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ABSTRACT

of the dissertation for the degree of Doctor of Philosophy

INVESTIGATION OF NADPH-GENERATING ENZYMES IN MAIZE SEEDLINGS GROWN UNDER ABIOTIC STRESS CONDITIONS

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Field of science:	Biology
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GENERAL CHARACTERISTICS OF THE RESEARCH

The relevance of the topic and the degree of completion. All living things, including plants are always subject to impacts of extreme factors of the environment of their habitat in this or other way[1]. In its relatively mild form, the plants build up multicomponent defense reaction with different and complex characteristics in the direction of reduction or elimination of complications of stress in plants and their adaptation to their habitat[2]. When the stress is severe and intolerable, the defense reaction of plants cannot cope with the outcomes caused by stress and this leads to their death[2]. It is worth to note that the defense reactions united under the term of phyto-immune have a kind and population peculiarity, as well as the individual one. Thus, whereas some kinds and populations can survive under the certain stress condition, the others cannot bear it. All the above mentioned shows how combined and even individual the defense reactions of plants in extreme conditions are[3]. The impacts of various stress factors are accompanied by the creation of reactive oxygen species (ROS) and this, in its turn, leads to the damage of cell components. Different non-fermented and fermented antioxidant systems have been formed by plants to neutralize the ROS.

Non-fermented antioxidant substances mainly include ascorbic acid, tocopherols, carotenes and carotenoids, flavonoids, anthocyanins[4].

Fermented systems include the enzyme systems such as superoxide-dismutase, catalase, polyphenoloxidases, and different peroxidases[5]. For the functioning of the majority of the fermented

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2 Kopecká, R. Abiotic Stress in Crop Production / R.Kopecká, M.Kameniarová, M.Černý [et al.]: [Electronic resource]. International Journal of Molecular Sciences, 2023, 24(7), 6603, URL: https://doi.org/10.3390/ijms24076603

3 Zhu, J. Abiotic Stress Signaling and Responses in Plants // Cell, –2016. 167, –p.313-324.

4 Munns, R., Tester, M. Mechanisms of salinity tolerance // Annu Rev, Plant Biol., –2008. 59, –p.651-681.

5 Haida, Z., Hakiman, M. A comprehensive review on the determination of enzymatic assay and nonenzymatic antioxidant activities // Food Science and Nutrition, –2019, 7, –p.1555-1563

antioxidant systems requires the participation of NADPH molecule. This is provided by the functioning of totally a number of NADPH - generating pro-oxidant enzyme systems existing in a cell[6]. These enzymes include Glucose-6-phosphate dehydrogenase (G6PDH, EC 1.1.1.49), Malate dehydrogenase (decarboxylating) (DMDH, malic enzyme, EC 1.1.1.40), and isocitrate dehydrogenase (NADP-ICDH, EC 1.1.1.42). The information about the role of these enzymes in the defense system has been covered in numerous materials[7].

Nevertheless, the case study into the role of NADPH in the protection of plants against the impacts of various stress factors, particularly under the combined impact of two or more stress is of relevant issues.

Object and content of the research. Activity dynamics of NADPH-generating enzymes in Zagatala locally improved, Zagatala-68, Zagatala-420, and Gurur genotypes of maize (*Zea mays* L.) plant taken from the Genetic Resources Institute of the Ministry of Science and Education of the Republic of Azerbaijan as an object of the research.

The purpose and tasks of the research. The purpose of the research is to assess the role of cytoplasmic forms of NADPH - generating G6PDH, DMDH, and ICDH enzymes, which play an important role in realization of response reactions against the stress in maize genotypes, cultivated under stress condition and perform as pro-oxidant enzymes in defense response and environmental adaptation of maize seedlings. To achieve the abovementioned objective, the tasks are as the following:

– Preparation of the cultivation condition of maize plant;

– Determination of activity of G6PDH, NADP-ME and NADP-ICDH enzymes in an extract obtained from corn seedlings;

– Study into the impacts of salt stress created through the

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[7] Corpas, F.J. Activation of NADPH-recycling systems in leaves and roots of Arabidopsis thaliana under arsenicinduced stress conditions is accelerated by knock-out of Nudix hydrolase 19 (AtNUDX19) gene / F.J.Corpas, S.Aguayo-Trinidad, T.Ogawa [et al] // J. Plant Physiol., –2016. 192, –p. 81-89

different rates of concentrations of Na^+- isocationic neutral salt (NaCl and Na_2SO_4) solutions on the biometric indicators of the development of maize seedlings and in this regard, on the activity dynamics of cytoplasmic forms of G6PDH, NADP-ME and NADP-ICDH enzymes;

– Analysis of the separate and combined impact of salt (100 mM NaCl) and drought stress on maize seedlings and the activity dynamics of enzymes;

– Determination of the combined impact of salt (100 mM NaCl) and γ - radiation on the development of maize seedlings and changes in the activity dynamics of G6PDH, NADP-ME and NADP-ICDH enzymes;

– Study the impact of stress condition created by the separate and combined effect of iron (III) oxide nanoparticles (γ-Fe_2O_3) with the γ-radiation, drought and salt stress on the development of maize seedlings and the activity dynamics of the cytoplasmic forms of the G6PDH, NADP-ME and NADP-ICDH enzymes;

– Monitoring of the changes in the absorption of mineral elements from the environment and their distribution within the tissues by maize seedlings in relation to stress condition;

– Assessment of the role of cytoplasmic forms of G6PDH, NADP-ME and NADP-ICDH enzymes in response reactions against the combined stress factors;

– Review of Electron Paramagnetic Resonance (EPR) under control and stress conditions for studying the paramagnetic centers in maize seedlings.

Research methods. Salt stress was created by irrigation with separate and combined solutions of NaCl and Na_2SO_4 salts, drought stress - by intermittent irrigation, radiation - by different doses of gamma rays, and the effect of Fe_2O_3 nanoparticles was studied.

The main points of the dissertation for defense:

– The involvement degree of cytoplasmic G6PDH, NADP-ME and NADP-ICDH enzymes in the formation of reducing potential related to the development of maize seedlings varies. This function is mainly performed by G6PDH in the early stages of development, and by NADP-ME and NADP-ICDH enzymes in the final stages respectively;

– Depending on the nature of the stress created in the course of the combined stress, the involvement degree of G6PDH, NADP-ME and NADP-ICDH;

– The joint impact of salt stress and ionizing gamma radiation leads to an increase in the negative effects of stress in maize seedlings and a decrease in the activity of prooxidant enzymes;

– The combined stress leads to severe changes in the nutrition of maize seedlings and the inter-tissue distribution of mineral elements;

– Iron (III) oxide (γ-Fe_2O_3) nanoparticles can draw out the negative impact of ionizing radiation, salt and drought stress on maize seedlings.

– Changes in the combined stress-related activity dynamics of G6PDH, NADP-ME and NADP-ICDH enzymes can be used as a valuable source of information in the creation of stress-resistant maize varieties;

– Stress factors cause the formation of (EPR) signals in maize seedlings.

Scientific innovation of research. The activity dynamics of cytoplasmic forms of G6PDH, NADP-ME, and NADP-ICDH enzymes performing the function of pro-antioxidant enzymes in the defense reaction against the stress in maize, especially the maize genotypes characteristic for Azerbaijan, under the influence of combined stress factors, have been comprehensively studied for the first time, and information on the extent of their engagement in this process in which situations has been obtained. It has been identified that in the early stages of the development of maize seedlings, the formation of NADPH potential is provided mainly by G6PDH enzyme, and in the final stages by NADP-ME and NADP-ICDH enzymes. During the combined stress, the degree of engagement of proantioxidant enzymes in the defense reaction against the consequences of stress differs depending on the nature of the stress. The combined impact of ionizing radiation and salt stress has a synergistic effect and thus, strengthens the negative impact of stress, and negatively affects the activity of pro-antioxidant enzymes. Either individual or combined stress causes severe changes in the course of feeding of maize seedlings and of the transfer process of mineral elements to the organs. Iron (III) oxide (γ-Fe_2O_3) nanoparticles can diminish the negative impact of control, drought, salt, and ionizing stress on maize seedlings.

Theoretical and practical significance of the research. Maize plant, which is used as a model plant for researches, enjoys significant strategic importance for its consumption in the world. On numerous occasions, this plant is subject to the impact of individual and combined abiotic stress factors negatively affecting its growth, development, and production. In order to neutralize these impacts and maintain the liveness capacity of plants, specific defense reactions have been formed during the evolution process and one of their important components is the pro-antioxidant enzymes. Therefore, the analysis of the engagement of these enzymes in the elimination process of damages caused by the various stress factors is definitely important.

In the conducted studies, it was determined that the activity of G6PDH and NADP-ME enzymes are mainly used in the process of eliminating the effects of NaCl salt, and NADP-ICDH enzymes is used in eliminating the complications of Na_2SO_4 salt. The stimulating effect of Iron (III) oxide (γ-Fe_2O_3) nanoparticles at low doses in both control and drought, salt and gamma radiation stress has been identified.

Approbation of the research. The main scientific conclusions of the dissertation have been submitted and discussed in the 9th International Scientific Conference on "Modern Innovative Approaches" dedicated to the 100th anniversary of Baku State University (Baku, 2019), Scientific-practical Conference on "Development of Ecologically Clean Agriculture in Azerbaijan" (Ganja, 2019), the 28th International Scientific-practical Conference on "International trends in science and technology" (Warsaw, 2021), the 11th International Conference on "Achievements and Problems in Biology" dedicated to the 120th anniversary of Mirali Akhundov, Professor of Baku State University (Baku, 2022), Republic scientific conference on "Actual problems of Biology in the context of continuous development" dedicated to the 100th anniversary of National Leader of the people of Azerbaijan Heydar Aliyev (Baku, 2023), the 2nd International conference on Protection of Biodiversity in Eurasia by Ege University (Izmir, 2024), as well as the seminars at the faculty of Biology at the Baku State University.

Organization where the dissertation was carried out. The main experiments of the dissertation work have been conducted in the scientific research laboratories of Baku State University, the irradiation of seeds in the High Technologies Park of the Ministry of Science and Education of the Republic of Azerbaijan, the EPR calculations in the Institute of Radiation Problems of the Ministry of Science and Education of the Republic of Azerbaijan, and the study of the organic and inorganic composition of the plant in the Analytical Center of the Institute of Geology and Geophysics accordingly.

Publications. Based on the dissertation, 19 scientific papers, such as articles, conference materials, and theses have been published in local and foreign journals.

Volume and structure of the dissertation. The dissertation work consists of an introduction (24 647 characters), 5 chapters (chapter I - 86 104 characters, chapter II - 16 292 characters, chapter III - 51 735 characters, chapter IV - 3 955 characters, chapter V - 18 826 characters) 23 paragraphs, 9 clauses, conclusion (3 443 characters), results (2 556 characters), recommendations (1 468 characters), a list of 187 different references, a list of abbreviations and appendixes. The paper contains 32 figures and 18 tables. The total volume of the work (excluding figures, diagrams, tables, a list of abbreviations and symbols and appendixes) consists of 209 026 characters, and 161 pages.

CHAPTER I. LITERATURE REVIEW

This chapter provides information with regard to the impact of abiotic stress factors on the plants, defense systems of plants against stress, the role of G6PDH, NADP-ME and NADP-ISDH enzymes among the NADPH-generating enzymes in their defense systems have been analyzed.

CHAPTER II. MATERIAL AND METHODS

As an object of the research, the Zagatala locally improved, “Zagatala-68”, “Zagatala-420”, and “Gurur” varieties of the maize plant (*Zea mays* L.) belonging to C_4 plants group were selected.

The seeds have been irrigated through the relevant salt solutions to create salt stress, and have been processed with 20-40 nm iron (III) oxide (γ-Fe_2O_3) nanoparticles in the "Vortex" blender to study the impact of iron nanoparticles[8].

The irradiation process with ionizing gamma radiation has been conducted in "RUHUND-20000" device with a Co^{60} source. Except for the control variant, the other variants have been exposed to ionizing gamma radiation at doses of the 50 Gy, 100 Gy, 150 Gy, 200 Gy, 250 Gy, 500 Gy and 750 Gy.

Amount of minerals has been determined in atomic Absorption Agilent technology 200 series AA with the accuracy of $n \cdot 10^{-5}$ $n \cdot 10\%$.

The activity of the enzymes has been determined spectrophotometrically, at a wavelength of 340 nm, in the "MRC" (Israel) spectrophotometer in accordance with the rate of reduction of NADP in 1.0 ml spectrophotometric cuvettes. mM NADPH/min/g wet weight has been used as the enzyme unit (Hans-Ulrich Bergmeyer method, 1950-1960). The reaction has been done at 25ºC, and the measurements have been repeated 3-5 times. Tissue: the extraction solution was taken in a ratio of 1g:5 ml. The preparation of the homogenate and determination of enzyme activity have been the same for all enzymes in terms of procedure, with the solutions used being different in composition[9, 10].

During the research, statistical analyses were conducted using IBM SPSS Statistics version 26.0. Student's t-test was employed to assess differences between groups. The analyses included calculations of standard deviations, confidence intervals, and standard errors for the obtained results. Differences were considered statistically significant at p-values ≤ 0.001, ≤ 0.01, and ≤ 0.05.

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CHAPTER 3. THE INDIVIDUAL AND COMBINED EFFECTS OF NACL AND NA_2SO_4 SALTS AT DIFFERENT CONCENTRATIONS ON MAIZE SEEDLINGS

In experiments, has been studied the combined effects of NaCl and Na_2SO_4 salts at different concentrations on corn plants.

3.1.The effect of different ratios of NaCl and Na_2SO_4 salts on the germination characteristics of maize seeds. Germination process of seeds has happened within a certain period of time, not a given one. In the control variant of Zagatala locally improved maize genotype, the germination process has been 53% after 48 hours of incubation period, 83% after 72 hours, and 95% after 96 hours, respectively. The same situation has been observed in the seeds of "Zagatala-68" and "Gurur" genotypes. Among the genotypes, relatively higher germination rate has been with regard to the Zagatala locally improved one, and relatively lower germination rate has been observed in "Gurur" genotype.

3.2. The individual and combined effects of different ratios of NaCl and Na_2SO_4 salts on the biometric parameters of maize seedlings. Taking into account the fact that the plants are more sensitive against the abiotic stress factors during the initial stages of their development, the impact of stress on the development of seedlings has been observed on 4^{th}, 8^{th}, and 12^{th} days of the germination process. Affect the developmental change of the root and stem tissue of maize genotypes has been given in Table 1.

As can be seen from the table (Table 1), both salts lead to an increase in stress. The gradual replacement of NaCl salt by Na_2SO_4 in the environment led to a further increase in this variation in proportion to the concentration of Na_2SO_4 salt in the environment. For example, in comparison with the control variant, while the development of the root and stem system under 100 mM NaCl salt stress condition has been 39.4% and 38.4%, respectively, under 100 mM Na_2SO_4 salt condition, the analogous figures have been 62.5% and 62.9%. According to the results, the Zagatala locally improved maize genotype demonstrated a relatively higher tolerance to both separate and combined salt stress, compared to the Zagatala-68 and Gurur genotypes.

Table 1. The individual and combined effects of NaCl and Na_2SO_4 salts at different ratios on the growth (cm) of seedlings in the Zaqatala local improved genotype

Days / Variants	Day 4	Day 8	Day 12
Control	leaf– 5.1±0.03 root– 3.2±0.19	leaf–7.4±0.31 root – 4.8±0.22	leaf–9.9±0.07 root – 7.3±0.05
NaCl 100 mM	leaf–3.5**±0.09 root – 2.9**±0.03	leaf–5.1***±0.33 root – 3.8*±0.09	leaf–6.0***±0.06 root – 4.5***±0.06
NaCl 75 mM 25 mM Na_2SO_4	leaf–3.3**±0.07 root – 2.6**±0.06	leaf–4.4***±0.33 root – 3.4** ±0.12	leaf– 5.2**±0.20 root – 4.2***±0.03
NaCl 50 mM 50 mM Na_2SO_4	leaf–3.0**±0.07 root – 2.3**±0.06	leaf–4.2***±0.33 root – 3.0*±0.20	leaf–5.0***±0.33 root – 3.8***±0.07
NaCl 25 mM 75 mM Na_2SO_4	leaf–2.7***±0.03 root – 2.0**±0.03	leaf–3.7***±0.33 root – 2.6**±0.17	leaf–4.4***±0.12 root – 3.1***±0.09
Na_2SO_4 100 mM	leaf– 2.2**±0.23 root – 1.7**±0.06	leaf– .1***±0.09 root – 2.3**±0.15	leaf–3.8***±0.09 root – 2.7***±0.09

Note: ***, **, * are statistically significant at $p \leq 0,001$ $p \leq 0,01$ and $p \leq 0,05$ levels of probability

3.3. The individual and combined effects of NaCl and Na_2SO_4 salts at different ratios on the activity dynamics of NADPH-generating enzymes in maize seedlings. With regard to the development of the Zagatala locally improved maize genotype seedlings, the activity dynamics of NADPH-generating enzymes and results of the individual and combined impact of NaCl and Na_2SO_4 salt solutions on the course of this process have been demonstrated in Table 2.

As can be seen from Table 2, with regard to the development of seedlings (control), the activity of the G6PDH enzyme gradually decreases and this decrease in 12-day-old seedlings is 35.6%

compared to 4-day-old seedlings. On the contrary, during this development phase, the activity of the NADP-ME and NADP-ICDH enzymes has increased by 37% and 13.4%, respectively in comparison with the initial period. This indicates that the formation of cytoplasmic NADPH potential in the early stages of the development of the Zagatala locally improved maize genotype seedlings is mainly done thanks to the activity of G6PDH enzyme, and in the later stages, mainly the activity of the NADP-ME and NADP-ICDH enzymes.

Table 2. The individual and combined effects of NaCl and Na_2SO_4 salts at different ratios on the activity (µM/min/g/wet weight) dynamics of NADPH-generating enzymes in the Zaqatala local improved genotype

Variants	G6PDH activity			DMDH activity			ICDH activity		
	Day 4	Day 8	Day 12	Day 4	Day 8	Day 12	Day 4	Day 8	Day 12
Control	103.3 ±0.11	80.4 ±0.19	66.5 ±0.47	77.6 ±0.52	95.4 ±0.41	106.3 ±0.38	93.6 ±0.22	108.1 ±0.41	106.6 ±0.61
100 mM NaCl	110.1^{**} ±0.21	99.8^{**} ±1.00	76.2^{*} ±1.27	88.7^{ns} ±0.67	117.3^{**} ±0.62	123.4^{**} ±1.22	96.8^{ns} ±1.15	105.5^{ns} ±1.06	108.3^{ns} ±1.08
50 mM NaCl+ 50 mM Na_2SO_4	97.8^{*} ±1.00	91.1^{**} ±0.95	75.4^{*} ±1.13	84.4^{*} ±0.55	99.7^{*} ±0.45	110.0^{*} ±1.55	98.3^{ns} ±1.12	109.8^{ns} ±1.40	113.6^{*} ±2.39
100 mM Na_2SO_4	92.3^{**} ±0.85	77.1^{ns} ±2.17	67.8^{ns} ±1..45	80.3^{ns} ±1.03	96.2^{ns} ±0.40	99.6^{*} ±2.97	105.7^{ns} ±29.71	121.1^{***} ±0.26	127.9^{**} ±0.47

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability, ns - non-significant

In Tables 3 and 4, a similar dependence is characteristic in the impact of stress factors on the activity of NADPH-generating enzymes in maize seedlings.

Interestingly, the total activity level of enzymes at different development stages of seedlings practically does not change.

The changed one is the degree of engagement of enzymes in the formation of the total NADPH potential. Thus, G6PDH is more actively engaged in performing this function in the first stage of development, and NADP-ME in the later stage. The engagement of the NADP-ICDH enzyme in this process is relatively stable.

Table 3. The individual and combined effects of NaCl and Na_2SO_4 salts at different ratios on the activity (µM/min/g/wet weight) dynamics of NADPH-generating enzymes in the Zaqatala-68 genotype

Variants	G6PDH activity			DMDH activity			ICDH activity		
	Day 4	Day 8	Day 12	Day 4	Day 8	Day 12	Day 4	Day 8	Day 12
Control	92.2 ±0.23	79.2 ±0.72	60.5 ±0.87	73.6 ±0.47	84.5 ±0.41	91.3 ±0.57	86.5 ±0.95	98.3 ±0.12	104.1 ±0.26
100 mM NaCl	108.4^{**} ±0.18	115.1^{**} ±1.25	103.3^{*} ±1.35	71.4^{*} ±0.58	83.5^{**} ±0.52	89.22^{**} ±1.13	95.3^{ns} ±1.09	106.7^{*} ±1.12	113.4^{ns} ±1.12
50 mM NaCl+ 50 mM Na_2SO_4	98.2^{*} ±0.98	87.7^{**} ±0.83	71.4^{*} ±1.02	81.3^{*} ±0.39	97.9^{*} ±0.38	106.8^{*} ±0.65	99.4^{*} ±1.02	108.8^{ns} ±1.21	111.7^{*} ±1.82
100 mM Na_2SO_4	87.7^{**} ±0.97	78.1^{ns} ±1.95	63.3^{ns} ±1.23	80.3^{*} ±1.05	96.2^{*} ±0.35	99.6^{*} ±1.32	105.7^{ns} ±18.3	121.1^{***} ±0.18	127.9^{**} ±0.32

Note: ***, **, * are statistically significant at $p \leq 0{,}001$ $p \leq 0{,}01$ and $p \leq 0{,}05$ levels of probability, ns - non-significant.

Table 4. The individual and combined effects of NaCl and Na_2SO_4 salts at different ratios on the activity (µM/min/g/wet weight) dynamics of NADPH-generating enzymes in the Gurur genotype

Variants	G6PDH activity			DMDH activity			ICDH activity		
	Day 4	Day 8	Day 12	Day 4	Day 8	Day 12	Day 4	Day 8	Day 12
Control	81.1 ±0.18	63.2 ±0.63	54.4 ±0.87	53.7 ±0.22	66.5 ±0.38	72.3 ±0.41	57.2 ±0.73	73.1 ±0.28	85.9 ±0.26
100 mM NaCl	85.3^{**} ±0.23	69.8^{**} ±0.89	58.2^{*} ±1.05	65.1^{*} ±0.49	76.3^{**} ±0.49	98.9^{**} ±0.91	61.2^{ns} ±0.97	77.4^{*} ±0.75	88.7^{ns} ±1.06
50 mM NaCl+ 50 mM Na_2SO_4	88.5^{*} ±1.21	76.3^{**} ±0.79	61.1^{*} ±0.99	72.2^{*} ±0.24	86.9^{*} ±0.47	97.3^{*} ±0.49	69.9^{*} ±1.89	89.8^{ns} ±0.95	101.7^{*} ±1.72
100 mM Na_2SO_4	66.8^{**} ±0.80	71.2^{*} ±1.70	55.4^{ns} ±0.95	60.7^{*} ±0.80	71.1^{*} ±0.29	77.3^{*} ±1.29	105.7^{ns} ±12.5	121.1^{***} ±0.22	127.9^{**} ±0.28

Note: ***, **, * are statistically significant at $p \leq 0{,}001$ $p \leq 0{,}01$ and $p \leq 0{,}05$ levels of probability, ns - non-significant

3.4. The effect of different ratios of NaCl and Na_2SO_4 salts on mineral nutrition in maize seedlings. The table below shows the impact of Na^+-isocationic neutral salt mixture taken at different ratios with a concentration of 100 mM on the ionic composition of the root and stem system in the Zagatala locally improved genotype maize seedlings (Table 5).

Table 5. Combined salt stress effects on mineral nutrition and element distribution in the Zaqatala local improved genotype

Variants	Organs	K	Na	Cl	Ca	Mg	P	S	Fe
Control	root	4,116	0,534	0,57	4,214	0,694	1,091	1,112	1,271
	leaf	1,020	0,007	0,26	0,721	0,203	0,545	0,220	0,031
100 mM NaCl	root	0,589	1,024	3,18	0,850	0,221	0,248	0,248	0,240
	leaf	0,954	0,171	2,56	0,592	0,215	0,414	0,152	0,031
75 mM NaCl + 25 mM Na_2SO_4	root	0,547	1,224	2,03	0,892	0,203	0,257	0,816	0,193
	leaf	0,954	0,244	2,36	0,564	0,299	0,441	0,220	0,023
50 mM NaCl + 50 mM Na_2SO_4	root	0,829	1,143	1,74	0,742	0,209	0,270	0,984	0,256
	leaf	1,145	0,334	1,78	0,842	0,389	0,598	0,352	0,046
25 mM NaCl + 75 mM Na_2SO_4	root	0,672	1,329	1,30	0,921	0,233	0,301	1,156	0,178
	leaf	1,419	0,252	1,34	0,585	0,335	0,502	0,280	0,038
100 mM Na_2SO_4	root	0,746	1,224	0,15	1,021	0,227	0,393	1,812	0,193
	leaf	1,692	0,386	0,28	0,792	0,269	0,628	0,940	0,101

According to the figures presented in Table 5, the amount of K^+ ions in 14-day-old the Zagatala locally improved maize genotype seedlings is 4.04 times higher in root tissues than in stem tissues. This ratio is characterized by a higher figure (76.3) for Na^+ ions. Cultivation of seedlings in 100 mM NaCl salt condition for 14 days causes severe changes in the dynamics of these cations. Thus, this condition leads to a decrease by 6.99 times in the amount of K^+ ions in the root system compared to the control. In the stem system, this indicator appears in a very slight form and the analogous figure is only 1.07. That is, although the salinity of the environment has a critically negative impact on the absorption of K^+ ions by root tissues and the ion (Na^+-K^+ exchange) exchange, it does not prevent its distribution within the tissues.

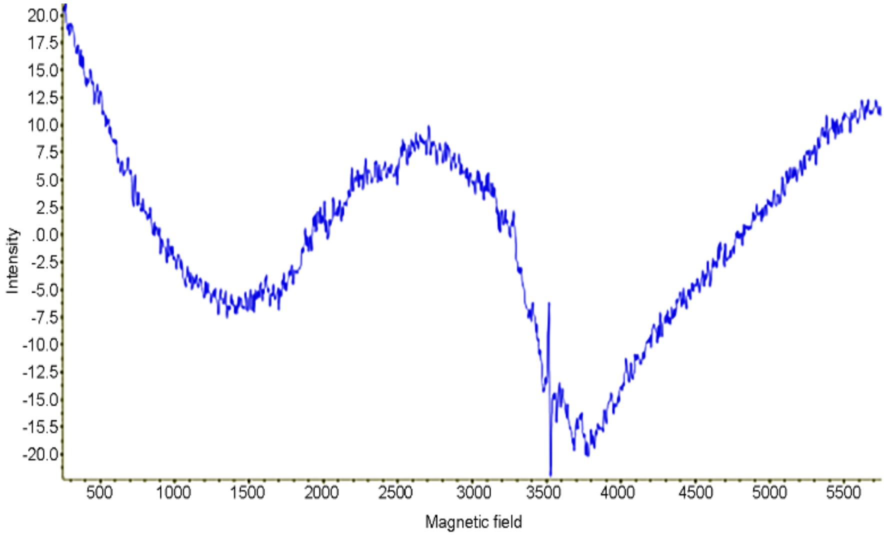
As expected, the increase of NaCl salt in the environment results in an extreme growth in the concentration, that is, accumulation of Na ions in both root (approximately 2.0 times) and stem tissues (approximately 24.4 times). Under the combined salt stress condition, the gradual replacement of NaCl salt by Na_2SO_4 salt leads to an even more severe accumulation of Na^+ ions in both root and stem tissues of seedlings in accordance with the concentration of Na_2SO_4 salt. That is, the replacement of Cl^- ions by SO_4^{2-} ions has a positive (synergistic) impact on the accumulation of Na ions within the tissues. The impact of combined salt stress on the absorption of K^+ ions by the root system and their distribution within the tissues differs from that of Na ions. Na_2SO_4 salt helps the accumulation of K^+ ions in the stem system to a certain degree, however, its level remains notably lower than that of the control variant. When it comes to the root system, the partial recovery of K^+ is higher at equimolar concentrations of salts.

3.5. Study of Electron Paramagnetic Resonance (EPR) in Maize Seedlings under Salt Stress Conditions

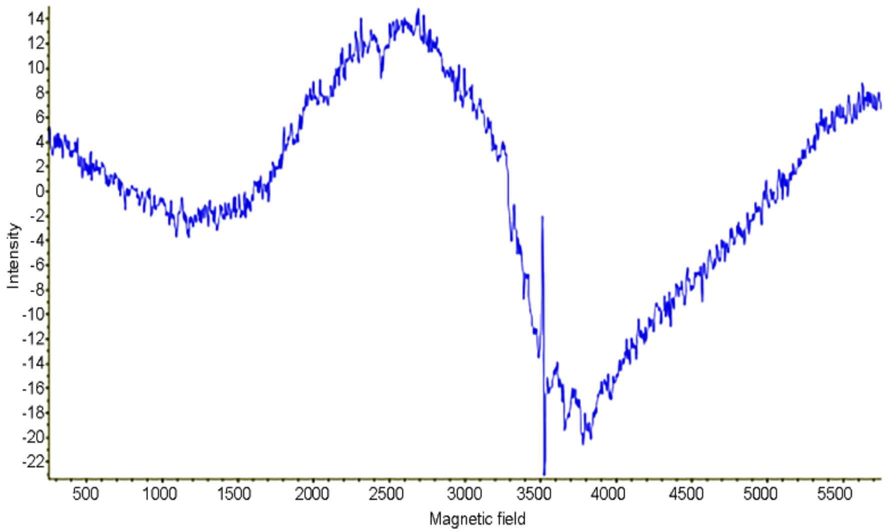
In our research work, Electron Paramagnetic Resonance (EPR) has been analyzed under the control and NaCl conditions in order to study the paramagnetic centers in seedlings of different genotypes of maize plant.

Paramagnetic centers in different genotypes of maize seedlings exposed to NaCl (100 mM) solution have been studied through the EPR method and comparatively analyzed with control samples (Figure 1 A and B).

Figure 1 A and B demonstrate the EPR results of the variants of Zagatala locally improved genotype cultivated under control and salt solution (NaCl) conditions. As can be seen from the figure, the intensity of the free radical signal (g=2.0023) in the control sample is significantly smaller than the intensity of the signal generated in the sample exposed to salt stress (A vs. B).



A-control



B-100 mM NaCl

Figure 1. EPR Spectra of the Zaqatala local improved Maize genotype under control (A) and 100 mM NaCl (B) conditions.

At the same time, when we compare the broad EPR signals generated in both samples, it can be clear that the amplitude of the broad EPR signal in Zagatala locally improved genotype exposed to salt stress is higher than in the control sample (Figure 1 A and B).

This arrangement has also been observed in other genotypes of maize plant. In other words, the amplitudes of both the free radical signal and the broad EPR signal have been higher than the amplitudes of the analogous signals of the control samples in all genotypes of maize plant exposed to salt stress.

CHAPTER 4. INDIVIDUAL AND COMBINED EFFECTS OF SALT (100 mM NaCl) AND DROUGHT STRESS ON MAIZE SEEDLINGS (ZAGATALA-68)

Salt and drought stress almost always accompany each other in nature which further accelerates the impact of stress. Therefore, a part of the experiments has been conducted in studying the combined impact of these two factors.

4.1. Effects of salt and drought stress on the biometric parameters of maize seedlings. The experiment was aimed at studying the development of maize seedlings Gurur genotype and the activity dynamics of NADPH-generating enzymes under separate and the combined effect of 100 mM NaCl and drought stress.

As can be seen from Table 6, during the development phase of maize seedlings, the biometric indicators of the plant almost doubled within the 4^{th} and 12^{th} days when the irrigation was carried out with distilled water, while under the impact of drought and salt stress, the development of seedlings has weakened. Despite the fact that the impact of both stress factors has been noticed with a relatively small difference in the initial phase of plant development (in 4-8-day-old seedlings), on the last (12^{th}) day, the delay has been relatively greater, and up to 2 times compared to the control, especially under the combined impact of drought and salt stress.

Table 6. Effects of salt and drought stresses on the growth dynamics (cm) of maize seedlings

Days / Variants	Day 4	Day 8	Day 12
Control	leaf – 4.7±0.1 root – 2.9±0.3	leaf – 6.5±0.2 root – 4.3±0.1	leaf – 9.2±0.2 root – 6.8±0.1
NaCl (100 mM)	leaf – 3.5**±0.09 root – 2.8^{ns}±0.03	leaf – 4.9*±0.18 root – 3.8*±0.06	leaf – 6.1**±0.07 root – 4.7**±0.06
Drought	leaf – 3.2**±0.17 root – 2.5**±0.03	leaf – 4.4**±0.09 root– 3.5**±0.07	leaf – 5.8***±0.07 root – 4.3**±0.13
NaCl (100 mM) +Drought	leaf – 3.0**±0.15 root – 2.1*±0.13	leaf – 4.1**±0.20 root – 3.2**±0.09	leaf – 5.2**±0.10 root – 4.0***±0.06

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability, ns - non-significant

4.2. Effects of salt and drought stresses on enzyme activity in maize seedlings. As can be seen from the tables (Table 7. and Table 8.), during the development phase of maize seedlings, a decrease in the activity dynamics of the G6PDH enzyme in the control variant and an increase in the activities of the NADP-ME and NADP-ICDH enzymes have been observed.

Table 7. Effects of salt and drought stresses on enzyme activity (µM/min/g/wet weight) in maize seedling leaves

Variants	G6PDH activity			DMDH activity			ICDH activity		
	Day 4	Day 8	Day 12	Day 4	Day 8	Day 12	Day 4	Day 8	Day 12
Control	102.5 ±0.3	81.3 ±0.21	67.1 ±0.27	78.6 ±0.33	96.2 ±0.39	107.1 ±0.47	93.9 ±0.64	104.4 ±0.57	107.5 ±0.72
NaCl (100 mM)	111.1** ±0.89	101.2*** ±0.42	78.4** ±1.27	89.3** ±0.44	118.2*** ±0.49	129.1** ±0.62	95.3^{ns} ±1.222	110.2*** ±0.07	112.3** ±0.35
Drought	107.2** ±0.40	96.1** ±0.62	81.3** ±0.67	92.3** ±0.50	126.5** ±1.15	138.0** ±1.11	96.3^{ns} ±1.00	112.6** ±0.64	101.3** ±0.29
NaCl (100mM)+ Drought	113.1** ±0.70	101.2* ±3.44	84.5** ±0.72	93.3** ±0.47	129.1** ±0.75	139.5*** ±0.26	98.4* ±0.91	115.2*** ±0.7	100.3** ±.32

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability, ns - non-significant

Table 8. Effects of salt and drought stresses on enzyme activity (μM/min/g/wet weight) in maize seedling roots

Variants	G6PDH activity			DMDH activity			ICDH activity		
	Day 4	Day 8	Day 12	Day 4	Day 8	Day 12	Day 4	Day 8	Day 12
Control	103.4 ±021	85.2 ±0.49	70.1 ±0.51	80.2 ±0.83	98.2 ±0.26	110.4 ±0.44	95.3 ±0.39	108.1 ±0.57	114.2 ±0.73
NaCl (100 mM)	114.2** ±0.59	103.2** ±0.93	80.3** ±0.35	92.4*** ±0.19	121.5*** ±0.19	133.2*** ±0.35	97.3*** ±0.03	109.2* ±0.22	112.5ns ±0.52
Drought	110.2* ±0.30	99.1** ±0.54	85.2** ±0.62	95.3** ±0.43	130.3*** ±0.55	141.3*** ±0.50	96.4ns ±0.95	113.2** ±0.27	116.1** ±0.12
NaCl (100mM)+ Drought	117.4** ±0.92	106.2*** ±0.35	87.3*** ±0.12	97.1** ±0.40	132.2** ±1.14	143.3** ±1.19	100.4* ±1.39	116.1** ±0.47	108.6* ±0.95

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability, ns - non-significant

The particular increase in the activity of DMDH enzyme can be related to the fact that the limitation of CO_2 absorption due to the closure of stomata in leaves with the outbreak of drought is eliminated by the DMDH enzyme.

CHAPTER V. INDIVIDUAL AND COMBINED EFFECTS OF SALT (100 mM NaCl) AND GAMMA RADIATION STRESSES ON MAIZE SEEDLINGS

5.1. Effects of salt and gamma radiation stresses, individually and in various combinations, on the biometric parameters and activity of NADPH-generating enzymes of maize seedlings (Zagatala-68). In accordance with Figure 2 and Figure 3, 100 mM NaCl salt solution has a significantly inhibitory effect on the development dynamics of seedlings. At the same time, the biometric indicators of seedlings cultivated under the combined impact of the low doses of radioactive radiation (50 Gy and 100 Gy) and salt stress (NaCl 100 mM) has been higher than those of the control, only salt and only radioactive radiation variants.

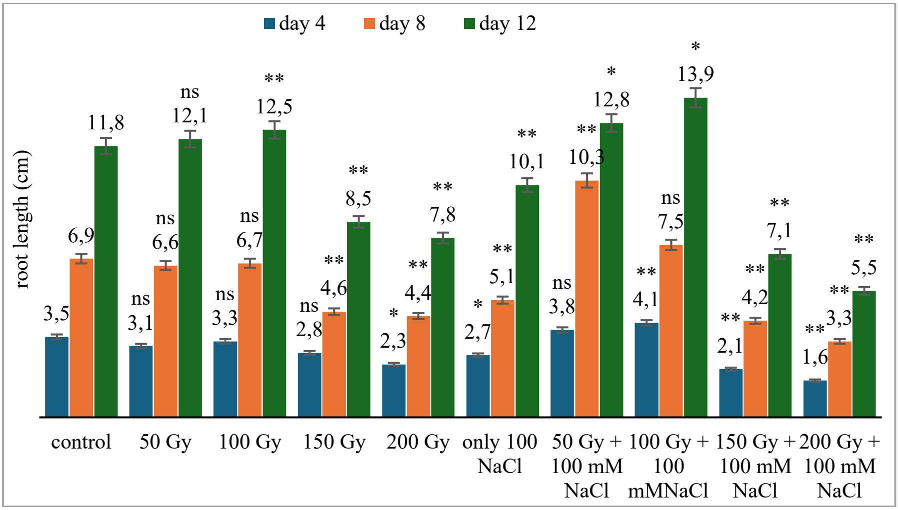


Figure 2. Effects of gamma radiation and salt stress on maize root growth (cm)

Note: **, * are statistically significant at p≤0,01 and p≤0,05 levels of probability, ns - non-significant

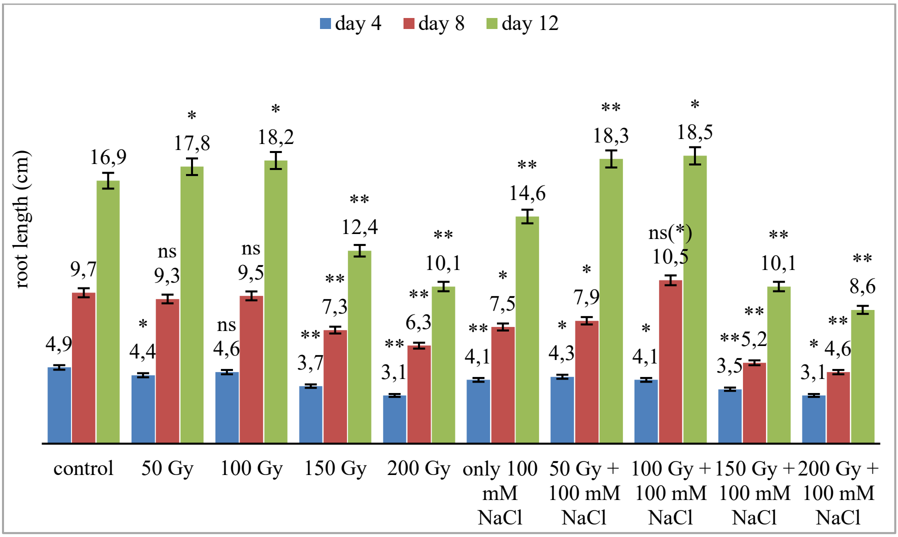


Figure 3. Individual and combined effects of gamma radiation and salt stress on root growth (cm) of maize seedlings

Note: **, * are statistically significant at p≤0,01 and p≤0,05 levels of probability, ns - non-significant.

With regard to the development of maize seedlings, the changes in the activity dynamics of NADPH-generating enzymes in the root system tissues of maize seedlings resulting from the stress factors are expressed in Figure 4, Figure 5, and Figure 6.

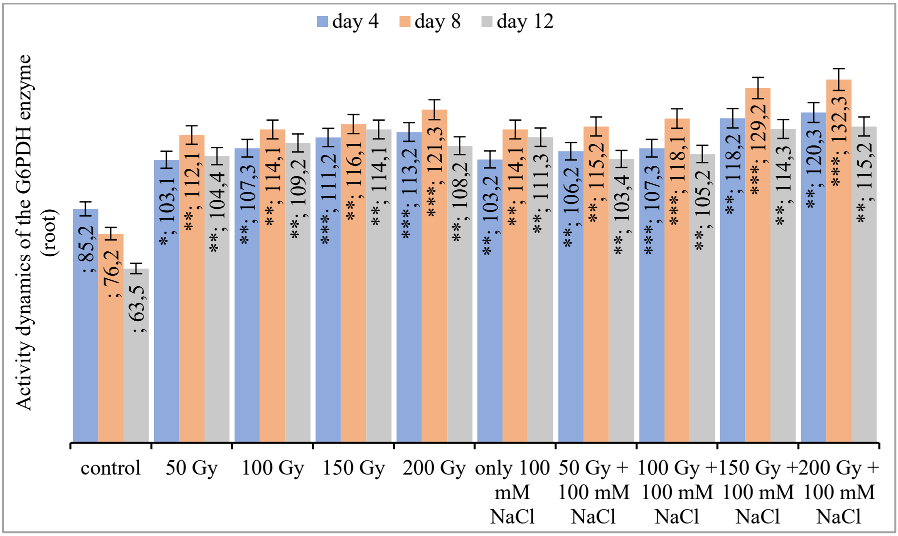


Figure 4. Individual and combined effects of gamma radiation and salt stress on the activity (μM/min/g/wet weight) dynamics of G6PDH enzyme in maize seedling root extracts

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability

As can be seen in Figure 4, during the 12-day cultivation period, the G6PDH enzyme in the root system of the seedlings of control variant gradually decreases and 71.4% of the initial activity remains. In all cases, stress condition generated by the individual and combined effect of radioactive radiation and NaCl salt solution are accompanied by the induction of enzyme activity and the maximum stimulation effect is observed on the 8th day of cultivation.

The activity of the DMDH enzyme has been recorded with the increasing dynamics both under control and impact of other stress factors with regard to the development of seedlings and increasing the dose of stress has induced the activity of this enzyme more (Figure 5). Similar dynamics are the case with the ICDH enzyme (Figure 6).

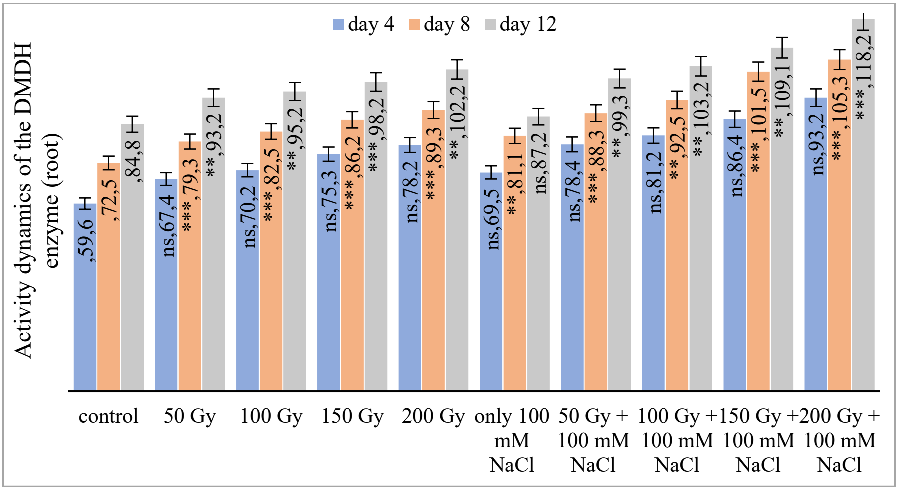


Figure 5. Individual and combined effects of gamma radiation and salt stress on the activity (μM/min/g wet weight) dynamics of DMDH enzyme in maize seedling root extracts

Note: ***, ** are statistically significant at p≤0,001 and p≤0,01 levels of probability, ns - non-significant.

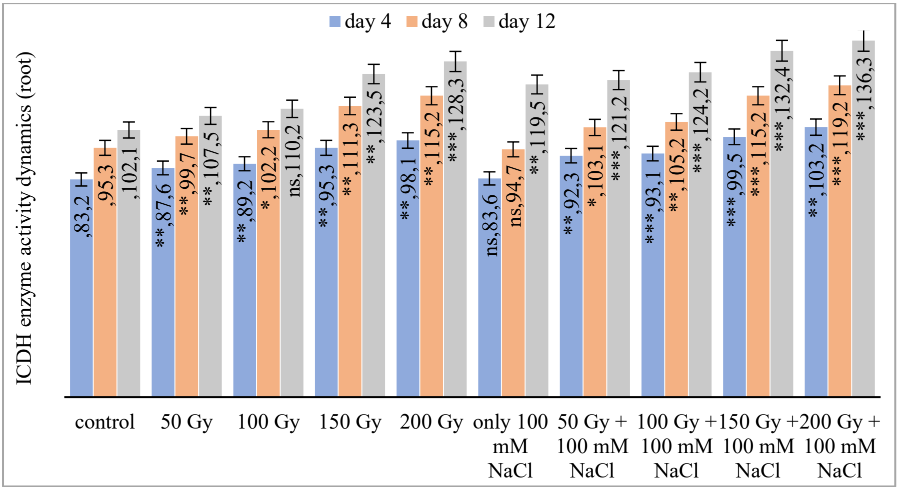


Figure 6. Individual and combined effects of gamma radiation and salt stress on the activity (μM/min/g wet weight) dynamics of ISDH enzyme in maize seedling root extracts.

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability, ns - non-significant.

With regard to the development of maize seedlings, the activity of the G6PDH enzyme in the control variant gradually decreases in the stem system tissues, as is the case with the root system tissues and 66.6% of the initial activity remains in the end of the experiments.

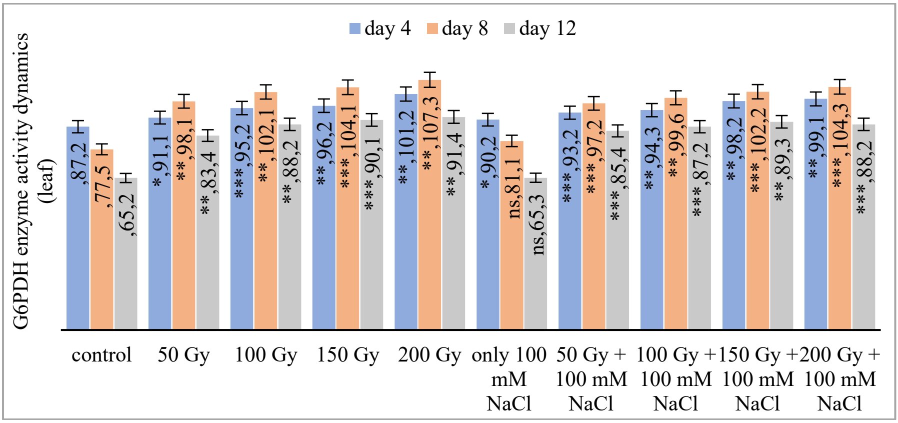


Figure 7. Individual and combined effects of gamma radiation and salt stress on the activity (μM/min/g wet weight) dynamics of G6PDH enzyme in maize seedling leaf extracts

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability, ns - non-significant

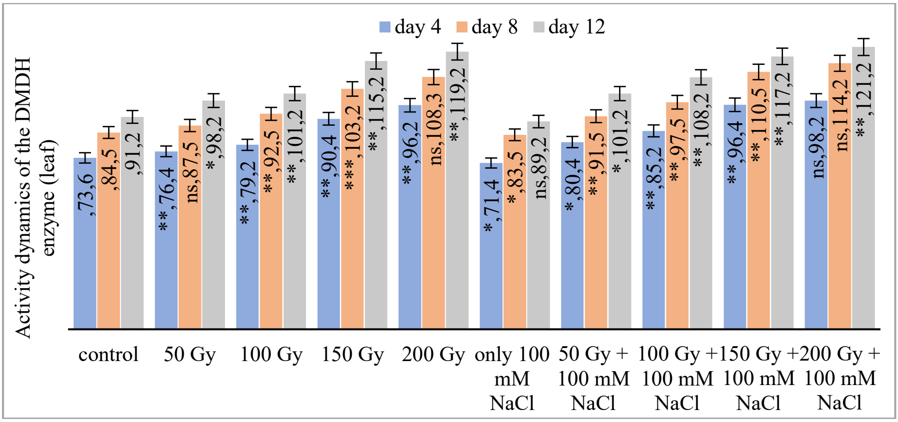


Figure 8. Individual and combined effects of gamma radiation and salt stress on the activity (μM/min/g/wet weight) dynamics of DMDH enzyme in maize seedling leaf extracts

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability, ns - non-significant.

Radioactive radiation leads to the stimulation of enzyme activity at all doses applied and the maximum effect appears on the 8th day of the experiments. On the contrary, the activity of the DMDH and ICDH enzymes in control variant increases with regard to the development of seedlings, and is additionally stimulated by both individual and combined impact of stress factors.

Thus, with regard to the development of seedlings, in the control variant, the activity of the G6PDH enzyme in the root system weakens compared to the initial period, whereas the activity of the DMDH and ICDH enzymes increases. In all variants, the impact of stress causes the induction of the activity of all three enzymes, and the induction effect is more visible on the 8th day of the experiment.

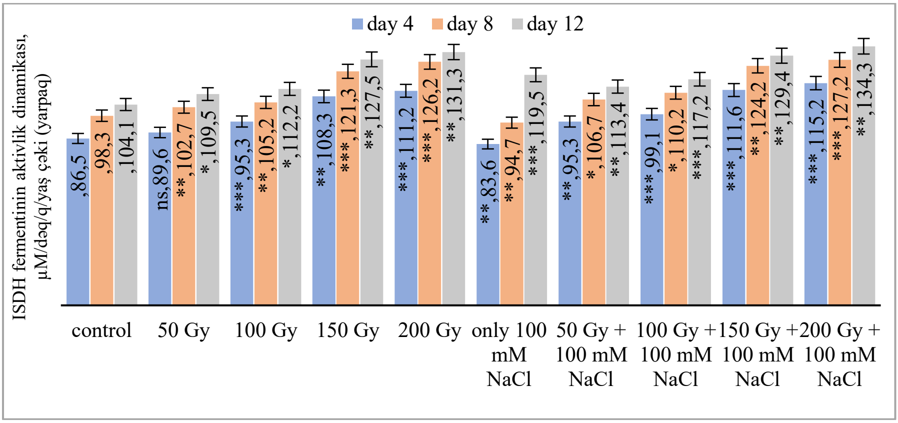


Figure 9. Individual and combined effects of gamma radiation and salt stress on the activity (µM/min/g/wet weight) dynamics of ICDH enzyme in maize seedling leaf extracts

Note: ***, **, * are statistically significant at $p \leq 0,001$ $p \leq 0,01$ and $p \leq 0,05$ levels of probability

5.2. Effects of two or more stress factors (100 mM NaCl, gamma radiation, and γ-Fe_2O_3) on maize (Zagatala-420) seedlings

The next stage of the research deals with the development of maize plant and the activity of enzymes under combined stress condition generated by the effects of ionizing gamma rays (250 Gy, 500 Gy, 750 Gy), salt solution (NaCl), and nanoparticles (γ-Fe_2O_3).

Under the stress condition created by the different doses of gamma rays separately and in combination with a salt solution, the development of a plant has significantly delayed rather than of the control variant. Increasing the dose of radiation further slowed down the development of a plant and led to its destruction at the doses of 500 Gy and 750 Gy. Therefore, a dose of 500 Gy has been considered a lethal dose for the maize plant and the experiments has been conducted only at a dose of 250 Gy.

With regard to the development of seedlings, in the control variant, only the activity of the G6PDH enzyme has decreased while NADP-DMDH and NADP-ICDH enzymes have advanced. In all other variants cultivated under the stress condition, the induction of the activity of all three enzymes in root and leaf cells during the first 10 days of the experiment, and their inhibition on the 15th day have been observed. This can be explained by the inhibition of the enzyme by the reaction product. The activity of the enzyme has been higher under the combined impact of stress factors. The results obtained are shown in Figure 10, Figure 11, Figure 12, Figure 13, Figure 14, and Figure 15.

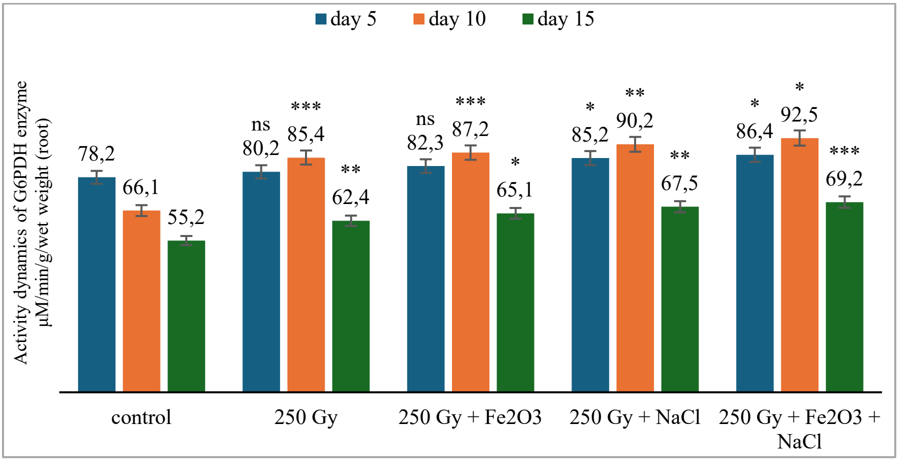


Figure 10. Individual and combined effects of gamma radiation, salt stress, and iron (ɪɪɪ) oxide nanoparticles on G6PDH enzyme activity (µM/min/g/wet weight) in maize seedling root extract

Note: ***, **, * are statistically significant at $p \leq 0{,}001$ $p \leq 0{,}01$ and $p \leq 0{,}05$ levels of probability, ns - non-significant

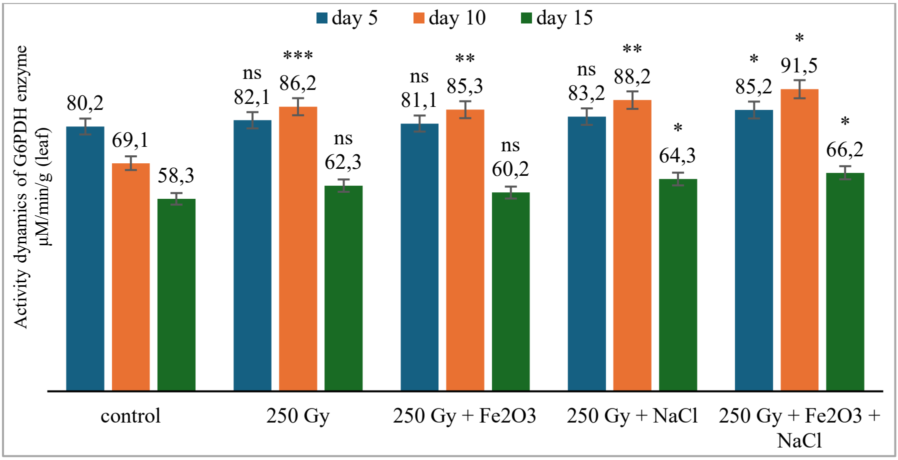


Figure 11. Individual and combined effects of gamma radiation, salt stress, and iron (ııı) oxide nanoparticles on G6PDH enzyme activity (µM/min/g/wet weight) in maize seedling leaf extracts

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability, ns - non-significant

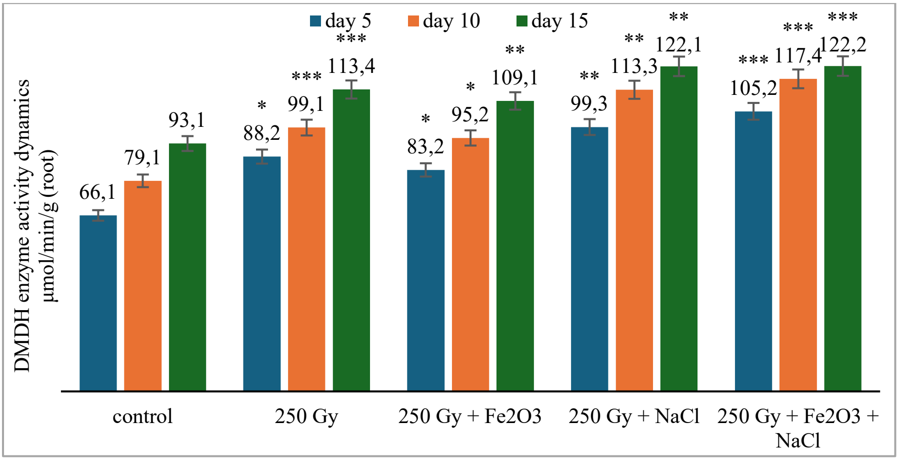


Figure 12. Individual and combined effects of gamma radiation, salt stress, and iron (ııı) oxide nanoparticles on DMDH enzyme activity (µM/min/g/wet weight) in maize seedling root extracts

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability

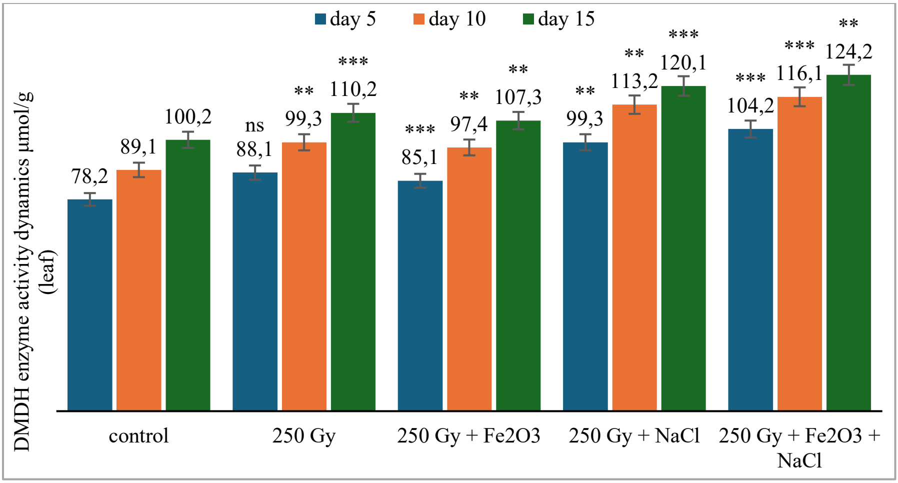


Figure 13. Individual and combined effects of gamma radiation, salt stress, and iron (ɪɪɪ) oxide nanoparticles on DMDH enzyme activity (µM/min/g/wet weight) in maize seedling leaf extracts

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability, ns - non-significant.

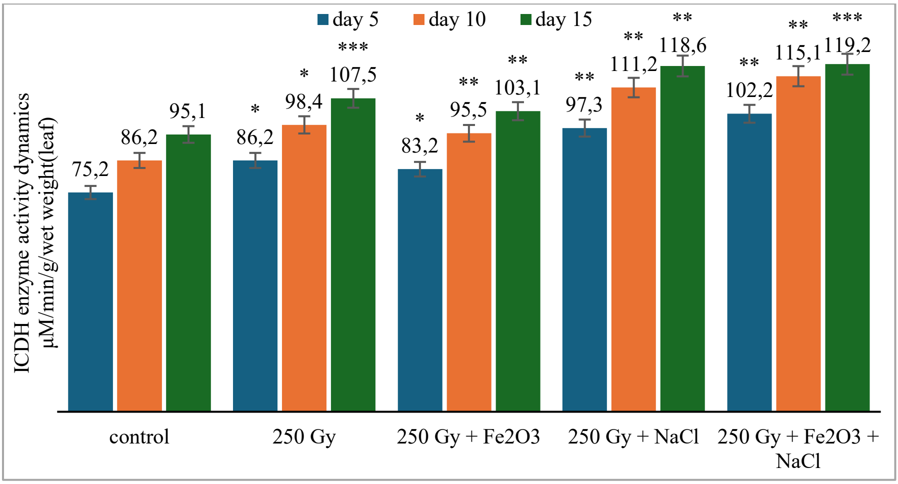


Figure 14. Individual and combined effects of gamma radiation, salt stress, and iron (ɪɪɪ) oxide nanoparticles on ICDH enzyme activity (µM/min/g/wet weight) in maize seedling leaf extracts

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability

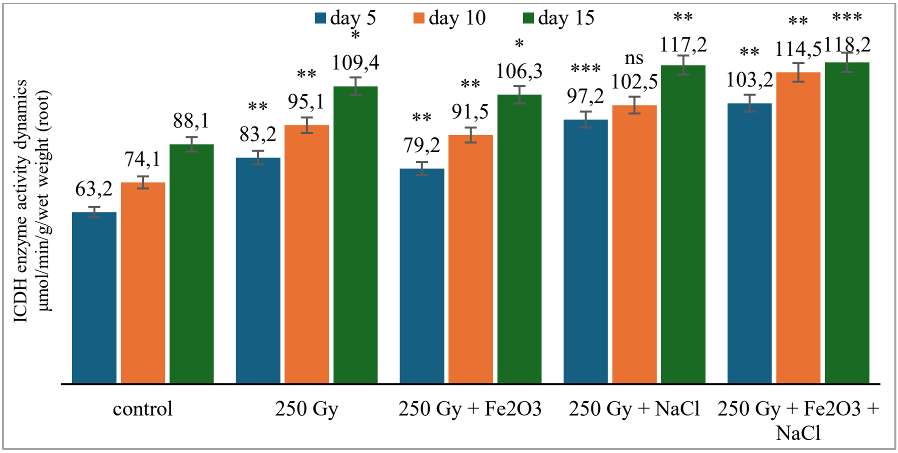


Figure 15. Individual and combined effects of gamma radiation, salt stress, and iron (ɪɪɪ) oxide nanoparticles on ICDH enzyme activity (µM/min/g/wet weight) in maize seedling root extracts

Note: ***, **, * are statistically significant at $p \leq 0,001$ $p \leq 0,01$ and $p \leq 0,05$ levels of probability, ns - non-significant

According to the results obtained, the activity of G6PDH enzyme is volatile; the observations show that the enzyme activity decreases in the control variant, whereas somewhat increases and again decreases under the impact of stress. Activity of DMDH and ICDH enzymes has been recorded as a generally increasing trend in character.

The results depicted in Figures 16 illustrate the effects of stress factors on the organic composition of maize seedlings. At a gamma radiation dose of 250 Gy, there was a 13.9% decrease in the organic content of root tissue and a 14.6% decrease in leaf tissue. When gamma radiation was combined with salt stress, the reduction in organic weight was 22.4% in the roots and 22.1% in the leaves. The addition of iron (III) oxide nanoparticles to the environment resulted in a decrease of 9.7% in root organic weight and 8.5% in leaf organic weight.

The findings from this study, particularly regarding the effects of NaCl and Na_2SO_4 salts on enzyme activity and mineral uptake, as well as the stimulatory effects of low-dose, short-term gamma radiation and iron (III) oxide nanoparticles on maize plants, hold significant practical implications. These results pave the way for future research in this field.

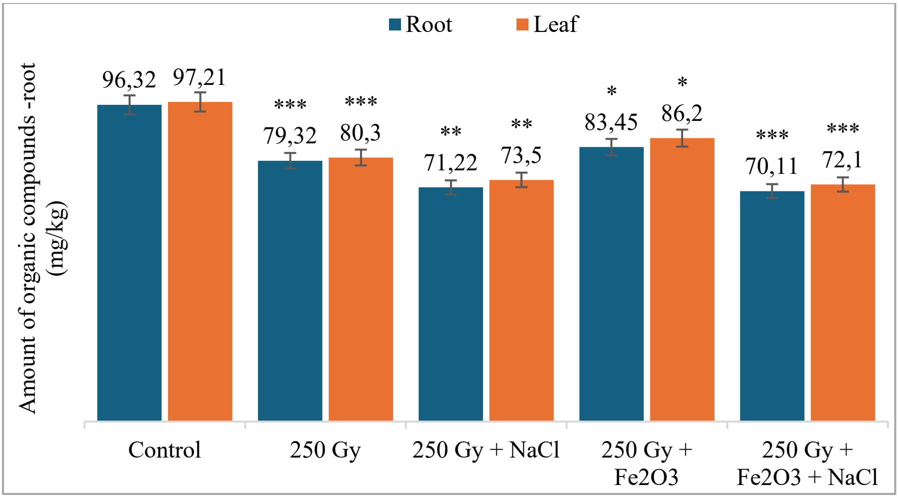


Figure 16. Individual and combined effects of gamma radiation, Salt stress, and Iron (III) oxide nanoparticles on organic biomass (mg/g/wet weight) of maize seedlings.

Note: ***, **, * are statistically significant at p≤0,001 p≤0,01 and p≤0,05 levels of probability

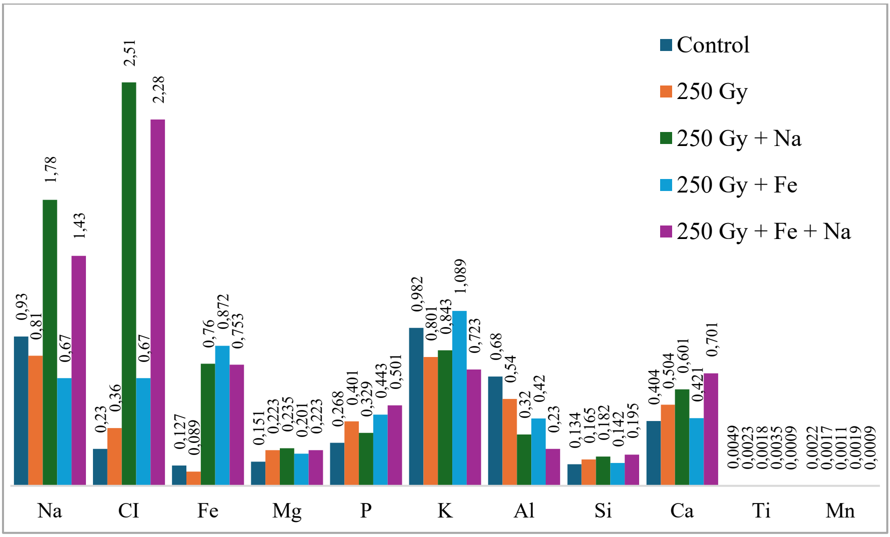


Figure 17. Individual and combined effects of gamma radiation, salt stress, and iron(ııı) oxide nanoparticles on inorganic biomass (mg/g/wet weight) of maize seedlings (leaf)

RESULTS

1. The individual and combined effects of NaCl and Na_2SO_4 salts negatively impact maize seed germination. Compared to the control, a 100 mM NaCl solution caused a 18–22% reduction in root development and a 16–19% reduction in leaf development. Similarly, a 100 mM Na_2SO_4 solution led to a 25–28% decrease in root development and a 20–24% decrease in leaf development. Increasing the proportion of Na_2SO_4 in the combined medium intensified these effects. [1; 5; 10].

2. The individual and combined effects of NaCl and Na_2SO_4 salts induce the activity of all three NADPH-generating enzymes in maize seedlings. Specifically, G6PDH and NADP-ME are primarily involved in mitigating the effects of NaCl, while NADP-ISDH plays a more significant role in counteracting the effects of Na_2SO_4 [8; 10; 12].

3. Regarding the development of maize seedlings, the overall level of reductive potential generated by cytoplasmic G6PDH, NADP-ME, and NADP-ISDH enzymes remains relatively constant. However, the contribution of G6PDH gradually decreases over time, while the roles of NADP-ME and NADP-ISDH enzymes increase [4; 5; 12].

4. Under drought stress, maize seedlings exhibit a 50% reduction in development compared to the control group. When combined with 100 mM NaCl, this reduction increases to 44%. The activity dynamics of enzymes show an increasing trend, with DMDH enzyme activity being particularly notable [6; 14; 15].

5. Na salts, iron (III) oxide nanoparticles (γ-Fe_2O_3), and gamma radiation significantly influence the uptake and distribution of mineral elements in maize seedlings. Na salts inhibit the uptake of K, Ca, Mg, P, and Fe, while the absorption of Al, Mn, and Ti remains largely unchanged. Under NaCl conditions, Na and Cl ions accumulate in root tissues, whereas under Na_2SO_4 conditions, Na, S, and Si ions accumulate [11; 18].

6. Gamma radiation has a stimulatory effect on maize seedling development at low doses (50 Gy), inhibitory effects at higher doses (150 Gy and above), and becomes lethal at 500 Gy. Enzyme activity dynamics, particularly for Q6PDH, differ from the control group; in

stress variants, activity increases during the first 10 days and decreases by the 15^{th} day [9; 12; 13].

7. Iron (III) oxide nanoparticles (γ-Fe_2O_3) at certain concentrations exhibit a stimulatory effect on maize plants, reducing the impact of stress factors like drought and gamma radiation. They positively influence the activity dynamics of NADPH-generating enzymes [11;18].

8. In various maize genotypes, salt stress (100 mM NaCl) leads to an increase in the amplitude of free radical signals and a broader EPR signal [12].

RECOMMENDATIONS

1. The tables depicting the individual and combined effects of NaCl and Na_2SO_4 salt stress on maize seedling development and the activity dynamics of NADPH-generating enzymes can be utilized in the field of plant breeding to develop new salt-tolerant maize varieties.

2. The tables illustrating the impact of abiotic stress factors, both individually and in combination, on maize seedling development can serve as a basis for preparing and evaluating action plans aimed at mitigating the effects of various stress factors on plants, to be used by the Ministry of Ecology and Natural Resources.

3. The findings regarding the development, organic and inorganic composition, and enzyme activation in maize seedlings under the low-dose and short-term stimulatory effects of abiotic stress factors can contribute to the agricultural sector by applying appropriate doses of stress factors to seeds, thereby enhancing maize productivity.

4. The materials obtained on the stimulatory effect of iron (III) oxide nanoparticles (γ-Fe_2O_3) on maize seedlings and their potential to partially alleviate the negative effects of other stress factors, such as gamma radiation, can be applied by the Ministry of Agriculture in relevant sectors.

5. The tables and diagrams depicting the activity of Q6PDH, NADP-ME, and NADP-ISDH enzymes in control and stress variants at different plant development stages can be used to study maize plants in relevant scientific research areas.

List of the research papers published with regard to the dissertation

1. Əliyeva N.Z., Məmmədov, Z,M., Əmrahov N.R., Duz stresinin qarğıdalı cücərtilərinin inkişafina və onların toxumalrında NADPH əmələ gətirən fermentlərin aktivlik dinamikasına təsiri / Bakı Universitetinin Xəbərləri Jurnalı. 2019, s.39-46.

2. Əliyeva N.Z., Məmmədov, Z,M., Duz və quraqlıq stresinin qarğıdlı cücərtilərinin qlükozo-6-fosfatdehidrogenaza və dekarboksilləşdirici-malatdehidrogenaza fermentlərinin aktivlik dinamiksına təsiri / BDU-nun 100 illiyinə həsr olunmuş "Müasir İnnovativ Yanaşmalar" mövzusunda IX Beynəlxalq Elmi Konfrans. 2019, s.20.

3. Əliyeva N.Z., Məmmədov, Z,M., Abiotik stres şəraitində becərilən qarğıdalı cücərtilərində bitkilərin müdafiə sistemində iştirak edən bəzi fermentlərin aktivlik dinamikasının tədqiqi. Azərbaycanda Ekoloji Təmiz Kənd Təsərrüfatının İnkişafı mövzusunda elmi-praktiki konfransı / Azərbaycn Dövlət Aqrar Universiteti. Gəncə. 2019, s.45-47.

4. Əliyeva, N.Z. Duz stresi şəraitində becərilən qarğıdalı cücərtilərində NADPH əmələgətirən İzositratdehidrogenaza fermentinin aktivlik dinamikasının tədqiqi. Nəsiminin 650 illik yubileyinə həsr olunmuş "Doktorant və Gənc Tədqiqatçıların XXIII Respublika Elmi konfransı, AMİU, 2019, cild-1, s.53-56.

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