

# Ultraviolet-C irradiation of wheat grains induces seedling resistance to leaf rust and powdery mildew disease

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# Highlights

- Grain treatment with UV-C improved wheat seedling resistance to leaf rust and powdery mildew disease.
- The most reduction in the disease parameter was detected in seedlings produced from UV-C treated germinated grains.
- Disease severity was significantly reduced in response to UV-C for 10 minutes by up to 68 and 63% for leaf rust and powdery mildew disease, respectively.
- UV-C radiation induces resistance in plants by promoting the accumulation of phenolics, oxidative enzymes, and total chlorophyll, in addition to the modification of phenylalanine ammonia-lyase mRNA expression levels.

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# Abstract

Ultraviolet-C (UV-C) irradiation of grains activated the antioxidant system and wheat seedlings' resistance to leaf rust and powdery mildew disease under greenhouse conditions. Two wheat cultivars (Gemmeiza-12 and Sids-1) with dry and germinated grains were treated with UV-C at three exposure times (5, 10, and 15 minutes). The results indicated that the percentages of disease severity and infection type for leaf rust and powdery mildew on wheat seedlings were significantly reduced when exposed to UV-C at all exposure times compared to the untreated control. The most effective treatments for both cultivars were obtained in seedlings grown from germinated grains treated with UV-C for 10 minutes. Furthermore, UV-C irradiation treatments improved plant resistance to infection by activating certain defense genes, thereby increasing the production of resistance compounds that support defense mechanisms against pathogens. Our results demonstrated that UV-C for 10 minutes can induce resistance in wheat seedlings while also increasing total chlorophyll, total phenolic compounds, phenylalanine ammonia-lyase, and peroxidase activity. In addition, phenylalanine ammonia-lyase mRNA expression levels were significantly increased in seedlings growing from germinated grains treated with UV-C for 10 minutes, as compared to both infected and uninfected controls. These findings demonstrate the potential for additional UV-C radiation treatments to enhance disease resistance.

# Introduction

Wheat (*Triticum aestivum* L.) is one of the world's most important cereals, providing calories and protein to approximately 85% of the global population (Ma *et al.*, 2014; Zhang *et al.*, 2017). Among the most significant plant diseases are leaf rust and powdery mildew, which cause substantial yield losses in wheat (Zhang *et al.*, 2016; Najeeb *et al.*, 2019; Arab *et al.*, 2021). *Blumeria graminis* DC E.O. Speer f. sp. *tritici* Em. Marchal (*Bgt*) syn. *Erysiphe graminis* DC causes powdery mildew (Gao *et al.*, 2018).

Once wheat is severely infected with powdery mildew, grain yield losses can reach 40% (Li et al., 2011). Under normal Egyptian growth conditions, B. graminis f. sp. tritici affects the majority of common wheat cultivars, resulting in a grain yield reduction of 26.68% in highly susceptible cultivars (Draz et al., 2019). Wheat is susceptible to a common and widespread foliar disease caused by Puccinia triticina Eriks (Huerta-Espino et al., 2011). Early leaf rust infection causes significant yield losses of up to 30% (Khan et al., 2013; Atia et al., 2021). Some studies have documented up to 60% yield reductions in highly susceptible wheat cultivars (Smith, 2008; El-Orabey et al., 2017; Arab et al., 2021). In Egypt, yield losses of wheat due to leaf rust have reached up to 50% (Thabet and Najeeb, 2017). The development of resistant varieties is considered the most practical, efficient, and sustainable method to manage these diseases (El-Shamy et al., 2016). However, chemical fungicides have been the standard method for managing wheat diseases. Nevertheless, their limitations necessitate the development of new methods, particularly for protective culture and organic agriculture. This century has witnessed an expansion of research into alternative physical techniques known as emerging technologies. In this manner, various physical methods are applied at various stages of plant growth, and the most effective, cost-effective, and environmentally safe method is to effectively control the diseases (Govindaraj et al., 2017). Pre-sowing physical techniques aim to increase crop yield by accelerating plant reaction speed to biotic and abiotic factors during and after germination (Thomas and Pothur 2017; Mariz-Ponte et al., 2018). The induction of resistance mechanisms by pre-sowing physical technique is similar to creating a stress memory in plants, which is associated with chromatin alterations, transcription elements, phytohormones, and stress-regulating metabolites (Conrath, 2011). Ultraviolet (UV) radiation has emerged as a promising technique for disease prevention among these physical methods (Araujo et al., 2016; Rifna et al., 2019).

UV radiation has traditionally been divided into three wavelength ranges: UV-A (320-390 nm), UV-B (280-320 nm), and UV-C (100-280 nm). Within these ranges, excess levels of UV-C radiation are both photochemically and biologically lethal. UV radiation is a significant factor in disrupting the normal biological functions of all organisms by causing DNA damage. Low-dose, nondetrimental UV-C exposures induce beneficial responses in the treated organism. Numerous studies have described how UV-C radiation induces resistance in plants by promoting the accumulation of flavonoids, phenolics, oxidative enzymes, and phytoalexins, in addition to the modification of cell walls and cell death (Turtoi, 2013; Urban et al., 2016; Vanhaelewyn et al., 2020). Furthermore, UV-C irradiation has been shown to stimulate the germination and growth parameters of maize and wheat grains (Rupiasih and Vidyasagar, 2016; Sukthavornthum et al., 2018; Sadeghianfar et al., 2019; Korotkova et al., 2020). Biochemical antioxidant enzymes like peroxidases and polyphenol oxidase have been shown to mitigate photo-oxidative stress by reducing reactive oxygen species (ROS) in plants. It is also considered a critical defensive component against pathogenic attacks (Zu et al., 2011). Furthermore, UV-C treatments applied to seeds have been demon-



strated to increase their resistance to pathogen attack (Brown *et al.*, 2001; Scott *et al.*, 2019; Aboul Fotouh *et al.*, 2019). However, no study has examined the impact of UV-C grain treatment radiation on the induction of disease resistance in wheat plants to fungal foliar diseases. Consequently, this research aimed to understand the effect of different durations of irradiation of wheat grain with UV-C on plant physiological and biochemical markers in wheat seedlings, which can enhance the resistance to powdery mildew and leaf rust disease under greenhouse conditions.

#### **Materials and Methods**

#### Plant and fungal

Gemmeiza-12 (highly susceptible to powdery mildew disease) and Sids-1 (highly susceptible to leaf rust disease) are two Egyptian wheat cultivars provided by the Wheat Research Section, Field Crop Institute, Agriculture Research Center (ARC), Giza, Egypt (Table 1).

The inoculum source for *B. garminis* f.sp. *tritici* (PGT) was obtained from field-grown wheat plants naturally infected with powdery mildew. The uredia of *P. triticina* were kindly provided by the Wheat Diseases Research Department, Plant Pathology Research Institute, ARC, Giza, Egypt. The following experiments were carried out in the greenhouses and laboratories of the Department of Plant Pathology, Faculty of Agriculture, Ain Shams University.

#### **Ultraviolet-C irradiation grain treatment**

The wheat grains of each cultivar were first disinfected with 1% NaOH for 5 minutes, then washed 3-4 times with sterilized distilled water. The grains were divided into two groups; the first group was immediately treated with UV-C. The other group was soaked in distilled water for 24 hours and then arranged on a plate coated with two layers of cotton. Grains were cultivated for two days in an incubator at 25°C until they germinated, then treated with UV-C. Dry and germinated grains were irradiated with UV-C at three exposure times (5, 10, and 15 min) using a UV-C fluorescent lamp (TUV 15 W G158T8, wavelength 254 nm, Phillips, Germany). In accordance with Brown et al. (2001), the targeted irradiation surface for plates was at a 20 cm distance from the lamp. After UV-C treatment, grains were placed in complete darkness all day (24 hours) to inhibit photoreaction activities. As controls, grains that were not exposed to UV-C were maintained. The treated grains (dry and germinated) were then planted at a rate of 5 grains/plastic pot (15 cm) containing clay soil. The experiment was conducted in a split-plot arrangement in a randomized complete design with five replicates in the greenhouse. After seven days, seedlings were inoculated with powdery mildew and leaf rust disease.

Table 1. Gemmeiza-12 and Sids-1 cultivars pedigree.

Genotypes	Pedigree	Year of release
Gemmeiza-12	OTUS/3/SARA/THB//VEECMSS97Y00227S-5Y-010M-010Y-010M-2Y-1M-0Y-0GM	2011
Sids-1	HD2172/Pavon "S"//1158.57/Maya74 "S" SD46-4Sd-2SD-1SD-0SD	1996



### Inoculation and assessment of leaf rust disease

The Sids-1 cultivar seedlings were inoculated with uredia of *P. triticina*, as described by Tervet and Cassel (1951). After inoculation, seedlings were incubated in dark, moist chambers for 24 hours, transferred to their designated greenhouse benches, and kept under observation for 15 days. Five pots without infection with the pathogen and untreated with UV-C served as controls (healthy plants), and disease severity was assessed 15 days after inoculation. Assessment of leaf rust was based on the symptoms observed on the entire plant of each replicate, which were classified as resistant or susceptible based on the infection types corresponding to Stakman *et al.* (1962), as shown in Table 2, and disease severity (%) was recorded according to Long *et al.* (1994).

#### Inoculation and assessment of powdery mildew disease

The Gemmeiza-12 cultivar seedlings were inoculated with *B.* garminis f.sp. tritici by shaking conidia from naturally infected plants collected from commercial wheat fields in several areas across Egypt. After inoculation, seedlings were kept in complete darkness at a relative humidity of 98% for 24 hours (El-Shamy *et al.*, 2012). The inoculated seedlings were maintained in the greenhouse at 25°C, 70-90% relative humidity, and kept under observation until evaluation. Five pots without infection with the pathogen and untreated with UV-C served as controls (healthy plants), and disease severity was assessed 15 days after inoculation. Disease severity of powdery mildew was measured by estimating the percentage of leaf area infected on the whole plant of each replicate using the modified Cobb scale of 0 to 100% (Peterson *et al.*, 1948). Infection types were scored using a modified 0-to-4 scale (Wang *et al.*, 2005) for recording the host response to infection, as depicted in Table 3.

#### **Determination of leaf chlorophyll**

Leaf chlorophyll content was measured 15 days after inoculation using a hand-held portable optical meter (Minolta SPAD-502 Plus chlorophyll meter, Tokyo, Japan). Soil plant analysis development (SPAD) measurements were performed on ten plants per treatment (Novichonok *et al.*, 2016). Afterward, chlorophyll *a* was determined by converting the SPAD values to mg/m<sup>2</sup> in accordance with Monje and Bugbee (1992) using Equation 1:

Chlorophyll (a)= $80.05+10.4 \times \text{SPAD}$  value

# Table 2. Infection types of wheat leaf rust.

# Assay of total phenolic compounds

Fifteen days after inoculation, 1 g of fresh wheat leaf samples were used to extract total phenolic compounds using ethanol according to the method presented by Swain and Hillis (1955). According to Vlase *et al.* (2014), the assay of the total phenols was carried out. A spectrophotometer (Unico-2100, Dayton, NJ, USA) was used to assess the optical density of the developed blue color at 725 nm. A catechol standard curve was utilized to measure the total quantity of phenols.

#### Extraction and assay of antioxidant enzyme activity

Five replicates of fresh leaf samples were collected from seedlings 15 days after inoculation, ground in liquid nitrogen, and then frozen at -80°C for further biochemical analysis. The techniques described by Biles and Martyn (1993) were primarily utilized to isolate peroxidase, as follows: 1 g of leaf tissue was ground in sodium phosphate buffer (2 mL, 0.1 M, pH 6.5). Samples were centrifuged for 20 minutes at 12000 rpm at 4°C. Peroxidase activity was estimated according to Liu et al. (2010) with 2.9 ml of sodium phosphate buffer (100 mM, pH 6.0) including 0.25% (v/v) guaiacol and hydrogen peroxide (100 mM). First, 100 µl of the crude enzyme extract was added to initiate the reaction. At 470 nm, absorbance variations were measured using a Unico UV-2100 spectrophotometer (Unico-2100, Dayton, NJ, USA). An increase in absorbance min<sup>-1</sup>/g<sup>-1</sup> of fresh weight represented the enzyme activity. Phenylalanine ammonia-lyase (PAL) activity was defined following the procedure of Solecka and Kacperska (2003) as follows: 1 g of leaf tissue was extracted in borate buffer (2 mL, 50 mM, PH 8.8). The extracts were centrifuged at 12000 rpm for 10 minutes at 4°C, then 1 mL of the supernatant was blended with sodium borate buffer (2 mL, pH 8.8) and 1 mL of 10<sup>-2</sup> M L-phenylalanine. After 1 hour of incubation at 30°C, the reaction was stopped by inserting 500 µl of HCl (6N). The mixture was then centrifuged at 12000 rpm for 10 minutes. Enzyme activity was conveyed as trans-cinnamic acid formed using a Unico UV-2100 spectrophotometer (Unico-2100, Dayton, NJ, USA) at 290 nm.

# **RNA** expression of phenylalanine ammonia-lyase

Reverse transcription polymerase chain reaction (RT-PCR) was used to assess the effect of UV light treatments on the expression of PAL. Using a total RNA purification kit (Bioscience,

Host	Infection type	Disease symptoms
Resistant	0	No uredia or other macroscopic signs of infection
	0;	No uredia but hypersensitive necrotic or chlorotic flecks present
	1	Small uredia surrounded by necrosis
	2	Small to medium uredia surrounded by chlorosis or necrosis
Susceptible	3	Medium-sized uredia that may be associated with chlorosis
	4	Large uredia without chlorosis or necrosis or rarely necrosis

(1)

#### Table 3. Infection types of wheat powdery mildew.

Host	Infection type	Disease symptoms
Resistant	0 0; 1 2	No visible symptoms Hypersensitive necrotic flecks Minute colonies with few conidia produced Colonies with moderately developed hyphae
Susceptible	3 4	Colonies with well-developed hyphae and abundant conidia, but colonies not joined together Colonies with well-developed hyphae and abundant conidia, and colonies mostly joined together



Dümmer, Germany), total RNA was extracted from the leaves of Sids-1 and Gemmeiza-12 seedlings obtained from irradiated germinated grains 15 days after inoculation. Subsequently, mRNA was reverse transcribed into cDNA using a one-step RT-PCR kit (QIAGEN, Hilden, Germany). The sequence of the forward wheat PAL primer is (PAL-F, 5- A A G C T G A T G T T C G C G C A G T T C T- 3), and the reverse primer is (PAL-R, 5- A A A C C A T A G T C C A A G C T C G G G T-3). The expression of the target gene was compared relative to the housekeeping wheat actin genes (actin-F, 5-C T C A T A C G G T C A G C A A T A C -3; actin-R, 5-A T G T G G A T A T C A G G A A G G A-3). In a thermal Eppendorf master cycler (T100TM thermal cycler, BIO-RAD, Segrate, Italy). This PCR reaction sequence consists of the following steps: the first step is reverse transcription at 50°C for 30 minutes, then denaturation at 94°C for 15 minutes, 30 cycles of 94°C for 30 seconds, 60°C for 30 seconds and 72°C for 30 seconds, and the last step is the final extension at 72°C for 1 minute. On 1.5% agarose gels stained with ethidium bromide, the amplification products were visualized and photographed using a gel documentation system (Bio-Doc Analyze, Biometra, Göttingen, Germany).

### Statistical analysis

Data were statistically analyzed using analysis of variance using SAS software (Cary, NC, USA). Duncan's multiple range test was utilized to identify homogenous groups of means that differ significantly at 5% ( $p \le 0.05$ ) (Duncan, 1955).

#### Results

# Effect of ultraviolet-C radiation on leaf rust and powdery mildew disease

As shown in Table 4, UV-C irradiation at all tested exposure times was associated with a reduction in disease severity and infection type in seedlings germinated from treated grains compared to those germinated from untreated grains. In addition, the degree of disease parameter reduction in both cultivars depended on the duration of UV-C exposure and the grain application form. The most effective treatment in both cultivars was obtained from seedlings grown from germinated grains treated with UV-C for 10 minutes. Data presented in Table 4 and Figure 1 demonstrate that treatment of Sids-1 germinated grains with UV-C for 10 minutes significantly reduced the severity of leaf rust disease to around 25% as compared to the infected control treatment (67%). In addition, there was a positive correlation between UV exposure times and infection type. The lowest infection type (1 and 0;) was obtained on seedlings grown from germinated grain treated with UV-C for 10 minutes, respectively, compared with the infected control treatment (4). The same decreasing trend was also observed for the Gemmeiza-12 cultivar. Treatment of germinated grains with UV-C for 10 minutes decreased the severity of powdery mildew disease to around 19% compared to the infected control treatment (60%). The lowest infection types (1 and 2) were obtained for seedlings grown from germinated grain treated with UV-C for 10 minutes, compared with the infected control treatment (4). Compared to the infected controls, disease severity was significantly ( $p \le 0.05$ ) reduced in response to UV-C for 10 minutes by up to 68 and 63% for leaf rust and powdery mildew disease, respectively.



**Figure 1**. Effect of UV- C grain irradiation treatments on infection type and severity of leaf rust (LR) caused by *Puccinia triticina* and Powdery mildew (PM) caused by *Blumeria graminis* f.sp *tritici* in seedlings of Sids-1 and Gemmeiza-12 wheat cultivars at 15 days post-inoculation under greenhouse conditions. wheat grains were irradiated with UV-C at three exposure times (5, 10 and 15 min) which **A**) control, **B**) UV- 5 min, C) UV- 10 min, **D**) UV- 15 min.

 Table 4. Effect of UV-C grain irradiation treatments on infection type and severity of leaf rust and powdery mildew disease in Sids-1 and Gemmeiza-12 cultivars at 15 days post-inoculation under greenhouse conditions.

Treatment		Sids - 1 (Leaf rust disease)				Gemmeiza-12 (Powdery mildew disease)			
	Germinated		Dry		Germinated		Dry		
	IT	DS %	IT	DS%	IT	DS%	IT	DS%	
Control	4	67 <sup>b</sup> ±1.45	4	78ª±1.66	4	$60^{\mathrm{C}} \pm 2.60$	4	72 <sup>b</sup> ±1.66	
UV-5m	2 & 3	46 <sup>d</sup> ±1.85	3	55 <sup>C</sup> ±2.88	3	$39^{\text{ef}}\pm2.08$	3 & 4	45d ±2.88	
UV-10m	0; & 1	25 <sup>j</sup> ±2.88	1 & 2	$34^{fgh}\pm 2.33$	1 & 2	$19^k \pm 1.73$	2	$29^{hij} \pm 2.08$	
UV-15m	2	33ghi±1.45	2	44 <sup>de</sup> ±2.33	2	$27^{ij}\pm 1.45$	3	$37^{fg}\pm\!\!1.66$	
LSD at 5%		5.44		5.44		5.44		5.44	

All the statistical differences were presented relative to the untreated control. Data are means of three replicates  $\pm$  SE; means with different letters within columns are significantly different by Duncan's multiple range test at (p≤0.05). DS: Disease severity. IT: Infection type, UV- 5/10/15 min: wheat grains were irradiated with UV-C at three exposure times (5, 10 and 15 minute).



# Physiological parameters and induction of resistance with ultraviolet-C radiation

To assess the induction of resistance induced by UV-C grain irradiation treatments in wheat seedlings infected with leaf rust and powdery mildew, the total of chlorophyll (SPAD value), chlorophyll *a*, and phenol compounds, as well as peroxidase and PAL enzyme activities, was measured.

#### **Chlorophyll content**

The maximum increase in SPAD value and chlorophyll a was observed in the leaves of non-infected seedlings grown from untreated grains (healthy controls), as shown in Figure 2. Moreover, our findings demonstrated that the concentrations of total chlorophyll and chlorophyll a in seedlings grown from UV-C pretreated grains at all exposure times were significantly higher compared to seedlings grown from untreated grains (infected controls) in both cultivars, Sids-1 and Gemmeiza-12, respectively. When germinated grains were irradiated with UV-C for 10 minutes, the total chlorophyll content of Sids-1 seedlings increased by 23.6% compared to infected control plants. During this exposure period, the chlorophyll concentration increased to 326.2 mg/m<sup>2</sup> compared to infected control plants. Similar effects were observed in Gemmeiza-12 seedlings, where the higher increases in the total chlorophyll concentration were 24 (SPAD value), and chlorophyll a increased with values of 330.3 mg/m<sup>2</sup> relative to infected control plants.

#### Enzyme and total phenolic compound activities

Total phenolic compounds significantly increased under all UV-C treatments in both cultivars (Figure 3). Values ranged from



Figure 2. Effect of UV-C grain irradiation treatments on total chlorophyll (A) and chlorophyll a content (B) in seedlings of Sids-1 and Gemmeiza-12 wheat cultivars at 15 days post-inoculation under greenhouse conditions. wheat grains were irradiated with UV-C at three exposure times (5, 10 and 15 min). cont., plant infected/untreated with UV; healthy, plant uninfected/untreated with UV. Error bars, standard error.

30 to 42 mg/g fw in the infected control. Under UV-C treatment for 10 minutes, they were increased to 69.4 in Sids-1 and 75 mg/g fw in Gemmeiza-12 seedlings derived from irradiated germinated grains, respectively. Furthermore, our results revealed a significant positive effect on antioxidant enzyme (resistance-related enzymes) activity under UV-C treatments (Figure 4). Germinated grains treated with UV-C for 10 minutes in both cultivars revealed a higher effect on the activation of the peroxidase and PAL enzymes in wheat seedlings as compared with the controls.



**Figure 3.** Effect of UV- C grain irradiation treatments on phenol content mg/g fw in seedlings of Sids-1 and Gemmeiza-12 wheat cultivars at 15 days post-inoculation under greenhouse conditions. wheat grains were irradiated with UV-C at three exposure times (5, 10 and 15 min). cont., plant infected/untreated with UV; healthy, plant uninfected/untreated with UV. Error bars, standard error.



Figure 4. Effect of UV- C grain irradiation treatments on (A) Peroxidase and (B) PAL enzymes activity in seedlings of Sids-1 and Gemmeiza-12 wheat cultivars at 15 days post-inoculation under greenhouse conditions. wheat grains were irradiated with UV-C at three exposure times (5, 10 and 15 min). cont., plant infected/untreated with UV; healthy, plant uninfected/untreated with UV. Error bars, standard error.

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#### **RNA expression of phenylalanine ammonia-lyase**

PAL genes were efficiently transcribed into mRNA, as evidenced by the presence of specific amplicons of expected molecular weight (104 bp) in both cultivars (Figure 5 A and B). However, the expression pattern of the PAL gene varied in the semi-quantitative RT-PCR analysis. The expression of PAL genes does not change in the 5-minute treatment compared to the infected, untreated control. The highest gene expression of the enzyme is recorded in the seedlings grown from germinated grains and treated with UV-C for 10 minutes in both cultivars, Sids-1 and Gemmeiza-12, infected with leaf rust and powdery mildew disease, respectively. As an internal control for cDNA synthesis, specific actin transcript amplicons were detected in all plants (Figure 5C).

## Discussion

UV irradiation has gained popularity in recent years since it promotes plant growth and increases resistance to biotic and abiotic stresses, thereby increasing crop yield. The pre-sowing treatment of seeds with ultraviolet radiation has received particular attention (Windram et al., 2012; Thomas and Puthur, 2017; Mariz-Ponte et al., 2018). Numerous studies have demonstrated that UV-C has a beneficial effect on the physiological and biochemical processes in seeds and plants, as well as on the health of seeds, germination, and seedling strength of a variety of crops (Rupiasih and Vidyasagar, 2016; Castronuovo et al., 2017; Sadeghianfar et al., 2019; Semenov et al., 2020; Hernandez-Aguilar et al., 2021). In the current study, UV-C irradiation of wheat grains (dry and germinated) at three exposure times (5, 10, and 15 minutes) increased resistance to leaf rust and powdery mildew disease. Similar patterns were observed in treated seedlings, which showed a significantly reduced severity and infection type of the pathogen compared with the infected, untreated control treatment. In both cultivars, the most effective treatments were obtained in seedlings grown from germinated grains treated with UV-C for 10 minutes,



Figure 5. Effect of UV-C grain irradiation treatments on RNA expression of PAL gene in seedlings growing from germinated grains of (A) Sids-1 and (B) Gemmeiza-12 wheat cultivars at 15 days post-inoculation under greenhouse conditions. wheat grains were irradiated with UV-C at three exposure times (5, 10 and 15 min). RNA expression of PAL gene compared to actin gene expression (Housekeeping gene) (C). M: (marker), 100 bp DNA Ladder (Bio science).

followed by UV-C for 15 minutes. It is suggested that the reaction was only caused by induced resistance because the pathogen was not directly exposed to UV-C light. The generation of wheat resistance via UV-C grain treatment matched the findings of Scott et al. (2019), which indicated that treatment of seeds with UV-C radiation had a positive effect on the decrease in disease incidence in tomato plants caused by Botrytis cinerea, Fusarium oxysporum f. sp. Lycopersici and Sclerotinia minor. According to Falconí and Mendizabal (2018), the treatment of lupin seeds with UV-C significantly reduces seedborne infections of anthracnose caused by Colletotrichum acutatum. Furthermore, Aboul Fotouh et al. (2019) and Siddiqui et al. (2011) illustrated that irradiation of germinated green bean, mung bean, and groundnut seeds with UV-C for 60 minutes decreased infection by root-infecting fungi, i.e., Rhizoctonia solani, Macrophomina phaseolina, and Fusarium spp. Moreover, Brown et al. (2001) stated that exposure of cabbage seeds to UV-C decreased the density of Xanthomonas campestris pv. campestris in infected leaves. On the other hand, Aarrouf and Urban (2020) indicated that exposure to UV-C light for one or 60 seconds increased plant resistance to Botrytis cinerea, Phytophthora capsici, and Plasmopara viticola in the leaves of lettuce, pepper, tomato, and grapevine plants. In contrast, Wang et al. (2018) explained that when UV-B radiation was used only prior to Puccinia striiformis f. sp. Tritici inoculation, the incubation period was shortened, and the infection efficiency, sporulation quantity, and disease index increased. All these effects of pre-treatment of seeds with UV-C radiation are related to two distinct processes: the direct germicidal activity of UV-C on pathogenic surface microbes and the stimulation of host resistance as a result of UV-induced stress reactions in treated tissues (Semenov et al., 2017).

Induction of resistance in plants with UV radiation has been related to the activation of different host defenses, including the accumulation of phenolic and flavonoid compounds combined with the stimulation of antioxidant mechanisms and delayed chlorophyll degradation (Sharma et al., 2012; Shin et al., 2013; Urban et al., 2016; Xu et al., 2019; Vanhaelewyn et al., 2020; Elshafei et al., 2021). The totals of chlorophyll, chlorophyll a, and phenol compounds, as well as peroxidase and PAL enzyme activity, were measured to evaluate the role of UV-C grain irradiation in inducing resistance in wheat seedlings. The current study found that different UV-C treatment exposure times significantly increased the aforementioned parameters compared to their corresponding controls. In both cultivars that were UV treated, a higher increase was obtained in seedlings grown from germinated grains that were UV-C treated for 10 minutes, followed by UV-C for 15 minutes. The increase in leaf total chlorophyll content corresponds to the results of other authors (Kacharava et al., 2009; Siddiqui et al., 2011; Sztatelman et al., 2015; Falconí and Mendizabal, 2018; Semenov et al., 2021). Chlorophyll's insensitivity to UV radiation may be linked to the activation of carotenogenesis or the stimulation of anthocyanidin synthesis. These latter compounds offer adequate defense against free radicals (Rice-Evans et al., 1997). In contrast, Middleton and Teramura (1993) found that UV radiation stimulated the biosynthesis of UV-absorbing compounds and carotenoids, thereby achieving a photoprotective function.

Based on the aforementioned findings, total phenolic compounds exhibited a significant increase under all UV-C treatments in both cultivars. Furthermore, our results demonstrated a significant positive effect on antioxidant enzyme activity under UV-C treatments. However, germinated grains treated with UV-C for 10 minutes in both cultivars showed a higher response to peroxidase and PAL activation in wheat seedlings when compared to controls. These results are consistent with Kacharava *et al.* (2009) and



Ouhibi et al. (2014), who illustrated that irradiation of kidney bean and lettuce seeds with low doses of UV-C enhanced the tocopherol, phenolic compounds, and flavonoids content in plant leaves. Similarly, McLay et al. (2020) concluded on the pre-treatment of lettuce seedlings with UV-B-induced phenolics, which act as phytoanticipins to restrict the growth of biotrophic pathogens (Bremia lactucae). Additionally, Falconí and Mendizabal (2018) demonstrated that seedlings grown from UV-C treated seeds revealed an enhanced concentration of the defense enzymes peroxidase and catalase compared to plants grown from untreated seeds. Similarly, Rivera-Pastrana et al. (2014) found a substantial increase in the activity of peroxidase and catalase on papaya peel as an effect of UV-C treatment compared to primary rates. Yongmei et al. (2018) revealed that the application of UV-B radiation before M. oryzae infection improved the activity of pathogenesis-related proteins like PAL, lipoxygenase, chitinase, and  $\beta$ -1,3-glucanase and the content of resistance-related elements, such as flavonoids and total phenols, thus enhancing the disease resistance of rice leaves to infection. It is well known that phenols play essential functions in plants as antifungal, antibacterial, and antiviral compounds (Gogoi et al., 2001; Hammerschmidt, 2005). The antioxidant enzymes peroxidases, catalase, glutathione reductase, and superoxide dismutase help plants reduce oxidative stress. In addition, antioxidant enzymes can protect plant cells from photo-oxidative damage by scavenging ROS produced by UV-induced stress (Rao et al., 1996). Peroxidase enzymes are associated with cross-linking cell wall components, lignin and suberin monomers polymerization, and consequent resistance in other host-pathogen relationships (Glazenner, 1982). The discovery of a priming-related expression profile for PAL after inoculation suggests that gene priming may also be essential for facilitating a rapid response to the initial plantpathogen interaction (Scott et al., 2018). PAL is a crucial rate-limiting enzyme in phenylpropanoid compound metabolism. In addition, it regulates the biosynthesis of flavonoids, a compound believed to be responsible for the resistance of crop leaves (Chandrasekaran et al., 2017; Li et al. 2018; Omar et al., 2021). PAL is also involved in the synthesis of phytoalexins, which have potent antimicrobial properties and contribute to the structural reinforcement of the cell through lignification and the production of salicylic acid (Dixon et al., 2002). In our study, RT-PCR data clearly revealed that the expression of the PAL gene was significantly upregulated in seedlings growing from germinated grains treated with UV-C radiation, as determined by RT-PCR. In agreement with our previous findings, the RNA and protein levels of the PAL gene are significantly upregulated in response to fungal infection, indicating its involvement in the host's immune response. These results agree with the findings of (Kobayashi et al., 2013; Atia *et al.*, 2021) who demonstrated that exposure of rose plants to low levels of UV radiation and infection with powdery mildew disease induced the expression of PAL genes, which are implicated in secondary metabolic pathways. According to Yongmei et al. (2018), increased UV-B radiation prior to Magnaporthe oryzae infection significantly increased the expression of resistance-related genes (OsPAL and OsCHT), enhancing rice leaf disease resistance. Additionally, Pombo et al. (2010) showed that pre-storage UV-C treatment of strawberry fruit reduces Botrytis cinerea losses. After 4 and 24 hours of storage, the expression and enzyme activity of PAL increased compared to the level found in the control.

#### Conclusions

According to the current study's findings, grain treatment with UV-C improved wheat seedling resistance to leaf rust and powdery mildew disease by activating the antioxidant system. The most significant decrease in the disease parameter was detected in seedlings produced from UV-C treated germinated grains. Therefore, it is possible that UV-C increased plant defense *via* multiple mechanisms, which requires further investigation at the level of resistance gene expression.

## References

- Aarrouf J, Urban L, 2020. Flashes of UVC light: an innovative method for stimulating plant defences. PLoS One 15:e02 35918.
- Aboul Fotouh MM, Maha HM, Moawad FG, Tag El-Din MA, Srour HAM, 2019. Enhancement of resistance against Rhizoctonia solani by glycine betaine and UV-C radiation in green bean (Phaseolus vulgaris L.). Arab Univ. J. Agric. Sci. 27:1829-41.
- Arab SA, El Shal MH, Eissa ST, Abou-Zeid MA, 2021. Assessment of some wheat genotypes for resistance to some diseases and their effect on yield and yield components. PCBMB. 22:73-8.
- Araujo SS, Paparella S, Dondi D, Bentivoglio A, Carbonera D,
  Balestrazzi A, 2016. Physical methods for seed invigoration:
  Advents and challenges in seed technology. Front. Plant Sci. 7:646.
- Atia AM, El-Khateeb EA, El-Maksoud RMA, Abou-Zeid MA, Salah A, Abdel-Hamid AME, 2021. Mining of leaf rust resistance genes content in Egyptian bread wheat collection. Plants 10:1378.
- Biles CL, Martyn RD, 1993. Peroxidase, polyphenoloxidase and shikimate dehydrogenase isozymes in relation to tissue type, maturity and pathogen induction of watermelon seedling. Plant Physiol. Biochem. 31:499-506.
- Brown JE, Lu TY, Stevens C, Khan VA, Lu JY, Wilson CL, Collins DJ, Wilson MA, Igwegbe ECK, Chalutz E, Droby S, 2001. The effect of low dose ultraviolet light-C seed treatment on induced resistance in cabbage to black rot (Xanthomonas campestris pv. campestris). Crop Protect. 20:873-83.
- Castronuovo D, Sofo A, Lovelli S, Candido V, Scopa A, 2017. Effects of UV-C radiation on common dandelion and purple coneflower: first results. Int. J. Plant Biol. 8:7255.
- Chandrasekaran M, Belachew ST, Yoon E, Chun SC, 2017. Expression of β-1,3-glucanase (GLU) and phenylalanine ammonia-lyase (PAL) genes and their enzymes in tomato plants induced after treatment with Bacillus subtilis CBR05 against Xanthomonas campestris pv. vesicatoria. J. Gen. Plant Pathol. 83:7-13.
- Conrath U, 2011. Molecular aspects of defence priming. Trends Plant Sci. 16:524-31.
- Dixon RA, Achnine L, Kota P, Liu CJ, Reddy MSS, Lang LJ, 2002. The phenylpropanoid pathway and the plant defence: a genomic perspective. Mol. Plant Pathol. 3:371-90.
- Draz IS, Esmail SM, Abou-Zeid MA, Essa TA, 2019. Powdery mildew susceptibility of spring wheat cultivars as a major constraint on grain yield. Ann. Agric. Sci. 64:39-45.



Duncan BD, 1955. Multiple ranges and multiple F test. Biometrics 11:1-42.

- El-Orabey WM, Nagwa I, El-Malik A, Ashmawy MA, Abou-Zeid MA, 2017. Reduction of bread wheat grain yield caused by leaf rust infection in common wheat varieties. Minufiya J. Plant Prot. 2:71-81.
- El-Shamy MM, Emara HM, Mohamed ME, 2016. Virulence analysis of wheat powdery mildew (Blumeria graminis f. sp. tritici) and effective genes in Middle Delta, Egypt. Plant Dis. 100:1927-30.
- El-Shamy MM, Sallam MEA, Awad HMF, 2012. Powdery mildew infection on some Egyptian bread wheat cultivars in relation to environmental conditions. J. Plant Prot. Path. Mansoura Univ. 3:363-72.
- Elshafei AA, El-Orabey WM, Fathallah FB, Esmail RM, Abou-Zeid MA, 2021. Phenotyping and validation of molecular markers associated with rust resistance genes in wheat cultivars in Egypt. Mol. Biol. Rep. 49:1903-15.
- Falconí CE, Yánez-Mendizábal V, 2018. Efficacy of UV-C radiation to reduce seedborne anthracnose (colletotrichum Acutatum) from andean lupin (lupinus Mutabilis). Plant Pathol. 67:831-8.
- Gao H, Niu J, Li S, 2018. Impact of wheat powdery mildew on grain yield & quality and its prevention and control methods. Ame. J. Agric. Forestry 6:141-7.
- Glazenner JA, 1982. Accumulation of phenolic compounds in cells and formation of lignin-like polymers in cell walls of young tomato fruits after inoculation with Botrytis cinerea. Physiol. Plant Pathol. 20:11-25.
- Gogoi R, Singh DV, Srivastava KD, 2001. Phenols as a biochemical basis of resistance in wheat against karnal bunt. Plant Pathol. 50:470-6.
- Govindaraj M, Masilamani P, Albert AV, Bhaskaran M, 2017. Effect of physical seed treatment on yield and quality of crops: a review. Agric. Rev. 38:1-14.
- Hammerschmidt R, 2005. Phenols and plant-pathogeninteractions: the saga continues. Physiol. Mol. Plant P. 66:77-8.
- Hernandez-Aguilar C, Dominguez-Pacheco A, Tenango MP, Valderrama-Bravo C, Hernández MS, Cruz-Orea A, Ordonez-Miranda J, 2021. Characterization of bean seeds, germination, and phenolic compounds of seedlings by UV-C radiation. J. Plant. Growth. Regul. 40:642-55.
- Huerta-Espino J, Singh RP, German S, McCallum BD, Park RF, Chen WQ, Bhardwaj SC, Goyeau H, 2011. Global status of wheat leaf rust caused by Puccinia triticina. Euphytica 179:143-60.
- Kacharava N, Chanishvili SS, Badridze GS, Chkhubianishvili E, Janukashvili N, 2009. Effect of seed irradiation on the content of antioxidants in leaves of kidney bean, cabbage and beet cultivars. Aust. J. Crop Sci. 3:137-45.
- Khan MH, Asifa B, Zahoor AD, Syed MR, 2013. Status and strategies in breeding for rust resistance in wheat. Agric. Sci. 4:292-301.
- Kobayashi M, Kanto T, Fujikawa T, Yamada M, Ishiwata M, Satou M, Hisamatsu T, 2013. Supplemental UV radiation controls rose powdery mildew disease under the greenhouse conditions. Environ. Control. Biol. 51:157-63.
- Korotkova I, Semenov A, Sakhno T, 2020. The ultraviolet radiation: disinfection and stimulation processes. Lambert: Academic Publishing, Saarbruecken, Saarland, Germany.
- Li H, Wang X, Song F, Wu C, Wu X, Zhang N, Zhon Y, Zhang X, 2011. Response to powdery mildew and detection of resistance genes in wheat cultivars from China. Acta Agron. Sin. 37:943-54.
- Li X, He Y, Xie C, Zu Y, Zhan F, Mei X, Xia Y, Li Y, 2018. Effects

of UV-B radiation on the infectivity of Magnaporthe oryzae and rice disease resistant physiology in Yuanyang terraces. Photoch. Photobio. Sci. 17:8-17.

- Liu F, Wei F, Wang L, Liu H, Zhu X, Liang Y, 2010. Riboflavin activates defense responses in tobacco and induces resistance against Phytophthora parasitica and Ralstonia solanacearum. Physiol. Mol. Plant P. 74:330-6.
- Long DL, Roelfs AP, Leonard KJ, Roberts JJ, 1994. Virulence and diversity of Puccinia recondite f.sp. tritici in the United States in 1992. Plant Dis. 78:901-6.\_
- Ma P, Xu H, Luo Q, Qie Y, Zhou Y, Xu Y, Han H, Li L, An D, 2014. Inheritance and genetic mapping of a gene for seedling resistance to powdery mildew in wheat line X39862. Euphytica 200:149-57.
- Mariz-Ponte N, Mendes RJ, Sario S, Melo P, Santos C, 2018. Moderate UV-A supplementation benefits tomato seed and seedling invigoration: a contribution to the use of UV in seed technology. Sci. Hortic. 235:357-66.
- McLay ER, Pontaroli AC, Wargent JJ, 2020. UV-B induced flavonoids contribute to reduced biotrophic disease susceptibility in lettuce seedlings. Front. Plant Sci. 11:594681.
- Middleton EM, Teramura AH, 1993. The role of flavonol glycosides and carotenoids in protecting soybean from ultraviolet-B damage. Plant Physiol. 103:741-52.
- Monje OA, Bugbee B, 1992. Inherent limitation of nondestructive chlorophyll meters. A comparison of two types of meters. HortScience 27:69-71.
- Najeeb KMA, Thabet M, Negm SS, EL-Deeb SH, 2019. Monitoring of Puccinia triticina Erikss. physiologic races and effectiveness of Lr-genes in Egyptian wheat during 2014-2016 growing seasons. Int. J. Agric. Technol. 15:35-54.
- Novichonok EV, Novichonok AO, Kurbatova JA, Markovskaya EF, 2016. Use of the atLEAF plus chlorophyll meter for a nondestructive estimate of chlorophyll content. Photosynthetica 54:130-7.
- Omar HS, Al Mutery A, Osman NH, Reyad NEA, Abou-Zeid MA, 2021. Genetic diversity, antifungal evaluation and molecular docking studies of Cu-chitosan nanoparticles as prospective stem rust inhibitor candidates among some Egyptian wheat genotypes. PLoS One 16:e0257959.
- Ouhibi C, Attia H, Rebah F, Msilini N, Chebbi M, Aarrouf J, Urban L, Lachaal M, 2014. Salt stress mitigation by seed priming with UV-C in lettuce plants: growth, antioxidant activity and phenolic compounds. Plant Physiol. Biochem. 83:126-33.
- Peterson RF, Campbell AB, Hannah AE, 1948. A Diagrammatic scale for estimating rust intensity on leaves and stem of cereals. Can. J. Res. 26c:496-500.
- Pombo MA, Rosli HG, Martínez GA, Civello PM, 2010. UV-C treatment affects the expression and activity of defense genes in strawberry fruit (Fragaria × ananassa, Duch.). Postharvest Biol. Tec. 59:94-102.
- Rao MV, Paliyath G, Ormrod DP, 1996. Ultraviolet □B□ and ozone-induced biochemical changes in antioxidant enzymes of Arabidopsis thaliana. Plant Physiol. 110:125-36.
- Rice-Evans C, Miller N, Paganga G, 1997. Antioxidant properties of phenolic compounds. Trends Plant Sci. 2:152-9.
- Rifna EJ, Ramanan KR, Mahendran R, 2019. Emerging technology applications for improving seed germination. Trends Food Sci. Tech. 86:95-108.
- Rivera-Pastrana DM, Gardea AA, Yahia EM, Martinez-Tellez MA, Gonzalez-Aguilar GA, 2014. Effect of UV-C irradiation and low temperature storage on bioactive compounds, antioxidant enzymes and radical scavenging activity of papa fruit. J. Food Sci. Technol. 51:3821-9.



- Rupiasih NN, Vidyasagar PB, 2016. Effect of UV-C radiation and hypergravity on germination, growth and content chlorophyll of wheat seedlings. AIP Conf. Proc. 1719, 030035.
- Sadeghianfar P, Nazari M, Backes G, 2019. Exposure to ultraviolet (UV-C) radiation increases germination rate of Maize (Zea maize L.) and sugar beet (Beta vulgaris) seeds. Plants 8:49.
- Scott G, Almasrahi A, Mansoorkhani FM, Ru-par M, Dickinson M, Shama G, 2019. Hormetic UV-C seed treatments for the control of tomato diseases. Plant Pathol. 68:700-7.
- Scott G, Dickinson M, Shama G, Rupar M, 2018. A comparison of the molecular mechanisms underpinning high-intensity, pulsed polychromatic light and low-intensity UV-C hormesis in tomato fruit. Postharvest Biol. Tec. 137:46-55.
- Semenov A, Korotkova I, Sakhno T, Marenych M, Hanhur V, Liashenko V, Kaminsky V, 2020. Effect of UV-C radiation on basic indices of growth process of winter wheat (Triticum aestivum L.) seeds in pre-sowing treatment. Acta Agric. Slov. 116:49-58.
- Semenov A, Sakhno T, Hordieieva O, Sakhno Y, 2021. Pre-sowing treatment of vetch hairy seeds, vicia villosa using ultraviolet irradiation. Global J. Environ. Sci. Manag. 7:555-64.
- Semenov AO, Kozhushko GM, Sakhno TV, 2017. Analysis of the role of UV radiation on the development and productivity of different cultures. Light Eng. Electricity 2:3-16. [Article in Ukrainian].
- Sharma P, Jha AB, Dubey RS, Pessarakli M, 2012. Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J. Bot. 2012:217037.
- Shin DH, Choi M, Kim K, Bang G, Cho M, Choi SB, 2013. HY5 regulates anthocyanin biosynthesis by inducing the transcriptional activation of the MYB75/PAP1 transcription factor in Arabidopsis. FEBS Lett. 587:1543-7.
- Siddiqui A, Dawar S, Zaki MJ, Hamiid N, 2011. Role of ultraviolet (UV-C) radiation in the control of root infecting fungi on groundnut and mungbean. Pak. J. Bot. 43:2221-4.
- Smith LM, 2008. Mapping of drought tolerance and leaf rust resistance in wheat. Degree Diss., Kansas State University, Manhattan, Kansas, USA.
- Solecka D, Kacperska A, 2003. Phenylpropanoid deficiency affects the course of plant acclimation to cold. Physiol. Plantarum 119:253-62.
- Stakman EC, Stewart DM, Loegering WQ, 1962. Identification of physiologic races of Puccinia graminis var. tritici. United States Department of Agriculture, Agricultural Research Service, Washington DC, USA.
- Sukthavornthum W, Bodhipadma K, Noichinda S, Phanomchai S, Deelueak U, Kachonpadungkitti Y, Leung DW, 2018. UV-C irradiation induced alterations in shoot proliferation and in vitro flowering in plantlets developed from encapsulated and non-encapsulated microshoots of Persian violet. Sci. Hortic. 233:9-13.
- Swain T, Hallis WE, 1955. The phenolic constituents of Prunus domestica. I. The quantative analysis of phenolic constituent. J. Sci. Food Agr.10:63-8.
- Sztatelman O, Grzyb J, Gabrys H, Banas AK, 2015. The effect of UV-B on Arabidopsis leaves depends on light conditions after treatment. BMC Plant Biol. 15:281.

- Tervet I, Cassel RC, 1951. The use of cyclone separation in race identification of cereal rust. Phytopathology 41:282-5.
- Thabet M, Najeeb KMA, 2017. Impact of wheat leaf rust severity on grain yield losses in relation to host resistance for some Egyptian wheat cultivars. Middle East J. Agric. Res. 4:1501-9.
- Thomas DT, Puthur JT, 2017. UV radiation priming: a means of amplifying the inherent potential for abiotic stress tolerance in crop plants. Environ. Exp. Bot. 138:57-66.
- Turtoi M, 2013. Ultraviolet light treatment of fresh fruits and vegetables surface: a review. J. Agroaliment. Processes Technol. 19:325-37.
- Urban L, Charles F, de Miranda MRA, Aarrouf J, 2016. Understanding the physiological effects of UV-C light and exploiting its agronomic potential before and after harvest. Plant Physiol. Biochem. 105:1-11.
- Vanhaelewyn L, Van Der Straeten D, De Coninck B, Vandenbussche F, 2020. Ultraviolet radiation from a plant perspective: the plant-microorganism context. Front. Plant Sci. 11:597642.
- Vlase L, Benedec D, Hanganu D, Madian G, Csillag I, Sevastre B, Tilea I, 2014. Evaluation of antioxidant and antimicrobial activities and phenolic profile for Hyssopus officinalis, Ocimum basilicum and Teucrium chamaedrys. Molecules 19:5490-507.
- Wang H, Qin F, Cheng P, Ma Z, Wang H, 2018. Effects of UV-B radiation intensity and timing on epidemiological components of wheat stripe rust. J. Integr. Agr. 17:2704-13.
- Wang ZL, Li LH, He ZH, Duan XY, Zhou YL, Chen XM, Lillemo M, Singh RP, Wang H, Xia XC, 2005. Seedling and adult plant resistance to powdery mildew in Chinese bread wheat cultivars and lines. Plant Dis. 89:457-63.
- Windram O, Madhou P, McHattie S, Hill C, Hickman R, Cooke E, 2012. Arabidopsis defense against Botrytis cinerea: chronology and regulation deciphered by high-resolution temporal transcriptomic analysis. Plant Cell 24:3530-57.
- Xu Y, Charles MT, Luo Z, Mimee B, Tong Z, Véronneau P, Roussel D, Rolland D, 2019. Ultraviolet C priming of strawberry leaves against subsequent Mycosphaerella fragariae infection involves the action of reactive oxygen species, plant hormones, and terpenes. Plant Cell Environ. 42:815-31.
- Yongmei H, Xiang L, Fangdong Z, Chunmei X, Yanqun Z, Yuan L, Ming Y, 2018. Resistance-related physiological response of rice leaves to the compound stress of enhanced UV-B radiation and Magnaportheoryzae. J. Plant Interact. 13:321-8.
- Zhang RQ, Sun BX, Chen AZ, Xing LP, Feng YG, Lan CX, Chen PD, 2016. Pm55, a developmental-stage and tissue-specific powdery mildew resistance gene introgressed from Dasypyrum villosum into commom wheat. Theor. Appl. Genet. 129:1975-84.
- Zhang Y, Bai Y, Wu G, Zou S, Chen Y, Gao C, Tang D, 2017. Simultaneous modification of three homoeologs of TaEDR1 by genome editing enhances powdery mildew resistance in wheat. Plant J. 91:714-24.
- Zu YG, Wei XX, Yu JH, Li DW, Pang HH, Tong L, 2011. Responses in the physiology and biochemistry of Korean pine (Pinus koraiensis) under supplementary UV-B radiation. Photosynthetica 49:448-58.