https://doi.org/10.15407/frg2026.01.028
UDC 581.192:58.081

THE INFLUENCE OF ABIOTIC STRESSES ON GROWTH AND CYTOKININ HOMEOSTASIS IN WINTER RYE *SECALE CEREALE* L. DURING EARLY ONTOGENESIS

I.V. KOSAKIVSKA, L.V. VOYTENKO, V.A. VASYUK, M.M. SHCHERBATIUK

M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine
2 Tereshchenkivska St., Kyiv 01004, Ukraine
e-mail: lesyavoytenko@gmail.com

The effects of heat stress (+40 °C for 2 hours), chilling (+4 °C for 2 hours), and moderate soil drought (four days without watering) on growth and cytokinin homeostasis in rye at 14th and 18th days of growth, and after recovery on 21st day were investigated. Morphometric analysis revealed that shoots were more sensitive to stresses, however, the root system recovered better in terms of fresh and dry weight. Cytokinin dynamics and distribution were organ-specific and stress-dependent. All stresses led to the accumulation of cytokinins in shoots and a decrease in roots, with the most significant changes observed under drought conditions. Stresses had prolonged effects on cytokinin levels, which remained lower than controls after recovery. The most significant alterations were found in *trans*-zeatinriboside accumulation, suggesting its potential role in adaptation to stress in rye. These findings provide a basis for further research into stress-resistance mechanisms in cereals, and the development of strategies to enhance their adaptability, in particular through the use of exogenous phytohormones.

Key words: *Secale cereale* L., chilling, cytokinins, heat stress, growth, soil drought, stress resistance.

In Ukraine, the reality of climate change — driven by both natural and anthropogenic factors — is becoming increasingly evident. This phenomenon is marked by a growing frequency of extreme weather events, and heightened contrast in climatic conditions between years and specific seasons [1, 2]. Temperature is one of the most critical environmental factors that affect plant growth, development, and productivity. Temperatures exceeding the optimal range induce heat stress, which adversely affects metabolism, inhibits photosynthesis, increases respiration, slows growth, and reduces yields [3, 4]. Conversely, low temperatures negatively impact both vegetative and reproductive growth, delay seed germination, and can cause partial plant mortality due to developmental abnormalities in embryos. Cold stress also impairs water and nutrient uptake, resulting in cellular dehydration, disrupted nutrient flow, and yield losses [5, 6]. Drought stress leads to stomatal closure, reducing the supply of carbon

Citation: Kosakivska I.V., Voytenko L.V., Vasyuk V.A., Shcherbatiuk M.M. The influence of abiotic stresses on growth and cytokinin homeostasis in winter rye *Secale cereale* L. during early ontogenesis. *Fiziol. rosl. genet.*, 2026, 58, No. 1, pp. 28—42. https://doi.org/10.15407/frg2026.01.028

dioxide to chloroplasts and suppressing photosynthesis [7]. It also inhibits aboveground growth [8] while stimulating root elongation [9]. Given the limited potential for expanding agricultural land in Ukraine, increasing the productivity of existing arable land is a pressing challenge. One promising approach is the development and cultivation of stress-resistant crop varieties.

Winter rye (*Secale cereale* L.) is one of the most important bread grains, and is the primary cereal grown in regions where wheat cultivation is difficult or not feasible [10]. Cultivated in Europe since ancient times, rye is genetically related to wheat and barley. It is the most cold-resistant among cereals, and is less dependent on soil fertility and moisture availability than wheat. Uniquely, rye can be cultivated without herbicides and, in many cases, without fungicides, making it suitable for sustainable and ecological farming [11].

The winter rye variety 'Boghuslavka' is a domestic Ukrainian cultivar bred by researchers of the Institute of Plant Physiology and Genetics of the National Academy of Sciences of Ukraine and the Nosivska Breeding and Research Station of the Chernihiv Institute of Agricultural Production. It is officially listed in the State Register and has been introduced into agricultural production. 'Boghuslavka' is a mid-season variety with moderate resistance to drought, frost, and diseases [12]. It is successfully cultivated at numerous Ukrainian farms. Given the current situation — where a significant portion of Ukraine's arable land is contaminated or degraded due to russian aggression — research into the biological traits of 'Boghuslavka' rye, an unpretentious and resilient crop, is both timely and relevant.

Phytohormones are key endogenous compounds involved in modulating physiological and molecular responses that enable plants to survive under adverse conditions [13—15]. Among these, cytokinins — adenine derivatives — are essential components of the phytohormonal complex [16, 17]. Cytokinins occur in active forms (such as isopentenyladenine, dihydrozeatin, *cis*-zeatin, and *trans*-zeatin) that bind to receptors, and in inactive forms such as ribosides and nucleotides. Cellular cytokinin homeostasis is maintained through a balance of biosynthesis, degradation, and conjugation [18]. In most plant species, *trans*-zeatin and its derivatives dominate due to their high activity, receptor affinity, and peak concentrations during periods of vigorous growth [19].

Cytokinins play a vital role in orchestrating complex plant responses to abiotic stresses. They can inhibit lipid peroxidation, stimulate protective protein biosynthesis, preserve membrane integrity, and delay premature tissue senescence. Under abiotic stress conditions, cytokinins are involved in the regulation of key metabolic processes, improving the efficiency of photosynthesis, nutrient uptake, enhancing the activity of antioxidant enzymes, and optimizing the structure of the root system. They also reduce the level of reactive oxygen species (ROS) and malondialdehyde (MDA), which leads to improved plant productivity and yield. Cytokinins interact closely with other phytohormones, including abscisic acid, ethylene, salicylic acid, and jasmonic acid, to modulate stress-protective pathways. This interaction contributes to the formation of plant responses to stress [20—22]. Their ability to quickly reprogram metabolic pathways enables plants to not only endure stress but also develop long-term adaptive strategies [15, 23].

Under extreme temperature conditions, cytokinins activate adaptive responses that protect cellular structures and functions [24]. In heat stress conditions, they stimulate the production of heat shock proteins (HSPs) — specifically small HSPs (sHSPs, such as HSP17.6 and HSP26.2), HSP70, and HSP90, which stabilize and repair denatured proteins and maintain membrane fluidity [25, 26]. Under low-temperature stress, cytokinins promote the synthesis of cryoprotectants such as sugars and amino acids that prevent intracellular ice crystal formation. They also regulate the production of unsaturated fatty acids, enhancing membrane fluidity and function at low temperatures [27, 28].

Under drought, cytokinins play a dual role in managing water homeostasis and growth. In aerial organs, cytokinin levels decrease to conserve water and suppress vegetative growth. In roots, cytokinin synthesis increases, facilitating their transport function to shoots and signaling the need for metabolic adjustment [29, 30]. Cytokinins also interact with other hormones, particularly abscisic acid (ABA), which plays a central role in drought response. While ABA induces stomatal closure to prevent water loss, cytokinins counterbalance this effect, supporting photosynthesis and ensuring a trade-off between gas exchange and water conservation. Moreover, cytokinins promote root elongation to enhance water uptake from deeper soil layers [31—33]. In wheat, ABA priming alters cytokinins homeostasis differently by species. In winter wheat, it can trigger cytokinins accumulation in shoots and roots to alleviate heat damage, while in spelt wheat, it may decrease shoot cytokinins to focus resources [34].

Cytokinins influence stress responses by regulating gene expression through chromatin modifications, facilitating quicker and more efficient adaptation [35]. These multifaceted roles highlight cytokinins as central players in plant adaptation to unfavorable environments. Their use in agricultural practices offers promising potential for mitigating the effects of abiotic stresses [36—39] — particularly in regions where cultivation is increasingly challenged by climate extremes. We hypothesized that temperature and drought stress trigger distinct changes in cytokinin accumulation and distribution in rye organs early in the growing season. These changes may activate stress-protective mechanisms, contribute to adaptation strategies, and offer valuable insights for developing approaches to screen resistant genotypes and environmentally friendly methods of inducing stress resistance. We leave the hypothesis unchanged — since it is a hypothesis.

The aim of this study was to investigate the effects of abiotic stresses (heat, chilling, and moderate soil drought) on growth parameters and the dynamics and distribution of endogenous cytokinins in the shoots and roots of young winter rye plants of the ‘Boghuslavka’ variety. Additionally, we aimed to analyze the patterns of post-stress restoration of cytokinin homeostasis.

Materials and Methods

Plant material and experimental design. 14-, 18-, and 21-day-old plants of winter rye *Secale cereale* L. cv. ‘Boghuslavka’ with medium drought and frost tolerance were used. Calibrated seeds were surface sterilized in 70 %

ethanol for 1—2 min, rinsed thoroughly with distilled water, then placed on moistened filter paper in cuvettes and germinated in the dark at 21 °C for 24 h. Uniformly germinated seedlings were transplanted into 2 L pots filled with calcined river sand and grown in a Vötsch growth chamber (Balingen, Germany) under the following conditions: 20 °C day/17 °C night, 190 μmol/(m^2 · s) photon flux density, 16 h photoperiod, and 65±5 % relative humidity. Plants were watered daily with 50 mL Knop solution per vessel.

Temperature stress treatments and sampling. To impose heat stress, 14-day-old plants were transferred to a thermostat at 40 °C for 2 h under 190 μmol/(m^2 · s) illumination. After treatment, plants were returned to control conditions and sampled at 21st days of age. For chilling stress, 14-day-old plants were exposed to 4 °C for 2 h under the same light intensity; subsequent recovery also continued until 21st day under control conditions.

Drought stress treatment and sampling. Moderate soil drought was induced by withholding water from 14-day-old plants for 4 days, until visible leaf wilting, and soil moisture declined to approximately 30 % field capacity (190 μmol/(m^2 · s); 20 °C). On day 18 (2—3 leaf stage), watering resumed, and plants were maintained under control conditions until 21st day (3—4 leaf stage).

Morphometric parameters measurements. Adaptive responses to heat, chilling, and drought were assessed by measuring shoot height, length of the longest root, and both fresh and dry weight of shoots and roots.

Extraction and purification of cytokinins. Shoots and roots (2 g each) were snapfrozen in liquid nitrogen and ground to a fine powder. The homogenate was transferred into test tubes containing 10 mL extraction solvent (methanol:water: formic acid, 15:4:1 v/v/v) and agitated at 4 °C in the dark for 24 h. After centrifugation (15000 rpm, 30 min, 4 °C), the supernatant was collected. The pellet was re-extracted with 5 mL solvent for 30 min under the same conditions, then recentrifuged. Combined supernatants were concentrated under reduced pressure at 40 °C to 1 mL. Lipophilic impurities, proteins, and pigments were removed on a C18 Sep Pak Plus cartridge (Waters), and cytokinins were retained on an Oasis MCX cartridge (6 cc/150 mg; Waters). Elution was achieved with 60 mL methanol containing 2.5 mL 26 % ammonia, brought to 100 mL with deionized water [40]. Eluates were evaporated to dryness and stored in the freezer.

Quantitative analysis of cytokinins. Cytokinin profiles were determined by HPLC-MS using an Agilent 1200 HPLC system with diode array detection (G1315B) coupled to an Agilent G6120A single quadrupole mass spectrometer. Separation was performed on an Agilent ZORBAX Eclipse Plus C18 column (4.6×250 mm, 5 μm particle size) in reversed phase mode [41]. Unlabeled standards of *trans*-zeatin (*t*-Z), *trans*-zeatinriboside (*t*-ZR), *trans*-zeatin-*O*-glucoside (*t*-OG), isopentenyladenine (iP), and isopentenyladenosine (iPA) (Sigma Aldrich, USA) were used for calibration. Detection employed a combined electrospray/chemical ionization source in positive ion mode. Cytokinin contents were calculated using Agilent OpenLAB CDS ChemStation (rev. C.01.09).

Statistical analysis. All experiments comprised three independent biological replicates, each independently repeated three times. Data were plotted in Microsoft Excel (Redmond, WA, USA) and analyzed using one way ANOVA in SPSS 16.0 (IBM SPSS Statistics, Chicago, IL, USA). Differences were considered significant at $p \leq 0.05$. Results are presented as mean±standard error (x±SE).

Results and discussion

Changes in growth parameters of winter rye under temperature stress and soil drought. Short-term exposure to high (+40 °C for 2 hours) and low positive (+4 °C for 2 hours) temperatures did not significantly affect the linear growth, fresh weight (FW), or dry weight (DW) of shoots and roots in 14-day-old winter rye plants ‘Boghuslavka’. However, by 21st day, the shoots of plants previously exposed to high (HT) and low (LT) temperatures showed reduced morphometric parameters compared to the control (C) plants. In particular, FW of HT-plant shoots decreased by 7.2 %. Root length in LT-plants remained comparable to control values (Table 1).

Under moderate soil drought (four days without watering), the shoot height of 18-day-old drought-stressed (SD) plants decreased by 14.3 %. FW of shoots and roots declined by 24.6 % and 22.5 %, respectively. Upon rewatering, 21-day-old plants still exhibited diminished shoot and root length — 8 % and 5 % below control, respectively. Biomass was reduced by 7 % in shoots and 6 % in roots, and shoot DW was 10 % lower (Table 1).

TABLE 1. Effect of short-term temperature stress (+40 °C and +4 °C, 2 h) and moderate soil drought (four days without irrigation) on the growth parameters of winter rye cv. ‘Boghuslavka’ (C — control, HT — high temperature, LT — low temperature)

Treatment	Shoots		Roots	
	Height, cm	FW/DW, mg	Length, cm	FW/DW, mg
C-plants. 14th day	18.3±0.9	119.2±6.0[1] 14.6±0.7[2]	15.0±0.8	121.3±6.3[1] 15.3±0.8[2]
HT-plants. 14th day	18.3±0.9	124.4±6.1[1] 13.8±0.7[2]	15.1±0.8	124.9±6.2[1] 15.7±0.6[2]
LT-plants. 14th day	18.1±0.9	126.3±6.3[1] 15.3±0.8[2]	14.9±0.6	124.2±6.2[1] 15.9±0.8[2]
C-plants. 21st day	23.7±1.2	150.1±7.5[1] 21.2±1.1[2]	17.2±0.9	135.0±6.8[1] 17.7±0.9[2]
HT-plants. 21st day	22.6±0.9	139.3±7.0[1] 20.5±0.4[2]	17.4 ±0.9	137.2±6.9[1] 17.9±0.9[2]
LT-plants. 21st day	21.2±1.1	141.9±7.1[1] 19.2±1.0[2]	17.6±0.9	139.2±7.0[1] 18.1±0.9[2]
C-plants. 18th day	21.0±1.0	126.3±6.4[1] 15.4±0.8[2]	15.6±0.8	120±5.9[1] 14.8±0.7[2]
SD-plants. 18th day	18.1±0.9	95.1±4.7[1]* 14.7±0.6[2]	15.0±08	93.3±4.7[1]* 13.8±0.7[2]
C-plants. 21st day	23.9±1.2	149.1±7.5[1] 19.1±0.9[2]	17.3±0.9	134.1±6.0[1] 16.7±0.8[2]
SD-plants. 21st day	22.1±1.1	138.4±6.9[1] 17.2±0.6[2]	16.4±0.8	126.2±5.0[1] 16.0±0.8[2]

Note. 1 — organ fresh weight; 2 — organ dry weight; * — significant difference at $p \leq 0.05$ compared to control; data presented are x±SE, n = 90.

Overall, shoots were more sensitive to abiotic stress in early vegetative stages, while the root system showed greater resilience.

Effect of temperature stresses on cytokinins homeostasis in winter rye. Five forms of cytokinins were identified in 'Boghuslavka' plants: *trans*-zeatin (*t*-Z), *trans*-zeatinriboside (*t*-ZR), *trans*-zeatin-*O*-glucoside (*t*-Z*O*G), isopentenyladenosine (iPA), and isopentenyladenine (iP). After short-term high-temperature stress (+40 °C, 2 h), total cytokinin content in shoots of 14-day-old plants increased by 42.1 %, while in roots it decreased by 9.0 %. These shifts were primarily driven by *t*-ZR, which increased 2.3-fold in shoots and decreased 1.1-fold in roots. In 14-day-old C- and HT-plants, zeatin-type cytokinins exceeded isopentenyl types by 36- and 19-fold, respectively (Fig. 1, Table 2).

By day 21 of recovery, total cytokinin content decreased by 6.8 % in shoots and 39.1 % in roots. Shoots exhibited reduced levels of all zeatin forms, while isopentenyl cytokinins — especially iPA — increased 7.9-fold. Root zeatin levels also dropped, most notably *t*-ZR (by half), whereas isopentenyl forms remained stable (20.0±0,9 ng/g FW). Overall, cytokinin levels during recovery were 45.5 % and 19.2 % lower in shoots and roots, respectively, compared to controls. *t*-ZR remained dominant but decreased 2.7-fold in shoots and 1.4-fold in roots. Isopentenyl forms increased 11.7- and 2.3-fold in shoots and roots, respectively, but remained 1.8- and 7.5-fold lower than zeatin forms (Fig. 1).

Under low temperature stress (+4 °C, 2 h), total cytokinin content in 14-day-old shoots increased by 43.2 %, with zeatin forms predominating. In roots, total cytokinin content dropped by 52.6 %. Zeatin levels were 2.8 times lower, while isopentenyl levels were 2.8 times higher than controls (Table 2). *t*-ZR was the dominant zeatin form. Isopentenyl forms, especially iPA, were mainly concentrated in roots, where iPA content was 1.9 times that of iP (Fig. 2).

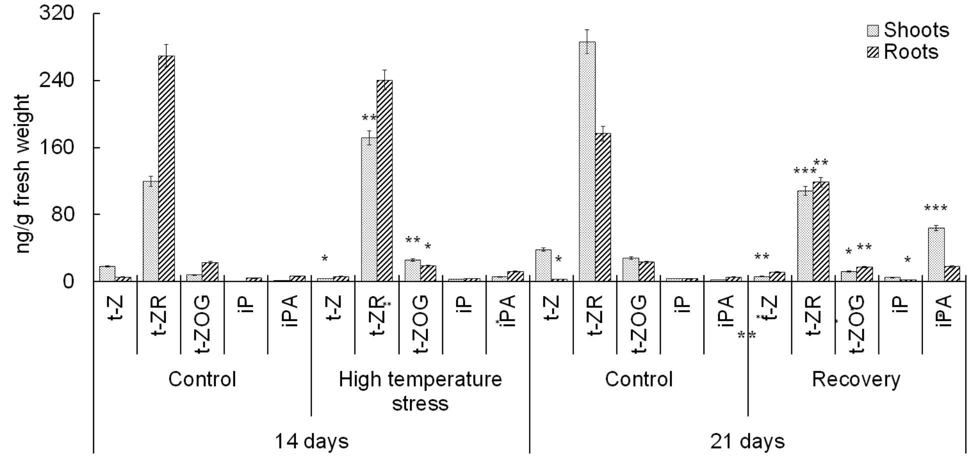

Fig. 1. Dynamics and distribution of endogenous cytokinins in 14-day-old *Secale cereale* cv. 'Boghuslavka' plants after high temperature stress (+40 °C, 2 h) and on the 21st day after recovery (ng/g FW). Notation (here and further in all figures): iP — isopentenyladenine, iPA— isopentenyladenosine; *t*-Z — *trans*-zeatin, *t*-ZR — *trans*-zeatinriboside, *t*-Z*O*G — *trans*-zeatin-*O*-glucoside (significance at: * — $p < 0.05$, ** — $p < 0.01$ and *** — $p < 0.001$ compared with the control; n = 3; x±SE)

TABLE 2. Total content of zeatin and isopentenyl cytokinin forms in 14-day-old Secale cereale cv. 'Boghuslavka' plants after short-term temperature stresses and on the 21st day after recovery (ng/g of FW) '(C — control, HT — high temperature, LT — low temperature)

Treatment	Cytokinin content	Shoots	Roots
C-plants. 14th day	*t*-Z, *t*-ZR, *t*-Z*O*G	145.6±7.3	297.8±14.9
	iP, iPA	1.8±1.1	10.5±0.5
HT- plants. 14th day	*t*-Z, *t*-ZR, *t*-Z*O*G	200.7±10.0*	264.7±13.2
	iP, iPA	8.7±0.4***	15.7±0.8
LT- plants. 14th day	*t*-Z, *t*-ZR, *t*-Z*O*G	205.3±10.2*	105.6±5.3**
	iP, iPA	5.7±0.3**	40.5±2.1***
C-plants. 21st day	*t*-Z, *t*-ZR, *t*-Z*O*G	352.3±17.6	202.6±10.1
	iP, iPA	5.9±0.3	8.8±0.4
HT- plants. 21st day	*t*-Z, *t*-ZR, *t*-Z*O*G	126.0±6.3***	150.8±7.5*
	iP, iPA	69.1±3.4***	20.0±0.9***
LT- plants. 21st day	*t*-Z, *t*-ZR, *t*-Z*O*G	214.6±10.7**	84.7±4.2***
	iP, iPA	19.8±1.0*	21.1±1.1***

Note. Significance at: * — $p < 0.05$, ** — $p < 0.01$ and *** — $p < 0.001$ compared with the control; n = 3; x±SE.

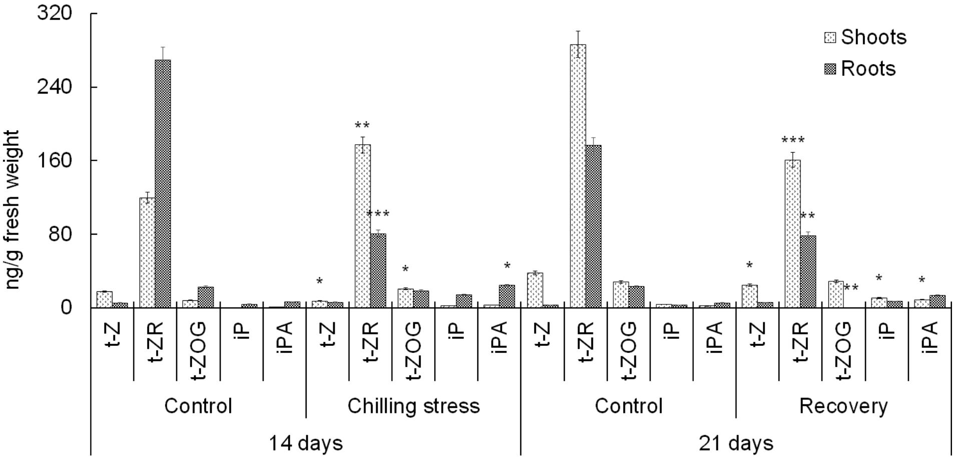

Fig. 2. Dynamics and distribution of endogenous cytokinins in 14-day-old *Secale cereale* cv. 'Boghuslavka' plants after low positive temperature stress (+4 °C, 2 h) and on the 21st day after recovery (ng/g FW) (significance at: * — $p < 0.05$, ** — $p < 0.01$ and *** — $p < 0.001$ compared with the control; n = 3; x±SE)

By day 21 post-stress, total cytokinin content in shoots rose to 234.4±11,7 ng/g FW, primarily due to a 3,5-fold increase in isopentenyl forms. In roots, cytokinin levels decreased by 27.5 % to 105.8±5,3 ng/g FW. While *t*-Z and *t*-ZR levels remained stable, *t*-Z*O*G declined to trace levels, and both iP and iPA were halved (Fig. 2, Table 2). Overall, recovered LT-plants showed 34.6 % and 50.0 % reductions in cytokinin content in shoots and roots, respectively. *t*-ZR remained dominant but decreased 1.8-fold in shoots and 2.2-fold in roots, while iP and iPA levels increased 3.4- and 2.4-fold, respectively, compared to controls.

Effect of moderate soil drought on cytokinins homeostasis in winter rye. Following four days of drought, total cytokinin content in 18-day-old SD-plant shoots increased by 47.2 %, while root levels decreased by 52.4 %. In shoots increases were driven by accumulation of *t*-ZR, *t*-Z*O*G, iP, and iPA; *t*-Z remained stable. In roots, zeatin forms (*t*-Z, *t*-ZR, *t*-Z*O*G) were higher than isopentenyl forms (iP, iPA) by 52.7 % and 46.9 %, respectively (Fig. 3, Table 3). By day 21 of recovery, shoot cytokinin levels remained 21.9 % above control, mainly due to increased *t*-Z, *t*-ZR, and iPA. Root cytokinin levels did not significantly change (1269.0±63,4 ng/g DW), though individual components shifted: *t*-Z increased 16.8-fold, *t*-Z*O*G stayed constant, and other forms declined. Overall, cytokinin content in recovered SD-plant shoots and roots was 6 % and 24.5 % below control levels, respectively. *t*-ZR remained the predominant form across all plants (Fig. 3).

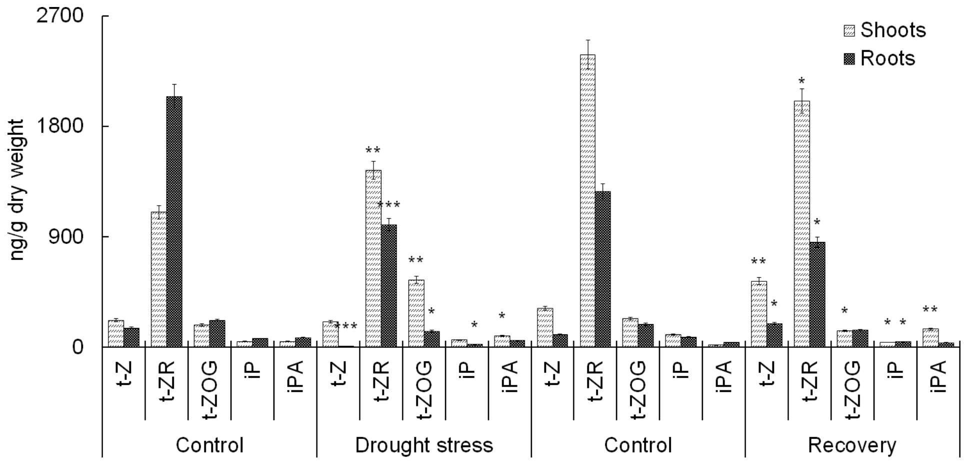

Fig. 3. Dynamics and distribution of endogenous cytokinins in 18-day-old *Secale cereale* cv. ‘Boghuslavka’ plants after moderate soil drought (four days without irrigation) and on the 21st day after recovery (ng/g DW) (significance at: * — $p < 0.05$, ** — $p < 0.01$ and *** — $p < 0.001$ compared with the control; n = 3; x±SE)

TABLE 3. Total content of zeatin and isopentenyl cytokinin forms in 18-day-old Secale cereale cv. ‘Boghuslavka’ plants after moderate soil drought and on the 21st day after recovery (ng/g of DW) ’(C — control, HT — high temperature, LT — low temperature)

Treatment	Cytokinin content	Shoots	Roots
C-plants, 18th day	*t*-Z, *t*-ZR, *t*-Z*O*G	1504.0±75.2	1142.4±57.1
	iP, iPA	96.0±4.8	79.3±4.1
SD-plants, 18th day	*t*-Z, *t*-ZR, *t*-Z*O*G	2201.4±110.1*	1562.7±78.1*
	iP, iPA	154.6±7.7**	123.9±6.2**
C-plants, 21st day	*t*-Z, *t*-ZR, *t*-Z*O*G	2935.6±146.8	1188.1±59.4
	iP, iPA	122.1±6.1	80.9±4.1
SD-plants, 21st day	*t*-Z, *t*-ZR, *t*-Z*O*G	2682.1±134.1*	1142.4±57.1*
	iP, iPA	189.7±9.5*	79.3±4.1

Note. Significance at: * — $p < 0.05$, ** — $p < 0.01$ and *** — $p < 0.001$ compared with the control; n = 3; x±SE.

The results indicate that winter rye exhibits complex, organ-specific adjustments in cytokinin homeostasis during and after exposure to abiotic stresses. These adjustments varied depending on the type of stress, with more pronounced and persistent effects observed under moderate soil drought.

Short-term temperature stresses did not significantly affect morphometric parameters of shoots and roots in winter rye plants. Moderate soil drought inhibited the growth of 18-day-old plants and had a delayed negative effect on the morphometric parameters of 21-day-old recovered plants. Shoots of winter rye at early stages of development were more sensitive to abiotic stresses, whereas the root system exhibited greater stress resistance.

Phytohormones, especially cytokinins, play a critical role in stress resistance mechanisms; however, cytokinins remain less studied in cultivated cereals. Cytokinins regulate growth rates and participate in chloroplast biogenesis, vascular differentiation, and nutrient mobilization [42—45] Maintaining cytokinin homeostasis in shoot and root apical meristems allows plants to quickly respond and adapt to environmental changes [46]. Temperature fluctuations negatively impact crop yields [47, 48], and the extent of damage depends on the developmental stage and duration of exposure [49]. Cytokinins, through interactions with other hormones, are key components of stress responses [23]. Notably, stress resistance can be activated by either an increase or decrease in endogenous cytokinin levels [42].

We observed that in 14-day-old plants, high temperature increased total cytokinin content by 7.5 %, while chilling caused a 21.6 % decrease. Under both stresses, zeatin forms dominated in shoots and roots, with active *trans*-zeatinriboside (*t*-ZR) prevailing. After heat exposure, *t*-ZR dominated in roots, whereas after chilling it dominated in shoots. The *t*-ZR content in shoots was similar under both stresses, but in roots, it was three times higher in HT-plants compared to LT-plants. Liu and Huang (2002) [50] reported that ZR mitigated high-temperature effects in *Agrostis palustris* by activating antioxidant defenses, reducing lipid peroxidation, and delaying leaf senescence.

The levels of isopentenyl-type cytokinins, dominant in roots, increased after both temperature stresses, with a 2.6-fold higher increase after chilling compared to heat. Inactive iPA was predominant under both stresses. In *Arabidopsis thaliana*, Todorova et al. (2005) [51] reported that high temperature (+38 °C, 24 h) induced more pronounced changes in zeatin, iP and dihydrozeatin accumulation than low positive temperature (+4 °C, 24 h). Similarly, a sharp decrease in cytokinin levels and photosynthetic activity was observed in maize seedlings subjected to brief heat shock (+47.5 °C, 2 min) [52]. In *Agrostis palustris* transgenic lines with elevated cytokinin levels, prolonged heat stress activated shoot and root formation and delayed leaf senescence, with iPA and ZR levels maintained or elevated compared to controls [53]. In *Triticum aestivum*, low-temperature exposure restructured cytokinin homeostasis, leading to the accumulation of active *t*-Z and iP [54].

Our study also revealed that moderate soil drought differentially affected cytokinin forms. After drought, total cytokinin content increased in shoots but decreased in roots of 18-day-old plants. In both temperature and drought stresses, zeatin forms predominated in rye, with their shoot content nearly double that in roots. Shoots primarily accumulated *t*-ZR and *t*-Z*O*G, while roots showed a general reduction in zeatin forms, especially *t*-Z (13.7-fold decrease). In both shoots and roots, *t*-ZR was the dominant form, with levels in shoots 1.4 times higher than in roots. Isopentenyl forms increased 1.6-fold in shoots and decreased 1.9-fold in roots, with iPA being dominant.

In 21-day-old recovered plants, total cytokinin content decreased by 25.3 % in HT-plants but remained unchanged in LT-plants. However, the total cytokinin levels in HS- and LT-plants were 35.8 % and 40.3 % lower than controls, respectively. In SD-plants, cytokinin content increased by 15.7 % after recovery but remained 12.7 % lower than controls. Zeatin forms dominated in both shoots and roots, with transport form *t*-ZR prevailing in shoots, and active *t*-Z and inactive *t*-Z*O*G prevailing in roots. Accumulation of isopentenyl forms in recovered HT-, LT-, and SD-plants was generally nonspecific, except in SD-plant roots, where levels were 1.5 times lower than controls, mainly due to active iP reduction. In recovered HT- and SD-plants, the shoot-to-root ratio of isopentenyl forms was 3.5 and 2.3 times higher, respectively, compared to 6.6 % in LT-plants. Inactive iPA was dominant across all experimental variants, except in recovered SD-plant roots.

Under drought, cytokinins regulate growth and stabilize photosynthetic processes [42, 55]. The rye photosynthetic apparatus was sensitive to temperature stresses, particularly chilling, as shown by decreased pigment levels [56]. A reduction of cytokinin levels in roots is often associated with improved drought tolerance [57, 58]. Transgenic barley with reduced cytokinins exhibited drought tolerance, better moisture retention, and higher yields [59]. In maize, higher cytokinin levels under drought inhibited leaf senescence, maintained photosynthetic rates, and improved yields [60]. However, drought suppressed *t*-ZR production and inhibited root growth in *Agrostis stolonifera* [61]. Changes in *trans*-ZR accumulation were most prominent, indicating its likely role in rye stress resistance regulation. Our results highlight the multifunctionality of cytokinins, with individual hormone forms likely regulating different components of the abiotic stress response. Specifically, *trans*-ZR may inhibit shoot growth while promoting root growth, with other cytokinin forms contributing to an anti-stress protective block.

Thus, cytokinin dynamics and distribution were organ-specific and stress-dependent. Nonspecific accumulation in shoots and reduction in roots were observed under all stress types. Abiotic stresses had prolonged effects on cytokinin homeostasis, with post-stress cytokinin levels generally lower than controls. The most significant changes occurred in *trans*-ZR accumulation, suggesting its involvement in after stress reaction and recovery in rye.

This publication presents results from research conducted under the project funded by the National Academy of Sciences of Ukraine № III-99-24.489 «Natural growth regulators in the induction of cereal plant resistance to heavy metals» (2024—2028).

Author Contributions: *study conception and design* — Iryna Kosakivska, Lesya Voytenko, Valentyna Vasyuk; *data collection* — Lesya Voytenko, Vasyuk Valentyna, Mykola Shcherbatyuk; *analysis and interpretation of results* — Lesya Voytenko, Vasyuk Valentyna, Iryna Kosakivska; *writing—original draft* — Iryna Kosakivska, Lesya Voytenko, Vasyuk Valentyna; *writing—review & editing* — Iryna Kosakivska, Lesya Voytenko, Vasyuk Valentyna.

All authors reviewed and approved the final version of the manuscript.

Conflicts of Interest: The authors declare no conflicts of interest.

REFERENCES

1. Karamushka, V., Boychenko, S., Kuchma, T. & Zabarna, O. (2022). Trends in the environmental conditions, climate change and human health in the southern region of Ukraine. Sustainability, 14, No. 9, 5664. https://doi.org/10.3390/su14095664
2. Vyshnevskyi, V.I. (2025). Climate change in Ukraine and its consequences. J. Landscape Ecol., 18, No. 4, pp. 150-174. https://doi.org/10.2478/jlecol-2025-0032
3. Narayanan, S. (2018). Effects of high temperature stress and traits associated with tolerance in wheat. Open Access J. Sci., 2, No. 3, pp. 177-186. https://doi.org/10.15406/oajs.2018.02.00067
4. Prasad, P.V.V., Pisipati, S.R., Mutava, R.N. & Tuinstra, M.R. (2008). Sensitivity of grain sorghum to high temperature stress during reproductive development. Crop Sci., 48, No. 5, pp. 1911-1917. https://doi.org/10.2135/cropsci2008.01.0036
5. Ji, H., Xiao, L., Xia, Y., Song, H., Liu, B., Tang, L., Cao, W., Zhu, Y. & Liu, L. (2017). Effects of jointing and booting low temperature stresses on grain yield and yield components in wheat. Agricult. Forest Meteorol., 243, pp. 33-42. https://doi.org/ 10.1016/j.agrformet.2017.04.016
6. Wu, Y., Wang, X., Peng, X., Ge, J., Cai, J., Huang, M., Zhou, O., Zhong, Y. & Jiang, D. (2023). Cold priming improves chilling resistance in wheat seedlings: Changing of photosystem II imprints during recovery from priming. Environ. Exp. Bot., 207, No. 1, 105220. https://doi.org/10.1016/j.envexpbot.2023.105220
7. Hu, W., Ren, T., Meng, F., Cong, R., Li, X., White, P.J & Lu, J. (2019). Leaf photosynthetic capacity is regulated by the interaction of nitrogen and potassium through coordination of CO_2 diffusion and carboxylation. Physiol. Plant., 167, No. 3, pp. 418-432. https://doi.org/10.1111/ppl.12919
8. Lind, C., Dreyer, I., López-Sanjurjo, E.J., von Meyer, K., Ishizaki, K., Kohchi, T., Lang, D., Zhao, Y., Kreizer, I., Al-Rasheid, K.A.S., Ronne, H., Reski, R., Zhu, J-K., Geiger, D. & Hedrich, R. (2015). Stomatal guard cells co-opted an ancient ABA-dependent desiccation survival system to regulate stomatal closure. Current Biol., 25, No. 7, pp. 928-935. https://doi.org/10.1016/j.cub.2015.01.067
9. Dietrich, D. (2018). Hydrotropism: how roots search for water. J. Exp. Bot., 69, No. 11, pp. 2759-2771. https://doi.org/10.1093/jxb/ery0340
10. Bushuk, W. (2001). Rye: Production, Chemistry, and Technology (2nd ed). St Paul, MN: AACC International, Inc. 239 p.
11. Arendt, E.K. & Zannini, E. (2013). 6 — Rye. Editor(s): Elke K. Arendt, Emanuele Zannini. In Woodhead Publishing Series in Food Science, Technology and Nutrition. Cereal Grains for the Food and Beverage Industries, Woodhead Publishing: 220-243e. https://doi.org/10.1533/9780857098924.220
12. Symonenko N.V., Skoryk V.V., Zhemoida, V. (2018). Results of the breeding work with winter rye to the Nosivska breeding research station. Plant Soil Sci., 268 [in Ukrainian]. https://agriculturalscience.com.ua/web/uploads/pdf/10847-23510-1-SM.pdf
13. Kosakivska, I.V., Babenko, L.M., Vasyuk, V.A., Voytenko, L.V. & Shcherbatiuk M.M. (2024). Chapter 2. Natural growth regulators as inducers of resistance in cereal plants against extreme environmental factors. In T.O. Yastreb, Yu.E. Kolupaev, A.I. Yemets, Ya.B. Blume (Eds.). Regulation of adaptive responses in plants. Published by Nova Science Publishers, Inc., New York: pp. 33-82. https://doi.org/10.52305/TXQB2084

14. Kosakivska, I.V., Shcherbatiuk, M.M., Vasyuk, V.A. & Voytenko, L.V. (2024 b). Phytohormones in growth regulation and the formation of stress resistance in cultivated cereals. Fiziol. rast. genet., 56, No. 2, pp. 130-150 [in Ukrainian]. https://doi.org/10.15407/ frg2024.02.130
15. Panozzo, A., Bolla, P.K., Barion, G., Botton, A. & Vamerali, T. (2025). Phytohormonal regulation of abiotic stress tolerance, leaf senescence and yield response in field crops: A comprehensive review. BioTech, 14, No. 1, 14. https://doi.org/10.3390/biotech14010014
16. Vedenicheva, N.P. & Kosakivska, I.V. (2017). Cytokinins as regulators of plant ontogenesis under different growth conditions. Kyiv: Institute of Botany NAS of Ukraine, Nash Format, 200 p. [in Ukrainian]. https://www.botany.kiev.ua/doc/kos_ved.pdf
17. Vedenicheva, N.P. & Kosakivska, I.V. (2020). Cytokinins in cereals ontogenesis and adaptation. Fiziol. rast. genet., 52, No. 1, pp. 3-30 [in Ukrainian]. https://doi.org/10.15407/frg2020.01.003
18. da Cunha Neto, A.R., dos Santos Ambrósio, A., de Jesus Rodrigues Resende, A., Régis Santos, B. & Nadal, M.C. (2025). From cell division to stress tolerance: the versatile roles of cytokinins in plants. Phyton-Int. J. Exp. Bot., 94, No. 3, pp. 539-560. https://doi.org/10.32604/phyton.2025.061776
19. Vedenicheva, N.P. & Kosakivska, I.V. (2016). Modern aspects of cytokinins studies: evolution and crosstalk with other phytohormones. Fiziol. rast. genet., 48, No. 1, pp. 3-19 [in Ukrainian]. https://doi.org/10.15407/frg2016.01.003
20. Mughal, N., Shoaib, N., Chen, J., Li, Y., He, Y., Fu, M., Li, X., He, Y., Guo, J., Deng, J., Yang, W. & Liu, J. (2024). Adaptive roles of cytokinins in enhancing plant resilience and yield against environmental stressors. Chemosphere, 364, 143189. https://doi.org/10.1016/j.chemosphere.2024.143189
21. Prasad, R. (2022). Cytokinin and its key role to enrich the plant nutrients and growth under adverse conditions-an update. Front. Genet., 13, 883924. https://doi.org/10.3389/fgene.2022.883924
22. Ullah, I., Toor, M.D., Basit, A. & Mohamed, H.I. (2024). Cytokinin Signaling in Plant Response to Abiotic Stresses. Abd-Elsalam, K.A., & Mohamed, H.I. (Eds.). Plant Growth Regulators to Manage Biotic and Abiotic Stress in Agroecosystems (1st ed.). CRC Press, pp. 26. https://doi.org/10.1201/9781003389507
23. Li, S.M., Zheng, H.X., Zhang, X.S. & Sui, N. (2021). Cytokinins as central regulators during plant growth and stress response. Plant Cell Rep., 40, No. 2, pp. 271-282. https://doi.org/10.1007/s00299-020-02612-1
24. Vedenicheva, N. & Kosakivska, I. (2024). Chapter. The regulatory role of cytokinins in adaptive responses of cereal plants. In book: Regulation of adaptive responses in plants, Nova Science Publication, USA, pp. 83-110. https://doi.org/10.52305/TXQB2084
25. Karunadasa, S., Kurepa, J. & Smalle, J.A. (2022). Gain-of-function of the cytokinin response activator ARR1 increases heat shock tolerance in Arabidopsis thaliana. Plant Signal. Behav., 17, No. 1, 2073108. https://doi.org/10.1080/15592324.2022.2073108
26. Xing, Y.H., Lu, H., Zhu, X., Deng, Y., Xie, Y., Luo, Q. & Yu, J. (2024). How rice responds to temperature changes and defeats heat stress. Rice, 17, p. 73. https://doi.org/10.1186/s12284-024-00748-2
27. Bhattacharya, A. (2022). Plant growth hormones in plants under low-temperature stress: A review. In: Physiological Processes in Plants Under Low Temperature Stress. Springer, Singapore. https://doi.org/10.1007/978-981-16-9037-2_6
28. Zheng, X.W., Cao, X.Y., Jiang, W.H., Xu, G.Z., Liang, Q.Z. & Yang, Z.Y. (2024). Cryoprotectant-mediated cold stress mitigation in litchi flower development: transcriptomic and metabolomic perspectives. Metabolites, 14, No. 4, p. 223. https://doi.org/10.3390/metabo14040223
29. Kaur, G. & Mishra, D. (2022). AtABCG14: a long-distance root-to-shoot carrier of cytokinin. Int. J. Plant Biol., 13, No. 3, pp. 352-355. https://doi.org/10.3390/ijpb13030029
30. Sakakibara, H. (2021). Cytokinin biosynthesis and transport for systemic nitrogen signaling. Plant J., 105, No. 2, pp. 421-430. https://doi.org/10.1111/tpj.15011
31. Bielach, A., Hrtyan, M. & Tognetti, V.B. (2017). Plants under stress: involvement of auxin and cytokinin. Int. J. Mol. Sci., 18, No. 7, p. 1427. https://doi.org/10.3390/ijms18071427

32. Wang, X-L., Qin, R-R., Sun, R-H., Wang, J-J., Hou, X-G., Qi, L., Shi, J., Li, X-L., Zhang, Y-F., Dong, P-H., Zhang, L-X. & Qin, D-H. (2018). No post-drought compensatory growth of corns with root cutting based on cytokinin induced by roots. Agricult. Water Manag., 205, No. C, pp. 9-20. https://doi.org/10.1016/j.agwat.2018.04.035
33. Werner, T., Nehnevajova, E., Köllmer, I., Novák, O., Strnad, M., Krämer, U. & Schmüllinget, T. (2010). Root-specific reduction of cytokinin causes enhanced root growth, drought tolerance, and leaf mineral enrichment in Arabidopsis and tobacco. Plant Cell, 22, No. 12, pp. 3905-3920. https://doi.org/10.1105/tpc.109.072694
34. Kosakivska, I.V., Voytenko, L.V., Vasyuk, V.A. & Shcherbatiuk, M.M. (2024 c). ABA-induced alterations in cytokinin homeostasis of Triticum aestivum and Triticum speltaunder heat stress. Plant Stress, 11, p. 100353. https://doi.org/10.1016/j.stress.2024.100353
35. Yamamuro, C., Zhu, J.K. & Yang, Z. (2016). Epigenetic modifications and plant hormone action. Mol. Plant, 9, No. 1, pp. 57-70. https://doi.org/10.1016/j.molp.2015.10.008
36. Kosakivska, I.V., Vasyuk, V.A., Voytenko, L.V. & Shcherbatiuk, M.M. (2022). Changes in hormonal status of winter wheat (Triticum aestivum L.) and spelt wheat (Triticum spelta L.) after heat stress and in recovery period. Cereal Res. Commun., 50, pp. 821-830. https://doi.org/10.1007/sr42976-021-00206-5
37. Kosakivska, I.V., Vedenicheva, N.P., Babenko, L.M., Voytenko, L.V., Romanenko, K.O. & Vasyuk, V.A. (2022). Exogenous phytohormones in the regulation of growth and development of cereals under abiotic stresses. Mol. Biol. Rep., 49, No. 1, pp. 617-628. https://doi.org/10.1007/s11033-021-06802-2
38. Kosakivska, I.V., Vasyuk, V.A., Voytenko, L.V. & Shcherbatiuk, M.M. 2023. The effects of moderate soil drought on phytohormonal balance of Triticum aestivum L. and Triticum spelta L. Cereal Res. Commun., 51, pp. 627-638. https://doi.org/10.1007/s42976-022-00332-8
39. Vedenicheva, N., Futorna, O., Shcherbatyuk, M. & Kosakivska, I. (2022). Effect of seed priming with zeatin on Secale cereale L. growth and cytokinins homeostasis under hyperthermia. J. Crop Improv., 36, No. 5, pp. 656-674. https://doi.org/10.1080/15427528.2021.2000909
40. Kosakivska, I.V., Shcherbatiuk, M.M. & Voytenko, L.V. (2020). Profiling of hormones in plant tissues: history, modern approaches, use in biotechnology. Biotechnol. Acta, 13, No. 4, pp. 14-25. https://doi.org/10.15407/biotech13.04.014
41. Shcherbatiuk, M.M., Voytenko, L.V., Kharkhota, M.A. & Kosakivska, I.V. (2021). Profiling of cytokinins in plant tissues: sampling, qualitative and quantitative analysis. Fiziol. rast. genet., 53, No. 4, pp. 346-368 [in Ukrainian]. https://doi.org/10.15407/frg2021.04.346
42. Cortleven, A., Leuendorf, J.E., Frank, M., Pezzetta, D., Bolt, S. & Schmülling, T. (2019). Cytokinin action in response to abiotic and biotic stresses in plants. Plant Cell Environ., 42, pp. 998-1018. https://doi.org/10.1111/pce.13494
43. Sosnowski, J., Truba, M. & Vasileva, V. (2023). The impact of auxin and cytokinin on the growth and development of selected crops. Agriculture, 13, No. 3, p. 724. https://doi.org/10.3390/agriculture13030724
44. Svolacchia, N. & Sabatini, S. (2023). Cytokinins. Current Biol., 33(1): R10-R13. https://doi.org/10.1016/j.cub.2022.11.022
45. Voytenko, L.V., Shcherbatiuk, M.M., Vasyuk, V.A. & Kosakivska, I.V. (2024). Role of cytokinins in the regulation the chilling stress response in Triticum aestivum and Triticum spelta. Dopov. Nac. akad. nauk Ukr., No. 3, pp. 69-76. https://doi.org/10.15407/dopovidi2024.03.069
46. Thu, N.B.A., Hoang, X.L.T., Truc, M.T., Sulieman, S., Thao, N.P. & Tran, L.S.P. (2017). Cytokinin signaling in plant response to abiotic stresses. In: Pandey G.K., ed. Mechanism of Plant Hormone Signaling Under Stress. Hoboken: John Wiley & Sons, Inc., pp. 71-100. https://doi.org/10.1002/9781118889022.ch4
47. Feng, Y., Li, Z., Kong, X., Khan, A., Ullah, N. & Zhang, X. (2025). Plant coping with cold stress: molecular and physiological adaptive mechanisms with future perspectives. Cells, 14, No. 2, 110. https://doi.org/10.3390/cells14020110

48. Kopecká, R., Kameniarová, M., Černý, M., Brzobohatý, B. & Novák, J. (2023). Abiotic stress in crop production. Int. J. Mol. Sci., 24, No. 7, 6603. https://doi.org/10.3390/ijms24076603
49. Feller, U. & Vaseva, I.I. (2014). Extreme climatic events: impacts of drought and high temperature on physiological processes in agronomically important plants. Front. Environ. Sci., 2, 39. https://doi.org/10.3389/fenvs.2014.00039
50. Liu, X. & Huang, B. (2002). Cytokinin effects on creeping bentgrass response to heat stress: II. Leaf senescence and oxidant metabolism. Crop Sci., 42, pp. 466-472. https://doi.org/10.2135/cropsci2002.0466
51. Todorova, D., Genkov, T., Vaseva-Gemisheva, I., Alexiva, V., Karanov, E., Smith, A. & Hall, M. (2005). Effect of temperature stress on the endogenous cytokinin content in Arabidopsis thaliana (L.) Heynh plants. Acta Physiol. Plant., 27, pp. 13-18. https://doi.org/10.1007/s11738-005-0031-5
52. Caers, M., Rudelsheim, P. & Van Onckelen, H. (1985). Effect of heat stress on photosynthetic activity and chloroplast infrastructure in correlation with endogenous cytokinin concentration in maize seedlings. Plant Cell Physiol., 26, pp. 47-52.
53. Xu, Y., Tian, J., Gianfagna, T. & Huang, B. (2009). Effects of SAG12-ipt expression on cytokinin production, growth and senescence of creeping bentgrass (Agrostis stolonifera L.) under heat stress. Plant Growth Regul., 57, pp. 281-291. https://doi.org/10.1007/s10725-008-9346-8
54. Kalapos, B., Novák, A., Dobrev, P., Vítámvás, P., Marincs, F., Galiba, G. & Vanková, R. (2017). Effect of the winter wheat cheyenne 5A substituted chromosome on dynamics of abscisic acid and cytokinins in freezing-sensitive chinese spring genetic background. Front. Plant Sci., 8, 2033. https://doi.org/10.3389/fpls.2017.02033
55. Prerostova, S., Dobrev, P.I., Gaudinova, A., Knirsch, V., Körber, N., Pieruschka, R., Fiorani, F., Brzobohatý, B., Černý, M., Spichal, L., Humplik J., Vanek T., Schurr U. & Vankova, R. (2018). Cytokinins: their impact on molecular and growth responses to drought stress and recovery in Arabidopsis. Front. Plant Sci., 9, 655. https://doi.org/10.3389/fpls.2018.00655
56. Romanenko, K., Babenko, L., Smirnov, O. & Kosakivska, I. (2022). Antioxidant protection system and photosynthetic pigment composition in Secale cerealesubjected to short-term temperature stresses. The Open Agricult. J., 16 (Suppl-1, M3), e187433152206273. https://doi.org/10.2174/18743315-v16-e2206273
57. Ramireddy, E., Hosseini, S.A., Eggert, K., Gillandt, S., Gnad, H., von Wirén, N. & Schmülling, T. (2018). Root engineering in barley: increasing cytokinin degradation produces a larger root system, mineral enrichment in the shoot and improved drought tolerance. Plant Physiol., 177, No. 3, pp. 1078-1095. https://doi.org/10.1104/pp.18.00199
58. Vojta, P., Kokáš, F., Husičková, A., Grúz, J., Bergougnoux, V., Marchetti, C.F., Jiskrová, E., Ježilová, E., Mik, V., Ikeda, Y. & Galuszka, P. (2016). Whole transcriptome analysis of transgenic barley with altered cytokinin homeostasis and increased tolerance to drought stress. New Biotechnol., 33, (5 Pt B), pp. 676-691. https://doi.org/10.1016/j.nbt.2016.01.010
59. Pospíšilová, H., Jiskrová, E., Vojta, P., Mrízová, K., Kokáš, F., Čudejková, M.M., Bergougnoux, V., Plíhal, O., Klimešová, J., Novák, O., Dzurová, L., Frébort, I. & Galuszka, P. (2016). Transgenic barley overexpressing a cytokinin dehydrogenase gene shows greater tolerance to drought stress. New Biotechnol., 33, Part (B), pp. 692-705. https://doi.org/10.1016/j.nbt.2015.12.005
60. Oneto, C.D., Otegui, M.E., Baroli, I., Beznec, A., Faccio, P., Bossio, E., Blumwald, E. & Lewi, D. (2016). Water deficit stress tolerance in maize conferred by expression of an isopentenyltransferase (IPT) gene driven by a stress- and maturation-induced promoter. J. Biotechnol., 220, pp. 66-77. https://doi.org/10.1016/j.jbiotec.2016.01.014
61. Xu, Y., Burgess, P., Zhang, X. & Huang, B. (2016). Enhancing cytokinin synthesis by overexpressing ipt alleviated drought inhibition of root growth through activating ROS-scavenging systems in Agrostis stolonifera. J. Exp. Bot., 67, No. 6, pp. 1979-1992. https://doi.org/10.1093/jxb/erw019

Received 12.02.2026. Accepted 02.03.2026. Published 01.04.2026

ВПЛИВ АБІОТИЧНИХ СТРЕСІВ НА РІСТ ТА ГОМЕОСТАЗ ЦИТОКІНІНІВ В ОЗИМОМУ ЖИТІ (*SECALE CEREALE* L.) НА РАННІЙ СТАДІЇ ОНТОГЕНЕЗУ

І.В. Косаківська, Л.В. Войтенко, В.А. Васюк, М.М. Щербатюк

Інститут ботаніки ім. М.Г. Холодного Національної академії наук України
01004 Київ, вул. Терещенківська, 2
e-mail: lesyavoytenko@gmail.com

Досліджено вплив теплового стресу (+40 °C, 2 год), охолодження (+4 °C, 2 год) й помірної ґрунтової посухи (чотири доби без поливу) на ріст і гомеостаз цитокінінів у 14- та 18-добових стресованих рослинах жита та після відновлення на 21-шу добу. Показано, що за морфометричними показниками чутливішими до стресів виявились пагони. Після припинення дії стресів за показниками маси сирої та сухої речовини краще відновлювались корені. Динаміка й розподіл цитокінінів залежали від виду стресу та органу рослини. Неспецифічне накопичення в пагонах та зменшення вмісту цитокінінів у коренях спостерігалися за всіх стресів і, зазвичай, найвиразніші зміни були за умов посухи. Продемонстровано пролонговану дію стресів на гомеостаз цитокінінів. У відновлених рослин загальний вміст цитокінінів поступався контролю. Найзначніші зміни відбулися в накопиченні *транс*-зеатинрибозиду, що свідчить про його участь у формуванні стрес-адаптації жита. Отримані результати закладають основу для подальшого дослідження механізмів стресостійкості у зернових культур і можуть сприяти розробці стратегій для підвищення їхньої адаптивної здатності.

Ключові слова: *Secale cereale L.*, ріст, цитокініни, тепловий стрес, охолодження, ґрунтова посуха, стресостійкість.

ORCID

І.В. КОСАКІВСЬКА — I.V. Kosakivska https://orcid.org/0000-0002-2173-8341

Л.В. ВОЙТЕНКО — L.V. Voytenko https://orcid.org/0000-0003-0380-0807

В.А. ВАСЮК — V.A. Vasyuk https://orcid.org/0000-0003-1069-9698

М.М. ЩЕРБАТЮК — M.M. Shcherbatiuk https://orcid.org/0000-0002-6453-228X