

UDC 581.1, 581.11, 581.132, 632.112

<https://doi.org/10.59849/0002-3078.2026.1.9>

EFFECTS OF DIFFERENT CONCENTRATIONS OF NaCl AND ZnSO₄ ON THE ANTIOXIDANT SYSTEM AND SOME ANABOLIC ENZYMES IN THE COTTON PLANT

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Summary: *The article investigates the effects of NaCl and ZnSO₄ at concentrations of 25, 50, 100, and 200 mM on the activity of antioxidant enzymes, catalase (CAT) and ascorbate peroxidase (APX), as well as carbon metabolism enzyme carbonic anhydrase (CA), and H⁺-ATPase in the root system of upland cotton (*Gossypium hirsutum* L.). The activity of CA and H⁺-ATPase enzymes was found to increase adequately in the presence of Zn²⁺ ions. During the ontogenetic phases of first true leaf formation (FTLF), budding (BP), and flowering (FP), a gradual increase in salt concentration up to 200 mM leads to an increase in CAT and APX activity, followed by a gradual decrease, which can be associated with the amount of H₂O₂ formed under stress conditions. Under salt stress, slight changes in lipid content do not depend on the nature of the salt. The increasing requirement of young plants for nicotinamide coenzymes results in the gradual activation of the studied enzymes and, consequently, in enhanced ATP synthesis. In contrast, under stress conditions, ATP content gradually decreases.*

Keywords: *Gossypium hirsutum* L., NaCl, ZnSO₄, CA, CAT, APX, H⁺-ATPase, tolerance

Introduction

The results of studies conducted at different times indicate that plant adaptation to unfavorable environmental conditions leads to the induction of genes responsible for certain biochemical and morphophysiological changes. As a result, low-intensity stress factors promote the formation of adaptive traits in plants under such conditions. However, when the intensity and duration of the stress factor are high, plants are unable to exhibit tolerance. Therefore, there is a need for careful investigation of the biochemical and morphophysiological changes occurring in plants under unfavorable environmental conditions.

Salinity is one of the major abiotic factors limiting plant growth and productivity. By 2050, more than 50% of cultivated land is expected to become saline [Wang et al., 2003]. Under salt stress conditions, the main causes of yield reduction include a decrease in photosynthetic intensity, a reduction in soil water potenti-

al due to the osmotic effects induced by salinization, improper irrigation practices, and global climate change [Zhang et al., 2020].

Salinity is considered one of the major abiotic factors limiting wheat and cotton production worldwide. It is known that cotton, a C₃ plant with significant fiber and oilseed value, is cultivated in more than 76 countries across over 32 million hectares globally. Despite its importance as a valuable industrial crop, information on the effects of salinity on physiological and metabolic processes during the reproductive development of cotton leaves and flowers remains insufficient [Babayev et al., 2023].

It has been established that at the onset of the FP in cotton, an intensification of respiration, photosynthesis, and overall metabolism is observed, along with an increase in the total content of carbohydrates and nitrogen [Madegowda, Jerry, 2014]. Studies indicate that any stress condition disrupts the balance between the generati-

on and scavenging of reactive oxygen species (ROS), resulting in alterations in the activity of the antioxidant defense system. In this regard, the investigation of functional changes in the antioxidant system under long-term exposure to high salt concentrations remains highly relevant.

It is well known that CAT, predominantly localized in peroxisomes, detoxifies H_2O_2 , a reactive oxygen species (ROS), by converting it into water and molecular oxygen in plant tissues. When stress generates low levels of H_2O_2 , APX, located in chloroplasts and the cytosol, compensates for CAT by carrying out H_2O_2 detoxification [Polesskaya, 2007].

Tavallali et al. have shown that the microelement zinc (Zn^{2+}) has a positive effect on plant development in saline soils, which depends on soil acidity, and that the influence of Zn^{2+} on plant growth occurs through the activation of antioxidants [Tavallali et al., 2010]. When zinc is deficient, plant growth and development, as well as certain metabolic processes such as RNA metabolism and protein synthesis, are slowed. Zinc protects biomembranes from oxidative and peroxidative damage, preventing the loss of integrity and functional properties of the plasma membrane [Zeinab, 2006].

The study revealed that soluble and membrane-bound forms of CA are present in the leaves of higher plants [Guliyev et al., 2003]. Numerous forms of CA have been shown to participate in maintaining a high intrathylakoid concentration of bicarbonate ions and in organizing photosynthetic proton transport. They are also involved in energy-related processes within the membranes and intracellular environment of root system cells, in the transport of CO_2 produced during respiration to the aerial organs, primarily to the leaves, and in mineral nutrition through ion exchange mechanisms, whereby protons are transferred to the rhizosphere via ion pumps [Babayev et al., 2023].

This article presents the results on the effects of high concentrations of NaCl and $ZnSO_4$ on the antioxidant defense system and, together with carboxylating enzymes, on the activity of ion pumps in the roots during the active developmental phases of ontogenesis in the Ganja 182 cultivar of *Gossypium hirsutum* L.

Materials And Methods

Plant material and growth conditions.

For the purpose of the study, the Ganja 182 cultivar of *Gossypium hirsutum* L. was selected as the experimental material. The cotton seeds were first surface-sterilized in a 3% H_2O_2 solution for 15 minutes, then rinsed several times with double-distilled water and germinated in Petri dishes placed in dark chambers. After 5 days, the germinated seeds were transferred into 16 vegetation pots filled with equal volumes of salt solutions at the respective concentrations. One pot served as the control. Five pots were treated separately with 25, 50, 100, and 200 mM NaCl, and another five pots were treated with $ZnSO_4$ solutions at the same concentrations. Samples were collected during the active developmental phases of the plant, namely FTLF, BP və FP. Since the values obtained in the control and 25 mM treatments were similar, the results for the 25 mM salt concentration were not included in the table.

Enzyme activity measurements. The activity of CA was determined by the electrometric method according to Wilbur and Anderson [Wilbur & Anderson, 1948]. CAT activity was assayed according to Kumar and Knowles [Kumar & Knowles, 1993], while APO activity was determined following the method of Lukatkin [Lukatkin, 2002].

Quantification of total proteins, pigments, adenine nucleotides, and nicotinamide coenzymes. The pigment content in leaves was determined spectrophotometrically according to Sims and Gamon [Sims & Gamon, 2002]. The lipid content was determined following the method of Ermakov et al. [Ermakov et al., 1987], and the total protein content was measured colorimetrically according to Lowry. The content of adenine nucleotides was determined according to Ermakova [Ermakova, 2005], and the content of nicotinamide coenzymes was assessed spectrophotometrically following Wahl and Kozaroff [Wahl & Kozaroff, 1962].

Measurement of gas exchange parameters. Gas exchange parameters-transpiration rate (T_r), photosynthetic intensity (P_n), stomatal conductance (g_s), and intercellular CO_2 con-

centration (C_i) were determined using the LI-6400XT infrared gas analyzer (LI-COR Biosciences, USA).

Statistical analysis. The values presented in the tables and the diagram represent arithmetic means and reflect the standard deviation. During the analysis of the final results, the mean values and their standard errors ($M \pm m$) were taken into account.

Results And Discussion

The results of our study on gas exchange parameters (P_n , T_r , C_i , and g_s) are presented in Table 1. As seen from the table, during the FP, there is a slight decrease in the intercellular CO_2 concentration, stomatal conductance, and transpiration rate across all salt treatments. In contrast, the photosynthetic intensity increases, while the other gas exchange parameters show a decrease in all treatments (Table 1).

Table 1

Effect of chloride and sulfate salts on the dynamics of changes in gas exchange parameters and pigment content in the leaves of cotton plants during active developmental phases

Variants	C, mM	Values of gas exchange parameters				Content of photosynthetic pigments					
		P_n	C_i	g_s	T_r	Chl a	Chl b	Chla/b	Chl (a+b)	Car	Chl/Car
First true leaf formation											
NaCl	C	10.8	233.0	0.36	1.29	0.19	0.11	1.73	0.38	0.24	1.17
	100	10.6	229.0	0.33	1.29	0.41	0.22	1.86	0.63	0.44	1.43
	200	10.2	227.0	0.32	1.27	0.22	0.23	0.96	0.45	0.26	1.73
ZnSO ₄	100	10.9	218.0	0.23	1.70	0.24	0.23	1.04	0.47	0.30	1.57
	200	10.5	216.0	0.23	1.69	0.18	0.14	1.29	0.32	0.16	2.0
Budding phase											
NaCl	C	14.3	243.0	0.49	1.58	0.27	0.11	2.45	0.38	0.24	1.1
	100	15.1	242.0	0.46	1.56	0.53	0.17	3.12	0.70	0.75	0.9
	200	14.5	241.0	0.43	1.55	0.23	0.11	1.09	0.34	0.32	1.0
ZnSO ₄	100	16.2	232.0	0.32	1.51	0.38	0.23	1.15	0.61	0.34	1.7
	200	15.9	235.0	0.37	1.51	0.15	0.14	1.0	0.29	0.12	2.4
Flowering phase											
NaCl	C	16.9	246.0	0.53	1.64	0.27	0.11	2.45	0.38	0.24	1.3
	100	16.9	241.0	0.53	1.64	0.44	0.44	1.0	0.88	0.61	1.3
	200	16.3	236.0	0.51	1.64	0.17	0.17	1.0	0.34	0.24	1.4
ZnSO ₄	100	17.4	233.0	0.50	1.63	0.4	0.35	1.14	0.75	0.19	4.0
	200	17.0	236.0	0.51	1.63	0.13	0.10	1.03	0.21	0.10	2.1

Note: P_n - $\mu\text{mol } CO_2 \cdot m^{-2} \cdot s^{-1}$, C_i - $\mu\text{mol } CO_2 \cdot m^{-2} \cdot s^{-1}$, g_s - $mmol H_2O \cdot m^{-2} \cdot s^{-1}$, T_r - $mmol H_2O \cdot m^{-2} \cdot s^{-1}$. Chl a - chlorophyll a, Chl b - chlorophyll b, Car - carotenoid, C - control. The statistical significance is less than 3%.

As seen from Table 1, the values of gas exchange parameters vary depending on the type of salt. Thus, although P_n increases over time under 100 mM NaCl and ZnSO₄, it decreases at higher concentrations. C_i and g_s decrease in the FTLF phase under stress from both salts, but in the BP and FP phases, they increase under 100–200 mM NaCl. Under 200 mM ZnSO₄, P_n accelerates in all three developmental phases. Only T_r remains relatively stable across all developmental phases and salt concentrations (Table 1).

As shown in Table 1, in each of the studied phases, except for P_n , the other gas exchange parameters in the control variants showed a slight increase following a similar trend. Accordingly, although the amounts of Chl a, Chl b, Car, and the Chl/Car ratio were relatively similar in the control variants, different results were obtained under salt treatment conditions. Thus, at a concentration of 100 mM NaCl, the values of gas exchange parameters decreased compared with the control, whereas the pigment con-

tent, in contrast, increased. Similar results were obtained in the presence of 200 mM NaCl. At 200 mM NaCl, the values of all studied parameters in all variants were noticeably lower than those obtained at 100 mM NaCl. In the presence of 100 and 200 mM ZnSO₄, compared with 100 and 200 mM NaCl treatments, P_n and T_r increased, whereas C_i and g_s decreased at both salt concentrations. The increase in P_n may be associated with reduced diffusion of C_i into the cell under stress conditions, when other parameters are decreased. Moreover, these results may also be attributed to reduced activity of enzymes whose substrate is CO₂.

Similar results to those observed in the FTLF were obtained in the BP across all variants. Thus, in the BP, due to the transition of the plant to a more advanced developmental stage, the contents of Chl a, Chl b, and Car under 100 and 200 mM NaCl and ZnSO₄ treatments were higher compared with the control variant. Similar trends were also observed in the total pigment content.

In the FP, although the P_n values at 100, 200 mM ZnSO₄ were higher than those at the corresponding NaCl concentrations, the values of T_r, C_i and g_s under ZnSO₄ treatment were lower compared with NaCl treatment. It was found that at 100 mM NaCl, the increase in the Chl a/b ratio was accompanied by a parallel increase in the Chl/Car ratio. As seen from the comparison of P_n with the Chl a/b and Chl/Car ratios in the FP, the values of these three parameters were as follows: under 100, 200 mM NaCl, the Chl a/b ratio was 1.0 and 1.0, while the Chl/Car ratio was 1.44 and 1.42. Under ZnSO₄ treatment, the Chl a/b ratio was 1.14 and 1.03, respectively, and the Chl/Car ratio was 3.95 and 2.1. Under both salt concentrations, the corresponding P_n values were 16.9, 16.3, 17.4, and 17.0, respectively. It can be concluded that, in discussing plant tolerance to stress conditions, the ratios of parameters provide more informative insights than their absolute values.

The analysis of these indicators demonstrates that under salinity conditions, irrespective

of the type and concentration of the salt, defense responses in plants are consistently higher than in the control variants. The main differences depend on the plant developmental stage, the type of salt, its plasticity, and its concentration. A specific mechanism was observed whereby, in the presence of NaCl, pigments exhibited more pronounced changes compared with gas exchange parameters, reflecting their physiological significance. These alterations appear to be associated with the induction of stronger stress under NaCl treatment. In contrast, ZnSO₄, being a milder and more physiologically plastic salt, does not cause severe disruption of physiological processes and is therefore more effective compared with NaCl.

Table 2 presents the effects of NaCl and ZnSO₄ on enzyme activity, as well as on the content of intermediate metabolites and biopolymers. As shown in the table, CA activity was more strongly stimulated by ZnSO₄ at concentrations of 50, 100, and 200 mM compared with NaCl treatment. The increase in CA enzyme activity up to a certain level, followed by a decline depending on exposure time and salt concentration, is associated with the physiological state attained by the plant under stress conditions. This pattern was more clearly pronounced in the presence of ZnSO₄ (Table 2).

The dynamics of changes in the contents of ATP and ADP, as well as NAD and NADP molecules, in cotton leaves under salt stress are presented in the figure. As seen in the figure, in the control variants, the levels of adenine nucleotides and nicotinamide coenzymes increased. In the presence of 50 mM NaCl, the oxidized forms (ADP, NADP) exceeded the reduced forms (ATP, NAD) in amount, whereas at 200 mM NaCl their contents decreased in all three developmental stages studied. Besides, under ZnSO₄ treatment at concentrations of 50, 100, and 200 mM, the levels of adenine nucleotides and nicotinamide coenzymes gradually declined over time in all developmental phases.

Table 2

Effect of chloride and sulfate salts on the dynamics of changes in enzyme activity and biopolymer content in the leaves of cotton plants during active growth phases

Parameters	NaCl, mM			ZnSO ₄ , mM		
	50	100	200	50	100	200
First true leaf formation						
CA	37±4.12	30±4.01	30.0±4.31	42±5.01	50±5.78	48.8±5.55
CAT	0.199±0.03	0.233±0.05	0.296±0.06	0.478±0.08	0.521±0.04	0.522±0.12
APX	0.604±0.08	0.701±0.09	0.734±0.09	1.591±0.51	2.23±0.18	2.1±0.22
ATPase	0.31±0.02	0.98±0.01	0.82±0.04	0.43±0.01	1.09±0.05	1.05±0.06
H ₂ O ₂	2.9±0.64	2.1±0.53	1.6±0.24	2.2±0.56	2.0±0.36	1.4±0.24
Protein	18.6±2.4	17.2±2.1	9.89±1.1	20.5±3.8	18.2±3.4	12.3±2.9
Budding phase						
CA	37±3.98	39±4.91	38.7±6.01	53±7.11	53±4.01	50.9±5.95
CAT	0.181±0.02	0.256±0.019	0.318±0.09	0.429±0.06	0.533±0.019	0.504±0.08
APX	0.324±0.05	0.683±0.02	0.735±0.09	1.647±0.62	2.5±0.093	2.4±0.1
ATPase	0.23±0.01	0.47±0.02	0.92±0.09	0.51±0.04	1.23±0.06	1.19±0.09
H ₂ O ₂	3.5±0.65	3.0±0.47	2.3±0.16	2.6±0.59	2.2±0.14	1.4±0.22
Protein	17.9±2.8	16.6±2.1	13.4±2.9	23.7±3.6	21.5±3.1	20.2±3.9
Flowering phase						
CA	49±6.63	50±3.62	48.6±4.72	54±4.08	53±0.03	36±4.65
CAT	0.135±0.04	0.251±0.02	0.310±0.08	0.460±0.07	0.47±0.06	0.421±0.07
APX	0.324±0.07	0.436±0.019	0.398±0.08	1.440±0.39	1.31±0.12	1.02±0.1
ATPase	0.24±0.02	0.49±0.02	0.88±0.02	0.57±0.03	1.27±0.09	1.22±0.08
H ₂ O ₂	3.8±0.66	3.1±0.62	2.8±0.31	2.9±0.61	1.8±0.12	0.9±0.06
Protein	18.3±3.1	17.5±2.1	15.8±2.2	24.8±4.9	25.5±4.7	24.7±4.9

Note: CAT-catalase ($\mu\text{mol H}_2\text{O}_2\cdot\text{g}^{-1}\cdot\text{min}^{-1}$), APX-Ascorbate peroxidase ($\mu\text{mol ascorbate}\cdot\text{g}^{-1}\cdot\text{min}^{-1}$), CA-EU mg/protein, H₂O₂-Hydrogen peroxide (mg/ml), First true leaf formation (FTLF), Budding phase (BP), Flowering phase (FP), C_{H+}-Hydrogen ion concentration at the corresponding pH ($\Delta\text{H}\cdot 10^{-4}$ eq)

The dynamics of changes in the contents of ATP and ADP, as well as NAD and NADP molecules, in cotton leaves under salt stress are presented in the figure.

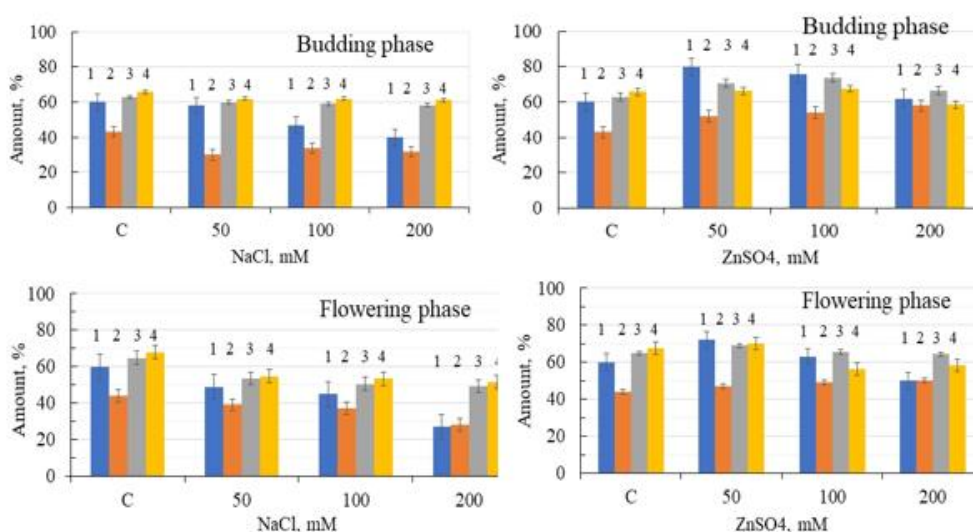


Figure. Effect of different concentrations of NaCl and ZnSO₄ on the dynamics of changes in adenine nucleotides and nicotinamide coenzymes in cotton leaves during active growth phases. 1-ATP, 2-ADP, 3-NAD, 4-NADP

As seen in the figure, in the control variants, the levels of adenine nucleotides and nicotinamide coenzymes increased. In the presence of 50 mM NaCl, the oxidized forms (ADP, NADP) exceeded the reduced forms (ATP, NAD) in amount, whereas at 200 mM NaCl their contents decreased in all three developmental stages studied. Besides, under ZnSO₄ treatment at concentrations of 50, 100, and 200 mM, the levels of adenine nucleotides and nicotinamide coenzymes gradually declined over time in all developmental phases.

Thus, the studies demonstrate that salt stress leads to a decrease in ATP content. In

contrast, the levels of nicotinamide coenzymes increase during the initial days of stress but decline as the stress persists. These findings suggest that at the early stage of stress, when young plants exhibit a gradually increasing demand for nicotinamide coenzymes, energy metabolism enzymes become progressively activated. As a result, ATP molecules, serving as the primary energy source, are synthesized. Under salt stress conditions, the organism enhances the utilization of its energy reserves as a protective mechanism, which consequently leads to a gradual depletion of ATP content.

Conclusion

The studies indicate that carbonic anhydrase and H⁺-ATPases function in coordination even under salt stress conditions. In the presence of Zn²⁺ ions in the medium, the rate of photosynthesis accelerates and photosynthetic productivity increases. With an increase in salt concentration up to 200 mM, catalase and ascorbate peroxidase activities also rise over time. However, their subsequent gradual decline may be explained by the destructive effects of excessive salt accumulation in leaves on cellular and tissue structures. It has been established that as plants age and stress intensity increases, the plants' adaptive responses to these factors also become stronger.

Lipid analysis revealed that since oil content is genotype-dependent, salt stress causes only minor changes in its level, and these changes do not depend on the nature of the salt. Furthermore, the steadily increasing requirement of young plants for nicotinamide coenzymes contributes to the progressive stimulation of enzymes involved in energy metabolism, ultimately enhancing ATP production, which functions as the main cellular energy source. Under salt stress, the organism enhances the efficient utilization of its energy reserves as a protective mechanism, leading to a gradual depletion of ATP content.

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PAMBIQ BİTKİSİNDƏ NaCl və ZnSO₄-ÜN MÜXTƏLİF QATILILARININ ANTIOKSİDANT SİSTEMİN VƏ ANABOLİZMİN BƏZİ FERMENTLƏRİNƏ TƏSİRİNİN TƏDQIQI

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Xülasə: Məqalədə adi pambıq (*Gossypium hirsutum* L.) bitkisinde NaCl və ZnSO₄ duzlarının 25, 50, 100 və 200 mM qatılıqlarında antioksidant fermentlərdən katalaza (KAT) və askorbat peroksidaza (APO), karbon mübadiləsi fermentlərindən karboanhidraza (KA), kök sistemində isə H⁺-ATF-aza fermentlərinin aktivliyinə təsiri tədqiq olunmuşdur. Müəyyən olunmuşdur ki, KA və H⁺-ATF-aza fermentlərinin aktivliyi Zn²⁺ ionlarının iştirakı şəraitində adekvat olaraq artır. Bitkinin ontogenezinin ilk yarpaqlama (İYF), qönçələmə (QF) və çiçəkləmə (ÇF) fazalarında duzların qatılığının 200 mM-dək tədricən yüksəlməsi KAT və APO fermentlərinin aktivliyinin artmasını, sonra isə tədricən azalmasını stres zamanı yaranan H₂O₂-nin miqdarı ilə əlaqədar olduğunu qeyd etmək olar. Duz stresində yağların miqdarının cüzi dəyişməsi duzun təbiətindən asılı olmur. Cavan bitkilərin nikotin kofermentlərinə ehtiyacının artması öyrənilən fermentlərin tədricən aktivləşməsinə və nəticədə ATF-in sintezinin artmasına gətirib çıxarır. Stres mühitində bunlardan fərqli olaraq ATF-in miqdarı tədricən azalır.

Açar sözlər: *Gossypium hirsutum* L., NaCl, ZnSO₄, KA, KAT, APO, H⁺-ATF-aza, davamlılıq

ВЛИЯНИЕ РАЗЛИЧНЫХ КОНЦЕНТРАЦИЙ NaCl и ZnSO₄ НА ANTIОКСИДАНТНУЮ СИСТЕМУ И НЕКОТОРЫЕ АНАБОЛИЧЕСКИЕ ФЕРМЕНТЫ У ХЛОПЧАТНИКА

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Аннотация: В статье исследуется влияние NaCl и ZnSO₄ в концентрациях 25, 50, 100 и 200 mM на активность антиоксидантных ферментов - каталазы (CAT) и аскорбатпероксидазы (APX), а также ферментов углеродного обмена: карбоангидразы (CA) и H⁺-АТФазы в корневой системе хлопчатника (*Gossypium hirsutum* L.). Установлено, что активность ферментов CA и

H⁺-АТФаза адекватно увеличивается в присутствии ионов Zn²⁺. В онтогенетических фазах формирования первого настоящего листа (FTLF), бутонизации (BP) и цветения (FP) постепенное увеличение концентрации солей до 200 мМ приводит к росту активности САТ и АРХ, за которым следует постепенное снижение, что может быть связано с количеством H₂O₂, образующегося в условиях стресса. При солевом стрессе незначительные изменения в содержании липидов не зависят от природы соли. Повышенная потребность молодых растений в никотинамидах коферментах приводит к постепенной активации изучаемых ферментов и, соответственно, к усилению синтеза АТФ. Напротив, при стрессовых условиях содержание АТФ постепенно снижается.

Ключевые слова: *Gossypium hirsutum* L., NaCl, ZnSO₄, СА, САТ, АРХ, H⁺-АТФаза, толерантность