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# Nocturnal Red Light Application Modulated the Fumonisin B1-Induced Changes in Glutathione Transferases of Different Wheat Cultivars

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## Abstract

Plant defense responses against *Fusarium* infection can be controlled by light. In this study, the effects of nocturnal red light were investigated on glutathione transferases (GSTs) in the leaves of the moderate- and high-*Fusarium* resistant wheat cultivars, GK Ígéret and GK Arató, respectively. GST activity increased in the light phase during the day, while it decreased after midnight. Since GST activity was lowest at midnight, we examined whether red light application at midnight could prevent the night-time drop in enzyme activity. We found that 15-min-long nocturnal red light application was effective to increase GST activity at dawn. The effects of red light pretreatments on GST expression and activity, as well as the oxidative stress induced by fumonisin B1 (FB1), were investigated. FB1 exposure increased GST activity and the expression of *GST* genes at dawn but nocturnal red light application in combination with the mycotoxin also increased GST activity and the transcript levels of the selected *GST*s in the resistant GK Arató. In addition to its effects on GSTs, it was discovered that, depending on the degree of tolerance, nocturnal red light increased the activity of the major antioxidant enzymes at dawn in both of the chosen wheat genotypes. These decreased FB1's oxidative stress-causing actions, resulting in lower lipid peroxidation and less cell viability loss when exposed to the mycotoxin. Pretreatment with nocturnal red light enhanced the activity of GST and antioxidant enzymes in wheat plant leaves, contributing to FB1 detoxification and reducing oxidative stress.

**Keywords** Antioxidant enzymes · Fumonisin B1 · Glutathione S-transferase · Red light · Toxin

## Introduction

Climate change and decreased water availability increase the risk of various infections spreading globally (Chakraborty et al., 2011; Magan et al., 2011). *Fusarium* species, such as *F. graminearum* and *F. oxysporum* are among the top five fungal pathogens threatening plant life and yield (Dean et al., 2012). *F. graminearum* infection mostly reduces grain quality and results in mycotoxin-contaminated cereals (Goswami and Kistler, 2004). Mycotoxins are produced by various *Fusarium* species, such as deoxynivalenol, zearalenone, or fumonisins, increase the pathogenicity of the fungi (Stępień et al., 2010). Among fumonisins, fumonisin B1 (FB1) has been identified as the most toxic compound, causing significant damage to various cereal crops and reducing yield (Deepa and Sreenivasa, 2019). *F. proliferatum*, *F. verticillioides*, and other species such as *F. oxysporum*, *F. nygamai*, and *F. fujikuroi* are the primary producers of FB1 (Cruz et al., 2013). FB1 is structurally similar to the sphingolipid intermediates sphinganine and sphingosine; thus, it inhibits the ceramide synthase activity disrupting sphingolipid metabolism and inducing cell death in both plants and animal cells (Yanagawa et al., 2017; Glenz et al., 2019). In plants, various phytohormones such as salicylic acid regulate FB1-induced cell death and/or defense mechanisms, which are highly dependent on the activation of detoxification processes and antioxidants (Iqbal et al., 2021). FB1 caused chronic and acute diseases in both animals and humans, and it is classified as a 2B group carcinogen by the International Agency for Research on Cancer (Stockmann-Juvala and Savolainen, 2008; Wild and Gong, 2010). The breeding of new resistant cultivars with a more effective detoxification system is critical to reducing the harmful effects of *Fusarium* species and their toxins (Bai and Shaner, 2004). In addition,

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another solution could be to develop and apply exogenous treatments that reduce fungal exposure and/or increase crop defense responses. As a result, new and innovative fungal disease management methods could improve plant protection and food safety.

Survivors of lethal FB1 treatment had significantly higher expression of glutathione transferase from the tau class and other genes that combat oxidative stress in the tomato root, according to previous observations (Harvey et al., 2008). GSTs are a diverse group of multifunctional enzymes that play an important role in the effective detoxification of xenobiotics through glutathione (GSH) conjugation and transportation to the vacuole (Nianiou-Obeidat et al., 2017). Plant GSTs are classified into 14 different classes in recent decades (Csiszár et al., 2014). As in other plant species, the phi (GSTF) and tau (GSTU) classes of GSTs are the largest groups in wheat, containing 38 and 26 *GST*-coding sequences, respectively, among the 98 members (Gallé et al., 2009). These two GST classes are characterized by the presence of a conserved Ser residue at their catalytic site and, if biologically active, by the formation of dimers (Nianiou-Obeidat et al., 2017). They are mostly involved in the detoxification of xenobiotics and the development of plant stress tolerance (Dixon and Edwards, 2010). Previously, it was discovered that expression of tau class GST genes, total GST activity, and GSH content are diurnally regulated in tomatoes, reaching a maximum at the end of the light period before decreasing in the dark (Gallé et al., 2018). These data indicate that light regulates GSTs in plants. Tepperman et al. (2001) discovered that a *GST* (AAD32887) from the tau group was transcriptionally activated rapidly when exposed to red light, but it was inhibited in phytochrome A (PHYA) mutants. Later, it was confirmed that another tau member of GST, AtGSTU20 interacts with FR-insensitive 219 (FIN219), implying that it is involved in the PHYA-mediated signaling network (Chen et al., 2007; 2017). In addition, *AtGSTU17* expression also depended strictly on PHYA (Jiang et al., 2010). Thus, it can be concluded that red light signaling is part of GST regulation and GST activity is dependent on the day/night time.

For many phytopathogens, such as *Fusarium* species, night-time darkness is a more favorable environmental condition than daytime light. Light can inhibit fungal metabolism, hyphal development, sexual reproduction, sporulation, and fungi virulence (Yu and Fischer, 2019). It was found that light decreased the amount of germinated macroconidia of *F. graminearum* (Beyer et al., 2004) and the biomass production of *F. verticillioides* (Velmurugan et al., 2010). At the same time, light has a positive effect on plant defense responses (Santamaría-Hernando et al., 2018). It was reported that red light, especially at night, can promote plant defense mechanisms against various phytopathogens (Gallé et al., 2021). Pretreatment with red light for 12 and 24 h reduced the wilt disease caused by *F. udum* in pigeon pea (*Cajanus cajan*) seedlings (Bansod et al., 2017). In the case of another fungus, the application of red light reduced the development of lesions by *Botrytis cinerea* and enhanced the accumulation of the antimicrobial compounds, as well as upregulating antioxidant defense-related and *GST* genes in grapevine (*Vitis vinifera*) leaves (Ahn et al., 2015). These findings suggest that red light treatment at night could be effective against fungal pathogens by enhancing the components of the antioxidant and detoxification systems such as GSTs.

The other aims of the experiments were to reveal the effects of nocturnal red light pretreatments on GSTs in the leaves of *Fusarium*-sensitive and resistant wheat cultivars. Our experiments were focused on whether nocturnal red light treatments could increase the expression of selected GST genes, the activity of GSTs, as well as the activity of key antioxidant enzymes, resulting in a more effective defense against FB1 toxin. Based on the analysis of GST enzymatic activity in the leaves, the effects of circadian rhythm and the optimal duration of red light exposure on GSTs were also investigated.

## Materials and Methods

### Plant Materials And Growth Conditions

Healthy grains of two wheat (*Triticum aestivum*) cultivars, *Triticum aestivum* cv. GK Ígéret, which is moderately resistant to *Fusarium*, and the highly resistant cv. GK Arató (Cereal Research Non-Profit Ltd., Szeged, Hungary) were germinated for 24 h in the dark at 27 °C. Fifteen healthy seedlings were placed in a pot containing modified Hoagland nutrient solution, as described earlier by Poór et al (2011), and they were grown for 10 d in a controlled environment: 200 µmol $m^{-2}$ $s^{-1}$ photosynthetic photon flux density (PSI, Drásov, Czech Republic), 12/12-h light/dark period (light phase starting from 06:00 until 18:00 h and 12 h dark period during the remaining daytime), 24/22 °C day/night temperatures, and 55%–60% relative humidity (Czékus et al., 2021). The nutrient solution was changed three times per week. The experiments were conducted on intact plants that were 10 d old.

### Treatments

Red light treatments were applied from the middle of the dark cycle at night with LEDs (V-TAC; Plovdiv; Bulgaria; 50 mW $m^{-2}$; 590–660 nm interval with a maximum at 630 nm) using a timer.

After pretreatments with red light, shoots were sprayed to runoff with 100 µM Fumonisin B1 (FB1) at 21:00

p.m. in the dark on the fourth day. FB1 with 100% purity (HPLC/ESI–MS) was obtained from Fumizol Ltd. (Szeged, Hungary). As a control treatment, double-distilled water was used. In three biological replications, the effects of FB1 were observed and analyzed 3 d after the treatments.

## Determination of the Activity of GST

Leaf tissue of wheat cultivars (250 mg) was homogenized with 1 mL of ice-cold extraction buffer (100 mM phosphate buffer [pH 7.0]; 1 mM phenylmethylsulfonyl fluoride, and 1% [w:v] polyvinyl-polyvinylpolypyrrolidone) and then centrifuged (12,000 × *g* for 20 min at 4 °C). This supernatant was used for the detection of GST as well as other antioxidant enzyme activity assays (Czékus et al., 2020).

As substrates, 1-chloro-2,4-dinitrobenzene and reduced glutathione (GSH) were used to measure GST activity. After adding 1-chloro-2,4-dinitrobenzene CDNB to the mixture, the absorbance increased for 3 min (KONTRON, Milano, Italy). One unit of GST corresponds to the amount of enzyme required to produce1 µmol conjugated product in 1 min (Gallé et al., 2009). The enzymatic activity was expressed as nkat $mg^{-1}$ protein. The protein content of each sample was determined using the Bradford (1976) method and a standard of bovine serum albumin. Sigma-Aldrich supplied all of the chemicals (St. Louis, MO, USA).

## RNA Extraction, cDNA Synthesis, and Expression Analysis by Quantitative Real-Time PCR

The Quick-RNA Miniprep Kit (Zymo Research, Irvine, USA) was used to extract total RNA from wheat leaves. Following the digestion of the genomic DNA by DNase I (Thermo Scientific, Waltham, MA, USA), samples were cleaned and concentrated using RNA Clean Concentrator-25 Kit (Zymo Research, Irvine, USA). cDNA synthesis was performed by MMLV reverse transcriptase (Thermo Scientific, Waltham, MA, USA). According to Czékus et al (2021), the transcript accumulation of the examined GST genes in wheat (Table 1) was determined via quantitative real-time reverse transcription-PCR (qRT-PCR; qTOWER Real-Time qPCR System, Analytik Jena, Jena, Germany). The qRT-PCR reaction was made up of 4.5 µL diluted (20X) cDNA template, 0.25 µL forward and 0.25 µL reverse primers of GSTs, and 5 µL of Maxima SYBR Green qPCR Master Mix (2X) (Thermo Scientific, Waltham, MA, USA) in double-distilled water at a final volume of 10 µL. After the initial denaturation step (7 min, 95 °C), the qRT-PCR program was assembled (7 min, 95 °C) by 40 repetitive cycles containing a denaturation step for 15 s at 95 °C followed by an annealing extension for 60 s at 60 °C. For data analysis, qTOWER Software 2.2 (Analytik Jena, Jena, Germany) was used. As a reference, elongation factor-1α and ribosomal

**Table 1** Primer pairs used for qRT-PCR

| Wheat genes | Genome locus identifier | Primer pair sequences (5′ – 3′) |
|---|---|---|
| *TaGSTU1A* | AJ414697 | F: 5′-GTGGTTGGTGGTTGTTGGTT-3′ |
| | | R: 5′-ATGGAAATGGAATGGCAG GT-3′ |
| *TaGSTU1B* | AJ414698 | F: 5′-CGGAGGGAAGGAACAAAT AA-3′ |
| | | R: 5′-CACTGACTGACCCAACCAAC-3′ |
| *TaGSTU2* | AJ414700 | F: 5′-CCGTGCTCGCTTGGAT-3′ |
| | | R: 5′-CGGACTCAGACACACACA AACA-3′ |
| *TaGSTU3* | AJ414701 | F: 5′-CCGCCTATGTGAACGACAA-3′ |
| | | R: 5′-GGGTCTCCTCCATCTTACCG-3′ |
| *TaGSTF3* | AJ440792 | F: 5′-CAAGAAGGTGCTGGAGGT GT-3′ |
| | | R: 5′-AAGGGGAAGTGGCTGAGGT-3′ |
| *TaGSTF6* | AJ441055 | F: 5′-CAAGAAGCCGTGATTTGCTA-3′ |
| | | R: 5′-GCGACACCAACAAGAAAA GA-3′ |
| *TaEF* | KX533924 | F: 5′-CCAAGACGAAGCAGAACA GA-3′ |
| | | R: 5′-ACACATCCAACGCAAGAGAa-3′ |
| *Ta18S* | AY049040 | F: 5′-GTGACGGGTGACGGAGAATT-3′ |
| | | R: 5′-GACACTAATGCGCCCGGTAT-3′ |

18S genes were used and the relative transcript accumulation was expressed by the $2^{(-\Delta\Delta Ct)}$ formula (Livak and Schmittgen, 2001).

### Determination of the Activity of Key Antioxidant Enzymes

To determine the activities of key antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and guaiacol-dependent peroxidase (POX), leaf samples were homogenized in the same way and with the same extraction buffer as described for the determination of GST activity (Horváth et al., 2015).

All enzymatic activities were determined by spectrophotometer (KONTRON, Milano, Italy) using the same supernatant. SOD (EC 1.15.1.1) activity was measured by determining the ability of the enzyme to inhibit the photochemical reduction of nitro blue tetrazolium (NBT) in the presence of riboflavin in the light (Beauchamp and Fridovich, 1971). One unit (U) is the amount of SOD required to inhibit NBT reduction by 50% when exposed to light. CAT activity (EC 1.11.1.6) was determined by measuring the consumption of $H_2O_2$ at 240 nm for 3 min at 25 °C ($\varepsilon_{240} = 39.4\ mM^{-1}\ cm^{-1}$) (Aebi, 1984). One unit of CAT activity means the amount of enzyme needed to decompose 1 µmol $min^{-1}$ $H_2O_2$. POX (EC 1.11.1.7) activity was measured following the increase of absorbance at 470 nm due to guaiacol oxidation ($\varepsilon_{470} = 26.6\ mM^{-1}\ cm^{-1}$) (Upadhyaya et al., 1985). The amount of enzyme producing 1 µmol $min^{-1}$ of oxidized guaiacol was defined as one U.

The concentration of soluble protein in samples was determined using the Bradford (1976) method with bovine serum albumin BSA as a standard. All required chemicals were purchased from Sigma-Aldrich (St. Louis, MO, USA).

### Determination of Glutathione Content

Two hundred and fifty mg of wheat leaves were homogenised with 1 mL of 5% (w/v) ice-cold trichloroacetic acid. Glutathione concentration was detected after centrifugation of the samples (12,000 × g, 20 min, 4 °C) using the supernatant, 100 mM phosphate buffer (pH 7.5), 1 mM 5,5′-dithiobis(2-nitrobenzoic acid) (DTNB), 1 mM NADPH, 1 U of glutathione reductase in the enzymatic assay. Samples were measured by spectrophotometer (KONTRON, Milano, Italy) at 412 nm (Griffith, 1980). All chemicals were purchased from Sigma-Aldrich (St. Louis, MO, USA).

### Determination of Malondialdehyde Content

One hundred mg of wheat plant leaf samples were homogenized with 1 mL of 0.1% trichloroacetic acid. Before the centrifugation (12,000 × *g*, 20 min, 4 °C), 0.1 mL of 4% butylated hydroxytoluene was added to the samples; 0.5 mL of supernatant was added to 2 mL of 0.5% thiobarbituric acid dissolved in 20% trichloroacetic acid and incubated for 30 min in boiling water. A spectrophotometer (KONTRON, Milano, Italy) was used to measure the absorbance of the samples at 532 nm and 600 nm. The extinction coefficient of 155 $mM^{-1}\ cm^{-1}$ was used to calculate the malondialdehyde content (Ederli et al., 1997). All required chemicals were obtained from Sigma-Aldrich (St. Louis, MO, USA).

### Determination of Cell Viability

According to Sun et al (2010), electrolyte leakage (EL) was measured as an indicator of cell viability. In 20 mL of double-distilled water, 100 mg of leaf samples were added and incubated for 2 h in the dark at room temperature. The electrical conductivity (C1) was then measured, and the samples were heated for 30 min at 100 °C. After cooling, the conductivity of the heated samples was measured as C2 using a conductivity meter (Mettler Toledo, Columbus, USA). The percentage of EL was calculated using the following formula: $EL\ [\%] = (C1/C2) \times 100$.

### Statistical Analysis

Each experiment includes at least three biological replicates (at least three plants per treatment), and the entire experiment was repeated three times. The results are presented as mean ± SE. Statistical analysis was accomplished using Sigma plot 11.0 software (SPSS Science Software, Erkrath, Germany). The differences between the treatments in the case of each plant cultivar were statistically analyzed by one-way ANOVA using Duncan's multiple range test. If $P \leq 0.05$, the means of each treatment were significantly different.

## Results

First, the GST activity was determined as a function of time for 24 h in the two selected wheat genotypes, in the *Fusarium* resistant GK Arató and the moderately resistant GK Ígéret. According to the data, GST enzyme activity was regulated by the circadian rhythm, increasing during the light period and peaking at the start of the dark period at 21:00. Then it decreased until midnight before the next light period started (Fig. 1). The GST enzyme activity showed more significant changes and higher levels in the light period in the resistant GK Arató cultivar as compared to GK Ígéret (Fig. 1). The circadian changes in the less resistant genotype were also much more moderate. At the same time, at 3:00 a.m., the lowest level of GST enzyme activity was observed (Fig. 1).

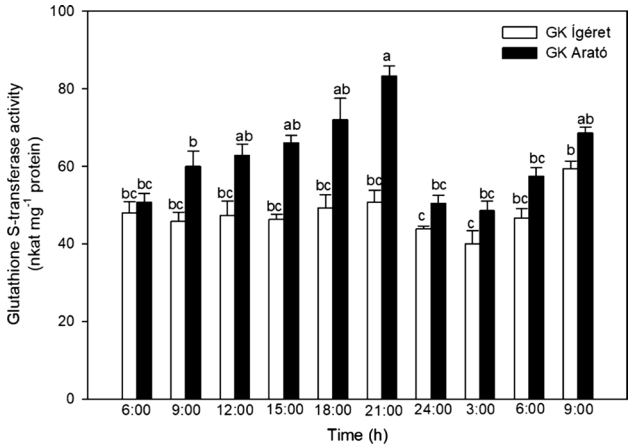


**Fig. 1** Changes in glutathione *S*-transferase enzyme (GST) activity during the day in the leaves of GK Ígéret (white columns) and GK Arató (black columns) wheat cultivars (Mean ± SE, $n = 9$). Bars denoted by different letters are significantly different at $P \leq 0.05$ as determined by Duncan's multiple comparison

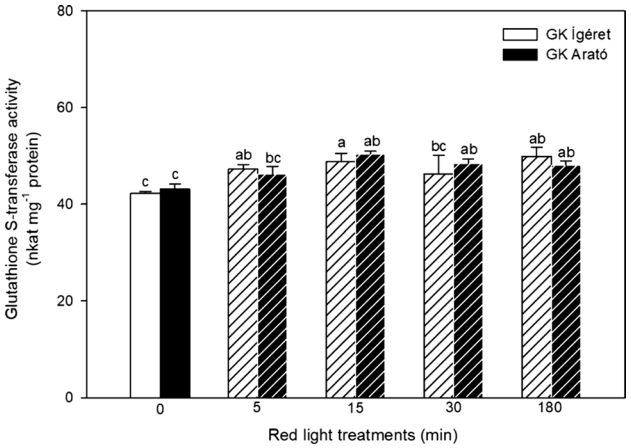


**Fig. 2** Changes in glutathione *S*-transferase enzyme (GST) activity after various long red light treatments at midnight (patterned columns) and measured at dawn (3:00 a.m.) in the leaves of GK Ígéret (white columns) and GK Arató (black columns) wheat cultivars (Mean ± SE, $n = 9$). Bars denoted by different letters are significantly different at $P \leq 0.05$ as determined by Duncan's multiple comparison

Since GST activity decreased from midnight until 3:00 a.m., we aimed to investigate whether FB1 or red light exposure can increase the enzyme activity in the leaves of the selected cultivars at dawn. Based on these results, the experiments were conducted in the middle of the night (near midnight).

The length of red light illumination, which is necessary to increase the GST enzyme activity at dawn (3:00 a.m.) was examined first in the two selected wheat cultivars. During the experiments, four-time intervals were used, with the length of illumination varying between 5, 15, 30, and 180 min. Enzyme activity measurements were carried out for 3 following the illumination. Based on these results, 5-min-long red light exposure at midnight was insufficient to significantly change GST enzyme activity in the moderately resistant GK Ígéret measured at 3:00 a.m., but it was effective in GK Arató (Fig. 2). After 15-min-long red light treatments at midnight, GST activity significantly increased in both wheat cultivars at 3:00 a.m. (Fig. 2). Similar changes were observed after the 30-and 180-min-long red light illumination as in the case of the 15-min treatment compared to the untreated controls in the dark (Fig. 2).

Our results showed that the 15-min-long treatment with red light proved to be the shortest and most effective to increase GST activity at dawn (3:00 a.m.); this time interval was used in the next experiments. It was also found that the 15-min-long nocturnal red light exposure for 3 d proved to be the shortest effective time interval but the effectiveness of treatments lasted until 1 wk. As a result, GST enzyme activity was elevated by 15-min-long red light exposure at 3:00 a.m. in both wheat cultivars (Fig. 3). The 3- and 4-day-long application of this red light treatment resulted in the highest GST enzyme activity in the less tolerant GK Ígéret while the 4- and 7-day-long red light application was the most effective in GK Arató (Fig. 3).

Thus, we chose a 4-day-long red light pretreatment before the FB1 exposure, and plants were illuminated for 15 min with the nocturnal red light during the 3-day-long mycotoxin exposure, too. Accordingly, sampling was carried out after 1 week of nocturnal red light and after 3 days of 100 µM FB1 treatments. Based on our results, it can be concluded that this red light exposure significantly increased the GST activity in both wheat cultivars in the dark cycle (Fig. 4).

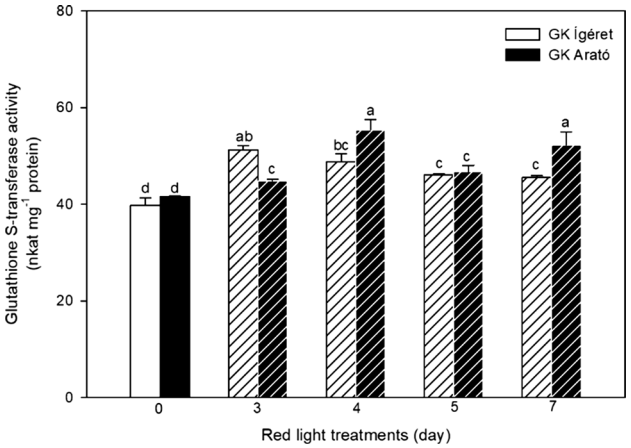


**Fig. 3** Changes in glutathione *S*-transferase enzyme (GST) activity after 15-min-long red light treatments at midnight (patterned columns) for several days and measured at dawn (3:00 a.m.) in the leaves of GK Ígéret (white columns) and GK Arató (black columns) wheat cultivars (Mean ± SE, $n = 9$). Bars denoted by different letters are significantly different at $P \leq 0.05$ as determined by Duncan's multiple comparison

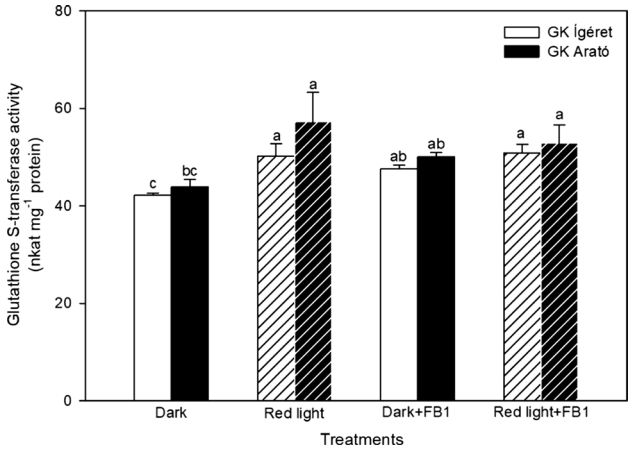


**Fig. 4** Changes in glutathione *S*-transferase enzyme (GST) activity after 15-min-long red light treatments at midnight (patterned columns) for 7 days and after 3-d-long 100 µM Fumonisin B1 (FB1) exposure on the fourth day of the nocturnal red light application (sprayed at 21:00 p.m.) in the leaves of GK Ígéret (white columns) and GK Arató (black columns) wheat cultivars. Measurements were carried out at 3:00 a.m. at dawn (Mean ± SE, $n = 9$). Bars denoted by different letters are significantly different at $P \leq 0.05$ as determined by Duncan's multiple comparison

As was expected, FB1 treatments also resulted in significantly higher GST activities compared to untreated control in both wheat cultivars at dawn (Fig. 4). However, the red light application before and during the FB1 exposure did not induce an additional increase in the enzyme activity compared to the FB1-treated plants (Fig. 4).

In the next step, we analyzed the expression of 6 selected (4 tau and 2 phi) wheat *GST* genes after the nocturnal red light treatments and the FB1 exposure. One week of 15-min-long red light treatment at midnight increased the expression of all *GST* genes in both wheat genotypes significantly (Fig. 5). At the same time, red light significantly increased the expression of *TaGSTU1B*, *TaGSTU2*, and *TaGSTF6* in the less tolerant GK Ígéret as compared to GK Arató (Fig. 5). FB1 exposure also elevated the expression of all *GST*s in both wheat cultivars under darkness, which was significantly higher in GK Ígéret as compared to GK Arató with one exception, *TaGSTU3* (Fig. 5B). In both wheat genotypes, the combined effect of nocturnal red light and FB1 caused significantly higher transcript accumulation of all GSTs as compared to untreated control(Fig. 5); however, the expression of *TaGSTU2*, *TaGSTU3*, *TaGSTF3*, and *TaGSTF6* significantly decreased under the combined effect of nocturnal red light and FB1 in GK Ígéret as compared to the FB1 treatments (Fig. 5). Similar changes were observed in the case of *TaGSTU3* and *TaGSTF6* in GK Arató (Fig. 5B, F). At the same time, nocturnal red light application and FB1 treatments increased the expression of *TaGSTU1A*, *TaGSTU1B*, and *TaGSTU2* increased upon the nocturnal red light application and FB1 treatments in the more resistant cultivar, GK Arató as compared to the FB1 treatments (Fig. 5A, C, E).

In addition to GSTs, the nonspecific effect of red light on plants was further investigated by the analysis of the changes in the activity of the key antioxidant enzymes. Firstly, the activity of SOD, which catalyzes the reduction of superoxide to hydrogen peroxide, was measured in the wheat cultivars' leaves. It was found that nocturnal red light significantly elevated SOD enzyme activity in both wheat genotypes at dawn (Fig. 6A). The highest activities in SOD were measured upon FB1 treatments, especially in the case of GK Ígéret, which was reduced by the nocturnal red light application in combination with FB1 in both genotypes, especially in GK Ígéret (Fig. 6A).

The activity of CAT was the highest after red light, especially in GK ígéret as compared to the control (Fig. 6B). Interestingly, FB1 did not influence CAT activity significantly in the wheat genotypes at dawn, but nocturnal red light elevated the activity of CAT under the FB1 exposure as compared to the control in both genotypes (Fig. 6B).

POX enzyme activity increased significantly, as did CAT and SOD activity when the nocturnal red light was applied at dawn (Fig. 6C). However, treatments with FB1 induced a significant increase in POX activity in GK Ígéret, but no changes in POX activity were observed in GK Arató after FB1 exposure (Fig. 6C). At the same time, the combined treatments with nocturnal red light and FB1 resulted in significantly higher POX enzyme activity compared to the dark controls and FB1, especially in the case of GK Arató (Fig. 6C). It can be concluded that high SOD activities after FB1 treatment can generate a higher amount of $H_2O_2$ in leaf tissues and red light exposure can reduce it by increasing the activities of $H_2O_2$ destructing enzymes CAT and POX.

The GSH content was the highest after FB1 exposure, especially in GK Ígéret as compared to the control (Fig. 7). Interestingly, red light did not influence GSH levels significantly in the selected wheat genotypes at dawn, but nocturnal red light elevated it under the FB1 exposure as compared to the control in GK Ígéret (Fig. 7).

The effects of FB1-induced oxidative stress on lipids were determined based on the measurements of MDA content in the leaves of the selected wheat genotypes. MDA content significantly increased after FB1 treatment, which was alleviated by the application of nocturnal red light in both wheat cultivars. Nocturnal red light treatments alone did not change significantly or decreased the MDA content (Fig. 8A).

Cell viability measured by EL from the leaves of both wheat genotypes increased significantly after FB1 exposure compared to the control but did not change significantly after nocturnal red light application alone or in combination with FB1 (Fig. 8B).

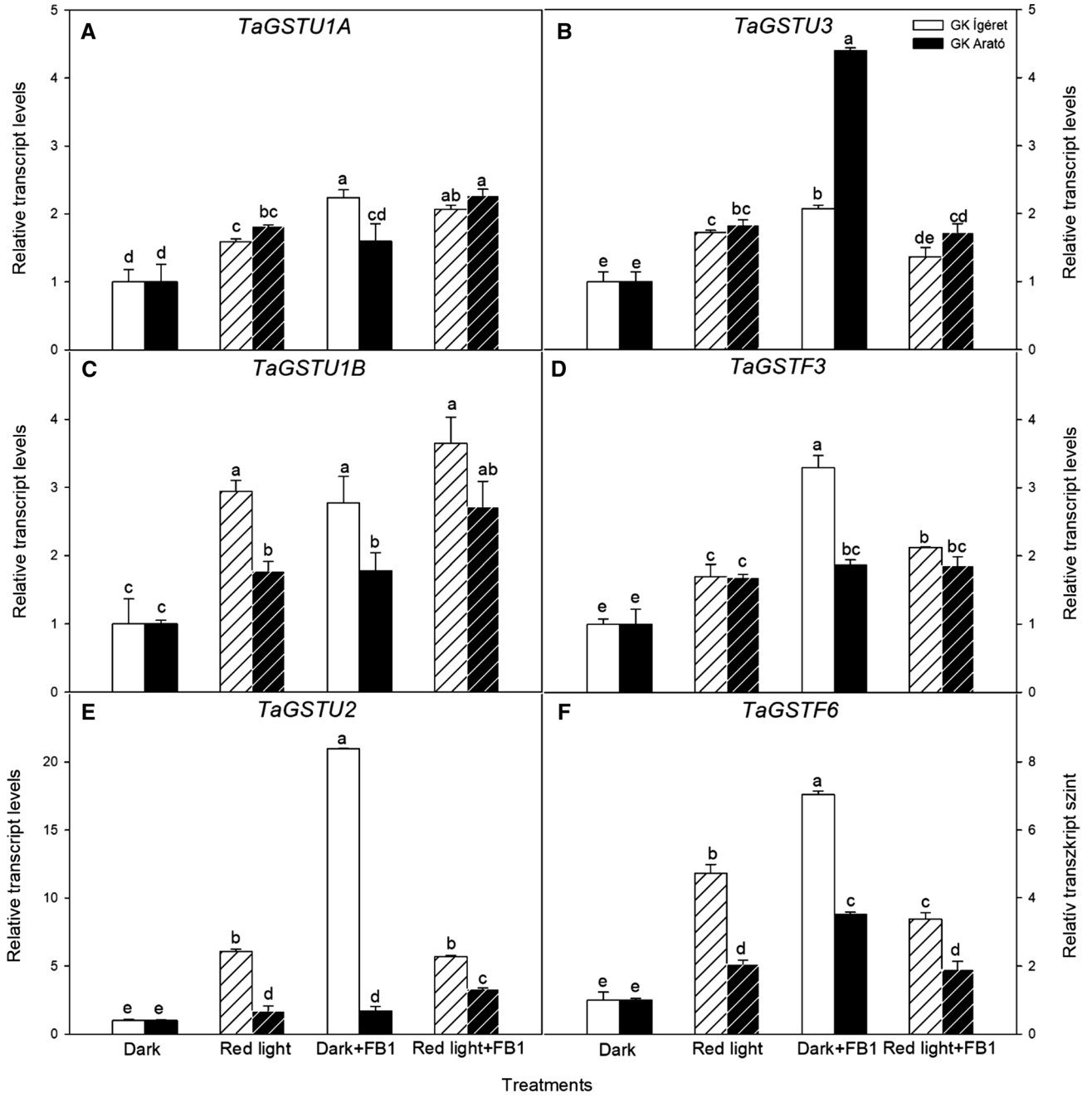


**Fig. 5** Changes in expression of selected glutathione *S*-transferase (GST)-coding genes (*TaGSTU1A,* **A***; TaGSTU3,* **B***; TaGSTU1B,* **C***; TaGSTF3,* **D***; TaGSTU2,* **E***; TaGSTUF6,* **F**) after 15-min-long red light treatments at midnight (patterned columns) for 7 days and after 3-d-long 100 µM Fumonisin B1 (FB1) exposure at the fourth days of the nocturnal red light application (sprayed at 21:00 p.m.) in the leaves of GK Ígéret (white columns) and GK Arató (black columns) wheat cultivars. Measurements were carried out at 3:00 a.m. at dawn (Mean ± SE, $n = 9$). Bars denoted by different letters are significantly different at $P \leq 0.05$ as determined by Duncan's multiple comparison

## Discussion

*Fusarium*-induced diseases resulted in a c.a. USD 2 billion loss in the United States in the period 1993–2001 (Xia et al., 2020). Therefore, the optimization of the fungicide application and the development of alternative methods for plant protection are the key questions in the agriculture and food industry (Shah et al., 2018; Paul et al., 2019). Results of basic and applied sciences can help this effort and provide new information, methods, and tools for practical purposes.

The regulation by the circadian clock provides the daily adaptation and optimization of physiological processes

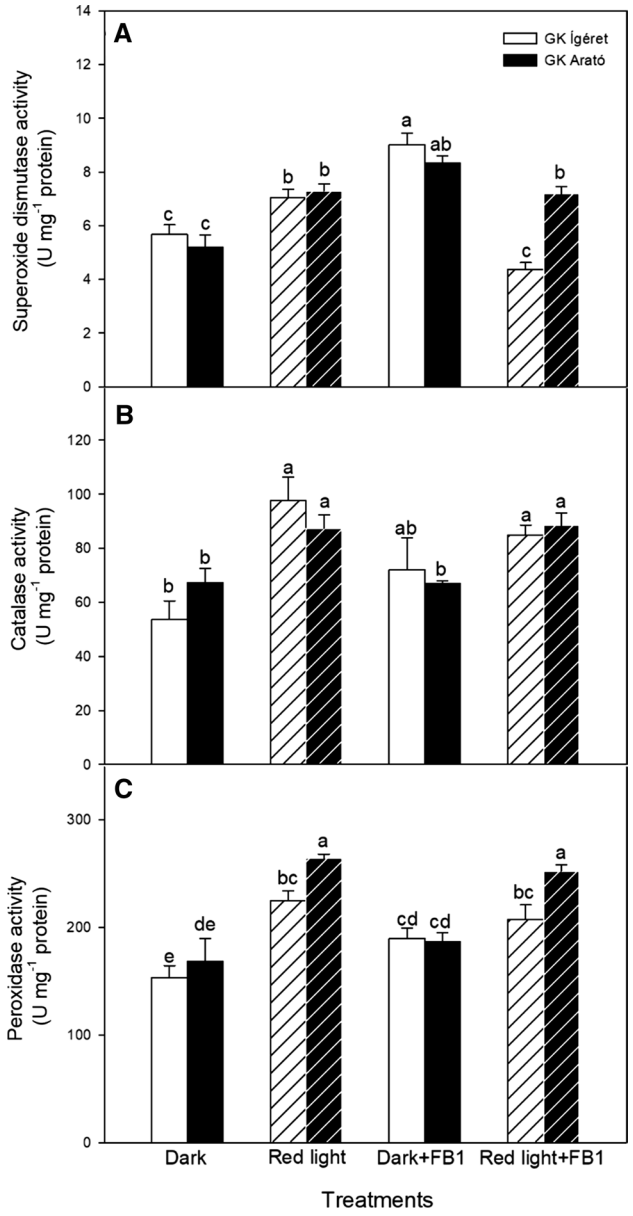


**Fig. 6** Changes in the activity of superoxide dismutase (SOD; **A**), catalase (CAT; **B**), and guaiacol-dependent peroxidase (POX; **C**) after 15-min-long red light treatments at midnight (patterned columns) for 7 days and after 3-d-long 100 µM Fumonisin B1 (FB1) exposure at the fourth days of the nocturnal red light application (sprayed at 21:00 p.m.) in the leaves of GK Ígéret (white columns) and GK Arató (black columns) wheat cultivars. Measurements were carried out at 3:00 a.m. at dawn (Mean ± SE, $n = 9$). Bars denoted by different letters are significantly different at $P \leq 0.05$ as determined by Duncan's multiple comparison

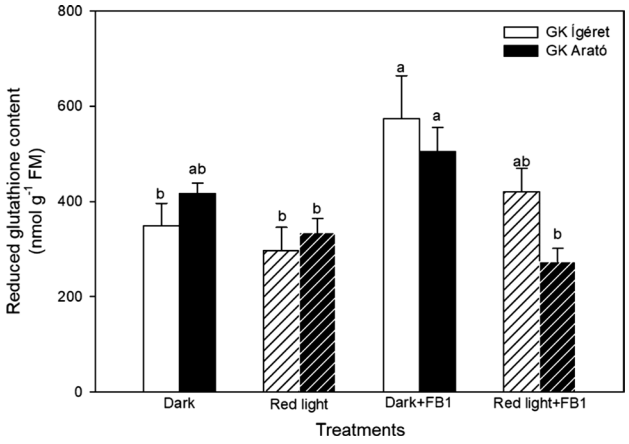


**Fig. 7** Changes in the reduced glutathione (GSH) content after 15-min-long red light treatments at midnight (patterned columns) for 7 days and after 3-d-long 100 µM Fumonisin B1 (FB1) exposure at the fourth days of the nocturnal red light application (sprayed at 21:00 p.m.) in the leaves of GK Ígéret (white columns) and GK Arató (black columns) wheat cultivars. Measurements were carried out at 3:00 a.m. at dawn (Mean + SE, $n = 9$). Bars denoted by different letters are significantly different at $P \leq 0.05$ as determined by Duncan's multiple comparisons

and the metabolism of plants to environmental changes. The endogenous circadian clock is adjusted to the actual environmental factors such as temperature (Greenham and McClung, 2015) or light conditions, the latter is mediated by photoreceptors, especially by phytochromes (red and far-red light receptors), and cryptochromes (blue light receptors).

First, we investigated the circadian effects on GST activity in two selected wheat genotypes: *Fusarium*-sensitive (GK Ígéret) and a resistant (GK Arató) cultivar to determine the most optimal night time to influence GST activity by a *Fusarium* mycotoxin, FB1. We found that GST enzyme activity increased in the light phase during the day by the regulation of the circadian clock, while it decreased in the late dark phase, especially at dawn (3:00 a.m.). Interestingly, GST enzyme activity in the *Fusarium* resistant GK Arató showed more significant changes and higher levels in the light period when compared to GK Ígéret. Similar results were observed in tobacco (Alderete et al., 2018) and tomato leaves (Gallé et al., 2018), where GST activity and expression levels of selected *GST* genes reached the maximum at the beginning of the dark period and their levels decreased at dawn.

The FB1-induced changes in the expression of 4 tau group (*TaGSTU1A*, *TaGSTU1B*, *TaGSTU2*, *TaGSTU3*) and 2 phi group (*TaGSTF3* and *TaGSTF6*) GST genes were examined at dawn. We found that the FB1 treatment increased the expression of all *GST* genes in both wheat genotypes in a genotype-dependent manner compared to untreated controls. Apart from the *TaGSTU3,* the transcript levels of other genes were significantly higher in the sensitive genotype, indicating that the response to FB1 in this cultivar was dependent on the de novo expression of the GST isoenzyme. Based on other results, members of the tau class of GSTs play an important role in plant acclimation to mycotoxins (Harvey et al., 2008), pathogens (Dean et al., 2005), herbicides (Thom et al., 2002), xenobiotics (Brazier-Hicks et al.,

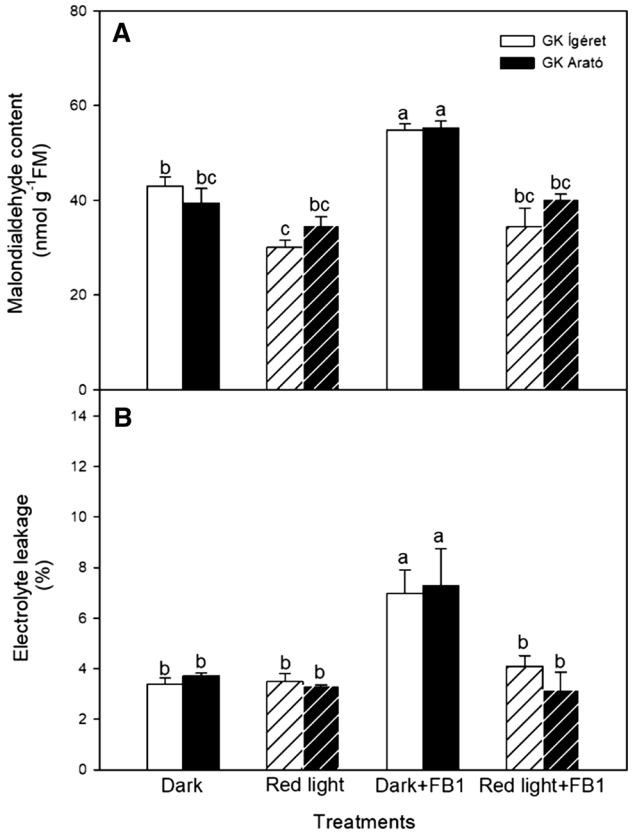


**Fig. 8** Changes in the malondialdehyde (MDA) content (**A**) and electrolyte leakage (**B**) after 15-min-long red light treatments at midnight (patterned columns) for 7 days and after 3-d-long 100 µM Fumonisin B1 (FB1) exposure at the fourth days of the nocturnal red light application (sprayed at 21:00 p.m.) in the leaves of GK Ígéret (white columns) and GK Arató (black columns) wheat cultivars. Measurements were carried out at 3:00 a.m. at dawn (Mean ± SE, $n = 9$). Bars denoted by different letters are significantly different at $P \leq 0.05$ as determined by Duncan's multiple comparison

2018), oxidative stress (Wagner et al., 2002), and other abiotic stressors (Cicero et al., 2015). Moreover, changes in the expression of tau class GSTs correspond to changes in GST activity (Thom et al., 2002). At the same time, members of the phi group were reported to participate mostly in the case of abiotic stressors (Nianiou-Obeidat et al., 2017).

It is well known that the expression of several members of tau class GSTs are phytochrome mediated and inducible by red light (Tepperman et al., 2001; Chen et al., 2007; 2017; Jiang et al., 2010). Wang et al (2019) collected the 5' cis regulating elements of all known wheat GSTs. Based on this research, there are several light-responsive elements in the promoter region of all examined *GSTs* (*TaGSTF3*, *TaGSTF6*, *TaGSTU1A*, *TaGSTU1B*, *TaGSTU2*, *TaGSTU3*; 4, 10, 12, 8, 19, 19), which further confirms the role of light in the regulation of plant GSTs.

While plant GSTs were part of the PHYA-mediated signaling network (Chen et al., 2007, 2017; Jiang et al., 2010), it was observed that the application of artificial red light by LEDs can influence GST enzyme activity and enhance the defense mechanism of plants, especially in the dark period when most of the plant pathogens, such as *Fusarium* species are most active (Yu and Fischer, 2019).

It was found that the application of nocturnal red light was effective in enhancing resistance against *Pseudomonas syringae* in tomatoes by elevating the expression of the biosynthetic genes of defense-related phytohormones such as salicylic acid and jasmonic acid (Yang et al., 2015). In addition, the beneficial effects of red light illumination in the defense against fungal pathogens were also reported. Red light regulated the metabolism of the reactive oxygen species by increasing the activity of SOD, CAT, and POX under *B. cinerea* infection, and in parallel, it decreased the oxidative stress in the leaves of tomatoes (Hu et al., 2017). Furthermore, red light elevated the accumulation of antimicrobial trans-piceid in grapevine (Ahn et al., 2015) and induced the accumulation of disease inhibitor polyphenols and flavonoids in strawberry leaves (Meng et al., 2019) under *B. cinerea* infection. At the same time, knowledge about the effects of red light on the detoxification of fungal toxins is scarce. Although there are some data about the induction of GST expression in grapevine after red light treatment (Ahn et al., 2015), extensive research has not been performed concerning the effects of red light on plant GSTs.

Based on our results, the red light exposure was performed at midnight (the middle of the dark period, 6 h after the end of the light cycle). First, the length of the red light illumination, which is necessary to increase GST enzyme activity at dawn (3:00 a.m.), was investigated. Finally, the 15-min-long red light treatment proved to be the most efficient because it significantly increased the GST enzyme activity of both wheat cultivars at dawn. In accordance with our results, others reported that inactive forms of phytochromes were activated and transported into the nucleus within minutes of being exposed to red light (Yamaguchi et al., 1999; Sheerin et al., 2015). Thus, 15-min-long red light treatment was enough to induce phytochrome-mediated signaling and increase the expression of *GST*s in wheat plants.

It was also found that the 4-d-long red light treatment effectively enhanced total GST activity in both wheat genotypes. Thus, the application of nocturnal red light for 4 d was enough to induce priming and change the stress memory of plants. The part of this priming is the changes in the chromatin pattern, accumulation of transcription factors, changes in phytohormone levels, changes in metabolite levels, and activation of antioxidant and detoxification systems (Hilker and Schmülling, 2019), which were reported also after red light exposure (Yang et al., 2015; Gallé et al., 2021).

Three days after mycotoxin exposure, the priming effects of nocturnal red light were tested in plants treated with FB1.

Based on our result, it can be concluded that both FB1 exposure and the 1-wk-long nocturnal red light treatment significantly increased the GST enzyme activity of both selected wheat cultivars at dawn in the dark period. However, the combined effect of light and FB1 exhibited only a slight increase in GST activity as compared to the FB1-treated plants. It was found that surviving the harmful effects of FB1 is associated with higher GST and antioxidant activity in tomato plants (Harvey et al., 2008). Based on our results that nocturnal red light treatments effectively induced the transcription and activity of GSTs, as well as the activity of key antioxidant enzymes at dawn, the use of nocturnal red light as priming can aid stress acclimation in mycotoxin-exposed plants.

The expressions of *TaGSTU1B*, *TaGSTU*2, and *TaGSTF6* genes were significantly higher upon red light treatment in GK Ígéret as compared to GK Arató. Based on the changes in transcript abundance of the selected *GST* genes, it can be concluded that the *Fusarium-sensitive* wheat was more sensitive to red light pretreatment. Apart from *TaGSTU1A* and *B* genes, the expression of all GSTs decreased in the sensitive GK Ígéret leaves under the combined nocturnal red light and FB1 treatment as compared to the mycotoxin-exposed plants. However, the red light was effective to induce the expression of *TaGSTU1A*, *TaGSTU1B*, *TaGSTU2,* and *TaGSTF6* in GK Arató, but the stimulating effect of red light during combined treatments remained only in the case of tau genes. Thus, it can be concluded that red light application as pretreatment elicited a gene-specific effect on the expression of GST coding sequences in the *Fusarium* resistant and sensitive wheat cultivar, which did not show a direct correlation with the total enzyme activities of tissues.

The nonspecific effects of red light on enzymatic antioxidant activities were investigated in addition to GSTs. It was observed that the nocturnal red light application significantly elevated SOD, CAT, and POX enzyme activities in both wheat genotypes at dawn. This effect of nocturnal red light is crucial in the aspect of plant defense mechanism because antioxidant enzymes are under circadian regulation and show the lowest activity at dawn (Poór et al., 2018). Interestingly, the highest SOD activity was detected after FB1 treatments, which was significantly reduced by the nocturnal red light application in the sensitive cultivar GK Ígéret. The higher activity of SOD can contribute to higher $H_2O_2$ accumulation upon FB1 application (Alscher et al., 2002), which can induce lethal oxidative stress in plants (Czarnocka and Karpiński, 2018). In GK Arató, the enzyme activities of CAT and POX, which regulate $H_2O_2$ decomposition with different affinities (Foyer and Noctor, 2009), were significantly lower after FB1 treatments compared to nocturnal red light application, and only slightly lower in GK géret. As a result, red light treatments were also effective in increasing CAT and POX activities in FB1-treated samples, particularly in the *Fusarium-resistant* GK Arató, contributing to a reduction in mycotoxin-induced high $H_2O_2$ accumulation. Aside from the changes in GST activities, the increased activity in key enzymatic antioxidants such as SOD, CAT, and POD is important effects of nocturnal red light on the wheat genotypes studied, particularly GK Arató, by reducing the degree of FB1-induced oxidative stress. Since it was discovered that FB1 induced lethal $H_2O_2$ accumulation and inhibited antioxidant enzyme activities such as CAT in other plant species, these are critical effects of nocturnal red light application (Xing et al., 2013; Zhao et al., 2015; Iqbal et al., 2021). These results are in accordance with the observation of other authors who measured reduced $H_2O_2$ levels and higher SOD, CAT, and POD activities during cucumber mosaic virus infection in *Nicotiana tabacum* when compared to white light (Chen et al., 2015) or in the case of *B. cinerea* infection in tomato leaves when exposed to red light (Hui et al., 2017).

Besides the key antioxidant enzymes, GSH levels were also determined upon treatments. GSH levels were significantly increased by FB1 exposure, especially in GK Ígéret. In this genotype, combined treatments also elevated GSH content in the leaves at dawn. GSH determines the redox status of cells and is the substrate of GST (Nianiou-Obeidat et al., 2017; Czarnocka and Karpiński, 2018). Earlier it was found that GSH levels were decreased by red light application in watermelon (Yang et al., 2018) but combined treatments with nematodes (Yang et al., 2018) or cucumber mosaic virus (Chen et al., 2015) elevated their accumulation in leaves as it was detected in GK Ígéret.

The cell death-promoting effects of FB1 were detected based on the changes in lipid peroxidation and loss of cell viability in the selected wheat cultivars. The beneficial effects of nocturnal red light via the activated detoxification of plants by GSTs and increased activities of antioxidant enzymes were confirmed because t reduced FB1-induced malondialdehyde MDA accumulation and EL increase in both wheat cultivars.

## Conclusion

Our results provided evidence for the first time for the positive effects of nocturnal red light treatments against the toxic effects of FB1 mycotoxin in wheat leaves depending on their *Fusarium* sensitivity. It can be concluded that nocturnal red light application can be an effective method to enhance detoxification processes e.g., by enhancing GST activity and transcription of selected GST coding genes at dawn when most of the phytopathogen fungi are more active. It can be concluded that red light was effective in inducing the expression of the selected *GST* genes in the resistant cultivar GK Arató, but the stimulating effect of red light compared to

FB1 remained only in the case of tau genes during a combined red light/FB1 treatment. In addition, the beneficial effect of the light pretreatment is the reduction of harmful oxidative stress and lipid peroxidation by enhancing the antioxidant enzyme activities (CAT and POX), especially in GK Arató, which are lower at dawn.

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## Declarations

**Conflict of interest** No conflict of interest is declared.



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