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# CHANGES IN TOTAL POLYPHENOLS, FLAVONOIDS, PHOTORESPIRATION, RESPIRATION AND GLYCOLATE OXIDASE ACTIVITY IN MAIZE PLANTS GERMINATED FROM SEEDS EXPOSED TO FREEZING STRESS

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KEYWORDS
Maize
Freezing
Total polyphenols and flavonoids
Photorespiration
Respiration
Glycolate oxidase

ABSTRACT
The aim of this study was to investigate the post-freezing effect of -4°C for 16 h (FS) applied to soaked maize seeds before germination on the levels of total polyphenols (TPC) and total flavonoids (TFC), photorespiration, total respiration and dark respiration, glycolate oxidase (GO) activity in maize plants grown under dark and light conditions. Exposure of maize seeds to subzero temperatures before germination followed by growth in the dark or in the light revealed after-effects of these factors on both TPC and TFC. The greatest inhibition of TPC by FS was achieved in etiolated sprouts (≈10%) and in 6-day-old plants in the light (≈9%), while the lowest level of TPC was observed in leaves of 8- and 17-day-old plants under light conditions. Photorespiration, total respiration, dark respiration, and glycolate oxidase activity in maize plants grown from seeds exposed to FS remained at reduced levels than in control samples. The suppression of these indices, apparently, in this case may be associated with a slowdown in the intensity of photosynthetic gas exchange in general.

## INTRODUCTION

Maize (*Zea maize* L.) as crop of tropical and subtropical origin is very susceptible to extreme temperature stresses, due to rapid global climate changes. The impact of extreme temperature stress mainly depends on duration, intensity, and timing of the stress (Bano et al., 2015; Waqas et al., 2021). The optimal temperature for maize growth, development and crop production is between 25 and 28°C, and a minimum growth temperature of 6–10 °C (Ma et al., 2022). Suboptimal temperature, defined as suboptimal chilling temperatures below 15 °C and above 0 °C significantly limits seed germination, seedling establishment, and subsequent plant growth, development and productivity (Ma et al., 2022; Meng et al., 2022; Cauş et al., 2022). Maize is also affected by freezing temperatures, the temperature below 0 °C. Frosts most often occur in early fall before harvest and can cause a variety of physical, mechanical, biochemical, and physiological changes in immature corn seeds (Woltz et al., 2006). Maize responds to cold stress through a series of morphological, physiological, biochemical and molecular changes (Zhou et al., 2022). In particular, during germination and subsequent growth of maize plants grown from seeds exposed to low positive and negative temperatures, changes in growth parameters occur (Cauş et al., 2022; Wijewardana et al., 2015; Hussain et al., 2020; Cauş et al., 2023) which are accompanied by changes in the production of secondary metabolites, including the content of polyphenols and flavonoids (Ray et al., 2024; Rao et al., 2024; Tian et al., 2025), the content of photosynthetic pigments and $CO_2$ exchange parameters (Ma et al., 2022; Grzybowski et al., 2019). An important role in plants for resistance against abiotic stresses is played by such metabolic way as photorespiration and the key enzyme of photorespiration, glycolate oxidase (Zelitch et al., 2009; Rojas et al., 2012; Voss et al., 2013; Chikov et al., 2019; Lu et al., 2013). To date, the most studied effects on photorespiration are those of high temperatures (Cui et al., 2016; Dusenge et al., 2019) and water deficit (Voss et al., 2013; Silva et al., 2015; Urban et al., 2017). As for the effects of other abiotic factors on plant photorespiration, including low and

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freezing temperatures, the available information on this issue is limited. Also, little is known about the combined effects of freezing stress to which seeds are exposed prior to germination and light conditions on germinated seed growth, subsequent plant growth, and whether these plant responses persist over longer periods of time.
In this regard, the aim of this work was to study the influence of freezing stress applied to corn seeds before germination on the content of polyphenols and flavonoids, photorespiration, respiration and glycolate oxidase activity in maize sprouts and plants, both in the dark and in the light.

## MATERIALS AND METHODS

The seeds of the Bemo 203 maize hybrid, provided by the Public Institution National Center for Seed Research and Production, Pașcani, RM, were used in this research. Studies to evaluate some biochemical properties of maize (*Zea mays* L) plants grown from seeds subjected to freezing stress (FS) of -4°C for 16 hours was carried out under controlled laboratory conditions with regulation of humidity, lighting and aeration. Maize seeds from the control and experimental variants were soaked in distilled water at 5°C for 36 hours. Then the seeds of the experimental variants, freed from water, were exposed to the action of FS, and the control seeds during this time were placed in a refrigerator at a temperature of 5°C. Subsequently, control and experimental seeds were sown simultaneously in containers on wet cotton discs and set for germination in a thermostat, in the dark, at an optimal temperature of 26°C and relative air humidity of 70-85%. The 2-day control and experimental germinated seeds were planted in pots with soil. Part of the pots with seedlings (control and experimental) were transferred for cultivation in a chamber with controlled conditions of lighting, aeration, humidity and temperature of 26°C, and another part of the control and experimental pots with seedlings were cultivated in the dark chamber at a temperature of 26°C and a relative air humidity of 70-85%. Epicotyl and leaf samples from control and experimental plants were taken from seedlings and plants aged 2 and 6 days, respectively, grown in the dark, and from those grown in the light for 6, 8 and 17 days, to be used in the determination of total polyphenols, flavonoids and glycolate oxidase (GO) activity. Photorespiration, total respiration and dark respiration were measured on intact 3ed leaves of maize plants, grown from seeds exposed to FS followed growth in soil under laboratory conditions at 26°C during of 17 days.
*Photorespiration*, *total respiration*, and *dark respiration* were measured on intact leaves of 17-day-old plants according to the method of Balaur et al. (2018). The determinations were carried out using the automated system PTM 48A, from the company "Bioinstrument" SRL, Republic of Moldova.
*Estimation of Total Polyphenols Content* (TPC). The total phenolics content in ethanolic extracts of sprouts' epicotyls and plants' leaves was determined spectrophotometrically at a wavelength of 700 nm using Folin-Ciocalteu reagent according to the procedure reported by Singleton et al. (1998), using μg standard gallic acid equivalent (GAE) per gram of FW.
*Determination of Total Flavonoids Content* (TFC). Total flavonoids content of ethanolic extracts of sprouts' epicotyls and plants' leaves was determined spectrophotometrically at 412 nm according to the method of Irshad et al. (2011) using standard quercetin equivalent (QE) as μg QE/g FW.
*Glycolate oxidase* (GO) activity was determined according to the method of Kolesnikov (1962).
*Statistical analysis of data.* The experiments were performed in three repetitions. In each repetition, 10 plants were used. Each experiment was repeated at least three times. Statistical processing of data was performed using the "Statistica 7" computer programs, using Basic Statistics, calculating the mean values and standard deviation of the data determined in three repetitions.

## RESULTS AND DISCUSSION

In response to low-temperature stress, including chilling and freezing injuries, plants respond through a myriad of physiological, biochemical and molecular changes (Zhou et al., 2025). Studies on the effects of subzero temperatures on maize have been conducted mainly at different stages of seed development and maturation, as well as the growth and development of plants from immature seeds formed under the influence of subzero temperatures (Woltz et al., 2006).
In addition to the fact that maize is sensitive to stress at low positive temperatures (Cauș et al., 2022) and negative temperatures (Cauș et al., 2023) at early growth stages with varying degrees of damage to germination and morphological parameters in different hybrids, it has been shown that another important factor affecting the growth and development of maize plants is light (Cauș et al., 2024). It is reported (Ning et al., 2016) that in maize seedlings, a complex mechanism of molecular regulation of phosphoproteins is realized during the de-etiolation process. Previous research (Cauș et al., 2024) with combined application of freezing stress to seeds before germination and subsequent growth of seedlings in the dark (etiolated seedlings) and in the light (green seedlings) for 6 days found that freezing significantly reduced carotenoids content in leaves of green seedlings, while in etiolated leaves the carotenoid content was not significantly altered by freezing, compared to the respective

controls. Numerous studies have shown that, along with carotenoids, other groups of polyphenols, including flavonoids, also play an important role in protecting plants from various abiotic stresses, such as temperature fluctuations, heavy metals, UV radiation, drought, etc. (Ray et al., 2024; Rao et al., 2025; Li et al., 2021; Samec et al., 2021; Shomali et al., 2022). To investigate whether the accumulation of polyphenols and flavonoids in maize seedlings varies depending on the freezing temperature applied to the seeds before germination and the light conditions during subsequent seedling growth, experiments (Figure 1) were conducted under controlled conditions.

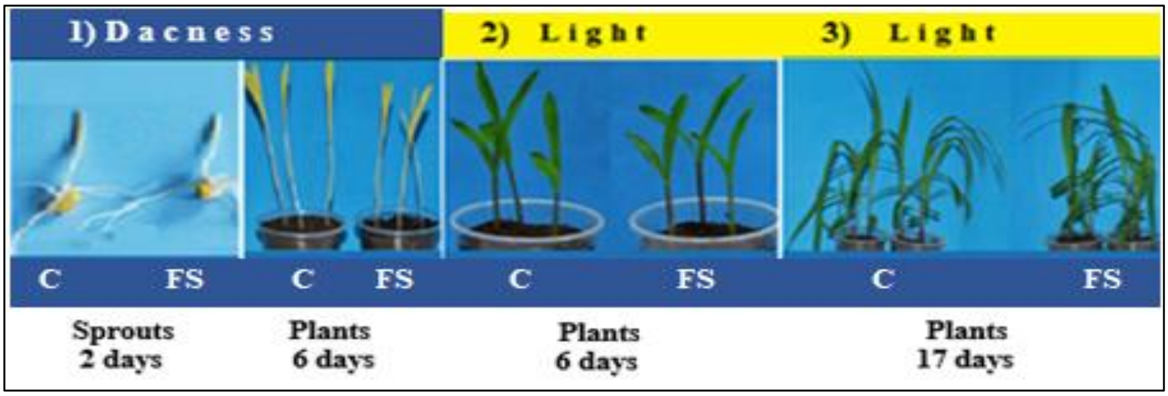


**Figure 1. Maize sprouts and plants, control (C) and experimental, the seeds of which were subjected to freezing stress (FS) at a temperature of -4°C for 16 hours before germination, followed by growing in the dark (1) or in the light (2) for 6 days, and plants (C, FS) which continued to grow in the light during of 17 days**

From the Figure 1.1 it is evident that 2- and 6-day-old maize seedlings grown in the dark are etiolated, while seedlings grown in the light are green in color (Figure 1.2, 1.3), indicating the presence of chloroplasts that synthesize chlorophyll pigments. Two-day-old sprouts and six-day-old plants germinated in the dark from seeds exposed before germination to freezing showed growth delaying and yellowing (Figure 1.1). Total polyphenols content (TPC) was significantly higher in both frozen and control seedlings, as well as in six-day-old plants under dark and light conditions (Figure 2A).

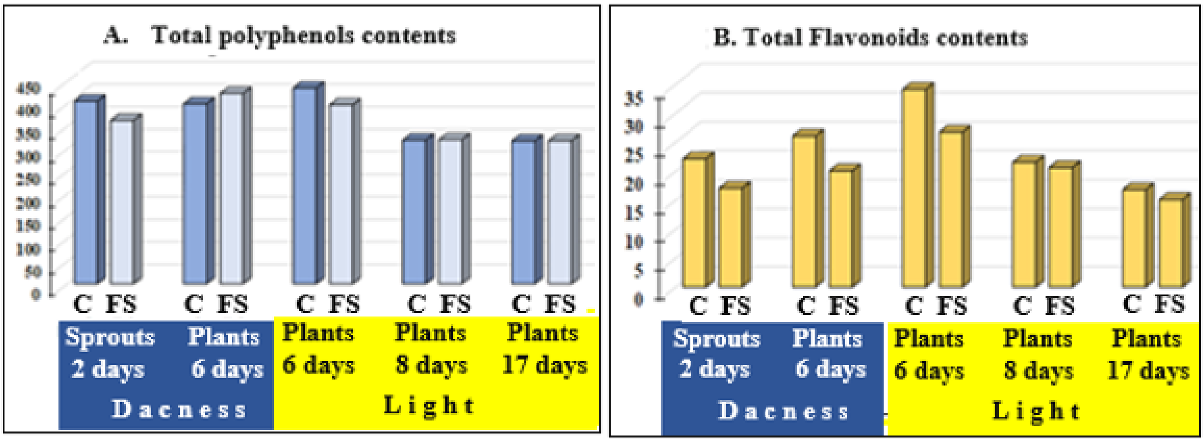


**Figure 2. Changes in A - total polyphenol content (TPC) and B - total flavonoid content (TFC) in sprouts and leaves of light and dark maize seedlings germinated from seeds subjected to freezing stress (FS) at -4°C for 16 hours before germination, and subsequent growth of plants from the corresponding germinated seeds in soil under controlled laboratory conditions**

As can be seen (Figure 2A), freezing stress applied to seeds before germination led to a decrease in polyphenols content under dark conditions in etiolated sprouts while in etiolated and stressed plants polyphenols contents is insignificant, only an increasing trend is observed. In plants grown in light, freezing stress decreased the polyphenols content in the leaves of 6-day-old plants and did not affect the polyphenols in the leaves of 8- and 17-day-old plants (Figure 2A). The lowest TPC levels were found in light-grown plants at 8 and 17 days of age, and polyphenol levels are similar in both freeze-treated and control plants. Moreover, the highest levels of polyphenols were found in sprouts and leaves of 6-day-old plants both in the dark
and in the light, compared with the polyphenols content in leaves of 8- and 17-day-old plants under light conditions (Figure 2A). This probably may be related to the more intensive physiological processes involving secondary metabolites as polyphenols that occur with plant aging under illumination. Exposure of maize seeds to subzero temperatures before germination followed by their growth in the dark or in the light revealed the aftereffect of

these factors on the total flavonoids content (Figure 2, B). In etiolated seedlings, freezing stress reduced flavonoid accumulation by 23%, whereas in plants of the same age (6 days), stress reduced it by 23% in etiolated and by 21.6% in green leaves compared to the corresponding control samples. At the same time, in the leaves of 8- and 17-day-old plants grown in light, the effect of reducing flavonoid content under the influence of freezing stress was preserved to a lesser extent, the decrease being 4 and 10% lower, respectively, compared to the control.

The fact that the effect of stress to which seeds are exposed before germination is subsequently manifested in plant growth processes, expressed by a decrease in the accumulation of flavonoid content, can be explained by the participation of these secondary metabolites in various physiological and biochemical reactions of plants under the respective conditions (Shomali et al., 2022). In maize (*Zea mays* L.), flavonoids, phenolic low molecular weight, with high antioxidant capacity play a protective role against various abiotic stresses and have a crucial role in growth and development of plants (Shomali et al., 2022; Falcone Ferreyra et al., 2012; Agati et al., 2013; Rius et al., 2016; Kumar et al., 2018; Righini et al., 2019; Kitashova et al., 2024). It is also mentioned the role of flavonoids as antioxidants and regulators in photorespiration (Agati et al., 2013). In a study with Arabidopsis mutants (Kitashova et al., 2024) was mentioned that flavonoid metabolism plays different roles in the early and late stages of plant cold acclimation. During the first 3 days of a 2-week cold acclimation period, flavonoid deficiency was observed to play a role in stabilizing C/N metabolism and photosynthesis, as well as on the proteome of the photorespiratory pathway. In the late stage of cold acclimation, flavonoid deficiency was found to cause a significant decrease in total protein amounts in studied *Arabidopsis* mutants.

Photorespiration, which links processes such as photosynthesis and respiration, is of great importance for the existence of plants. This process involves a complex of cellular organelles such as chloroplasts, mitochondria, and peroxisomes. In recent years, a number of studies have appeared indicating that photorespiration is involved in plant responses to the effects of unfavorable environmental factors of various natures (water deficit, high temperatures, salinity, low temperatures, heavy metals (Voss et al., 2013; Kangasjarvi et al., 2012; Hodges et al., 2016; Szymanska et al., 2014; Zhang et al., 2024). Photorespiration is a light-induced process of $O_2$ absorption with oxidation of photosynthesis intermediates and release of $CO_2$. The monitoring of photorespiration intensity in intact leaves of maize 17-day-old plants grown from seeds exposed to freezing stress before germination and subsequent cultivation under light conditions, revealed that the dynamics of changes in the photorespiration intensity during the measurement process was represented by a curve with several peaks, giving it an undulating character (Figure 3A).

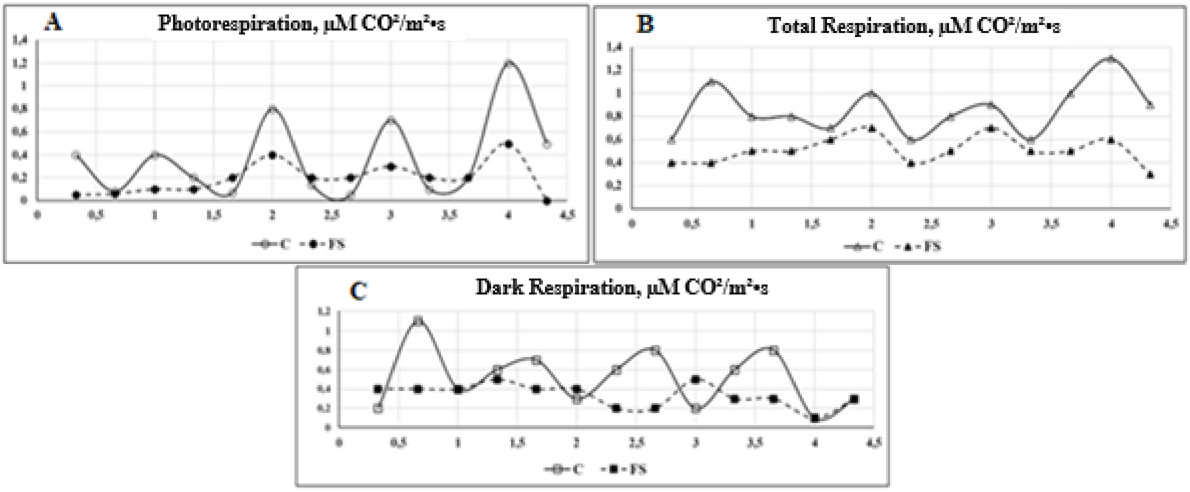


**Figure 3. Photorespiration, total respiration and dark respiration in leaves of intact maize plants, grown from seeds exposed to FS of – 4 °C for 16 h before germination and subsequent growth in soil under laboratory conditions at 26 °C. The measurements were performed on leaf 3 of 17-day-old maize plants**

In plants grown from seeds that were preventively subjected to frost shock, a decrease in the intensity of photorespiration was observed, the modification curve of which also had an undulating character and was at a lower level than the control throughout the monitoring period. Under a light condition the efflux of carbon dioxide from maize leaves to air was higher than that of plants grown from freezing stress exposed seeds. And the initial rate of $CO_2$ efflux from control leaves was eight times higher than that of FS plants (Figure 3A). Inhibition of photorespiration in this case may be associated with a slowdown in photosynthetic metabolism in general (Kangasjarvi et al., 2012). As mentioned above photorespiration is closely related to the processes of photosynthesis and respiration. The entire complex chain of interconnected processes of production and transformation of photosynthesis products is carried out by respiration. This process occupies a central place in the cellular metabolism of consumption, production and delivery of assimilates to organs. The photosynthesis rate of maize, a cold sensitive crop, is highly dependent on the temperature conditions (Wu et al., 2024). This is supported by our data on a significant decrease in chlorophyll pigments and the intensity of photosynthesis in maize seedlings grown from seeds imposed to frost stress (Cauș et al., 2024). Symptoms of impaired photosynthetic rate in maize plants due to exposure of seeds to low temperatures prior to germination were observed even in plants returned to optimum growth temperatures and maintained for 17 days (Cauș et al., 2024). There are evidence that cold-induced inhibition of photosynthesis plays an important role in limiting early growth in maize (Cauș et al., 2023). So, the respiratory capacity curves are probably related to photorespiration and photosynthetic activity of the leaf apparatus, restructuring its functioning. In Figure 3 are shown representative measurements of photorespiration, total and dark respiration on unfolded leaf 3 of 17-day-old plants (Figure 1) grown from freeze-treated seeds.

It can be seen that young corn plants germinated from seeds treated by freezing (-4°C for 16 hours) and, after returning to the optimal temperature of 26°C in the light for 17 days, showed lower respiration levels, compared to control plants. Frost stress applied to seeds before germination causes a decrease in the rate of total respiration as well as dark respiration of 17-day-old plants (Figure 3B, C). Dark respiration (also called mitochondrial respiration) is the controlled oxidation of reduced carbohydrates, producing $CO_2$, reducing equivalents (NAD(P)H and $FADH_2$), and resulting in respiratory $O_2$ consumption and ATP production (Siedow et al., 2000). Thus, on the third leaf of 17-day-old maize plants (Figure 3) it is evident that the characteristics of $CO_2$ gas exchange during photorespiration, respiration and dark respiration change in a similar way. But, as can be seen (Figure 3B, C), changes in the development of these physiological processes occur at a lower level during the observation period in the leaves of plants obtained from seeds subjected to frost stress, compared to the control.

In the process of photorespiration, the primary product is glycolic acid, and its further metabolization is associated with the glycolate pathway. The key enzyme of photorespiration is glycolate oxidase (GO). Glycolate oxidase (GO) plays an important role in plant photorespiration because it is the only enzyme that catalyzes the oxidation of glycolate to glyoxylate and hydrogen peroxide ($H_2O_2$) in peroxisomes. It is known from the literature (Chikov et al., 2019; Popov et al., 2003; Dmitrieva, 2005) that in C4 plants the key enzyme of photorespiration, GO, is found both in bundle sheath cells and, in the mesophyll cells. GO genes are involved in a wide variety of physiological processes in response to abiotic stresses (Dellero et al., 2016) and also strongly regulate photosynthesis, possibly through Rubisco activase inhibition by feedback mechanism (Xu et al., 2009).

To examine the consequences of the effect of exposing soaked maize seeds before germination to freezing stress temperature of 4°C for 16 hours on GO activity, germination and initial growth in the dark were examined with subsequent transfer of plants to light and the optimal temperature of 26°C (Figure 1). Specific GO activity was also determined to establish possible correlations between GO activity level and photorespiration. Representative results on changes in GO activity in maize plants grown from seeds subjected to freezing stress are shown in Figure 4.

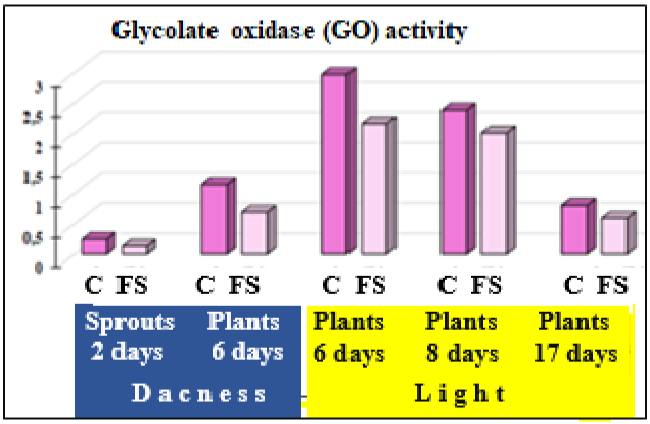


**Figure 4. Effect of freezing stress (FS) of – 4 °C for 16 h applied to the maize seeds before germination and the subsequent cultivation of plants from respective germinated seed in soil under controlled laboratory conditions on glycolate oxidase (GO) activity in leaves during the growth**

GO activity is present in both etiolated and green maize tissues. The results show that maize GO differs in the level of enzymatic activity in the leaves of control and experimental plants (Figure 4). It can be observed that the activity of GO increases, starting with etiolated sprouts and 6-day-old plants in the dark, reaching the highest value in the leaves of 6-day-old plants in the light, after which it begins to decrease in the leaves of 8- and 17-day-old plants. Similar results were obtained in studies with seedlings of C4 plants, such as maize, sorghum and amaranth, where it was shown that on the 6-7th day of greening, the growth of GO isoform activity in the studied plant species practically slows down (Iventyev et al., 2005). Also, GO activity in plants germinated from seeds treated by freezing is at a lower level than in controls (Figure 4). Freezing stress decreased GO activity in dark-grown sprouts by 47%, in leaves of 6-day-old plants grown in both dark and light by 39% and 27%, respectively, and in 8- and 17-day-old plants grown in light by 15% and 26%, respectively, compared to the respective controls. Can also be observed that GO in plants of the same age (6 days) is a light-activated enzyme, the maximum effect being observed in both the control and experimental leaves grown in the light (≈2, 6 and 3 times higher in the control and experimental variants, respectively), compared to those in the dark (Figure 4). Previous studies (Dmitrieva et al., 2005) have also demonstrated that GO in maize leaves is functionally active in both green and etiolated plants. And during the greening period, the activity of GO in maize leaves was noted to increase by 4.9 times.

Comparative analysis of the results on photorespiration intensity (Figure 3 A) and GO (Figure 4) demonstrates that there is a positive correlation between the activities of these two reactions in maize leaves under stress conditions. The data on the increase in GO activity in maize leaves, correlating with the intensity of photorespiration (Figure 3A), as well as with previous results on the content of chlorophyll pigments during the greening period of plants (Cauș et al., 2024), confirm the relationship of this enzyme with photorespiratory metabolism. Similar results were obtained in studies with C4 plants (Dmitrieva, 2005; Yventyev et al., 2005), which established a relationship between changes in the activity of GO isoforms and the dynamics of chlorophyll accumulation.

## CONCLUSION

Our results show that exposing of water – soaked maize seeds before germination to freezing stress temperature of -4°C for 16 hours subsequently weakened polyphenols accumulation and reduced flavonoids content during maize plant growth.

Freezing stress treatment applied to maize seeds before germination induces processes that decrease the level of plant photorespiration, total respiration, dark respiration, and glycolate oxidase (GO) activity in the leaves of 17-day-old maize plants.

GO from maize leaf cells was shown to be a light-activated enzyme. In both control plants and plants grown from seeds exposed to frost stress, of the same age, when transferred to light, GO activity was 2,6 and 3 times higher, respectively, than in plants grown in the dark.

Overall, the obtained data suggest that when soaked maize seeds are exposed to freezing stress of -4°C for 16 hours before germination, the cultivated plants subsequently show suppression of photorespiration, total respiration, dark respiration and glycolate oxidase (GO) activity, which, in this case, may apparently be associated with a slowdown in the intensity of photosynthetic gas exchange in general.

## ACKNOLEDGMENTS

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## REFERENCES

1. Agati G., Brunetti C., Di Ferdinando M., Ferrini F., Pollastri S., Tattini M. *Functional roles of flavonoids in photoprotection: New evidence, lessons from the past*. Plant Physiology and Biochemistry, 2013, 72: 35-45.
2. Baluar N., Badicean D., Peterhaensel C., Mereniuc L., Vorontsov V., Terteac D. *The peculiarities of carbon metabolism in the ears of C3 cereals $CO_2$ exchange kinetics, chloroplast's structure and ultrastructure in the cells from photosynthetic active components of the ear*. Journal of Tissue Culture and Bioengeering, 2018, 1: 1-14.
3. Bano S., Aslam M., Saleem M., Basra S., Aziz K. *Evaluation of maize accessions under low temperature stress at early growth stages*. The Journal of Animal and Plant Sciences, 2015, 25 (2): 392-400.
4. Cauș M., Dascaliuc A., Borozan P. *Effect of negative temperature shock on the primary resistance of maize hybrids*. Annals of the University of Craiova, Biology, Horticulture, Food products processing technology, Environmental engineering, 2023, 28 (64): 27-32.
5. Cauș M., Dascaliuc A., Borozan P. *Responses of seed germination and seedling growth of different maize hybrids to low positive temperature stress*. Annals of the University of Craiova, Biology, Horticulture, Food products processing technology, Environmental engineering, 2022, 27(63): 1453-1475.
6. Cauș M., Platovschii N. *Effects of hypothermic stress applied to seeds before germination on the parameters of the photosynthetic apparatus of maize plants*. Annals of the University of Craiova, Biology, Horticulture, Food products processing technology, Environmental engineering, 2024, 29(65): 128-133.
7. Chikov V.I., Akhtyamova G.A. *Photorespiration and its role in the regulation of photosynthesis and plant productivity*. American Journal Plant Sciences, 2019, 10: 2179-2202.

8. Cui L.-L., Lu Y., Li Y., Yang C., Peng X.-X. *Overexpression of glycolate oxidase confers improved photosynthesis under high light and high temperature in rice*. Frontiers in Plant Science, 2016, 7.
9. Dellero Y., Jossier M., Schmitz J., Maurino V.G., Hodges M. *Photorespiratory glycolate-glyoxylate metabolism*. Journal of Experimental Botany, 2016, 67 (10): 3041-3052.
10. Dmitrieva E.A. *Regulatory properties and physiological role of glycolate oxidase isoforms in maize leaves*. PhD Dissertation abstract. Voronezh, 2005, 162 p. RSL OD, 61: 05-3/1011.
11. Dusenge M.E., Duarte A.G., Way D.A. *Plant carbon metabolism and climate change: elevated $CO_2$ and temperature impacts on photosynthesis, photorespiration and respiration*. New Phytology, 2019, 221: 32-49.
12. Falcone Ferreyra M.L., Casas M.I., Questa J.I. Herrera A.L., Deblacio S., Wang J., Jackson D., Grotewold E., Casati P. *Evolution and expression of tandem duplicated maize flavonol synthase genes*. Frontiers in Plant Science, 2012, 3: 101.
13. Grzybowski M., Adamczy J., Jończyk M., Sobkowiak A., Szczepanik J., Frankiewicz K., Fronk J., Sowinski P. *Increased photosensitivity at early growth as a possible mechanism of maize adaptation to cold springs*. Journal of Experimental Botany, 2019, 70 (10): 2887-2904.
14. Hodges M., Dellero Y., Keech O., Betti M., Raghavendra A.S., Sage R., Zhu X.G., Allen D.K., Weber A.P.M. *Perspectives for a better understanding of the metabolic integration of photorespiration within a complex plant primary metabolism network*. Journal of Experimental Botany, 2016, 67: 3015-3026.
15. Hussain H.A., Men S., Hussain S. *Maize tolerance against drought and chilling stresses varied with root morphology and antioxidative defense system*. Plants, 2020, 9, 720.
16. Irshad M., Shreaz S., Manzoor N., Khan L.A., Moshahid M., Rizvi A. *Anticandidal activity of Cassia fistula and its effect on ergosterol biosynthesis*. Pharmaceutical Biology, 2011, 49, 7: 727-733.
17. Iventyev A.N., Popov V.N., Eprintsev A.T., Puzyrev A.B. *Physicochemical and properties of glycolate oxidase isoforms from C4 plants*. Proceedings of Voronezh State University. Series: Chemistry. Biology. Pharmacy, 2005, 1: 113-115.
18. Kangasjärvi S., Neukermans J., Li S., Aro E.M., Noctor G. *Photosynthesis, photorespiration, and light signalling in defense responses*. Journal of Experimental Botany, 2012, 63 (4): 1619-1636.
19. Kitashova A., Lehmann M., Schwenkert S., Munch M., Leister D., Nagele T. *Insights into physiological roles of flavonoids in plant cold acclimation*. The Plant Journal, 2024, 120: 2269-2285.
20. Kolesnikov P. A. *Koloremetricheskie metodi opredelenia aktivnosti oxidazi glikolevoi kisloti i reduktazi glioksalovoi kisloti*. Russian journal Biohimia, 1962, 27(2): 193-196.
21. Kumar V., Suman U., Rubal, Yadav S.K. *Flavonoid secondary metabolite: Biosynthesis and role in growth and development in plants*. In Recent Trends and Techniques in Plant Metabolic Engineering; Springer, 2018: 19-45.
22. Li B., Fan R., Sun G., Sun T., Fan Y., Bai S., Guo Y.S., Huang S., Liu J., Zhang H., Wang P., Zhu X., Song C.P. *Flavonoids improve drought tolerance of maize seedlings by regulating the homeostasis of reactive oxygen species*. Plant and Soil, 2021, 461 (4): 1-17.
23. Lu Y., Li Y., Yang Q., Zhang Z., Chen Y., Zhang S., Peng X.X. *Suppression of glycolate oxidase causes glyoxylate accumulation that inhibits photosynthesis through deactivating Rubisco in rice*. Physiologia Plantarum, 2013, 150: 463-476.
24. Ma Y., Tan R., Zhao J. *Chilling tolerance in maize: Insights into advances—toward physio-biochemical responses and QTL/Genes' Identification*. Plants, 2022, 11, 2082.
25. Meng A., Wen D., Zhang C. *Dynamic changes in seed germination under low-temperature stress in maize*. International Journal of Molecular Science, 2022, 23, 5495.
26. Ning D.L., Liu K.H., Liu C.C., Liu J.W., Qian C.R., Yu Y., Wang Y.F., Wang Y.C., Wang B.C. *Large-scale comparative phosphoprotein analysis of maize seedling leaves during greening*. Planta, 2016, 243 (2)Ș: 501-517.
27. Popov V.N., Dmitrieva E.A., Eprintsev A.T., Igamberdiev A.U. *Glycolate oxidase isoforms are distributed between the bundle sheath and mesophyll tissues of maize leaves*. Journal of Plant Physiology, 2003, 160, 8: 851-857.
28. Rao M.J., Zheng B. *The role of polyphenols in abiotic stress tolerance and their antioxidant properties to scavenge reactive oxygen species and free radicals*. Antioxidants, 2025, 14, 74.
29. Ray A., Kundu S., Mohapatra S.S., Sinha S., Khoshru B., Keswani C., Mitra D. *An insight into the role of phenolics in abiotic stress tolerance in plants: Current perspective for sustainable environment*. Journal of Pure and Applied Microbiology, 2024, 18 (1): 64-79.
30. Righini S., Rodriguez E.J., Berosich C., Grotewold E., Casati P., Falcone Ferreyra M.L. *Apigenin produced by maize flavone synthase I and II protects plants against UV-B-Induced damage*. Plant Cell and Environment, 2019, 42: 495-508.
31. Rius S.P., Emiliani J., Casati P.P. *Epigenetic regulation in leaves of high-altitude maize landraces: Effect of UV-B Radiation*. Frontiers in Plant Science, 2016, 7, 523.
32. Rojas C.M., Mysore K.S. *Glycolate oxidase is an alternative source for $H_2O_2$ production during plant defense responses and functions independently from NADPH oxidase*. Plant Signaling and Behavior, 2012, 7: 752-755.
33. Šamec D., Karalija E., Šola I. Vujcic Bok V., Salopek-Sondi B. *The role of polyphenols in abiotic stress response: The influence of molecular structure*. Plants, 2021, 10, 118.
34. Shomali A., Das S., Arif N., Sarraf M., Zahra N., Yadav V., Aliniaeifard S., Chauchan D.K., Hasanuzzaman M. *Diverse physiological roles of flavonoids in plant environmental stress responses and tolerance.* Plants, 2022, 11, 3158.
35. Siedow J.A., Day D.A. *Respiration and Photorespiration*. In B. B. Buchanan, W. Gruissem, & R. L. Jones (Eds.), *Biochemistry and Molecular Biology of Plants*; 1st ed., American Society of Plant Physiologists: Rockville, Md: USA, 2000, 30: 676-728.
36. Silva E.N., Silveira A.G., Ribeiro R.V., Vieira S.A. *Photoprotective function of energy dissipation by thermal processes and photorespiratory mechanisms in Jatropha curcas plants during different intensities of drought and after recovery*. Journal of Environmental and Experimental Botany, 2015, 110: 36-45.
37. Singleton V.L., Orthofer R., Lamuela-Raventos R.M. *Analysis of total phenols and other oxidation substrates and antioxidants by means of folin-ciocalteu reagent*. Methods in Enzymology, 1998, 299: 152-178.

38. Szymańska R., Ślesak I., Orzechowska A., Kruk J. *Physiological and biochemical responses to high light and temperature stress in plants.* Environmental and Experimental Botany, 2017, 139: 165-177.
39. Tian, X., Chen L., Sun L., Gong K., Liu K., Guo Y. *Omics analysis revealing flavonoid content during maize grain germination*. Metabolites, 2025, 15, 107.
40. Urban L., Aarrouf J., Bidel L.P.R. *Assessing the effects of water deficit on photosynthesis using parameters derived from measurements of leaf gas exchange and of chlorophyll a fluorescence*. Frontiers in Plant Science, 2017, 8: 2068.
41. Voss I., Sunil B., Scheibe R., Raghavendra A.S. *Emerging concept for the role of photorespiration as an important part of abiotic stress response*. Plant Biology, 2013, 15: 713-722.
42. Waqas M.A., Wang X., Zafar S.A., Noor M.A., Hussain H.A., Nawaz M.A., Farooq M. *Thermal stresses in maize: Effects and management strategies*. Plants, 2021, 10, 293.
43. Wijewardana C., Hock M., Henry B., Reddy K.R. *Screening corn hybrids for cold tolerance using morphological traits for early-season seeding*. Crop Science, 2015, 55: 851-867.
44. Woltz J., TeKrony D.M., Egli D.B. *Corn seed germination and vigor following freezing during seed developmen*t. Crop Science, 2006, 46: 1526-1535.
45. Wu A., Truong S.H., McCormick R. van Oosterom E.J., Messina C.D., Cooper M., Hammer G.L. *Contrasting leaf-scale photosynthetic low-light response and its temperature dependency are key to differences in crop-scale radiation use efficiency*. New Phytologist, 2024, 241, 6: 2435-2447.
46. Xu H., Zhang J., Zeng J., Jiang L., Liu E., Peng C., He Z., Peng X. *Inducible antisense suppression of glycolate oxidase reveals its strong regulation over photosynthesis in rice*. Journal of Experimental Botany, 2009, 60: 1799-1809.
47. Zelitch I., Schultes N.P., Peterson R.B., Brown P., Brutnell T.P. *High glycolate oxidase activity is required for survival of maize in normal air*. Plant Physiology, 2009, 149: 195-204.
48. Zhang Z., Zhu G., Peng X. *Photorespiration in plant adaptation to environmental changes*. Crop and Environment, 2024, 3: 203-212.
49. Zhou L., Ullah F., Zou J., Zeng X. *Molecular and physiological responses of plants that enhance cold tolerance*. International Journal of Molecular Science, 2025, 26, 1157.
50. Zhou X., Muhammad I., Lan H., Xia C. *Recent advances in the analysis of cold tolerance in maize*. Frontiers in Plant Science, 2022, 13, 866034.