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Role of cytokinins in the regulation the chilling stress response in *Triticum aestivum* and *Triticum spelta*

Presented by Academician of the NAS of Ukraine V.V. Morgun

The research is devoted to the study of the effect of chilling (+4 °C, 2 h) on cytokinin homeostasis in 14-day stressed and 21-day restored plants of winter wheat (Triticum aestivum L.) cv. "Podolyanka" and spelt wheat (Triticum spelta L.) cv. "Frankenkorn". Our study revealed that chilling induces complex changes in the content and distribution of cytokinins in plants that are species- and organ-specific. After chilling, the total cytokinin content in the roots of winter wheat cv. "Podolyanka" increased threefold due to the accumulation of trans-zeatin-O-glucoside, trans-zeatin, isopentenyladenine and isopentenyladenosine. Stress did not affect trans-zeatin riboside accumulation in roots but induced a fourfold increase in its content in the shoots of winter wheat cv. "Podolyanka". The total content of cytokinin in the roots of spelt wheat cv. "Frankenkorn" decreased by 1.4 times due to decline in trans-zeatin-O-glucoside and trans-zeatin riboside content, while in shoots, it decreased by 1.2 times owing to reduced trans-zeatin-O-glucoside and isopentenyladenine levels. Prolonged exposure to chilling was manifested by an increase in hormone levels in both 21-day-old species. Our data revealed common and distinct traits in cytokinin homeostasis between winter wheat cv. "Podolyanka" and spelt wheat cv. "Frankenkorn" during rapid adaptation and the recovery period, providing new insights into the response of these species to chilling.

***Keywords**: Triticum aestivum, Triticum spelta, cytokinins, chilling, recovery.*

Introduction. Abiotic stresses have a detrimental effect on the growth and productivity of cereal crops, significantly affecting the world's most vital group of monocotyledonous plants that have served as food and other basic human needs for millennia. These stresses cause approximately 50% of crop losses, with low temperatures alone accounting for 7% [1]. Annually, 85% of the

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world's wheat acreage is affected by spring frosts, which mainly occur in March and April during early development [2]. Low temperatures adversely affect vegetative and reproductive growth of wheat, delay seed germination and lead to partial death of plants due to impaired embryo development. The rate of water and nutrients absorption by seedlings decreases, which leads to dehydration of cells, disruption of nutrient processes and yield losses in the range of 10—30% [3]. Cold stress in wheat plants alters photosynthesis, respiration and substances transport intensity [4], inducing structural and functional reorganization of photosynthetic and energy apparatus [5], and triggered changes in endogenous phytohormone balance [6].

Phytohormones are important endogenous regulators of physiological and metabolic processes in plants under both normal and stressful conditions [7, 8]. They represent promising targets for biotechnological approaches aimed at improving and increasing plant productivity in desired direction. Current research in field of phytohormones is mainly focused on cell and tissue culture and modern omics approaches [9]. Recently, phytohormone engineering has emerged as an important platform for the development of stress-tolerant plants. However, the success of phytohormone utilization depends on the fundamental study of the mechanisms of stress tolerance enhancement. Phytohormones belonging to the cytokinin family play a crucial role in the regulation of plant growth and development. They control cell division, meristem formation, photosynthesis, aging and the uptake of macro- and microelements [10—12]. Cytokinin synthesis primarily occurs in the root apical meristem, with the hormone translocating to the aerial part via the transpiration stream. Zeatin-type cytokinins, including *trans*- and *cis*-zeatin (*t*-Z, *c*-Z), *trans*-zeatin riboside (*t*-ZR), and zeatin-*O*-glucoside (Z*O*G), are predominant in the xylem, while isopentenyl-type cytokinins, such as isopentenyladenine (iP) and isopentenyladenosine (iPA) are prevalent in the phloem [13]. Recent studies have increasingly demonstrated the ability of cytokinins to mitigate both abiotic and biotic stressors [11, 14, 16]. However, the precise role of cytokinins in response of plants to low temperatures remains incompletely understood. Our study **aims** to investigate the involvement of endogenous cytokinins in the formation of the responses to short-term chilling in the related wheat species *Triticum aestivum* and *T. spelta*.

Materials and method. Fourteen- and twenty-one-day-old plants of winter wheat (*Triticum aestivum* L. cv. "Podolyanka") and spelt wheat (*Triticum spelta* L. cv. "Frankenkorn") were examined under laboratory conditions from 2022 to 2023. The "Podolyanka" wheat variety is known for its winter hardiness and drought resistance, high yield and adaptability to various growing conditions, while "Frankenkorn" spelt wheat variety exhibits frost resistance and environmental versatility [16, 17]. Calibrated seeds were sterilized in 80% ethanol solution, washed with distilled water, placed in cuvettes filled with water for three hours and germinated in a thermostat at a temperature of +24 °C for 21 hours. The germinated seeds were then planted in 2-liter containers filled with calcined river sand. Plants were grown under controlled conditions at a temperature of +20 °C, a light intensity of 190 μmol/(m^2·s), a photoperiod of 16/8 h (day/night), and relative air humidity 65 ± 5%. Substrate moisture was maintained at 60% of full moisture capacity with daily watering using Knop's solution at a rate of 50 ml per vessel. Fourteen-day-old plants with 2-3 leaves were divided into two groups: one group was exposed to +4 °C temperature 190 μmol/(m^2·s) light intensity for 2 hours (LT-plants), and the other group, which served as a control (C-plants), continued to grow under initial experimental conditions. Plants were recovered by growing under controlled conditions until the twenty-first day (3-4 leaf phase). Shoots and roots of both 14- and 21-day-old LT- and C-plants were selected for the study.

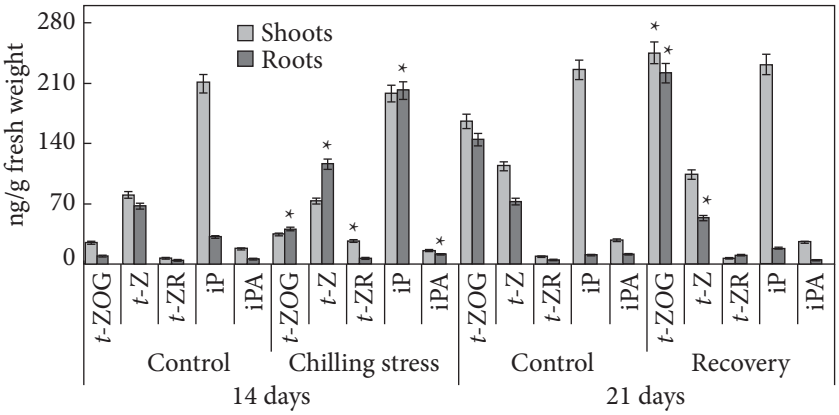

Fig. 1. Accumulation and distribution of endogenous cytokinins in *Triticum aestivum* L. cv. "Podolyanka" plants after chilling stress (+4 °C, 2 h) and during recovery period (ng/g FW). iP — isopentenyladenine; iPA — isopentenyladenosine; *t*-Z — *trans*-zeatin; *t*-ZR — *trans*-zeatin riboside; *t*-Z*O*G — *trans*-zeatin-*O*-glucoside. * — significant difference at $P \leq 0.05$ vs. control; data are the mean ± SE, $n = 9$

Extraction, purification and quantitative determination of endogenous *t*-Z, *t*-ZR, *t*-Z*O*G, iPA and iP were performed following the method outlined in article [18].

The experiments were conducted with three biological and three analytical replicates. Analysis and calculation of the phytohormone content were performed using Agilent OpenLAB CDS ChemStation Edition (rev. C.01.09) chromatograph software. Statistical analysis was performed using the program Statistix v. 10.0 ("Analytical Software", USA). One-way analysis of variance (ANOVA) was used, and differences between mean values were considered significant at $P \leq 0.05$.

Results and discussion. Five forms of cytokinins were identified in "Podolyanka" winter wheat and "Frankenkorn" spelt wheat plants: *t*-Z, *t*-ZR, *t*-Z*O*G, iPA, and iP. Active forms of cytokinins *t*-Z and iP were predominant in 14-day-old control winter wheat plants, with their content in shoots being 1.2 and 6.6 times higher than in roots, respectively. The level of *t*-ZR approached the limit of the method sensitivity (Fig. 1). In 14-day-old control spelt wheat plants, *t*-ZR dominated among the active forms, with content in shoots and roots at 62.2 ± 3.1 and 54.8 ± 2.7 ng/g FW (fresh weight), respectively. In spelt wheat roots, the level of *t*-Z*O*G was 1.9 times higher, while in winter wheat, it was 2.6 times lower than in shoots. iPA in the organs of both species was present in trace amounts (Fig. 2). In shoots and roots of 21-day-old control winter wheat plants, the total cytokinin content increased by 59.4% and 79 %, amounting to 542.4 ± 27.1 ng/g FW and 214.8 ± 10.7 ng/g FW, respectively. Accumulation of *t*-Z*O*G, *t*-Z and iPA was observed in both organs, with amounts in shoots being 0.9, 1.6 and 2.4 times higher than in roots (see Fig. 1).

In shoots and roots of 21-day-old control spelt wheat plants, the total cytokinin content increased by 145,6% and 172.2%, amounting to 336.0 ± 16.8 ng/g FW and 434.5 ± 21.7 ng/g FW, respectively. *t*-Z*O*G, *t*-ZR and iPA were accumulated in both organs of spelt wheat plants. The levels of *t*-Z*O*G and iPA in roots were 2.2 and 3.3 times higher than in shoots, whereas the contents of *t*-Z, *t*-ZR and iPA were in a close range (see Fig. 2). Among the isopentenyl forms, iP (225.6 ± 11.38 ng/g FW) was predominant in shoots of 21-day-old control winter wheat plants, while iPA was predominant in spelt wheat roots (73.8 ± 3.4 ng/g FW) (see Fig. 1, 2).

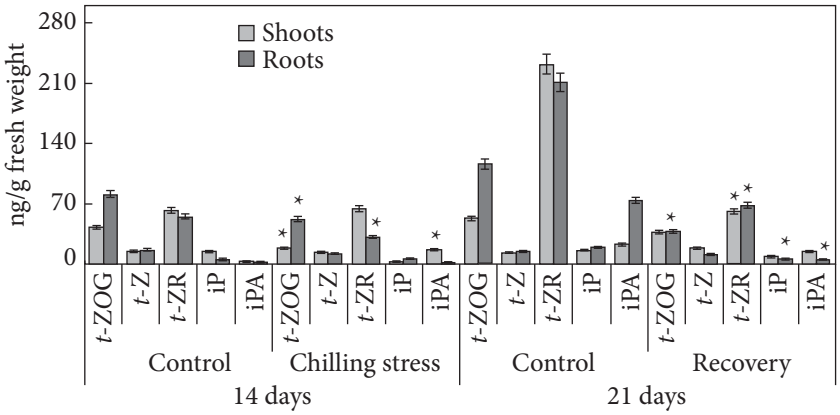

Fig. 2. Accumulation and distribution of endogenous cytokinins in *Triticum spelta* L. cv. "Frankenkorn" plants after chilling stress (+4 °C, 2 h) and during recovery period (ng/g FW). iP — isopentenyladenine; iPA — isopentenyladenosine; *t*-Z — *trans*-zeatin; *t*-ZR — *trans*-zeatin riboside; *t*-ZOG — *trans*-zeatin-*O*-glucoside. * — significant difference at $P \leq 0.05$ vs. control; data are the mean ± SE, $n = 9$

After short-term chilling, the total cytokinin content in the roots of 14-day-old winter wheat plants increased threefold, reaching 377.6 ± 18.9 ng/g FW. This increase was due to the increase of *t*-ZOG, *t*-Z, iP and iPA content by 4.2-fold, 1.7-fold, 6.4-fold and 2.0-fold, respectively. In shoots, the total cytokinin content remained elevated and amounted to 349.1 ± 17.5 ng/g FW. Low positive temperature did not affect the *t*-ZR accumulation in roots, but led to fourfold increase of the hormone level in shoots (see Fig. 1). Conversely, in 14-day-old spelt wheat plants, chilling caused a 1.5-fold and 1.2-fold decrease in total cytokinin content in roots and shoots, respectively, amounting to 103.9 ± 5.2 ng/g FW and 114.9±5.7 ng/g FW. The changes in roots were attributed to 1.6-fold and 1.7-fold reduction in *t*-ZOG and *t*-ZR levels, while shoot alterations involved a 2.3-fold and 5.4-fold decrease in *t*-ZOG and iP levels. The content of *t*-Z in both organs, *t*-ZR in shoots and both isopentenyl forms in roots remained within the control range (see Fig. 2).

During the recovery period, the total cytokinin content in the shoots of 21-day-old winter wheat plants increased by 75.9% to 613.9 ± 30.7 ng/g FW, while in roots it decreased by 18.2% and amounted to 309.1 ± 15.5 ng/g FW. These values were 13.2% and 43.9% higher than the corresponding values in unstressed 21-day-old control plants. The recovered plant shoots were dominated by *t*-ZOG, iP and *t*-Z, which were 245.4 ± 12.3 ng/g FW, 231.8 ± 11.6 ng/g FW, and 104.3 ± 5.2 ng/g FW. *t*-ZOG and iP exceeded controls by 47,9% and 2,7%, while *t*-Z content was 8.3% lower. In recovered plants roots, *t*-ZOG content was 53.6% higher than control, reaching 221.6 ± 11,1 ng/g FW. *t*-Z, *t*-ZR and iPA levels in shoots and *t*-Z and iPA levels in the roots did not reach control values (see Fig. 1).

In shoots and roots of spelt wheat plants recovered at 21 days after stress, total cytokinins content increased by 20.7% and 23.8%, reaching 138.7 ± 6.9 ng/g FW and 128.6 ± 6.4 ng/g FW, respectively. These values were 58.7% and 70.4% below the control values. *t*-ZOG and *t*-ZR dominated in recovered plants, distributed evenly between shoots and roots. Their levels were 30.5% and 73.9% lower in shoots and 32.6% and 67.9% in roots compared to control. *t*-Z content in shoots and roots of recovered plants was at control levels, while isopentenyl form levels were lower (see Fig. 2).

In general, the total cytokinin content in 14-day control spelt wheat plants was 1.6 times lower than in winter wheat. By the day 21, the accumulation of cytokinins in both species was equally high. When exposed to low positive temperature, the cytokinin content in 14-day-old winter wheat plants increased 1.6 times, while in spelt it decreased 1.4 times. After recovery, the level of cytokinins in 21-day-old winter wheat and spelt wheat plants increased by 1.3 and 1.2 times. Winter wheat plants exhibited a 21.9% higher total cytokinin content, while spelt wheat showed a 65.3% lower content compared to control non-stressed plants (Table).

We previously demonstrated that after short-term chilling (+2 °C, 2 h), the total cytokinin content in the roots and shoots of 14-day-old winter wheat plants of the frost-resistant variety "Volodarka" decreased. Hormone accumulation occurred mainly in shoots, with *t*-ZR predominating in roots and *t*-Z in shoots. Additionally, we established that after chilling, the level of zeatin-type cytokinins significantly decreased in the roots of the heat-resistant winter wheat variety "Yatran 60", while it increased in the shoots [19]. Other researchers reported that under low-temperature stress in *Triticum monococcum* wheat plants, cytokinin levels decreased, but during the adaptation phase (after 21 days), active hormone forms increased, reaching maximum values [20]. In response to chilling (+4 °C), bioactive cytokinin levels decreased in winter and spring wheat plants. After 3—7 days of exposure to low positive temperature, endogenous cytokinin levels increased, but diminished by the 21st day, with winter wheat plants showing faster and more pronounced responses [21]. Studies of cytokinin content changes during short- and long-term low-temperature treatment revealed significant differences between sensitive and cold-resistant wheat genotypes. The cold-resistant genotype showed decreased levels of active cytokinin forms in response to cold stress, accompanied by activation of the gene encoding isopentenyltransferase, a key enzyme cytokinin biosynthesis [22].

Conclusions. Our study revealed that after short-term chilling stress, the total cytokinin content in the roots of 14-day-old winter wheat plants increased threefold due to *de novo* biosynthesis and accumulation of cytokinins, such as *t*-ZOG, *t*-Z, iP and iPA. Low positive temperature did not affect *t*-ZR accumulation in roots, but induced a fourfold increase in its content in winter wheat shoots. Conversely, after exposure to low positive temperature, the total cytokinin content in the roots of 14-day-old spelt wheat plants decreased by 1.4-fold due to a decline in *t*-ZOG and *t*-ZR content, while in shoots, it decreased by 1.2-fold due to reduction in *t*-ZOG and iP levels. Cytokinins have been shown to promote shoot growth and simultaneously inhibit root system growth. We believe that the increase in the content of endogenous cytokinins in the roots of winter wheat plants after chilling mediates the inhibition of growth processes, which increases

Total cytokinin content in *Triticum aestivum* L. cv "Podolyanka" and *Triticum spelta* L. cv "Frankenkorn" plants exposed to chilling stress (+4 °C, 2 hour) and in recovery period, ng/g FW

Option experiment	14-day-old		21-day-old	
	C-plants	LT-plants	C-plants	After recovery
Triticum aestivum	460.2 ± 23.1	726.7 ± 36.3*	757.2 ± 37.9	922.9 ± 46.1*
Triticum spelta	296.4 ± 14.8	218.8 ± 10.9*	770.5 ± 38.5	267.3 ± 13.4*

Note. Data are the mean ± SE, $n = 9$. * Significant difference at $P \leq 0.05$ vs. control.

resistance. The prolonged effect of chilling was manifested by an increase in the level of the hormone in both 21-day-old species. In general, chilling stress caused complex changes in the content and distribution of cytokinins, the characteristics of which depended on the species and plant organ. Our data revealed common features as well as organ and species specificities of cytokinin homeostasis of winter wheat and spelt plants during rapid adaptation to chilling stress and during the recovery period, which provided new insights into the response of these related wheat species to low positive temperature at early vegetative stages.

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ЦИТОКІНІНИ У ФОРМУВАННІ РЕАКЦІЇ-ВІДПОВІДІ НА ОХОЛОДЖЕННЯ В РОСЛИНАХ *TRITICUM AESTIVUM* І *TRITICUM SPELTA*

Робота присвячена дослідженню впливу охолодження (+4 °С, 2 год) на гомеостаз цитокінінів у 14-добових стресованих та 21-добових відновлених рослин озимої пшениці (*Triticum aestivum* L.) сорту “Подолянка” та спельти (*Triticum spelta* L.) сорту “Франкенкорн”. Показано, що охолодження зумовлює комплексні зміни у вмісті і розподілі цитокінінів, які є видо- та органоспецифічними. Після охолодження загальний вміст цитокінінів (нг/г сирої речовини) у коренях пшениці зріс утричі за рахунок накопичення *транс*-зеатин-*O*-глюкозиду, *транс*-зеатину, ізопентеніладеніну та ізопентеніладенозину. Стрес не вплинув на накопичення *транс*-зеатинрибозиду у коренях, але спричинив збільшення його вмісту в чотири рази в надземній частині озимої пшениці “Подолянка”. Загальний вміст цитокінінів у коренях спельти “Франкенкорн” зменшився в 1,4 раза за рахунок зниження вмісту *транс*-зеатин-*O*-глюкозиду і *транс*-зеатинрибозиду, а в надземній частині — в 1,2 раза за рахунок зниження рівня *транс*-зеатин-*O*-глюкозиду та ізопентеніладеніну. Віддалений ефект охолодження виявився у підвищенні рівня цитокінінів у обох видах рослин. Визначені загальні і специфічні зміни цитокінінового гомеостазу озимої пшениці “Подолянка” та спельти “Франкенкорн” під час швидкої адаптації і в період відновлення додають нові знання про реакцію споріднених видів пшениці на охолодження на ранніх етапах вегетації.

Ключові слова: *Triticum aestivum, Triticum spelta, цитокініни, охолодження, відновлення.*