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MOLECULAR MECHANISMS OF SALT TOLERANCE: THE SOS PATHWAY AND ASSOCIATED GENES

Annotation. Soil salinization is one of the most important abiotic stress factors that negatively affects plant growth, development, and productivity. This stress significantly reduces plant vitality by disrupting physiological and biochemical processes. The main problems caused by salinity are osmotic stress,

ion toxicity, and nutrient imbalance, which disrupt photosynthesis, water exchange, and cell turgor. Cotton (*Gossypium spp.*) is one of the most important natural fiber crops in the world. Although it is moderately salt-tolerant, it is especially sensitive to salinity during seed germination and seedling stages. Several molecular defense mechanisms are involved in developing salinity tolerance in plants, among which the SOS (Salt overly sensitive) pathway is one of the most important. This pathway regulates intracellular Na^+ ions through SOS1, SOS2, and SOS3 proteins. In response to salt stress, an increase in intracellular Ca^{2+} ions activates the SOS pathway, and these proteins interact to enhance the plant's salt tolerance. This article analyzes the salt stress responses and molecular defense mechanisms in plants, particularly in cotton, and highlights the importance of genetic approaches in developing salt-tolerant varieties.

Key words: Food and Agriculture Organization (FAO), salinity, **SOS1**, **SOS2**, and **SOS3** genes, **AtNHX1**, **CycC1**, transcription factors **AP2/ERF**, **bZIP**, **NAC**, **MYB**, and **WRKY**

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МОЛЕКУЛЯРНЫЕ МЕХАНИЗМЫ УСТОЙЧИВОСТИ К СОЛЕВОМУ СТРЕССУ: СИГНАЛЬНЫЙ ПУТЬ SOS И СВЯЗАННЫЕ С НИМ ГЕНЫ

Аннотация. Засоление почвы — один из важнейших абиотических стрессовых факторов, негативно влияющих на рост, развитие и продуктивность растений. Этот стресс резко снижает жизнедеятельность растений за счёт нарушения физиологических и биохимических процессов. Основные проблемы, возникающие в результате засоления, включают осмотический стресс, ионную токсичность и нарушение баланса питательных веществ, что приводит к сбоям в фотосинтезе, водообмене и тургоре клеток. Хлопчатник (*Gossypium spp.*) является одной из важнейших природных волокнистых культур в мире. Хотя он считается умеренно солеустойчивым, на стадии прорастания семян и рассады он особенно чувствителен к засолению. В формировании устойчивости к соли у растений участвуют несколько молекулярных защитных механизмов, одним из важнейших из которых является путь SOS (Salt overly sensitive). Этот путь регулирует концентрацию ионов Na^+ в клетке с участием белков SOS1, SOS2 и SOS3. В ответ на солевой стресс повышение уровня ионов Ca^{2+} в клетке активирует путь SOS, и эти белки взаимодействуют между собой, повышая устойчивость растения к соли. В данной статье рассматриваются реакции растений, особенно хлопчатника, на солевой стресс и молекулярные механизмы защиты, а также

подчеркивается значение генетических подходов в создании солеустойчивых сортов.

Ключевые слова: Продовольственная и сельскохозяйственная организация (ФАО), засоление, гены **SOS1**, **SOS2** и **SOS3**, **AtNHX1**, **CysC1**, транскрипционные факторы **AP2/ERF**, **bZIP**, **NAC**, **MYB** и **WRKY**

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**O'SIMLIKLARNING SHO'RLANISHGA QARSHI
HIMOYALANISHINING MOLEKULAR MEXANIZMI**

Annotatsiya. Tuproq sho'rlanishi o'simliklarning o'sishi, rivojlanishi va mahsuldorligiga salbiy ta'sir ko'rsatuvchi eng muhim abiotik stress omillaridan biridir. Bu stress fiziologik va biokimyoviy jarayonlarning buzilishi orqali o'simliklar hayotiy faoliyatini keskin pasaytiradi. Sho'rlanish tufayli yuzaga keladigan asosiy muammolar — bu osmotik stress, ion toksikligi va oziq moddalari muvozanatining buzilishi bo'lib, ular fotosintez, suv almashinuvi va hujayra turgorini izdan chiqaradi. G'o'za (*Gossypium* spp.) dunyodagi eng muhim tabiiy tolali ekinlardan biri hisoblanadi. U o'rtacha sho'rga chidamli ekin bo'lsa-da, ayniqsa urug' unishi va ko'chat bosqichlarida sho'rlanishga sezgir hisoblanadi. Sho'rlanishga qarshi chidamlilikni shakllantirishda o'simliklarda bir nechta molekulyar himoya mexanizmlari mavjud bo'lib, ularning eng asosiylaridan biri bu SOS (Salt overly sensitive) yo'lidir. Ushbu yo'l SOS1, SOS2 va SOS3 oqsillari orqali hujayradagi Na^+ ionlarini tartibga soladi. Tuz stressiga javoban hujayra ichida Ca^{2+} ionining ko'payishi natijasida SOS yo'li faollashadi va bu oqsillar o'zaro ta'sirlashib, o'simlikning tuzga chidamliligini oshiradi. Ushbu maqolada o'simliklarning, xususan g'o'zaning, tuz stressiga javob reaksiyalari va molekulyar himoya mexanizmlari tahlil qilinadi, shuningdek, sho'rlanishga chidamli navlarni yaratishda genetik yondashuvlarning ahamiyati yoritiladi.

Kalit so'zlar: Oziq-ovqat va qishloq xo'jaligi tashkiloti FAO, sho'rlanish SOS1, SOS2 va SOS3 genlari *AtNHX1* *CycC1* *AP2 / ERF*, *bZIP*, *NAC*, *MYB* va *WRKY* transkripsiya faktorlari (TF)

Introduction. Plants thrive under the influence of a large number of abiotic and biotic factors. Some of them have positive effects and some have negative effects. One of the abiotic factors with such a negative effect is a high content of salt in the soil, namely salinity. This abiotic stress can adversely affect plant growth, development, and productivity by disrupting the physiological and biochemical processes required for plant development and yield [] In December 2024, in Bangkok, the Food and Agriculture Organization of the United Nations (FAO) published the first major global report on salt-affected soils in 50 years. The report shows that nearly 1.4 billion hectares of land (more than 10% of the total

land area) are subject to salinity, while another one billion hectares are at risk due to climate change and the anthropogenic factor [5]. The report also noted that 70% of this indicator falls on the share of 10 countries (Afghanistan, Australia, Argentina, China, Kazakhstan, the Russian Federation, the United States, Iran, Sudan and Uzbekistan). [5]. On the territory of the country, 1,746.6 thousand hectares are covered with various levels of salinity, of which 65,2 thousand hectares are strong, 439,4 thousand hectares are medium and 1,242 thousand hectares are low-salinity. Notably, as a result of the Aral Sea tragedy, more than 5.5 million hectares of land have been turned into salt deserts [12]. For the rational use of these lands, it is necessary to study the mechanisms of resistance to the salt stress factor in plants and to develop salt-tolerant goose varieties based on this obtained data.

Effect of salinity on plant physiology and molecular mechanisms.

Plants respond to this stress in various ways, that is, by preventing the ingress of salts (at the cellular or whole plant level), by taking more water from the soil, by reducing the concentration of salts in the cytoplasm, and so on. Salt stress has four main harmful and dangerous effects on plant growth: Insufficient availability of water for the plant due to high osmotic stress caused by the high accumulation of dissolved salts in the soil; ionic toxicity caused by high concentrations of sodium (Na^+), chloride (Cl^-) and magnesium (Mg^{2+}) ions; It has been proven that disturbance of the specific ions imbalance and the accumulation of toxic ions adversely affect the growth and development processes of plants, yield. In addition, important physiological processes such as photosynthesis, lipid metabolism, and protein synthesis are also significantly impaired or disrupted under salinity conditions [14].

The economic significance of the goose plant and the need to study salt tolerance. Cotton (*Gossypium spp.*) is one of the most economically important crops in the world, as it serves as the main source of natural fiber, accounting for about 35% of the total fiber used in the world [3]. However, high concentrations of salt in the soil caused by agricultural practices and climate change pose a serious

threat to the growth and yield of the cotton plant [9]. Despite the fact that the goose is classified as moderately resistant to salt (7.7 dS m^{-1}), under salinity conditions it has a serious impact on the quality of fiber, which is considered a staple product, along with a decrease in plant growth, number and yield. Understanding the negative effects of soil salinization on the goose is critical to effective management of cotton cultivation and increased yields. The effect of salinity on the geese plant is observed at different stages of germination, seedling, vegetative and maturity stages. However, the germination and young seedling stages of seeds are particularly susceptible to salinity stress compared to their other stages [2].

The effect of salt stress on plants. Salinity causes osmotic stress in the plant cell due to ion imbalance disturbance and lack of water. This leads to many transient biophysical changes such as a decrease in cell turgor pressure, contraction of the plasma membrane, and changes in the structure of the cell wall [11]. Salinity has a significant impact on physiological processes such as transpiration rate in goose plants, leaf temperature, osmotic potential and water status, photosynthetic activity, and total water composition of leaves. Salinity has two detrimental effects on photosynthesis. First, it causes plant stomas to become clogged, i.e., leaf mouthpieces, which lowers CO_2 levels in their cells. Secondly, it damages photosynthetic membranes and reduces the ability to absorb CO_2 . This decline is not only due to the disruption of the stomata but also includes non-stomatal elements, such as the breakdown of photosynthetic pigments. These changes disrupt the overall efficiency of the photosynthetic process, the subsequent response to stress in plants [11].

The main genes related to the salt tolerance of the cotton. Plants, including cotton plants, also have protective mechanisms against salt stress, one of which is the *Salt Overly Sensitive* (SOS) pathway. Due to the high content of salt in the soil, large amounts of Na^+ ions enter the cytoplasm of plant cells. Three basic processes of plant defense mechanisms in preventing this have long been studied: (1) minimizing the ingress of Na^+ ion into cells; (2) Maximize the transfer of Na^+ into vacuole; and (3) perform the removal of Na^+ from the cell [11]. A few

decades ago, as a result of extensive genetic studies, it was determined that the role of SOS genes in increasing NaCl homeostasis and salt tolerance in *A. thaliana* is significant. SOS genes are mainly made up of three components, which are: *SOS1*, *SOS2* and *SOS3*. In the family of SOS proteins of Arabidopsis, *SOS2* and *SOS3* are located in the cytoplasm and *regulate the balance of K⁺ and Na⁺ ions in and out* of the cell by regulating *SOS1* in the plasma membrane, which is involved in increasing the salt tolerance of plants [Error: Reference source not found]. In the cells of plants in a saline soil environment, the Na⁺ contained in salt enters the stem tissues in the first 2 minutes and then within 10 minutes the protective mechanism is activated and these ions are excreted from the root tissue through xylem tissues [13]. The penetration of a large amount of Na⁺ ions into the cell from the external environment leads to an increase in the concentration of Ca²⁺ in the cell cytoplasm. This process is carried out with the help of kinase – signaling proteins of various receptors. Studies have shown that lipids present in plasma membrane, such as glycosyl inositol phosphoryl ceramide (GIPC), interact with the sphingolipids Na⁺ and contribute to the activation of Ca²⁺ flow pores. In addition, abscisic acid (ABA) activates Ca²⁺ signaling in response to stress. ABA controls the release of Ca²⁺ ions from internal reserves, such as endoplasmic mesh and vacuole. This process is controlled by the activation of ABA receptors. When ABA levels increase, it interacts with Ca²⁺-sensory proteins such as CIPK (CDPK) and PP2C (protein phosphatase). These proteins control the intracellular concentration of Ca²⁺ ions and cause Ca²⁺ to enter or exit the cell to transport the desired signals [7]. Increased Ca²⁺ ions in the cytoplasm *bind to SOS3* proteins. The *SOS3* gene encodes a protein that binds myristilated calcium that acts as a calcium sensor, and this protein senses an increase in the Ca²⁺ ion in the cytoplasm stimulated by excess Na⁺ entering the cytoplasm. *SOS3* belongs to a unique family of calcium-binding proteins that contain two pairs of EF arm structures with four approximate metal binding sites. In this protein, the N terminal and C terminals (the side where the N terminal amino groups are present, the side where the C terminal carboxyl group is present) and the two pairs present near the N terminal

side come to an active state after bonding with the calcium ion using EF hands. *The serine/threonine protein kinase SOS3, which belongs to the SnRK3 (Sucrose non-enzymatic 1-related protein kinase 3) family* of SOS3 protein kinases, is capable of interacting and activating SOS2. SOS2 contains the N-terminal kinase catalytic domain and the regulatory domain at the novel C-terminal, similar to that found in Suc nonfermenting1 (SNF1) and AMP-activated protein kinase AMPK.

(Serine/threonine protein kinases (Ser/Thr kinases) are a category of enzymes that activate or reduce their substrate proteins by phosphorylating the hydroxyl groups of serine or threonine amino acids [6]. These complex compounds activate the *SOS1* gene by phosphorylation. During salt stress, *the expression of SOS1 gene is partially controlled by SOS3 and SOS2. The SOS1 gene activates Na⁺/H⁺ antiporter activity under saline conditions. For the SOS1 gene to work, SOS2 and SOS3 must combine to form a complex. Recent studies in Saccharomyces cerevisiae have provided additional experimental evidence for the interaction between SOS3 and SOS2 proteins, as well as the involvement of this complex in regulating the expression of the SOS1 gene.* [4].

In addition, SOS2 has a positive effect on the anti-porter activity of the tonoplast (vacuole membrane) Na⁺/H⁺ anti-porter, which holds Na⁺ ions in the vacuole. Apart from this, it also controls the activity of the vacuolar H⁺/Ca²⁺ substitute CAX1, which is involved in maintaining intracellular calcium balance. [16] The *SOS1* gene was first identified in Arabidopsis and *designated as AtNHX1 – AtNHX8. AtNHX7 (or AtSOS1)* is an important component in the SOS signaling pathway. *AtSOS1* is located in the plasma membrane and acts mainly in the epidermis cells at the stem tip and in the parenchyma at the xylema-symplast border of the stem, stem, leaf. This *SOS1* controls its release outside the cell and the transport of Na⁺ ions in plants in environments where the concentration of tonillar Na⁺ increases. *SOS1* manifests itself as a homodimer, with each monomer having 12 transmembrane domains in its N-terminal region and a cytosolic domain, a cyclic nucleotide binding domain, and an auto-inhibition domain at the C-terminal. SOS proteins have been implicated in regulating the salinity resistance

of plants [9]. Overexpression of *SOS1* resulted in decreased accumulation of Na^+ in the xylem and in the stem stream moving from the stem to the leaf [16]. In addition to Arabidopsis, the physiological roles of *SOS1* genes bound in soybean, maize, tomato, goose crops have been studied [9]. The SOS signal transduction pathway is the main regulatory mechanism of ion homeostasis, initially regulates the breakdown of Na^+ in the roots. However, if the external salt content is high and persistent, and this initial line of defense cannot protect the roots from excessive salt accumulation, the Na^+ entering the stem will eventually reach the conductive tissue. Plants tend to maintain a certain concentration of Na^+ ions in the root tissues even under conditions of salt stress, thereby trying to prevent ion toxicity. The rate of accumulation of Na^+ in plant branches is determined by the precise absorption of Na^+ into the roots and the rate of its transition from the root to the shoots. Mechanisms of ionic homeostatic regulation play an important role in the salt resistance of the SOS signaling pathway and the protection of various tissues and organs from salt stress. *The results of the reverse genetic approach in T. salsuginea* showed that transgene lines diluted by the RNAi of the *SOS1* gene led to an overaccumulation of Na^+ ions in pericyclic (pericycle is a single-layered meristema or promeristema cells located in the central part (stele) of plant roots), and an increase in the Na^+/K^+ ratio was observed in root xylema parenchyma cells, which indicates a serious disturbance of ion balance [6].

There are significantly greater associations between salinity stress regulation and *families of transcription factor (TF) such as AP2/ERF, bZIP, NAC, MYB, and WRKY*. For example, MYB proteins are members of a superfamily of TFs encoded by Arabidopsis genes with a highly conserved DNA-binding (*MYB*) domain. During the salt treatment, *MYB42* is directly bound to *SOS2*. It then accelerates the promoter and its activity [15].

Disruption of the subunit of the plant mediator complex CycC1 (CycC1 (Cyclin C1)) — one of the components of the mediator complex, especially the subcomplex called the CDK8 module) increases salt-associated *SOS1* gene expression and salt resistance in Arabidopsis because CycC1; 1 inhibits the

activation of RNA polymerase II by capturing the *SOS1* promoter. *cycc1*; The *SOS1* mutation in mutant 1 increased its salt resistance. In addition, *CycC1*; 1 *can directly interact with the WRKY75* transcription factor, which can bind directly to the *SOS1* promoter and activate its expression. *Cycc1*; In contrast to mutant 1, *WRKY75* had reduced *SOS1* expression and salt tolerance in mutant 75. *CycC1*; Activity 1 inhibits the activation of *WRKY75* transcription factor activity. Thus, *cycc1*; The increase in *SOS1* expression and salt tolerance in mutant 1 is associated with the correct expression of *WRKY75* activity. In addition, *CycC1* in response to high salinity; The expression of 1 is suppressed and *the expression of WRKY75* is enhanced [8].

Conclusion. Thus, each plant has different mechanisms of defense against different stress factors, in particular salinity. Experiments in this area show that *SOS* pathways are an effective means against salinity. The *SOS1* gene activity of the *SOS* pathway is important in the excretion of salt ions entering the cell outside the cell. *The SOS2 and SOS3 genes play an important role in acting as a signaller and activating SOS1 gene activity by sensing the amount of salt ions* entering the cell. Working with this gene is a bit of a challenge, as the *SOS1* gene is very large in the fight against salinity. Therefore, *boosting the activity of the SOS2 and SOS3 genes* can confer higher efficacy. In addition, the study of the activity of these genes, which belong to the *families of MYB and WRKY*, which are involved in the management of these genes, is important in combating salt stress. Because transcription factors *MYB42* and *WRKY75* directly affect *SOS* genes, that is, because increased activity of these transcription factors leads to increased *SOS* gene activity, increasing the activity of these TFs may be one of the promising pathways against salinization. Also, the activity of the *CycC1* mediator complex has an inverse effect on *SOS* genes, meaning that this complex occurs due to a decrease in the activity of the *WRKY75* transcription factor. Slowing down the activity of this mediator complex can be one of the measures to combat salinity. Currently, the creation of a new plant against salinization, in particular goose varieties, is of great importance for the economy and future of our country.

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