Interactive Relationships Between Water Status, Antioxidant Protection Systems, Inherent Rezistance And Plant Cross-Tolerance

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Abstract

In this study, we examined the cross-tolerance of soybean plants to low and high temperature stresses induced by relative drought in the early stages of ontogenesis, and the possible involvement in its formation of the ability of water status self-regulation and antioxidant protection systems.The plants of two soybean varieties, with different potential for drought resistance, served as a subject of study. It has been demonstrated that exposure of plants to moderate hydric stress at the earliest stages of development induces resistance to hypo- and hyper- temperature stresses, as well as to repeated drought. It is argued that non-specific reactions, such as the ability to maintain water homeostasis in tissues and activate antioxidant protection systems, are involved in plant cross-tolerance formation. The obtained data showed that cross-tolerance may be the result of two distinct phenomena: as a consequence of previous plant exposure to another type of stress (inducible cross-tolerance) and / or as a genetic property specific to certain varieties, to demonstrate resistance to more stress types (inherent cross-resistance).

Keywords — cross-tolerance, cross-stress-memory, non-specific reactions, water homeostasis, antioxidant protection systems.

I. INTRODUCTION

Under conditions of global warming, the negative impact of droughts repeated over time, accompanied by heat, hail and temperature drops, as well as extreme rainfall fluctuations, is catastrophic for plant productivity and rural economy. The negative impact of limiting climatic factors is further complicated by negative anthropic activity, atmospheric pollution and increased ß - ultraviolet radiation [1].Fluctuations in environmental conditions with adverse character, but not necessarily fatal in general are regarded as stressogenic factors. Such repetitive events may cause cellular degradation, the discordance of key physiological processes, and morphological changes with severe effects on productivity [2].

As sedentary organisms, plants in the ever-changing environment are inevitably subjected to the most unfavorable factors.Fluctuations of environmental conditions with adverse character, but not necessarily fatal, in general are regarded as stressogenic factors. Plants cannot avoid stressful situations. During phylogenesis, plants have developed mechanisms that allow them to adapt and survive drought periods. Recently it has been established that pre-exposure of the plant organism to various conditions of moderate abiotic stress (drought, cold, high temperatures, salinization, etc.) can change the response later, increasing the resistance to repeated exposures. Attempts are being made to demonstrate the existence of cross-tolerance in plants: plant exposure to a moderate stress factor often induces resistance to other types of stress [1-5].Lately, a number of attempts have been made to explain the mechanisms of cross-tolerance phenomenon, but the problem is far from being solved [1; 3; 5; 6]. It is assumed that the acclimatization and formation of stress memory to a certain type of stress prevents the deterioration caused by other stressors by providing cross-memory to stress and complex tolerance [7].It is assumed that the acclimatization and formation of stress memory to a certain type of stress prevents the deterioration caused by other stressors by providing cross-memory to stress and complex tolerance [7]. This phenomenon is explained by the fact that the mechanisms of acclimatization to different factors are partially identical [8].In the few existing papers it is mentioned that the possible mechanisms underlying cross-tolerance are the accumulation of different proteins, amino acids, transcription factors or protective metabolites, as well as epigenetic and/or morphological changes [9; 10]. Therefore, the importance of knowing the mechanisms of plant cross-tolerance is indisputable and has direct implications for the development of strategies of crop harvest adapting and maintaining.

The aim of this paper consists in the elucidation of cross-tolerance manifestation in plants pre-exposed to moderate water stress at the initial stages of ontogenesis, and to involve non-specific reactions such as the ability to maintain water homeostasis in tissues and activate antioxidant protection systems in its formation.

II.MATERIAL AND METHODS

The plants of *Glycine max* (L.) Merr, Moldovitsa and Magia varieties, selected in the Research Institute of Field Crops "Selection", which have a production potential of 3000 to 3500 and 2870 to 3200 kg / ha respectively, were used as objects of study.Based on the assumption that high productivity comes in contradiction with resistance to unfavorable factors, it can be assumed that plants of Magic variety, which differs from Moldovitsa variety in potentially higher productivity, are more susceptible to drought.

Plants used in experiments with different humidity conditions, conducted in the Greenhouse of the Institute of Genetics, Physiology and Plant Protection were grown in Mitcherlih pots with a 30 kg capacity of absolutely dry soil.The moisture regime was maintained by watering the plants according to the weight of the pots with soil and plant respectively.Drought-induced stress was modelled by reducing the watering level from 70% of total soil water capacity (TWC) to 40% TWC humidity.

Scheme of experiment:

I variant - control, humidity 70% TWC (total water capacity of the soil);

II variant - humidity 70 - 40% TWC.

Water stress conditions lasted for 7 days. After 7 days of drought, moisture level had been restored up to the optimal level.In order to appreciate the particularities of the water status in the plants, the following indices were determined: total water content - by drying the samples to a constant weight at 105 ° C; leaf saturation deficit - expressed as a percentage of full saturation; the water retention capacity in the tissues was characterized by the amount of water retained after 2 hours of experimental fading and expressed as a percentage of its initial content. SOD activity was determined by the method of inhibiting the photochemical reduction of nitroblutetrazolium, described in detail by [11]. CAT activity was estimated after [12] by spectrophotometric determination at λ 240 nm of H2O2 decomposition; GwPX - after intensity of guaiacol oxidation (2 - methoxy - phenol) as hydrogen donor in the presence of H2O2, λ 470 nm; APX - by monitoring the ascorbate oxidation rate at λ 290 nm [13]; GR - by reducing oxidized glutathione in the presence of NADP · H [14]. The homogenization of plant material and extraction was carried out as described in [15]. The content of proline in plant leaves was determined by the method of [16]. The plant constitutive resistance to dehydration, heat and low positive temperatures was determined after the formation of the first trifoliate leaf by the method proposed by [17], as well as by the degree of modification/ stabilization of the physiological processes in the plants under the influence of stress factor.About the formation of cross-tolerance, it was concluded by the property of plants pre-exposed to moderate hydric stress at the stage of the first trifoliate leaf to withstand water and heat stress (42 ℃; 4 ℃) compared to the control plants' resistance. The results were statistically analyzed using the software package "Statistics 7" for computers.

III.RESULTS AND DISCUSSION

More and more evidences are being gained in favor of the idea that the main trigger of the general adaptation reaction in plants both to water potential reducing in the soil and other factors may be the decrease of turgor pressure.The homeostatic capacity of water in the organism is the primary condition for plant resistance not only to moisture deficiency but also to the various external factors such as heat, cold, frost, salinization, xenobiotics, etc.Changing the parameters of water status is a non-specific response of plants to a variety of stressing factors, and the character modification can be used to obtain information about plant sensitivity or tolerance to drought [18 - 20].The threshold level of moisture, which conditions significant stressogenic changes in the physiological processes of plants, differs depending on the variety, species and culture.In the given researches, it was found that under optimal conditions soybean plants Moldovitsa and Magia lack significant differences in water content parameter.The degree of hydration depending on the functional state and the ontogenesis stage varies in the range of 83.1-72.5 g of water per 100g f.w. for Moldovita plants and 81.7 - 71.8 g for Magia plants (Table 1).The amplitude of variation of water content in leaves at the "flowering - pods formation" phase is rather insignificant - 10.6 and 9.9 percent respectively. Correspondingly, the saturation deficit is 7.5 to 11.5% from the full saturation in the leaves of the first variety and 8.10 - 12.6% in the leaves of Magia plants (Table 1).Changing the humidity regime and the occurrence of water deficiency in soil is reflected on the water status of plants by diminishing tissue hydration.The lack of moisture at the stage of "first trifoliate leaf" had reduced the degree of hydration in plants of both varieties, but especially in representatives of Magia variety.

Table 1. Drought impact on water status parameters in plant leaves of *Glycine max*(L.)Merr at the initial stages of ontogenesis

Variety	Soil humidity, % TWC	WC, g·100g^{-1} f.w.*		SD, % of full saturation		WRC, % water retained from the initial content Remained water, g·100 g. m. p.	
		M ± m	Δ, %	M ± m	Δ, %	M ± m	Δ, %
Moldovitsa	**Control, 70**	83,14±0,36		7,47±0,14		50,59 ±0,50	
	Drought, 70 -40	75,75±0,32	-8,89	19,42±0,23	159,97	56,66 ± 0,33	12,0
Magia	**Control, 70**	81,73±0,40		8,04± 0,20		53,90±0,52	
	Drought 70 -40	73,50±0,86	-10,07	21,59±0,14	168,53	56,91±0.88	5,58

*WC - water content; f.w.- fresh weight; SD-saturation deficit; WRC - water retention capacity

As a consequence of the tissue dehydration, the leaf turgidity in the Moldovitsa plants decreased by 11% and in plants of the Magia variety - by 13.6%, which created an increase of the saturation deficit by 159 and 168% compared to values of the saturation deficit in control plants.This data demonstrates indirectly that the representatives of the first variety have a higher water retention capacity.Under conditions of moderate humidity insufficiency occurs an increase of the water retention capacity: in the Moldovitsa plants the amount of water retained after 2 hours of experimental wilting was by 12.0% higher compared to the control plants, and in the Magia plants - by 5.8%. Thus, the different impact of the drought on the water status in leaves of soybean plants of Moldovitsa and Magia varieties is conditioned majorly by their different capacity to retain water in tissues.Changing the water retention capacity in cells and tissues is an integral factor in regulating plant endogenous response to adverse environmental factors, because only the intracellular water provides cooperative enzyme restructuring, the effects of concentration and compartmentalization.As mentioned above, the parameters of water status in the plant are used as quantitative criteria of plant resistance to stressful climatic factors everywhere and for a very long time.Analysing the data obtained from the point of this postulate it can be concluded that the inherent resistance to low humidity in Moldovitsa plants is somewhat higher compared to Magia plants due to increased water retention capacity.

Much of the damage caused by drought is associated with oxidative cellular destructions due to excessive formation of the ROS caused by cell dehydration.It is considered that plant ability to control the content of ROS often correlates with resistance to unfavorable factors. A positive correlation between oxidative stress and drought stress tolerance was found, as well as a significant negative correlation between the oxidative stress tolerance and the baseline concentration of ROS [10; 21; 22]. Adapted plants possess the ability to retain ROS production coupled with effective antioxidant protection. According to the data (Table 2),obtained in determining the content of malondialdehyde, in

Table 2. Antioxidant protection capacity of soybean plants *Glycine max* (L.) Merr under the conditions of drought at the phase "First trifoliate leaf"

Parameters	Variety			
	Moldovitsa		Magia	
	M±m	Δ, %	M±m	Δ, %
MDA, μM · g^{-1} fr. w.	12,52±0,15* / 19,87±0,27**	58,71	15,02±0,20 / 29,83±0,25	98,60
SOD, conv. un.· g^{-1} fr. w.	195,02±2,73 / 283,65±4.82	45,45	183,29±2,05 / 245,52±3,07	33,95
CAT, mM · g^{-1} fr. w.	6,06±0,07 / 8,63±0,09	42,41	6,49±0,08 / 7,85±0,06	20,96
APX, mM · g^{-1} fr. w.	2,41±0,04 / 3,65±0,06	51,45	1,13±0,02 / 1,58±0,03	39,82
GR, mM· g^{-1} fr. w.	158,63±3,19 / 219,08±4,98	38,11	173,09±3,62 / 197,38±3,75	14,03
GPX, mM · g^{-1} fr. w.	76,39±1,17 / 106,49±2,11	39,40	73,53±1,27 / 92,01±1,84	25,13
GwPX, mM · g^{-1} fr. w.	43,59±0,83 / 57,12±0,78	31,04	62,74±1.29 / 68,68±1,40	9,47

* - under favorable conditions; ** - under moderate drought.

soybean plants Moldovitsa under conditions of moderate humidity insufficiency the process of formation of ROS is lower compared to the Magia variety plants.Moldovita soybean plants have the capacity to maintain the content of malondialdehyde at a significantly lower level, both under optimum humidity conditions and under a soil moisture deficiency, unlike Magia plants.Content of MDA formed in the leaves of Moldovitsa variety after dehydration is about 1.58-fold higher compared to content in leaves of the control plants and about 1.96-fold or higher for the plants of Magic variety.The differences in the MDA content and the intensity of oxidative stress in these plants can be explained by the different degree of activation of the antioxidant protective enzymes.

In Moldovitsa plants, the stress caused by moderate humidity deficiency (7 days, 40% CTA) in the soil at the "first trifoliate leaves" phase, the activation of the enzyme protection system increased by 40.74%, and in the Magia plants the activation of the antioxidant enzymes constituted about 22.5% from the total enzyme activity in control plant leaves (70% TWC). The antioxidant enzyme protection capacity, manifested by the activity of SOD, CAT, APX and GPX, is reliably higher in these plants. It is required to note the significant SOD (by 45%) and APX (by 51%) content increase. In Magia plants, moderate water stress increased the activity of these enzymes by only 33.9% and 39.8% compared to non-stressed plants. As a consequence of the increased degree of dehydration and relatively low activation of antioxidant protective enzymes, the MDA content increased about twice.

One of the plant responses to the action of stressors is the content increase of membrane compounds and macromolecules with protective functions. Such compounds as proline, glutamate, glycine-betaine, mannitol, sorbitol, fructans, sucrose, oligosaccharides have the property to maintain the degree of hydration of the proteins [23;24] and increase water retention capacity. Proline and ascorbic acid content (Table 3) increase following the apparition of the oxidative stress was registered in leaves of both soybean varieties, but it was reliably more significant in Moldovitsa variety. They are also characterized by the ability to maintain a more stable level of carotenoid content, which, as it is known, plays an important role in protection of chloroplast and chlorophyll from the destruction by singlet oxygen molecules.

Tabele 3. Content change of non-enzymatic antioxidants in the leaves of soybean plants *Glycine max* (L.) Merr exposed to drought stress at the phase "First trifoliate leaves"

Variety	Humidity, % TWC	carotenoids, mg · $100g^{-1}$fr.w.		Ascorbic acid, mg%· g^{-1} fr.w.		proline, µM· 10^{-3} g fr.w.	
		M ± m	Δ, %	M ± m	Δ, %	M ± m	Δ, ori
Moldovitsa	Control, 70	41,90±0,58		30,73±0,23		4,59±0,09	
	Drought, 70 -40	35,48±0,41	-15,32	42,22±0,39	+37,39	34,63±0,23	+7,55
Magia,	Control, 70	40,62±0,53		31,77±0,78		6,93±0,10	
	Drought, 70 -40	33,80±0,29	-16,78	40,79±0,69	+28,39	15,58±0,12	+2,25

It is now well established that free proline has a polyfunctional role, which is manifested, among others, in the property to neutralize reactive oxygen species.Low-molecular mass organic compounds ensure, as mentioned above, the protection of macromolecules (including enzymes, membrane proteins and lipids) from dehydration, increase the water retention capacity, may bind reactive oxygen species that are formed in plant cells under drought conditions [25 - 27].

Thus, the obtained data demonstrate that tolerant plants differ in a higher content of ascorbate, proline, carotenoids, and higher activity of superoxide dismutase (SOD), catalase (CAT), peroxidases (PX), glutathione reductase (GR). By more stable water status and higher antioxidant capacity under conditions of moderate humidity deficiency are characterized Moldovitsa plants (Table1; 3; Figure 1).It is considered that by the antioxidant protection capacity, as well as by the water homeostatic capacity, one can judge about the constitutive resistance of the plants subjected to unfavorable factors [6;28]. Judging by the degree of physiological parameters change (fig. 1) under the action of water stress at the initial stages of ontogenesis it can be concluded that Moldovitsa plants have higher constitutive resistance compared to Magia plants.

The formalized notion for the resistance of a system (including living organisms) implies that a system with high resistance to external action is characterized by an insignificant deviation of its parameter values from normal followed by their rapid and complete return to initial state after the action has ceased. The expression of the effect of the unfavorable factor is represented by the degree of change of the vital processes in plants compared to the intensity of plant processes under optimum conditions.

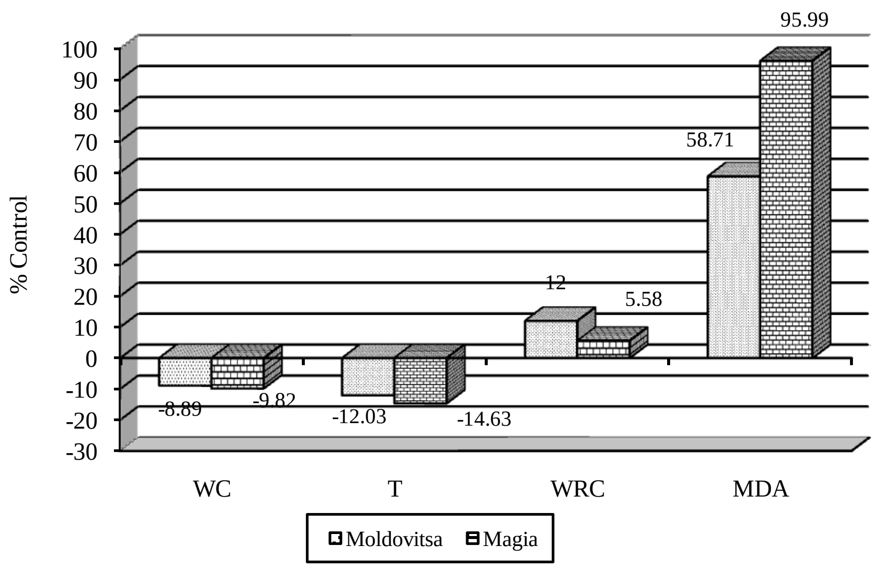


Fig.1. Degree of change in water content (WC), turgidity (T), water retention capacity (WRC) and malondialdehyde (MDA) content in soybean plant under conditions of moderate moisture insufficiency.

The data presented in Figure 1clearly demonstrates thedifferent reaction to drought of the plants of the two soybean varieties at the initial stage of ontogenesis: a more significant deviation of the water status parameters and the antioxidant protection system was recorded in the representatives of the Magia variety. The antioxidant protection capacity of Moldovitsa soybean plants is ensured by both increasing the activity of antioxidant enzymes and by increasing the content of non-enzymatic antioxidants.

Therefore, dehydration of soybean tissue, induced by the occurrence of drought conditions, results in the formation of reactive oxygen species (ROS) coupled with lipid peroxidation, which is confirmed by the increase of malondialdehyde content. Drought of the same intensity and duration makes a stronger oxidative stress more likely to occur in plants with a lower potential of water status self-regulation. Water status change and accelerated generation of reactive oxygen species cause the activation of protective systems: intensifying antioxidant enzyme activity and increasing the content of compounds with protective function - proline, ascorbate, glutamate, etc.

Changing the water status and ROS formation are nonspecific reactions in response to the action of various environmental factors: drought, cold, heat, salinization, gas, xenobionts, etc. The leaf water emission is intensified by increasing cell membrane permeability, coupled, on the one hand, with the inhibition of metabolic and energy reactions in general, on the other - by reducing the mobility of the ions, their diffusion, and consequently, with the braking of bioelectric activity of the membranes. Ion diffusion reduction under conditions of dehydration is associated with decrease of electrical conductivity and increased electrical resistance of tissues [29]. Starting with works of Dexter S., Tottingham W. and Graber L. [30], the determination of membrane permeability by multiple measurement of the electrical conductivity was used as a test criterion for studying the action of various adverse factors on the plant. In the current paper (tab. 4), characterizing the plant tolerance was also performed using the method based on the use of biophysical indices - the degree of change in the electrical resistance of leaf tissues under the influence of stress factor and the degree of restoration of the test-criterion. These methods are based on the determination of the degree of damage under the action of the stress factor(s) and the ability to restore the functions after the improvement of the external environment conditions [17]. Data is presented in Table 4.

Table 4.Effect of preliminary water stress at the phase" first trifoliate leave" on cross-tolerance of soybean plants

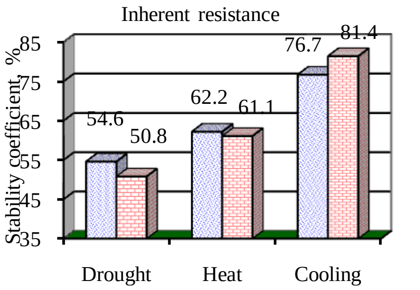
Variants	R_1, * kOm	R_2, ** kOm	Δ_1, %	R_3, *** kOm	Δ_2, %	Coef. of stability	Coef. of affectation
Plants, Magia variety							
Dehydration							
Control, optimal	641,1±12,8	920,0±22,1	43,5	677,5+11,5	5,7	50,8	49,2
Water stress, preliminary	625,8±10,8	903,5±22,8	44,4	632,5±12,5	1,1	54,5	45,5

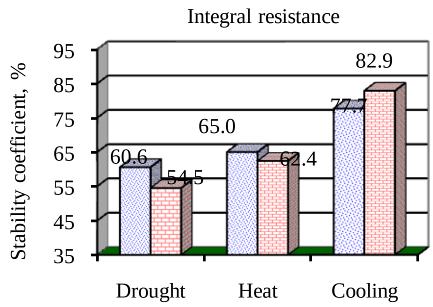
Cooling(4°C)							
Control, optimal	554,4±7,2	882,5±24,7	59,2	329,4±3,6	-40,6	81,4	18,6
Water stress, preliminary	902,5±18,0	1338,3±26,7	48,3	620,7±11,9	-31,2	82,9	17,1
Heat(40°C)							
Control, optimal	650,0±14,9	929,2±22,3	42,9	624,2±11,8	-4,0	61,1	38,9
Water stress, preliminary	890,0±15,1	1232,0±27,1	38,4	883,1±9,7	-0,8	62,4	37,4
Plants, Moldovitsa variety							
Dehydration							
Control, optimal	648,5±4,3	1107,0±2,9	70,70	484,5±0,7	-25,29	54,60	45,40
Water stress, preliminary	649,0±9,7	970,10±0,2	49,48	583,6±5,8	-10,08	60,60	39,40
Cooling(4°C)							
Control, optimal	573,2±13,8	896,7±6,4,5	56,44	383,3±1,7	-33,13	76,7	23,3
Water stress, preliminary	1094,0±9,8	1304,0 ±6,2	19,20	1127,9±10,5	3,10	77,7	22,3
Heat(40°C)							
Control, optimal	646,5±3,6	1033,8±3,2	59,91	503,5±5,5	-22,12	62,2	37,79
Water stress, preliminary	924,4±6,4	1315,6±4,4	42,34	856,1±5,9	-7,39	65,0	35,0

* R1 - electrical resistance value of plant tissues under optimum conditions; ** R2 - electrical resistance value of plant tissues under stress conditions; *** R3 - electrical resistance value of plant tissues after restoring optimum conditions.

The characteristics obtained by using the biophysical indices as a test-criterion correspond to the characteristics of the drought resistance obtained by determining the functional parameters - after the capacity of self-regulation of the water status and the antioxidant protection capacity in plants (Table 1-4).

According to the conception of the bi - component nature of the resistance [31 -33], which includes the constitutive component and the induced component, it is necessary to mention that the constitutive resistance is the capacity of plants, which row under optimal conditions, to respond to the action of the unfavorable factor; induced resistance is the intensified part of the resistance of plants adapted to moderate unfavorable conditions.The resistance of plants pre-exposed to drought stress for the first time is ensured only by the initial constitutive component. The data presented in Figure 2 demonstrates the different degree of the inherent resistance of the soybean plants pre-exposed to the action of the moderate drought at the "first trifoliate leaf" phase.





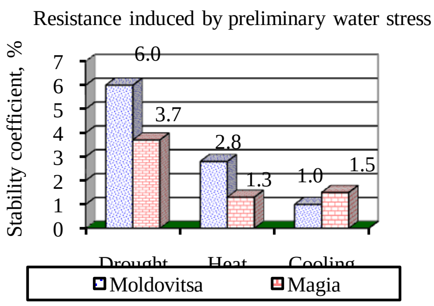


Fig. 2. The manifestation of cross-tolerance to plants under the influence of the preliminary water stress.

The inherent resistance to a moderate drought is higher for Moldovitsa variety compared to Magia variety.The results obtained (Figure 2) show that plants of the studied varieties have inherent tolerance not only to moderate humidity insufficiency but also to unfavorable temperature conditions - to hypo - and hyperthermic stresses. The inherent resistance of plants of these varieties to heat (+40^{0}C) is 62,2 and 61,1; to cooling (+4° C) and 76,7 and 81,4% respectively.Moldovitsa plantshave an increased inherent resistance to drought and heat, while Magia plants have higher inherent resistance to low temperatures of 4 - 5°C.Plants that had undergone moderate water stress more easily withstood heat (40°C) and low temperatures (4°C). Low temperature tolerance rate increase, induced by preventive water stress conditions, was 1,0% for Moldovitsa plants and 1,5% for Magia plants; the heat tolerance increase, induced by preventive water stress conditions, was 2,8 and 1,3% respectively. The resistance of plants to repeated droughts increased by 6,0 and 3,7% compared to the resistance of the control plants (Figure 2).

Therefore, the data confirms the idea that the action of an unfavorable factor of moderate intensity activates mechanisms that ensure the tolerance to other stressors.It has been demonstrated that there is strong positive correlation (r = 1) between inherent resistance and water retention capacity; and negative between the inherent resistance and the content of malondialdehyde, the coordination of which decreases under drought conditions (Table 5). At the same time, the dependence of cross-tolerance formation on inherent tolerance of plants, which undergone moderate stress at the early stages of ontogenesis, was demonstrated.Plant

Table 5. Correlation between inherent resistance, self-regulation of water status and antioxidant protection in soybean plants *Glycine max*(L.) Merr

Variety	Humidity, %TWC	drought/ WRC		drought/ MDA		heat/WRC		heat/ MDA		cold/WRC		cold/MDA	
		r	R^2	r	R^2	r	R^2	r	R^2	r	R^2	r	R^2
Moldovitsa	Control,70	1	1	-0,99	0,98	1	1	-1	1	0,99	0,98	-1	1
	Water stress, preliminary	0,93	0,86	-0,89	0,79	0,90	0,81	-0,89	0,79	0,91	0,83	0,87	0,76
Magia	Control, 70	0,99	0,98	-0,91	0,83	0,99	0,98	-1	1	0,99	0,98	-0,99	0,98
	Water stress, preliminary	0,88	0,77	-0,82	0,67	0,87	0,76	-0,81	0,65	0,88	0,77	0,79	0,62

pre-exposure to moderate water stress causes the true increase in tolerance to dehydration and heat and insignificant - to hypothermic stress.

Therefore, soybean plants, Moldovitsa variety in particular, possess inherent cross-tolerance, and the preliminary exposure of plants to moderate water stress causes the increase of cross-resistance due to the induced tolerance rate.

Hence, plants exposed in the initial stages of ontogenesis to the action of a certain stress factor (moderate short-term drought) become more tolerant to other unfavourable factors - dehydration, heat, cooling. Cross-tolerance depends on the inherent resistance potential, the self-regulation capacity of the water status, the activity of antioxidant protection systems.

IV. CONCLUSIONS

1. Plants exposed in the initial stages of ontogenesis to the action of a certain stressor (moderate short-term drought), become more tolerant to the action of other unfavourable factors: dehydration, heat, low temperatures.

2. The manifestation of cross-tolerance may be the result of two distinct phenomena: the increased stress tolerance being a consequence of previous exposure of plants to another type of stress (induced cross-tolerance), and/or specific genetic property of the species to provide resistance to several types of stress (inherent cross-tolerance).

3. The possible mechanisms that correlate with cross-tolerance are the inherent resistance potential, the water status self-regulation ability, the activity of antioxidant protection systems, including the ability to accumulate low-molecular weight antioxidants, and protective metabolites. The manifestation of cross-tolerance is closely related to the removal of ROS, especially with the activation of SOD, APX, CAT and GR.

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