and a decrease in the size and number of starch inclusions. At this time, small vacuoles appeared in the cytoplasmic compartment, in which, probably, sequestering ions that entered the cell are isolated. Another object of research, characterized by high salt tolerance, was *Limonium gmelinii*, whose leaves had salt glands. Through these glands, the salts arriving with the residue were removed to the surface of the leaf, bypassing the chlorophyll-bearing cells. The chloroplasts of this object in the control variant were literally clogged with numerous starch inclusions, while the fate of the lamellar system and the stroma was quite small. Lamellae, both grana and stroma, packed so tightly that it was difficult to see their clarity. Under the influence of salt stress (800 mM NaCl), after 24 hours the leaves lost turgor, the volume and number of starch inclusions decreased, the stroma became brighter, and small vacuoles appeared in the cytoplasm, although they were much less frequent than in *Artemisia lercheana*. Recovery of turgor and ultrastructure of chloroplasts on the 3rd day was not significant. *Thellungiella salsuginea* tentatively belongs to the group of exceptions in relation to the action of NaCl. Indeed, 24 hours after adding 250 mM NaCl to the neutral medium, no changes in the ultrastructure of chloroplasts were observed. Only long-term growing of plants in a saline environment (400 mM NaCl) led to a reduction of the lamellar system and swelling of the grains, while the amount of starch inclusions decreased to an insignificant extent. *Cytoplasmic vacuolization*, as a way of protecting cytoplasmic biological polymers from contact with salt entering the cell, was more strongly expressed in *Thellungiella salsuginea*, compared to previously

studied objects. Obtained characteristics of the state of chloroplasts in response to salt stress from different groups of halophytes, allow us to further decipher the impact of high salt concentrations on the photosynthetic apparatus and the activity of its individual components, which ultimately will make it possible to assess the potential productivity of various ecotypes of halophytes under conditions of salt stress [Kurkova et al., 2008].

In addition to the tissue level of combating salt stress, plants have ion balance maintenance systems at the cellular level as well. By maintaining a low level of cytotoxic sodium and chlorine ions in the cytosol, plant cells can perform all necessary metabolic functions. One of the main means of increasing the tolerance of plants against salt stress is maintaining a sufficiently high level of potassium in relation to sodium in the cytoplasm. Deposition of cytotoxic ions in the central vacuole, which occupies 90% of the cell volume, is one of the main conditions for overcoming salt stress. In addition, the accumulation of potassium ions in the vacuoles of plants serves as a universal depot for the subsequent use of this ion by the cell in the metabolic processes of the cytoplasm. That is why a detailed study of the functions of ion transporters and vacuole channels is very important [Isayenkov et al., 2010, Isaenkov, 2011].

CHAPTER 3. ECOLOGICAL MANAGEMENT OF ELECTROPHYSIOLOGY OF PROCESS

Plants have developed signaling systems that allow coordination of molecular processes in response to changes in environmental conditions. Studies of long-distance signals that provide the development of a systemic response have traditionally focused primarily on phytohormones, as well as on other signaling molecules. At the same time, it is well known that plants are capable of generating and propagating various types of electrical signals in response to various stimuli, such as changes in temperature and illumination, mechanical damage, and others. The spread of the stress signal causes changes in the concentration of quite important secondary messengers in the cell. Such changes underlie the transformation of an electrical signal into a functional response. The consequence of the modification of functional activity caused by the stress signal is a change in the resistance of plants against the action of adverse factors [Vodeneev, 2019].

The generation and propagation of electrical signals is one of the mechanisms of the formation of the plant's systemic response to the spatially inhomogeneous effect of stressors. Specifically, electrical signals induce the development of a systemic response that includes both short-term and long-term inactivation of photosynthesis. Short-term inactivation is mainly associated with an increase in intracellular pH, which leads to a decrease in the entry of carbon dioxide into cells, and with a decrease in intracellular pH, which directly affects the processes of the light stage of photosynthesis. A possible mechanism for inducing electrical signals of prolonged inactivation is an increase in the concentration of stress hormones (ABA and jasmonic acid) in plant leaves. It is quite likely that the final role of the systemic photosynthetic response consists in increasing the resistance of the plant against the action of stressors, which opens up significant prospects for the use of such a response in the management of the

resistance of cultivated plants and in monitoring their condition, for example, by registering changes in the photozyme reflection index [Sukhov, 2019] .

All plant organisms are under the constant influence of the electric field of the atmosphere, which under normal weather conditions is mainly characterized by a positive potential that increases by an average of 130 V/m. Since air is a good dielectric and contains few carriers of electric charges, the current density determined by the electric field of the atmosphere is not high and is 3×10^{-16} A/cm². Shielding plants from the external electric field when placing them under a Faraday grid leads to a slowdown in growth processes [Medvedev, 2012].

The main electrical characteristic of a plant cell is its membrane potential, which corresponds to the state of the cell during physiological rest, when the metabolism is in equilibrium. Living structures always have a more negative charge than the environment. Membrane potential determines all types of electrical activity in living organisms. The gradients of electrical potentials recorded between different areas of plant tissues or between tissues and showing different levels of metabolism in these areas or in these tissues are often called metabolic potentials. The damage potential (variable or demarcation) is the fluctuation of electrical potentials between the damaged and undamaged (intact) part of the plant. A damaged area is always electrically neutral in relation to an undamaged one [Yurin et al., 1991].

The cytoplasm of living cells is negatively charged in relation to the surrounding environment, as there is a difference in electrical potential that can serve as a driving force for ion transport. At the same time, the entry of cations, including potassium, into the middle of the cell and the exit of anions from it are facilitated. That is why cells have special mechanisms for maintaining ion homeostasis. Usually, the concentrations and, accordingly, the chemical potentials of most ions in cellular compartments are not the same, which is the reason for their passive diffuse movement toward a lower electrochemical potential [Skulachev, 1989].

A direct reaction to temperature effects is a change in membrane fluidity. Under the influence of high temperature, the number of unsaturated phospholipids in membranes increases. At the same time, hydrogen and electrostatic interactions between polar groups of proteins in the middle of the liquid phase of the membrane decrease, and integral proteins interact more strongly with the lipid phase. As a result, the composition and structure of the membrane changes, and as a result, membrane permeability increases and the release of water-soluble substances from the cell. Increased fluidity of membrane lipids at high temperature can be accompanied by loss of activity of membrane-bound enzymes and disruption of electron carriers [Kretovych, 1980].

Passive flows of substances through the membrane are the main cause of the potential difference on the membrane - the membrane diffuse potential, which can be determined by considering the contributions of all ion flows that pass through the membrane. Under normal conditions, not all anions and cations penetrate the membrane quite easily. Many divalent cations cannot easily enter or leave the cell passively, which means that their mobility in the membrane is very low. Such ions do not usually make a significant contribution to the ion fluxes through the plasmalemma to significantly affect the membrane diffusion potential. For many plant cells, the total ion flow consists mainly of the movement of K^+ , Na^+ , and Cl^- ions, which are present inside and outside plant cells in significant concentrations. Usually, in some cases, a real flow of other ions is possible, for example H^+ , Ca^{2+} , OH^- , HCO_3^- . Thus, the properties and physiological state of a particular membrane, the external and internal concentrations of K^+ , Na^+ and Cl^- , and in special cases, as already noted, other ions, really affect the value of the diffuse potential. However, limiting the number of ions to these three considered is quite sufficient for determining the diffusion potential of many membranes [Krutetskaya, Lonsky, 1994].

In biological systems, some portion of the potential difference may be due to charges immobilized or fixed on some solid phase bordering the aqueous

medium. This special type of diffuse potential is called the Donnan potential. An example of a solid phase in which the Donnan potential occurs in plants is the cell wall. Pectin and some other compounds of the cell wall contain a significant number of immobilized carboxyl groups (-COOH), the dissociation of which with the release of a proton gives the cell wall a total negative charge, which contributes to the attraction of divalent calcium cations to it. The overall effect is the exchange of H^+ for Ca^{2+} . As a result of this attraction, there is a higher osmotic pressure in the cell wall than in the surrounding aqueous solution. The region containing immobilized charged particles is called the Donnan phase. At equilibrium between the Donnan phase and the adjacent aqueous solution, an electric potential arises – the Donnan potential. Relative to the external solution, the potential of the cell wall is negative. If the immobilized or fixed ions are placed in a flat layer, then mobile ions of the opposite sign are concentrated in the adjacent layer – the resulting formation is called an electric double layer. Layers containing cations are quite often formed in aqueous solutions on each side of a biological membrane, which usually acts as a Donnan phase, which has a negative total charge. Donnan phases are also found in the cytoplasm, where the occurrence of immobilized charges is often caused by proteins that are fixed in the cytoplasm because they cannot freely diffuse either through the plasmolemma or through the tonoplast. Cytoplasm contains a significant number of protein molecules, which are known to be bipolar compounds, and the pH characteristic of cytoplasm, many of them carry a negative charge [Yurin et al., 1977].

In plant cells, there are at least four types of membrane transport of ions - passive diffusion, facilitated diffusion, primary-active and secondary-active transport. Nonspecific passive diffusion of ions does not require special mechanisms and occurs when various hydrophilic pores appear in the membrane. according to the principle of passive diffusion, that is, according to the gradient of the electrochemical potential, the transport of ions through various channels also occurs. Facilitated diffusion is provided by special carrier proteins. The

primary active transport of ions in the vast majority of cases is carried out by transport ATPases – ion pumps, the source of energy for which is the hydrolysis of ATP or pyrophosphate. In the membranes of chloroplasts and mitochondria, during the operation of primary-active ion transport systems, the source of energy is the activity of redox chains. If the energy source is the ion concentration gradient created on the membrane, then the process is called secondary active transport. This transport ensures the transfer of monosugars, amino acids, anions and a number of cations into the cell. In plant cells, the concentration gradient of protons created by various H⁺ pumps is most often used. The term "ion pump" is used to describe various active transport systems capable of pumping ions against an electrochemical potential gradient [Plonsy, Barr, 1992].

Transport proteins allow many small polar molecules to pass through cell membranes, but they are unable to transport macromolecules such as proteins, polynucleotides, or polysaccharides. However, in most cells, certain macromolecules can pass bidirectionally across plasma membranes, and some cells are even able to absorb large cellular particles. The mechanisms of these processes are significantly different from the mechanisms of transport of small molecules or ions [Plonsy, Barr, 1991, Alberts et al., 1994, Kamkin, Kiseleva, 2008, Kovbasenko, 2021].

Plasmodesms provide intercellular symplast transport of low molecular weight substances and regulatory macromolecules - RNA and proteins. Research in recent years shows that the permeability of plasmodesmata is subject to fine regulation, including calcium signaling, as well as changes in the redox status of cells, in which thioredoxins play a rather important role [Domashkina et al., 2019].

The process of diffusion is closely connected with the movement of water in the plant. The system of water flow motors in plants is usually divided into lower, upper and intermediate. In turn, the analysis of the driving forces is detailed to: assessment of the ways of water transfer and the conditions of their switching,

the contribution of hydrostatic pressure in the form of the suction effect of transpiration with the accompanying effect of tension of water threads and participation in the regulation of the transfer of the stomatal apparatus, the contribution of root pressure, assessment of the causes of self-oscillations of cells, the role of aquaporins, the contribution of the capillary component, the phenomenon of transfer polarity, the tasks of verifying the intermediate of the (stem) engine, mechanisms of signal connections between the upper and lower engines (the list can be continued) with the conclusion that most of these dynamic processes each have their own Achilles heel, which complicates the transfer process, especially in the off-season period [Anisimov, Suslov, 2019].

It is believed that redox reactions take place in the central vacuole, as well as in any point of the cellular space, with the participation of redox proteins capable of forming redox chains, within which redox pathways of electron transfer occur. Redox chains are united by mobile electron donors into a single redox system. The study of redox elements and modeling of vacuolar redox chains will reveal redox processes characteristic of the vacuole, which will expand our understanding of the role of this compartment in redox metabolism, and possibly redox signaling of the plant cell [Pradedova et al., 2017a].

Biological electrogenesis, or bioelectrogenesis, is understood as a whole complex of mechanisms leading to the generation of bioelectric potential. Bioelectrogenesis of higher aquatic plants has a complex nature. This is due not only to the fact that the mechanisms, in particular active and passive, which are at its core, are significantly different, but also to the fact that plant cells have numerous membrane structures, each of which is characterized by certain electrical properties [Oprytov et al. , 1991].

The basis of the modern membrane concept of bioelectrogenesis was laid by Hodgkin and Horowitz [Hodgkin, Horowicz, 1959] and continued in the works of Oprytov, Kogan and other researchers [Kogan, 1969, Oprytov et al., 1988, 1991]. This concept is based on the following provisions [Hodgkin, Horowicz,

1959, Kogan, 1969, Vorobyev, 1988, Oprytov et al., 1988, 1991, Thain, Wildon, 1996, Gradmann, Hoffstadt, 1998, Tarchevsky, 2002, Pyatygin, 2003, Davies, 2004]: 1) place electrogenesis is the surface membrane (electrical potential differences can also occur on intracellular membranes, but the electrical properties of the cell are determined mainly by electrogenesis on the surface membrane); 2) the potential difference on the surface membrane is ionic in nature, not electronic as in metals; 3) the generation of potential differences on the surface membrane is due to the occurrence of ionic asymmetry, that is, the unequal distribution of cations and anions on both sides of it.

One of the most important functions of the cell membrane is the regulation of ion permeability of a living cell. Until recently, this function was exclusively attributed to channel-forming proteins embedded in the lipid bilayer. However, quantized current fluctuations, outwardly indistinguishable from current fluctuations in channel-forming proteins, were detected in purely lipid bilayer membranes at the temperature of the lipid phase transition. In the scale of amplitudes of current fluctuations, they were in the nanoampere range, and in the scale of life time – fractions of a second [Antonov, 2015].

Selective transport of various substances and ions is one of the main functions of biological membranes. This process ensures the active exchange of the cell and its organelles with the surrounding environment, serves as the basis of all bioenergetic mechanisms, determines the effectiveness of the processes of reception and transmission of excitation, in other words, makes the cell a perfect dynamic system. Active and passive transport of substances, osmosis, filtration and bioelectrogenesis occupy a rather important place among the numerous phenomena occurring in the cell. There are various methods of diffusion transfer: diffusion of oil-soluble substances through the lipid part of the membrane, transfer of hydrophilic substances through the pores formed by membrane lipids and proteins, facilitated diffusion with the participation of special carrier molecules, selective transport of ions through ion channels. However, in the process of

evolution, a living cell has created a special way of transportation, which is called active transport. In this case, the transfer of substances occurs against the difference in concentration, and therefore is combined with the use of energy, the universal source of which in the cell is the ATP molecule. Passive transport through membranes, or simple diffusion, is the transfer of substances through the membrane from an area with a higher concentration to an area with a lower concentration. This process is described by the law of simple diffusion, or simply Fick's law: the amount of substance transferred per unit of time through a unit of surface area is directly proportional to the concentration gradient of the dissolved substance in the middle of the membrane. This law is valid only for uncharged, neutral molecules. And for all charged particles, regardless of their size, lipid bilayers are largely impermeable: the charge of ions and a high degree of hydration prevent their passage through the hydrocarbon part of the bilayer. Passive transport is carried out as follows: oil-soluble substances dissolve in the hydrocarbon region and thus diffuse through the bilayer. An example of such diffusion is osmosis [Plonsy, 1991].

Under most stress conditions, the permeability of plant cell membranes changes. Along with this, one of the earliest responses to any biotic or abiotic stress is the accumulation of ROS in the cell. At the same time, it was found that the increase in diffuse water permeability of membranes during wounding stress is caused by the activation of aquaporins. At this time, the permeability of the lipid bilayer practically does not change over time. It was shown that the main mechanism of activation of aquaporins during wounding stress is the oxidation of thiol groups of aquaporins. With the additional induction of ROS with the help of paraquat, the directionality of the change in diffusion permeability of aquaporins changes, which indicates the connection of other, not direct, mechanisms of their regulation. Thus, the directionality of changes in diffuse water permeability of membranes depends on the level of oxidative stress [Sibgatullin et al., 2015]. The main biological process leading to the formation of the superoxide radical is

electron transport associated with mitochondrial membranes. Usually, the reductive transformation of oxygen into water with the participation of oxides requires the sequential transfer of electrons, which is accompanied by the formation of free radicals [McCord, Fridovich, 1970]. It is assumed that the redistribution of electron flows in the electron-transport chain of chloroplasts, namely the decrease in the intensity of $O_2\bullet^-$ formation at the level of photosystem 1 and the activation of the photoformation of hydrogen peroxide, is one of the mechanisms of plant resistance against osmotic stress and salinity [Stryzh, 2010].

The role of the external structure bordering the external environment is performed by the cellulose cell wall of the plant cell with an amorphous matrix of polymeric pectin molecules, which carries a negative surface charge of the order of 0.02 Ev/m^2 [Clarkson, 1978, Vorobyev, 1988]. The presence of this charge gives the cell wall quite distinct cation-exchange properties [Vorobyev, 1988].

The plasma membrane is the main structural barrier that separates the contents of the plant cell from the external environment, and has a much more complex and compact organization, specially adapted for transport and a number of other functions [Opritov et al., 1991].

The difference in electric potential between the internal environment of a living cell and the external solution is called the membrane potential or resting potential. The membrane potential arises as a result of the diffusion of electrolytes through a membrane that is permeable to some ions and poorly permeable to other ions. The main cause of the emergence of the membrane potential is the selective ion permeability of the cell membrane in combination with the uneven distribution of ions between the cell and the environment [Clarkson, 1978].

In higher plants, two types of electrical signals are distinguished - action potential and variable potential. An action potential occurs in response to non-traumatic actions, and a variable potential occurs in response to damage. Both of these types of electrical reactions represent a transient depolarization of cells. The action potential of higher plants has properties quite characteristic of all living

organisms. Unlike the action potential, the variable potential shows dependence on the intensity of the action, and has an irregular phase of depolarization, and especially, repolarization, the parameters of the variable potential change as it propagates. The generation of the action potential is connected with the occurrence of passive flows of ions, as well as with a change in the activity of the electrogenic pump – the proton ATPase of plasma membranes. The occurrence of the pulse is caused by the activation of potential-dependent calcium channels and the entry of divalent calcium ions into the cell. An increase in the concentration of divalent calcium ions leads to activation of chlorine channels and inactivation of proton ATPase. Propagation of electrical signals occurs mainly along conductive bundles. Although a variable potential is classified as a propagating electrical signal, this type of electrical response is a local response that occurs in response to a chemical or hydraulic signal. Electrical signals cause short-term changes in a number of processes during their propagation. There is a prediction that the final goal of the changes in the functional state of the plant induced by electrical signals is the growth of its non-specific resistance [Vodeneev, 2015].

A rather important role in the development of the plant's systemic response to local external actions is played by fast remote signals. Such signals include propagating electric reactions, represented in higher plants by variable potential, action potential [Opritov et al., 1991, Sibaoka, 1991, Stahlberg et al., 2006] and system potential [Vodeneev et al., 2012]. It is known that the variable potential arises under the action of damaging stimuli and its spread occurs with a decrease in the amplitude and speed of the reaction [Stahlberg et al., 2006, Vodeneev et al., 2012]. According to existing ideas, the variable potential is, in fact, a local electrical response to the propagation of a hydraulic signal [Stahlberg et al., 2006] or a chemical signal [Vodeneev et al., 2012]. It was found that the radioactive label is able to spread through the plant at a speed comparable to the speed of the variable potential. Blocking the chemical signal prevents propagation of the

electrical response. This indicates the possibility of spreading the variable potential in accordance with the chemical hypothesis [Akinchyts et al., 2013].

The generation of a variable potential is mainly associated with a transient change in the activity of H⁺-ATPase of plasma membranes [Stahlberg et al., 2006, Julien et al., 1991]. Spreading, variable potential and action potential are capable of causing a complex of physiological changes in the tissues and organs of higher plants that were not directly exposed to the factor, including changes in the activity of photosynthesis, respiration, gene expression, etc. [Bulychev et al., 2004, Fromm, Lautner, 2007].

The ionic mechanism of variable potential generation in higher plants was studied, and specifically, the role of hydrogen, chlorine and calcium ions in this process was investigated. The use of an H⁺-ATPase inhibitor, an anion channel blocker, and removal of divalent calcium cations from the extracellular environment led to a significant decrease in the response amplitude. A transient decrease in the concentration of hydrogen ions and an increase in the concentration of chlorine ions in the solution in the experimental cuvette were recorded, which was accompanied by the generation of a variable potential. The obtained results indicate the participation of the initial flow of chlorine ions in the development of depolarization during the generation of a variable potential, and also confirm the expected participation of divalent calcium ions and the proton pump in the development of a variable potential. Therefore, it can be stated that the mechanism of generating a variable potential has a complex nature. At the same time, both the occurrence of passive flows of calcium and chlorine ions, which go along the electrochemical gradient, and the change in the activity of the electrogenic pump [Akinchyts et al., 2011] contribute to its formation.

It is shown that the development of the photosynthetic response induced by the variable potential is probably due to the entry of protons into the cell. The effect of changes in the concentration of protons can be associated with a change in the activity of carbonic anhydrases [Grams et al., 2009], aquaporins [Gallé et

al., 2013], enzymes of the Calvin cycle [Wolosiuk et al., 1993], a change in the ratio of carbon dioxide to HCO_3^- [Bulychev et al., 2001], by translocation and change in activity ferredoxin:NADP⁺-reductases [Alte et al., 2010], as well as the growth of non-photochemical quenching [Müller et al., 2001].

The following sequence of events during the generation of a variable potential is proposed. An increase in the concentration of calcium ions in the cell causes a decrease in the activity of H^+ -ATPase, as well as the activation of anion channels, which leads to the appearance of an outflow of chlorine, which makes a significant contribution to depolarization. It can be assumed that the subsequent decrease in calcium concentration initially leads to the inactivation of chlorine channels, with suppressed activity [IIW1] H^+ -ATPase, and the subsequent decrease leads to the reactivation of H^+ -ATPase, which makes the main contribution to the formation of the repolarization phase of the variable potential. According to the results obtained during the work, the generation of a variable potential is accompanied by shifts in the intracellular concentrations of hydrogen and calcium ions [Vodenev et al., 2014]. It is quite likely that these shifts associated with the generation of excitation potentials are the basis of the transformation of the signal, which is palpated, into a functional response [Krupenina, Bulychev, 2007, Pyatigyn et al., 2008, Grams et al., 2009].

Electrical signals, specifically, variable potential, cause changes in the passage of many physiological processes, including the inactivation of the dark stage of photosynthesis and the activation of respiration – these processes can increase the ATP content in leaves. And on the other hand, precisely the increase in the concentration of ATP in the plant organism can be one of the mechanisms of its resistance to stressors. Thus, the question of the increase in ATP content under the action of a variable potential is one of the keys to a correct understanding of the functional role of electrical signals [Surova et al., 2015]. It should also be noted that in plant cells the contribution of electrogenic transport systems to the membrane potential is much higher than in mammalian cells. All

this is manifested in the fact that the value of the membrane potential of a plant cell significantly exceeds the value of the diffusion, and specifically, the equal potassium potential. High values of the membrane potential in plant cells are primarily created due to the transport of hydrogen ions from the cytoplasm to the environment [Medvedev, 2012].

Membranes, as a natural barrier, are the first to be affected by stress factors. Being dynamic structures, membranes are able to react quickly enough to deviations in the conditions of their existence. However, the changes that occur in the membranes involve a whole cascade of shifts in the metabolism of the entire cell. The permeability of membranes increases, the membrane potential of the plasma membrane depolarizes, the acidity of the cytoplasm shifts to the acidic side, and the activity of hydrogen ions increases. Shifts in the functional activity of membranes are accompanied by rearrangements in their structure, which in the initial stage show an increase in their stability until the action of the stressor reaches tension. In a complex phospholipid molecule, all the most important elements are strictly determined qualitatively and quantitatively [Chernavskaya, 1989, Plonsy, Barr, 1991, Antonov, 1997].

Cell membranes perform a number of specific and rather finely regulated functions, which make them not only irreplaceable for ensuring the normal life of the cell, but also promising from the point of view of creating new generations of nano-objects based on them. The functional activity of biological membranes in normal and pathological conditions is determined by the peculiarities of their molecular composition, as well as the degree and dynamics of changes in their physical and chemical properties in various processes. Understanding these relationships at the molecular level is necessary not only for deepening our fundamental knowledge, but also for the rational construction of membrane supramolecular systems with given properties. The membrane is often considered as an inert homogeneous medium, the main function of which is the accommodation of membrane proteins. However, the results of recent

experimental and computational work have shown that cell membranes are extremely dynamic systems, and their action is strongly dependent on local features and fluctuations of their structure, hydrophobic and electrical properties [Efremov, 2015].

At the cellular level, the action of the membrane potential can occur due to non-specific changes in the polarization of cell membranes and their permeability. However, this is not the only course of action. Membrane potential can also affect not only the cytoplasmic membrane of the cell, but also other subcellular formations, and specifically, the nucleus. Membrane potential can also cause genetic effects [Kholodov, 1971].

Membranes play a rather important role in the functioning of cells and in the structural organization of cellular structures. They are a key barrier that protects the contents of the cell from the external environment. Membranes include various lipid-protein complexes that carry out the transfer of various molecules and ions through the membrane. It is known that membrane lipids, such as phospholipids, consist of a hydrophilic part and a hydrophobic "tail" and form a stable bilayer to which various protein complexes are bound. Proteins that form channels, as well as ATPases, have a globular or unfolded structure and are immersed in hydrophobic areas of the lipid bilayer of the membrane. Peripheral proteins interact electrostatically with the outer layers of the lipid bilayer by polar groups of amino acids and do not penetrate the membrane. The most important energy processes take place in the membranes of mitochondria – respiration and ATP synthesis. Mitochondria are functionally dependent organelles [Bakeeva et al., 1978]. In higher plants, mitochondria are single and have either a spherical or cylindrical shape [Logan, Leaver, 2000].

Under conditions of stress, mitochondria form dense clusters grouped around chloroplasts or in other areas of the cytosol. The formation of "giant mitochondria" is accompanied by an increase in the generation of ROS. Antioxidants prevent both the formation of "giant mitochondria" and the growth

of ROS generation by these organelles [Scott, Logan, 2008, Zhang et al., 2009]. The morphology of isolated mitochondria most likely shows their functional state [Claypool et al., 2006]. Mitochondria are key links in energy, redox and metabolic processes in the cell [Nagata et al., 1987, Scott, Logan, 2008].

Cellular respiration is concentrated in the mitochondria, which is necessarily combined with the "leakage" of electrons, that is, the one-electron reduction of oxygen and the formation of the superoxide radical. Superoxide quickly dismutates with the formation of hydrogen peroxide - the longest-lived representative of ROS, which can give rise to more active ROS, especially the hydroxyl radical in the Fenton reaction. In addition, superoxide, reacting with nitric oxide, causes the formation of the active peroxytrifluoromethyl radical. All ROS produced in mitochondria are extremely dangerous for the cell, and normally their production is balanced by various antioxidant systems located both in mitochondria and in the cytoplasm. Pronounced mitochondrial dysfunction may be incompatible with normal cell functioning [Chernyak, 2010]. Approximately half of ROS production by mitochondria is catalyzed by respiratory complex I, and the other half by dihydrolipoyl dehydrogenase. In the presence of ammonium ions, up to 90% of the formed peroxide is due to the activity of dihydrolipoyl dehydrogenase [Kareeva, 2017].

It is shown that during thermal action, inhibition of electron transport occurs mainly with the participation of mobile carriers of plastoquinone nature. Moreover, it is shown that both the level of plastoquinone reduction and the sizes of the photoactive and non-photoactive plastoquinone pools change. It was established that the slowing down of the recovery rate of plastoquinone is partly caused by a change in the rate of their diffusion in the lipid bilayer of thylakoid membranes. Therefore, it was predicted that the slowing down of electron transport may also be caused by a change in the rate of diffusion of other mobile carriers of thylakoid membranes [Pshybytko et al., 2010].

Cl⁻/H⁺ exchange through the membrane isolated from root cells of the salt-accumulating halophyte *Suaeda altissima* was revealed. Plants were grown in aqueous culture in the presence of NaCl. When a Cl⁻ concentration gradient directed to the middle of the vesicles is created on the membrane, the transmembrane transfer of H⁺ from the vesicular lumen to the external environment is registered. Cl⁻/H⁺ exchange was accompanied by the generation of an electric potential on the membrane ("minus" in the middle of the vesicles). The identified Cl⁻/H⁺ exchanger functioned in the pH range from 7 to 8, with an optimum of 7.5, which corresponds to the cytoplasmic pH value. In addition to the experimental indicators that demonstrate the function of Cl⁻/H⁺ exchange, the expression in the roots of one of the genes belonging to the CLC family was also shown. At the same time, it was hypothesized that the Cl⁻/H⁺- antiporter in the roots of *Suaeda altissima* can perform the following functions: 1) active export of Cl⁻ from the cytoplasm; 2) reduction of the driving force of Na⁺ influx due to membrane depolarization; 3) depolarizing the plasmalemma, the Cl⁻/H⁺-antiporter activates the H⁺-ATPase, which leads to an increase in ΔpH. An increase in ΔpH, in turn, stimulates the export of Na⁺ from the cytoplasm through the Na⁺/H⁺ antiporter [Shuvalov et al., 2011].

The decisive role of ferredoxin in thermoinduced inhibition of electron transport in chloroplasts was established. It is shown that the increase in the level of reducibility of ferredoxin is the cause of inhibition of linear and cyclic electron transport. The regulatory role of the redox state of ferredoxin in the formation of the size of the photoactive plastoquinone pool, as well as its redox state during heat stress, was revealed [Pshybytko, 2017].

A weak variable magnetic field and short-term hyperthermia caused similar disturbances in photosystems and electron flow, which allows predicting commonality in the mechanisms of their effects in plant cells. It is likely that this is related to a small protective effect on the speed of the Hill reaction, revealed in

the case of pretreatment of plants with an alternating magnetic field before the next hyperthermia [Synitsyna et al., 2014].

The main mechanism of the growth of damage to photosystem 2 (PS 2) by high temperature, which is observed during the preliminary induction of variable potential (VP), is the inhibition of transpiration activation during heating. Such a decrease in total transpiration, which mirrors the closure of stomata caused by VP, leads to a stronger heating of the leaf at the same external temperature, which is the reason for the increase in damage to FS 2, which probably plays a protective role, reducing the probability of damage to photosystem 1 by reactive oxygen species, which arise due to the flow of electrons from FS 2. The final result of changes in the stability of the photosynthetic apparatus caused by VP is probably an increase in the general resistance of the plant against increased temperature. Therefore, it can be considered that the spread of VP is a rather important mechanism of adaptation of the plant against changes in the environmental conditions [Surova et al., 2017].

It is shown that the movement of such ions, for example, sodium and chlorine, which are part of the same salt, along the xylem of the stem of some plants is fundamentally different: chlorine passes freely with the xylem flow, and sodium with a large decrement. Since these are the anion and cation of the same salt, (+)- and (-)-charges, this cannot help but determine the occurrence of a difference in electrical potentials between xylem sections that differ in length of the stem. Although, of course, the decrement of sodium is a consequence of rather intense ion exchange processes between the xylem exudate and living cells of the surrounding tissues, instead of sodium, potassium, calcium, probably a proton and other ions are released into the exudate, but when exchange equivalence is observed, a difference in electrochemical potentials arises due to differences in the ionic composition of different parts of the solution. On the other hand, potential currents arising between different sections of the same liquid, but moving at different speeds, have been known for a long time. And finally, with a

narrow and long capillary channel for liquid (xylem vessel), the limit of the change of solutions reaches first the first, and only then the second measuring electrode, which leads to the occurrence of a wave biphasic electrophysiological reaction. However, biphasicity can also be a consequence of the irritating or damaging effect of the new solution on the cells and tissues of the plant (phases: irritation - inhibition). In the model experiments, the impulse movement of the perfusate along the vessels was tested, for which a plunger pump was used. It turned out that the hydraulic pulses caused synchronous pulsations of the electric potential difference, which indicates a close connection between the hydrodynamic parameters of the xylem flow and the occurrence of the electric potential difference between the basal and apical sections of the stem segment. However, at a higher concentration of salts in the perfusate (>10 mM NaCl), electrical pulsations disappear, which is most likely due to the shunting of the difference in electrical potentials due to the high electrical conductivity of the xylem perfusate. This is confirmed by the fact that non-electrolytes, in particular sucrose and glycerol, even in much higher concentrations (up to 500 mM), did not shunt the pulsation of the difference in electrical potentials. A biological model was also used, where instead of a stem, a cylinder was taken from the tissue of a potato tuber, hermetically cut into a glass or plastic tube, and instead of a xylem vessel, a longitudinal channel was pierced in it, through which the "perfusion" of the object was carried out. Of course, the hydraulic and electrical (osmotic) pressure of such a model was much lower. In this case, pulsations of the electric potential difference did not occur either on water or on NaCl solutions of any concentration. But several pulses of the difference in electric potentials (<10) still "skipped" at the very moment of changing the solutions. The pulsations of the electric potential difference in this and other cases are most likely connected not with a change in the speed of the solution, but with the occurrence of excess pressure in the part of the stem closest to the pump. Having reached its maximum, this pressure is quickly absorbed, thanks to the movement of the solution through

the xylem, the speed of which decreases rapidly, possibly to a complete stop. On the same model, with a non-impulse supply of the solution, the transition curves were recorded when changing water to salt and vice versa. They turned out to be different for different salts and concentrations. When passing from water to salts or acids of different concentrations, the potential may initially become positive, but then this process will gradually change to negation. Sometimes there is a transition through 0 (change in polarity). When transitioning to alkali, both phases have the opposite sign of changes (initially negation, and then positivity). Washing with water after each action gives a reaction of the reverse direction, which passes at a lower speed and often in one phase. If an object, i.e. potato tissue, is not placed in such a model system, the transition curves are also recorded, but in a different way. The difference between the first and second curves gives the actual search value – wave-like two-phase changes in the difference in electrical potentials of a plant object, which have characteristic features for different electrolytes. Hydrochloric acid acted in the same way as NaCl, but the amplitude of the response was several times (up to 5) higher, and NaOH caused a response in the opposite direction – all comparisons in equimolar concentrations. The effect of each electrolyte was gradual, but the shunting effect was strongly imposed. Thus, with an increase in NaCl concentration from 1 to 5 mM, the amplitude of the reaction increased by 1.5-2 times, from 5 to 10 mM – by 1.2-1.5 times, and from 20 to 50 mM - almost did not increase. The speed parameters of the reaction also changed somewhat. On the main object – the xylem vessels of the stems - sometimes only transient curves were also recorded, and in other cases (unlignified lilac stems) stable levels of the difference in electric potentials for different solutions were obtained. The considered models make it possible to understand the reasons for these differences [Zakharin, Panichkin, 2007].which have characteristic features for different electrolytes. Hydrochloric acid acted in the same way as NaCl, but the amplitude of the response was several times (up to 5) higher, and NaOH caused a response in the opposite direction - all

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It was shown that in response to the salinity of the nutrient solution in plants from the Fabaceae family, the ionization constant of the carboxyl groups of polygalacturonic acid in the walls of all organs decreases, while the dissociation constants of the carboxyl groups of oxycinnamic acids and phenolic OH groups are little dependent on the strength of the external solution. The ion exchange capacity of the polymer matrix of the cell walls of the root, stem and lower layer of leaves of *Sicer arietinum* and *Visia narbonesis* increases with the level of

salinity of the nutrient solution by 10-20%. At all concentrations of sodium chloride in the medium, the capacity for ion exchange of cell walls is higher than that of roots and leaves, since the cell walls of the stem contain significantly more carboxyl groups of polygalacturonic acid [Jalalikhonarmad, 2007]. It was also found that at a low ionic strength of the external solution, that is, a high rate of transpiration, the apoplastic path of water movement is decisive, since under these conditions the hydraulic resistance of the root is low, which ensures rapid absorption of water [Steudle, Peterson, 1998].

It has been established that additional illumination with blue light increases the resistance of potato plants against chloride salinity. The protective effect of the short-wave range of the spectrum can primarily be caused by the accumulation of components of non-enzymatic antioxidant protection systems - carotenoids and proline [Kovtun et al., 2019].

It was found that under salt (NaCl) stress the plant *Mesembryanthemum crystallinum* switches from C3 photosynthesis to CAM (Crassulacean acid metabolism). A plant normally uses C3 carbon fixation, but when it experiences water or salt stress, it can switch to Crassulacean acid metabolism. This effect was pronounced if the plant was grown in an environment rich in red light. It has also been shown that light with a low H/F ratio (red light / far red light), in contrast to light with a high H/F ratio, induces the formation of pinitol, a soluble carbohydrate that accumulates in a number of plant species under a range of conditions stress. When studying the influence of red and far-red light on the content of chlorophyll pigment in *Mesembryanthemum crystallinum* L., it was found that red light stimulated chlorophyll biosynthesis in both normal and saline plants. The red and far-red forms of phytochrome also regulated the ratio of chlorophyll a to chlorophyll b and the biosynthesis of yellow and orange pigments. Based on the results obtained in this work, it was shown that phytochromes also regulate the transition of plants from the vegetative period to the generative period of development [Cockburn et al., 1996].

It was also shown that an increase in the content of the active form of phytochromes leads to an increase in the content of carotenoids and flavonoids, as well as to increased stability of the photosynthetic apparatus of plants. A decrease in the content of phytochromes is accompanied by a decrease in the stability of the photosynthetic apparatus. Changes in the phytochrome system also lead to rapid regulation of the expression of genes that encode photosynthetic proteins and antioxidant enzymes that change in their activity. Phytochromes interact with stress signaling components, and as a result, contribute to the fine regulation of photosynthesis processes and the stability of the photosynthetic apparatus to changes in the surrounding environment [Kreslavski et al., 2018].

The effect of red and far-red light on phytochrome content and FS2 activity under salt stress in etiolated seedlings of two wheat genotypes was studied. The results of the study showed that with the increase in the concentration of sodium chloride, the content of phytochrome and the efficiency of PS2, measured by fluorescence parameters (F_v/F_m), decrease. Under the action of red (660 nm) light, the content of phytochrome and the efficiency of FS2 was higher than under the action of red light (730 nm). A direct correlation between the content of phytochrome and the efficiency of FS2 was also found. The conducted studies showed that the soft wheat variety differed from the durum wheat variety in relatively high tolerance against salt stress. In the soft wheat variety Pirshakhin, the content of phytochrome and the efficiency of FS2 was higher than in the durum wheat variety Shark under salt stress. As the concentration of sodium chloride increases, the content of phytochrome in wheat seedlings decreases. The content of phytochrome in these seedlings is in direct correlation with the efficiency of FS2 work [Azizov et al., 2019].

The process of energy conversion begins with the excitation of the chromophore of the chlorophyll molecule by a quantum of light, that is, a photon, with the subsequent transition of an electron to a higher energy level. The return of an excited, i.e. unstable, chlorophyll molecule to its initial state is possible as a

result of the transformation of its excess energy: 1) into heat (molecular movement) and light from a longer wavelength (in the case of the so-called deactivating fluorescence, in solution); 2) into the energy of the resonance wave of excitation of an exciton, but not an electron, that occurs between neighboring chlorophyll molecules; 3) in the process of transferring a high-energy electron to the nearest acceptor molecule, and during the subsequent return to the initial state due to the acceptance of a low-energy electron from the donor molecule [Chentsov, 1997, Deichman, 2017].

CHAPTER 4. ECOLOGICAL MANAGEMENT OF SALT TOLERANCE DIAGNOSTICS

Stability diagnosis methods must satisfy a number of requirements: have sufficient differentiating ability to separate objects according to their level of stability; be reliable; have quantitative evaluation criteria; be characterized by technical simplicity; not high labor intensity [Goncharova, 2011a, 2011b]. Various methods of diagnosing salt resistance should be based on the determination of shifts in certain physiological and biochemical parameters in response to salinity. At the same time, sufficiently low as well as excessively high salt concentrations can provide the necessary differentiation of samples [Martinez-Cob et al., 1987, Sergeeva et al., 2011]. Assessment of salt resistance based on the intensity of post-illumination or growth of isolated tissues also shows intracellular mechanisms of homeostasis restoration [Tretyakov, 1980, Freytag et al., 1990; Jain et al., 1990].

The intensity of salinity is measured in various indicators, and specifically, in molar units, which are used in laboratory experiments. The salinity of water used for irrigation is assessed by its electrical conductivity or osmotic potential. In the SI system, the unit of electrical conductivity is the siemens - the reciprocal of the Ohm. Usually, the higher the concentration of salt in water, the higher the electrical conductivity of water and the lower its osmotic potential [Chirkova, 1997; 2002].

Thus, cytogenetic and biochemical assessment methods at the cellular level include the assessment of the frequency of chromosomal disorders and mitotic activity in meristems, the intensity of lipid peroxidation and the accumulation of proline in plant tissues, the state of their pigment system and the balance of the elemental composition [Vykhreva et al., 2002; Chirkova, 2002; Gupta, Huang,

2014]. Physiological and molecular markers of resistance are also being developed [Abdel-Hamid, 2014].

Soil salinization has a rather strong depressing effect on the growth and productivity of cultivated plants. On the one hand, the influence of salts can be considered as a factor that stimulates osmotic stress. On the other hand, chloride or sulfate salinity has a toxic effect due to the accumulation of sodium in the cells. At the same time, the threshold level for most plants is 40 mM/l NaCl [Munns, Tester, 2008]. Salt stress, like any other stress, has a rather negative effect on biochemical and physiological processes, growth parameters and development, depending on the resistance of plants. Biochemical changes such as the level of hydrogen peroxide or superoxide radicals activate the antioxidant defense system. The activity of antioxidant enzymes can be used as a marker to assess plant resistance to stress [Asada, 1999, Ros-Barcelo et al., 2002, Janda et al., 2003, Foyer, Noctor, 2005, Chen et al., 2006, Couee et al., 2006, Jaleel et al., 2007, Polesskaya, 2007, Hernandez et al., 2010, Koshkin, 2010, Sinkevich et al., 2011, Cavaiuolo et al., 2013, Rogers, Munne-Bosch, 2016, Oliynyk et al., 2017, Kovbasenko et al., 2018, 2019, 2019a , 2021, 2021a, Teslyuk et et al., 2018, Grygoryuk et al., 2020, Kovbasenko, 2021a, Kovbasenko, Kovbasenko, 2021, 2021a, 2021b].

Salinity, that is, an excess of salts in the aqueous phase of the soil layer, where the root system functions, is most often represented by sodium cations in close combination with chlorine, sulfate, or carbonate anions. Soils with carbonate-sodium salinity, with very rare exceptions, are absolutely unsuitable for use in agriculture. The term "salt tolerance" in agronomic and physiological literature is used in relation to chloride and sulfate-sodium salinity [Shikhmuradov, 2014]. One of the main features of plant salt tolerance is the ability of plant cells to maintain an optimal ratio of K^+/Na^+ in the cytosol [Maathuis, Amtmann, 1999; Tester, Darenport, 2003]. Under normal conditions, cytosol K^+ is about 150 mM [Wyn Jones et al., 1979; Leigh, Wyn Jones, 1984]

and cytosolic Na⁺ in lower limits [Carden et al., 2003], this ratio is much greater than 100, indicating normal cell metabolism.

Halophytes have physiological and biochemical mechanisms that allow them to cope with high soil salinity. Among these mechanisms, along with the ability to control the flow of ions into plant organs, a rather important role belongs to the processes of antioxidant protection, as well as structural and functional modulations of the biological membranes of the plant cell [Parida et al., 2004, Bose et al., 2014, Rozentsvet et al. , 2017].

It is quite likely that the first mechanism that ensures the resistance of plants against salinity may be the low permeability of the plasmolemma of root cells for these ions [Richter, 1927; Gushchin, 1938] and rather high sorption capacity of roots [Evdokimov, 1970].

Different intensity of transport of absorbed sodium and chlorine ions in the plant is noted in the literature. The highest concentration of sodium ions was found in the roots [Prat, Fathi-Ettai, 1990], and chlorine ions – in the leaves [Walker et al., 1987]. In the growing tissues of barley, the concentration of sodium and chlorine in the stretching zone was significantly higher than in dividing cells [Munns et al., 1988]. It is likely that inhibition of the transport of these ions through the plant leads to a significant increase in salt tolerance.

The protective effect of sodium chloride on plants of crystal grass (*Mesembryanthemum crystallinum* L.) is manifested mainly in the improvement of the water status of plants under the conditions of the toxic effect of copper. This process includes a decrease in the osmotic potential of cell juice, which allows plants to more effectively absorb water and accumulate proline - a universal stress-protective compound, as well as differential expression of aquaporin genes, proteins that take an active part directly in cellular water transport [Volkov et al., 2007].

To compare the ion-transporting and ion-correcting ability of the root system and aerial organs of the whole plant, mainly under NaCl-stress conditions,

the xylem perfusion method of the stem was used. The effect of decrement (incomplete passage) shown earlier on stems was also found for roots, although the long-term kinetics for organs differed significantly. After a day, sodium passed through the root almost without decrement, and the concentration at the outlet was 0.90-0.95 of the nominal value. For the stem, this value ranged from 0.3 to 0.6 and was maintained at this level for a week or more. The situation is similar in relation to the second effect – enrichment of the perfusate with potassium and calcium ions. Both of these effects, as well as a decrease in the perfusion rate at high concentrations of NaCl in the perfusate, are a manifestation of what we conventionally call salt resistance, i.e., such changes under the influence of salt stress that prevent the further development of stress (penetration of salts) or slow it down. Salt resistance can be considered as an alternative to salt tolerance. It was found in glycophytes, which do not have salt resistance (by definition). Traditionally, the main role in the mineral nutrition of the whole plant is attributed to the root, and in conditions of salt stress, the root determines the stability or resistance of the whole organism. The conducted studies showed that the resistant function of the stem was much stronger than that of the root. On the root, in addition to xylem, there is also radial transport of ions, which is usually associated with "active" systems and regulatory mechanisms. However, radial transport is localized in the absorption zone of the root, which is relatively small in length - a few centimeters. Above is the leading part of the root system, where the same ion-correcting mechanism is possible during xylem transport (sodium decrement), as in the vessels of the stem. Why is the ion-correcting function of the root obliged to: radial or xylem transport? The answer to this question was quite simple. By perfusing NaCl (100 mM) through the root in the reverse direction, so that the perfusate flowed from the tips of the roots, a high decrement of sodium was registered, its concentration at the outlet was 36.6 mM, and when cutting off the tips of the roots by approximately 2-3 cm (open vessels) it did not change. However, at subsequent cuttings of the lower third of the roots, then the

middle and then the upper (sequential reduction of the length of the xylem paths in the roots), the sodium concentration at the outlet was 58.0, 73.3, and 95.8 mM, respectively. That is, when the length of the xylem was shortened, the sodium decrement decreased and at the very end reached the zero mark. And the opening of the vessels into the solution, the actual shunting of the radial transport, practically did not affect the decrement. Therefore, the observed ion-correcting function of roots (not lasting) under salt stress is related not only to "active" radial transport, but also to "passive" xylem transport. From the point of view of the water-salt exchange of plants, the structural and functional schemes of the stem and root are quite similar. Each of these organs actually consists of plant tissue, i.e. a combination of symplast and apoplast, between which there is a continuous water-salt exchange through cell plasmodes. However, in such a "static" form, this system tends to quickly establish a dynamic equilibrium, after which the processes of regulation of water-salt exchange are stopped. In order for this not to happen, a continuous flow of the solution is needed, which, bringing fresh portions of the external solution for a while, continuously disturbs this equilibrium. Such a scheme, according to researchers, is a "universal transport system" that works at the level of organs and the whole plant. In this case, the xylem flow is the exciting force, the "driver" of the universal transport system, or in other words, the entire water-salt exchange of the entire plant. Obtained for plants subjected to salt stress, these images are quite likely to characterize ion transport processes under normal conditions as well [Zakharin, 2007].

Using the method of electronic cytochemistry to detect chlorine ions, based on the binding of chlorine ions by stem ions with the formation of electron-dense AgCl granules in the cells, showed that chlorine ions are concentrated in the specified pinocytotic intussusceptions and multivesicular bodies. In the halophyte *Suaeda altissima*, the survival strategy at a high concentration of salt in the external environment is based on the translocation of sodium and chlorine ions absorbed by the roots into above-ground organs and their deposition in cell

vacuoles. And this, in turn, leads to a decrease in the water potential, thanks to which the flow of water to above-ground bodies is stopped. The conducted study shows that the process of pinocytosis is involved in the deposition of ions in the halophyte *Suaeda altissima*, thanks to which these ions enter the vacuole from the apoplast, bypassing the cytoplasmic compartment [Kurkova et al., 2007].

In irrigated agriculture, the increase in salinity tolerance of cultivated plants will reduce the requirements for leaching, reduce the costs of irrigation schemes and the need for fresh water [Pitman, Lauchli 2002].

As an express indicator, it is quite convenient to use the degree of suppression of the regeneration activity of stem cuttings under salinity conditions, which was analyzed on the example of a significant number of herbaceous plants. It was noted that the degree of reduction in the regeneration activity of cuttings under salinity conditions can be considered as a test indicator, and the concentrations of salts that inhibit rhizogenesis in sensitive species and varieties are in lower regions than in resistant ones [Alieva, Yusufov, 2013]. For semi-woody and woody cuttings of fruit plants, such an express assessment is especially relevant, because it allows early monitoring of plant salt tolerance [Sincliar, Hoffman, 2003].

A rather close connection between the implementation of regeneration processes in grape cuttings under salinity conditions and the changes that occur at the cellular level, in particular the content of chlorophyll and the state of membranes, was revealed. This approach makes it possible to correctly assess the integral response of the response of the plant organism and can be used in the assessment of salt tolerance [Alieva, 2016].

A representative sample of genotypes with contrasting indicators of salt resistance was screened in the conditions of a microvegetation experiment on artificial media. Gene-specific primers were designed for the sequences of the *SrIk* gene described for the model species *Medicago truncatula*, and their effectiveness was tested in the polymerase chain reaction with the genomic DNA

of other species of the genus *Medicago* from the VIR collection, which differ in their resistance to salt stress. Amplified fragments of the *Srlk* gene were subjected to restriction analysis using a set of endonucleases, which allowed for the first time to identify and describe the intraspecific polymorphism of the nucleotide sequence of *Srlk* in *Medicago sativa*, which had not been previously studied. The comparison of the detected nucleotide sequence polymorphism of the *Srlk* gene in different *Medicago sativa* genotypes with their salt tolerance indicators will allow further development of CAPS (*Cleavage Amplified Polymorphic Segments*) markers, which allow to distinguish allelic variants of the *Srlk* gene in salt-tolerant and salt-sensitive genotypes of alfalfa by sowing, without using a rather expensive procedure sequencing [Vyshnevskaya et al., 2010].

Accumulation of sodium and proline ions in the cell sap of *Thellungiella salsuginea* (Pall.) OE Schulz. was 2 times higher than similar indicators for cells of *Arabidopsis thaliana* (Heynh.). At the same time, an increase in the volume of the vacuoles of *Thellungiella salsuginea* (Pall.) OE Schulz cells was noted. and the presence of characteristic ultrastructural signs of a highly energized state of mitochondria. It is likely that *Thellungiella salsuginea* (Pall.) OE Schulz. implements the strategy of several "lines of defense" and resists salinity not only at the level of the whole plant, but also at the level of cells [Nosov et al., 2010].

The reaction to NaCl salinity (100 mM) of wild herbaceous plants (*Geum urbanum* L., *Thalictrum aquilegifolium* L., *Plantago major* L., *Artemisia lerchiana* L.), whose decorative forms can be used in urban landscaping, was studied. *Geum urbanum* L. and *Thalictrum aquilegifolium* L., in contrast to *Plantago major* L. and *Artemisia lerchiana* L., were characterized by high sensitivity to the action of NaCl. This was expressed in the rapid loss of turgor, the dying of the leaves of the lower tier, stunted growth and a high percentage of non-adapted plants. Marker biochemical indicators were used to assess the stress state of plants: the content of proline and sodium ions, the activity of superoxide dismutase and guaiacol peroxidase. All studied plants, to one degree or another,

accumulated sodium ions in the stems and root system. Significant differences were found in the accumulation of proline, the activity of superoxide dismutase and guaiacol peroxidases. Plants with less sensitivity to salinity (*Plantago major* L. and *Artemisia lerchiana* L.) were characterized by a greater accumulation of proline in the stems and a high activity of guaiacol peroxidases in the stems and root system. And the plants *Geum urbanum* L., *Thalictrum aquilegifolium* L., on the contrary, possessed a higher constitutive activity of superoxide dismutase [Kartashov et al., 2011].

Vacuolar Na^+/H^+ -antiporters take the most active part in maintaining a low concentration of Na^+ in the cytosol of plant cells. Energy for their work is produced by H^+ -ATPase and H^+ -pyrophosphatase. Amino acid sequences of antiporters usually contain 9-12 hydrophobic domains in their N-terminal part and a hydrophilic section of 100 amino acid residues in the C-terminal part. The greatest identity in the amino acid sequences of various vacuolar Na^+/H^+ -antiporters is observed in the hydrophobic region, which determines the ion-exchange activity of the antiporter, and the least in the hydrophilic region, which is associated with the regulatory activity. Three isoforms of the vacuolar Na^+/H^+ -antiporter HvNHX1-3 were studied in barley seedlings of different varieties, which differ in their resistance to salt stress. Cytochemical study showed that all three HvNHX1-3 proteins are present in the same cells of almost all root tissues, both in the tonoplast and in prevacuolar vesicles. It was also established that the content of all three isoforms in the vacuolar membranes of barley seedlings increases during salt stress and that this process is more pronounced in the resistant variety. It is also shown that the quantitative growth of HvNHX1-3 under stressful conditions is related to the regulation of HvNHX1-3 expression at the transcriptional and translational levels. The obtained results indicate in favor of the fact that varietal salt tolerance of barley is correlated with the intensity of Na^+/H^+ exchange on vacuolar membranes under control conditions and with the ability to regulate it under stress conditions. The final dimensions of the vacuole

volume impose restrictions on their ability to maintain a low concentration of sodium ions in the cytosol of plant cells for a long time, and therefore an interpretation of the relationship between salt resistance and the intensity of Na^+/H^+ exchange on vacuolar membranes, different from the compartmentalization of sodium ions, is proposed [Roslyakova et etc., 2010].

The ability of the membranes of the microsymbiont to ensure salt resistance of the symbiotic system of leguminous crops was studied. For this purpose, the ion permeability of the membranes of bacteria with weak (50 mM NaCl – *Bradyrhizobium lupini*) and relatively high (400 mM NaCl – *Sinorhizobium meliloti*) salt resistance was compared. At the same time, the permeability of the Na^+ -cytoplasmic membranes of free-living and symbiotizing forms of rhizobia, as well as the peribacteroid membrane of symbiosomes of lupine and alfalfa tubers was determined. It was shown that the content of sodium ions in the cells of pure cultures of both types of rhizobia increases as the concentration of salt in the nutrient medium increases. Despite the fact that the two species of rhizobia differ in salt tolerance, their cytoplasmic membranes were equally easily permeable to sodium ions. In the fractions of symbiosomes and bacteroids, the content of sodium ions increased with increasing salt concentration in the incubation medium. And therefore, the membranes of microsymbionts of both lupine and alfalfa cannot serve as a reliable barrier for the entry of sodium ions into their cells. The peribacteroid membranes of the symbiosomes of these legumes are also a weak barrier for chlorine ions. The addition of ATP to a suspension of symbiosomes from lupine and alfalfa nodules caused the generation of an electrical potential ($\Delta\phi$) on the peribacteroid membranes. Subsequent introduction of monovalent penetrating ions (NO_3^- and Cl^-) into the incubation medium led to the dissociation of $\Delta\phi$ on the peribacteroid membranes. The half-life $\Delta\phi$ for nodule symbiosomes of both types of leguminous plants was the same. The obtained results allow us to state that the functioning of the nitrogen-fixing symbiotic system of lupine and alfalfa under conditions of salt stress is due to

either the low sensitivity to NaCl of the biological polymers of the microsymbiont, or the ability of the host plant to maintain ion homeostasis in the cells of the central tissue of the nodule [Khailova, Andreev, 2010].

Haloxylon aphyllum (Minkw.) Iljin, family *Chenopodiaceae* (leafless, black saxaul) is one of the main edifiers of the Kyzylkum desert, forming huge, tens of kilometers long, populations. However, this species is localized mainly in the lowland parts of the microrelief. Such selectivity of its distribution is quite surprising considering the highest resistance to arid climate among plants of species with NADP-ME type C₄-photosynthesis. In the conditions of the constancy of the regional climate, the main factor in the formation of saxaul populations is the increase in soil salinity when the topography of the area decreases [Shuiskaya et al., 2010].

It is shown that with the increase in the concentration of NaCl in the growing medium of winter wheat seedlings from 1 to 150 mM, an increase in the content of photosynthetic pigments is observed. At the same time, there is also an increase in the ratio of chlorophyll *a* to chlorophyll *b*, and a decrease in the ratio of the sum of chlorophylls to carotenoids; increase in the amount of auxiliary pigments. All this testifies to the protective role of the latter under the action of salinization. With increasing time of exposure of seedlings in a solution of high concentration of NaCl, the nature of the effect of salinity on the content of photosynthetic pigments changes: first, an increase in the number of photosynthetic pigments is noted, and then - a decrease. It should also be noted that winter wheat seedlings treated at a later age retained their viability even in the presence of 300 mM NaCl. Usk proves that the sensitivity of a plant organism to salinity is determined by the stage of its development [Yakovets, Adamovych, 2018].

Solving the problem of successful use of saline areas involves the search for salinity-resistant wheat varieties. In this regard, previously, based on the determination of germination energy, seed germination, raw and dry mass, an

assessment of salt resistance of six varieties of soft wheat was carried out: Sudarynya P1, Darya P1, Lyubava P2, which are yarrows and Elegy, Mroya P2, Oda , which are winter. For further research, the salt-tolerant varieties Elegiya and Darya P1, salt-sensitive Mroya P2 and Lyubava P2 were selected. To confirm the obtained results, the seedlings of the selected varieties were grown by the roll method in glass vessels containing solutions of the following composition: 0.1 mM CaSO₄ (control); 0.1 mM CaSO₄, 200 mM NaCl. On the 14th day, the length of roots and stems was determined. On the basis of the obtained results, it can be concluded that the earlier assessment of salt resistance of wheat varieties based on growth tests was also confirmed by the method of water cultures [Yakovets, Svadkovskaya, 2018].

Using the proposed method, we screened salt tolerance of the main varieties of tomato (Table 1).

Table 1 – Parameters of the main varieties of tomato plants

Options research	Root length, mm	The length of the stems, mm
Mild grade		
Control, water	14.6 ± 0.4	13.8 ± 0.3
0.1 mM CaSO ₄	10.1 ± 0.5	9.8 ± 0.4
200 mM NaCl	10.0 ± 0.5	9.7 ± 0.4
Horiv variety		
Control, water	14.9 ± 0.2	14.2 ± 0.2
0.1 mM CaSO ₄	10.9 ± 0.3	10.3 ± 0.4
200 mM NaCl	10.8 ± 0.4	10.2 ± 0.3
Boyan variety		
Control, water	14.8 ± 0.2	14.1 ± 0.3
0.1 mM CaSO ₄	10.7 ± 0.3	10.2 ± 0.4

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200 mM NaCl	10.5 ± 0.3	10.1 ± 0.4
Bobrytsky variety		
Control, water	15.0 ± 0.2	14.5 ± 0.5
0.1 mM CaSO ₄	11.3 ± 0.4	10.8 ± 0.2
200 mM NaCl	11.1 ± 0.3	10.6 ± 0.3
Borivsky variety		
Control, water	14.9 ± 0.4	14.2 ± 0.3
0.1 mM CaSO ₄	10.8 ± 0.6	10.2 ± 0.4
200 mM NaCl	10.7 ± 0.4	10.0 ± 0.2
Dawn variety		
Control, water	14.3 ± 0.4	13.6 ± 0.2
0.1 mM CaSO ₄	10.0 ± 0.3	9.7 ± 0.6
200 mM NaCl	9.9 ± 0.2	9.6 ± 0.5
Flora variety		
Control, water	14.1 ± 0.1	13.4 ± 0.4
0.1 mM CaSO ₄	9.8 ± 0.5	9.5 ± 0.3
200 mM NaCl	9.6 ± 0.4	9.3 ± 0.5
Variety Kyiv 139		
Control, water	14.2 ± 0.3	13.5 ± 0.4
0.1 mM CaSO ₄	9.9 ± 0.2	9.6 ± 0.4
200 mM NaCl	9.7 ± 0.2	9.4 ± 0.3
Kort Konservnyi Kyivskyi		
Control, water	14.0 ± 0.4	13.3 ± 0.4
0.1 mM CaSO ₄	9.7 ± 0.3	9.4 ± 0.3
200 mM NaCl	9.4 ± 0.3	9.2 ± 0.2

One of the rather important and integral indicators that can be used to judge the degree of influence of salinity on cultivated plants is their growth, which is

one of the main indicators of the physiological state of plants [Shevelukha, 1987; Daskalyuk et al., 1992; Kostyuk et al., 1994; Veselov et al., 2007; Zaitseva et al., 2009]. A different degree of reduction in the length of the root and the height of the aerial part was noted depending on the type (NaCl, Na₂SO₄) and salinity level (5.0, 7.5 and 10.0 g/l) [Orlova, Kanevskaya, 2015].

A rather important importance in the mechanism of plant salt tolerance of the processes of the exchange of phenolic compounds was established, and the special role of lignin in adaptation was shown, which can be a biochemical marker of cell aging and salinity of the environment, as well as the specificity of the response to the effect of the qualitative composition of salts and their concentrations. In an actively metabolizing cell, phenolic compounds are in the form of glycosides or simple or complex esters with low metabolic activity. Therefore, the increased level of free forms of phenolic compounds in plants against the background of salinity will contribute to the growth of their functional activity. Less polar free forms of phenolic compounds within functional concentrations stabilize cell membranes due to hydrogen and hydrophobic bonds, and their high antiradical and antioxidant activity increases the resistance of membranes against damage. In addition, phenolic compounds can be used as spare respiratory substrates, which is especially important in stressful situations [Dostanova, 1994].

It was found that the absorption of silicon by plants is combined with sodium and calcium, and therefore, in conditions of soil salinity, plants are able to intensively accumulate silicon, which contributes to the growth of their resistance to salinity [Kemecheva, 2003; Sheujen, Kemecheva, 2003, Hattori et al., 2009, Inal et al., 2009, Tale, Haddad, 2011, Kovbasenko, Kovbasenko, 2018].

The metabolic response of wheat seedlings under combined water and salt stress is non-additive and differs significantly from the response under each of these stresses separately. Initiation of proline synthesis requires not only the

presence of salt in plant cells, but also the creation of drought conditions [Ivanov, Kosobryukhov, 2014].

The fact of the formation of megamitochondria or a mitochondrial network in the cells of wheat roots when the work of the first and third complexes of the electron transport chain is blocked has been revealed. At the same time, it can be predicted that along with changes in the functional activity of mitochondria, that is, a decrease in the level of respiration, ATP, $\Delta\psi_m$, a change in their morphology is one of the possible ways of adaptation against stressful actions [Ponomareva et al., 2014].

It has been established that intervarietal and intravarietal differences occur under conditions of salt stress. It has been experimentally shown that the selection of promising salt-resistant samples using laboratory methods for determining germination energy, germination, determination of free proline content and peroxidase activity, their evaluation on saline soils in field conditions allow to achieve positive results within a short period of time and create salt-resistant samples and varieties of wheat [Sedlovsky et al., 2014].

Zucchini and pumpkin are quite similar in shape and are characterized by approximately the same salt tolerance. And therefore their reaction of their isolated cotyledons to salinity was of the same type. From the isolated cotyledons of both these cultures, it is possible to judge the specificity of their reaction to the level and type of salinity. In this sense, isolated cotyledons can be considered as a simpler model for assessing the sensitivity of plants to salinity. This provision deserves to be checked on objects that differ in salt resistance [Abdurakhmanov, 2011].

The reaction of plants to the stress effects of chlorine ions was noted mainly in the early stages of lupine seed germination. This causes a plant response reaction in the form of accumulation of individual components of the system, especially anti-stress proteins-protease inhibitors. Indicators of the activity of the

proteolysis system can be successfully used in agricultural practice [Domash et al., 2011].

One of the rapidly progressing methods of studying miRNAs is the third-generation deep sequencing (NGS) method, which allows you to quickly and accurately determine the sequence of miRNAs and pre-miRNAs, as well as measure their quantities. This method was used to study the diversity of miRNAs in the plant *Thellungiella salsuginea*. At the same time, it was possible to show that under normal conditions, 42 families of known miRNAs, which number 110 representatives, are expressed. Also, 8 new miRNAs expressed only in *Thellungiella salsuginea* were discovered; the difference from *Arabidopsis thaliana* is 7.2%. It was shown that, under normal conditions, microRNAs associated with the regulation of HD-ZIP, MYB, SBP transcription factor genes are expressed most intensively, while miRNAs associated with the regulation of auxin signal perception factors are expressed to a lesser extent, the expression of which is activated upon action stressors of various physiological nature, including NaCl [Pashkovsky, 2011, Pashkovsky et al., 2013]. At the same time, it was established that microRNAs take part in the primary response to salinity. The obtained information indicates the probable suppression of mRNA of some antioxidant and respiratory enzymes, genes of biosynthesis of hormones, cellulose and transcription factors, which in turn are able to regulate a whole complex of other genes. The expression of miRNA in plants under stress indicates both a possible slowdown in the biosynthesis of hormones necessary for the redistribution of energy between metabolic processes, and the activation of mechanisms that change the sensitivity of cells and tissues to already formed hormones [Pashkovsky et al., 2015]. miR398 expression was only detected in light-grown calli, which may indicate inactivation of miR398-mediated gene regulation in the dark. This can be explained by a possible transition to a heterotrophic type of nutrition and degradation of chloroplasts in calli that grew in the dark. In the callus lines of *Thellungiella salsuginea* grown in the light, the

expression of miR398 had a stress-inflammatory character and was inactivated in the first hours after treatment with a stressor [Pashkovsky et al., 2011].

It is believed that the salt-resistant varieties of cultivated plants maintain the necessary K^+/Na^+ ratio in the leaves, but do not spend additional energy on the selective absorption of these ions, the reverse transport of sodium in the root and its removal into the soil solution. It is assumed that there is a compartmentalization of salinizing ions in the stems, which contributes to the formation of a high osmotic potential in addition to the synthesis of organic osmolytes [Ladatko, Doseeva, 2010].

The study of salt resistance of tall varieties of durum wheat and their short-stemmed analogues with different stunting genes showed that the salt resistance of short-growing analogues with the Rht 1 gene is similar to that of tall forms. The salt resistance of short-stemmed lines with the Rht 3 gene and other genes was slightly higher than the salt resistance of tall forms. The revealed tendency to increase salt resistance in short-stemmed forms is associated with the weak permeability of biological membranes of short-stemmed forms and with strong compaction and smaller cell sizes of short-stemmed forms [Alderov, 1991].

The possibility of diagnosing the resistance of grapes to salinity was studied using the example of two varieties - Pinot Gris (I) and Sauvignon Green (II) - by comparing the indicators of stem and root formation, as well as the accumulation of biological mass of lignified stem cuttings during cultivation in NaCl solutions (A) 10^{-1} , 10^{-2} , 10^{-3} M and Na₂SO₄ (B) 10^{-1} , 10^{-2} , 10^{-3} M at room temperature and lighting, and the control is water. The biological mass of roots according to the variants for grade I was significantly lower than the control, and for type II it was significantly higher, with the exception of variant 10^{-2} B. Under salinity conditions, varieties I and II differed in the sensitivity of root formation and stem growth. And therefore the ratio of dry mass of stems/roots ("polarity coefficient") also changed. The ratio in I increased with salinity, while in II there was a tendency to decrease. Thus, according to the sum of these indicators, I is less

resistant to salinity A and B, while in II there is an advantage of the biological mass of roots over stems, which indicates its higher resistance [Aliyeva, 2015a].

The conducted studies show that the fluorescent probe dihydroethidium can be used to study the reaction of ROS synthesis under salt stress in bryophytes. This substance shows a fairly high degree of specificity for superoxide, compared to hydrogen peroxide, but is probably capable of detecting hydroxyl and other radicals as well. The results of the work also demonstrate that in the moss *Physcomitrella patens*, salinity causes the synthesis of superoxide and hydroxyl radicals, which is inhibited by natural antioxidants, such as superoxide dismutase, reduced glutathione, and spermine [Zvonarev et al., 2015]. At the same time, the study of soil microflora involves the selection of resistant natural strains for the purpose of their further research in the field of biological use [Kulesh et al., 2016].

Cells and tissues cultured *in vitro* are a promising model for studying salt tolerance of plants. A comparative analysis of salt tolerance of winter triticale samples using *in vitro* callus cultures was carried out. The work used 5 varieties of winter triticale from the collection of the Dagestan VIR station named after E. Vavilova: Almaz, PRAG5301-1934, Timbo and Triskell. Embryos were cultured on Murashige and Skoog medium with the addition of 2,4-D hormones, BAP and NaCl with concentrations of 85 and 165 mM. All variants were cultivated in a climate chamber at a temperature of $24 \pm 1^\circ\text{C}$. The stability of triticale was determined by the intensity of callus formation and proline content. A decrease in growth rates under salinity conditions was expressed in the calli of the *Timbo* sample. In the sensitive specimen Timbo, callus was formed only on medium with a lower concentration of NaCl (85 mM). High growth characteristics were found in the *Triskell* variety. The studied varieties of winter triticale also differed in the accumulation of proline. The intensity of proline accumulation under salinity conditions in callus tissues of winter triticale variety samples was higher in salt-resistant forms – *Triskell*, PRAG5301-1934 [Khabieva et al., 2019].

A conclusion was made about the positive effect of glutathione-S-transferases on plant growth under the influence of drought, salinity, and low temperatures [Kuluev et al., 2017].

A new methodological approach is proposed - the use of fragments of aseptically obtained juvenile seedlings from seeds, which are uniform in habit and stage of development. Aseptically obtained seedlings of two genotypes of tomato (*Solanum lycopersicum* L.) served as plant material for the study: the YLF selection line and the Recordsman variety. For this purpose, in 8-10-day-old tomato seedlings at the stage of the beginning of the formation of the first true leaf, the root and part of the hypocotyl were cut off so that their size was about 2 cm, after which they were transferred to culture vessels with nutrient medium $\frac{1}{2}$ MS containing 0.2 mg/l IMC for the induction of rhizogenesis and different concentrations of NaCl (0-250 mM). On the 8th day of cultivation, the frequency of rhizogenesis was determined (%), morphometric characteristics of the roots and stem part of tomato seedlings were performed according to the following indicators: number (pcs) and length (cm) of regenerated roots, raw and dry biological weight of roots and stem part of the seedling (mg). The indicators of the intensity of dark respiration and true photosynthesis of tomato seedlings were established with the help of a previously developed control system of photosynthetic and diesel CO₂ gas exchange of plants, isolated organs and tissues *in vitro*. Roots regenerated under different conditions of NaCl salinity, as well as fragments of the middle part of the hypocotyl, cotyledons and true leaf were fixed for light and transmission electron microscopy. In addition, an immunocytochemical analysis of the α -tubulin cytoskeleton of the cells of the meristematic zone of the root in seedlings of two different tomato genotypes under NaCl salinity conditions *in vitro* was carried out. As a result of the research, it was established that at the early stages of development (seedling stage), the studied tomato genotypes differ significantly in their resistance to NaCl salinity according to the indicators of raw and dry biological mass of regenerated roots, the stem part of seedlings, the intensity of

dark respiration and true photosynthesis. Experimentally established sublethal concentrations of NaCl, which were 150 and 250 mM for the YALF line and the Recordman variety, respectively. It has been demonstrated that changes in the size and shape of cells of various tissues of the hypocotyl and cotyledons can be used as cytological indicators for the comparative assessment of tomato genotypes for resistance or sensitivity to salinity. Transmission electron microscopy revealed significant differences between tomato genotypes in the structural organization of the chloroplast and nuclear compartments in spongy mesophyll cells of cotyledon leaves under conditions of 150 mM NaCl. The use of antibodies against α -tubulin made it possible to study the organization of the microtubule network in the interphase cells of the root of tomato seedlings of the YLF line and the Recordman variety under NaCl salinity conditions *in vitro*, as well as to reveal the morphological changes of the tubulin cytoskeleton characteristic for each genotype at different concentrations of the stress factor. The proposed methodological approach can be quite successfully applied not only for the comparative evaluation of different tomato genotypes under NaCl salinity conditions, but also in the case of other abiotic stress factors, for example, drought, heavy metals and others, as well as plant objects that have the ability to root regeneration *in vitro* [Khaliluev et al., 2017].

The verification of the researched method of agrochemical melioration on seedlings of deciduous species showed that in the range of sodium chloride content of 100-300 g/m² in the rhizosphere of the studied cultivars, the stability of seedlings, according to the parameters of their morphological structure and production characteristics, is successively reduced in the series: petioled oak - small-leaved linden – sharp-leaved maple. The effectiveness of using meliorant (dolomite flour) in a dose that can be recommended for maple and linden is manifested at the level of salinity of the rhizosphere < 100 g NaCl/m² in the range of soil acidity: for maple at pHKCl 4.7-5.2, for linden at pHKCl 5.3-6.0. Under the action of meliorant in the leaves of the sharp-leaved maple, the participation

of sodium ions in the ion balance decreases up to 5 times in the absence of an increase in the transport of calcium and potassium ions into the leaves; in small-leaved lindens, the introduction of meliorant into the rhizosphere homeostatizes a two-fold decrease in the concentration of sodium ions in the leaf apparatus with an adequate increase in the content of potassium and calcium ions [Budkevich et al., 2017].

A preliminary assessment of rice plants for salt resistance and the selection of the most promising samples can be carried out based on a complex of morpho-physiological indicators: 1) the amount of above-ground biological mass at salinity in relation to the fresh control in the budding and flowering phase; 2) the size of the total leaf surface of the plant, the area of the leaves of the main stems and the level of their reduction under conditions of stress, in relation to the fresh control, in the flowering phase; 3) the number of green leaves on the main stems under salinity in relation to the fresh control, in the flowering phase; 4) leafiness ratio of the main stems; 5) photosynthetic potential on a saline substrate during the "germination - tillering - tuber" period. The final assessment of rice varieties and samples for salt resistance is given by the level of grain yield reduction under salinity conditions in relation to the fresh control [Ladatko, 2006].

The molecular aspects of the mechanisms of stress signal transmission through the ABA-dependent pathway with the participation of ABF transcription factors were studied. The new model plant *Thellungiella salsuginea*, closely related to *Arabidopsis*, which shows higher resistance to salinity and low temperatures, was used as an object of research. Using the RACE-PCR method, 4 genes encoding ABF were identified. Analysis of ABF expression by real-time PCR revealed a persistent induction of ABF in *Thellungiella* in response to stress. Interestingly, unlike *Arabidopsis*, ABF is expressed at a higher level in *Thellungiella* even under normal growth conditions. This gives reason to claim some re-adaptation of *Thellungiella* plants against stress. An analysis of the amino acid sequences of ABF revealed a motif in their C-terminal region, which is

classical for binding to 14-3-3 regulatory proteins. To test the possibility of interaction of ABF with protein isoforms previously identified in *Thellungiella*, 14 genetic constructs were created and yeast two-hybrid analysis was performed. Six of the eight 14-3-3 isoforms tested interacted with ABF, and the intensity of this interaction appeared to be isoform-specific. Replacing serine with alanine in the potential motif, the phosphorylation of which is necessary for binding to 14-3-3 proteins, led to a complete loss of interaction. The obtained results indicate that the regulation of the activity of ABF transcription factors in *Thellungiella* can be carried out by phosphorylation of a specific C-terminal motif followed by the interaction of 14-3-3 proteins with it. This interaction should lead to the stabilization of the dimeric structure of the ABF transcription factors themselves, which cannot help but affect the efficiency of their work. The variety of isoforms of the interacting 14-3-3 proteins, as well as their functioning in the form of dimeric structures, indicates the potential possibility of the formation of various protein complexes with the participation of ABF transcription factors, which in turn can lead to the branching of the signaling pathway at the level of transcription [Vysotskyi and etc., 2010].

A direct relationship between the activity of cell wall lectins and the degree of resistance of winter wheat plants against stress factors of abiotic and biotic nature was revealed, which makes it possible to use this indicator for rapid diagnostics of the resistance of various varieties [Timofeeva et al., 2010].

For the model object *Medicago truncatula*, the key role of the *Srlk* (Salt-induced Receptor-like Kinase) gene in the perception and transmission of the signal about the high concentration of sodium and chlorine ions in the root zone was shown. The transcription factor ZptA2-1 is activated in response to the signal from *Srlk* and ensures the plant's response to stress. Based on the synteny of legume genomes, the sequence of the *Srlk* and ZptA2-1 genes was identified in the rather important fodder and amelioration crop alfalfa (*Medicago* sp.). The allelic diversity of these genes was studied in 18 samples of alfalfa from the world

collection of VIR, growing in contrasting regions. The Srlk sequence was sequenced in 167 alfalfa plants, and the ZptA2-1 sequence was sequenced in 92 plants. The identified non-synonymous SNPs can be associated with the variability of alfalfa varieties in resistance to salt stress [Dzyubenko et al., 2014].

Under conditions of action of stressors, the polarity coefficient changes, which shows the ratio of the biological mass of stems and roots - it increases with salinity [Abed Al Aziz, Yusufov, 1991; Yusufov, Aliyeva, 2014]. Thus, the roots of poplar microclones on a medium with 100 mM NaCl had an increased content of malondialdehyde; the level of superoxide dismutase and catalase also changed, and the leaves were severely damaged under these conditions. Also, the length of internodes, the size and shape of the leaf can serve as signs for monitoring the effects of salt stress on grape plants [Chanteele, Hoffman, 2003].

To assess the salt resistance of cultivated plant varieties, a method of evaluating the D_{50} indicator is recommended – the average time in days, the survival of the variety after salinization of the environment. To do this, young plants of 2-3 weeks of age are watered with NaCl solution (50 mM) and the time is marked when 50% of the plants of each variety die. The greater the value of D_{50} , the higher the salt resistance of this variety [Flowers, Leo, 1995].

It was established that in the early phases of the development of durum wheat plants (seedlings and tillers), the studied samples show weak resistance, and in the later phases, salt resistance increases. The growing salt resistance to the earing phase is a manifestation of the organism's adaptation to the accumulation of toxic ions. It is quite likely that this circumstance is a very important point for the survival of the organism in conditions of increasing salinity due to evaporation of water and drawing of salts to the root layer during the growing season [Shikhmuradov, Magomedov, 2010].

In conditions of salinity, a number of other physiological indicators also change [Parvaiz, Satyawati, 2008; Bayuelo-Jiménez et al., 2012]. In the conditions of abiotic stress caused by salinity, as well as a number of other factors,

the reaction of plants can be evaluated by various physiological and biochemical indicators: the activity of the components of the antioxidant system - superoxide dismutase, peroxidase, the formation of malondialdehyde, the content of proline, chlorophyll, the relative content of water [Keshavkant et al., 2012; Wu et al., 2013]. During salinization, the concentration of soluble hexoses and other organic substances in the total and raw biological mass of fruits decreases. An increase in the content of proline and soluble sugars was noted under salinity, drought and other stress factors in plant tissues and callus cultures of a fairly significant number of species [Dashek et al., 1981; Rus-Alvares, Guerrier, 1994; Benhassaini, 2012, etc.].

With the help of cell selection methods, lines and varieties of cultivated plants resistant to salinity are screened [Ochatt et al., 1998].

CHAPTER 5. SOURCE MATERIAL FOR ECOLOGICAL MANAGEMENT OF CLASSICAL SELECTION

The bottleneck of any breeding program is the lack of a reliable, receptive, inexpensive method that allows for quick selection. In most cases, field selection for salt resistance remains the main tool, despite its time limitation and dependence on environmental conditions [Zhu, 2000; Munns, James, 2003]. In the mechanisms of salt resistance, it is necessary to distinguish between the direct effect of an excess of salinizing ions on the plant [Cheeseman, 1988] and a change in the water-physical and mineral regime under the influence of an excess of salts in the soil solution [Gardner, 1967].

Many potential criteria or traits were used for selection for salt resistance, in particular: 1) variation of plants in the degree of growth or productivity [Greenway, 1962]; 2) plant survival at high salinity [Well, Fossey, 1998]; 3) degree of similarity [Well, Fossey, 1998]; 4) degree of elongation of roots or leaves [Well, Fossey, 1998]; 5) leaf damage and reduction of carbon dioxide and assimilation [Well, Fossey, 1998]; 6) loss of chlorophyll and damage to the photosynthetic apparatus [Krishnarai et al., 1993]; 7) removal of sodium ions [Garcia et al., 1995]; 8) K^+/Na^+ discrimination [Aschraf, Khanum, 1997]; 9) removal of chlorine ions [Rogers, Nobel, 1992]. Many of these criteria are quite often completely unrelated to each other, resulting in different estimates of salt tolerance.

But the main feature of salt tolerance of plants is the ability of plant cells to maintain the optimal K^+/Na^+ ratio in the cytosol [Maathuis, Amtmann, 1999; Tester, Darenport, 2003].

The importance of maintaining the optimal K^+/Na^+ ratio for salt tolerance of plants is quite relevant and is discussed in the literature [Gorham et al., 1991; Gaxiola et al., 1992; Cuin et al., 2003]. It is also likely that such an optimal ratio

can be preserved by limiting the accumulation of sodium ions in plant tissues, or by preventing the loss of potassium ions from the cell. This is a model of the mechanism that is in the center of attention of breeders [Heenan et al., 1988; Ashraf and Khanum, 1997]. However, there have not been any large-scale actions on salt tolerance of plants, which are based on changes in the ability of plants to retain potassium ions in their tissues. The importance of the latter ability is given special importance in studies conducted on *Arabidopsis* SOC (supersalt-tolerant) mutants, which brought to the fore the importance of potassium homeostasis for salt tolerance [Liu, Zhu, 1998; Zhu et al., 1998; Rus et al., 2004; Shabala et al., 2005]. Electrophysiological analysis of root currents showed that all major elucidated potassium ion systems exhibit higher K^+/Na^+ selectivity in *Thellungiella halophila* (CA Meyer) relative to salt tolerance than in *Arabidopsis thaliana* [Volkov et al., 2004]. And other studies have shown that the better selectivity of the allocation of the transport system for potassium ions over sodium ions is an improvement in the definition of salt tolerance [Rodriguez-Navarro, 2000].

At the same time, the literature offers various methods of evaluating selection samples for salt resistance, which are based on various indicators [Ivanov, Udovenko, 1970; Udovenko, 1975; Stasilyunas, 1978; Eswara, Reddy, 1984; Koval, 1985; Bliss et al., 1986; Ashraf et al., 1987; Polonsky, Malyshevskaya, 1989].

The research established noticeable intravarietal differences of Sarepta mustard plants (*Brassica juncea* Czern.) against the action of salinity, which are in the range of 100-200 mM NaCl. At the same time, the concentration of 300 mM is critical and almost completely suppresses the germination of seeds of all studied varieties. Similar varietal differences were obtained when studying the growth of seedlings. As a result, it was possible to establish that the Slavyanka variety is the most resistant to chloride salinization, and the Lera variety is

characterized by medium resistance. The Donsky variety was the least salt-tolerant [Grynin et al., 2007].

Different samples of individual plant species show a high degree of variability against salt tolerance [Epstein et. al., 1980; Chen et al. al., 2007], there are also reports in the literature about different accumulation of glycine-betaine and proline among genotypes of grain crops [Wyn Jones, Storey, 1978; Rhodes et al. al., 1989; Colmer et al. al., 1995; Jiang and Zhang, 2003].

The revealed ecotypes of *Thellungiella salsuginea* contrasting in resistance to negative temperatures and high concentrations of NaCl represent a real opportunity for establishing genetic diversity that determines resistance, QTL analysis, as well as for researching regulatory mechanisms that ensure plant resistance against abiotic stress [Leonova et al., 2007].

It was established that *Distichlis spicata* (Poaceae) has a specific defense mechanism that reliably isolates the metabolically active zone of photosynthetic cells from the salt flow from the roots to the surface of the leaf plates [Lubimov, Byl, 2007].

It was determined that the salt resistance of *Cicer arietinum* L. varieties varies in the series: ILC482 > Hachem > Bivaniij. In addition, it was shown that, in conditions of salinity of the environment, in chickpea plants, in contrast to age and rank, the largest decrease in the accumulation of dry mass occurs, while in *Vicia narbonesis* L. and *Lathyrus sativus* L. this indicator has similar values [Meychyk et al. , 2007a].

Screening of 20 varieties of winter triticale was carried out, as a result of which, by analyzing seed germination and growth indicators of seedlings under conditions of chloride salinity, 5 salt-resistant ones were distinguished: Triskell, Sotnyk, PRAG5301-1934, Almaz, Timbo. A comprehensive evaluation of the reaction to salinity was carried out for the selected variety samples based on physiological and biochemical indicators. The varietal specificity of the reaction of winter triticale to the effect of salt stress caused by the action of NaCl in a wide

range of concentrations (85-350 mM) was established. Differences between cultivars in terms of germination and seed germination energy, starting with a concentration of 250 mM NaCl, and growth rates at 165 mM NaCl. The least pronounced decrease in indicators was noted in the Triskell sample. The greatest sensitivity was shown by the variety sample Timbo, in which similarity decreased starting with the 165 mM NaCl variant. At a high concentration of NaCl (350 mM), seed germination decreased to 40% in the Triskell variety, and to 4% in the Timbo variety. The most pronounced differences were noted in the 300 mM NaCl variant, which is fashionable to recommend as a selective agent for evaluating salt tolerance based on indicators of germination and germination energy [Khabyeva, 2018].

Wheat varieties were screened for resistance to NaCl based on growth indicators and the anatomical structure of leaves and roots under salinity conditions. For this, plants were grown for 7 days in solutions containing different concentrations of NaCl: control, 50 mM NaCl; 100 mM NaCl. According to the linear growth of aerial organs and roots, the studied varieties can be arranged as follows: aerial organs - Kazakhstan-skaya early (85%) > Kazakhstan-3 (81%) > Kaiyr (69%) > Chagala (53%) > Meltun (28%); roots - Kazakhstan early (94%) > Kazakhstan-3 (88%) = Kaiyr (88%) > Meltun (81%) = Chagala (81%). According to the accumulation of biological mass, these varieties are located in the following order: aerial organs - Kazakhstan early (88%) > Kazakhstan -3 (75%) = Kayyr (75%) > Chagala (56%) > Meltun (50%); roots – Kaiyr (90%) > Mel-turn (83%) > Kazakhstan early (80%) > Kazakhstan -3 (75%) > Shagala (66%) [Atabaeva et al., 2013].

The greatest interest is represented by 10 samples of winter wheat from the breeding school of the second year, which showed high salt resistance on the salt stress of NaCl - 1.68% and 2% for 7 days. Samples No. 263, 268, 277, 293, 266, 288 were characterized by high similarity and germination percentage (91-100%). Samples No. 263, 277, 293, 266 showed the same high similarity and resistance

to Na₂SO₄ salt stress – 1.68%. From the control nursery, 4 winter wheat samples potentially resistant to salinity are of interest - Nos. 368, 42, 428, 512 [Sedlovsky et al., 2013].

When analyzing the obtained results, it was concluded that the degree of stimulatory effect of NaCl salt on growth processes in plants is largely determined by varietal differences of the studied culture. The more salt-resistant wheat variety "Zernogradskaya" was characterized by the least physiological changes than the studied variety "Kharkovskaya-46", in the seedlings of which fairly noticeable changes were noted already in the first hours of seed germination [Lutsenko, Galaktionova, 2013, Lutsenko, Fedorenko, 2014].

During the study of 18 varieties of spring wheat of different origin, the following were found in the group with high resistance to salinity: Satu, Skorospelka, Tyumenskaya 80, Omskaya 20, Ziryanovka, Lutescens 70 [Bome, 2008].

In laboratory conditions, determination of salt-resistant samples using the energy of germination, germination, determination of free proline and peroxidase activity, determination of germination in conditions of high salt content on field sites in Kyzylorda, samples were selected: 179 - Navruz, 30 - 10AYTIR-56, 342 - Navruz-2, 6966H1, 412 – Naz x Obry, 392 – Almaly x ГФ70/2 [Sedlovsky et al., 2014].

The results of the conducted experiments showed the effectiveness of interspecies hybridization for the creation of new starting selection material, allowed to identify stress-resistant and productive interspecies hybrids (*Triticum turgidum* x Saratovskaya-29 F2, *Triticum compactum* L. x Leningradka F4 BC2), promising for further selection and genetic research [Terletsкая and etc., 2014].

The cuttings of the two grape varieties Agadai and Husayne differed in the rates of morphogenesis and survival. But in general, the Agadai variety turned out to be more resistant to salinity [Alieva, 2011].

Cultivation of triticale seedlings in NaCl solutions inhibited the growth of roots and aerial parts in all varieties; the greatest decrease in these indicators was observed in varieties Kaskad*PG511 and Zymohor, and the least - in variety 03-128T33. The size of the roots decreased to the greatest extent in both variants of NaCl solutions (86 and 164 mM) in the variety Sotnyk, and the smallest - in the variety 03-128T33. The highest indicators of the size of the aerial part under conditions of both levels of salinity were noted in the 03-128T33 variety, and the lowest - in the Zymohor variety. In the 03-128T33 variety, under conditions of model salinity, the highest increase in biological mass of roots and above-ground part was observed. At the same time, the most intense accumulation of proline in seedling tissues occurred in the less resistant varieties Kaskad and Zymohor, and the least in the variety 03-128T33. A higher proline content was observed in the above-ground organs of all varieties of winter triticale under salinity conditions. A comprehensive evaluation of the salt resistance of the varieties revealed the best resistance in the 03-128T33 variety, and the worst in the Zymohor variety [Khabyeva, Aliyeva, 2015].

When cultivating cuttings in solutions of low concentrations of salts, it is not possible to judge the reaction of grape varieties to different salinity of the environment. The Husayne variety shows resistance against chloride and sulfate salinization at medium concentrations of solutions. The Muscat white variety is the most tolerant against chloride salinity. And the Sauvignon variety is green - against sulfate salinity. All studied varieties show a higher tolerance against chloride salinity compared to sulfate salinity. The Pinot Gris variety is less resistant to any salinity of the environment. The reaction of cuttings to salinity can be used to judge the tolerance of grape varieties to the type of salinity [Aliyeva, 2008]. When 80 mm of sodium chloride was added to the nutrient medium, 100% death of the rootstock of the Riparia Gloire de Montpellier grape was noted, 40% survived in Ruggera 140, and 70% of the explants survived and retained the ability to grow in Solonis x Riparia 1616 [Ivanov et al., 2014] .

As a result of laboratory screening of 29 millet genotypes, varieties and samples that showed resistance against chloride salinization at the juvenile stage of development were identified. These include samples k-9989, k-3137, Barnaulskoe kormovoe, Zolotistoe kormovoe, k-9520, k-9842 and Kokchetavskoe 66, which accumulated the maximum percentage of raw biological mass, as well as samples k-1437, Shortandynskoe 7, Shortandynskoe 10, Kokchetavskoe 66, Barnaulskoe Kormovoe, k-3742 and k-10278, which were characterized by high similarity at all three salinity levels studied (75 mM, 100 mM, 150 mM). These genotypes, as the most adaptive, are valuable as source material for their inclusion in breeding programs to create more salt-tolerant forms [Rysbekova et al., 2019].

Barley samples from Ethiopia: k-17554, k-19975, k-20029, k-20048, k-22752, k-23450, k-25009 were found to be resistant to soil salinization. Barley samples k-17554, k-22752 and k-25009 are characterized by complex resistance against powdery mildew, toxic aluminum ions and chloride soil salinity [Abdullaev et al., 2019].

Samples of cultivated oat species resistant to salinity were selected in Dagestan. They are represented by local and selection varieties of different ecological and geographical origin, the formation of which took place in areas with fairly widespread soil salinization. Among them are k-11444 (Israel), k-11527 (Algeria), k-7012 (Dagestan), k-4664 (Turkey) [Ahadova, Kurkiev, 2019].

The assessment of the resistance of intact tomato seedlings to NaCl made it possible to draw up the following descending series: Volgogradskyi > Novichok > Aran > Red Star > Titan > Torch [Samedova, Aliyeva, 2008].

On the MS agar medium with 200 mM NaCl, potato root growth was inhibited least of all in the Jubilee Zhukov variety (by 23.8%), and more strongly in the Zhukovsky early (by 94.7%) and Malinovka (by 84.1%) varieties [Mytyna et al., 2010].

The results of the assessment of salt resistance showed that at a concentration of NaCl salt solution of 6.5 g/l, soft wheat was not susceptible to salinization, while triticale and winter durum wheat were close to highly resistant. And when growing seedlings on a salt solution with a concentration of 9.8 g/l, winter durum wheat was the most sensitive. Triticale and common wheat are classified as highly resistant [Pomynov, Orlova, 2010].

It was established that of the varieties of winter wheat created in the breeding institutions of the city of Saratov, the variety *Lutescens 72*, created in the Saratov DAU named after E. Vavilova [Pronin, Nazarov, 2010].

As a result of the screening of samples of perennial alfalfa (*Medicago* sp.), salt-resistant varieties *Medicago sativa* variety *Nadezhda* (k-40812), *Medicago varia* variety *Tibetskaya* (k-25782), *Medicago sativa* (k-8958), *Medicago varia* variety *Rambler* (k- 33299), *Medicago coerulea* (k-12821) [Vyshnevskaya et al., 2014].

As a result of targeted research, it was established that samples of the species *Hordeum procerum* and *Hordeum jubatum* have the highest potential salt tolerance among the studied species at all levels of assessment. Several samples of these species maintained viability for up to a year *in vitro* culture under the maximum stress load of 0.3 M NaCl. When the load was reduced to 0.2 M, regeneration of calli was observed. Wild barley *Hordeum procerum* forms long-proliferating suspension cultures. This property made it possible to check the resistance of samples of the species against the action of different concentrations of NaCl at the cellular level. It was found that *Hordeum procerum* is characterized by a reaction of neutralization of an aggressive environment by part of the cells of the suspension, which allows the survival of other cells of the suspension, and the viability of the cells is preserved even at 0.6 M NaCl. Species of the *Hordeum* section: *Hordeum vulgare*, *Hordeum murinum*, *Hordeum bulbosum* are less resistant to the action of chloride salinity. The threshold concentration of NaCl for these species is 0.2 M on average [Chernov, Pendynen, 2014].

Varietal differences of Sarentan mustard plants (*Brassica juncea* L.) were revealed, which are based on different ability to regulate the supply of sodium and chlorine ions and the intensity of proline accumulation. The Lera variety was the least resistant, and the Slavyanka variety was the most resistant to salinization [Grynin, 2010].

CHAPTER 6. ECOLOGICAL MANAGEMENT OF CELL SELECTION

It should be noted right away that at present there is no unified scheme of cell selection that could be universally applied to different families of plants. The literature contains various information regarding the use of various biotechnological objects and criteria for *in vitro* selection [Smith, McComb, 1981, Shamyna, 1984, Kuznetsov et al., 1990, Sydorov, 1990, Sodi et al., 1990, Eattathottam, 1991, Belyanskaya et al., 1994, Dragiiska et al., 1996, Tsuru et al., 1999, Almansouri et al., 2000; Dias et al., 2002, Kosulina et al., 2007, Elwan, 2007; Arzani, 2008; Ayed-Slama et al., 2015].

In works on cellular selection of plants for resistance against ionic stresses, the method of direct selection was most often used, in which toxic concentrations of salts were used as a selective agent. However, creating stressful selective conditions *in vitro* identical to those in nature is extremely difficult. In natural conditions, in addition to the toxic effect of ions, other factors are imposed, and more specifically, the presence of various other substances, the acidic pH value of the environment and other factors. For selection at the cellular level, nutrient media are offered, which, even if not completely, corresponded to natural stress conditions, and would ensure the expression of the resistance trait and provide the opportunity to select the necessary options. Thus, cellular mechanisms of tolerance to salinity are important for cultured *in vitro* cells and whole plants, and selection at the cellular level represents a real prospect of obtaining salinity-resistant forms of plants [Hasegawa et al., 2000, Dasgupta et al., 2008].

For example, on the basis of somaclonal variability of flax *in vitro* culture, salinity-resistant forms were obtained [McHughen, Swartz, 1984].

To study the salt tolerance of cultivated plants, the most convenient model is resistance at the level of cells, tissues, and simple organismic reactions, and therefore seedlings and young plants are often used to study the genetic

mechanisms of salt tolerance [Shan et al., 1987]. It should also be borne in mind that even on seedlings, the study of the inheritance of salt tolerance faces a number of difficulties. The greatest success can be achieved in the analysis of the inheritance of cellular mechanisms of salt resistance. At the same time, it was noted that the cellular mechanisms of salt resistance differ not only between species and genera, but also between varieties of the same crop [Wong et al., 1983, Kishor et al., 1985]. Molecular genetic mechanisms of plant salt resistance are also known. Salt stress can cause changes in gene expression at the mRNA level [Ramagopal, 1987, Robinson et al., 1990]. At the level of a whole adult plant, almost all researchers share the opinion that salt resistance is a dominant or semi-dominant trait [Udovenko, 1989; Subbarao et al., 1990, etc.].

In order to obtain tolerant samples of corn, selection of salt-resistant calli obtained from immature embryos was carried out. 4 lines and 4 hybrids of corn served as the material for the study. In the work, we used the callus tissue obtained on the shields of immature embryos induced in a modified medium N6 supplemented with 10 mg/l AgNO₃, 2 mg/l 2,4-D, 0.1 mg/l ABA and 30 g/l sucrose. 30-45 days after induction, the control sample of calli was continued to be cultivated on the induction nutrient medium, and the calli of the experimental variant were transplanted to the same medium, but supplemented with 6 g/l NaCl, and cultivated for 30 days. Then, the chloride load was removed and callus growth was evaluated during the 30-day recovery period. The initial diameter of the calli before transplanting to a medium with salt averaged 5.85 ± 0.58 mm. The largest callus diameter was recorded in the PLS61 line – 6.79 ± 0.27 mm, and the smallest – in the DK267 line – 5.08 ± 0.38 mm. A tendency to decrease the growth rate of calluses under the influence of sodium chloride was also revealed. The studied genotypes differed in the degree of growth inhibition, the greatest inhibition was noted in the DK298 × DK267 hybrid. After removing the chloride load, an increase in the growth rate was observed, but it was weaker than in the control sample. On a stressful background, the selected calli were the ones with the lowest

degree of suppression and the highest recovery rate after the removal of salt stress [Konoshchuk et al., 2013].

Two selective agents - PEG-6000 and mannitol - were tested for the purpose of selecting corn plants tolerant to several abiotic stresses by the method of cell selection. At the same time, it was shown that the selective system with mannitol is more effective, as it provides a more complete elimination of sensitive cells and a higher viability of regenerating plants. Among the plants regenerated from cells resistant to mannitol, samples with increased tolerance not only against drought, but also against salinity and against low positive and negative temperatures were selected: R91m7, N31m4, A188xR91m19, 29, 30. Thus, it is shown that through selection *in vitro* on media with osmotic mannitol (0.8 M) plants can be obtained, tolerant against several abiotic stressors that cause dehydration of plant tissues [Al-Kholany, Dolgikh, 2007, Al-Kholany, 2010].

When creating a selective background in cell selection for drought resistance, along with traditional osmotic agents (PEG, mannitol, sorbitol), NaCl is often used, as it allows simulating not only salt, but also osmotic stress and obtaining salt- and drought-resistant forms [Oshmarina and etc., 1983; Levenko, 1991; Ignatova, 2011]. In addition to osmotic stress, NaCl salinity causes the toxic effect of an excess of inorganic sodium and chlorine ions, ionic imbalance and oxidative stress in plants, as a result of which there is a violation of cellular metabolism and a decrease in plant productivity. Salt toxicity, as a rule, is due to a rather high content of Na⁺ ions. It is believed that the ability to remove these ions is consistent with salt tolerance of plants [Munns et al., 2003; Garthwaite et al., 2005]. The toxic effect of salinity is quite closely related to the accumulation of an excess of sodium ions compared to potassium and calcium ions [Azimov, 1974; Lynch et al., 1988; Vidal et al., 1990]. Salt stress in plant cells is the main reason for the combination of osmotic and ionic stress due to a rather high concentration of monovalent sodium ions in the soil [Hasegawa et. al., 2000]. A marker of oxidative stress is high enzymatic activity of superoxide dismutase,

which catalyzes the reaction of superoxide radical conversion into hydrogen peroxide. A decrease in the concentration of hydrogen peroxide is possibly associated with the activity of other enzymes of the plant antioxidant system, in particular with catalase and glutathione reductase [Hernandez et al., 2010].

Different isoforms of superoxide dismutase "work" quite actively in the middle of cells and are controlled at different stages of plant development, as well as by the environment [Van Camp et al., 1997]. In the process of the superoxide dismutase reaction, hydrogen peroxide is formed, which is less active compared to the superoxide radical, and is utilized by other enzymes [Kordyum et al., 2003; Apel, Hirt, 2004; Polesskaya, 2007].

Long-term salt stress resulted in inhibition of benzidine, guaiacol and ascorbate peroxidase activities in *Zinnia elegans* Jacq. [Plotnikov et al., 2019].

It has been established that the expression of about 1,500 genes changes in plants under the influence of salt stress [Ma et al., 2006]. The resistance of plants against salinity is largely determined by the ability of cells to maintain a high ratio of K^+/Na^+ in the cytoplasm, which is ensured by the coordinated operation of proton pumps, ion channels and transporters of K^+ and Na^+ , among which NHX - tonoplast antiporters undoubtedly play an important role [Kryvosheeva, Belyaev, 2013]. It was found that the presence of Na^+ in the lumen of endocytic structures, as well as a certain contribution of endocytosis to the accumulation of Na^+ and Cl^- by cells during salinity. Thus, along with the traditional function of regulating the content of membrane proteins, in particular, ion transporters, endocytosis directly participates in the transport of ions and their deposition in vacuoles [Mayorova et al., 2016]. At the same time, it was established that the peroxidase activity and the ability to form proline are significantly higher in potentially salt-tolerant wheat samples [Sedlovsky et al., 2013].

It is shown that the change in the expression of the Δ -ornithine aminotransferase gene does not affect the proline level: transgenic tobacco plants, which carry the main genetic constructs for increasing and decreasing the

expression of the Δ -ornithine aminotransferase gene, do not differ from the control plants in terms of proline content either under normal conditions or under saline conditions stress. It was found that the change in the expression of the Δ -ornithine aminotransferase gene in transgenic plants affects the growth characteristics of stems and roots in normal conditions and under salt stress: 1) the introduction of a genetic construct into the plant genome that enhances the expression of the Δ -ornithine aminotransferase gene leads to increased root formation in the norm and increased resistance to salt stress; 2) the introduction of an antisense suppressor of Δ -ornithine aminotransferase expression into the plant genome leads to reduced root formation under salt stress. It was shown that the level of expression of the Δ -ornithine aminotransferase gene in tobacco is different in tissues and organs: 1) the highest level of Δ -ornithine aminotransferase mRNA is observed in the zones of active growth (callus, seedlings, apical meristem, first leaf); 2) the minimum level of Δ -ornithine aminotransferase mRNA is observed in differentiated tissues (stem, leaf). At the same time, a new hypothesis was formulated about the role of the Δ -ornithine aminotransferase gene in plants: the change in growth characteristics in response to a change in the expression of the Δ -ornithine aminotransferase gene, as well as the localization of the expression of this gene in the growth zones, allows us to predict that the Δ -ornithine aminotransferase gene takes part in plant growth processes, and probably participates in the protection of growth zones in salt stress languages [Gerasimova, 2011].

It is assumed that the Cl^-/H^+ antiporter of the Golgi apparatus is involved in the export of cytoplasmic Cl^- into the vacuole and into the periplasmic space in the cells of the root of the halophyte *Suaeda altissima* through, respectively, endocytosis and exocytosis structures [Balnokin et al., 2013, Shuvalov, 2013]. Currently, the full-length cDNA sequences of two genes from the eugalophyte *Suaeda altissima*, SaCLCa1 and SaCLCc1, have already been cloned. It was established that the genes of the anion transporters SaCLCa1 and SaCLCc1 are

expressed both in the roots and in the leaves of *Suaeda altissima*. The expression of SaCLCa1 and SaCLCc1 changes in organs in response to changes in the concentration of NaCl and NO₃⁻ in the environment [Nedelyaeva, 2019]. In recent years, the method of QTL analysis (Quantitative Trait Loci), which is based on the use of molecular markers for the localization of a quantitative trait on a chromosome map, has received significant development [Chesnokov, 2009].

Functional identification was carried out Cl⁻/H⁺-antiporter and analysis of the Cl⁻/H⁺ exchange carried out by it in *Nicotiana tabacum* L. Analysis of the activities of marker enzymes in the membrane fraction isolated in the two-phase system showed that this fraction is enriched with vesicles of the plasmolemma and the Golgi apparatus. ΔpCl-dependent proton transfer through the membrane was recorded by the change in differential absorption (ΔA₄₉₂₋₅₄₀) ΔpH-indicator acrylic orange, and the generation of a negative transmembrane electric potential (Δψ) accompanying the Cl⁻/H⁺ exchange was recorded by the change in differential absorption (ΔA₄₉₂₋₅₄₀) Δψ- sufranin O indicator. When ΔpCl was created on the membrane, directed to the middle of the vesicles, the release of a proton from the vesicles was observed, i.e., the alkalinization of the vesicular lumen occurred, which was accompanied by the generation of an electric potential with a "minus" sign in the middle of the vesicles. This information indicates the existence of a Cl⁻/H⁺ antiporter in the membrane. ΔpCl-dependent proton release from vesicles was detected in all *Nicotiana tabacum* L. plants, regardless of whether sodium chloride was contained in the culture medium or not. However, Cl⁻/H⁺-antiporter activity was higher in plants grown in the presence of 50 mM NaCl than in plants grown on non-saline medium. Thus, the presence of Cl⁻/H⁺-antiporter in the membrane fraction isolated from tobacco roots is a constitutive feature, but NaCl in the culture medium increases their activity. Since anion-proton antiporters are not detected in plants in the plasma membrane, there is a high probability that the detected Cl⁻/H⁺ exchange refers to the Golgi apparatus.

Therefore, it is assumed that the Golgi apparatus takes part in the intracellular transport of chloride [Kozgunova et al., 2017].

The main role in the process of removing sodium homeostasis from the cell is played by proteins - sodium-proton antiporters. The activity of Na/H antiporter was registered in plasma membranes of barley, tobacco, table beet, *Atriplex nummularia*, tomato, wheat, blue-green and salt-resistant algae *Dunaliella salina*. Potato regenerants transformed with the barley antiporter gene HvNHX2 with the help of *Agrobacterium* were obtained. The results of PCR analysis of transgenic plants showed that the gene integration was successful. The results of the work indicate the possibility of using the HvNHX2 gene for genetic engineering of salt-tolerant plants [Bayat et al., 2008].

In rapeseed plants, 56 genes encode putative transcription factors that change the speed of their work under salt stress. Among such genes, which are more than 5-fold upregulated under this stress, belong to the AP2-EREBP family (ATERF11, CBF4 / DREB1D, CBF1 / DREB1B, ATERF4 / RAP2.5, DREB2A, CBF1 / DREB1B, DREB2A and ATERF11), Basic-Helix-Loop-Helix (bHLH) family (AtbHLH17), Basic region leucine zipper family (AtbZIP55 / GBF3), C2H2 family (ZAT10, ZAT12 / RHL41, ZAT6 and ZAT102 / RHL41), Heat stress family (ATHSFA1E), Homeobox family (ATHB-7), NAC family (ANAC036, ANAC029 / ATNAP, ANAC055 / ATNAC3, ANAC047, ANAC072 / RD26, ANAC002 / ATAF1, ANAC019 and ANAC032) and the WRKY family (WRKY, ATWRKY40 and ATWRKY33). These transcription factors are induced in response to salt stress signals transmitted by sensing and signaling molecules. After that, complex gene regulatory networks, which consist of transcription factors and other proteins, regulate the expression of numerous genes [Shokri-Gharelo, Noparvar, 2018].

The study of salinity tolerance of alloplasmic wheat on the cytoplasm of *Aegilops crassa* *in vitro* culture showed that foreign cytoplasm had different

effects on salinity, depending on the interaction with the nucleus, but generally increased salinity [Hou Ning et al., 2000].

In salt-tolerant wheat cell lines, the presence of three POD eozyme changes and four additional EST bands was shown; their K⁺/Na⁺ ratio is increased (0.788 at a NaCl concentration of 0.9%). The content of proline in hardy lines and their offspring was 6.93 times higher at a Nad concentration of 1.2%; additional bands of gliadin were detected [Wang Ming-gang et al., 1999].

Examples of the selection of cell lines resistant to different concentrations of sodium chloride and the regeneration of plants that maintain salt tolerance are presented in Table 2.

Table 2 – Examples of salt-tolerant cell lines and plants obtained through cell culture [Timofeeva, 2006]

Starting material for breeding and its ploidy	NaCl concentration	Results of cell selection
<i>Medicago sativa</i> (2n)	0.17 M	Callus
<i>Medicago sativa</i> (2n=2x, 2n=4x)	0.08-0.17 M	Plants
<i>Citrus sinensis</i> (2n)	0.08-0.17 M	Callus
<i>Nicotiana tabacum</i> (2n)	0.17 M	Suspension, plants
<i>Datura innoxia</i> (2n)	0.17-0.34 M	Callus, plants
<i>Pennisetum americanum</i> (2n)	0.19 M	Embryogenic suspension
<i>Ipomea batatas</i> (2n)	0.17 M	Suspension
<i>Crepis capillaris</i>	0.12 M	Suspension
<i>Oryza sativa</i>	0.17 M	Embryogenic callus, plants

Simultaneously with the synthesis of ROS in the plant, monovalent potassium ions are released from the cells. After organogens, potassium is the most abundant element in the plant cell, involved in a wide range of metabolic transformations and regulatory interactions. This metal also plays the role of a key generator of osmotic, chemical and electrical gradients in the plant cell. In agricultural practice, potassium is used as a means of combating stresses, mainly salinity [Munns, Tester, 2008].

The fact that the increase in the volume of the apoplast of the crystal grass due to the thickening of the middle plate, as well as the filling with polysaccharides of the compartments formed between the cell wall, was observed only in the second variant (– Fe + NaCl) indicates that NaCl induces the formation of pectin substances. The main component of these substances is polygalacturonic acid, thanks to which the cell wall has a negative charge. The growth of free carbonyl groups of uronic acids in the apoplast can probably contribute to the sequestration of toxic sodium ions. In addition, the growth of the apoplast volume in the crystal grass probably allows plants to accumulate more water in salinity conditions [Paramonova, 2013]. It is also believed that the ratio of the thickness of the exoderm to the thickness of the endoderm is a rather important indicator of plant resistance to salinity [Gomes et al., 2011; Singh and Prasad, 2009].

One of the mechanisms that ensure the resistance of cultivated plants against salinity can be the low permeability of the plasma membrane of cells for these ions. At the same time, different intensity of transport of Na⁺ and Cl⁻ ions in the plant is noted, and its suppression leads to a significant increase in salt tolerance. In response to salt stress, molecular and physiological-biochemical reactions are observed in the plant aimed at adaptation of the plant organism against the changed conditions of the surrounding environment. One of the main features of plant salt tolerance is the ability of plant cells to maintain an optimal K⁺/Na⁺ balance in the cytosol [Tester, Davenport, 2003]. In the mechanisms of salt tolerance, it is necessary to distinguish between the direct effect of an excess

of salinizing ions on plants [Cheeseman, 1988] and a change in the water-physical and mineral regime under the influence of an excess of salts in the soil solution [Gardner, 1967].

One of the modern breeding directions for creating highly productive salt-resistant varieties is *in vitro* selection. The possibility of obtaining cell variants resistant to salt stress is due to somaclonal variability, the mutagenic effect of growth regulators of the nutrient medium, as well as the effect of a selective factor. *In vitro* selection for resistance to salt stress is usually carried out in callus cultures [Reshetnikov et al., 2014]. It is assumed that the mechanism of *in vitro* variability is similar to spontaneous mutations and is caused by ROS [Micke, Donini, 1993, Anonymous, 1995].

Salt-resistant somaclones of Pokkali rice were studied. *In vitro* culture regenerated 1190 primary regenerants of the Pokkali variety from the calli of mature seeds. Among the SC2 generation, 26 promising plants were selected, and 10 lines were selected for further selection. According to agronomic indicators, grain quality and polypeptide composition, they differed significantly from the base population [Mandal et al., 1999]. In the suspension culture of cereals, a tendency to accelerate the passage of all phases of development and a significant decrease in cell viability was revealed, but at the same time, the ability of somatic cells of salt-tolerant genotypes to restore viability after severe salt stress was shown, which gives prospects for cell selection. The possibility of regeneration and production of viable plants with pronounced resistance to drought and salinity *in vitro* was shown [Terletsckaya, 2013].

Osmotic stress *in vitro* inhibits the growth of many cultures. In the suspension culture of carrot cells with a decrease in water potential, a decrease in the raw and dry mass of non-adapted cells was noted [Fallon, Phillips, 1989]. In heterotrophic and photomixotrophic pine calli, water stress, especially at a water potential of -2.5 MPa, also caused inhibition of growth and a decrease in cell volume [Valluri et al., 1990].

As a result of research, it was found that during direct selection on a medium with 1.2% NaCl until the end of the 1st passage in the triticale line 38/1296 and the Aubriy variety, about 53 and 41% of calli survived, respectively. After 3 passages under selective conditions, the proportion of living calli in both genotypes was 34.6 and 22.7%, respectively. By the end of the 6th passage, 10.1% of resistant calli survived in the 38/1296 line on a medium with 1.2% NaCl, and 7.9% in the Obry variety. When stepwise selection was carried out with a gradual increase in the concentration of sodium chloride in the medium from 0.6 to 1.2%, the viability of callus cultures in both genotypes was comparatively higher. Thus, during the 6th passage on the medium with 1.2% NaCl, 18.1% of live calli were recorded in the 38/1296 line, and 10.2% in the Obry variety. Thus, stepwise selection turned out to be more effective, since as a result of its application, a larger share of salt-resistant callus forms was selected in both genotypes of winter triticale compared to direct selection [Pykalo, 2016, Pykalo et al., 2017].

In response to high salt stress, various genes begin to regulate molecules that directly or indirectly participate in plant defense [Tuteja, 2007]. Susceptibility or tolerance against stress under the influence of a high concentration of sodium chloride in plants is a coordinated action of quite a few genes that respond to stress [Rains, Epstein, 1965, DeRose-Wilson, Gaut, 2011]. Cellular toxicity caused by a high content of monovalent sodium ions is the predominant ionic toxicity, which leads to the inhibition of various processes, such as the absorption of monovalent potassium ions, the inactivation of vital enzymes and the inhibition of photosynthesis [Flowers, Läuchli, 1983, Murguía et al., 1995, Tsugane, 1999].

It has been shown that lines of genetically modified tobacco plants that express an antisense suppressor of the Arabidopsis proline dehydrogenase gene are characterized by increased resistance to salt stress [Kolodiazhnaya et al., 2007]. Against the background of salinity, a change in gene expression is shown for species and varieties contrasting in terms of salt resistance [Gulic, Dvorak, 1987]. Expression of HKT transporter genes is quite important for characterizing

salt tolerance of wheat. In durum and soft wheat varieties Orenburgska 10 and Orenburgska 22, there is a 3-4 times increase in the expression of HKT genes under salt stress. The increase in the expression level of the HKT family genes in roots and leaves under salt stress conditions is associated with the rapid restoration of the K^+/Na^+ ion balance and the protective function [Fedoreeva, 2019]. In general, susceptibility or tolerance against stress under the influence of a high concentration of sodium chloride in plants is a coordinated action of a fairly large number of genes that respond to this stress [Flowers, Läuchli, 1983, Murguía et al., 1995, Jabnourne et al., 2009, DeRose-Wilson, Gaut, 2011, Munns et al., 2012].

The organization of the actin cytoskeleton (a dynamic network consisting of actin microfilaments, both individual and assembled into dense bundles, in which constant processes of synthesis and decomposition of components take place) under salt stress is closely related to the functioning of the SOS (salt overly sensitive) regulatory pathway, aimed at maintaining Na/K homeostasis in the cell. The organization of actin filaments in *Arabidopsis* root rhizoderm cells in *sos3* mutants differed from the organization of the actin cytoskeleton in wild-type seedling cells and showed hypersensitivity against salinity [Ye et al., 2013].

It has been shown that glycophytes under the conditions of the complex action of salinity and heavy metals are exposed to even more intense stress than when they are isolated [Smolders, McLaughlin, 1996, Huang et al., 2006], while halophytes are characterized by a strategy of induction of protective mechanisms that ensure the reduction of the toxic effect of copper in the conditions of the combined action of this metal and salinity [Helal et al., 1998, Fitzgerald et al., 2003, Demirezen, Redd, 2006, Volkov et al., 2010].

It was established that the features that distinguish calli tolerant to salinity of the resistant genotype are a decrease in cell length, the appearance of spherical embryogenic cells, the initiation of embryos, and the presence of cells with signs of programmed cell death. Histochemical and cytochemical methods revealed extracellular substances of polysaccharide and protein nature, cells that are

released with signs of programmed cell death in the process of tissue adaptation of resistant varieties against stress. Ultrastructural features of cultured wheat cells under salt stress were also revealed [Bishimbaeva et al., 2011].

During adaptation to salinity and water deficit *in vitro* culture, the activity of glucose-6-F-DH increased by 1.5 times in experimental sugar beet plants. At the same time, a decrease in K_m from 0.15 to 0.12 mM was observed in all components of this hybrid. The general activity of ICL also increases, and the affinity for the substrate increases more than 8 times [Zemlyanukhina et al., 2011].

It was established that the lower resistance to salinity of the salt-sensitive corn hybrid *in vitro* culture, compared to the salt-tolerant one, is associated with inhibition of the activity of the H^+ -ATPase enzyme, the activity of which is compatible with the mechanism of the Na^+/H^+ -antiporter in glycophyte-type plants and promotes removal from cells of "excess" Na^+ ions [Kabuzenko, Omelchenko, 2011].

The Na^+ -transporting enzyme of halotolerant microalgae - Na^+ -ATPase, whose work does not depend on the proton gradient on the membrane, can be a promising resource for the creation of transgenic plants capable of growing on both saline and alkaline soils. Na^+ -ATPases were found in two species of marine green microalgae *Tetraselmis viridis* and *Dunaliella maritima*. Na^+ -ATPase is a primary active mechanism and due to the energy of ATP hydrolysis, it is able to quite effectively remove excess Na^+ ions from the cytoplasm in a wide range of external Na^+ concentrations and pH values. The Na^+ -ATPase gene is cloned (Gen Bank: FN691482.1) [Popova et al., 2013].

In the plasmolemma of the marine microalga *Dunaliella maritima*, the P-type Na^+ -ATPase functions, which is responsible for Na^+ -homeostasis in this organism. In order to identify the Na^+ -ATPase gene in *Dunaliella*, the transcript of the microalga *Dunaliella tertiolecta* was analyzed. An *in silico* search of the assembled *de novo* transcriptome did not reveal ATPases similar to known Na^+ -ATPases. Among other P-type ATPases, two enzymes similar to H^+ -ATPases

were found. Knowing the identified *in silico* transcript sequences of these enzymes, the corresponding full-length sequences of two ATPases, DmHA1 and DmHA2, were cloned from *Dunaliella maritima*. The expression of DmHA1 and DmHA2 in conditions of hyperosmotic salt shock was investigated by the qRT-PCR method. A sharp increase in the concentration of NaCl in the medium led to a significant increase in the expression of DmHA2 and suppression of the expression of DmHA1. This information shows that DmHA2 ATPase is involved in Na⁺ homeostasis of cells of *Dunaliella maritima*, and is likely to be a Na⁺-transporting enzyme. To confirm the functioning of the DmHA2 protein as a Na⁺-ATPase, experiments are being conducted on the heterologous expression of this enzyme in a yeast mutant devoid of Na⁺ export systems from cells [Popova et al., 2019].

Salt resistance in hexaploid wheat *Triticum aestivum* (AA BB DD gene) is controlled by numerous genes that manifest themselves both at the cellular level and at the level of the whole plant. It was shown that the genes located in the long arm of chromosome 4D are responsible for the control of the whole plant over the transport of sodium ions to the aerial part of the stem in hexaploid wheat. Tetraloid wheat (*Triticum durum* L.), possessing the AABB genome, lacks an organismic mechanism to resist salt stress due to the absence of the D genome. In this case, cellular mechanisms of resistance come to the fore. Therefore, the study of the effect of salt stress on the growth of durum and soft wheat cells and the selection of cell lines resistant to salinity with subsequent degeneration of altered plants acquires not only theoretical, but also practical significance [Gorham et al., 1987]. It was found that the genes that control the increased ratio of potassium and sodium ions in the leaves and determine the higher salt tolerance of hexaploid wheat are located in the long arm of chromosome 4D [Foster et al., 1988]. It has also been shown that under conditions of oxidative (10 µM methylviologen, MV) and salt stress (250 mM NaCl), as well as under the influence of drought, an

increase in the expression of genes of the ATG8 family is observed [Ryabov et al., 2016].

A sign of K^+/Na^+ differentiation contributes to the growth of salt tolerance in soft wheat compared to hard wheat and is present in the genome of *Aegilops tauschii*. Evaluation of this indicator in parental forms and synthetic hexaploid lines obtained from crossing durum wheat with the specified *egilops*, which indicates the presence of this feature in the latter and demonstrates its successful transfer with the *egilops* genome into synthetic hexaploids. The most productive synthetics had the same K^+/Na^+ ratio as the saline control S24. Highly reliable correlations between K^+/Na^+ differentiation and raw weight of plants in the studied set of genotypes were revealed. In the backcross program of the best synthetics with the drought-resistant Opata variety, significant differences of the studied indicator from the same recurrent parent were found. At the same time, the rather high selection potential of two synthetic lines, tolerant to lodging under irrigation and to several other biotic stresses, is noted [Pritchard et al., 2002]. Overexpression of the HAL1 gene in yeast provides salt tolerance due to high internal concentration of K^+ and reduced concentration of Na^+ . The gene was introduced into the tomato genome from *Agrobacterium tumefaciens*. The progeny of transgenic plants showed increased resistance to salinity in the presence of 1-4 copies of the HAL1 gene. These plants are characterized by increased retention of K^+ [Gisbert et al., 2000].

The common wheat salt tolerance gene regulates the K/Na balance, which is localized in the D genome. A new source of K/Na^+ allocation, which creates the salt tolerance of durum wheat lines 149 in *Triticum monococcum* C68-101, and a QTL of low Na^+ concentration in the leaves have been identified. $NaCl$, in chromosome 2AL. The genes of wheat chromosome 2AL and rice chromosome 4L had good overall collinearity for reverse sequence in the chromosomal segment including the $NaCl$ locus. Two putative Na transporter genes were mapped to chromosome 2AL. In particular, the TtNKT7-A1 gene was

polymorphic between salt-tolerant and sensitive lines and was cleaved compatible with Nax1. The TmHKT7-1S gene was localized in the same VAS ~145 t. n., as well as TtNKT7-A1. Both genes had 83% amino acid identity, but only TtNKT7-A2 was expressed in the roots of the salt-tolerant line 149, consistent with the physiological role of NaCl in reducing Na⁺ concentration in leaf blades. TtNKT7-A2 can control the unloading of Na⁺ from the xylem in roots [Chang et al., 2005].

When studying salt-tolerant tall varieties of durum wheat and their short-stemmed analogues with various genes for stunting, it was established that the salt resistance of short-growing analogues with the Rht1 gene is adequate to that of tall forms. The salt resistance of short-stemmed lines with the Rht3 gene and other genes was slightly higher than the salt resistance of tall forms. At the same time, the revealed tendency to increase salt resistance in stunted forms is associated with weak permeability of biological membranes of short-stemmed forms and with strong compaction and smaller sizes of cells of stunted forms [Alderov, 1991].

Currently, many transgenic varieties of plants resistant to salinity have been created by cell breeding methods. The table presents only some of the main crops (Table 3).

Table 3. Transgenic plants, tolerant to salinity

Gene	Gene function	Plant	Source of information
ZFP, ZF	Transcription factor	<i>Arabidopsis thaliana</i>	Seong et al., 2007; Xu et al., 2007
DREB			Kasuga et al., 1999, 2004;
HSF			Yokotani et al., 2008
ERF		<i>Nicotiana</i>	Xu et al., 2007

CHAPTER 6

		<i>tabacum</i>	
LOS4, PDH45	DNA helicase	<i>Pisum sativum</i>	Sanan-Mishra et al., 2005
hva1	LEA	<i>Triticum aestivum</i>	Sivamani et al., 2000
P5CS	Synthesis of		Aida, 2005
RDH	proline	<i>Arabidopsis thaliana</i>	Nanjo et al., 1999
codeA	Accumulation of		Hayashi et al., 1997
betA	glycine betaine	<i>Nicotiana tabacum</i>	Lilius et al., 1996
		<i>Orysa sativa</i>	Takabe et al., 1997

Genetic analysis of cleavage in the progeny of wheat varieties with different salinity tolerance 1:2:1 showed that this trait is determined by one large gene. 520 primers were used to amplify the gene pools of both parental forms, of which only one OPZ09 determined the polymorphism of the 590 p fragment. n. in parents and F1 and F2 populations. The specific OPZ09-590 fragment is a RAPD marker linked to the salt tolerance gene [Weng Yue-Jin, Chen Dao-Ming, 2002]. Effective selection of genotypes with low sodium accumulation already in F2 is confirmed by the realized inheritance value from 0.43 to 0.90 [Rao et al., 1999].

Thanks to the use of foreign mixed lines, it was possible to establish that the chromosomes of the first and fifth homologous groups of wheat and rye carry genes that control the salt tolerance of seedlings. At the same time, it was also found that the Novosibioska 67 wheat variety is more resistant to salinity than the Sarativska 29 variety [Shchapova, Kravtsova, 1999]. It was also noted that the content of glycine-betaine in the cells of plants exposed to stress is a dominant

trait with a high degree of inheritance. All this makes it possible to use this indicator in breeding and genetic studies [Grumet et al., 1985].

The study of salinity tolerance in 8 wheat varieties with different efficiency of callusogenesis and regeneration under salinity showed no differences between control callus and callus on medium with 10 g/l NaCl in terms of the height of regenerated plants, the length of the ear and the number of seeds per ear. When irrigated with water containing less than 20 g/l of NaCl, the seeds of the saline plum regenerant showed better root and coleoptile growth and photosynthesis [Zair et al., 2003].

An integrated osmolyte (osm) gene was introduced into the binary vector in wheat plants using genetic engineering methods. The damaging effect of salt stress was assessed by the degree of inhibition of root growth of wheat seedlings when they were grown on media with different concentrations of NaCl. An increase in salt tolerance was found in the transgenic line: seedlings of this line were able to form roots on medium with a high concentration (250 mM) of NaCl. The resistance to salinity of plants of the transgenic line was significantly higher than that of the non-transformed original variety [Sadam-Nuri, Sohansanzh, 2008].

A cloned cDNA encoding a proline transporter, *Hordeum vulgare* (HvProT) from plant roots under salt stress. HvProT has a size of 2161 p. n. and it is similar in amino acid sequence to similar proteins of rice, *Arabidopsis* and tomato. Treatment with 200 mM NaCl induced the formation of HvProT transcripts in roots after 30 min. HvProT has a fairly high affinity for L-proline ($K_m = 25 \mu\text{M}$) and depends on the pH gradient. Gene expression is highest in root cap cells under salt stress [Bohnert, Shen, 1999].

The study of salt-resistant and sensitive varieties of barley showed the influence of salinity on the structure of chloroplasts: disorientation of the lamellar system, which is more pronounced in the sensitive variety. The meristem of the root tips undergoes various disturbances - vesiculation of the plasmolemma,

accumulation of lipid droplets, vacuolization of the cytoplasm, damage to mitochondria [El-Banna, Attia, 1999].

The yeast Mn-superoxide dismutase (Mn-SOD) gene was introduced into rice protoplasts by electroporation. The total activity of the enzyme in transgenic plants was 1.7 times higher than in the control. Imposition of salt stress (100 mM NaCl) caused a decrease in superoxide dismutase activity in both cases, but it was more pronounced in the control. The activity of overexpression of Mn-SOD and cytosolic Cu/Zn-SOD under salt stress did not change in either transgenic or control plants, the activity of chloroplast Cu/Zn-SOD in the control significantly decreased. At high salinity, the ascorbate peroxidase activity of the transformants was 15 times higher than in the control [Tanak et al., 1999].

Overexpression of superoxide dismutase genes in some transgenic plants contributed to their resistance to salinity (Table 4).

Table 4. Increased resistance to salt stress in transgenic plants expressing superoxide dismutase (SOD) genes

Expressing enzyme	Culture	Source of information
Mn-SOD	arabidopsis	Gao et al., 2003
Cu, Zn-SOD	tobacco	Badawi et al., 2004
Fe-SOD	tomato	Serenko et al., 2009

The strategy for the selection of additional stress tolerance genes is considered, which is based on the functional screening of cDNA libraries by expression in yeast, and specifically, the Arabidopsis genes SRL1 and RCY1, which encode proteins of similar SR-splicing factors. When overexpressed in transgenic Arabidopsis plants, these genes significantly increase tolerance to drought and salinity throughout their development [Bourgon et al., 2007]. Salt tolerance is achieved by DNA transformation of Na⁺/H⁺ exchange polypeptides,

95% homologous to those of Arabidopsis, to remove monovalent cations from the cytosol [Blumwald et al., 2005].

Transformation of Arabidopsis with the XVSAP1 gene under the CaMV35S promoter, nos terminator and under bar selection led to the constitutive accumulation of the corresponding protein in leaves. Transgenic plants *in vitro* culture showed increased viability under osmotic, salt, and temperature stress [Deal et al., 1999].

Isolated Arabidopsis genes AtHA13a and AtHAL3b. Both of these genes were induced by salt stress, and the AtHAL3a gene was most strongly expressed in plants, especially in seeds, in the absence of stress. An increased content of AtHA13a mRNA in seed embryos and in the phloem of various tissues is also shown. AtHAJ3 proteins are highly homologous to a group of fungal, plant, and animal proteins and some flavoproteins of prokaryotes. Transgenic plants with AtHA13a function have altered growth rate and tolerance to salt and osmotic stress [Espinosa-Ruiz et al., 1999]. In addition, it was shown that overexpression of the NtHAL3 gene led to an increase in proline synthesis and increased resistance to salt and osmotic stress, as well as to lithium ions [Yonamine et al., 2004].

Overexpression of the VaCDPK21 gene greatly increases the resistance of *Vitis amurensis* Rupr cell lines. and Arabidopsis thaliana plants against salt stress. In transgenic plants of Arabidopsis thaliana, the expression of stress marker genes AtCOR15, AtCOR47, AtCAT1, AtCSD1, AtNHX1, AtKIN1, AtRD26, AtRD29B increases under salt exposure. Thus, the VaCDPK21 gene is a weak positive regulator of grape resistance against salt stress [Khristenko, 2018].

In rapeseed plants, there are three levels of regulation of gene expression formed in response to salinity. The first level affects the stage of transcription through specific protein factors, which are the main elements interacting with other proteins, especially with RNA polymerases, and acting cis/trans elements in

the regulatory regions of the genome. However, many other mechanisms are still waiting to be studied [Shokri-Gharelo, Noparvar, 2018].

It was also noted that epigenetic events are another gene regulation mechanism found in rapeseed. Epigenetic regulation of stress-responsive genes has been shown to play a key role in plants under various conditions [Chinnusamy, Zhu, 2009, Luo et al., 2012]. It was established that when plants were transferred to salinity conditions after their preliminary treatment with osmotic stress, histone modification occurred, as a result of which plants accumulated fewer sodium ions [Sokol et al., 2007]. A change in DNA methylation and histone modification of rapeseed plants in response to environmental salinity is shown. Under these conditions, de novo methylation and demethylation events occur at CpCpGpG sites [Labra et al., 2004].

Genes with epigenetic modifications are still less known. Ethylene-sensitive element binding factor (EBF) is one of the genes that undergoes methylation in rapeseed DNA under salt stress conditions [Guangyuan et al., 2012]. The role of miRNA at the post-translational stage in rapeseed plants treated with salt was also studied. MicroRNA is a non-coordinating RNA with a length of 20 to 24 nucleotides. It is also reported that more than 340 miRNAs participate in the post-translational regulation of salt-sensitive genes in rapeseed [Jian et al., 2016].

Research on other cultures under salt stress showed that in *Arabidopsis* many transcription factors, as well as superoxide dismutase and laccase genes - glycoproteins containing a significant amount of copper - are under the control of miRNA [Stief et al., 2014]. Therefore, the discovery of the key role of miRNAs in adaptation against various types of stress and their impact on plant growth and development implies the use of this type of RNA in the future as a new promising target for increasing tolerance against adverse environmental conditions [Zhang, 2015].

One of the mechanisms of plant salt tolerance is the compartmentalization of Na⁺ outside the cytosol. Overexpression of the vacuolar Na⁺/H⁺ antiporter in *Arabidopsis* plants stimulated growth and development in soil when watered with water containing 200 mM NaCl. Salt tolerance was correlated with increased content of AtNHX1 transcripts and Na⁺/H⁺ antport activity [Apse et al., 1999, Apse, Blumwald, 2007].

In *Arabidopsis*, SOS1-3 (salt overly-sensitive) genes have been identified, which are involved in the mechanisms of salt resistance: at high NaCl salinity, the content of intracellular calcium ions increases, which binds to the transport protein SOS3, and then activates SOS2-serine-threonine- by kinase [Sanders, 2000].

The participation of *Arabidopsis* sos4 (salt overly sensitive 4) mutations in the critical role of vitamin B6 in plant salinity tolerance was studied. At the same time, 4 sos4 mutants and the SOS4 gene were characterized. Sos4 mutants are hypersensitive to monovalent lithium, potassium, and sodium ions. Under NaCl salinity conditions, they accumulate more sodium ions and retain less potassium ions than the wild type. SOS4 encodes pyridoxal kinase, which is involved in the biosynthesis of vitamin B6. Addition of pyridoxine to the growth medium partially removes the salt tolerance defect of the mutant, and SOS4 is expressed in all tissues [Hamada et al., 1999].

Tobacco leaf discs were transformed through *Agrobacterium tumefaciens* carrying the plasmid pBIBnNHX1, with the nptII and vacuolar Na⁺/H⁺ antiporter genes. 32 transgenic plants were regenerated, in which the antiporter gene BnNHX1 is expressed to varying degrees. Such plants have increased salt tolerance and can grow on medium with 200 mM NaCl. The transgene was inherited according to the Medlelov scheme 3:1 [Wang et al., 2004].

A new genetic model was created - transgenic tobacco plants carrying a heterologous antisense suppressor of proline dehydrogenase. It is shown that the partial suppression of the PDH gene is accompanied by an increase in the

resistance of plants to salinity, which makes it possible to publicize the hypothesis of the possibility of controlling salt resistance by increasing the activity of this enzyme. At the same time, a new approach for obtaining stress-resistant forms of plants is proposed, based on the use of genetic constructs - suppressors in PDH [Tytov, 2008].

The *Cicer arietinum* ПАР2 gene encoding a new transcription factor of the AP2 family was isolated. Recombinant CAP2 protein specifically binds to dehydration response elements and transactivated reporter genes. SAR2 is a monocopy (low-copy) benzitron gene, the product of which is localized in the nucleus. Dehydration and salinity, as well as ABA and auxin treatment stimulated the production of SAR2 mRNA. Expression of CAP2 under the 35S promoter in tobacco caused an increase in leaf size and the number of lateral roots. Transgenic plants were more resistant to water deficit and salinity, highly expressed stress response genes NtERD10B and NtERD10C and auxin response genes IAA4.2 and IAA2.5 [Shukla et al., 2006].

In the absence of salt stress, growth and photosynthesis of transgenic (DnaK1) and control tobacco plants did not differ. An increase in NaCl concentration caused a decrease in the intensity of carbon dioxide assimilation of the control to 40%, while in transgenics it was 85% of the norm. Salt stress decreased the total content of protein and ribulose biphosphate carboxygenase and oxygenase in both cases, but less so in the transgene [Sugjno et al., 1999].

The study of salt resistance of pollen of tomato lines showed that 85.5% of the variability in pollen viability is due to the action of salt stress, 3% of the variability is determined by the genotype, and 10.7% is determined by the interaction of these factors [Saltanovych, Makovey, 2000].

The expression of bacterial genes encoding enzymes of proline biosynthesis leads to an increase in the content of free proline in plant cells and increased resistance to salt stress. This system can be used to obtain cultivated plants resistant to various stresses [Pyruzyan et al., 2002].

Molecular cloning and differential expression of the vacuolar Na⁺/H⁺ antiporter gene in *Suaeda salsa* under salt stress was performed. A Na⁺/H⁺ antiporter cDNA clone of 2262 bp was isolated. p. with an openly read frame 1665 p. n. The amino acid sequence is similar to that of AtNHX1 and OsNHX1. Gene expression increased with salinity. The authors concluded that OsNHX1 is a Na⁺/H⁺ antiporter [Ma et al., 2004].

Salt tolerance of cultivated plants is influenced not only by nuclear but also by cytoplasmic genes [Shevyakova, 1981]. The maternal effect in the inheritance of salt tolerance of plants has been noted more than once [Shevyakova, 1981, 1982, Udovenko, 1989, etc.]. The rather important role of additive and dominant effects of genes in the manifestation of the salt tolerance trait of plants was also noted [Akbar et al., 1986].

The rather complex process of salt tolerance inheritance in cultivated plants is most likely determined by the presence of numerous factors that control this trait. It is assumed that the resistance of plants at a certain stage of development can be controlled by a small number of genes, and if we consider this process as a whole, then it turns out that this feature is quite complex and practically does not lend itself to classical genetic analysis [Corver et al., 1988].

A positive correlation was found between the expression of the HVA1 protein (family III LEA proteins) and tolerance against water deficit and salt stress in barley plants [Ingram, Bartels, 1996]. For a number of plants, a positive correlation has been shown between the growth of cultured tissues on osmotic media and the drought resistance of plants [Kopertech, 1995; Barakat, Abdel-Latif, 1996; Tabori et al., 2009]. Physiological evaluation of plants obtained by cell selection methods showed the inheritance of the drought resistance trait during seed propagation [Jaleel et al., 2009; Mahmood et al., 2012].

Osmoresistant corn plants were obtained in selective *in vitro* systems using mannitol and PEG [Dolgikh, 2004, 2005; Al-Kholany, Dolgikh, 2008, Al-Kholany, 2010; Al-Kholany et al., 2010; Matheka et al., 2008], lavender and sage

were obtained with mannitol and sodium chloride [Ehorova, 2012; Egorova, Stavtseva, 2013], salt-resistant and cold-resistant wheat and winter barley [Tantau et al., 2004], and with proline and sodium chloride - rice plants [Khadeeva et al., 2000], and only with sodium chloride - salt-resistant and drought-resistant wheat [Nikityna et al., 2014; Mahmood et al., 2012]. There are also known scientific studies aimed at the selection of salt-resistant trees against NaCl: cherries [Ochatt, 1996], margoza [Shivanna et al., 2013], palms [Jameel M. Al-Khayri, 2002; Mahmoud., Yaish et al., 2015] and apple trees [Wang, 2004; Ji-Hong Liu, 2006]. The resistance of plants against drought at the cellular level is expressed in the tolerance of cells to the presence of osmotically active substances in the cellular environment [Dolgikh, 2004]. It is likely that one of the mechanisms that provides resistance against salinity may be the low permeability of the plasma membrane of cells to these ions. One of the main features of plant salt tolerance is the ability of plant cells to maintain an optimal K^+/Na^+ balance in the cytosol [Tester et al., 2003].

The selection of stable salt-resistant lines of potatoes, capable of growing on media containing 60-450 mM NaCl, was carried out. Calli grown on media containing 120 or 150 mM NaCl had greater crude weight than those grown on other media. Replacing NaCl with KS1 or Na₂SO₄ revealed that the decrease in crude mass was mainly due to the presence of Na⁺. When PEG-6000 was added to the medium instead of salt, the salt-tolerant lines were unable to overcome PEG-6000-induced water stress. Whole plants regenerated from salt-resistant callus showed resistance to salt stress when their wet and dry weight was washed with 90 mM NaCl, and they produced more tubers per plant under salinity conditions. Salt-resistant plants differed phenotypically from the control plants in the shape of the leaf and in the color of the skin and pulp of the tuber, which were pink. RAPD prints with 70 different primers showed that the salt-resistant regenerants differ from the control and genotypically. The Kennebec potato variety, which is not resistant to salt, served as a control, from which salt-resistant

plants were selected [Ochatt et al., 1998]. It was shown that salt stress in control cells of ginseng (*Panax ginseng*) leads to an increase in gene expression (PgCDPK1c, PgCDPK2b, PgCDPK2c, PgCDPK3b, PgCDPK4a), a decrease in gene expression (PgCDPK1b, PgCDPK3a) and the appearance of new genes (PgCDPK3c). It should also be noted that there are transcripts in the sequence of which a number of catalytic subdomains are missing (PgCDPK4as). The rol genes act in a similar way to the effect of salt stress: the expression of a number of genes increases or decreases, "short" CDPK transcripts appear. The difference is that certain CDPK genes are upregulated or downregulated and different subdomains of CDPK genes are excised. Thus, it is shown that the rol genes affect the fundamental mechanisms that regulate the protective reactions of plants [Kiselev, Hryshchenko, 2008].

It is shown that successful physiological adaptation of regenerating sugar beet plants *in vitro* to high salinity occurs on selective media with a sublethal salt concentration within 2%. The degree of resistance of the explants depended on the number of passages on selective media. The frequency of regeneration during the primary passage was 3.3-4.8%; secondary mating increased it by 2 times and amounted to 6.1-8.6%. The obtained microclones on a selective nutrient medium (2% salt) retained the ability to grow and form roots, compared to the control ones (without selection), in which inhibition of growth and development processes was observed. The results of the conducted research made it possible to select and multiply *in vitro* the components of the sugar beet hybrid with signs of resistance to salinity. Further passaging of selected regenerants on media with sorbitol at a concentration of 0.45-0.40 M increased osmotic resistance by 1.5-1.9 times [Cherkasova, Fedoryn, 2018].

A comparative analysis of fodder beet callus lines resistant to sulfate and chloride salinity obtained from explants of diploid and tetraploid plants was carried out. At the same time, it was found that chloride salinity is more toxic to callus cultures than sulfate salinity. Cell lines obtained from tetraploid explants of

the Kyivsky variety were more resistant to both types of salinity, compared to lines obtained from diploid explants of the Ursus and Panfil'skyi varieties [Gubanova et al., 2000].

The response to chloride and sulfate salinization of fodder beet lines with cross-resistance against the toxin of the causative agent of bacteriosis and low temperatures was studied. Cell lines resistant to three stress factors were selected - a toxin, a causative agent of bacteriosis, low temperatures, as well as one of the types of salinity - chloride or sulfate. Regenerative plants were obtained from them and their cytosynthesis analysis was carried out [Gubanova et al., 2002]. Similar results were obtained in other laboratories [Swaaij et al., 1986, Kuznetsov et al., 1991].

Nitrate reductase is the first enzyme in the nitrogen assimilation chain. The activity of this enzyme is quite strongly reduced under the influence of various stressors (salinity, drought, heavy metal ions), which is observed *in vitro* and *in vivo* in plants and at the cellular level. Cell lines that do not assimilate nitrates can be obtained using chlorate. Chlorate, an analogue of nitrate, also acts as a substrate for normal nitrate reductase and is reduced to the toxic compound chlorite. And chlorate-resistant plant cells are characterized by nitrate reductase defects. Tungsten ions (W^{6+}) also have an inhibitory effect on nitrate reductase activity. This ion replaces molybdenum as a cofactor of the enzyme. Almost all W-containing enzymes are inactive, with few exceptions. With this phenomenon in mind, a selective system containing both nitrates as a single form of nitrogen and tungsten anions was created. Stable cell lines of soybean *Glycine max* L were selected on this medium. After several passages on medium with the addition of tungsten anions, stable cell lines were transferred to selective media containing vanadium anion (V^{5+}). This anion is another toxic inhibitor of nitrate reductase activity. Selected soybean cell cultures showed resistance against both types of anions. Although it is known that the mechanisms of toxic action of tungsten and vanadium ions are not the same. Resistant soybean cell lines were grown under

alternative stressor conditions for more than three years. To test the phenomenon of complex stability of nitrate reductase, cell lines growing on media with the addition of tungsten and vanadium were transferred to a selective medium with chlorate. Resistant cell variants grew successfully on all types of selective media. Growth of cultures in the presence of a nitrate reductase inhibitor indicates its stability. A selective medium with tungsten ions is a new way of selecting plant cell lines with a stable form of nitrate reductase [Mykhalskaya et al., 2008, Sergeeva, Bronnikova, 2016]. At the same time, the salt resistance of tobacco plants obtained using barium ions was very close to the level of resistance of natural halophytes [Sergeeva, 2016].

In experiments on selective media containing concentrations of barium ions toxic to wild-type cell cultures, resistant tobacco cell lines were selected. It is known that barium ions have an inhibitory effect on the transport of potassium ions from the cell. Taking into account this ionic antagonism, a hypothesis was proposed about the possibility of selecting variants with an increased level of salt resistance. Cultivation of barium-resistant cell lines on a selective medium with the addition of seawater salts only confirmed the validity of this prediction. Regenerants were obtained from tobacco cell lines resistant to barium ions and salinity, which were also tested for salt resistance. It was established that the selected cell cultures and regenerative plants withstood a lethal dose of salinity (20.0 g/l) of sea water salts for tobacco. To clarify the possible mechanism of resistance in callus cells and plants grown on a saline background, the content of free proline was measured. The level of free proline fluctuated during the passage, but the dynamics of its changes coincided at the cellular level and at the level of the whole plant. In terms of absolute value, the value exceeded this indicator, noted during cultivation on the control medium by 37-64 times in plants and by 13-22 times in cell lines. The change in the level of free proline indicates the benefit of its active use to maintain the vital activity of the body in conditions of salinity. This phenomenon is one of the possible mechanisms of salt resistance in

tobacco cell lines selected on media with barium ions and regenerants from them [Poretskaya et al., 2008].

Resistant wheat lines were selected on selective media that contained doses of Ba²⁺ cations lethal to cell cultures. Barium-resistant cell lines were tested under conditions of direct action of sulfate-chloride and sulfate salinities. The selected lines were characterized by complex resistance to both types of salt stress [Sergeeva, Bronnikova, 2017].

Correlative relationships between salinity resistance of the whole plant *in vivo* and callus tissues *in vitro* are noted in the literature, both positive [Almansouri et al., 2000, Terletsкая, 2008] and negative [Nosov, 1999].

A comparative evaluation of the growth parameters of three lines of wheat regenerants obtained from the callus culture of immature embryos on selective (0.42% NaCl) and one on control (without NaCl) media was carried out under conditions of salt stress (1.68% NaCl). and their parent forms. The genotype of the donor plant had a significant effect on the growth characteristics. The regenerant of the selective medium from the Minusa variety did not differ in any of the indicators (length of roots, stems; weight of roots, stems) from the parent form both in control (distilled water) and under stress conditions. One of the regenerants from the selection line KS-1607, obtained from a saline environment, had indicators lower than the parental form in both conditions, but exceeded the regenerant from an explant from the same ear obtained from a neutral environment (weight, root length, stem weight in the control, mass of roots in the version with NaCl). The second regenerant from the same line from the selective medium surpassed the parental form in stem mass both on the control and on the saline medium. Thus, for the most part, the regenerants that were selected on a selective medium had a higher regeneration potential than the rest of the forms. The ambiguity of the response to stress of regenerants obtained on selective media caused the need to increase the efficiency of the selection of salt-resistant forms of wheat *in vitro*, for example, by correcting the stressor level in the selective

media. A two-fold increase in the concentration of NaCl in the selective medium (up to 0.84%) led to a significant inhibition of callus culture morphogenesis compared to the control, with a moderate level of formation of full-fledged regenerants (15-20%). The concentration of NaCl equal to 1.68% caused callus necrosis in the majority of studied genotypes. And only from the selection line KS-1607 under these conditions, full-fledged regenerative plants were obtained. The last observation only emphasizes the value of this line for the selection of stress-resistant forms of wheat *in vitro*. Thus, the possibility of obtaining salt-resistant forms of wheat according to the technology proposed by the authors is shown; the pressure level of salt stress necessary for the selection of salt-tolerant regenerants is determined; a promising genotype for use in this technology was discovered [Stupko et al., 2008, Stupko, 2009].

Stimulation of the growth of callus tissues of Jerusalem artichoke (*Helianthus tuberosus* L.) caused by the addition of exogenous proline to the nutrient salt medium also does not directly confirm its role as a protective factor. In the presence of 1.5% NaCl in the nutrient medium, the growth of calli is inhibited. But when 0.2% proline is added to the medium with 1.5% NaCl, the negative effect of salt stress is significantly slowed down: under these conditions, the rate of proliferation is partially restored [Popov et al., 2001]. During *in vitro* cultivation, the use of exogenous proline can increase the frequency of regeneration of shoots of a number of cultures, there are data on the increase in the content of endogenous proline during somatic embryogenesis [Rastagi et al., 2008]. Free proline can be one of the factors involved in the growth and differentiation of sunflower cells *in vitro*. Moreover, the indicator of free proline content can be used for primary screening of sunflower explants [Komisarenko et al., 2014]. The organ specificity of the accumulation of free proline in the inbred line of corn and the line carrying dsRNA suppressor of the proline dehydrogenase gene in response to various osmotic stresses was established. In L-390 control plants, the level of free proline in the initial stages of stress decreased in the stems,

and increased in the roots. In the stems of T0 seedlings, the level of free proline was determined by the type of osmotic stress: it decreased in the presence of mannitol and increased in salinity, relative to the control indicators. One of the components of the general genetic control system associated with changes in the content of free proline in the early stages of the stress response is the cucurbit proline dehydrogenase gene [Sergeeva et al., 2014].

When plants are exposed to stress agents, their cells synthesize protective amino acids, in particular proline. Therefore, analogs of proline are often used as a selective factor for selection at the cellular level, among which azetin-2-carboxylic acid and hydroxyproline proved to be the most effective. With the use of these selective substances, salt- and drought-resistant forms of potatoes, carrots, tobacco and soybeans were selected. In selected clones resistant to amino acid analogues, an increase in the intracellular level of proline was observed, but a direct relationship between the level of salt resistance and the proline content in cells was not noted [Riccardi et al., 1983, Drydze, 1990, Kishor et al., 2005, Hayat et al. ., 2012].

The peculiarities of the effect of salt stress on callusogenesis and morphogenesis in the culture of isolated tissues of essential oil geranium (*Pelargonium roseum* Willd.) during several passages were investigated. Sublethal concentrations of NaCl (0.75%) were detected for non-morphogenic and morphogenic callus cultures, selection of resistant lines was carried out. The advantage of using morphogenic callus cultures for *in vitro* selection was shown, regenerative plants were obtained, and their preliminary analysis was carried out [Egorova, 2009].

Studies of the influence of salinity on the processes of morphogenesis of regenerating plants of hanging birch (*Betula pendula* Roth) of positive genotypes revealed that the NaCl concentration of 0.5% is lethal for hanging birch plants of the studied clones and sublethal for regenerants of hybrid genotype No. 52-84/8. This gives reason to predict the possibility of obtaining, as a result of mutagenesis,

lines of somaclonal variants of this genotype, resistant to chloride-sodium salinization and their use for further stepwise selection and creation of valuable breeding material [Konstantynov, 2014].

As a result of the conducted research, some features of the effect of salt stress on the development of callus cultures of two varieties of narrow-leaved lavender (*Lavandula angustifolia* Mill.) during several passages were revealed. Sublethal concentrations of NaCl (0.7-0.8%) were detected and resistant cell lines were selected. The advantage of using for *in vitro* selection of calli of the fourth passage, compared to the first, as well as the effect on the degree of salt resistance of the calli of the variety, mutagenic treatment with colchicine and the duration of the action of the stress factor is shown. It was established that at sublethal concentration of NaCl, the cultivation of callus tissues is possible for no more than three passages, and with selective ones - for six passages [Egorova, 2011].

In order to develop methods of cell selection, the effect of abiotic stress factors in *Lavandula angustifolia*, *Salvia sclarea*, *Coriandrum sativum*, *Pelargonium* spp. with the use of different varieties and biotechnological objects [Egorova, Stavtseva, 2006, Yegorova, 2012, Egorova, 2012]. And specifically, for geranium, when analyzing the effect of NaCl on callus cultures, it was established that a more effective approach in selection for salt resistance is the introduction of NaCl into the nutrient medium for the induction of morphogenesis and the selection of morphogenic calli against the background of a stress factor. The stability analysis of selected *in vitro* regenerants showed their increased tolerance against NaCl at the level of isolated meristems, compared to the original variety [Ehorova, 2012]. For lavender, sublethal concentrations of NaCl (0.7-0.9%), mannitol (8-11%) were determined, and the specifics of the effect of these substances on callus and morphogenesis, depending on the passage, callus type, and composition of the nutrient medium, were identified. Selection schemes for resistance against osmotic stress and low temperatures *in vitro* were developed, the advantage of using morphogenic calli and pre-treatment with colchicine for

selection of resistant lines and plant regeneration was established. In the selected resistant lines of lavender, an increase in proline content and differences in the cytophysiological parameters of the callus cell population in the growing cycle were found, compared to the control lines [Egorova, 2012, Egorova, 2012, 2014].

From leaf explants of diploid fodder beet plants of the Panfilsky variety, callus lines resistant to the toxin of the causative agent of bacterial spot (*Pseudomonas syringae* pv. *aptata*) were obtained, characterized by heterogeneity in the number of sets of chromosomes in the cell. A high level of chromosomal and morphogenetic variability was found in 12 regenerants obtained from them. During the cytological study, plants of different levels of ploidy were noted: 2 diploids ($2n = 2x = 18$), 2 triploids ($2n = 3x = 27$), 5 tetraploids ($2n = 4x = 36$) and 3 aneuploid plants with the number of chromosomes from 19 to 37. A fairly high level of karyotypic instability was found in all regenerated plants. Fodder beet cell lines resistant to chloride and sulfate salinity were also obtained. Several dozen plants were regenerated from them, most of which (80%) had a diploid karyotype. Mixoploid ($2x$ and $4x$) and aneuploid plants with an approximately tetraploid number of chromosomes were also found. From chloride-resistant callus lines, mainly diploid (65%) and tetraploid (24%) plants were regenerated, in which a significant (up to 10%) number of cells with mitosis disorders was noted [Chugunkova et al., 1999].

To select resistant cell lines, the method of stepwise selection was used according to the schemes: 1.5% NaCl (3 passages) – 2.0% NaCl (3 passages) – 2.5% NaCl (3 passages) – the main medium of MS (3 passages); 2.0% Na₂SO₄ (3 passages) – 2.5% Na₂SO₄ (3 passages) – 3.0% Na₂SO₄ (3 passages) – basic MS medium (3 passages). Thus, several selection cycles were carried out and 2 sugar beet callus lines resistant to chloride salinity and 3 to sulfate salinity were obtained. For direct selection of resistant lines, 2.0% NaCl and 2.5% Na₂SO₄ were used as selective agents. Pieces of callus tissue weighing 15-20 mg were placed in Petri dishes with sublethal doses of salts. Resistant clones were selected

after 6 weeks. It was found that by the end of the first passage, up to 32% of calli survived on NaCl medium and up to 37% on Na₂SO₄. According to the standard scheme of cell selection, calli were tested under selective and non-selective conditions. After three passages in selective conditions with sublethal doses of salts, the number of viable calli decreased to 20% on average. After the next two passages on medium without a selective factor and checking growth under selective conditions, 2.6 to 4.8% of resistant clones were isolated. Along with the experiments on the transfer of callus lines with cross-resistance against the toxin of the causative agent of bacteriosis and low plus temperatures immediately to media with sublethal doses of salts, the selection of these lines was carried out on media with a gradual increase in the concentration of the selective factor (stepwise selection). As a result of successive selections, calli were selected, which are able to grow on selective media with 2.5% NaCl, 3.0% Na₂SO₄ and stably maintain stability. It was found that unlike lines resistant only to chloride or sulfate type of salinity, the concentration in the medium of 2.5% NaCl, 3.0% Na₂SO₄ did not lead to the death of cross-resistant calli. The obtained cell lines, resistant to three stress factors, had the following morphological characteristics: a dense callus with a globular structure of light yellow or brown color on NaCl medium and dark yellow on Na₂SO₄ medium. Brown and dark yellow calluses were able to regenerate shoots. The frequency of regeneration in the obtained cell lines resistant to a complex of stress factors was at the level of 17%. Sometimes the seedlings morphologically differed significantly from the control variants. It should be noted that callus cultures resistant to a complex of stress factors and sulfate salinity (3k/2, 8k/2, 11k/2) better tolerated the check of stability of signs during 10 passages (up to 75.5% of planted calli). In lines resistant to low temperatures, bacterial toxin and chloride salinity (3k/1, 8k/1, 11k/1), up to 66.6% of calli remained viable at the end of transplantation. A significant number of regenerative plants were obtained from cell lines that grew stably on media with various stress factors. In beet regenerating plants, obtained on environments with

sublethal doses of salts and the toxin of the causative agent of bacteriosis and planted in the soil (vegetation vessels) were tested for resistance to bacterial leaf spot. Affection of the selected regenerants with bacteriosis (causing agent *Pseudomonas syringae* pv. aptata) was assessed on a five-point scale. The concentration of the pathogen in the suspension was 10⁷ cells/ml. Infection with the pathogen was carried out at the stage of 8-10 pairs of leaves. Regenerative plants obtained from unstable cell lines served as controls. It was established that control plants were affected by the disease by 80-90%, the degree of damage was 4-5 points. The degree of bacteriosis of the leaves of regenerating plants with complex resistance was at the level of 1-2 points, and the development of the disease was 15-20%. So, as a result of consistent complex work using cell selection methods, callus lines of sugar and fodder beets were obtained, resistant both to individual and complex stress factors, including the toxin of the causative agent of bacteriosis, low plus temperatures, as well as to one of the types of salinity - chloride or sulfate. Checking the stability of signs of resistance against a complex of stress factors proved the resistance of most callus lines and regenerating plants obtained from them [Chugunkova, Shevtsov, 1998, Chugunkova, 2009].

As a result of the conducted research, it was established that the successful physiological adaptation of regenerating plants against strong salinity occurs with an alternating light regime (darkness - 4 days, then light for 30 days), which precedes two-time hard selection in the process of growing on a selective nutrient medium with a sublethal concentration of salt within 2%. This made it possible to obtain relatively stable components of the sugar beet hybrid with high viability, the use of double crossing under salt stress conditions allowed to increase the degree of resistance of microclones to 66.0-81.7%. It was established that osmotic stress causes the accumulation of a significant amount of proline in the cytoplasm of cells, which exceeds the control by 7-11 times, depending on the genotype. At

the same time, the proline content can serve as an indicator for the selection of osmotic-resistant microclones [Cherkasova, Zhuzhzhhalova, 2013].

A wheat cell line resistant to 1% NaCl was obtained as a result of stepwise selection. After subcultures on a saline medium, and then on a salt-free medium, a line was obtained, which in terms of raw mass, proline content, and soluble protein prevails over the original form. Salinity tolerance is defined as a physiological adaptation of a non-mutational type [Liu et al., 1999]. Other studies have shown that the selection of cell lines of spring wheat *in vitro*, proliferating on a saline medium and retaining regenerative abilities, should be carried out at a concentration of sodium chloride up to 1.2-1.3% [Nikityna et al., 2013].

The evaluation of the morphogenetic and regeneration potential of 6 spring wheat varieties of different ecological and geographical origin in the culture of immature embryos *in vitro* was carried out. At the same time, the efficiency of dedifferentiation of cell lines of genotypes under conditions of salt stress and under control was evaluated. The frequency of morphogenesis was higher in 2015 and amounted to 91.5%, and under conditions of stress in 2014, this indicator was 87.2%. An ambiguous reaction of the studied genotypes of spring wheat to the frequency of regeneration was established [Bychkova, 2016]. In cereals, the frequency of callusogenesis, morphogenesis, and regeneration depends on a number of factors [Bregitzer, 1992; Avksentieva, Petrenko, 2009; Zobova et al., 2011; Nikitina, Khlebova, 2015].

In 6 varieties of rice (Pusa Basmati 1, Basmati 370, Type III, Pant Dhan 4, CSR-10 and Pokkali), the growth of embryogenic callus, plant regeneration and the content of proline and total protein under salt stress on agar medium containing 0; 0.5; 1.0; 1.5 and 2.0% NaCl. 4 weeks after inoculation, the raw mass of callus decreased with increasing salt concentration in the medium in all 6 varieties. The frequency of regeneration of plants from salt-stressed callus was lower, compared to the control. After 15 and 30 days after inoculation, the content

of proline increased several times, while the content of total protein significantly decreased with increasing salt concentration [Shankhdhar et al., 2000].

In the course of the research, we obtained plants of red fescue (*Festuca rubra* L.) and fennel (*Agrostis stolonifera* L.) *in vitro*, resistant to high concentrations of sodium chloride. Stable cell lines of fescue and meadowsweet were selected on modified MS medium with 1% and 2% NaCl. Regeneration and rooting of plants from the surviving clones was carried out on MS media with 1% and 2% NaCl, and then the regenerants were transplanted into the soil [Gladkov et al., 2014].

As a result of the research, some features of the effect of salt stress on the development of callus cultures of two varieties (Stepnaya, Sineva) of narrow-leaved lavender (*Lavandula angustifolia* Mill.) during several passages were revealed. Sublethal concentrations of NaCl (0.7-0.8%) were also detected and resistant cell lines were selected. The advantage of using for *in vitro* selection of calli of the fourth passage, compared to the first, as well as the effect on the degree of salt resistance of the calli of the variety, mutagenic treatment with colchicine and the duration of the action of the stress factor is shown. It was also established that at sublethal concentration of NaCl, it is possible to cultivate callus tissues for no more than three passages, and with selective ones - for six passages [Egorova, 2011].

One of the main features of plant salt tolerance is the ability of their cells to maintain an optimal K^+/Na^+ balance in the cytosol [Maathuis, Amtmann, 1999, Tester et al., 2003]. Under normal conditions, cytosol K^+ is about 150 mm [Wyn et al., 1979; Leigh, Wyn, 1984] and cytosol Na^+ in lower limits [Carden et al., 2003], this ratio reaches 100 units, revealing normal cell metabolism. Under conditions of salinity, the K^+/Na^+ ratio decreases. This occurs as a result of an excessive accumulation of sodium ions in the cytosol and an increase in the outflow of potassium ions from the cell, which leads to sodium chloride-induced depolarization of the membrane under salinity conditions [Cakirlar et al., 1981;

Leigh et al., 2001; Shabala, 2003; Zhu et al., 2003]. It follows that the ability of cells to store potassium ions can influence the improvement of salt tolerance of plants [Shabala, 2003].

Salt stress *in vitro* was modeled by adding NaCl to the medium in concentrations of 0, 50, and 100 mM. Leaf area and total length of grape roots were used as indicators of salt tolerance. Salt stress *in vivo* was provided by irrigation for 75 days with water containing NaCl in concentrations of 0, 80, 100, and 120 mM. Salt tolerance of plants was evaluated on the basis of agrobiological parameters (leaf area, stem length, stem load, stem lignification) and yield analysis (cluster characteristics, bush yield, mass concentration of sugars, titrated acidity and pH of juice). The water potentials of the leaves were also determined as indicators of the water balance of plants and the electrical conductivity of the soil as an indicator of salinity. Reactions to salt stress of plants grown *in vitro* and in pot culture showed a complete correlation [Ryff, Berezovskaya, 2020].

A fairly effective method of creating barley regenerants on selective media with a high concentration of NaCl and low pH is the use of callus tissues obtained in the culture of immature embryos with a double selection of stress-resistant forms at the stages of callus proliferation and plant regeneration [Konysheva, 2004].

Carrying out cell selection in two stages made it possible to obtain salt-resistant cell clones that retain the property of embryogenicity. In the process of selection, an indicator of the embryogenic capacity of the callus tissue has a rather significant value when evaluating salt resistance, along with growth characteristics. The revealed correspondence between the high embryogenic ability of clone A 188 and its highest salt resistance allows us to predict that the effective selection of resistant forms in the initially embryogenic cell line is complicated without taking into account the embryogenicity of the tissue. The production of regenerant corn plants from salt-resistant cell lines made it possible to assess the possibility of realizing the salt-resistance characteristics of cells at

the level of the whole organism. Regenerative plants and their progeny, as well as hybrids obtained as a result of backcrossing with the original non-solestic line showed signs of salt tolerance when tested under different conditions. At the same time, salt tolerance was inherited as a dominant nuclear trait [Laryna, 1995].

In vitro mutagenesis can also be useful for the selection of salinity-resistant forms of wheat, as it increases the frequency and spectrum of mutations in combination with faster production of plants [Morgun et al., 2016].

The results of experiments on the determination of the content of total soluble cell protein, free proline and the activity of the main enzyme of the oxidizing chain of the pentose-phosphate cycle in microclones of blooming Weigela plants (Weigela florida "Variegata" Bunge ADC) indicate that they are well adapted to salinity conditions and the presence of ions heavy metals, in particular copper, organisms [Zemlyanukhina et al., 2017].

Experimental confirmation of the hypothesis was obtained, according to which the hydraulic signal, and not the signal of a hormonal nature, is the "primary messenger of water deficit", which is generated in the roots in response to salt stress or soil drought and instantly spreads through the continuous water phase of the plant, transforming in the cells of aboveground organs into chemical regulatory signals and inducing the formation of effective protective mechanisms [Kholodova et al., 2006].

An effective method using *Agrobacterium tumefaciens* (strain AGL1; patent No. 2004120871) was used for the genetic modification of the meadowsweet *Agrostis stolonifera* L. To select transgenic plants, three selection systems were used: 1. Only kanamycin 150 mg/l was used as a selective agent. 2. 1% and 2% NaCl were used as a selective agent; 3. Kanamycin and NaCl were used as a selective agent. When using kanamycin as a selective agent, the selection efficiency of green plants was about 1%, but the genes that carried them were not always present in the selected plants. The most efficient (20% of transgenic plants) selection system for transgenic plants was screening on medium

containing 2% NaCl. Under these conditions, no control plants survived, in contrast to the use of a 1% NaCl concentration, where survival of control plants was 10%. But the plants selected on a medium with 2% NaCl showed the presence of the proline dehydrogenase gene from *Arabidopsis thaliana* in the antisense orientation under the control of the 35S promoter of the cauliflower mosaic virus and the selector gene NPTII, which gives plants resistance to kanamycin in its genome during PCR analysis [Danilova et al. , 2008].

As a result of agrobacterial transformation, lines of genetically modified tobacco plants carrying an antisense suppressor of the *Arabidopsis* proline dehydrogenase gene were obtained, which were characterized by a decrease in proline dehydrogenase activity and an increased proline content. As a marker gene, the phosphonemycin transferase gene was introduced, which causes resistance against kanamycin. A number of experiments were conducted that showed the resistance of the obtained plants against various stressful actions. These plants have been shown to be resistant to toxic concentrations of sodium chloride. Moreover, both seedlings and plants at later stages of development were resistant. For control plants, a concentration of 400 mM was toxic, while genetically modified plants were able to survive for a month on 500 mM NaCl. Also, these plants were able to withstand toxic concentrations of heavy metal salts: nickel, cadmium, mercury and lead for 2-3 weeks. In addition, they were characterized by higher resistance to high temperatures, as well as to drought and osmotic stress [Kolodiazhnaya et al., 2008].

It was experimentally established that to remove agrobacterium after co-cultivation with barley in various recipient systems, it is best to use timentin (450-550 mg/l), which practically does not cause cell death, both in callus and in barley embryo culture, unlike cetofaxim , which showed toxicity in the studied concentration range (150-500 mg/l) [Bakulyna, 2016].

A comparison was made of the efficiency of the selection of plants regenerating from explants after treatment with agrobacteria with the P5KS gene,

on a medium with 25, 50 and 100 mg/l kanamycin. Selection of plants on medium with 50 mg/l kanamycin was effective for explants of rapeseed, stevia and aspen. In addition, since the expression of the P5KS gene increases the salt tolerance of plants, direct selection of transformants was carried out on MC medium with different concentrations of NaCl (100, 150, 200 mM). Rapeseed and oil radish plants selected on medium with 100 and 150 mM sodium chloride were transferred to medium with 200 and 250 mM NaCl. Some of the plants were able to grow at these concentrations, while the majority died. When breeding on media with 50 mg/l kanamycin, most of the plants that developed from rapeseed and radish explants lost their green color and subsequently died. At the same time, several plants were selected that retained their green color after cultivation for several months on a medium with kanamycin [Syutykova et al., 2008].

The analysis of the level of CpNpG site-specific methylation of nuclear DNA and the study of the specificity of methylation of some genes of *Mesembryanthemum crystallinum* plants growing under salt stress showed that under salt stress (0.5 M NaCl) when C3 photosynthesis is switched to the CAM pathway assimilation of carbon dioxide in facultative halophytic plants *Mesembryanthemum crystallinum* level of CpNpG-methylation of their nuclear of the genome in CCWGG sequences increases twofold and is associated with hypermethylation of satellite DNA. At the same time, the pattern of methylation of CCWGG sequences in the 51 promoter region of the phosphoenolpyruvate carboxylase gene, the key enzyme of C4 photosynthesis and CAM, as well as nuclear ribosomal DNA does not change. Also, specific CpNpG-hypermethylation of satellite DNA was detected under conditions of expression of a new metabolic program. The functional role of CpNpG-hypermethylation of satellite DNA is probably related to the formation of a specialized chromatin structure, which simultaneously regulates the expression of a large number of genes in *Mesembryanthemum crystallinum* plant cells during their adaptation to salt stress and switching to CAM metabolism. At the same time, a satellite DNA

fraction of *Mesembryanthemum crystallinum* plants was also isolated. Experiments on its analysis and localization on the chromosomes of *Mesembryanthemum crystallinum* plants are also being conducted, as well as research on the "CAM-specific" chromatin structure [Dyachenko et al., 2007].

Plants develop quite a number of biochemical and molecular defense mechanisms during salt stress [El-Esawi et al., 2019]. Biochemical pathways leading to products and processes that increase salt tolerance are likely to act additively and synergistically [Parida, Das, 2005]. Biochemical strategies include: 1) selective accumulation or exclusion of ions; 2) control of ion absorption by roots and transport to leaves; 3) compartmentalization of ions at the cellular level and the whole plant; 4) synthesis of compatible soluble substances; 5) changes in the photosynthetic pathway; 6) changes in the structure of membranes; 7) activation of antioxidant enzymes; 8) changes in hormonal status [Parida, Das, 2005].

It has been shown that the genes whose action may be associated with the increase in salt tolerance of plants are divided into three main functional groups: 1) genes that control the absorption and transport of salt ions - salt overly sensitive (SOS1, SOS2, SOS3, SOS4); 2) genes responsible for osmotic function (P5CS mod, codA, P5CS, otsA, otsB, AtTPS1, AtTPS2, mt1D, S6PDH, OemaT1, imt1); 3) genes that could provide accelerated growth of plants in saline soil, namely candidate genes, probably those involved in signaling pathways, which include sensors, hormones, transcription factors, protein kinases and other signaling molecules, such as calmodulin, binding proteins: it is assumed that such genes are activated when plants are exposed to various abiotic stressors [Munns, 2005, Parihar et al., 2015].

Features of the development of symptoms of programmed cell death induced by NaCl, as well as modification of growth processes in response to NaCl in wild-type *Arabidopsis thaliana* and lines lacking the ROS-activated K⁺ channel GORK were revealed. The experiments used the natural ecotype WS-0

(Wassilewskija), as well as the knockout mutant *gork1-1*, which lacks the outward-rectifying K⁺ channel GORK. Whole plant culture was grown vertically from seeds in Petri dishes (100% Murashige and Skoog medium, 0.35% phytoigel, 1% sucrose, pH 6.0) using standard protocols. To analyze the growth processes, the medium replacement technique was used, the stressor was introduced into the medium for 4 days. It was shown that replacing the control medium with medium with 75-200 mM NaCl caused inhibition of primary root elongation. It was found that *gork1-1* roots were less sensitive to these treatments compared to the wild type. The maximum effect (inhibition by 60%) was found for the treatment of 200 mM NaCl. In *gork1-1*, this effect was 2 times weaker. Programmed cell death was induced by incubating plants in 200 mM NaCl solution for 15 hours. To detect the development of morphological symptoms of programmed cell death, 10 samples of 50 cells each, separately for trichoblasts and atrichoblasts, were analyzed. Viability of root cells was determined using Evans Blue dye. The test for the activation of caspase-like proteases was carried out using the CaspACE FITC-VADfmk in situ marker kit. Treatment of plants with 200 mM NaCl for 15 h significantly stimulated the number of symptoms of programmed cell death in wild-type roots. The FITCVAD-fmk signal was significantly lower in *gork1-1* plants. The share of atrichoblasts with morphological symptoms of programmed cell death in WS-0 plants was about 45%, and in *gork1-1* roots - only 15%. For root hairs, these indicators were 50% in WS-0, 25% in *gork1-1*. NaCl-induced programmed cell death was accompanied by a violation of the integrity of the plasma membrane and gave a positive test with Evans Blue. Roots treated with high levels of NaCl showed a higher level of CaspACE FITC-VAD-fmk fluorescence compared to the control. This indicates the induction of caspase-like proteases involved in the processes of programmed cell death. In the *gork1-1* line, activation of protease activity was less pronounced. The obtained results allow us to draw the following conclusions: 1) when NaCl is added to the medium, the growth rate of the main root of *Arabidopsis* sharply decreases; 2) an increase in

NaCl concentration induces the development of morphological and biochemical symptoms of programmed cell death; 3) in plants lacking the GORK K⁺ channel, the symptoms of programmed cell death are less pronounced, which indicates the involvement of these channels in the response to stress [Matskevich et al., 2018]. Along with that, it was established that the ROS-sensitive center in the structure of GORK (Cys-151) is of key importance in the activation of GORK K⁺ channels under the action of ROS under salt and oxidative stress. The elimination of functional Cys-151 caused a significant decrease in plant sensitivity to salt and oxidative stress [Samokhina et al., 2018].

Under conditions of salt stress (two-hour treatment with 25 mM NaCl), 363 and 106 transcripts were identified in chickpea (*Cicer arietinum* L.) plants, which were characterized by increased and decreased expression in roots and nodes, respectively [Molina et al., 2011]. At the same time, among the upregulation of transcripts after salt treatment, there were genes associated with redox reactions. A comparative transcriptome analysis of gene expression in pepper plants exposed to 400 mM NaCl revealed activation of genes encoding cytochrome P450, ubiquinol oxidoreductase, CDPK substrate protein 1, succinate dehydrogenase, selenium-binding protein, and others. At the same time, the genes encoding the TF 9 homeodomain, sterol C-methyltransferase, malate dehydrogenase, and fumarate hydratase were repressed [Lee, Choi, 2013].

However, proteomic approaches can contribute to a deeper understanding of the molecular mechanisms of resistance of agricultural plants against saline environments [Zhuang et al., 2014]. It was shown that during salt stress in plants, proteins involved in signaling, ion transport, energy (photosynthesis, respiration, ATP formation), carbohydrate, protein, lipid metabolism, metabolism of osmolytes, phytohormones, stress proteins, associated with pathogenesis, osmotic stress, antioxidant enzymes, as well as cytoskeletal proteins/enzymes that accept participation in secondary metabolism, in particular in lignin biosynthesis and cyanate degradation, and others [Kosová et al. 2013]. In potato plants under the

stress of 90 mM NaCl, 322 and 305 proteins were identified with up- and down-regulation in the stems of two cultivars "Kennebec" and "Concord", respectively [Aghaei et al., 2008]. Osmotin-like proteins, BTSH, calreticulin proteins, TSI-1 protein, protein inhibitors were marked by marked upregulation. Under stress caused by 150 mM NaCl, a significant decrease in the level of proteins involved in photosynthesis, primary metabolism (triose phosphate isomerase, glyceraldehyde-3-phosphate dehydrogenase), nitrogen and amino acid metabolism, polyamine synthesis (arginine decarboxylase, S-adenosylmethionine decarboxylase, agmatine deiminase) [Evers et al., 2012]. The use of the proteomic approach revealed a total of 23 proteins in tomato seedlings (*Solanum lycopersicum*) in response to the action of 120 mM NaCl. These proteins were divided into 6 functional categories: 1) BTSH; 2) enzymes involved in detoxification; 3) proteins related to carbohydrate metabolism; 4) proteins responsible for transcription and translation; 5) ATP synthases; 6) proteins of photosynthetic metabolism [Chen et al., 2009]. And in tomato seedlings, 40 and 36 proteins were identified with significant quantitative changes in leaves and roots, respectively, the main part of which was proteins related to degradation, metabolism and protein folding, and photosynthesis [Manaa et al., 2011].

In vitro selection for resistance against sulfate salinity has so far been much less successful than against chloride salinity, which is due to the rather high phytotoxicity of sulfate anions and strong absorption of sodium cations [Dubrovnaya, 2017]. The influence of different types of salts (NaCl, KCl, Na₂SO₄, seawater salts) on callus cultures of rice was analyzed in terms of growth indicators, accumulation of proline and toxic ions in tissues. It was established that, among the studied salts, the stronger inhibition of the growth of callus cultures was caused by the inhibitory effect of KCl. According to the obtained results, among the studied genotypes of rice, in general, a different response of calli to the action of selective agents was found. The researchers came to the conclusion that the accumulation of specific toxic ions is a rather important aspect

of the effect of salt stress on rice callus cells, and the accumulation of proline serves as an indicator of resistance against osmotic stress [Lutts et al., 1996].

Also, a possible selective factor that somewhat mimics sulfate-chloride salinity is common sea salt, which is added to the nutrient medium in concentrations that will inhibit cell growth *in vitro* culture. When studying the effect of increasing salinity levels (0, 0.6 and 0.9 g of sea salt) on the growth and some chemical indicators of wheat callus, a positive correlation was found between the content of total nitrogen and the ratio of potassium ions to sodium in cells with increasing sea salt concentration [Aly et al., 2007].

A strategy for transgene-induced activation of genetic programs of plant protection against salt stress is proposed in the model of facultative halophytic plants *Mesembryanthemum crystallinum*. Based on the use of CpG-CpHpG site-specific DNA methyltransferases, a strategy for creating model plants with transgene-induced unigenetic activation of genetic programs of protection against abiotic and biotic stresses was developed. Methods of regeneration and transformation of *Mesembryanthemum crystallinum* plants have been developed. A specialized construct containing a modified EcoRII methylase gene under the control of the 35S CaMV promoter was obtained and agrobacterial transformation of *Mesembryanthemum crystallinum* plants was carried out with it. In the obtained transgenic plants, the connection between the adaptation of *Mesembryanthemum crystallinum* plants against salt stress and wave deficiency and hypermethylation of CCWGG-repetitive sequences in their genome will be investigated [Dyachenko et al., 2010].

To study the role of enzymatic DNA methylation in the modification of metabolism and adaptation against stressful conditions, model plants were obtained with transgene-induced methylation using the DNA methyltransferase EcoRII, which methylates the internal cytosine in the CCWGG sequence. Such plants are expected to receive a more complete protective response to salt and water stress. Methods of regeneration and transformation of *Mesembryanthemum*

crystallinum plants have also been developed. A specialized construct containing the EcoRII methyltransferase gene was obtained, which modifies the attachment of the nuclear localization signal of the SV40 virus under the control of the 35S RNA promoter of the cauliflower mosaic virus. Genetic transformation of *Mesembryanthemum crystallinum* plants was carried out with the obtained construction with the help of antibacterial infiltration, transgenic plants of the first generation were obtained. Restriction analysis of the genome of the obtained transformants showed protection of their genomic DNA from hydrolysis by specific methyl-sensitive endonucleases, which indicates the functional activity of the transgene. Transformed plants differed phenotypically from control plants. The proposed method will reveal the relationship between hypermethylation of specific sequences in the genome of *Mesembryanthemum crystallinum* and the adaptation of these plants against salt stress and water deficit when switching complex metabolic programs of the defense response [Cherevatenko et al., 2012].

An increase in salt tolerance of plants was noted when the Na⁺/H⁺-antiporter gene was overexpressed in them. Potato varieties Skoroplodny and Jubilee Zhukov transformed with the gene of the vacuolar Na⁺/H⁺-antiporter of barley HvNHX2 under the control of the 35S promoter. It was established that *in vitro* culture Yubilei Zhukov variety has higher growth parameters than Skoroplodny. At the same time, the reaction of individual transgenic lines to 100 mM and 200 mM NaCl on MC medium was studied. The following parameters were also studied: the growth of stems and roots, the number of internodes and leaves, wet and dry masses, as well as the accumulation of sodium. At an increased salt concentration, a decrease in most of the morpho-physiological characteristics of all analyzed lines was noted. At 100 mM NaCl, the growth of transgenic lines of Skoroplodny and Yubilei Zhukov varieties was significantly higher than that of the original genotypes. The growth of stems of transgenic lines of the Jubilee Zhukov variety was higher than that of non-transgenic plants of the original variety. On medium with 200 mM NaCl in all lines except JZ9161(2),

there is practically no growth of roots and stems. According to all measured growth indicators, this line is the most salt-tolerant. At 100 mM NaCl, the original genotype of the Skoroplodny variety accumulates more sodium ions than the transgenic lines. In contrast, the two transgenic lines of the Jubilee Zhukov variety have a significantly higher sodium ion content at 100 mM NaCl [Lypatnikova et al., 2010].

An attempt was made to demonstrate that NaCl is capable of causing ROS generation in *Physcomitrella patens* (Hedw.) Bruch & Schimp. cells. A technique for measuring ROS in cells using the fluorescent probe dihydroethidium and an adapted Somet technique for determining DNA breaks was developed. In the course of the research, it was found that NaCl in concentrations above 200 mM causes a significant increase in the fluorescence intensity of dihydroethidium. This effect increased with NaCl concentration, reaching a maximum value at 300 mM. Superoxide dismutase reduced NaCl-induced dihydroethidium fluorescence by 40-45% at 200-300 mM NaCl and by 60% at 400 mM NaCl. This information shows that approximately half of the dihydroethidium signal is due to the reaction with $O_2^{\bullet-}$. Thiourea, which is a negatively specific hydroxyl radical scavenger, reduced NaCl-induced dihydroethidium fluorescence by 20% at 200 mM NaCl and by 30% at 300 and 400 mM NaCl, respectively. This indicates that part of the dihydroethidium signal is caused by reaction with hydroxyl radicals. Other low-molecular-weight antioxidants, such as reduced glutathione, dimethyl sulfoxide, and spermine also partially inhibited the NaCl-induced dihydroethidium signal. These substances caused a 40-50% decrease in the dihydroethidium signal at 200-300 mM NaCl and 25-30% at 400 mM NaCl. Thus, it was shown that salinity causes the generation of ROS, including its most reactive ones, such as hydroxyl radicals. Comet-based techniques were adapted for the analysis of DNA breaks: the neutral Comet assay for detecting double-strand breaks and the alkaline Comet assay, which is sensitive to single-strand DNA breaks. The results of the Comet-tests showed that protonema treatment with 100 mM NaCl causes a significant

increase in double- and single-strand DNA breaks. Treatment with 300 and 500 mM NaCl increased the number of DNA double-strand breaks by 3-3.5 and 4-4.5 times, respectively, compared to the control. The number of single-strand breaks progressed in approximately the same way with increasing salt concentration in the medium. The induction of DNA double-strand breaks can be associated with the activation of the processes of programmed cell death, previously registered for NaCl treatments of various plant tissues. At the same time, the appearance and increase in the number of single-strand breaks can be explained from the point of view of oxidative DNA damage, similar in nature to the action of genotoxic factors. Thus, it was shown that NaCl causes DNA damage, which manifests itself in the accumulation of single- and double-strand breaks and can be associated with the increasing production of highly reactive ROS, such as hydroxyl radicals [Zvonarev et al., 2018]. Using a model system for the analysis of ROS synthesis and DNA destruction - the protonema of *Physcomitrella patens*, the qualitative composition of ROS generated during salinization was investigated, and the observed "programmed" (double) and "genotoxic" (single) DNA breaks were evaluated. At the same time, it was shown that the dominant ROS under the action of NaCl is the superoxide anion radical, and also hydroxyl radicals are synthesized in significant quantities, and to a lesser extent, hydrogen peroxide. Tests based on the COMET technique showed that treatment with 100-500 mM NaCl causes a significant increase in both double- and single-strand DNA breaks. Hydroxyl radical scavengers such as thiourea or dimethylsulfoxide inhibited the formation of DNA breaks in response to NaCl. Thus, NaCl induced both "programmed" and "genotoxic" DNA damage in a hydroxyl-dependent manner [Zvonarev et al., 2019].

Under conditions of increased NaCl content, the transgenic potato lines with the expression of the *HvNHX2* transgene had a significant number of leaves, were taller, and accumulated biological mass more actively. It is quite likely that the increase in salt resistance of transgenic lines is associated with the

preservation of a higher content of potassium ions in stem and root tissues than in non-transformed plants, which allowed transgenic lines to maintain a lower water potential and better saturate their tissues with water [Kryvosheeva et al. 2014]. In addition, a high ratio of K^+/Na^+ in the cytosol during salinity is quite important due to the ability of sodium ions to replace potassium ions in the sites required for the activation of more than 50 enzymes, which causes the metabolic toxicity of sodium ions [Tester, Davenport, 2003]. More successful compartmentalization of sodium ions in the vacuole due to the expression of HvNHX2 could also increase the resistance of the studied transgenic potato lines against 150 mM NaCl [Kryvosheeva et al., 2014].

The effect of salinization of different intensities on transgenic tobacco plants obtained by agrobacterial transformation, expressing the barley HvPIP2;1 gene under the control of the constitutive 35S promoter, was studied. Cuttings from leaves of different layers were incubated for two days in NaCl solutions with a concentration of 100 to 500 mM, and then their raw weight and osmotic potential of the juice were determined. During incubation in 100 mM NaCl solution, the mass of cuttings increased, mainly due to water absorption. The increase in mass of cuttings from the leaves of transgenic plants expressing the HvPIP2;1 gene was, on average, one and a half times greater than in the control, that is, in plants transformed with the "empty" vector. It is obvious that the greater accumulation of crude mass in transgenic plants expressing barley aquaporins was associated with their increased ability to absorb water. Against the background of a high concentration of NaCl, the mass of cuttings from leaves, on the contrary, decreased due to water loss. The level of loss was 6-fold higher in HvPIP2;1 transgenic plants compared to the control, which was probably due to a higher permeability of cell membranes to water. Aquaporins are able to conduct water both inside and outside the cells, and the direction of the water current depends on the water potential gradient. The nature of the change in leaf mass and the change in their osmotic potential showed that the plants were able to maintain the

osmotic potential gradient against the background of lower salt concentrations, and under these conditions, the increase in membrane permeability to water in HvPIP2;1 transgenic plants ensured a greater influx of water into the cells. And against the background of high salt concentration, the mechanism of osmotic adaptation was no longer effective, and the leaves lost water, which made HvPIP2;1 transgenic plants more accessible due to a decrease in their water-holding capacity. Plants are able to change the expression of aquaporin genes depending on the availability of water for plants. Constitutive increased expression of aquaporin genes increases the resistance of plants to a weak water deficit, but reduces it to a strong one. This information is quite important for the biotechnology of creating varieties of cultivated plants resistant to water deficit [Sharipova et al., 2019].

The study of salinity tolerance of alloplasmic wheat on the cytoplasm of *Aegilops crassa* *in vitro* culture showed that foreign cytoplasm did not have the same effect on salinity, depending on the interaction with the nucleus, but generally increased salinity [Hou Ning et al., 2000].

Among the studied genes (*hliB*, *sigD*, *rbpA*, *rpl3*, *rpoA*) in the cyanobacterium *Synechocystis*, differences in the expression change during cold and salt stress were observed. This fact deserves attention if we talk about genes controlled by a two-component regulatory system, which are controlled by the same histidine kinase under cold and salt stress, but by different response regulators. In this case, it is possible to predict the interaction of calcium on the response regulators of some two-component regulation systems. It should also be noted that among the found calcium-dependent genes there were both those regulated by the Hik33 histidine kinase and those with unknown regulation mechanisms. This fact indicates the possibility of participation of calcium ions in various regulatory systems. So, as a result of the research, it was shown that calcium plays a rather important role in the regulation of the expression of stress-dependent genes in the cyanobacterium *Synechocystis* and can be both a part of

various regulatory systems and play a certain role in changes in DNA supercoiling [Bachyn, Los, 2015].

One of the strategies to protect plants against the effects of abiotic stressors is the creation of transgenic plants with genes for the synthesis of osmoprotectants, specifically, glycine betaine. Glycine betaine is synthesized in organisms from glycine or from choline by two different metabolic pathways. In the bacterium *Arthrobacter globiformis*, one choline oxidase enzyme is required for the synthesis of glycine betaine. A genetic construct was created with the *codA* gene under the control of the CaMV35S promoter. The gene is translationally fused with the signal sequence from the tomato RBPK small subunit gene, which encodes a transit peptide that directs choline oxidase to the chloroplast, where choline, the substrate for glycine betaine synthesis, is most accessible to choline oxidase. With this construction, tobacco plants were transformed and the physiological and biochemical changes of transgenes under the influence of NaCl and Na₂SO₄ were studied. It was shown that plants with *codA* expression were more resistant, compared to the control, that is, non-transgenic plants, having better physiological and biochemical indicators, as well as a better developed root system and stems [Raldugina et al., 2019].

With the help of qRT-PCR, the expression of the genes of nitrate transporters SaNRT2.1, SaNRT2.5, SaNRT3 and anion channels SaSLAH1.1, SaSLAH1.2 in the halophyte *Suaeda altissima* at different concentrations of NaCl (0 mM, 250 mM and 750 mM) and nitrate (15 mM and 0.75 mM) in the medium. Primers for qRT-PCR were selected for private cDNA sequences lying in the middle of the coding regions of the indicated genes. Amplification of partial sequences was carried out based on the affinity of SaNRT2.1, SaNRT2.5, SaNRT3, SaSLAH1.1 and SaSLAH1.2 with their homologues from the halophytes *Suaeda fruticosa* and *Suaeda glauca* - closely related species of *Suaeda altissima*. Nucleotide sequences of homologues from *Suaeda fruticosa* and *Suaeda glauca* were determined by in silico analysis of de novo transcripts of these

halophytes. Arrays of short RNA reads for the assembly of transcriptomes were taken from the SRA (DNA and RNA Sequence Read Archive, NCBI) database. The expression of these genes was organ-specific and changed characteristically for each gene in response to changes in NaCl and nitrate concentrations in the medium [Shuvalov et al., 2019].

Among the genes that are more than 5-fold upregulated under salt stress belong to the AP2-EREBP family (ATERF11, CBF4 / DREB1D, CBF1 / DREB1B, ATERF4 / RAP2.5, DREB2A, CBF1 / DREB1B, DREB2A and ATERF11), Basic-Helix-Loop-Helix (bHLH) families (AtbHLH17), Basic region leucine zipper family (AtbZIP55 / GBF3), C₂H₂ family (ZAT10, ZAT12 / RHL41, ZAT6 and ZAT102 / RHL41), Heat stress family (ATHSFA1E), Homeobox family (ATHB-7), NAC family (ANAC036 , ANAC029 / ATNAP, ANAC055 / ATNAC3, ANAC047, ANAC072 / RD26, ANAC002 / ATAF1, ANAC019 and ANAC032) and the WRKY family (WRKY, ATWRKY40 and ATWRKY33) [Lee et al., 2008].

A multi-stage scheme of cell selection of spring red for resistance to chloride salinity has been developed, which makes it possible to select cell lines and regenerative plants resistant to the negative effects of the stress factor. It was established that 1.5% concentration of NaCl in the nutrient medium is the limit for conducting *in vitro* selection of spring ryegrass. The share of cell structures obtained from the explant of the Stepovy 1 variety that retained viability at the specified salinity level was 5.9%, Peremoha - 8.4%, Euro 12 and Klondike - 0.8% of the initial amount of biomaterial. Long-term cultivation of spring red cell lines caused a decrease in regeneration capacity. A total of 381 regenerating plants were obtained, of which 39.9% were in the presence of NaCl. The content of sodium chloride in the regeneration medium reduced the yield of plants by 45.4% on average by genotype. During the transition from the cellular level to the level of the whole plant, 58.8% of the studied genotypes retained resistance to the selective factor. In the plant material induced on the regeneration media of the

control variant, the preservation is 41.5%, obtained under the action of NaCl - increases to 84.9%. A total of 224 plant lines resistant to chloride salinity at the intact plant level were identified [Lyubchenko et al., 2019, Lyubchenko, 2020].

The study of the influence of chloride and sulfate salinity on the induction and proliferation of callus revealed differences in sensitivity between varieties against different types of salts. As a result of cell selection for salinity resistance on tetraploid and hexaploid wheat varieties, stable cell lines and regenerative plants were obtained [Dias, 1994].

The regularities of *in vitro* formation of stress-resistant cell lines and regenerants of spring durum wheat on selective media containing osmotic components were studied. A comprehensive physiological assessment of the reaction of the obtained somaclonal lines in terms of resistance to excess salinity and osmotic stress was carried out [Bychkova, 2018].

As a result of the conducted studies, the principle possibility of adaptation of callus cultures of cultivated soybean (*Glycine max*) against osmotic stress during passage on a nutrient medium with an increased concentration of NaCl has been shown. The adaptation scheme used in the research made it possible to increase the value of the growth index during the breeding process. On the nutrient medium containing NaCl at a concentration of 0.2% in the first and second passages, the value of the growth index increased slightly relative to the control - from 83.4% to 84.3%, respectively. At the same time, the value of the growth index increased from 35.3% to 80.1% during the first, second and third passages on the nutrient medium containing NaCl at a concentration of 0.5%. The established dependence may indicate the successful use of the stepwise selection method in the production of *Glycine max* callus cultures. Resistant to osmotic stress [Bugara, Yunusova, 2016].

With the use of a selective system with sodium chloride, direct and stepwise *in vitro* selection was carried out, selection of winter triticale callus lines resistant to simulated salt stress was carried out. In the 38/1296 line and the Aubrii variety,

5 and 4 resistant callus lines were isolated, respectively, which had a high level of survival on a selective medium with a 1.2% NaCl content and preserved morphogenetic potential. Regenerative plants were obtained from resistant cultures, their growth, rooting and transfer to *in vivo* conditions were optimized. Seed generation R1 was obtained from induced regenerants, and its resistance to simulated salt stress was analyzed [Pykalo, Dubrovna, 2017]. Research on the production of salinity-resistant genotypes of triticale by biotechnological methods is extremely limited, so there are only isolated works on the selection of *in vitro* salt-resistant forms in the literature [Cheng-he et al., 1986, Wang, 1998, Sudyova et al., 2002].

For obtaining regenerating plants of wheat. and specifically, somaclones use immature embryos more effectively. When evaluating the resistance of genotypes against various stress factors, in particular heavy metals, moisture deficiency, excess salinity, etc., it is possible to use mature embryos, where the formation of any morphogenic lines already indicates the stability of the genotype [Bychkova et al., 2016].

The analysis of photomorphogenesis processes in calli of different ploidy levels of winter wheat species *Triticum monococcum* L. (Au), *Triticum polonicum* L. var. *villosum* (AuB) and *Triticum aestivum* L. (AuBD), obtained from immature and mature embryos at two levels of auxin. The photosynthetic activity of callus tissues was investigated in the dynamics of *in vitro* cultivation on the medium for proliferation both under optimal conditions and under conditions of edaphic stress (salinity - NaCl, 0.63% and drought - PEG-6000, 16% wt./vol). Cytological analysis of tissues of calluses formed under conditions of osmotic stress revealed the presence of degenerative processes of photomorphogenic tissues: first, pronounced plasmolysis of vacuolated cells, which determine the biological mass of calluses and a decrease in the number of these cells in the structure of calluse tissue, and then - plasmolysis of meristematically active cells, as well as destruction chlorophyll-containing areas and tracheo-like structures, especially in less resistant forms. In general, the

results of evaluating the photosynthetic activity of plant tissues recorded *in vitro* culture allow for a more specific analysis of the dynamics of photosynthetic activity of various types of wheat under normal and stressful conditions at different levels of plant organization [Terletsckaya et al., 2016, 2018].

It was established that one of the mechanisms of adaptation to stressful conditions is the growth of genetic instability and, accordingly, the expansion of genetic diversity, which in specific conditions manifests itself at the level of the cell population. During cell selection, multiple point mutations or deletions can occur, specifically, in the binding sites with primers to LTR repeats of the retrotransposon Cassandra, which lead to the disappearance of individual amplicons in the spectra of amplification products [Zinchenko et al., 2013].

Salinity tolerance of plants can be increased as a result of *in vitro* selection against one salinity factor - osmotic stress. For example, tomato cells adapted against water stress induced by PEG-6000 were resistant to NaCl. Increased salt tolerance was found in carrot cell lines selected on a medium containing minitol as an osmotic agent at a high concentration (99-870 mM). It follows from the given results that the adaptation of cells against osmotic stress is also used for the selection of salt-tolerant variants, and research of this kind arouses interest for studying them both in interaction and independently of each other [Butenko, 1999].

Somaclonal variability is very well manifested in the cellular selection of plants, in connection with the use of abiotic and biotic factors as a selective agent. For example, as a result of cell selection *in vitro*, regenerative plants of Brassica juncea were obtained that were resistant to salinity [Jain et al., 1990, Kirti et al., 1991]. However, salt-tolerant Brassica plants were obtained by overexpression of the AtNHX1-antiporter Na⁺/H⁺ from Arabidopsis thaliana [Zhang et al., 2001].

Using the developed methods of direct regeneration of plants from explants, a series of experiments on agrobacterial transformation was carried out using a genetic construct with a proline synthesis gene (pyrroline-5-carboxylate

synthetase (P5KS) cDNA from *Medicago truncatula*, located under the control of the 35S promoter of the cauliflower mosaic virus; except moreover, the structure contains the neomycin phosphotransferase II gene). Optimal concentrations of agrobacterial suspensions, exposure of cocultivation after treatment with agrobacteria were selected [Syutykova et al., 2008].

At the moment, genetic engineering methods have already obtained and brought to field trials a significant number of different transgenic varieties, which are characterized by resistance to adverse environmental factors. For example, corn and soybean varieties resistant to drought, cold, and salinity were created [Warwick et al., 2009].

In parallel cultivation of transgenic and non-transgenic lines of *Agapanthus L'Hér.*, similar somaclonal variations were noted using the *gusA* reporter gene as an example [Mori et al., 2007]. The degree of somaclonal variability in transgenic plants can be correlated with the stress caused by tissue culture [Sala et al., 2000; Labra et al., 2001].

It is known that proline biosynthesis occurs as a result of such abiotic stresses as salt and drought [Molinari et al., 2004; Zhu et al., 2005]. Tobacco plants were obtained [Kishor et al., 1995; Hong et al., 2000], rice [Zhu et al., 1998; Su et al., 2004] and *Arabidopsis* [Nanjo et al., 1999; Ma et al., 2008], which overexpress the P5CS enzyme, and showed resistance against salt stress.

As is known, the change in proline content in plant cells correlates with salinity resistance. The work used a genetic engineering construct created on the basis of the binary vector pBI101 with a conserved fragment of the proline dehydrogenase gene from *Arabidopsis thaliana* in the antisense orientation under the control of the 35S promoter of the cauliflower mosaic virus and the selective NPTII gene that gives plants resistance to kanamycin. In the selected transgenic lines under salt stress (1% and 2% NaCl), which continued for 7 days, the content of free proline was approximately 2 times higher, compared to the control plants. And in the absence of stress, the level of proline in both transgenic and non-

transgenic plants was approximately the same. A conclusion was made about the effectiveness of the selection of transgenic plants on a medium containing 2% NaCl, than in the presence of kanamycin, which allows to exclude the gene for resistance to kanamycin [Danilova et al., 2008].

It is assumed that proline performs quite a number of functions in the plant cell, taking an active part in providing a response to various stress factors of the environment, since its level increases in response to drought, salinity, an increase or decrease in temperature, the toxic effect of heavy metals, various infections, deficiency nutrients, atmospheric pollution, ultraviolet radiation, etc. [Kolodyazhnaya et al., 2008, Grygoryuk et al., 2020, Kovbasenko, 2021, Kovbasenko et al., 2021, 2021a].

Currently, one of the approaches to creating forms of plants with increased salt tolerance is transformation with genes that encode proteins of various ion transporters, for example, H⁺-ATP, H⁺-pyrophosphatase, Na⁺/H⁺-antiporter. Transgenic tobacco plants were obtained, expressing the membrane H⁺-pyrophosphatase gene of *Rhodospirillum rubrum* (RPP) under the control of the 35S promoter. As a result of the research, it was noted that the beginning of the flowering phase in transgenic plants occurred 7-8 days earlier than in control plants. A comparison of the obtained seed material showed that the number of seed pods on transgenic plants was 2 times more compared to control, and the number and weight of seed material in transgenic plants was more than one and a half times more, respectively. Chlorophyll content in the leaves of control and transgenic plants was also determined. The experiment showed that the amount of chlorophyll in the leaves of transgenic plants is more than 1.5 times higher than in control plants. The obtained results may indicate that the expression of the membrane H⁺-pyrophosphatase gene of *Rhodospirillum rubrum* not only increases the salt tolerance of plants. but also has a stimulating effect on their biological productivity [Dyakova, Rakityn, 2008].

The presence of genetic control of the salt tolerance trait in higher plants has already been proven for rice, wheat, barley, and rye [Schachtman et al., 1982, Foster et al., 1995]. It was also established that the expression of the Fe-superoxide dismutase gene leads to an increase in the resistance of transgenic tomato plants against salt stress and ultraviolet irradiation [Nodelman, 2013]. Screening for salinity resistance of cultivated and wild tomato species was carried out *in vitro* using stem apices [Cano et al., 1998].

At the same time, the prevailing opinion is that this trait is polygenic and is controlled by at least three genes in barley plants [Koval, Koval, 1996]. There is information in the literature that the main biotechnological method of creating tolerant strains is so far only somacolonial variability [Nabors et al., 1974, 1980, Orton, 1980].

Thellungiella salsuginea (known as halophilla) has a small genome, which is 92% homologous to the *Arabidopsis* genome, a short life cycle, a significant number of seeds, is self-pollinating and can be quite easily transformed by soaking the inflorescences into a suspension of agrobacteria. The ability of this plant to grow in areas with both low temperatures and soil salinity makes it unique for studying resistance mechanisms common to these stresses. In conditions of cold stress, the aerial part of plants is mainly affected by the damaging effect of low temperature, while in conditions of salinity, the root system is first exposed to the toxic effect of salts. And as the salt stress develops, the above-ground part of the plants is adversely affected by the accumulation of salts. In this regard, it was predicted that photosynthetic stems of *Thellungiella salsuginea* can make a significant contribution to the adaptation of this plant against high concentrations of NaCl and Na₂SO₄. To test this prediction, stems obtained by *in vitro* clonal micropropagation technologies were used. Two ecotypes were chosen as objects - Saratov and Yakutsk. The seeds of this plant were selected in the natural places of vegetation of these plants. Researches were carried out in sterile conditions. *Thellungiella salsuginea* seeds were germinated on an agar medium according to

Murashige and Skoog (MS). To initiate the growth of adventitious stems after 25-30 days, plants grown from seeds without leaves and roots were transplanted onto an agar medium containing vitamins, 2% sucrose, 0.025 mg/l 6-BAP and 0.1 mg/l IMC. After three passages, when plants adapted to *in vitro* conditions, cuttings (without roots and leaves) were planted on MS medium (1/2 concentration of mineral salts) containing 2% sucrose, 0.1 mg/l IMC (control option) and salt concentration (NaCl — 100, 200, 300, 500, 600, 700 mM; Na₂SO₄ — 10, 25, 50, 75, 100, 200 mM). After 30 days of cultivation, the accumulation of raw biological mass of the aerial part, the formation of roots, and the content of Na⁺ and K⁺ ions were determined. A decrease in the accumulation of biological mass was observed with increasing NaCl concentration. Suppression of the growth of stems under sulfate salinity was noted in the Yakutsk ecotype, while in the Saratov ecotype at 10 and 25 mM Na₂SO₄ the increase in biological mass increased. In contrast to the stems, the process of root formation in salinity conditions was sharply inhibited. The roots of the two studied ecotypes were practically not formed already at 50 mM Na₂SO₄. With chloride salinization, there were no roots in the Saratov ecotype already at 200 mM, and in the Yakutsk ecotype, starting from 300 mM. However, the absence of roots did not always have a significant effect on the accumulation of biological mass of the above-ground part of plants. The absence of roots in the Yakutsk ecotype at 300 and 500 mM NaCl led to a decrease in biological mass by only 16 and 20%, respectively, compared to 200 mM NaCl. In the Saratov ecotype, inhibition of root formation at concentrations of 200 and 300 mM NaCl, compared to 100 mM NaCl caused a decrease of only 9% and 5%, respectively. The absence of roots at 50 mM Na₂SO₄ reduced the growth of stems in the Yakutsk ecotype by 35%, and in the Saratov ecotype by 37%, compared to 25 mM Na₂SO₄. High concentrations of NaCl and Na₂SO₄ increased the concentration of sodium ions in the stems of both ecotypes, but the content of potassium ions remained at the level of the control variants. Thus, photosynthetic stems of *Thellungiella salsuginea* at high concentrations of salts,

to a greater extent chloride salinity, under *in vitro* conditions, have a defense system and can support growth in the absence of roots. The ambiguity of the effect of NaCl and Na₂SO₄ on the process of root formation implies the need to use different types of salinity when studying the mechanisms of plant salt tolerance [Ovchinnikova, Leonova, 2008].

Among the known signaling pathways in eucaryotic organisms, the TOR (Target of Rapamycin) signaling system is a central component of the perception and transduction of exogenous environmental signals and coordinates the growth of cells and the whole organism. The key element of the TOR signaling system is the TOR kinase [Bersimbaev, Kravchenko, 2016]. In *Arabidopsis thaliana* mutant lines with overexpression of the TOR gene and RNAi lines with reduced expression, it was found that the level of TOR gene transcripts is positively correlated with plant size and its resistance to salt stress [Deprost et al., 2007].

The common wheat salt tolerance gene regulates the K—Na balance and is localized in the D genome. A new source of K\Na⁺ allocation, which creates salt tolerance of durum wheat line 149 in *Triticum monococcum* C68-101, and a QTL of low concentration of monovalent sodium ions in leaves were discovered, NaCl, in chromosome 2AL. The wheat chromosome 2AL and rice chromosome 4L genes had good overall collinearity, but reversed sequence in the chromosomal segment that includes the NaCl locus. In chromosome 2AL, 2 putative Na-transporter genes were mapped. The TtNKT7-A1 gene was polymorphic between salt-tolerant and sensitive lines and was cleaved compatible with Nax1. The TmHKT7-1S gene was localized in the same VAS ~145 t. n., as well as TtNKT7-A1. Both genes had 83% amino acid identity, but only the TtNKT7-A2 gene was expressed in the roots and sheaths of the salt-tolerant line 149, corresponding to the physiological role of NaCl in reducing the concentration of sodium ions in the leaf plates with retention of the same ions in the sheaths. The TtNKT7-A2 gene can control the unloading of Na⁺ from the xylem in roots and sheaths [Shannon, 1997].

A sign of K^+/Na^+ differentiation promotes the growth of salinity tolerance in soft wheat compared to hard wheat and is present in the genome of *Aegilops tauschii*. Evaluation of this indicator in parental forms and synthetic hexaploid lines obtained from crossing durum wheat with the indicated *egilops* revealed a lower K^+/Na^+ indicator in parental forms of durum wheat compared to elite synthetics, which indicates the presence of this trait in the latter and demonstrates successful transfer it with the genome of *Egilopsis* into synthetic hexaploids. The most productive synthetics had the same K^+/Na^+ ratios as the saline control S24. Highly reliable correlations between K^+/Na^+ differentiation and raw plant weight in the studied set of genotypes were also found. In the backcross program of the best synthetics with the drought-resistant *Opata* variety, reliable differences of the studied indicator from that of the recurrent parent were revealed. A fairly high selection potential of two synthetic lines, tolerant to lodging under irrigation and many biotic stresses, is noted [Pritchard et al., 2002].

Genetic analysis of cleavage in the progeny of wheat varieties with different salinity tolerance 1:2:1 showed that this trait is determined by one large gene. 520 primers were used for the amplification of gene pools of both parental forms, of which only one OPZ09 determined the polymorphism of 590 p. n. in parents and F1 and F2 populations. The specific fragment OPZ09-590 is a RAPD marker. Grafted with a salt tolerance gene [Weng Yue-Jin, Chen Dao-Ming, 2002].

Currently, there are a number of works on obtaining salt-resistant lines of cultivated plants by methods of cell selection. Most studies have been conducted on the selection of chlorine-resistant lines of agricultural crops: spring wheat, sorghum, oats, rice, sugar beet, cotton, castor, rapeseed, sugar cane, tomatoes, carrots, tobacco, etc. [Liu, Yeh, 1982, Nabors et al., 1982, Bhaskaran et al., 1983, Rodriguez et al., 1986, McHughen, 1987, Butenko et al., 1988, Jeschke, Wolf, 1988, Kishor, 1989, Rahman, Kaul, 1989].

CHAPTER 7. ECOLOGICAL MANAGEMENT OF INFLUENCE OF GROWTH REGULATORS

An effective method of increasing plant stress resistance is the use of phytohormones. There are three variants of hormonal influence - before the onset of the stressor (pre-adaptation, priming), simultaneously with the onset of the stressor (stress period) and after the stressor (recovery stage) [Danilova et al., 2018, 2019].

Induced mutagenesis has long been widely used in genetics and breeding to obtain true mutants. One of the reasons for the genetic diversity of cultured cells is a violation of their hormonal balance. This can lead to a change in the kinetics of the cell cycle, possibly mitosis, as a result of which cells with a different number of chromosomes appear. The cytogenetic structure of cell populations largely depends on the ratio of phytohormones that regulate cellular and tissue homeostasis. Cultivation of cells on artificial media containing, as a rule, exogenous phytohormones significantly disrupts the hormonal balance, as a result of which morphological and cytogenetic diversity of cell populations may occur. The use of different phytohormones at different stages of the microevolution of cell populations (primary culture, formation of a strain, and maintenance of the formed strain) can have different effects on the cytogenetic features of cultured cells. The effects of different synthetic and natural phytohormones can differ significantly. The genetic composition of cells cultured *in vitro* can also be influenced by other components of the nutrient medium: individual mineral elements, sugars, vitamins, yeast extract, coconut milk, etc., as well as the culture regime [Timofeeva, 2006]. The basis of morphogenesis is cytodifferentiation, which can be defined as the selection by cells of one of the many programs specified by the genotype of a given organism. The implementation of the cell differentiation program in the induction of callus tissue

is largely determined by the content of physiologically active substances (phytohormones, enzymes, structural proteins, etc.) in the cell [Gaponenko, 1987].

Against the background of salinity, the depression of plant growth is caused by a decrease in the content of gibberellin-type growth stimulants in the tissues, which leads to inhibition of the processes of cell division and stretching [Orton, 1980; Synelnikova, 1981].

The optimal selective nutrient medium according to the Hamburg recipe with a sorbitol content of 0.45 M at pH 3.5 and BAP-0.2 mg/l was found, where seed germination from 15.0% to 22.7% was observed in all sugar beet genotypes and was maintained regenerative capacity of seedlings. Their repeated cultivation under selective conditions showed a high tolerance against drought and soil acidity, and the number of resistant regenerants varied from 58.0% to 73.5% [Cherkasova et al., 2019].

The protective effect of jasmonic acid under the action of salinity (100 mM NaCl) was evaluated. The research was carried out on potato plants (*Solanum tuberosum* L.) of the mid-ripening Luhivska variety. Regenerative plants were budded and cultivated in test tubes on a modified MC nutrient medium in the absence (control) and in the presence of jasmonic acid in concentrations of 0.001; 0.1 and 10 μ M under optimal growing conditions or with the addition of sodium chloride. After 28 days of cultivation, growth (stem length, root length, number of tiers and leaves, plant mass) and physiological (proline content and photosynthetic pigments, determination of osmotic potential of cellular exudate) plant characteristics were evaluated. At the same time, it was shown that jasmonic acid (0.1 and 10 μ M) exhibits a pronounced protective effect on potato plants under conditions of salt stress. The protective effect is manifested in the partial removal of the negative effect of NaCl on the main photosynthetic pigments and the maintenance of the osmotic status of the cellular content during salinization [Efimova et al., 2019]. It was established that *Arabidopsis det2* plants,

characterized by a reduced endogenous content of brassinosteroids, are characterized by a higher sensitivity against salinity, compared to wild-type plants [Zeng et al., 2010]. An assessment of the salt tolerance of test-tube plants-regenerants of Luhivska medium-ripening potatoes against chloride salinity was carried out, based on the daily dynamics of morphological and physiological indicators. At the same time, the protective effect of jasmonic acid was demonstrated, significantly reducing the inhibitory effect of salt on the growth and development of potato plants in vitro [Mukhamatdinova et al., 2019].

It was shown that exogenous epibrassinolide at intensive salinization significantly stabilized some physiological indicators - the content of photosynthetic pigments, proline, soluble phenols and the level of osmotic potential. The identified changes ultimately contributed to reducing the negative impact of salinity on the photosynthetic apparatus and plant growth [Efimova et al., 2013].

The obtained experimental results indicate that the transcription factor MYC2/JIN1 takes part in the induction of the antioxidant system by jasmonic acid, and quite likely, in other reactions necessary to maintain the cellular homeostasis of plants under conditions of salt stress. At the same time, the greatest effect of jasmonic acid on the activity of antioxidant enzymes and the content of photosynthetic pigments under salt stress was also manifested in *jin1* mutant lines, which indicates the presence of alternative signaling pathways not related to the MYC2/JIN1 transcription factor, with the help of which the protective effect of exogenous jasmonic acid [Yastreba et al., 2015]. Similar results were obtained by other researchers [Shakirova et al., 2013; Avalbaev et al., 2016; De Ollas et al., 2016].

The activities of glucose-6-phosphate dehydrogenase (GL-6-F-DH), proline and nuclear characteristics of the cells of the apical meristem of the roots are supposed to be used as ecological and biochemical markers of adaptation against salt stress of flowering weigela (*Weigela florida* Bunge A.DC.

"variegata") . The specific activity of GL-6-F-DH under the influence of sodium chloride decreased by 2.5 times compared to the control in the first passage, and under the influence of copper chloride - by 3.7 times, and by the end of the adaptation period, it was restored to the level of control values. Salinity conditions caused by sodium chloride in the first passage led to a 1.4-fold increase in peroxidase activity, and pollution conditions caused by copper chloride - by 1.9 times. By the end of the experiment, the activity of peroxidase in the experimental and control plants was equal. All this indicates the formation of microclones of weigela flowering adaptation mechanisms against the increased content of sodium and copper chlorides in in vitro culture [Voronina, 2020].

Free proline under stress has a multifunctional biological effect, which manifests itself not only in osmoregulatory, but also in antioxidant, energetic and other functions that ensure the maintenance of cellular homeostasis and its transition to a new adaptive state [Kuznetsov, Shevyakova, 1999]. Variants with salinity differed in the maximum content of proline in the above-ground organs of seeded oats, especially on soil with a neutral pH, which indicates the osmoregulatory role of this amino acid [Ustinova, 2019]. In most cases, the phenomenon of proline accumulation is associated with resistance to stress. This is confirmed by the better adaptation and survival of proline-accumulating species in conditions of water deficit and salinity [Franko, Melo, 2000].

Based on the information about the high degree of homology of cereal lectins, it is assumed that wheat germ agglutinin (WAG) can exert a growth-stimulating and protective effect on the division of root cells of rice and barley seedlings. It was found that treatment with 1 mg/l of AZP led to the activation of the mitotic index of the apical meristoma of the roots of both species. A comparative analysis of the balance of phytohormones, treated and untreated AZP plant roots showed that wheat lectin causes similar changes in the state of the hormonal system, associated with the sequential accumulation of ABA, IOC and cytokinins. Pre-treatment of rice and barley seedlings for 24 hours with AZP

revealed a protective effect on the mitotic index of cells under conditions of 7-hour salinity. The seedlings pre-treated with AZP and exposed to short-term salinity were characterized by a significantly lower level of stress-induced accumulation of ABA and the content of growth activator hormones - IOK and cytokinin at a level close to the control. Treatment of rice and barley seedlings with AZP immediately after exposure to 2% NaCl contributed to the acceleration of the recovery of the mitotic activity of the cells of the tips of the roots of rice and barley to almost the same extent as that of wheat. Acceleration of the repair of growth processes under the influence of AZP is due to the accelerated accumulation of IOK and cytokinins in experimental plants. Thus, the ability of AZP to actively affect the state of the hormonal system before the action of salinity and in the post-stress period makes a rather important contribution to the realization of its re-regulating and anti-stress effect not only on wheat plants, but also on other cereals [Bezrukova et al., 2007]. The detected effect of AZP probably contributes to strengthening the barrier properties of cell walls and reducing the level of toxic effects of NaCl on AZP pre-treated plants [Lubyanova et al., 2008]. Blue light had the strongest effect on the activity of soluble lectins under salinity conditions: an increase of up to 174% was observed. Red light had the same effect on cell wall lectins - the activity increased and was 122% of the control level. It is likely that the growth of lectin activity under the influence of different spectral composition under salinity occurs both due to the regulation of lectin accumulation and, to a greater extent, due to the acceleration of the maturation of its precursors, that is, at the post-translational level [Yakushenkova et al., 2013].

Установлено, що NaCl в усіх дослідних варіантах призводить до зменшення маси проростків рису сорту Лиман та довжини їхніх осьових органів. Під дією солі спостерігалось зниження оводненості тканин коренів. У стеблах зниження оводненості було не значним, порівняно із контролем. А у проростках рису, насіння яких було оброблене Агатом-25К, оводненість

тканин в умовах засолення була вищою, ніж у проростках, вирощених у тих же умовах, але без обробки препаратом. Під дією засолення спостерігалися ультраструктурні зміни ядра, мітохондрій, ендоплазматичного ретикулума, апарата Гольджі. Характер та ступінь цих змін залежали від концентрації хлориду натрію. Так, при середньому та сильному рівні засолення спостерігалось помітне зростання ядерця; кристи мітохондрій мали розширені внутрішньокристинні проміжки, знижувалося число рибосом на мембранах гранулярного ендоплазматичного ретикулума і при цьому виявили розширення його каналів, відмічалися випадки порушення цілісності мембран. Усе це може свідчити про суттєве порушення метаболічних процесів у клітинах. Обробка насіння Агатом-25К призводила до значного відновлення тканин та клітинних органоїдів в умовах засолення. Під дією Агата-25К відновлення мітотичної активності у проростаючому насінні рису відбувається швидше, ніж у варіантах із засоленням. Використання Агата-25К у контрольному варіанті досліду не викликало змін активності пероксидази та вмісту проліну. А при дії NaCl зростав вміст вільного проліну у коренях та стеблах проростків рису. Крім того, відмічено зростання активності пероксидази. Із зростанням концентрації солі рівень проліну та активність пероксидази також зростали. Попередня обробка насіння Агатом-25К знижувала активність фермента в умовах підвищеного вмісту хлориду натрію у середовищі та зменшувала концентрацію проліну у тканинах проростків. При цьому необхідно відмітити, що при слабкому та середньому рівнях засолення активність пероксидази під впливом Агату-25К знижувалася у більшій мірі, ніж при сильному. А конкретно, при засоленні 0,1 М і 0,15 М зниження активності фермента відбулося на 30% і 25%, відповідно, у той же час як при рівні засолення 0,2 М цей показник склав усього 10%. У цьому ж варіанті досліду спостерігалось і найменше зниження вмісту проліну. Зміна активності пероксидази та концентрації проліну при засоленні у проростках рису є

порушенням метаболічних процесів у клітинах, які виражаються у зниженні показників росту. Ці фізіолого-біохімічні порушення у певній мірі можуть бути нівельовані дією регулятора росту Агат-25К. Проведеними дослідженнями показано, що регулятор росту рослин Агат-25К може виступати як стимулятор росту, що контролює мітоз та впливає на антиоксидантний захист культурних рослин при засоленні [Луценко, Марушко, 2007]. Агат-25К – препарат на основі продуктів метаболізму бактерій *Pseudomonas fluorescens* Н16, містить рослинні біостимулятори, флавоноїди та мікроелементи [Мотовилин и др., 1999]. Біодукс (д.р. – арахідонова кислота) підвищує активність лектинів, ефективність хлорофіл-білкових комплексів та підвищує адаптацію рослин проти стресів [Ямалеев и др., 2014].

It was established that in wheat plants the drug Stifun (extract of plants *Secale cereale* L., preparation form - water-soluble powder) to a certain extent prevents the decrease in the activity of amylases, proteinases and their inhibitors caused by the action of sodium chloride salting and cadmium acetate. It was found that in normal wheat plants and under chloride salinity, the effect of Stifun application is comparable to the effect of epin-extra in terms of the degree of influence on the activity of amylases, proteinases and their inhibitors [Kalimullina, 2019]. It has been shown that the mechanism of the re-regulating effect of stifun is manifested in the increase in the intensity of respiration and cell stretching, along with changes in the levels of ABA and IOC and in the increase in the content of individual forms of cytokinins: isopentenyladenosine, zeatin, zeatin riboside, dihydrozeatin riboside in the roots and dihydrozeatin riboside in the stems. An increase in the number and volume of wheat meristematic cell nuclei under the action of this plant growth regulator was also established, which indicates that it activates rRNA synthesis. The detected changes in the content of individual free amino acids in wheat plants when using stifun indicates an increase in the adaptive potential of plants against stress factors. Stifun has a protective

effect on *Allium fistulosum* plants, which is expressed in the reduction of clastogenic and aneugenic effects of stressors. It was also established that treatment with stifen does not cause changes in the expression activity of the phytochelatin synthase gene PCS1 in rice seedlings, but reduces its level of stressor-induced transcription [Lubyantsev, 2009].

Soil salinization suppresses the growth of glycophytic plants, which include all cultivated plants, reducing their productivity. Due to the aridity of the climate and the use of irrigated agriculture, the areas of saline soils are constantly increasing, which requires the study of the mechanism of the growth-depressing action of salinity and the increase of salt resistance of plants. One of the rather effective ways of increasing the resistance of plants against salinity is the introduction of growth-stimulating bacteria into the rhizosphere of plants [Dodd, Perez-Alfocea, 2012].

It was found that the effect of 2% NaCl on wheat seedlings led to a significant increase in the content of salicylic acid in them, which is not surprising, because salicylic acid is a key mediator of signaling pathways that lead to the activation of the body's defense systems in response to the action of different types of stress factors [Horvath et al., 2007, Smith et al., 2009, Vlot et al., 2009, Dmitriev et al., 2015]. Pre-sowing treatment with salicylic acid leads to a gradual and consistent, within 14 days, growth of the fate of the alternative respiratory pathway in the stems, and the cytochrome pathway in the roots. An increase in the share of alternative respiratory pathways in stems stimulates a decrease in the accumulation of hydrogen peroxide, and as a result, a decrease in the degree of lipid peroxidation [Rakhmatullina, 2007].

It should also be noted that endophytic bacteria are the object of increased interest in order to widely use them in plant breeding [Sturz et al., 1997, Tokala et al., 2002, Mischra et al., 2009, Stajkovic et al., 2009, Rajendran et al., 2012, Korir et al., 2017, Igehon, Babalola, 2018].

At the same time, the same pre-treatment of wheat seeds with suspension culture of *Bacillus subtilis* strain 10-4 (10⁵ CFU/ml) caused an almost two-fold accumulation of salicylic acid in seedlings before stress, which is consistent with the information available in the literature [Savada et al., 2006, Turan et al. al., 2014] and may point in favor of a salicylate-dependent implementation pathway protective action of these bacteria. Indeed, seedlings previously treated with a suspension culture of *Bacillus subtilis* strain 10-4 were characterized by a significantly lower level of stress-induced accumulation of salicylic acid, which is probably a consequence of these bacilli's pre-alarming effect on plants before the subsequent stress through the activation of salicylate-dependent signaling pathways [Lastochkina et al., 2014].

It was found that the effect of 2% NaCl on wheat plants led to a significant accumulation of proline in them, while in seedlings pretreated with *Bacillus subtilis* 10-4 and 10-2 the level of its accumulation was significantly lower, which is a consequence of the pre-adaptive action of these bacilli on plants against the next action of the stressor. In favor of this, indicators show a decrease in the accumulation of malondialdehyde - the end product of lipid peroxidation - in seedlings pre-treated with *Bacillus subtilis* 10-4 and 10-2 strains, compared to untreated wheat seedlings [Lastochkina et al., 2013].

The introduction of auxin-producing (*Pseudomonas mandelii* IB-Ki14) or cytokinin-producing (*Bacillus subtilis* IB-22) bacteria into the wheat rhizosphere reduced the negative effects of salinity. Inoculation with both strains immediately increased plant transpiration, which required an increase in water availability from the roots. In the case of auxin-producing bacteria, the solution to this problem turned out to be a decrease in the water potential of the leaves, which provides an increase in the driving force for raising water, as well as an increase in the mass of roots under the influence of inoculation. In plants treated with cytokinin-producing bacteria, the optimization of the water balance along with the increase in root mass was facilitated by the increase in hydraulic conductivity, which

determined the greater effectiveness of the growth-stimulating effect of these bacteria on plants [Arkhypova et al., 2020].

The conducted studies revealed that the treatment of wheat seedlings with salicylic acid leads to significant changes in the balance of ROS and the activity of antioxidant enzymes, which plays a rather important role in the manifestation of the pre-adaptive and anti-stress effect of this phytohormone on wheat plants against salinity and other toxic silts [Shakirova et al. ., 2013, Maslennikova, Shakirova, 2015, 2015a]. It is assumed that the exogenous treatment of cucumber plants with salicylic acid serves as a protective mechanism for increasing their resistance to salinity, which is confirmed by a decrease in the content of proline and the activity of lipid peroxidation in cotyledons [Abylova, Ramazanova, 2011] and changes the pro-oxidant-antioxidant balance when the environment is salinized. changing the level of lipid peroxidation and the activity of the antioxidant system [Abylova, 2010].

Salicylic acid solutions of 1 mM maximally induced the activity of lipid peroxidation, and 1 mM and 3 mM maximally inhibited the activity of superoxide dismutase during cultivation of isolated cucumber cotyledons for 6 hours. These results are probably related to the fact that salicylic acid increases the amount of hydrogen peroxide not by activating superoxide dismutase, but by inhibiting the activity of enzymes capable of degrading hydrogen peroxide. The obtained results indicate that salicylic acid in concentrations of 0.1 and 1 mM is an inducer of systemic resistance and exhibits a protective effect on cucumber plants in conditions of environmental salinity [Abylova, Khametova, 2008].

Analysis of TADHN gene expression in wheat plants in response to sodium chloride salinization revealed a significant increase in the transcription level of the dehydrin gene, while pretreatment of plants with fluridone reduced, but did not prevent, the stress-induced increase in this indicator. Plants pre-treated with salicylic acid were characterized by a significantly lower level of salinity-induced increase in the expression of the TADHN gene, which may indicate a lower level

of the damaging effect of stress on them. At the same time, fluridone did not prevent, but almost 50% inhibited the stress-induced expression of the TADHN gene in seedlings pretreated with salicylic acid. The obtained results indicate the implementation of both ABA-dependent and alternative ABA pathways of wheat dehydrin gene expression regulation in untreated and pre-treated plants with salicylic acid [Allagulova et al., 2011].

A comparative analysis of the effects of treatment of wheat plants with phytohormones 24-epibrasinolide, 6-benzylaminopurine and salicylic acid, which are characterized by growth-stimulating and anti-stress effects and transcriptional activity of the TADHN dehydrin gene, was carried out. The sensitivity of the studied gene to each of the three phytohormones was revealed, which indicates its possible involvement in the spectrum of protective action of these hormones against various stress interactions. Using fluridone, an inhibitor of the biological synthesis of ABA, it was shown that the transcriptional regulation of the dehydrin gene TADHN in wheat plants is realized through both endogenous ABA-dependent and independent signaling pathways [Klyuchnikova et al., 2012].

It is shown that the basis of the implementation of the regulatory effect of ABA in the formation of plant stress resistance lies in the induction of the expression of numerous ABA-sensitive genes, among which a special place is assigned to the genes of protective proteins, and specifically, dehydrins. Dehydrins belong to LEA (Late Embryogenesis Abundant) proteins of late embryogenesis, which are characterized by high hydrophilicity, thermal stability and the mandatory presence of a conservative 15-link K-segment (EKKGIMEKIKEKLPG) capable of forming an amphiphilic α -helix [Allagulova et al., 2003, Shakirova et al., 2010].

As a result of the analysis of the indicators of the experiment on the influence of the growth regulator on the activity of catalase in plant tissues of corn plants under conditions of salt stress, a positive regulatory effect of Zircon on the investigated indicator was noted. At the same time, a dynamic uniform growth of

the activity of the catalase enzyme was revealed during the entire time period under investigation. The activity of the enzyme when adding a growth stimulator in all variants of the experiment, compared to the control and variants of saline solutions, was reduced during the entire period of the analyses. Thus, after 5 minutes, the activity of catalase in plant tissues of the aerial part in the 50 mM NaCl option is 22.7% higher than in the Zircon 0.05% + 50 mM NaCl option, and in the 200 mM NaCl option it is increased by 11.3% , compared to the option Zircon 0.05% + 200 mM NaCl. Catalase activity in plant root tissues after 5 minutes of the experiment in the 100 mM NaCl variant is 44% higher than in the Zircon 0.05% + 100 mM NaCl variant, and in the 150 mM NaCl variant it is increased by 28.9%, compared to the Zircon variant 0.05% + 150 mM NaCl [Sobchuk, Chmelyova, 2017]. Similar results were obtained on soybeans - pre-sowing treatment with Zircon leads to the induction of anti-stress mechanisms, thanks to which the resistance of *Glycine max* L. against abiotic stress increases [Chmelyova, Ryzhih, 2017].

As a result of the research, a positive effect of the growth regulator Zircon on the mitotic activity of the cells of the apical meristem of the roots of corn seedlings (*Zea mays* L.) was revealed under conditions of salt stress (50 mM; 100 mM; 150 mM; 200 mM). Pre-soaking of seeds in 0.05% solutions of the studied synthetic growth regulator will stimulate the mitotic activity of the cells of the apical meristem of the roots of corn seedlings, which can be used to enhance the processes of root growth, which will ultimately lead to an increase in their absorptive capacity, and as a result, to increase plant productivity [Chmelyova et al., 2016, Chmelyova, Sobchuk, 2017].

Zircon stimulates the growth of the assimilation surface of leaves and provides them with photosynthetic pigments [Seregina, 2008, Naumenko, 2010].

We established the influence of salinity on the change in peroxidase activity in tomato plant seedlings under the influence of signaling molecules (Table 5).

Table 5. Effect of salinity on peroxidase activity in tomato plant seedlings

Options research	Enzyme activity, in mg-eq/min.:	
	in 24 hours	in 48 hours
Control, distilled water	11.51 ± 0.22	11.49 ± 0.23
100 mM NaCl	14.23 ± 0.34	14.37 ± 0.32
100 mM NaCl + 1.0 µM jasmonic acid	17.45 ± 0.31	17.49 ± 0.30
100 mM NaCl + 5.0 µM jasmonic acid	18.67 ± 0.42	18.78 ± 0.41
100 mM NaCl + 10.0 µM salicylic acid	17.22 ± 0.22	17.26 ± 0.30
100 mM NaCl + 50.0 µM salicylic acid	17.98 ± 0.12	18.03 ± 0.19
100 mM NaCl + 0.01 µM epine	17.39 ± 0.23	17.44 ± 0.31
100 mM NaCl + 0.05 µM epine	18.58 ± 0.21	18.60 ± 0.32

The choice of effective endophytic strains of bacteria as the basis of drugs to increase the resistance and productivity of cultivated plants should be based on the ability of endophytes to compensate for those plant properties that do not allow the macrosymbiont to form sufficiently high productivity and resistance to stresses, including depending on the effect of specific adverse agroclimatic conditions and anthropogenic environmental factors. The influence of endophytic bacteria on the resistance of plants against moisture deficit and salinity can be characterized by variety-strain specificity. The protective effect of endophytes on plants under the conditions of the specified stress factors is manifested in the improvement of growth indicators, a decrease in the level of accumulation of

malondialdehyde, asorbate and proline in the tissues of inoculated plants, compared to non-inoculated ones [Garypova, 2019].

One of the most important mechanisms used by bacteria of the PGPR group to stimulate plant growth is the reduction of the hormone ethylene, which is produced in plant cells in excessive amounts in response to adverse environmental factors. Rhizosphere bacteria producing 1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase) can reduce the amount of "stress" ethylene synthesized by the plant by deamination of the immediate precursor of ethylene 1-aminocyclopropane-1-carboxylate (ACC). In this regard, one of the urgent tasks of modern biotechnology is the creation, with the help of genetic and genetic engineering approaches, of highly active strains of rhizospheric bacteria capable of oversynthesis of ACC deaminase, and the development of means of their use to stimulate the growth of cultivated plants, as in normal environment, as well as in the presence of biotic and abiotic stress factors. On the basis of the rhizospheric bacteria *Pseudomonas mendocina* and *Pseudomonas putida*, ACC-deaminase-producing strains were created, which increase the resistance of plants against environmental stress factors, such as soil salinization and its contamination with heavy metals [Zhardetskyi et al., 2012].

In the experiments with medium salinity, wheat seedlings not inoculated and treated with the bacterium *Azotobacter* (*Azotobacter vinelandii* ЁБ 4) were transplanted into Petri dishes on a 1% sucrose solution, and in the experiment - on the same medium with an additional 1% NaCl content. In another variant, with the effect of moisture deficit, seedlings were planted on a 10% PEG-6000 solution in a 0.5% sucrose solution, and control seedlings were on a sucrose solution. When the environment was salinized, the inhibition of root growth in non-inoculated plants was approximately 2.5 times stronger than in inoculated ones. Seedlings inoculated with the biological fertilizer Azolen more quickly overcame the short-term effect of a lack of nutrients; the roots of non-inoculated seedlings did not grow even after 48 h of the experiment, while treated seedlings showed

the ability to grow 20 h after stress. Root and coleoptile growth rates of Azolene-treated plants remained higher compared to untreated plants (7.7% and 13.8%, 2.8% and 11%, respectively). Since under the influence of various stress factors plants can include the same signaling pathways and activate the same classes of protective proteins, it becomes clear that the inoculation of plants with the bacterium *Azotobacter vinelandii* ЁБ 4 also increases their resistance to chloride salinization of the environment, as well as to moisture deficiency, simulated by PEG-6000 [Ivanova, 2012].

A liquid form of the complex-acting biological preparation RIZOKOM-2 was created based on an association of three strains of salt-resistant wheat rhizobacteria *Bacillus subtilis*, which possess multifunctional properties (phosphorus and potassium-mobilizing ability, antagonistic activity against wheat phytopathogens, root-forming and growth-stimulating activity). The drug is recommended for pre-sowing treatment of wheat seeds. The physical method of adsorption immobilization was used to prepare the dry preparation form of this biological preparation. Phosphorite flour, kaolin, sand, soil, coal dust and biocompost were used as fillers. The viability and physiological activity of salt-resistant rhizobacteria of wheat stored for three years on sterile media were studied. Phosphorite flour and biocompost were selected as effective carriers. The technological and apparatus schemes and laboratory regulations for obtaining the dry form of the biological preparation RIZOKOM-2 for the cultivation of winter wheat on saline soils have been developed [Zakiryeva, Djumaniyazova, 2015].

The results of the research allow us to conclude that the *Bacillus megaterium* 501 GR strain is sufficiently resistant to high concentrations of NaCl and Na₂SO₄ and can be used for inoculation of plants on soils salted with chloride and sodium sulfate. Conversely, Na₂CO₃ is toxic for this bacillus, which is due to a rather high alkaline reaction of the substrate, and therefore the use of *Bacillus megaterium* 501 GR on sweetened soils has no prospects. Inoculation of corn seeds with a liquid culture of *Bacillus megaterium* 501 GR and the drug Mega-1

reduces salt stress in plants caused by the toxic effect of sodium chloride, increases salt resistance at the initial stages of their development, acting as a growth stimulator, and to some extent as a plant protector [Lysina, Kichko, 2019].

One of the promising ways to solve the problem of soil salinity is the use of new microbial biotechnologies that significantly improve the phosphate regime of the soil, because there is a direct correlation between the degree of soil salinity and the degree of their phosphatization - highly saline soils are simultaneously highly phosphatized [Menyailo et al., 1994]. It was found that strains of bacteria *Bacillus* sp., 80, 83 and 113 help assimilate the applied phosphorus fertilizers. The use of an association of four strains stimulated the root formation of cotton seedlings in variants with phosphoric fertilizers and without the introduction of ampos. This fact indicates an increase in the rate of use of applied phosphorus fertilizers and the possibility of more effective use of soil reserves of insoluble phosphates without the use of phosphorus fertilizers on moderately saline soils. Thus, on the basis of the conducted experiments, it can be asserted that the isolated new salt-resistant strains of phosphate-mobilizing bacteria, which have growth-stimulating and root-forming ability, can be used in the development of new microbial biotechnologies for agriculture [Narbaeva et al., 2008].

The use of biological preparations of complex action Rizokom-1 and Serhosil for growing cotton on saline soils contributed to the improvement of biometric indicators - the development of the root system and the above-ground part of cotton plants is stimulated due to the improvement of root and leaf nutrition with macro- and microelements. Rizokom-1 is created on the basis of salt-resistant rhizobacteria and is used for pre-sowing treatment of seeds, and Serhosil is created on the basis of green microalgae for foliar feeding of plants [Babina, Narbaeva, 2015]. The dry form of the biological preparation Rizokom-2 was developed using the adsorption immobilization method. The viability and physiological activity of salt-resistant wheat rhizobacteria of the genus *Bacillus*, which were stored for 4 years on sterile media, were studied. Phosphorite flour

and biocompost were selected as effective carriers. Technological, equipment schemes and laboratory regulations for obtaining the dry form of the biological preparation Rizokom-2 for growing winter wheat on saline soils were also developed [Zakiryayeva, Djumaniyazova, 2015]. It was established that under conditions of stress, when the access of nutrients is limited, and during salt stress, the production of secreted ribonucleases of the genus *Bacillus* intensifies [Kharitonova et al., 2017].

The introduction of auxin-producing (*Pseudomonas mandelii* IB-Ki14) or cytokinin-producing (*Bacillus subtilis* IB-22) bacteria into the rhizosphere of wheat plants reduced the negative effects of salinity [Arkhylova et al., 2020].

It was established that salicylic acid causes oxidative stress in cucumber seedlings when salinized with sodium ions, revealed by the accumulation of malondialdehyde and the increase in peroxidase activity. A significant increase in the level of one of the key osmoprotectors - proline, which was expressed to a greater extent in the presence of salicylic acid, in all variants of the experiment indicates that sodium and potassium ions cause both osmotic and oxidative stress in seedlings. A negative proportional relationship was found between proline content and superoxide dismutase activity, which was especially pronounced in the presence of salicylic acid. It is likely that the high level of proline and high activity of peroxidase compensated for the low activity of superoxide dismutase during salinization [Abylova, 2010].

The conducted studies indicate the dependence of the effect of salicylic acid solutions on the pH of the medium. Moreover, different growth indicators do not have the same importance for evaluating the effect of salicylic acid. In this regard, the root system and the value of the polarity coefficient turned out to be the most sensitive. The results of the study of the exogenous action of salicylic acid depending on the pH of the solutions, even on one object, have methodological significance for isolating its effect from the influence of the pH of the solutions. The same concentration of salicylic acid at different pH values can be both

stimulating and depressing. These effects require specification when studying the physiological role of salicylic acid on other plants [Abylova, Khametova, 2007].

Numerous scientific studies have shown that salicylic acid helps to increase the resistance of rolin against salinity [Kolupaev et al., 2003, Sakhabutdinova et al., 2003, Ma et al., 2006, Yang, Zhang, 2006, Deef, 2007, Joseph et al. , 2010, Lapa et al., 2011, etc.].

In recent decades, researchers have drawn attention to the possibilities of gibberellic acid [Kaya et al., 2009]. It is known that treatment of tomato plants with gibberellic acid reduces stomatal resistance, which allows plants to use water in salinity [Maggio et al., 2010].

As a result of the conducted experiments, no protective effect of melafen (melamine salt of bis (oxy) methyl phosphinic acid) on the growth of barley seedlings under salt stress conditions was found. However, this does not completely exclude that under other conditions, with plants of a different age of barley or other crops, the protective effect of melafen under the action of high salt concentrations may be detected [Zubkova et al., 2010]. At the same time, it was established that melafen exhibits a membranotropic effect on the energy of mitochondria, and in very low concentrations it changes the physicochemical properties of the lipid bilayer of the membrane, increasing the activity of RNA polymerase 1, affects the expression of the early light-induced protein gene of barley chloroplasts under stress conditions, and also causes melafen-induced tyrosine phosphorylation of proteins of the dark phase of photosynthesis at concentrations of 10^{-8} – 10^{-6} M [Osypenkova et al., 2007, Alekseeva et al., 2009, Karimova, 2010, Kuznetsov et al., 2010]. It was also found that melafen in small doses prevented changes in the fatty acid composition of mitochondria, had a significant effect on microviscosity, the level of lipid peroxidation, activated electron transfer during the oxidation of NAD-dependent substrates, and also changed the structural characteristics of pea plant membranes [Zhygacheva et al., 2014]. The influence of the drug melafen on the increase in the intensity of

photosynthesis and the content of chlorophyll and stimulated cyclic photophosphorylation was also shown. It also induced the intensity of breathing. At the same time, its effect on the third segment of ETC of mitochondria is assumed. An increase in the rate of thermogenesis under the influence of this drug was revealed, which characterizes the efficiency of energy use by cells. It has been shown that using protein synthesis inhibitors, cell growth under the action of this drug is more closely related to protein synthesis on cytoplasmic ribosomes [Kashina, 2007]. It was also established that melafen affects the plastic and energy metabolism of the cell, namely, it increases the efficiency of oxidative phosphorylation, reduces the generation of ROS, which prevents damage to cell membranes and the induction of lipid peroxidation [Zhygacheva et al., 2007, 2010]. It is also significant that the addition of this drug to the culture of chlorella algae cells has a positive effect on the rate of photosynthesis and cell growth [Loseva et al., 2007].

A comparison of the morphological parameters of plants grown in a saline environment showed that in the presence of melafen (10⁻⁸ M - 10⁻¹⁰ M), an increase in stem length, leaf surface area, and hydration of plant leaves was observed, compared to the variant without this drug. The plants were treated in two ways: prior to the introduction of NaCl into the nutrient medium and with the simultaneous introduction of NaCl and melafen into the nutrient medium. The method of application of the drug had a minor effect on the hydration of the leaves. With the simultaneous introduction of NaCl and melafen into the nutrient medium, an increase in stem height and biological weight of plants by 6-7% was noted, compared to the previous introduction of melafen. The effect of this drug was most significantly manifested when comparing indicators of oxidative stress. In conclusion, it is claimed that the drug melafen at a concentration of 10⁻⁹ M contributed to the growth of plants, reducing the level of oxidative stress and survival of calendula plants (*Calendula officinalis* L.) in conditions of increased salinity [Stetsenko, 2015].

It was found that salinization accelerated the lignification of the cell walls of the central cylinder of wheat roots compared to the control, while this process occurred significantly more intensively in the roots of seedlings pretreated with methyl jasmonate. The totality of the obtained results indicates the ability of methyl jasmonate to show a protective effect on plants in conditions of environmental salinity, which is manifested in a significant decrease in the level of the growth-inhibiting effect of sodium chloride in wheat seedlings pretreated with methyl jasmonate [Lastochkina et al., 2010].

In vegetation experiments, it was found that pre-treatment of seeds with 10⁻⁷ M Metiur and Ivin drugs enhanced the salt resistance of corn even in the presence of 0.1 M NaCl, and the effect of Metiur was stronger and persisted throughout the growing season, especially with additional spraying during the transition to generative development. In a field experiment on saline soils, the use of Metiur increased grain yield by 11%. In experiments on seedlings exposed to NaCl, it was found that seed treatment with drugs reduced the level of lipid peroxidation in tissues by activating the antioxidant defense system, and also normalized osmotic homeostasis, enhancing the synthesis of soluble sugars and amino acids. The ability of the drugs, especially Metiura, to maintain the lipid composition, as well as the activity of H⁺-ATPases of the plasmalemma and tonoplast, which contributes to the functioning of their Na⁺/H⁺-antiporters, was demonstrated on membrane preparations. The dependence of the adaptogenic effect of drugs on their structure was also studied, and it was also shown that the presence of side SH in the Metiura molecule determines its antioxidant activity *in vitro*, which is carried out by the antiradical pathway [Palladina, Rybchenko, 2010].

It has been shown that Tebulak (a by-product of potato processing) in a concentration of 0.3-0.5% has an activating effect on the proteinase-inhibitory system of germinating seeds of narrow-leaved lupine and winter rye under salinity conditions. Thus, the activity of neutral proteases in lupine seeds increased by an

average of 50%, compared to the control, and by 36%, compared to the version with 0.1 M NaCl. The increase in the activity of alkaline protease (BAPase) was on average 20% in relation to the variant with salinity. The use of this drug neutralized the effect of the stressor and changed the activity of the investigated proteases in germinating winter rye seeds. Thus, a 0.5% concentration contributed to an increase in the activity of neutral and alkaline proteases by 17.8% and 30% in relation to 0.1 M NaCl. Under stressor conditions, this drug increased the activity of trypsin inhibitors, antioxidant activity, proline content, and accelerated the growth and development of seedlings and 20-day-old plants. Thus, the conducted studies provide a certain contribution to the understanding of the mechanism of action of this drug and show the prospects of its use on crops of agricultural plants to reduce the negative effects of salinity [Domash et al., 2011].

The influence of pretreatment of seeds for one day with 1% solutions of amino acids (methionine, serine, threonine) on the content of photosynthetic pigments in 10-day-old seedlings of winter wheat of the Elegia variety grown under this salinity (150 and 300 mM NaCl) was investigated. Comparing the effect of the tested amino acids with each other, it can be stated that threonine has the greatest protective effect among them: pre-treatment with this amino acid increases the resistance of winter wheat seedlings against subsequent salinization. Moreover, on the second day of exposure to 150 mM NaCl, a significant increase in the content of photosynthetic pigments was recorded, and with increasing exposure in a solution of this concentration up to three days, no significant changes in the content of photosynthetic pigments were detected. Moreover, under the action of NaCl of high concentration (300 mM), the level of the content of photosynthetic pigments did not differ from the control value. In second place in terms of protective properties, you can put the amino acid serine. And the protective effect of methionine was manifested only when exposed to 150 mM NaCl for three days [Yakovets, Zynovych, 2018].

At the same time, it has been shown that ABA is one of the key signaling elements that regulate many aspects of plant growth and development and the regulation of responses to stress, including salinity [Leung, Giraudat, 1998; Rock, 2000; Shinozaki, Yamaguchi-Shinozaki, 2000, Barrero et al., 2005, Batygina et al., 2010, Cutler et al., 2010, Gilmanova et al., 2012, Seldymirova et al., 2017, Kruglova et al., 2018] . In addition to protein phosphatases of the PP2C type, protein phosphatases of other types have been shown to be involved in ABA signal transmission, and the most obvious role was demonstrated for PP2A. Thus, mutations leading to disruption of PP2As activity led to ABA-hypersensitive seed germination, seedling development and root growth, as well as expression of ABA-regulated genes. At the same time, it was found that mutant plants showed increased resistance to salinity and high concentrations of sugars [Pernas et al., 2007]. However, it was established that ABA treatment of Arabidopsis leaves, rice seedlings, or bean roots increased the resistance of these plants against salt stress [Khadri et al., 2006]. In addition, it was found that pre-treatment of plants with 1 μ M ABA under salinity significantly improved their physiological state, which was manifested in an increase in biological mass, a decrease in oxidative stress indicators, unlike plants that experienced a deficiency of the ABA hormone as a result of the action of the herbicide fluridone. It was shown that exogenous ABA affects the quantitative content of putrescine and cadaverine in the leaves of crystal grass (*Mesembryanthemum crystallinum* L.) under salt stress, which indicates the regulatory role of ABA on metabolically active diamines [Stetsenko, 2014]. In the literature, there is also an opinion about the possible involvement of exogenous ABA in callus cultures as a stress agent [Rai et al., 2011].

It was found that in wheat calli, the osmotic stress caused by the action of NaCl salt led to the accumulation of not only sodium and chlorine ions in the cells, but also ABA [Fazeli-nasab et al., 2012], as well as an increase in the content of proline, total soluble carbohydrates, activation of catalase and peroxidase enzymes, synthesis of new proteins, possibly salt shock proteins [Khuder, AL-

Taei, 2015]. Similar results were also obtained in rice calli [Ahmad et al., 2007, Alhasnawi et al., 2017].

ABA has a rather significant effect on the expression of a large number of genes that are involved in the formation of responses to abiotic stressors, the activation of which is extremely necessary for plant adaptation [Ingram, Bartels, 1996; Busk, Pages, 1998; Rock, 2000; Shinozaki, Yamaguchi-Shinozaki, 2000; Xiong et al., 2002, Shevchenko, 2012]. The protein SAD1 (supersensitive to ABA and drought) is one of the subunits of the small ribonucleoprotein complex U6, which takes part in various stages of RNA processing. At the same time, it was clearly shown that the mutation in this gene led to the appearance of hypersensitivity in plants to ABA, drought and salt stress, and also affected the expression of stress response genes, while the expression of ABA biosynthesis and signaling genes changed - AOO3, LOS5, PP2C, ABI1 [Xiong et al., 2001]. All these results made it possible to predict that the SAD1 protein is a rather important negative regulator of the early stages of hormone signaling. As is known, there is a connection between the regulation of gene expression through miRNA and responses to ABA. HYL1 (HYPONASTIC LEAVES 1), is one of the three deacylases in eukaryotes, which takes part in the first stages of mRNA degradation, it has been shown that mutation of the HYL1 gene leads to the formation of negative responses to ABA. Disturbances in LBA1/UPF1 (LOW BETA-AMYLASE 1) are components of nonsense-mediated mRNA degradation, which is a rather important mechanism for removing mRNA with immature stop codons, and also affects the formation of responses to ABA [Yoine et al., 2006].

The obtained indicators of the comparative analysis of the effect of methyl jasmonate and cytokinin BAP on the content of dehydrin and proline proteins in normal conditions and during salinity indicate the involvement of these osmoprotectants in the spectrum of the protective effect of both phytohormones on wheat plants [Avalbaev et al., 2014].

During the action of 24-epibrasinolide on millet seedlings, a decrease in endogenous proline content and an increase in the activity of superoxide dismutase and other antioxidant enzymes were noted. Despite the decrease in proline content in leaves, the salt tolerance of millet plants treated with 24-epibrasinolide was significantly higher than that of control plants. It can be predicted that 24-epibrasinolide induces other stress-protective systems, the functioning of which fully compensates for the lack of proline accumulation. One of them can be the antioxidant system. It is quite natural that this does not exclude the participation of other defense systems in the development of salt tolerance of millet seedlings under the action of 24-epibrasinolide [Vainer et al., 2014]. The comparison of various indicators of the viability of grape cuttings indicates the possibility of using epibrasinolide to reduce the effects of salinity and heavy metals on plants in isolated organs. At the same time, the reaction of cuttings and seedlings to the action of sodium chloride and copper sulfate, as well as the previous treatment with the hormone, turns out to be species- and variety-specific. The possibility of increasing the viability of cuttings, which is observed both under favorable cultivation conditions and under stress, is shown to be of practical importance for hard-to-root tree cuttings [Aliyeva, 2014].

The protective effect of steroid hormones is determined by their chemical structure, effective concentration, lighting conditions, and duration of NaCl action. The lowest protective activity at intensive chloride salinization is shown for 28-homobrasinolide; on day 3.5, the hormone did not change the growth and physiological indicators of seedlings, on day 7 a slight decrease in the negative effect of salt was observed. 24-epicastasterone showed the highest protective effect in case of intensive chloride salinization in white light. The most effective concentration of this hormone was 10^{-7} M. Brassinolide in concentrations of 10^{-9} and 10^{-8} M demonstrated a high protective effect during long-term salting in white light; with a short-term effect of salinity, the use of brassinolide was not effective. The highest protective effect at long-term salinity both in the dark and

in the light is shown for 24-epibrasinolide, regardless of the concentration chosen for the study. The highest protective effect in terms of growth indicators of rapeseed seedlings was noted at concentrations of 10^{-9} and 10^{-7} M. At the same time, the content of all groups of photosynthetic pigments, regardless of hormone concentration, was restored to control values. As a result of the research, it was established that the manifestation of the negative effect of NaCl is characterized not only by the intensity of the salt action, but also depends on the presence or absence of lighting. It was also found that 24-epibrasinolide showed the highest protective effect at intense salinity, followed by brassinolide, 24-epicastasterone, and 28-hombobrasinolide [Efimova et al., 2015]. It was also established that the ketone-containing brassinosteroid 24-epicastasterone had the most pronounced stress-protective effect on rapeseed plants [Kolomeychuk et al., 2019]. Brassinosteroids contribute to the growth of resistance and express adaptation of plants against constantly changing conditions of their vegetation. The action of exogenous 24-epibrasinolide in agrocenosis on plants increases the balance of their growth and development depending on the level of nutrition. The effectiveness of exogenous 24-epibrasinolide increases in conditions of deviation from the optimal supply of plants with nutrients [Voronina, 2008].

The stress-protective effect of pre-treatment of plants of *Solanum tuberosum* L. mid-ripening variety Luhivska and early-ripening variety Zhukovsky early with brassinosteroids under chloride salinity is shown. The protective effect of brassinosteroids was assessed by physiological (osmotic potential of cellular exudate, degree of lipid peroxidation, content of photosynthetic pigments, proline, activity of antioxidant enzymes) indicators. In addition, the relative expression level of a number of stress-regulated genes - proline metabolism, antioxidant enzymes, Na^+/H^+ antiporter, and others in response to the action of exogenous brassinosteroids was determined by real-time PCR. The reason for the decrease in proline content in response to priming with

brassinosteroids was also established, and possible mechanisms of the protective effect of steroid hormones were shown [Murgan et al., 2019].

After treatment of isolated bean leaves with epinome (0.025 ml/l), which were cultivated in 10 mM NaCl, the proline content was determined on the 7th day. The results showed a noticeable decrease in its content under conditions of salinity; when treated with epinome - 0.2 mg/g, and in the control - 0.8 mg/g [Samedova, 2008].

Spraying barley plants at the beginning of the budding or flowering phase with epibrassinolide or homobrassinolide in a concentration of 10-5 mg/l helped to increase the resistance of plants of this crop to salinity [Vokebaeva, 1991]. It is assumed that the effect of brassinosteroids on the resistance of plants to cold and salinity is related to their effect on the structure and functions of membranes [Korableva, Platonova, 1995, Khripach et al., 2003, 2004].

It was shown that exogenous 24-epibrassinolide reduced the negative effect of salinity on growth indicators, the content of photosynthetic pigments, the level of proline, total soluble phenols, including flavonoids, the value of the osmotic potential and the intensity of lipid peroxidation. The hormone showed the strongest protective effect if it acted during or after salt action. It is predicted that the protective effect of 24-epibrassinolide under conditions of salt stress is based on its antioxidant effect, however, it is not due to the hormone-induced accumulation of proline and low molecular weight phenolic compounds [Efimova et al., 2016].

The conducted studies indicate that brassinosteroids showed a pronounced protective effect on rapeseed plants under salinity conditions. At the same time, chloride salinization stimulated the accumulation of analyzed endogenous steroid hormones. The basis of the protective action of brassinosteroids under salt stress is likely to be their ability to prevent the destruction of photosynthetic pigments and stimulate the accumulation of low molecular weight phenolic compounds, while reducing the intensity of oxidative stress. Another, rather unexpected,

ability of brassinosteroids is the restriction of the entry of toxic sodium ions into plant cells and the combined maintenance of an elevated level of potassium ions. It turned out that under these conditions, the introduction of 24-epibrassinolide together with NaCl allowed plants to reduce energy and structural costs for the biological synthesis of proline, which also contributed to the increase in the resistance of rapeseed plants to salinity [Efimova et al., 2015a]. It was established that the regulation of the quantitative level of cytokinins in wheat seedlings by 24-epibrassinolide is made by a change under its influence in the enzymatic activity and expression level of the cytokinin oxidase gene. Treatment with 24-epibrassinolide causes rapid inhibition of enzyme activity and cytokinin oxidase gene expression in roots and then in stems. And stopping treatment with 24-epibrassinolide leads to a gradual recovery of these indicators in the same sequence [Yuldashev, 2009]. The effect of 24-epibrassinolide on the lipoxygenase signaling cascade was also revealed, which was manifested in a change in the content of oxylipins, which are formed from linoleic acid. The effect of 24-epibrassinolide is regulated at the level of lipoxygenases, which catalyze the formation of hydroperoxides of unsaturated fatty acids. It was found that 24-epibrassinolide increases the content of hydrogen peroxide in plant cells, which indicates its activation of the superoxidase signaling system [Fedyna, 2006].

It was shown that short-term pretreatment of potato plants of the Luhivska variety with steroid hormones - 24-epibrassinolide and 28-homobrassinolide induced the transition of plants of this culture to a priming state, which was manifested in their ability to respond to "terminated" salt stress by more effective accumulation of proline and carotenoids, which have pronounced antioxidant and stress-protective properties [Efimova, 2019]. It was found that treatment of Bentham tobacco plants with brassinolide increased their salt tolerance [Zhu et al., 2016].

It was shown that trace elements selenium and zinc, used for pre-sowing treatment of cereal seeds, stimulated protective mechanisms in the plant organism

and reduced the negative effect of abiotic stresses of various nature, in particular, dehydration, salinity, the action of heavy metals and herbicides on the grain productivity of wheat, barley and triticale [Osypova et al., 2014].

A comparative assessment of the effect of selenium (1-100 μM) in the form of sodium selenite (Na_2SeO_3) and nanoparticles (nanoSe) on the content of low molecular weight antioxidants and the activity of catalase and peroxidase enzymes under salt stress was carried out. Interest in the use of nanoSe is due to its possible higher efficiency in the activation of Se-dependent enzymes. Differences in the effectiveness of Na_2SeO_3 and nanoSe in low concentrations on enzymatic activity were not noted either in control or under stress conditions. But Na_2SeO_3 in a higher concentration reduced peroxidase activity during salinization. When using nanoSe, a decrease in peroxidase activity was not noted. At the same time, nanoSe stimulation of catalase activity was detected. It is assumed that nanoSe regulation of antioxidant systems leads to the formation of plant resistance mechanisms against salt stress [Zaprudskaya et al., 2019].

There is also information in the scientific literature, which shows that the introduction of small doses of selenium (0.01% - 0.00001%) under conditions of water and salt stress leads to an increase in the synthesis of proline and an increase in its content in the plants of the eastern gorse, barley and beans [Vykhreva, 2001; 2011; Akbulut, Çakır, 2010; Usubova, 2012]. In another study, treatment of barley plants with selenium under conditions of oxidative stress led to a decrease in the accumulation of proline to the control level and below [Skrypnyk, 2009]. It was also predicted that the decrease in proline content under stress conditions in the presence of selenium is due to the fact that selenium itself induces antioxidant properties, reducing the content of ROS in the middle of the cell. Thus, the participation of proline in the neutralization of ROS is necessary to a lesser extent [Soldatov, Raschyotova, 2013].

In a series of sterile experiments, the influence of the use of selenium as a factor in increasing the resistance of plants against adverse environmental

conditions was studied in terms of its influence on the formation of nitrates in wheat seedlings. In these experiments, the existence of the process of endogenous formation of nitrates during seed germination was established. The conducted studies showed that stressful situations caused by the increase in the content of HH_4Cl and NaCl in the environment increased the intensity of this process. In the same experiment, at an increased concentration of Na_2SO_4 , no additional endogenous formation of nitrates was noted, compared to the control bkz stress, eggs were detected when the environment was salted with chloride salts [Yakovlev, 2014].

In corn ($r = 0.84$) and barley ($r = 0.91$) plants, a correlation was found between the indicators of the net productivity of photosynthesis and the dry matter content of the plants against the background of salinity. This indicates that 6-BAP and ivin against the background of salinity have a significant effect directly on the processes of photosynthesis, rather than on the outflow of assimilates into growing organs, this is especially well expressed in barley plants. Also, the correlation dependence between the indicators of pure photosynthesis and the regenerative activity of chloroplasts increased significantly. The correlation coefficient was the highest in barley plants and was 0.91, which shows the dependence of assimilate utilization processes in growth processes [Zhyzhyna, Kabuzenko, 2013].

The drug 6-BAP showed a significant positive effect on the germination energy of barley and corn seeds on a saline background. Synthetic plant growth regulator ivin showed a strong stimulating effect at the later stage of germination and contributed to the growth of germination of barley and corn seeds on a saline background. At the same time, its significant effect on the mitotic activity of the root meristem of the studied plants is noted. One of the mechanisms of the stimulating effect of ivin on the germination of cereal seeds under salinity conditions is the increase in the mitotic index of the germ meristem [Zhyzhyna, Kabuzenko, 2006]. Suppression of meristem activity by salt was manifested in an

increase in the total time of the cell cycle, which directly depends on the concentration of the salt solution. The duration of the cell cycle in the wheat meristem on the background of a 0.3% NaCl solution increased by 34.4% compared to the control, which depended on the duration of interphase and the initial stage of prophase [Kabuzenko, 1997]. However, there are known facts about the positive influence of substrate salinity on the accumulation of root mass during the slow growth of stems [Yoneva, Petrov-Spiridonov, 1995].

The set of obtained results demonstrates a clear protective effect of pretreatment with sodium nitroprusside - a donor of nitrogen oxide on wheat seedlings against the effects of salt stress, which generally affects the maintenance of their physiological and biochemical processes at a level that is difficult to control. The basis of this effect is the prevention by nitric oxide of sharp stress-induced changes in the state of the hormonal system of wheat plants [Maslennikova et al., 2016]. It is known that when a signal of a biotic or abiotic nature is transmitted in a plant cell, there are changes in the cytosolic concentration of calcium ions and the level of nitric oxide. In the experiment, exogenous NO stimulated the release of calcium ions from cellular depots in the closing cells of the stomata of *Vicia faba* and affected the activity of enzymes, including protein kinases, as well as Ca²⁺-dependent K⁺- and Cl⁻-dependent channels [Garcia-Mata et al., 2003]. The participation of nitric oxide in the reprogramming of the genome of plant cells has also been experimentally confirmed [Besson-Bard et al., 2008, Kolupaev, Karpets, 2009, Krasylenko et al., 2010, Moreau et al., 2010, Kovbasenko et al., 2019]. At the same time, changes in the expression level of many plant genes under the action of NO were shown [Grun et al., 2006]. However, an increase in tyrosine protein nitration was also shown in olive leaves under salt stress conditions [Valderrama et al., 2007].

It was established that an experimental change in the intracellular content of nitric oxide leads to a change in the intracellular content of hydrogen peroxide. Is this effect a consequence of a change in the NO content or can it be related to

the non-specificity of the action of the used modulators. It is still not clear. However, the possibility of the influence of nitric oxide on the level of intracellular hydrogen peroxide is being studied [Molassiotis, Fotopoulos, 2011]. In this regard, it can be argued that NO nitric oxide can be involved in the regulation of the expression of not only the *CYCD3;1* gene, but also the *CDKA1;1* gene, and the regulatory effect of NO on the expression of *CDKA1;1* can be mediated by a change in the redox status of cells [Sibgatullina et al., 2017].

The contribution of NO-dependent modifications to RNA biochemistry remains practically unexplored until now. However, taking into account the mechanism of micellar oxidative nitrosylation, when the place of generation of active modifying agents is hydrophobic phases, including the cores of macromolecules, in the world of nucleic acids namely massive RNAs should be the main targets of these modifications, because in DNA the ratio of the surface to volume is much higher than that of RNA [Beda, Nedospasov, 2007].

Cells of many organs and tissues of higher plants respond to fusicoccin treatment with an increase in volume, which may be associated with its effects such as stomatal opening, cell growth and elongation. One of the most striking hormonal properties of fusicoccin is its anti-stress activity, especially during salinity and temperature changes [Muromtsev et al., 1987].

A promising method of increasing plant resistance to salinity is the use of adaptogens. The influence of para-aminobenzoic acid adaptogen on the resistance of narrow-leaved lupine plants against salt stress was studied. At the same time, an increase in the intensity of growth processes in plants was established, which was associated with a 1.35-1.50 times increase in the number of dividing cells in the meristem of the roots of seedlings. Therefore, the positive effect of the para-aminobenzoic acid adaptogen on the resistance of narrow-leaved lupine plants to salt stress may be associated with the activation of nonspecific mechanisms of resistance to stress [Kunitskaya et al., 2011].

Silicon performs a fairly significant number of functions in the life of plants, and it is especially important in stressful situations. The role of silicon can be compared with the role of secondary organic metabolites that perform protective functions in plants. Looking at the multitude of roles that silicon plays in plants against various stresses, the world scientific opinion recognizes that there is still a long way to go before developing a unified theory of silicon in biology and agriculture [Epstein, 2009].

It has been established that silicon contributes to the growth of plant resistance against salinity and oil pollution [Reichert, Norton, 1994, Matichenkov, Calvert, 2000]. In conditions of salt stress, the introduction of active forms of solid and liquid silicon into the nutrition system increases the salt tolerance of crops. The inclusion of silicon in nutrient mixtures has a positive effect on plants at an early stage of their development. This effect is universal because it is observed on agricultural crops from different botanical families with different physiological and biochemical characteristics of growth and development: rice, cauliflower, tomato, corn, sweet pepper, watermelon, cucumber, and others. In the conditions of a vegetation experiment on sand and gray forest soil, as well as in field experiments on tropical ferruginous soil in West Africa, it was shown that active forms of silicon: monosilicic acid and diatomite increase the resistance of tree crops, such as *Jatropha* L., against salt stress. Reduction of salt poisoning of plants by active forms of silicon is explained by a decrease in the intensity of sodium transport through the apoplast of plants. This ability is strengthened in the series: root - stem - leaf. The introduction of active forms of silicon into the ecosystem stimulates the blocking of sodium in the roots of plants and prevents its transport through the plant. The cell walls of barley roots prevent the transfer of sodium from the apoplast to the symplast, but the cell walls of stems and leaves do not have this ability [Matychenkov, 2014]. It was established that an increase in sodium chloride in the solution from 0.3 to 1.2% led to a sharp decrease in the percentage of germinated barley seeds. Adding amorphous silicon dioxide or

commercial preparations containing silicon to the solution together with sodium chloride stimulated the reduction of the negative effect of sodium chloride and increased the number of germinated seeds compared to the control. At the same time, the highest effect was observed in the presence of the drug Zamsil when it was diluted 1000 times. The concentration of monosilicic acid in the solution in this case was 150.6–151.4 mg Si/l [Matychenkov et al., 2005]. Silicic acid interacts well with organic and inorganic compounds, forms soluble complexes [Dietzel, 2000]. Sometimes soluble silicon compounds include colloidal particles and silicic acid gels [Banerjee et al., 2006].

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A scientific direction has been developed in the theoretical and practical aspects of the chemistry of organosilicon compounds: selective synthesis of physiologically active silicon compounds (FASC) - activators of specific processes that occur during the development of plants in ontogenesis, which includes the development of targeted methods of their synthesis, methods of modification, study of physicochemical properties and physiological activity.

Synthesized FASKs will increase the natural resistance of plants against biogenic and abiogenic stresses, as well as the quality and quantity of plant products. New technologies for the synthesis and application of biologically active organosilicon compounds are essential for solving major global problems [Loginov, 2012].

The research results indicate the presence of a mechanism in plants that ensures the active and rapid redistribution of silicon in plant tissues. At the same time, the transfer of silicon goes to tissues that are more prone to stress. This conclusion confirms the work of the Japanese researcher Ma (1990-2006). he showed that in rice there are special transport proteins responsible for silicon transport. A fragment responsible for the synthesis of these proteins was found and identified in DNA. It is assumed that not only in rice, but also in plants there is a similar mechanism responsible for providing the plant with silicon and its transport [Ma, 2007].

The positive effect of silicon on plant growth in conditions of soil salinity is manifested in an increase in the activity of the photosynthetic apparatus [Kosobrukhov, Matichenkov, 2004], a change in the ratio of potassium and sodium in the xylem [Ahmad et al., 1992], an increase in the activity of a number of enzymes [Bradbury, Ahmad, 1990], regulating metabolic processes in plants. An increase in the content of monosilicic acid in the soil solution prevents the absorption of sodium from the soil. Thus, with the improvement of silicon nutrition, not one, but several mechanisms of regulation of physiological functions operate. It is also assumed that silicon inhibits invertase and acid phosphatase in rice plants [Aleshin, 1982a].

It was found that the absorption of silicon is closely related to sodium and calcium, and therefore, in conditions of soil salinity, plants are able to intensively accumulate silicon, which contributes to the growth of their resistance to salinity [Kemecheva, 2003; Sheuzhen, Kemecheva, 2003].

The biological activity of silatranes [general formula $N(CH_2CH_2O)_3Si-X$], according to the paradigm adopted by researchers, is due to the presence of a

donor-acceptor bond N – Si, which stimulates the formation of an unusual compact tricyclic structure and a high dipole moment of molecules, which in turn provides them high permeability to cell membranes, stabilizing them [Adamovych, 2014]. An alternative hypothesis is based on the ability of silatranes to hydrolyze and form nanosized silicon in water environments [Zelenkov, Potapov, 2016].

The mechanism of effect of silatranes on metabolic processes in the cell is partly due to their membranotropic properties. This determines their high solubility in lipids and the ability to specifically interact with various organic substances. In certain concentration ranges and depending on the nature of the substituent bound to the silicon atom, silatranes contribute to a decrease in the level of lipid peroxidation and an increase in plant resistance under stress conditions [Gong et al., 2008].

The mechanism of action of silatranes is determined by their atran heterocycle, the significant dipole moment of which gives their molecules high permeability to cell membranes, and the rigidity of the molecular structure increases the resistance of membranes against adverse factors. Their easy biodegradability and lack of toxic effect in a wide range of concentrations are also important. The high polarity of molecules allows them to be embedded in the lipid double layer of cell membranes in such a way that the negatively charged fragments of their structures remain on the surface of the membrane, and the biogenic fragment is included in the alkyl chains of lipids. Silatran and protatran adsorbed in the double layer of the membrane interact with polar groups of proteins and lipids. This stabilizes the cell membrane and stimulates the activity of the mitochondrial apparatus, optimizing the course of their metabolic processes. Protatran stimulates the elongation and division of cells, taking part in the processes of their differentiation. Penetrating into cells, it binds to specific receptors affecting the functional activity of membranes, polyribosomes, and the nuclear apparatus. The complex of protatran with the receptor, entering the

nucleus, activates the synthesis of all forms of RNA, including matrix ones, which stimulates the process of formation of new polyribosomes and synthesis of proteins in the cytoplasm [Karmin, 1986, Gong et al., 2008, Karsunkina, 2011].

The fairly high polarity of the molecules of the active substance of the drug "Energia-M" allows them to be embedded in the lipid bilayer of cell membranes in such a way that the negatively charged fragments of their structures remain on the surface of the membrane, and the biogenic fragment is rooted in the alkyl chains of lipids. Silatran and protatran adsorbed in bilayer membranes interact with polar groups of proteins and lipids. This stabilizes the cell membrane and stimulates the activity of the mitochondrial apparatus, optimizing the course of their metabolic processes. Protatran stimulates the stretching and division of cells, taking part in the processes of their differentiation. Penetrating into cells, it binds to specific receptors that affect the functional activity of membranes, polyribosomes and the nuclear apparatus. The complex of protatran with the receptor, entering the nucleus, activates the synthesis of all forms of RNA, including matrix ones, which stimulates the formation of new polyribosomes and the synthesis of proteins in the cytoplasm [Voronkov and Baryshok, 2005, 2010, Voronkov et al., 2014a, 2014b, Myrskov et al. etc., 2016].

It was shown that exogenous application in low concentrations of JO3⁻ (< 40 M) improves the response of plants to soil salinization with sodium chloride. The action of JO2 under these conditions led to a decrease in the concentration of toxic ions such as Na⁺ and Cl⁻. In addition, treatment of plants with JO3⁻ contributes to an increase in the concentration of sugars in the leaves, which participate in osmotic regulation. An increase in the activity of a number of antioxidant enzymes under its influence was also established. In this connection, the researcher came to the conclusion that iodine can be considered a useful element for counteracting the harmful effects of salt stress [Rocio, 2011].

5-aminolevulinic acid (ALA), a precursor of chlorophyll and heme in low concentrations, acts as a plant growth regulator, mitigating the negative effects of

salt. The effect of 125 mM NaCl on the rate of endogenous ALA formation, heme and ATP content, cytochrome c oxidase activity, and respiration rate in cotyledons of 7-day-old cucumber seedlings grown in the presence or absence of exogenous ALA was studied. It was shown that NaCl significantly reduces the length and biological mass of roots, the mass of roots (by 60% and 30%, respectively) and hypocotyls of hypocotyls (by 70% and 70%), reduces the biological mass of plants by 50% and only slightly (by 14%) reduces the biological mass of cotyledons. At the same time, NaCl significantly increases the rate of synthesis of endogenous ALA and the content of heme in cotyledons, keeps the rate of respiration and the content of ATP almost at the level of control plants, and slightly (by 20%) reduces the activity of cytochrome c oxidase. It is assumed that the activation of the synthesis of endogenous ALA in cotyledons stimulates the biosynthesis of heme and thereby supports the respiratory process as the main source of energy in the absence of photosynthesis, which contributes to the formation of resistance of cotyledons against NaCl. Addition of exogenous ALA to the growing medium (10 and 60 mg/l) increases the biomass of hypocotyls, cotyledons and seedlings by 12% and 24%, 7% and 12%, 20% and 29%, respectively, compared to the variants where one salt is present. At the same time, in cotyledons, exogenous ALA does not increase heme content, respiration rate, and only slightly increases ATP level and cytochrome c oxidase activity, compared to plants grown on the same salt. The obtained results allow us to predict that exogenous ALK acts mainly as a plant growth regulator. stimulating growth processes and thereby increasing the resistance of the seedling against the action of NaCl [Averina et al., 2011].

CONCLUSIONS

The aggravation of the ecological situation due to the negative anthropogenic impact on the environment (irrigation, application of mineral fertilizers, man-made pollution with waste, etc.) makes the problem of adaptation of plants against salinity one of the most important in physiology and agriculture. The study of the mechanisms of salt resistance involves the study of the adaptive reactions of the whole organism, and more specifically, the enzyme systems that ensure the life of plants under conditions of stress [Zemlyanukhina et al., 2008]. It is known that the mechanisms of resistance of plants against stresses work at different levels of biological organization - cellular, tissue, organismal, population. And vital activity under stress is possible only when the organism is able to show sufficient resistance at any of these levels [Terletskaya, 2008].

Stress-tolerance of plant cells is a consequence of induced differential expression of genes, signal integration and coordination of various physiological, metabolic and biochemical reactions. Genetic regulation of resistance is carried out at the transcriptional, post-transcriptional, and post-translational levels [Vij, Tyagi, 2007].

Global climate changes only intensify the effect on plants of negative environmental factors, including soil salinization, which spreads especially quickly on irrigated lands, reducing the productivity of agriculture. The emergence of a state of salt stress under the influence of various factors is the result of a violation of their osmotic, and sometimes also ionic homeostasis, accompanied by secondary oxidative stress. Salinity is a particularly strong and irreversible stress factor for plants due to the presence of sodium ions as the main cation in salts. At the cellular level, sodium is quite toxic for all plant species, which is why it is not possible to create salt-resistant varieties of plants using classical breeding methods [Palladina, Rybchenko, 2010].

CONCLUSIONS

In response to salt stress, the plant reacts with numerous molecular, metabolic and physiological reactions, aimed at the synthesis of protective macromolecules, the formation of protective systems and the adaptation of the plant organism to the changed environmental conditions. At the same time, the resistance of halophytes is determined by the functioning of constitutive protective mechanisms, while the salt resistance of glycophytes is based on stress-induced protective systems [Munns, Tester, 2008, Kuznetsov, 2009].

The effect of salinization largely depends on the characteristics of the soil, the presence of water, climatic conditions and other factors. Therefore, the effect of salt on a plant is complex. It is believed that research on halophytes can play a significant role in solving this problem. However, the resistance of plants against salinity is ensured by the extremely complex work of dozens of genes. As a result, it is necessary to look for alternative ways that would help reveal more general relationships between indicators, which would create a basis for adequate modeling of the adaptation process against salinity. And modeling, in turn, would contribute to attracting our attention to the genes that ensure salt resistance from these positions, and would not be reduced to looking for a needle in a haystack of information about genes that are important for the adaptation of plants against salinity [Ivanishchev, 2019].

Cell and tissue selection provides the use of more complex selection schemes, increasing its efficiency, and it is a fairly convenient model for the analysis of plant morphogenesis when grown against the background of salt stress factors in controlled conditions [Bajaj, Gupta, 1986].

The negative effect of salt leads to a low water potential in the soil, which prevents the normal flow of water into the plant. Chloride salinity is the most common and toxic. The damaging effect of a high concentration of salts is associated with the disruption of membrane structures, especially the plasma membrane, as a result of which its permeability increases, the ability to selectively

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accumulate substances is lost. In this case, salts enter the cell passively, which significantly increases cell damage [Efimova et al., 2017].

Despite the rather high interest in this field, the mechanisms of the effect of increased levels of NaCl on the plant cell are still not fully understood. At the same time, the distribution and transport of Na⁺ and Cl⁻ ions in the system of the whole plant play a rather important role in the formation of the mechanisms underlying plant salt tolerance. It is believed that salt-resistant plants have the ability to avoid the accumulation of Na⁺ and Cl⁻ ions in actively metabolizing cells, depositing these ions in those parts of the plant that do not bear a significant metabolic load [Balnokin, 2012]. Of the organismic mechanisms of resistance, attention is focused on a strong root system and drought resistance [Vedrov, 1984; Nikulin, Lyashok, 1990; Zimnytskyi, 1991]. It is believed that the main mechanism of resistance against chloride salinity in glycophytes is their ability to limit the transport of chloride into the stem [Popova et al., 2008].

Mechanisms of plant adaptation at the population level are based on intraspecific (intravariate) polymorphism of genetic systems that increase the rate of response of the population. This is based on the idea of using multiline varieties [Sozynov et al., 1986]. It should also be noted that there is some similarity between the main mechanisms of resistance against biotic and abiotic stresses. In these cases, in addition to specific genes responsible for resistance against this or that factor, extremely many complex systems also take an active part in adaptation, the effect of which is not direct, but pleiotropic in nature. The latter include, for example, genetic systems that control the rate of development, which allow the plant to avoid adverse factors to some extent [Bidinger et al., 1987].

The resistance of plants against salinity is largely determined by the ability of cells to maintain a high ratio of K⁺/Na⁺ in the cytoplasm, that is, cellular homeostasis, which is ensured by the coordinated work of proton pumps, ion channels and transporters of potassium and sodium ions, among which there is no doubt a rather important role NHX-antiporters of the tonoplast play a role

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[Isayenkov et al., 2010, 2011, Kryvosheeva, Belyaev, 2013, Rakhmankulova, Shuiskaya, 2015]. In the cell walls of plants, the number of active sites capable of exchanging H^+ for Na^+ of the external environment increases, and as a result, the effect of toxic concentrations of Na^+ on the cytoplasmic content of the cell decreases. Therefore, the physiological role of ion exchange reactions in the cell wall is to maintain a low concentration of sodium ions in the aqueous space of the apoplast during sharp changes in the concentration of NaCl in the external environment, and at the same time the movement of divalent calcium ions from the cell wall into the aqueous space of the apoplast and further, it is probably a rather important element of ion homeostasis regulation in the cell during adaptation to salinity conditions [Meychyk, Ermakov, 2013].

Cation-exchange properties of cell walls are determined by the presence of carboxyl groups of α D-polygalacturonic and oxycoric acids, as well as phenolic groups, and ion-exchange properties by amino groups. In response to the salinity of the nutrient solution in halophytes and glycophytes, the ionization constant of carboxyl groups decreases, and therefore the number of ionogenic groups capable of exchanging a proton for a cation of the external environment increases accordingly. As a result, the solution in the cell membrane phase will contain fewer sodium ions than the external solution. Under conditions of salt stress, the concentration of protons and calcium ions in the solution in the plasmolemma increases due to exchange reactions between the cations of the external solution and the ionized carboxyl groups of the polymer matrix of the cell walls, which leads to a change in the transport functions of the plasma membrane [Nikolaeva, 2005].

It is believed that salt-resistant plants have the ability to avoid the accumulation of sodium and chlorine ions in young tissues and generative organs, depositing these ions in those parts of plants that do not carry a significant metabolic load [Orlova et al., 2015].

CONCLUSIONS

The adaptation systems of plants at the cellular level are closely related to the accumulation of certain metabolites and the fine organization of intracellular structures. Commonly recognized mechanisms of cellular adaptation are an increase in proline concentration as a response to an adverse effect, stress proteins, water retention due to cytoplasmic colloids, and induction of protein synthesis on polyribosomes. The relative simplicity of biochemical mechanisms and a significant set of works on biochemical genetics make the cellular level of adaptation the most accessible for genetic study [Kueh, Brigh, 1982, Grumet et al., 1985, Samsonov, 1988].

When studying the mechanisms of resistance in isolated in vitro salt-resistant cell lines, it was shown that the ability to penetrate salt ions is not impaired in a number of clones and, at the same time, the osmotic gradient necessary for the functioning of the cell is maintained. These lines were characterized by a truly halophytic type of resistance, in which they accumulated significantly higher concentrations of ions than sensitive lines, and, moreover, required an increased salt content in the medium for normal growth [Balasubramanian et al., 2004].

A promising method of protecting cultivated plants against salt stress is the use of phytohormones. One of the mechanisms of action of salicylic acid on plant cells is a change in the proton conductivity of membranes (especially and primarily - plasmalemma), which leads to acidification of the cytoplasm and a sharp increase in energy expenditure (due to the work of ATPases) for the extraction of protons from cells and the absorption of potassium ions [Gordon et al., 2003]. Both auxins and brassinosteroids can induce the expression of genes encoding enzymes that weaken the cell wall, which indicates the interaction of auxin and brassinosteroid signaling pathways at the level of gene expression [Hardtke et al., 2007]. Brassinosteroids exert their regulatory effects on the plant cell through a two-component system that includes a serine-threonine protein kinase located in the plasma membrane, which is similar in structure to the Toll

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receptors of animals, and more specifically to the Toll receptors of *Drosophila melanogaster* L. [Belkhadir, Chory, 2006, Gendron, Wang, 2007]. It has been established that jasmonic acid regulates gene expression during plant development, as well as for the activation of protective reactions against biotic and abiotic stresses [Stumpe, Feussner, 2006; Creelman, Mullet, 1997; Wasternack, Parthier, 1997; Ziegler et al., 2000; Delker et al., 2006].

The positive effect of silicon on plant growth in conditions of soil salinity is manifested in an increase in the activity of the photosynthetic apparatus [Kosobrukhov, Matichenkov, 2004], a change in the ratio of potassium and sodium in the xylem [Ahmad et al., 1992], an increase in the activity of a number of enzymes [Bradbury, Ahmad, 1990, Guerriero et al., 2016], regulating metabolic processes in plants

The resistance of halophytes to salt stress is ensured by various factors. In particular, the ability of roots to accumulate or release certain ions [Lauchli, 1984], to control the absorption and transport of ions into the shoot [Flowers et al., 1997], selective xylem transport to other parts of the plant [Jeschke et al., 1984], to accumulate ions by osmotic adaptation [Bernstein, 1961], to compartmentalize ions in the cell [Flowers et al., 1997], to accumulate soluble organic substances [Pollard, Wyn Jones, 1979], etc.

The revealed mechanisms of inducing resistance of plants against abiotic stresses by growth regulators will contribute to increasing their tolerance against salinity.

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