

THE "PHOTOSYNTHESIS–GROWTH–STRESS MEMORY" RELATIONSHIP IN PLANTS UNDER CONDITIONS OF MOISTURE FLUCTUATION AND RECURRENT DROUGHT: MANAGEMENT OPTIONS

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ABSTRACT. The effect of co-activation of the stress-memory formation potential under repeated drought of *Glycine max* (Merr.) L. plants was recorded using cytokinin (CK), thiourea (TH) and, especially, complex preparation Polyel. *Glycine max* plants (Merr.) L. of Moldovitsa, Nadejda and Magia varieties, exposed to two cycles of "drought–rehydration" at the "first trifoliate leaf" and "flowering - pods formation" phases served as test subjects. The tolerance-inducing effect manifests itself by maintaining the content of assimilatory pigments, photosynthesis and growth processes at a significantly higher level. After the restoration of the optimal moisture background, plants pre-treated with CK, TH and the preparation Polyel, which endured moderate stress in the initial stages of

ontogenesis, had restored functional processes. The information obtained in this work certainly opens the management perspective of the ability to form stress memory, adaptation and tolerance of plants to the unfavourable fluctuation of humidity and recurrent drought. The management possibilities of plant adaptation and tolerance are discussed.

Keywords: plants; adaptation; resistance; growth; photosynthesis; transpiration; productivity; cytokinin compounds; antioxidant preparation.

INTRODUCTION

Repeated droughts caused by climate change often have catastrophic



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consequences for plant productivity. Urgent actions are needed to reduce the climate risk in all spheres of activity, including agriculture (FAO, 2022). Currently, the problem of crop productivity and resistance to the impact produced by climate change on Earth represents the main and most critical matter for the food security of the population (IPCC, 2022).

Water deficit is considered the strongest abiotic stress factor, limiting plant growth and productivity and threatening food security and nutrition. Data have accumulated on plant responses to stress caused by dehydration under drought conditions (Chaves *et al.*, 2003; Kramer and Boyer, 1995; Levitt, 1986). In many physical-geographic areas on Earth, plants are subjected to recurrent episodes of drought that vary in severity and length. There is a growing interest in learning more about how plants react to repeated droughts.

Recently, it has been demonstrated that plants can "remember" past incidents from the external environment and can use these memories for an appropriate response if these events are repeated, enduring them more easily (Walter *et al.*, 2011). Such plants form a "stress memory". Abiotic stress that occurs at different stages of ontogenesis creates a high risk of damage, but previous stress events can provide plants with protection against subsequent stress. Multiple exposures to drought conditions provide a faster and more appropriate plant response to a new stress situation compared to plants that have not been previously exposed to drought stress. However, little is known about which mechanisms are involved in

the manifestation of stress memory. From the published data (Bhattacharjee, 2005, 2012; Jacques *et al.*, 2021; Munne-Bosch, 2013) and the results of our own investigations (Ștefîrță *et al.*, 2021), the key systems, linked to plants reactions to recurrent drought and formation of stress memory in plants, are those coupled with self-regulation of water homeostasis (Bartoli *et al.*, 1999; Kramer and Boyer, 1995; Ștefîrță *et al.*, 2020), formation and neutralisation of reactive oxygen species (ROSs), and activation of the antioxidant potential (Asada, 2006; Foyer and Shigeoka, 2011; Shinozaki and Yamaguchi-Shinozaki, 1999; Ștefîrță *et al.*, 2021). With the creation and accumulation of numerous substances with a protective effect, such as particular proteins, amino acids, carbohydrates, etc., the modest rise in ROS level conditions the expression of protective genes and the beginning of adaptive processes (Bhattacharjee, 2012; Bruce *et al.*, 2007). Another possibility for preserving the memory of ecological stress is the morphological changes of the plant, which remain stable for a longer time than the metabolic changes (Bartoli *et al.*, 2013; Kalapos *et al.*, 1996). The production and yield of plant biomass are considered the main macroscopic indicators of drought stress memory because they integrate different molecular mechanisms and physiological processes involved in the plant's response to repeated stress (Abid *et al.*, 2017; Perveen *et al.*, 2015a, b).

Abid *et al.* (2017) consider the production and yield of plant biomass the main macroscopic indicators of drought stress memory since the plant's reaction to repeated stress is governed

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by a variety of molecular pathways and physiological processes. The importance of knowing the mechanisms that ensure plant accommodation and tolerance to repeated ecological impacts over time and elucidation of the factors that induce them is indisputable. Although knowledge of the mechanisms that allow plants to tolerate drought has increased considerably in recent years (Bartoli *et al.*, 2013; Ding *et al.*, 2012; Kinoshita and Seki, 2014), there is relatively little information regarding the improvement of tolerance to adverse moisture fluctuation and stress caused by recurrent drought. In this context, there is a need to explore some methods or ways of inducing stress memory and tolerance to often extreme fluctuations of external factors and repeated ecological stress. One of the key ways to increase stress tolerance is the application of agents that activate native protection mechanisms. Based on these findings, it has been suggested that drought effects can be managed using plant growth regulators, phytohormonal compounds, etc. (Aimar *et al.*, 2011; Fleta-Soriano, 2015; Liu *et al.*, 2022; Ștefiriță *et al.*, 2021). An effective way to protect the seeds is to increase natural plant resistance using tolerance-enhancing compounds by applying antioxidants and phytohormones (cytokinins, auxins) as factors for intensifying antioxidant protection, stabilising growth, delaying ageing, etc. (Ștefiriță *et al.*, 2021). In this sense, the real mechanisms involved in increasing plant tolerance to drought are persistently studied through the exogenous application of phytohormonal

compounds, knowing that they increase the ability of plant tissues to retain water, activate biosynthesis and accumulate phytomass, which ultimately ensures the formation of a plant phenotype with a wider norm of reaction to adverse conditions and reduce crop losses under repeated drought (Wahid *et al.*, 2017).

Currently, the physiological mechanisms underlying drought stress memory are not entirely clear. We aimed to test the possibility of inducing stress memory and improving plant performance, including through changes in photosynthesis, growth and productivity under recurrent drought conditions through the exogenous application of cytokinin-type compounds.

The specific objective of this work consisted of evaluating the particularities of plant growth regulation when using cytokinin-type compounds and the exogenous induction of stress memory and plant tolerance to repeated stress caused by drought.

Working hypothesis: Polyel preparation with a positive impact on the primary non-specific reactions of the plant's response to the action of drought – water homeostasis and antioxidant protection capacity – can induce stress tolerance in plants to unfavourable humidity fluctuations and repeated water stress through co-activation of morphophysiological mechanisms and optimisation of growth and development processes. The possibility of managing the effects of recurrent drought through the exogenous use of the new bioactive Polyel preparation with significantly

expressed antioxidant properties was verified.

MATERIALS AND METHODS

Glycine max L. (Merr) cultivars Nadejda, selected in the IGFPP, Moldovitsa and Magia, selected in the Research Institute for Field Crops "Selectia", served as study objects. Polyel preparation, obtained in the Institute of Chemistry from the Republic of Moldova (patent MD 1348 2020.02.29; patent MD 4647, 2020.04.30), is a beige powder consisting of coordinating compounds of iron(III), cobalt(III), micro- and macroelements, vitamins, and NO₃⁻ ions. Polyel represents a complex of active substances, including nicotinamide (vitamin PP) and micro- and macroelements (Ștefîrță *et al.*, 2020), possesses significant antioxidant properties (Ștefîrță *et al.*, 2021), and regulates water homeostasis in plant tissues exposed to unfavourable humidity conditions (Ștefîrță *et al.*, 2021). The evaluation of the compensatory reactions induced by cytokinin, thiourea and Polyel was carried out under conditions of controlled soil water content and repeated water stress.

The plants were grown in Mitcherlich vegetation pots with a capacity of 40 kg, pre-treated with cytokinin, thiourea and Polyel and exposed during ontogeny to drought-moisture recovery cycles, according with Scheme for "**first trifoliolate leaf**" and "**flowering - pods formation**".

In the periods of Critical Water Needs, plants were subjected to drought cycles of 7 days each, followed by recovery periods. At the end of each

cycle of stress and, respectively, of restoring the optimal humidity, new, fully developed leaves were harvested and analysed.

The intensity of transpiration and photosynthesis as well as the stomatal conductance were measured with the LCpro-SD portable analyzer. The net rate of these three parameters was established in accordance with the scheme of experiences at photosynthetically active radiation (PhAR) from 1000 μmol photon flux density m⁻²s⁻¹. While leaf temperature, air humidity and CO₂ concentration were recorded according to their values from the environment. All measurements were made in the morning between 8 and 11. The photosynthetic pigment content was determined using the spectrophotometric method in 80% acetone extracts. The determination of growth processes was performed every 3 days, both during the stress action period and during the post-stress period.

The statistical analysis of the obtained data was done in the "Statistics 7" environment. The degree of change in the assimilatory pigment content, growth speed and photosynthesis intensity were used as indicators to quantify the stress intensity and the effect of the compounds used on the formation of plant stress memory and tolerance to humidity fluctuations and to the action of repeated moderate drought.

RESULTS

Drought at the "first trifoliolate leaf" phase conditioned the reduction of chlorophyll content by 17.75% and chlorophyll b by 15.56% in the leaves of Moldovitsa and by 24.29 and 17.01%,

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respectively, in the leaves of Magia (Table 1). Thereafter, the total content of the assimilatory pigments was reduced. The destruction of chloroplasts and the

significant reduction of assimilation pigments inevitably led to the inhibition of the photosynthesis process.

Scheme of the experiment at the phase "first trifoliolate leaf"

Variant	Plants pre-treatment	Soil moisture (% TWC)
I	untreated	70
II	untreated	
III	Cytokinin	40 (moderate drought)
IV	Thiourea	
V	Polyel	

Scheme of the experiment at the phase "flowering – pods formation"

Variant	Plants pre-treatment	Soil moisture (% TWC)	Drought cycles
I	untreated	70	-
II	untreated	70 - 40	First cycle
III	Cytokinin		
IV	Thiourea	70 - 40 - 70 - 40	2
V	Polyel		

Note: TWC- total water capacity of soil

Table 1 – The content of the assimilation pigments (mg/100 g fr. m.*) in the leaves of soybean plants exposed to recurrent drought conditions

Variety	Variants, Moisture, % TWC**	Chlorophyll a		Chlorophyll b		Chlorophyll a + b	
		M ± m	Δ, %M	M ± m	Δ, %M	M ± m	Δ, %M
<i>at the "first trifoliolate leaf" phase</i>							
Moldovitsa	Control, 70	138.22±3.21		58.47±1.01		196.68±2.73	
	Drought, 70-40	113.68±2.18	-17.8	49.37±0.89	-15.6	163.05±3.08	-17.1
Magia	Control, 70	95.28±1.07		39.28±0.65		134.56±1.70	
	Drought, 70-40	72.14±1.98	-24.3	32.60±0.54	-17.0	104.73±2.42	-22.2
<i>at the "flowering - pods formation" phase</i>							
Moldovitsa	Control, 70	165.03±2.98		77.31±1.62		242.34±3.18	
	Drought, first cycle	137.48±1.89	-16.7	64.49±1.12	-16.6	201.97±3.02	-16.7
	Drought, second cycle	153.78±2.13	-6.8	70.02±0.98	-9.4	223.80±1.9	-7.6
Magia	Control, 70	158.34±2.02		71.96±0.96		230.29±3.02	
	Drought, first cycle	122.92±1.87	-22.4	57.19±0.75	-20.5	180.08±2.52	-21.8
	Drought, second cycle	138.12±2.75	-12.8	61.94±0.81	-13.9	200.06±3.01	-13.1

Notes: *- fresh mass; **- total water capacity of the soil

Water stress at the "first trifoliate leaf" phase caused a decrease in the photosynthesis intensity of Moldovitsa and Magia plants by 29.37 and 47.35%, respectively, compared to the intensity of the assimilation process under optimal humidity conditions (Table 2). A negative influence was recorded in plants exposed to drought for the first time in the "flowering – pods formation" phase. The assimilation process in representatives of the Moldovitsa variety was reduced 2.7 times and in Magia by 3.6 times. Previously stressed plants withstood the repeated stress more adequately; repeated drought conditioned the reduction of photosynthesis by 45.11% in the Moldovitsa variety and by 47.5% in the Magia variety. Strong inhibition of carbon dioxide assimilation in leaves

under insufficient moisture was a result not only of the decrease in the pigment content but also of the reduction in stomatal conductance, leaf dehydration and transpiration intensity (Table 2).

The stomatal resistance against CO₂ diffusion under conditions of insufficient humidity increased in Moldovitsa and Magia plants by 2.1 and 3.15 times, respectively, at the "first trifoliate leaf" phase and by 1.8 and 2.6 times, respectively, at the "flowering – pods formation" phase. Consequently, the intensity of transpiration in the twice-stressed plants of both varieties constituted 40.4–44.3% of the value of the process recorded in the plants from control variant and 53.1–60.2% in those exposed to drought for the first time at this development phase.

Table 2 – The intensity of photosynthesis, transpiration and stomatal conductance in *Glycine max* (Merr.) L. plants exposed to recurrent drought conditions

Variety	Variants, Moisture % TWC	Stomatal conductance, mmol·m ⁻² ·sec ⁻¹		Transpiration, μmol·m ⁻² ·sec ⁻¹		Photosynthesis, μmol·m ⁻² ·sec ⁻¹	
		M ± m	Δ, % C	M ± m	Δ, % C	M ± m	Δ, % C
<i>at the "first trifoliate leaf" phase</i>							
Moldovitsa	Control, 70	0.063±0.002		1.66±0.04		2.69±0.12	
	Drought, 70-40	0.030±0.001	-52.4	0.67±0.01	-59.6	1.90±0.09	-29.4
Magia	Control, 70	0.050±0.001		1.55±0.06		2.45±0.08	
	Drought, 70-40	0.020±0.001	-60.0	0.59±0.01	-61.9	1.29±0.07	-47.4
<i>at the "flowering – pods formation" phase</i>							
Moldovitsa	Control, 70	0.081±0.003		1.88±0.04		4.70±0.19	
	Drought, first cycle	0.044±0.001	-54.3	0.88±0.01	-53.2	1.76±0.07	-62.6
	Drought, second cycle	0.067±0.002	-17.3	1.12±0.05	-40.4	2.68±0.09	-45.1
Magia,	Control, 70	0.072±0.002		1.76±0.07		3.73±0.15	
	Drought, first cycle	0.028±0.001	-61.4	0.70±0.02	-60.2	1.05±0.03	-71.9
	Drought, second cycle	0.049±0.002	-31.9	0.98±0.05	-44.3	1.96±0.02	-47.5

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Plant resilience to recurrent droughts increased under the influence of substances having cytokinin activity. In these plants, stress memory manifests itself more obviously by minimising or mitigating the negative impact of subsequent stress on the assimilatory pigment content (*Table 3*) and photosynthesis intensity (*Table 4*). Under repeated conditions of humidity deficiency, the total chlorophyll content in the leaves of the plants from control variant was kept at a higher level compared to the plants from control variant exposed to water stress for the first time in the "flowering – pods formation" phase. Pre-treatment of plants with cytokinin, thiourea and Polyel ensured the maintenance of chlorophyll *a* + *b* content at a correspondingly higher level by 7.89, 13.48 and 17.83% under conditions of water content fluctuation and repeated water stress compared to the pigment content in the leaves of control plants exposed to repeated drought. Destruction of chloroplasts and significant reduction of assimilation pigments inevitably led to the inhibition of the photosynthesis process (*Table 4*). A particularly negative influence was recorded in plants exposed to drought for the first time in the "flowering – pods formation" phase.

In the control (untreated) plants exposed to a second cycle of drought, the process of carbon dioxide assimilation was preserved at a higher level by 18.2% compared to the plants exposed to the action of water stress for the first time at the "flowering - pods formation" phase. In twice-stressed and pre-treated plants, stomatal conductance and photosynthesis intensity decreased

by 1.27 and 1.65 times, respectively, while in plants exposed to the first stress at the "flowering – pods formation" phase, stomatal conductance and photosynthesis intensity suffered an impact of 1.73 and 1.95 times, respectively. The transpiration intensity was 54.8 and 60.45% of the value of the process recorded in the control plants under an optimal humidity background.

Growth maintenance under conditions of insufficient moisture represents an adaptive reaction associated with the organism's resistance to drought. In this work, the growth of the plant as a whole was strongly marked by humidity conditions (*Figure 1*). After 3 days of moderate moisture deficiency (40% TWC), the growth speed of these plants was reduced by 37.9% compared to the growth speed of control plants under an optimal moisture background. The impact produced by drought on the pre-treated plants manifested itself in a reduction of the diurnal growth rate by 28.4, 19.8 and 13.12% (*Figure 1*).

The improvement of humidity conditions ensured a significant intensification of the growth processes of the plants preventively exposed to water stress (*Figure 1* and *Figure 2*). It should be noted that the ability to restore growth processes in plants pre-treated with the investigated physiologically active substances (PHAS) manifests itself significantly better than in untreated plants.

Table 3 – Assimilatory pigment content (mg/100 g fr. m.) in the leaves of soybean plants under conditions of repeated water stress at the "flowering - pods formation" phase

Parameters Variants	Chlorophyll a		Chlorophyll b		Chlorophyll a + b		Carotenoids	
	M ± m	Δ, % C optim	M ± m	Δ, % C optim	M ± m	Δ, % C optim	M ± m	Δ, % C optim
Control, optim	171.78±4.8		76.63±2.5		248.41±7.7		52.2±1.52	
Control, drought first cycle	123.07±3.5	-28.4	53.33±1.5	-30.4	176.40±5.6	-29.0	36.5±1.15	-30.0
Control, drought second cycle	134.70±3.9	-21.6	58.5±1.6	-23.7	193.2±6.0	-22.2	41.7±1.33	-20.1
CK, drought second cycle	145.34±4.2	-15.4	63.07±1.8	-17.7	208.41±6.7	-16.1	44.5±1.37	-14.8
Thiourea, drought second cycle	153.83±4.9	-10.5	65.41±2.0	-14.6	219.24±7.0	-11.7	44.9±1.52	-14.0
Polyel, drought second cycle	158.12±4.8	-7.9	69.53±1.8	-9.3	227.65±6.8	-8.4	45.1±1.27	-13.6

Notes: compared to the control plants in optimal humidity conditions

Table 4 – Photosynthesis, stomatal conductance and transpiration of soybean plants under conditions of repeated water stress at the "flowering - pods formation" phase

Parameters Variants	Stomatal conductance, $\text{mmol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$		Transpiration intensity, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$		Photosynthesis intensity, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$	
	M ± m	Δ, % M*	M ± m	Δ, % M*	M ± m	Δ, % M*
Control, optim	0.052±0.002		1.77±0.05		3.12±0.09	
Control, drought first cycle	0.030±0.001	-42.31	0.97±0.03	-45.20	1.60±0.04	-48.72
Control, drought second cycle	0.041±0.001	-21.15	1.07±0.04	-39.55	1.89±0.03	-39.42
CK, drought second cycle	0.045±0.002	-13.46	1.12±0.03	-36.72	2.28±0.05	-26.92
Thiourea, drought second cycle	0.048±0.001	-7.69	1.37±0.04	-22.60	2.81±0.08	-9.94
Polyel, drought second cycle	0.050±0.002	-3.85	1.45±0.03	-18.07	2.95±0.10	-5.45

Notes: compared to the control plants in optimal humidity conditions

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On the fourth day after restoring optimal levels of soil moisture, the growth rate of untreated plants was 32.64%, those pre-treated with cytokinin – 30.48% and those treated with thiourea and Polyel – with 22.23 and 8.35%, respectively lower than in control plants (*Figure 2*). Plants pre-treated with this preparation restored their growth processes more quickly. After 10 days under improved levels of soil moisture, the growth rate of these plants was restored to the values of the control plants, which were not exposed to drought. The growth rate of untreated plants remained inhibited even after 10 days of moisture improvement. In the current investigation, a tendency to accelerate the growth speed of plants exposed to the action of a new cycle of drought at the "flowering – pods formation" phase compared to plants exposed for the first time to drought at this phase of development was recorded (*Figure 3*).

The degree of inhibition of the growth rate of plants exposed to the first cycle of drought at the "flowering – pods formation" phase was 37.4–54.9%. The growth speed of plants repeatedly exposed to drought was 35.6–54.1% higher compared to that of control plants. Repeated drought had a significantly smaller impact on the degree of change in the growth rate of plants pre-treated with CK, Thiourea and Polyel. In these plants, the ability to restore growth processes was mean significantly higher than in the untreated plants with the studied compounds. The results of the investigations led to the conclusion that CK, Thiourea and Polyel had the effect of intensifying the formation of stress-memory and increasing the tolerance of plants to repeated drought conditions caused by the fluctuation of soil moisture, which was manifested by maintaining growth processes at a higher level compared to untreated plants.

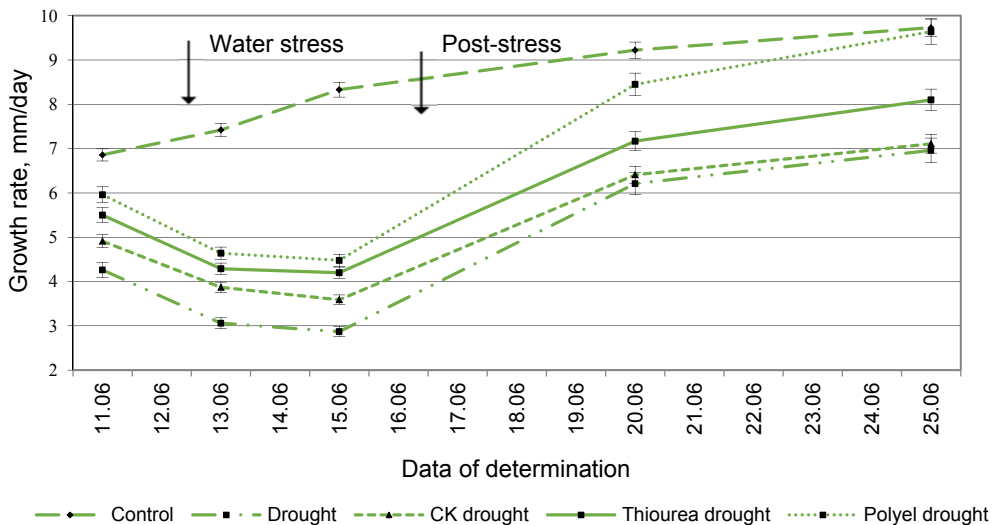


Figure 1 – The growth dynamics of soybean plants, cv. Moldovitsa, pre-treated with cytokinin-type compounds, and exposed to moderate drought at the "first trifoliolate leaf" phase

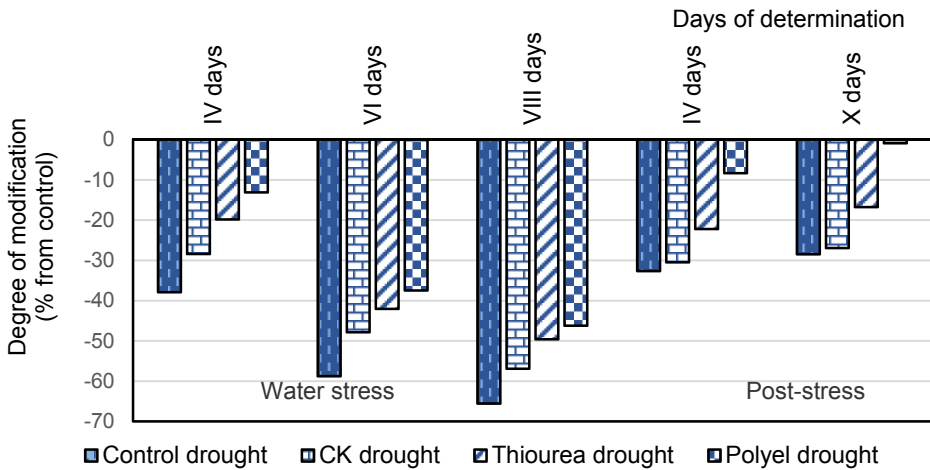


Figure 2 – The degree of modification (% from control) of the plant growth rate of *Glycine max* (Merr) L. variety Nadejda pre-treated with cytokinin-type compounds and exposed to the moderate drought at the "first trifoliolate leaf" phase

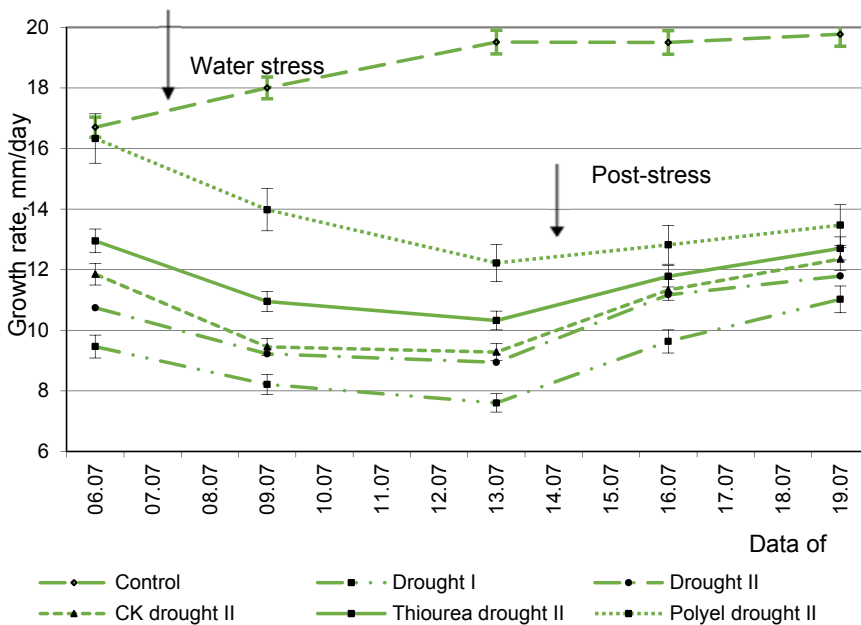


Figure 3 – The growth dynamics of soybean plants pre-treated with cytokinin-type compounds and exposed to moderate drought at the "flowering - pods formation" phase

DISCUSSION

Resistance is a genetically determined hereditary trait that does not

manifest itself under optimal conditions but is expressed only when humidity and temperature reach a certain threshold level. Resistance as a characteristic is

formed in the first stages of leaf development and its increase coincides in time with the period of leaf growth through cell division. As mentioned previously, the change in water status and accelerated generation of ROSs is one of the common primary responses to different stress factors (Asada, 2006; Bartoli *et al.*, 1999; Foyer and Shigeoka, 2011; Kramer and Boyer, 1995; Shinozaki and Yamaguchi-Shinozaki, 1999; Ștefăriță, 2020). On the one hand, ROSs serve as signalling molecules and activators of protection systems; on the other hand, dehydration and ROSs cause chlorophyll degradation, peroxidic oxidation of membrane phospholipids, chloroplast destruction and reduction of the carbon fixation rate with a direct impact on plant growth and productivity. The degree of change in the assimilatory pigment content under the influence of repeated stress confirms the conclusion about the formation/existence of stress memory in plants. The impact of the second drought cycle at the "flowering – pods formation" phase was truly weaker compared to the degree of decrease in the content of assimilatory pigments in plants exposed to drought of the same duration and intensity for the first time at this phase of development (Table 1). The chlorophyll content in the leaves of plants exposed to repeated stress (70-40-70-40% TWC) was maintained at a higher level compared to the pigment content in the leaves of plants exposed to drought for the first time (70-40% TWC). In the Magia variety, the changes in the pigment content in the leaves were more significant compared to the plants of the Moldovitsa variety (Table 1), which demonstrates a less pronounced

manifestation of stress memory and a less significant adaptation effect.

The destruction of chloroplasts and the significant reduction of assimilation pigments inevitably led to the inhibition of the photosynthesis process (Table 2). Repeated drought caused changes in the photosynthesis process of the same characteristic but was quantitatively less significant compared to carbon assimilation in plants exposed to stress for the first time during generative development. Changes in photosynthesis have been highlighted in several studies regarding water stress-induced memory (Leufen *et al.*, 2020). Kim *et al.* (2020) demonstrated that a single incidence of water stress at the initial stages of ontogeny in *Glycine max* plants can improve the plant's response to subsequent stress by mitigating its impact on photosynthesis, thus sustaining the state of carbon assimilation at a higher level.

Therefore, in plants that have endured moderate stress at the beginning of vegetation, a "stress memory" is formed – the ability to react adequately to subsequent stress. The first incidence of stress leaves an imprint that influences the plant's response to the subsequent occurrence of unfavourable conditions. The dependence of stress memory formation on genotype-specific characteristics is specified.

Tissue dehydration under drought conditions greatly affects stomatal conductance and constrains gas exchange and plant growth (Scoffoni *et al.*, 2012). Stomatal closure reduces water loss through transpiration but inevitably leads to the deceleration of photosynthesis because of the

chlorophyll content decline and the access of carbon dioxide at the chloroplast level. Some of these reactions are directly induced by changes in the water status of the cells, while others are conditioned by changes in endogenous phytohormone content. A lack of moisture inevitably affects the transport of phytohormones through the phloem and xylem and disrupts the growth and development processes. Dehydration conditions the decrease in phytohormone levels of the growth stimulator class, namely indolyl acetic acid (IAA), gibberellin (GA), and cytokinin (CK), and the accumulation of "stress hormones", namely ethylene (ET) and abscisic acid (ABA) (Dobra *et al.*, 2010). Adverse conditions of the external environment, especially drought, inhibit the delivery of CK from roots to aerial organs. As a result, shoot growth is reduced, and the leaves fall prematurely. CK influences a wide spectrum of physiological and biochemical processes and has a positive effect on the production process: formation and operation of the photosynthetic apparatus, transport and distribution of assimilates, growth, development, storage of reserve substances, etc. (Davies *et al.*, 2005). Together with the water flow, cytokinins are also transferred from roots to shoots due to which the stomata's state, and, consequently, water consumption, the process of assimilation of carbon dioxide, as well as the growth by elongation of cells, were regulated. Cytokinins increase their water attraction capacity towards leaves and growing organs.

Their action is explained by the phytohormones' ability to open the

stomata's ostiols, intensify transpiration, and stimulate growth processes and biosynthesis in cells. It has been demonstrated that the exogenous use of cytokinins restrains the premature senescence of leaves and intensifies photosynthesis and plant growth under drought conditions (Ștefîrță *et al.*, 2021). Stress memory and faster and more efficient plant responses to subsequent stress can be induced in the absence of primary stress by the application of phytohormones, of abscisic (ABA), jasmonic (JA), salicylic (SA) and beta aminobutyric acids (Aimar *et al.*, 2011; Fleta-Soriano *et al.*, 2015; Fleta-Soriano and Munné-Bosch, 2016; Liu *et al.*, 2022; Ștefîrță *et al.*, 2021). Phytohormones have been shown to be a dominant factor in mediating plant adaptation and stress memory formation. Plant resilience to recurrent droughts increased under the influence of substances having cytokinin activity.

Plant pre-treatment with solutions of cytokinin-type compounds diminishes the negative impact of water stress and amplifies the formation/activation of plant stress memory under recurrent drought. Plants previously stressed and pre-treated with CK, Tu and Polyel endured repeated stress significantly better than untreated plants. The large gap between the decrease in photosynthetic pigment content and inhibition of photosynthesis demonstrates that strong inhibition of carbon dioxide assimilation in leaves under conditions of moisture deficit is a result not only of the decrease in the pigment content but also of the reduction in stomatal conductance and leaf dehydration. Stomatal closure reduces water loss through transpiration, but it

inevitably leads to a reduction in photosynthesis because of the decrease in the content of chlorophyll and the access of carbon dioxide at the chloroplast level. Significantly smaller changes were recorded in plants pre-treated with cytokinin, thiourea and, especially, Polyel.

In summary, the information in the specialised literature and the results of our own investigations show that the mechanisms coupled with self-regulation of water homeostasis, formation and neutralisation of ROSs, and intensification/stabilisation of the synthesis of compounds with regulatory and protective functions are correlated with the formation of plant stress memory and have tangents to the regulation of morphogenesis, growth and development. The effect of co-activation of the stress memory formation potential under repeated drought of *Glycine max* (Merr.) L. plants were recorded using cytokinin, thiourea and, especially, the complex preparation of Polyel. The tolerance-inducing effect manifests itself by maintaining the content of assimilatory pigments, photosynthesis and growth processes at a mean significantly veridical higher level. After the restoration of the optimal moisture background, plants pre-treated with CK, Tu and, especially, the preparation Polyel, which endured moderate stress in the initial stages of ontogenesis, restored their functional processes. The information obtained in the work certainly opens the management perspective of the ability to form stress memory, adaptation and tolerance of plants to the unfavourable fluctuation of humidity and recurrent drought.

CONCLUSIONS

Plant exposure to moderate moisture deficit, as well as pre-treatment with cytokinin-type compounds at the initial stages of ontogenesis, induces the formation of stress memory, which ensures a more adequate reaction and tolerance to the repeated occurrence of drought at the stages of generative development.

Stress memory and plant adaptation to fluctuating humidity and recurrent drought involve adjusting the content of assimilatory pigments, photosynthesis and plant growth.

Pre-treatment of plants with cytokinin-type compounds significantly reduced the harmful effects of recurrent drought on photosynthesis, growth and biomass accumulation both during the action of the repeated stress factor and in post action after the improvement of moisture conditions. Moderate and short-term water stress also lessens the harmful effects of repeated drought conditions.

After restoring the optimal moisture background, plants pre-treated with CK, Tu and, especially, with Polyel preparation, which endured moderate stress in the initial stages of ontogenesis, had restored their functional processes more thoroughly.

Plant exposure to moderate water deficit, as well as pre-treatment with cytokinin-type compounds at the initial stages of ontogenesis, present options for stress memory management, adaptation and tolerance of plants to conditions of unfavourable moisture fluctuations and recurrent drought.

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The "photosynthesis–growth–stress memory" relationship in plants

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