The Thesis of the PhD Dissertation

Kalpita Singh

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Hungarian University of Agriculture and Life Sciences

Redox control of physiological and biochemical processes in maize

Kalpita Singh

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The PhD School

Name: Doctoral School of Agricultural and Food Sciences

Discipline: Crop and Horticulture Sciences

Head: Prof. Dr. Melinda Kovács
Professor, MTA member
Institute of Animal Physiology and Nutrition,
Hungarian University of Agriculture and Life Sciences

Supervisors: Dr. Gábor Kocsy
Scientific advisor
Agricultural Institute, HUN-REN Centre for
Agricultural Research

Dr. Dávid Polgári
Assistant Professor
Hungarian University of Agriculture and Life Science

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Approval of the Supervisor

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Approval of the Head of Doctoral School Approval of the Supervisor

1. BACKGROUND OF THE WORK AND ITS AIMS

Maize is utilised globally, either as a staple food, fodder crop or in the production of ethanol. Its origin can be traced back to ancient civilisations of the Mayans and Aztecs. Hundreds of years of domestication and selective crop breeding techniques have significantly improved maize production (YANG et al., 2023). The development and registration of the first inbred maize hybrid (Mv5) in Hungary, Europe and the release of the first commercial maize hybrid in the USA mark the milestone steps for mankind in maize improvement programmes (JÁNOSSY et al., 1957; MARTON, 2013; TROYER, 1995). A significant increase in maize production and demand has been observed over the years. However, with shifting habits along with the population boom, the demand for maize has increased. This inflated demand, together with changing climate conditions, necessitates the need to develop stress-resilient crops (CGIAR, 2024). In order to develop stress-tolerant crops, we first need to understand the signalling triggered in plants when faced with stress. Under unfavourable environmental conditions, stress-specific molecular sensors are activated in the cells that are in contact with the stimuli. As a result, the change in cellular redox homeostasis stimulates the antioxidant system and modifies the transcriptome and metabolome. To further strengthen the stress signal perceived, a series of protein phosphorylations is initiated, including the Mitogen-Activated Protein Kinase (MAPK) cascade and sucrose non-fermenting-1-related protein kinase 2 (SnRK2) modules (ZHANG et al., 2023). It is essential to understand that instead of a single chain reaction, stress perception, signalling, and ultimately adaptation are a network of cross-communications with nodes and molecules affecting multiple other ones at different layers. For instance, the ROS wave triggers the antioxidant system that initiates ROS scavenging, but at the same time stimulates hormone production, such as abscisic acid (ABA) and jasmonic acid (JA), which further complements ROS production via NADPH and boosts antioxidant enzymes to maintain ROS balance (DEVIREDDY et al., 2021). These changes govern

transcriptional reprogramming and exhibit stress adaptive responses such as the accumulation of osmoprotectants, biosynthesis of antioxidants, amino acid profile modifications, and changes in carbon and nitrogen assimilation (ZHANG et al., 2023). Therefore, understanding redox alteration and its crosstalk with other components, such as hormones, amino acids, and thiols, could provide helpful insights to not only curb the global hunger but also fight against the prevailing nutritional hunger. The focus of the present study is to understand the holistic network of simultaneous modulations in the hormonal profile, carbohydrates, organic acids, amino acids, polyamines, phenylpropanoids, and the redox system at the metabolic and genetic level by the application of two reductants (ascorbate -Asc, and sodium hydrosulfide- NaHS, H_2S donor) and one oxidant (hydrogen peroxide- H_2O_2). The main problem addressed in the study is the influence of 3 different redox compounds on the internal redox chemistry of the plants governing metabolism and hormone interaction with the redox homeostasis to modulate seedling growth.

The following were the set objectives for the study:

- To characterise the effects of three redox compounds (Asc, H_2O_2, and NaHS) on seedling growth and cellular redox homeostasis in maize.
- To investigate the redox-modulated regulation of the central carbon and nitrogen metabolism (carbohydrates, organic acids, amino acids, and polyamines) to identify redox-sensitive metabolic pathways.
- To identify and analyse redox-dependent specific changes in the hormonal profile at the transcriptional and metabolic levels.
- To explore the interplay between redox homeostasis and holistic plant metabolism to understand the simultaneous changes in metabolic pathways in response to redox imbalance.

2. MATERIALS AND METHODS

2.1. Plant material and treatments

Seeds of *Zea mays* L. cultivar 'Ivanka' (Hungarian maize hybrid) were obtained from the Maize Breeding Department of HUN-REN ATK, Martonvásár, Hungary. After surface sterilisation, the seeds were germinated for 4 days at 25 °C. After the emergence of the root and coleoptile, they were cultivated for 7 days in half-strength Hoagland solution at 25 °C with a 12/12 hours light and dark cycle in a growth chamber (Poleco). The seedlings were then treated with 5 mM Asc, 5 mM H_2O_2, and 1 mM NaHS by adding them to the nutrient media in three parallel sets for each treatment, along with the controls. The used concentrations of the chemical reagents were determined based on the preliminary experiments. Sampling was done after 3 and 7 days. All the biochemical measurements were performed using the shoot samples.

2.2. Measurements of stress markers- electrolyte leakage, lipid peroxidation, and H_2O_2

Electrolyte leakage was measured in one cm-long leaf segments using a conductometer, following the method of GULYÁS et al. (2014). For the calculations, a ratio of ECactual/ECtotal was used, and the results were presented as percentage electrolyte leakage.

Lipid peroxidation was determined by the endogenous levels of MDA in the shoot samples, following the methodology of DE PAULA et al. (1996). The concentration of MDA was calculated using an extinction coefficient of 155 $mM^{-1}cm^{-1}$.

Endogenous H_2O_2 content of shoot samples was measured using the Ferrous Oxidation-Xylenol Orange assay (FOX1) solution containing 0.1 mM xylenol orange, 100 mM D-sorbitol, and 0.127 mM ammonium Fe sulfate prepared in 2.5 M H_2SO_4. The absorbance was measured at 560 nm. The reaction was based on

the H_2O_2-dependent oxidation of ferrous ions to ferric ions, which were detected using xylenol orange at 560 nm (KELLŐS et al., 2008).

2.3. Measurements of thiols

The measurement of total and oxidised thiols was done following the protocol of TARI et al. (2002). For oxidised thiols, 200 µL of the supernatant was mixed with 300 µL 0.2 M 2-[cyclohexylamino]ethane-sulphonic acid (CHES, pH 8.5) and 15 µL of 50 mM N-ethylmaleimide (NEM) to block reduced thiols. The mixture was vortexed and incubated at room temperature for 15 minutes. Excess NEM was removed by washing the solution three times with 500 µL toluene. To reduce the oxidised thiols, 10 µL of 9 mM dithiothreitol (DTT) was added to 20 µL of distilled water with 300 µL extract, and the mixture was incubated for 1 hour at room temperature. Subsequently, 20 µL of 15 mM monobromobimane (mBBr) was added, and the samples were incubated in darkness for 15 minutes. The reaction was stopped by adding 250 µL of 0.25% (v/v) methanesulphonic acid (MSA). For total thiols, the extract was mixed with 2-[cyclohexylamino]ethane-sulphonic acid (CHES, pH 8.5) and DTT and the subsequent steps were as described for oxidised thiols. The samples were measured by HPLC using an Alliance 2690 system equipped with a fluorescent detector (Waters, Milford, MA, USA).

2.4. Measurements of antioxidant enzymes

The enzyme activity was determined using the MES/KOH extraction buffer, consisting of 50 mM MES, 40 mM KCl, and 2 mM $CaCl_2$ at pH 6.0 (MURSHED et al., 2008). The enzyme activity of ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), and catalase (CAT) was measured following the detailed protocol mentioned by SINGH et al. (2025). The enzyme

activity was calculated on a protein basis, measured according to BRADFORD (1976).

2.5. Gene expression analysis

For RNA extraction, 100 mg of the sample was pulverised in liquid nitrogen and mixed with TRIzol reagent (DirectzolTM RNA miniprep kit, Zymo Research). Total RNA was extracted as per the instructions of the RNA extraction kit (DirectzolTM RNA miniprep kit, Zymo Research) and was treated with DNase I. The cDNA was synthesised according to SINGH et al. (2025), and the gene expression was measured with the gene-specific primers using qPCR. The primers were designed by Primer-BLAST and manual work, following the proper principles of primer designing (YE et al., 2012). For the calculation of primer efficiencies, LinRegPCR was used (RAMAKERS et al., 2003). The calculation of relative gene expressions was done by the Pfaffl method (PFAFFL, 2001).

2.6. Measurements of hormones, flavonoids, and phenylpropanoids and metabolite profiling

Extraction of the samples was performed following VRHOVSEK et al. (2012) and PÁL et al. (2019). Quantification of hormones, flavonoids, and phenylpropanoid intermediates was performed on a Waters Acquity I-class UPLC system equipped with a PDA detector and coupled to a Xevo TQ-XS triple-quadrupole mass spectrometer fitted with a UniSpray^{TM} (US) ion source (Waters Corp., Milford, MA, USA). Separation of phenolic compounds was achieved on an HSS T3 column (1.8 µm, 100 x 2.1 mm) as described by (VRHOVSEK et al., 2012). The Xevo TQ-XS operated in multiple-reaction monitoring (MRM) mode following the method of PÁL et al. (2019).

Metabolite extraction and derivatisation for GC-MS were carried out as outlined by GONDOR et al. (2021). Extraction was performed using methanol, while derivatisation was performed using methoxyamine hydrochloride in pyridine and

N-trimethylsilyl-N-methyltrifluoroacetamide. Derivatised samples were injected into a 30 m HP-5MS UI column (30 m x 0.25 mm, 0.25 μm film thickness) using helium as the carrier gas at a constant flow of 1 mL minute^{-1}. The injector was operated in split mode at 230 °C. Metabolite identification was based on analytic standards, Kovats retention indices, and mass spectral matching against the Wiley 229 and NIST 2.3 libraries.

2.7. Measurements of N-containing compounds- free amino acids and polyamines

Free amino acids were measured from 300 mg of samples, extracted using 2 mL cold 10% TCA with constant shaking for 1 hour at room temperature (GULYÁS et al., 2017). Following filtration through a 0.2 μm pore membrane filter, sample detection was conducted using an automatic amino acid analyser (Ingos Ltd., Czech Republic) fitted with an Ionex Ostion LCP5020 cation exchange column. The separation of free amino acids was achieved through a Li^+-citric buffer system (Ingos Ltd., Czech Republic).

The quantification of polyamines in the shoot samples was achieved by preparing their dansyl derivatives as described by NÉMETH et al. (2002) and SMITH AND DAVIES (1985). The polyamine residue was dissolved in 1 ml of methanol, ultrafiltered through nylon membranes, and then assayed.

2.8. Statistical analysis

Statistical differences were calculated by one-way analysis of variance (ANOVA) using GraphPad Prism 10. Fisher's Least Significant Difference (LSD) test was performed as a post hoc test, with the expressed means considered significantly different at $p \leq 0.05$. For the statistical analysis, three biological replicates were utilised per treatment, with each replicate consisting of a mixture of 5 individual plants. The heatmaps in the result section were created using the software MultiExperiment viewer (MeV).

3. RESULTS AND DISCUSSION

3.1. The effect of redox compounds on growth, cellular redox homeostasis, and stress markers

The three compounds affected growth differently. A significant reduction was noted after Asc and H_2O_2 treatment in shoot length, fresh weight and root fresh weight after 7 days **(Fig. 1)**.

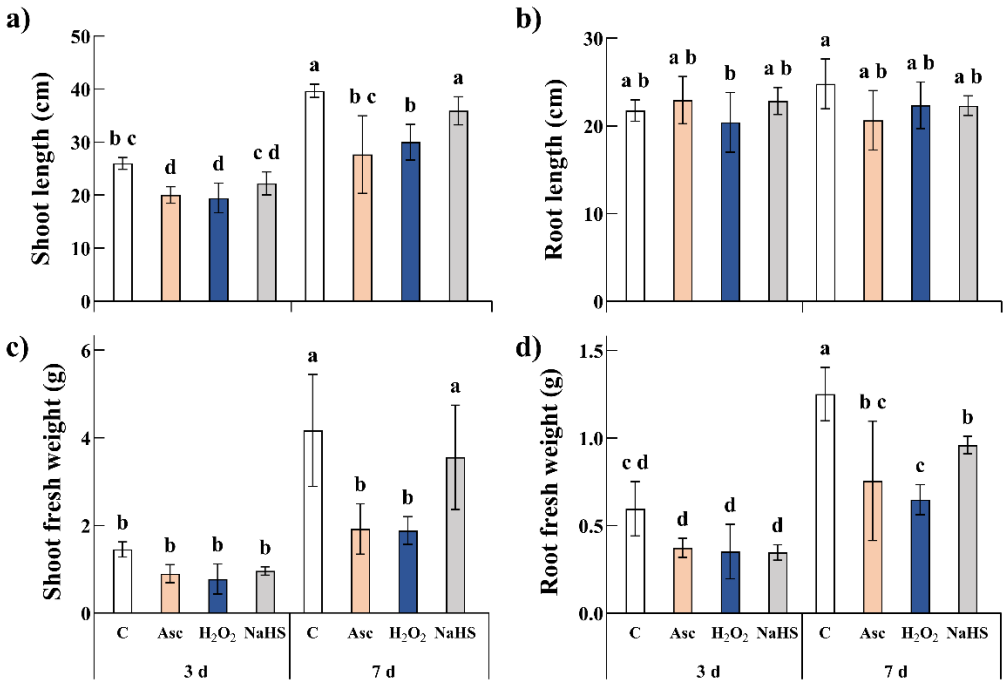

Figure 1: The effect of 5 mM ascorbate (Asc), 5 mM hydrogen peroxide (H_2O_2), and 1 mM sodium hydrosulfide (NaHS) on the growth parameters of maize seedlings along with the controls (C), after 3 and 7 days of the treatments. (a) shoot length, (b) root length, (c) shoot fresh weight, (d) root fresh weight. Values marked with different letters are significantly different from each other at $p < 0.05$ levels (One-way ANOVA followed by Fisher's Least Significant Difference (LSD) Test for the data obtained with three biological replicates each).

In the case of redox state, Asc-treated plants had a low ratio of reduced glutathione to oxidised glutathione and reduced cysteine to oxidised cysteine **(Fig. 2a, b)**.

Whereas NaHS shifted the redox balance towards a more reduced side. In the case of H_2O_2, a very high reduced to oxidised cysteine ratio was observed **(Fig. 2b)**. Thus, the redox state was in the order of NaHS<H_2O_2<Asc from reduced to oxidised cellular state.

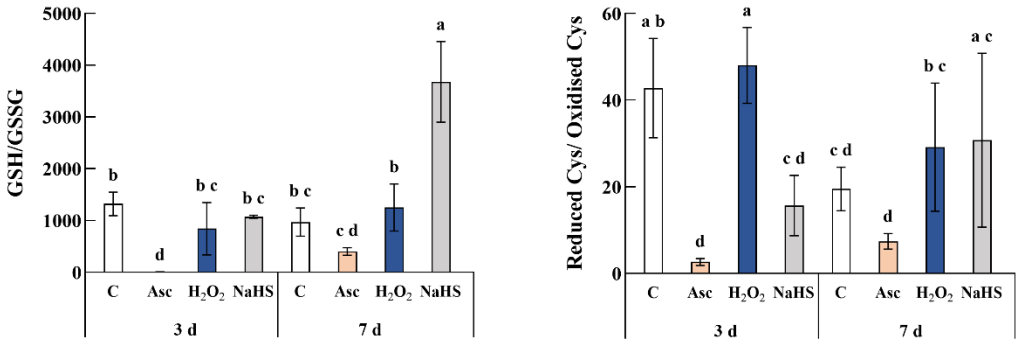

Figure 2: The effect of 5 mM ascorbate (Asc), 5 mM hydrogen peroxide (H_2O_2), and 1 mM sodium hydrosulfide (NaHS) on the cellular redox balance of maize seedlings along with the controls (C), after 3 and 7 days of the treatments. (a) reduced to oxidised glutathione ratio (GSH/GSSG) and (b) reduced to oxidised cysteine ratio. Values marked with different letters are significantly different from each other at $p < 0.05$ levels (One-way ANOVA followed by Fisher's Least Significant Difference (LSD) Test for the data obtained with three biological replicates each).

As a consequence of altered redox homeostasis, electrolyte leakage and lipid peroxidation were the highest and lowest after Asc and NaHS treatment, respectively **(Fig. 3a, b)**. In the case of endogenous H_2O_2, Asc had the lowest level after 7 days, and NaHS had the highest levels amongst the three treatments **(Fig. 3c)**.

The three chemical treatments negatively affected the cellular redox balance. As a consequence, higher electrolyte leakage, lipid peroxidation, and biomass reduction were observed. These results are in accordance with the previous findings of ASGHAR et al. (2023b), who observed a significant reduction in plant biomass after the application of 5 mM Asc and H_2O_2 in wheat plants after 3 and 7 days.

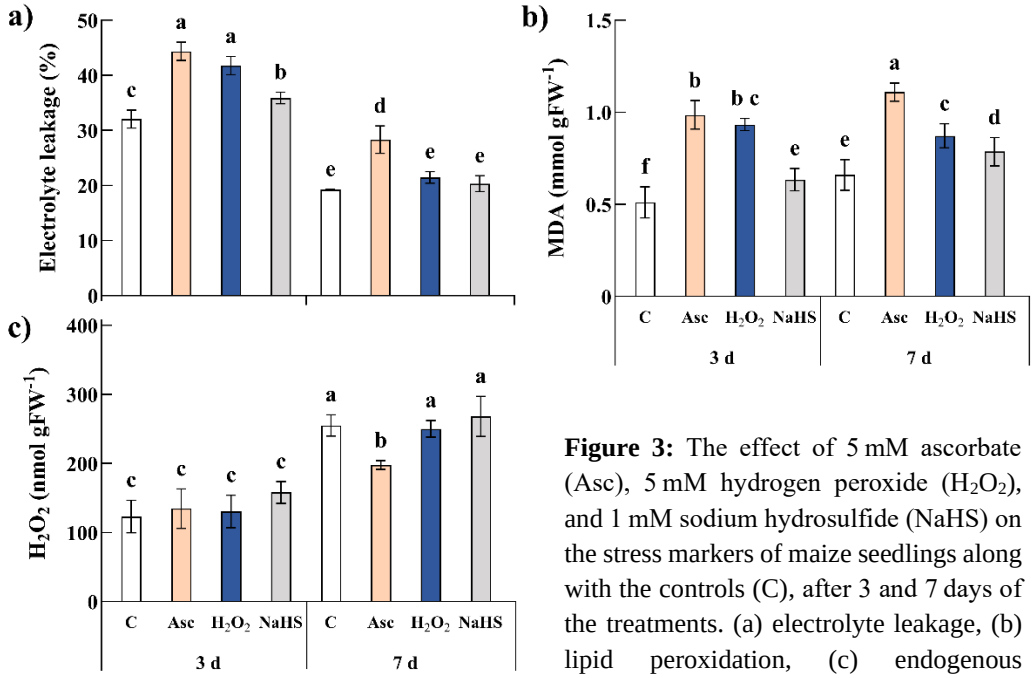

Figure 3: The effect of 5 mM ascorbate (Asc), 5 mM hydrogen peroxide (H_2O_2), and 1 mM sodium hydrosulfide (NaHS) on the stress markers of maize seedlings along with the controls (C), after 3 and 7 days of the treatments. (a) electrolyte leakage, (b) lipid peroxidation, (c) endogenous hydrogen peroxide (H_2O_2). Values marked marked with different letters are significantly different from each other at $p < 0.05$ levels (One-way ANOVA followed by Fisher's Least Significant Difference (LSD) Test for the data obtained with three biological replicates each).

3.2. The effect of redox compounds on the antioxidant enzymes

The activity of the antioxidant enzymes, including APX, MDHAR, DHAR, and GR, was measured. APX showed the highest activity following H_2O_2 application. DHAR enzyme activity peaked after prolonged Asc application **(Fig. 4a, b)**. MDHAR and GR activity increased following prolonged Asc and H_2O_2 application, while being lowered after 7 days of NaHS addition amongst the three treatments **(Fig. 4c, d)**. The gene expression of the related genes (*cytosolic MDHAR2*, *peroxisomal APX*, and *cytosolic GR*) correlated with the enzyme activity as well **(Fig. 4f)**. In conclusion, Asc and H_2O_2 had activated the Asc-GSH cycle to scavenge accumulating H_2O_2. This high antioxidant enzyme activity after Asc and H_2O_2, while lower antioxidant enzyme activity could be a possible explanation for the observed endogenous H_2O_2 levels.

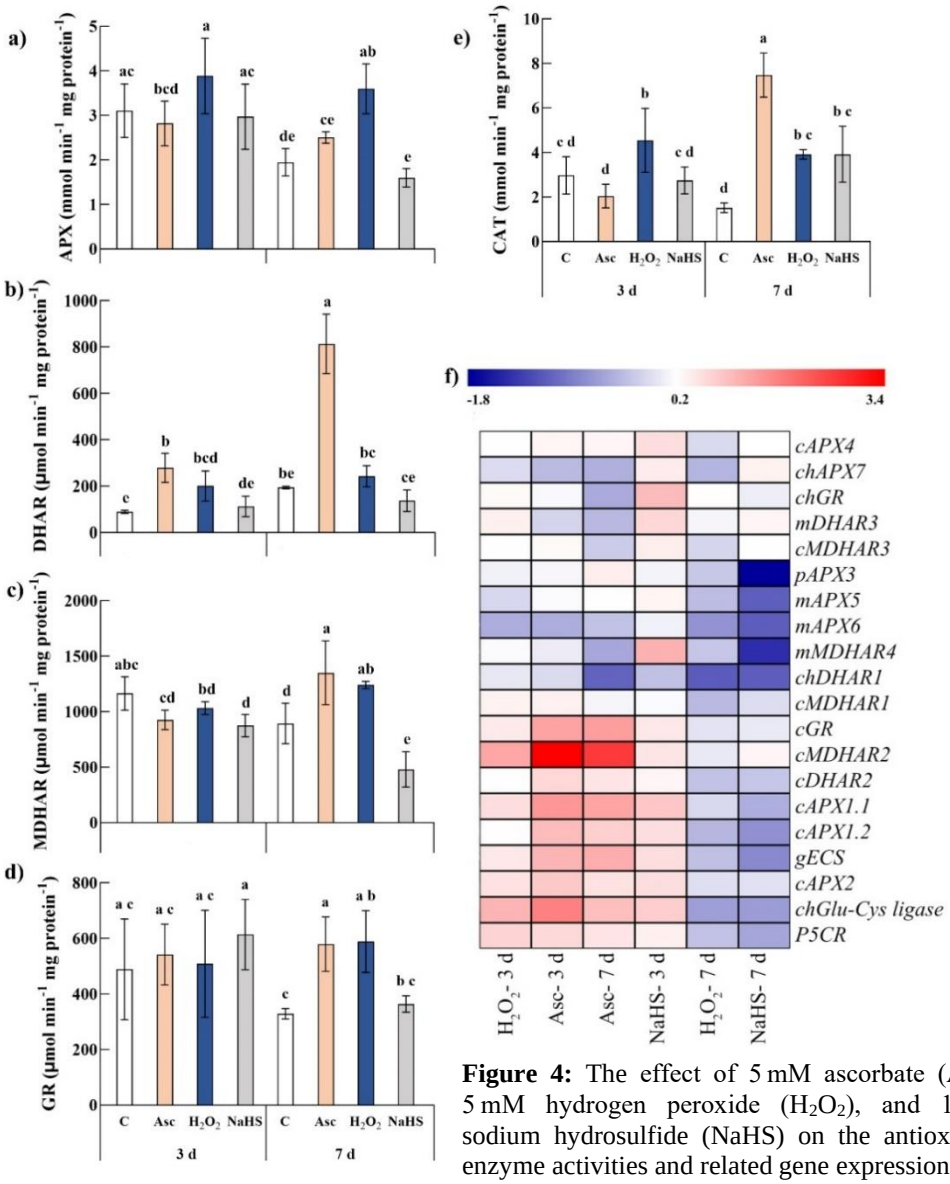

Figure 4: The effect of 5 mM ascorbate (Asc), 5 mM hydrogen peroxide (H_2O_2), and 1 mM sodium hydrosulfide (NaHS) on the antioxidant enzyme activities and related gene expression in maize seedlings along with the respective controls (C) after 3 and 7 days of treatment. (a) ascorbate peroxidase (APX), (b) dehydroascorbate reductase (DHAR), (c) monodehydroascorbate reductase (MDHAR), (d) glutathione reductase (GR), (e) catalase (CAT), (f) the expression of the genes related to antioxidants. For the graphs, values marked with different letters are significantly different from each other at $p \leq 0.05$ levels (One-way ANOVA followed by Duncan's multiple range test for the data obtained by three biological replicates each). For the heatmap, the letter at the beginning of the gene name - *c, ch, m, p* refers to cytosolic, chloroplastic, mitochondrial and peroxisomal, respectively. *MDHAR: monodehydroascorbate reductase, GR: glutathione reductase, APX: ascorbate peroxidase, gECS: gamma-glutamylcysteine synthetase, Glu-Cys ligase: glutamine-cysteine ligase, DHAR: dehydroascorbate reductase, P5CR: δ1-pyrroline-5-carboxylate reductase*. The colours represent the $\log_2$ values of the relative gene expression in treated plants with respect to the control.

To understand the redox-specific changes in carbon metabolism, some of the metabolites from the glycolysis and TCA cycle were measured. The glucose levels were comparable amongst the treatments, except after 7 days of NaHS treatment **(Fig. 5)**. From the metabolites of the TCA cycle, Asc had the lowest level of citric acid, while H_2O_2-treated plants had the highest level. In contrast, H_2O_2 exhibited the lowest level of α-ketoglutaric acid after both days. Likewise, Asc and H_2O_2 had the lowest level of succinate **(Fig. 5)**. Interestingly, NaHS-treated plants had the highest level of malic acid. The redox changes caused a metabolic reprogramming of glycolysis and the TCA cycle, which could be due to disturbed photosynthesis, limited availability of components for energy production and ultimately affected amino acid synthesis and other metabolites. The Asc and H_2O_2-mediated redox shift was accompanied by decreased levels of the intermediates of the TCA cycle. Similar results of lower accumulation of α-ketoglutaric acid and aconitic acid were noted in wheat (ASGHAR et al., 2023a).

µg gFW $^{-1}$	C-3	Asc-3	H_2O_2-3	NaHS-3	C-7	Asc-7	H_2O_2-7	NaHS-7
Succinate	a 25.95± 7.19	b 17.24± 3.22	bc 14.95± 4.11	b 17.72± 3.89	bd 13.69± 3.88	d 7.3± 2.23	cd 8.81± 1.01	b 16.37± 4.96
Malic Acid	ac 289.45± 37.24	ac 286.6± 13.12	c 231.88± 70.83	ac 298.44± 11.43	bc 278.83± 23.88	bc 266.41± 39.27	ab 315.86± 46.92	a 362.32± 71.59
Oxo-proline	a 220.59± 35.20	de 29.11± 5.67	bcd 71.89± 27.36	bc 80.93± 23.94	ce 55.79± 15.43	e 8.31± 1.80	bc 83.65± 4.12	b 112.85± 58.83
α-ketoglutaric acid	ab 60.41± 15.35	bd 40.17± 9.36	d 24.3± 5.84	bd 44.3± 13.63	a 69.27± 16.38	cd 33.6± 11.21	d 22.61± 6.33	abc 51.19± 17.77
D-arabinose	c 5.58± 1.24	b 9.63± 1.68	bc 7.11± 1.78	bc 6.26± 0.62	c 5.37± 1.65	b 9.46± 2.36	a 14.38± 3.67	bc 6.21± 1.77
D-ribose	ab 89.75± 19.63	a 109.12± 24.52	bc 70.33± 2.47	ab 85.71± 18.03	c 56.79± 10.15	c 57.85± 9.73	bc 68.47± 6.47	c 54.47± 7.91
Citric acid	bc 116.78± 2.85	bc 105.74± 17.79	ab 139.5± 16.06	cd 98.11± 14.28	bc 118.7± 9.44	d 69.79± 23.11	a 156.18± 28.34	ab 140.26± 35.12
D-glucose	b 204.9± 17.36	b 242.9± 22.61	b 237.21± 17.14	b 246.57± 10.32	b 237.85± 15.91	b 257.17± 21.65	b 240.35± 24.59	a 339.75± 120.15
Myo-inositol	d 57.32± 11.59	b 114.4± 12.8	ab 117.9± 23.13	bc 96.17± 11.09	cd 74.4± 13.41	ab 122.37± 15.57	a 151.19± 35.56	cd 68.79± 23.57
Sucrose	b 10.53± 2.97	a 16.74± 4.21	c 5.66± 1.82	a 15.38± 2.8	bc 8.78± 3.43	bc 9.54± 1.48	bc 10.02± 2.88	bc 8.63± 0.81

Minimum Maximum

Figure 5: The effect of 5 mM ascorbate (Asc), 5 mM hydrogen peroxide (H_2O_2), and 1 mM sodium hydrosulfide (NaHS) on the metabolite profile after 3 and 7 days of the treatments along with the respective controls (C). The numbers 3 and 7 refer to the sampling day after treatment. Colouring is done individually for each row, with blue representing the lowest level and red

representing the highest level. Values marked with different letters are significantly different from each other at $p \leq 0.05$ levels (One-way ANOVA followed by Fisher's Least Significant Difference (LSD) Test for the data obtained with three biological replicates each).

3.4. Effect of Asc, H_2O_2, NaHS on amino acids at transcriptional and metabolic levels

Altered redox balance affected photosynthesis and sugar metabolism. As a consequence, the amino acid profile was severely modified. H_2O_2 and Asc sustained an opposite effect on total amino acid levels after 3 days, with H_2O_2 increasing them and Asc lowering them **(Fig. 6b)**. However, after 7 days, Asc continued to decrease them significantly, while H_2O_2-treated plants exhibited levels similar to those of the control. The level of cysteine precursors- serine and glycine exhibited a unique accumulation only after H_2O_2 treatment **(Fig. 6a)**. In addition, NaHS-treated plants had the highest accumulation of proline. This could probably be the reason that the least membrane damage was noted in NaHS-treated plants. H_2O_2-treated plants also had a high level of polyamine precursors-arginine and ornithine **(Fig. 6a)**. From the aromatic amino acids, H_2O_2 treatment also resulted in a high level of tyrosine. The arogenate dehydrogenase enzyme (involved in tyrosine biosynthesis) gene expression was the highest after H_2O_2 treatment, reflecting the results obtained at the metabolite level **(Fig. 6c)**. It is possible that the plants may initiate the accumulation of Tyr as a response mechanism to withstand H_2O_2-induced oxidative stress. Similar results were obtained by EL-MOGY et al. (2024). Glutamine synthase (involved in nitrogen assimilation) level was higher in NaHS-treated plants, pointing to better nitrogen assimilation in these plants **(Fig. 6c)**.

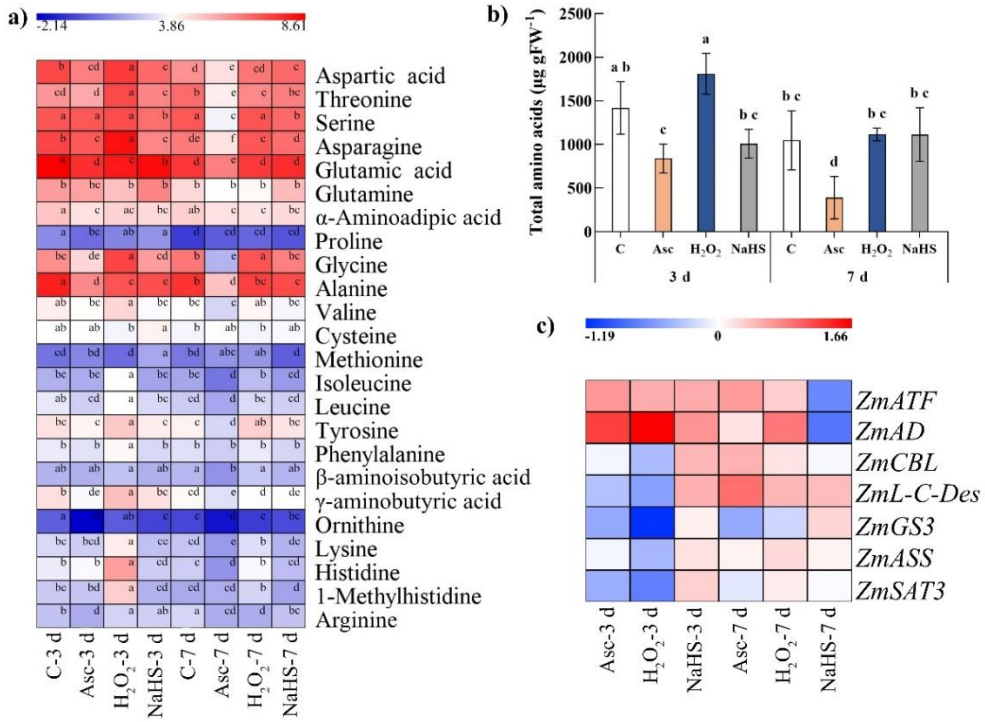

Figure 6: The effect of 5 mM ascorbate (Asc), 5 mM hydrogen peroxide (H_2O_2), and 1 mM sodium hydrosulfide (NaHS) on a) the free amino acids, b) total amino acids, and c) the relative gene expression after 3 and 7 days of the treatments along with the respective controls (C). The numbers 3 and 7 refer to the sampling day after treatment. For the heatmaps, the colours represent the $\log_2$ values of the average of three biological replicates used to measure the endogenous levels of the amino acids and the relative gene expression, with blue indicating lower levels and red indicating higher levels. Boxes marked with different letters are significantly different from each other at $p \leq 0.05$ levels (One-way ANOVA followed by Fisher's Least Significant Difference (LSD) test for the actual data obtained with three biological replicates each). The heatmap was created using the software MultiExperiment Viewer (MeV). *ZmATF- Zea mays aminotransferase y4uB; ZmAD- Zea mays arogenate dehydrogenase; ZmCBL- Zea mays cystathionine beta-lyase chloroplastic; ZmL-C-Des- Zea mays L-cysteine desulfhydrase chloroplastic; ZmGS3- Zea mays Glutamine synthetase 3; ZmASS- Zea mays argininosuccinate synthase; ZmSAT3- Zea mays serine acetyltransferase*

3.5. Changes in secondary metabolites as a result of redox change

Plant metabolism is tightly regulated by redox processes, and vice versa (BERGONCI et al., 2023). Thus, to understand the redox-mediated changes in the

amounts of flavonoids, the components of phenylpropanoid pathways were investigated. A depletion of cinnamic acid was noted after 3 days of H_2O_2 **(Fig. 7a)**. This pointed out the possibility that under oxidative stress, an increased production of phenylpropanoids and flavonoids was initiated, which might have caused its depletion. The accumulation of ferulic acid, which is also an antioxidant and a downstream product of cinnamic acid, was observed **(Fig. 7a)**. Thus, in Asc and H_2O_2-treated plants, the depletion of cinnamic acid and accumulation of ferulic acid, 3,4-hydroxybenzoic acid, indicated an increased synthesis of ROS-scavenging compounds.

Likewise, redox-and time-dependent changes were noted in the case of flavonoids. Dihydrokaempferol and related compounds levels were the lowest after H_2O_2 treatment, while naringenin and related compounds were highest after 3 days of NaHS treatment **(Fig. 7b)**. Luteolin increased in response to Asc and NaHS treatment after 3 days. It remained higher after 7 days in Asc, but not in NaHS-treated plants **(Fig. 7b)**. Comparable patterns were reported in Chinese cabbage, where 100 μM salicylic acid (SA) increased trans-ferulic acid, kaempferol, and quercetin levels under salt stress (LINIĆ et al., 2021).

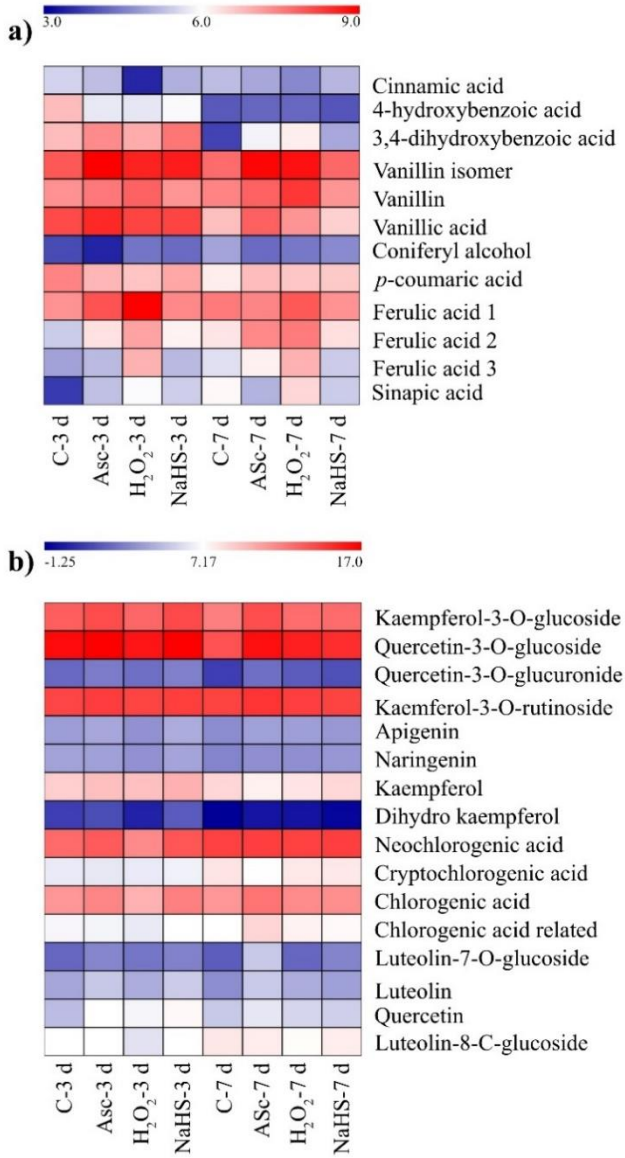

Figure 7: The effect of 5 mM ascorbate (Asc), 5 mM hydrogen peroxide (H_2O_2), and 1 mM sodium hydrosulfide (NaHS) on phenylpropanoids in maize seedlings along with the controls (C) after 3 and 7 days of the treatments. (a) phenylpropanoids, and (b) flavonoids. The numbers 3 and 7 refer to the sampling day after treatment. The colours represent the $\log_2$ values of the average of three biological replicates used to measure the endogenous levels of the various compounds. The heatmap was created using the software MultiExperiment Viewer (MeV).

3.6. Altered hormonal profile under redox imbalance

Phenolic compounds serve as the precursor for hormone synthesis. Interestingly, the levels of SA, ABA, and JA were higher after Asc and H_2O_2 treatment **(Fig. 8a)**. In the case of NaHS-treated plants, the levels were comparable to those of control plants. A similar pattern was observed at the transcriptional level as well. For instance, the expression of ABA synthesis genes (*ZmVP14-1*, *ZmVP14-2*, and *ZmNCED*) was higher, while that of the catalysis-related genes (*ZmABA8ox1a*,

ZmABA8ox3a) was highly downregulated in Asc and H_2O_2-treated plants **(Fig. 8b)**. Redox-dependent changes in hormones were observed at the metabolite and transcriptional levels, with a more oxidising environment promoting the accumulation of SA, ABA, and JA, while a reduced environment coincided with their lowest levels. Results similar to ours of hormone accumulation were obtained in rice (ZHOU et al., 2020), wheat (ASGHAR et al., 2023a), and Arabidopsis (BULLEY et al., 2021).

a)

ng g^{-1} FW^{-1}	3 d				7 d			
	C	Asc	H_2O_2	NaHS	C	Asc	H_2O_2	NaHS
Bound *o*HCA	b 9488.00	b 10775.00	a 12362.33	b 9575.00	b 9519.00	c 6054.00	a 12497.00	c 5718.00
Free SA	c 22.00	b 38.00	bc 31.33	bc 25.33	c 23.67	a 62.67	bc 30.00	c 24.33
Bound SA	de 284.33	b 460.67	bc 383.67	cd 359.00	e 251.00	a 567.33	bc 403.67	bc 373.67
Auxin	a 2.15	ab 1.86	ab 2.04	ab 1.90	ab 2.02	b 1.34	ab 1.65	ab 1.82
ABA	d 4.38	b 65.90	a 117.50	d 9.57	d 5.47	c 32.23	b 53.93	d 3.74
PA	d 2.42	bc 8.71	a 20.73	d 3.82	d 3.49	cd 5.94	b 10.75	d 2.20
DPA	d 7.37	cd 25.57	a 155.50	cd 21.50	cd 13.16	c 33.23	b 92.77	d 12.00
JA	ab 160.33	ab 202.00	a 236.00	ab 182.33	b 90.10	ab 199.67	ab 160.00	b 103.35
JA-LE/ILE	a 6.41	a 7.58	a 8.29	a 5.58	a 3.01	a 6.43	a 6.03	a 5.16

Minimum — Maximum

b)

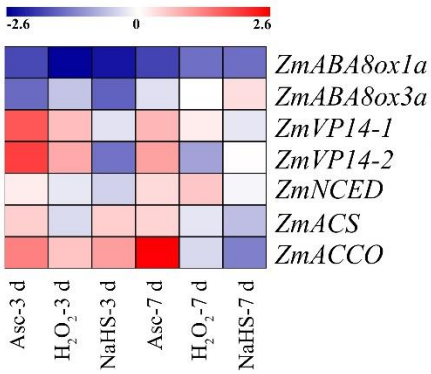

Figure 8: The effect of 5 mM ascorbate (Asc), 5 mM hydrogen peroxide (H_2O_2), and 1 mM sodium hydrosulfide (NaHS) on a) the hormonal profile, b) the relative gene expression of the hormones related genes of maize seedlings along with the respective controls (C) after 3 and 7 days of the treatments. For a) the colouring is applied individually to each row, while for b) the overall heat map is coloured (created using MultiExperiment Viewer MeV), representing $\log_2$ values with blue (lowest) and red (highest). Values marked with different letters are significantly different from each other at $p \leq 0.05$ level (One-way ANOVA followed by Fisher's Least Significant Difference (LSD) Test for the data obtained with three biological replicates each). *o*HCA: *ortho*-hydroxycinnamic acid, SA: salicylic acid, ABA: abscisic acid, PA: phaseic acid, DPA: dihydrophaseic acid, JA: jasmonic acid, JA-LE/ILE: JA-isoleucine/ leucine, *ZmVP14*: *Zea mays viviparous 14*, *ZmACCO: 1-aminocyclopropane-1-carboxylic acid oxidase*, *ZmACS: 1-aminocyclopropane-1-carboxylate synthase*, *ZmABAox1a/3a: abscisic acid oxidase 1a/3a*, *ZmNCED: nine-cis epoxycarotenoid dioxygenase*.

4. CONCLUSION AND RECOMMENDATIONS

The redox imbalance negatively affects plant growth and development, ultimately leading to yield loss. From the perspective of the current global climate scenario, the yield losses are projected to increase further. Thus, imposing the need to develop climate-resilient crops by understanding oxidative stress-mediated changes in the plant metabolism. In the current study, we could simulate the disturbing effects of environmental stresses on the redox environment using oxidants and reductants. The three compounds- Asc, H_2O_2, and NaHS- altered the redox homeostasis to a varying degree, as was evident by the measurement of membrane damage, electrolyte leakage and endogenous H_2O_2 levels. Furthermore, due to redox imbalance, the antioxidant system is activated in plants. In the current study, Asc and H_2O_2 triggered the activity of the antioxidant enzymes (APX, MDHAR, DHAR, GR, and CAT). Such changes were manifested at the transcriptional level as well after these two treatments. The redox imbalance and damaged photosynthetic apparatus negatively affected carbon metabolism, as was evident with the metabolites of glycolysis and the TCA cycle. Consequently, this affected the downstream processing of amino acids and subsequently polyamines and phenolic compounds. As a result, total amino acid content was significantly lower in Asc-treated plants, and H_2O_2 resulted in its significant decrease from 3 to 7 days of the treatment. NaHS-treated plants had levels similar to the control. This accordingly corresponded to the changes in the accumulation of polyamines, phenylpropanoids, and flavonoids. In addition, these phenolic compounds serve as the precursor for the biosynthesis of phytohormones. Therefore, a modified hormonal profile was expected. The hormones accumulate under stressful conditions to help induce tolerance and survival. The accumulation of ABA, SA, and JA could be a stress response to further stabilise the cellular redox balance, as phytohormones are known to trigger the antioxidant machinery as well.

In light of the present results, future studies can be focused on the specific redox sensors, such as Quiescin sulfhydryl oxidase 1 (boosts plant immunity), the subcellular distribution of these antioxidant compounds, and their interaction with other signalling molecules. Studies with mutants and transgenic plants could be conducted to analyse the direct functional involvement of the identified compounds at the molecular level. Practical use of modulating the redox environment to induce stress protection, regulating growth and development can be conducted. Furthermore, gene editing, seed coating or spraying with certain redox compounds could be investigated under varied or combined stresses, imitating field conditions. The redox-modulating effect by modifying GSH metabolism to ultimately influence plant physiology and stress response is of benefit to increase amino acid accumulation, resulting in improved nutritional quality as well.

5. NEW SCIENTIFIC RESULTS

1. Asc, H_2O_2, and NaHS have specific physiological effects, since only Asc and H_2O_2 decreased the growth, chlorophyll content and increased lipid peroxidation.
2. Asc shifts the GSH-dependent redox environment in a more oxidising and NaHS in a more reducing direction, while its intermediate state occurs after H_2O_2 addition.
3. The more oxidising redox environment after Asc -treatment activates some antioxidant enzymes (CAT, DHAR) at the gene expression and activity level.
4. The redox compounds control the metabolism in a specific way, since lower level of several compounds of glycolysis, tricarboxylate cycle and nitrogen metabolism (amino acids, polyamines, NO) was detected after Asc and H_2O_2 application compared to NaHS treatment.
5. Different redox regulation of some phenolics and flavonoids occurs by the three studied compounds since they exhibited a greater increase after Asc and H_2O_2 addition compared to the effect of NaHS.
6. The specific interaction between the hormonal and redox system is indicated by greater SA, JA and ABA levels after Asc and H_2O_2 treatments compared to NaHS addition.

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7. THE PUBLICATIONS OF THE AUTHOR IN THE FIELD

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1. Kocsy, G., Gulyás, Z., Kulman, K., Jobbágy, K., **Singh, K.**, Panda, S.K. (2025). Redox Regulation of the Response to Abiotic Stresses by MicroRNAs and Transcription Factors in Plants. In: Panda, S.K., Khan, M.A. (eds) Plant

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1. **Singh K.**, Pál M., Kocsy G. (2023): Redox control of polyamine metabolism in maize. 3rd Plant Polyamine Research Workshop. 12-13 October 2023, Budapest and Martonvásár, Hungary. Book of Abstracts (2023), p. 28.
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3. **Singh K.**, Jobbágy K., Kulman K., Szalai G., Hamow, K.Á., Kocsy G. (2024): Redox modulation of hormones and metabolites in maize. FIBOK 2024, April, Martonvásár, Hungary. ISBN 978-615-6448-45-3.
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5. **Singh, K.**, Jobbágy, K., Kulman, K., Szalai G., Hamow, K.Á., Kocsy, G. (2024): Redox balance and growth modulation in maize under oxidative stress. XIV. Magyar Növénybiológiai Kongresszus: Összefoglaló kötet (2024) p. 93.

Oral and Poster presentations

1. **Singh, K.** (2024): Redox modulation of hormones and metabolites in maize at FIAtal NÖVénybiológusok ELŐadássorozatát PLANT BIOLOGISTS lecture series on March 2024, Debrecen, Hungary.
2. **Singh K.**, Pál M., Kocsy G. (2023): Redox control of polyamine metabolism in maize. 3rd Plant Polyamine Research Workshop. 12-13 October 2023, Budapest and Martonvásár, Hungary.
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5. Soltész, A., Jobbágy, K., **Singh, K.** and Gulyás, Z. (2025): Ectopic expression of wheat *TaCbf14* and *TaCbf15* genes in barley induces cold tolerance and reveals trichome- and anthocyanin-associated responses. 8th Conference on cereal biotechnology and breeding. 10-13 November 2025, Budapest, Hungary.
6. Jobbágy, K., **Singh, K.**, Kalapos, B., Farkas, Z., Ahres, M., Soltész, A., Galiba, G., Kocsy, G. and Gulyás, Z. (2025): Characterisation of auxin transport-related *HvACT1* and *HvGNOM* in barley. 8th Conference on cereal biotechnology and breeding. 10-13 November 2025, Budapest, Hungary.
7. **Singh, K.**, Jobbágy, K., Kulman, K., Szalai, G., Hamow, K.Á., Gulyás, Z., Kocsy, G. (2025): Redox-mediated changes in hormones and metabolites in

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8. Kulman, K., Jobbágy, K., **Singh, K.**, Török, A.L., Cadar, O., Vanková, R., Szalai, G., Ahres, M. and Kocsy, G. (2025): Redox regulation of the response to cadmium in wheat. Plant Biology Europe 2025, 25-28 June 2025, Budapest, Hungary.

Mobility scholarships received

1. Pannónia Scholarship for Stipendium Hungaricum students for a short-term mobility research at Karl-Franzens-Universität Graz, Institut für Biologie, Graz, Austria. Financed by the Hungarian University of Agriculture and Life Sciences for the years 2025 (contract number: PANP-00005-001/2024/SMT-G-024) and 2026 (contract number: PANP-00005-001/2024/SMR-G-005).
2. "PROM - Short-term academic exchange" to the University of Lublin, Poland, financed by the National Agency for Academic Exchange and co-financed by the European Union (application number: PROM.IN.SD.2026:9).