ISSN 1392-3196 / e-ISSN 2335-8947
Zemdirbyste-Agriculture, vol. 109, No. 1 (2022), p. 21–26
DOI 10.13080/z-a.2022.109.003

Effect of pre-sowing priming of seeds with exogenous abscisic acid on endogenous hormonal balance of spelt wheat under heat stress

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Abstract

Pre-sowing priming of seeds with exogenous phytohormones affects plant growth, development and resistance. However, it remains unclear, whether the effect of exogenous hormones on growth is direct, or whether it is associated with changes in the level and distribution of endogenous hormones. The dynamics and distribution of endogenous abscisic (ABA), indole-3-acetic (IAA), gibberellic (GA_3) and salicylic (SA) acids in spelt wheat (*Triticum spelta* L., 'Frankenkorn') plants grown from seeds primed with ABA (10^{-6} M) were analysed. Fourteen-day-old, water-germinated and ABA-primed plants that had been exposed to a heat stress (2 h at +40°C) and 21-day-old plants after recovery were studied. Endogenous ABA, IAA, GA_3 and SA were found to dominate in shoots of 14-day-old plants. On the 21st day, the pattern of distribution of all phytohormones, except GA_3, remained unchanged. However, most of the endogenous GA_3 was transferred to the roots. Pre-sowing priming of seeds with exogenous ABA induced changes in the balance of endogenous hormones. In shoots and roots of 14-day-old water-germinated, heat-stressed plants, accumulation of endogenous ABA and SA was enhanced, and the content endogenous of IAA and GA_3 decreased. In the recovery period, the amount of SA in 21-day-old plants increased, and the ABA content was reduced; endogenous GA_3 and IAA accumulated in the roots. In 14-day-old, exogenous ABA-primed plants, after heat stress maximal concentrations of endogenous ABA were recorded in shoots (46.8 ± 2.3 ng g^{-1} FW) and roots (32.3 ± 1.6 ng g^{-1} FW). In roots of 14-day-old exogenous ABA-primed, unstressed plants, the content of endogenous IAA reached a maximum (53.9 ± 2.7 ng g^{-1} FW). The maximum concentration (39.7 ± 2.0 ng g^{-1} FW) of endogenous GA_3 was recorded on the 21st day after recovery in roots of exogenous ABA-primed plants. The SA content in shoots and roots of exogenous ABA-primed, heat-stressed plants increased by 31% and 44.7%, respectively, while in non-primed ones – by 15.9% and 12.8%.

In summary, the pre-sowing priming of spelt wheat seeds with exogenous ABA induced differentiated prolonged changes in the dynamics and distribution of endogenous ABA, IAA, GA_3 and SA in shoots and roots of 14- and 21-day-old water-germinated plants (controls) and high temperature (heat stress) conditions. This suggests that the response to heat stress is associated with changes in the level and distribution of endogenous hormones in young spelt wheat plants caused by pre-sowing priming of seeds with exogenous ABA.

Keywords: abscisic acid, gibberellic acid, indole-3-acetic acid, heat stress, priming, recovery, salicylic acid, *Triticum spelta*.

Introduction

Spelt wheat (*Triticum spelta* L.) is a husked-wheat species with 42 chromosomes and is closely related to common wheat (*Triticum aestivum* L.). Spelt wheat is unpretentious to growing conditions, cold- and winter-tolerant, resistant to excess moisture. High nutritional qualities and adaptability to organic farming make spelt wheat popular in many European countries (Lacko-Bartošová et al., 2010; Escarnot et al., 2012; Babenko et al., 2018). Spelt is taller than common wheat plants, has a larger leaf area, higher chlorophyll content and vegetative biomass (Ruzhitska, Borysova, 2018). Compared to *T. dicoccum*, the leaves of *T. spelta* have thicker mesophyll and more stomata. Stems of *T. spelta* are characterized by narrower ring of sclerenchyma with smaller vascular bundles than in *T. dicoccum* and fewer vascular bundles in the parenchyma (Kirilenko et al., 2016). The ultrastructure of spelt wheat leaf mesophyll cells is typical of cultivated cereals: in chloroplasts of regular lens shape a well-developed thylakoid system submerged in a fine-grained stroma is clearly observed (Babenko et al., 2019). Compared to common wheat, the grain of spelt wheat cultivars has higher content of total soluble protein and the protein from soluble fractions. In spelt wheat, the grain hardness is lower and the content of dry gluten in grains is higher (Ruzhitska, Borysova, 2018).

Please use the following format when citing the article:
Kosakivska I. V., Voytenko L. V., Vasyuk V. A., Shcherbatiuk M. M. 2022. Effect of pre-sowing priming of seeds with exogenous abscisic acid on endogenous hormonal balance of spelt wheat under heat stress. Zemdirbyste-Agriculture, 109 (1): 21–26. DOI 10.13080/z-a.2022.109.003

The main abiotic stressors are high temperature and drought that adversely affect the metabolism, ontogenesis and yield of cereals. Since the beginning of the century, the ambient temperature has risen and is expected to rise further. It is predicted that with an average air temperature increase of 1°C worldwide wheat production will decline by 6% (Asseng et al., 2015). At higher temperatures, the duration of ontogenesis, photosynthetic activity, stability of cell membranes, relative water content and leaf area index, total biomass and wheat yield decrease (Narayanan, 2018).

One of the critical periods of wheat ontogenesis is the three-leaf stage. At this stage, seedlings transition from drawing upon seed reserves for nutrition to the absorption of nutrients through the root system. A successful biotechnological approach that can improve stress resistance is the use of physiologically active substances for pre-sowing priming and foliar treatment of plants (Akter, Islam, 2017). Among the phytohormones involved in abiotic stress tolerance, a special role plays abscisic acid (ABA) (Vishwakarma et al., 2017; Olds et al., 2018). In drought conditions after foliar treatment of wheat plants with exogenous ABA, dry biomass and photosynthetic pigment content increase, photoassimilate transport from leaves and stems to grain improves and grain protein content increases (Travaglia et al., 2010). Under water deficiency and salt stress, treatment of wheat plants with exogenous ABA stimulated an increase in shoot height and biomass, induced proline accumulation, inhibited lipid peroxidation and the formation of reactive oxygen species (ROS) (Kaur, Asthir, 2020). Foliar treatment of wheat plants with exogenous ABA accelerated grain filling and starch accumulation, enhanced nutrient remobilization, increased yield, endogenous zeatin riboside and auxin content (Yang et al., 2014).

In our previous studies (Kosakivska et al., 2019; 2020 a), it was shown that pre-sowing priming of seeds with exogenous ABA promoted resistance to high temperature and soil drought and induced root system growth of winter and spelt wheat plants. After short-term heat stress, in spelt wheat plants, the content of endogenous ABA increased, while that of endogenous IAA declined, and the lowest amount of IAA was found in the roots (Kosakivska et al., 2020 b). In this study, the effect of pre-sowing priming of seeds with exogenous ABA on the dynamics and distribution of endogenous abscisic (ABA), indole-3-acetic (IAA), gibberellic (GA_3) and salicylic (SA) acids in shoots and roots of spelt wheat water-germinated plants (controls) and at heat stress conditions and after recovery was investigated.

The aim of the study was to determine, whether the response to heat stress is associated with changes in the level and distribution of endogenous hormones in young spelt wheat plants caused by pre-sowing priming of seeds with exogenous ABA. The study of adaptation mechanisms will provide useful information for the selection of stress-resistant cultivars of cereals considering future extreme climatic changes.

Materials and methods

Plant material. The experiment was performed in 2018–2019 at the M. G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine. Plants of spelt wheat (*Triticum spelta* L., cultivar 'Frankenkorn') were studied. It is a medium-sized, resistant to lodging, frost-resistant and environmentally friendly genotype. Spelt wheat seeds were obtained from the collection of the National Centre for Plant Genetic Resources of Ukraine in Kharkiv. Calibrated seeds were sterilized in 80% ethanol solution, washed with distilled water, placed for 3 h in a cuvette with water. Thereafter, the seeds continued to germinate in water (1st control) and were primed in 10^{-6} M ABA solution (2nd control) in a thermostat at +24°C for 21 h. This concentration of exogenous abscisic acid (ABA) for seed priming was determined as physiological. Water-germinated seeds were planted in 2-litre vessels; as the substrate, river sand sterilized by calcination was used. Plants were grown under controlled conditions at a temperature of +20°C, light intensity of 190 µmol m^{-2} s^{-1}, photoperiod of 16/8 h (day/night), relative air humidity of 65 ± 5% and substrate humidity of 60% from full moisture content. The plants were watered with 50 ml of Knop solution per vessel daily.

Abiotic stress treatment and sample collection. To simulate heat stress, 14-day-old water-germinated and ABA-primed plants were placed in a thermostat for 2 h at +40°C under the illumination of 190 µmol m^{-2} s^{-1}. The first group of plants was grown in water for up to 14 days, half of which were then exposed to heat stress, and then all plants were continuing to grow for up to 21 days under the conditions described above. The second group of plants after priming of seeds with exogenous ABA also grew to 14 days, half of which were exposed to heat stress, and then all plants were continuing to grow for up to 21 days under the conditions described above. In the controls and the experiment with heat stress, there were selected shoots and roots of 14- and 21-day-old water-germinated and ABA-primed plants.

Extraction of abscisic (ABA), indole-3-acetic (IAA), gibberellic (GA_3) and salicylic (SA) acids. Shoot and root samples (2 g) were frozen and ground in liquid nitrogen using 10 ml of extraction solution: methanol, distilled water and formic acid in a ratio of 15:4:1. The homogenate was incubated in the dark for 24 h at +4°C. The extracts were centrifuged at 15,000 rpm for 30 min at +4°C. After separation of the supernatant, 5 ml of extraction solution was added to the precipitate, extracted for 30 min and then centrifuged under the same conditions. The combined supernatants were evaporated to an aqueous residue of 5 ml under reduced pressure in a vacuum evaporator at +40°C. Further purification of phytohormones was performed on two solid-phase extraction (SPE) columns Sep-Pak C18 Plus and Oasis MCX 6 cc, 150 mg^{-1} (Waters Corp.) (Kosakivska et al., 2020 d). To remove lipophilic substances, proteins and pigments, the column Sep-Pak C18 Plus was used. On the column Oasis MCX, sorption and separation of phytohormones of different classes were performed. Elution of IAA, ABA, GA_3 and SA was performed with 100% methanol. The eluent was evaporated to dryness in concentrator flasks using a vacuum rotary evaporator at a temperature not exceeding +40°C. Before analysis, the dry residue was reduced to 200 µl with 45% methanol.

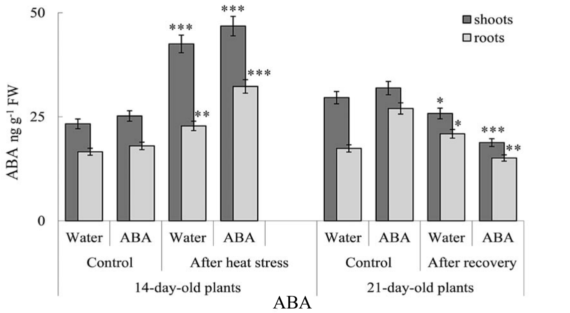
Analytical quantification of phytohormones ABA, IAA, GA_3 and SA was performed using high performance liquid chromatography (HPLC) on a 1200 LC/MS instrument (Agilent Technologies Inc., USA) with a diode-array detector G1315B and a single quadrupole mass-selective detector G6120A (Agilent). Chromatographic separation was carried out using a ZORBAX Eclipse Plus C18 column (Agilent) with a lipophilic-modified sorbent, particle size 5 µm (reversed-phase chromatography). After chromatographic separation of the samples with a volume of 20 µl solvent system (methanol, deionized water and acetic acid in a volume ratio of 45:54.9:0.1), IAA and ABA were screened in the UV absorption range at analytical wavelengths of 280 and 254 nm, respectively. To determine the content of SA samples, a volume of 10 µl was separated by a system of solvents (acetonitrile, deionized water and acetic acid in a volume ratio of 45:54.9:0.1) and screened for SA in the UV absorption range at analytical wavelength of 302 nm. After separating an aliquot of 20 µl with a solvent system (acetonitrile, deionized water and acetic acid in a volume ratio of 30:69.9:0.1), GA_3 was quantitatively detected by the mass detector signal, because the response to GA_3 of the diode-matrix detector was too weak. During detection of IAA and ABA, the speed of the mobile phase of the solvents was 0.7 ml min^{-1}, SA – 0.8 ml min^{-1} and GA_3

– 0.5 ml min^{-1}. As chemical standards for calibration, unlabelled IAA, ABK, GA_3 and SA, manufactured by Sigma-Aldrich (USA), were used. The content of analytes in the samples was monitored using a mass spectrometer (MS) in the combined mode (electrospray and chemical ionization at atmospheric pressure) with ionization of molecules of analytes in negative polarity. For quantitation of GA_3, with the molecular weight of 346, the signal of the MSD SIM (single selected ion monitoring) mass detector (setting 50% of the scan time for monitoring of the 345 m/z value [346-H]$^-$) was used.

Statistical analysis. All measurements were performed with 3 biological and 3 analytical replicates. The content of phytohormones was analysed and calculated using OpenLAB CDS ChemStation Edition (Agilent) (rev. C.01.09), a program for controlling the HPLC/MS instrument and processing the data. Statistical analysis was carried out with software *Statistica*, version 6.0 (StatSoft Inc.). For testing differences between mean values, the Bonferroni-corrected ANOVA criterion considered to be significant at $P < 0.05$ (Van Emden, 2008) was used.

Results and discussion

Effect of priming of spelt wheat seeds with exogenous ABA on level and distribution endogenous ABA. Pre-sowing seed priming with exogenous ABA induced a slight increase in endogenous ABA content in 14-day-old plants. After a heat stress (2 h at +40°C), the content of endogenous ABA in shoots and roots of primed plants increased 1.9- and 1.8-fold, in non-primed ones – 1.8- and 1.4-fold. After heat stress, maximum concentration (46.8 ± 2.3 ng g^{-1} FW) of endogenous ABA was observed in shoots of primed plants. In all treatments, endogenous ABA dominated in shoots of 14-day-old plants (Figure 1).

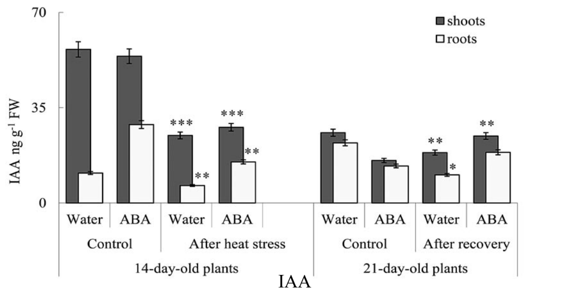


Note. Significant at * – $P < 0.05$, ** – $P < 0.01$ and *** – $P < 0.001$ compared to the controls at 14- and 21-day of vegetation; the bars denote coefficient of variation (CV).

Figure 1. Effect of pre-sowing priming of spelt wheat seeds with exogenous abscisic acid (ABA) (10^{-6} M) on the dynamics and distribution of endogenous ABA in 14- and 21-day-old plants

During spelt wheat growth, the content of endogenous ABA in shoots of 21-day-old water-germinated plants (1st control) increased 1.3-fold. At the same period, in roots of with exogenous ABA-primed plants, the increase of endogenous ABA content reached 50%, while in non-primed ones the changes were within the margin of error. During the recovery period, the content of endogenous ABA decreased in heat-stressed plants. The minimum concentration (15.1 ± 0.8 ng g^{-1} FW) of endogenous ABA was recorded in roots of 21-day-old, exogenous ABA-primed, heat-stressed plants (Figure 1). Thus, the priming of seeds with exogenous ABA induced the accumulation of endogenous ABA in spelt wheat plants after heat stress and inhibited the accumulation of the phytohormone during the recovery period.

Effect of seed priming with exogenous ABA on level and distribution of endogenous IAA. Endogenous IAA dominated in shoots of spelt wheat plants: the maximum concentration (56.4 ± 2.8 ng g^{-1} FW) was measured in shoots of 14-day-old non-primed plants. Pre-sowing seed priming with exogenous ABA induced more than a 2-fold increase (22.8 ± 1.4 ng g^{-1} FW) of the endogenous IAA content in roots of 14-day-old plants. After heat stress, the endogenous IAA content decreased significantly in all treatments in 14-day-old, water-germinated, heat-stressed and ABA-primed, heat-stressed plants. However, the content of endogenous IAA in shoots and roots of ABA-primed, heat-stressed plants was higher by 12.1% and 136%, respectively than that in water-germinated, heat-stressed ones (Figure 2).



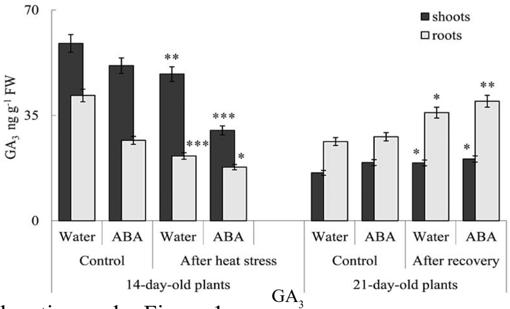
Explanation under Figure 1

Figure 2. Effect of pre-sowing priming of spelt wheat seeds with exogenous abscisic acid (ABA) (10^{-6} M) on the dynamics and distribution of endogenous indole-3-acetic acid (IAA) in 14- and 21-day-old plants

During spelt wheat growth, the content of endogenous IAA in shoots of 21-day-old, water-germinated and ABA-primed, unstressed plants declined: in ABA-primed ones – by 71.1%, in non-primed ones – by 54.3%, compared to 14-day-old plants. In contrast, in roots of non-primed plants, the endogenous IAA content doubled, while in ABA-primed ones it declined 1.7-fold. After recovery of 21-day-old ABA-primed plants, the content of endogenous IAA increased in shoots by 57.7%, in roots – by 36.8%, while in non-primed ones it decreased in roots by 53.4%, in shoots – by 28.3% (Figure 2). Thus, after heat stress, the content of endogenous IAA reduced, but the phytohormone content in 14-day-old, ABA-primed plants was higher than in non-primed ones. In the recovery period, seed priming with exogenous ABA induced the accumulation of endogenous IAA.

Effect of seed priming with exogenous ABA on level and distribution of endogenous GA_3. Endogenous GA_3 dominated in spelt wheat shoots of 14-day-old plants. The maximum concentration (58.9 ± 2.9 ng g^{-1} FW) of the endogenous GA_3 occurred in non-primed plants. Pre-sowing seed priming with exogenous ABA inhibited the accumulation of endogenous GA_3 in shoots and roots of 14-day-old plants by 12.6% and 35.8%, respectively. Some drop in the endogenous GA_3 content occurred after heat stress: in shoots and roots of ABA-primed plants – by 41.7% and 33.0%, in non-primed ones – by 17.3 and 48.3% (Figure 3). In shoots of 21-day-old, ABA-primed, water-germinated plants (controls), the endogenous GA_3 content decreased 2.7-fold compared to that in 14-day-old ones, while in non-primed ones it decreased 3.7-fold, but in roots of ABA-primed plants it increased by 4.5%, and in non-primed ones it declined by 37.8%.

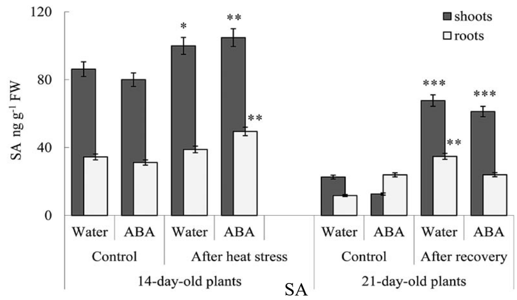
Following recovery, the endogenous GA_3 content in shoots and roots of non-primed plants rose by 20.8% and 34.2%, in ABA-primed ones – by 6.2% and 42.2%. The prolonged effect of seed priming with exogenous ABA was more pronounced in the accumulation of endogenous GA_3 in roots (10.6%), while in shoots this enhancement was only 6.8% (Figure 3). Thus, seed priming with exogenous ABA inhibited the accumulation of endogenous GA_3 in shoots and roots of 14-day-old plants after heat stress and induced an increase of its content after recovery.



Explanation under Figure 1

Figure 3. Effect of pre-sowing priming of spelt wheat seeds with exogenous abscisic acid (ABA) (10^{-6} M) on the dynamics and distribution of endogenous gibberellic acid (GA_3) in 14- and 21-day-old plants

Effect of seed priming with exogenous ABA on level and distribution of endogenous SA. Endogenous SA dominated in spelt wheat shoots of 14-day-old plants. Maximum concentration (104.8 ± 5.2 ng g^{-1} FW) was observed in shoots of ABA-primed, heat-stressed plants. Pre-sowing seed priming with exogenous ABA inhibited the accumulation of endogenous SA in roots of 14-day-old, water-germinated, unstressed plants by 9.6%. After heat stress, the SA content increased in shoots and roots of ABA-primed plants by 30% and 58.6% and in those of non-primed ones by 15.9% and 12.8% (Figure 4).



Explanation under Figure 1

Figure 4. Effect of pre-sowing priming of spelt wheat seeds with exogenous abscisic acid (ABA) (10^{-6} M) on the dynamics and distribution of endogenous salicylic acid (SA) in 14- and 21-day-old plants

In 21-day-old, ABA-primed, water-germinated plants (control), endogenous SA dominated in roots, and its content in shoots reached a minimum of 12.6 ± 0.6 ng g^{-1} FW. During the recovery period, non-primed plants were characterized by a 3-fold increase in the content of endogenous SA in shoots and roots. In ABA-primed plants, the content of endogenous SA in shoots significantly increased (4.9 times), and in roots this index remained unchanged. In the recovery period, the content of endogenous SA in shoots and roots of ABA-primed plants was lowered by 9.6% and 31.0% compared with non-primed ones (Figure 4).

Thus, pre-sowing priming of spelt wheat seeds with exogenous ABA solution induced specific changes in the dynamics and distribution of endogenous phytohormones in the organs of 14-day-old plants after a short-term heat stress. In shoots and roots, the contents of endogenous ABA and SA increased, and those of IAA and GA_3 reduced. In the recovery period, the amount of SA rose in shoots of 21-day-old plants, the ABA content decreased, and GA_3 and IAA accumulated in roots.

Discussion

Successful cultivation of highly productive stress-resistant cereals requires a deep understanding of the mechanisms of behaviour and management of metabolic and growth processes, a key role in which belongs to the phytohormones. Plants respond to stressors by switching between and interactions among different hormonal signalling pathways. ABA plays an important role in integrating various stress signals and controlling downstream stress responses. Because a universal response to any stressor is an increase in endogenous ABA, exogenous hormone treatment may be perceived by the plant as a stress signal and trigger cellular defence mechanisms (Tuteja, 2007; Ng et al., 2014).

Pre-sowing seed priming optimizes conditions for triggering metabolic processes during germination, minimizes the occurrence and manifestation of problems associated with the quality and structure of seeds and assures uniform strong germination (Muhie, 2018). This simple cost-effective approach mitigates the negative effects of moisture deficiency, soil salinity and temperature fluctuations (Ali et al., 2013; Kaya et al., 2013) and activates antioxidant systems (Eisvand et al., 2010). Wheat endogenous phytohormones are extremely sensitive to external and internal factors (Abhinandan et al., 2018). Affected by high temperature, drought and salinity, cultivated cereals normally exhibit rapid increase of the endogenous ABA content (Gietler et al., 2020). It was found that after a short-term heat stress young spelt wheat plants showed some rise in the endogenous ABA and SA content, while the content of endogenous IAA and GA_3 decreased (Figures 1–4).

A higher content of endogenous ABA and a decrease of the IAA content were observed under the same conditions in *Triticum aestivum* 'Podolyanka' (Kosakivska et al., 2020 c). Other researchers (Wu et al., 2019) have reported that heat stress in rice plants resulted in the accumulation of endogenous ABA and a decline in the content of endogenous GA_1, IAA and active forms of cytokinins. In barley anthers under high temperature conditions, expression of the auxin biosynthesis *YUCCA* gene was repressed, and the content of endogenous IAA decreased (Sakata et al., 2010). However, some reports indicate that in barley plants an increase in temperature by 4°C above the optimum caused a decrease in ABA in shoots and an increase in roots during 20 min of stress (Kudoyarova et al., 2014). An increase in the content of endogenous ABA, IAA and gibberellins in rice grains after heat stress was reported by Yang et al. (2014). During the flowering stage, heat stress induced sterility of rice spikelets through the inhibition of pollen tube elongation in the pistil, which was associated with a decrease in auxin content (Zhang et al., 2018).

Results of our experiment demonstrate that pre-sowing priming of spelt wheat seeds with exogenous ABA led to changes in the balance of endogenous hormones in water-germinated plants (controls). Thus, pre-sowing seed priming with exogenous ABA induced the accumulation of endogenous ABA and SA and a decline of IAA and GA_3 content in shoots of 14-day-old plants. Similar dynamics manifested in roots of ABA-primed plants, except for IAA, the content of which increased. On the 21^{st} day, in shoots of ABA-primed plants, ABA content remained higher than in shoots of non-primed ones, IAA and SA content was lower and that of GA_3 was higher; roots had the same distribution of phytohormones, except for SA (Figures 1–4). In our previous study (Kosakivska et al., 2019), it was found that pre-sowing priming of spelt wheat seeds with exogenous ABA significantly mitigated the negative effect of short-term heat stress on the growth of 14- and 21-day-old plants. Other researchers have reported that the heat resistance of maize seedlings (Gong et al., 1998) and suspension culture of *Bromus inermis* (Robertson et al., 1994) enhanced after the priming with exogenous ABA. Treatment with exogenous ABA (100 μM) improved heat resistance of rice pollen by activating antioxidant enzymes enhancing biosynthesis of heat shock proteins and accelerating metabolism of sugars and carbohydrates. At the same time, due to a decrease in transpiration, the leaf temperature increased, which caused damage to plants (Islam et al., 2018).

Following a short-term heat stress, nonspecific and specific changes occurred in the balance of endogenous hormones of water-germinated and ABA-primed plants (controls). Namely, the trend to increase the content of stress phytohormones ABA and SA and to decrease that of growth phytohormones IAA and GA_3 in shoots and roots of 14-day-old plants continued. However, the accumulation of ABA and SA was more pronounced in ABA-primed plants, and the content of endogenous IAA was maintained at a higher content than in non-primed ones. In contrast, ABA-primed, heat-stressed plants inhibited the accumulation of endogenous GA_3 more strongly than non-primed ones. In the recovery period, the amount of SA increased in 21-day-old plants, and the amount of ABA decreased. Endogenous GA_3 and IAA accumulated in roots. At the same time, in shoots of non-primed, heat-stressed plants the content of endogenous ABA and IAA declined, and that of GA_3 and SA increased, while in roots a high concentration of ABA was maintained (Figures 1–4).

Thus, our findings indicate that pre-sowing seed priming with exogenous ABA affects the balance of endogenous hormones of spelt wheat plants under water-germination (controls) and heat stress conditions. We suggest that changes in the dynamics and distribution of endogenous ABA, IAA, GA_3 and SA caused by pre-sowing seed priming with exogenous ABA can improve stress tolerance through regulation of metabolic and growth processes.

Conclusions

1. The results of this experiment showed that endogenous abscisic acid (ABA), indole-3-acetic acid (IAA), gibberellic acid (GA_3) and salicylic acid (SA) dominated in spelt wheat shoots of 14-day-old plants. On the 21st day, the distribution of all phytohormones, except GA_3, remained unchanged; the endogenous GA_3 was transferred to the roots.

2. It was identified that pre-sowing seed priming with exogenous ABA induced differentiated prolonged changes in the dynamics and distribution of endogenous ABA, IAA, GA_3 and SA in 14- and 21-day-old plants.

3. After short-term heat stress (2 h at +40°C), in shoots and roots of 14-day-old plants, the accumulation of endogenous ABA and SA enhanced, and the content of endogenous IAA and GA_3 decreased. In the recovery period, which lasted 7 days, the amount of SA in 21-day-old plants increased and the ABA content reduced; endogenous GA_3 and IAA accumulated in roots.

4. Maximums in the endogenous ABA content were recorded after heat stress in shoots (46.8 ± 2.3 ng g^{-1} FW) and roots (32.3 ± 1.6 ng g^{-1} FW) of 14-day-old, ABA-primed plants. The maximum of endogenous GA_3 content (39.7 ± 2.0 ng g^{-1} FW) occurred on the 21st day after recovery in roots of ABA-primed plants. The content of endogenous IAA in roots of 14-day-old ABA-primed, unstressed plants (2nd control) reached a maximum of 53.9 ± 2.7 ng g^{-1} FW. The SA content increased in shoots and roots of ABA-primed, heat-stressed plants by 31% and 44.7%.

5. The obtained data revealed that response to heat stress is associated with changes in the level and distribution of endogenous hormones in spelt wheat plants caused by pre-sowing seed priming with exogenous ABA. The balance of endogenous hormones of plants under water-germination (controls) and heat stress conditions was affected with exogenous ABA.

The results of the study suggest that changes in the dynamics and distribution of endogenous ABA, IAA, GA_3 and SA caused by exogenous ABA application can improve stress tolerance through regulation of metabolic and growth processes.

Acknowledgements

The publication contains the results of research conducted within the project funded by the National Academy of Sciences of Ukraine I III-90-19.463 “Hormonal regulation of growth and development of cereals under the influence of negative climatic factors” (2019–2023).

Received 17 02 2021
Accepted 08 10 2021

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Speltų sėklų apdorojimo prieš sėją egzogenine abscizo rūgštimi įtaka augalų endogeniniam hormonų balansui karščio streso sąlygomis

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Santrauka

Sėklų priešsėjinis apdorojimas egzogeniniais fitohormonais turi įtakos augalų augimui, vystymuisi ir atsparumui. Tačiau vis dar neaišku, ar egzogeninių fitohormonų poveikis augimui yra tiesioginis, ar jis susijęs su endogeninių fitohormonų kiekio ir pasiskirstymo pokyčiais. Buvo tirta endogeninių abscizo (ABA), indolo-3-acto (IAA), giberelino (GA_3) bei salicilo (SA) rūgščių dinamika ir pasiskirstymas speltos (*Triticum spelta* L., ‘Frankenkorn’) augaluose, išaugintuose iš sėklų, apdorotų ABA (10^{-6} M). Tirti 14 dienų amžiaus augalai, kurie buvo veikiami trumpalaikio karščio streso (2 val. +40 °C temperatūroje), ir 21 dienos amžiaus augalai po atsigavimo. Nustatyta, kad 14 dienų amžiaus augalų ūgliuose dominavo endogeninės ABA, IAA, GA_3 ir SA rūgštys. Dvidešimt pirmą dieną visų fitohormonų, išskyrus GA_3, pasiskirstymo pobūdis buvo nepakitęs, tačiau didžioji dalis endogeninės GA_3 susikaupė šaknyse. Sėklų apdorojimas prieš sėją egzogenine ABA sukėlė endogeninių fitohormonų pusiausvyros pokyčius. Karščio stresą patyrusių 14 dienų amžiaus augalų ūgliuose bei šaknyse endogeninių ABA ir SA kiekis padidėjo, o IAA ir GA_3 – sumažėjo. Po karščio streso 21 dienos amžiaus augaluose SA kiekis padidėjo, o ABA – sumažėjo; endogeninės GA_3 ir IAA kaupėsi šaknyse. Endogeninės ABA didžiausia koncentracija po karščio streso buvo užfiksuota ūgliuose (46,8 ± 2,3 ng g^{-1} žalios masės) ir šaknyse (32,3 ± 1,6 ng g^{-1} žalios masės). Endogeninės IAA didžiausia koncentracija (53,9 ± 2,7 ng g^{-1} žalios masės) nustatyta ABA apdorotų 14 dienų amžiaus augalų šaknyse; endogeninės GA_3 didžiausia koncentracija (39,7 ± 2,0 ng g^{-1} žalios masės) užfiksuota 21 dieną po atsigavimo ABA apdorotų augalų šaknyse. SA kiekis karščio streso paveiktų augalų ūgliuose ir šaknyse padidėjo atitinkamai 31 ir 44,7 %, ABA neapdorotų – 15,9 ir 12,8 %.

Apibendrinant eksperimento duomenis galima teigti, kad speltų sėklų priešsėjinis apdorojimas egzogenine ABA sukėlė skirtingus endogeninių ABA, IAA, GA_3 ir SA dinamikos bei pasiskirstymo pokyčius 14 ir 21 dienos amžiaus augalų ūgliuose bei šaknyse kontrolinių variantų ir karščio streso sąlygomis. Tai rodo, kad reakcija į karščio stresą yra susijusi su endogeninių fitohormonų kiekio ir pasiskirstymo pokyčiais jaunuose speltų augaluose, kuriuos sukėlė sėklų apdorojimas prieš sėją egzogenine ABA.

Reikšminiai žodžiai: abscizo rūgštis, apdorojimas, atsigavimas, giberelino rūgštis, indolo-3-acto rūgštis, karščio stresas, salicilo rūgštis, *Triticum spelta*.