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RESEARCH ARTICLE

α-Tocopherol application as a countermeasure to UV-B stress in bread wheat (*Triticum aestivum* L.)

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Abstract
The source of energy for all photoautotrophic organisms is light, which is absorbed by photosynthetic processes and used to transform carbon dioxide and H_2O into organic molecules. The majority of UV-B light (280 to 320 nm) is absorbed by stratospheric ozone layer, although some of it does reach at the Earth's surface. Because of the sedentary lifestyle of plants, this form of abiotic stress is unavoidable and can induce growth and even cell death. Ten-day-old calli generated from mature Kirik wheat embryos were subjected to UV-B radiation for 0, 2, 4, and 6 h to examine the function of exogenous α-tocopherol, a lipophilic antioxidant, in wheat tolerance to UV-B radiation stress. The calli were then moved to a callus medium containing α-tocopherol (0, 50, and 100 mg/l) and cultivated there for 20 days after being subjected to UV-B stress. For plant regeneration, embryogenic calli were put on a medium for plant regeneration after 30 days. The findings of this investigation demonstrated that an increase in UV-B exposure period resulted in a substantial drop in the relative growth rate of callus, the rate of embryogenic callus, the rate of responding embryogenic callus, and the number of plants in each explant. On the other hand, with the application of α-tocopherol, all these parameters improved, and the best result was observed in the application of 100 mg/l of α-tocopherol in terms of plant regeneration under UV-B stress.

Keywords Plant regeneration · Wheat · In vitro · UV-B stress · α-Tocopherol

Introduction

Wheat has been a crucial cereal crop in providing people's nutritional needs throughout history (Aydin et al. 2016a). It is a form of food that people in all geographic regions of the world require. The reason for this is that it is adapted to high altitudes, can be cultivated quickly and readily, has a high nutritional value, is easier to store and keep, and has a greater bread quality than other cereal crops. According to the data of FAO 2021, the wheat cultivation area in the world was 220.76 million ha and the production amount was 770.87 million tons (FAO 2021).

The expansion of wheat production to wide areas raises awareness of production techniques, resulting as output under stressful conditions and in marginal locations. This circumstance increases the amount of yield obtained from the unit area. Plants are exposed to many abiotic stresses such as ultraviolet (UV). This situation leads to serious reductions in the yield of agricultural products in particular (Láposi et al. 2009; Sigmaz et al. 2015).

Solar radiation is the universe's primary source of energy and is essential for plant growth and development. Plants are exposed to varying levels of UV-B light throughout their life cycle. Furthermore, although UV-B radiation is a minor component of solar radiation, it can have multiple effects on life systems due to its high energy (Mariotti et al. 2021). UV-B influences plant growth by modifying morphological, physiological, and molecular responses (Kanungo et al. 2022). Common climatic characteristics such as precipitation patterns and temperature have a considerable influence on the efficiency of UV-B radiation (Puranik et al. 2022). UV-B effects also vary with species, altitude, latitude, time of the day, day of the year, cloud cover, and other meteorological conditions (Rai et al. 2022). UV-B is received by plants as an environmental signal and a possible

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abiotic stressor that affects plant development and response (Shi and Liu 2021). UV-B rays have the potential to damage cells due to the high energies, which is one of their most critical properties. Reactive oxygen species (ROSs), which builds in the cell as a result of severe UV-B stress, damages numerous cellular components such as DNA, RNA, proteins, and membrane lipids, as well as causing metabolic problems (Foyer and Noctor 2009). It has been shown that exposure to UV-B radiation induces several reactions in higher plants. Diverse enzymatic and non-enzymatic antioxidants help plants survive oxidative stress by removing ROSs. These antioxidants are substances that slow down the oxidation of fats (Mackerness et al. 2001).

α-Tocopherol, which is found in the cell membrane and has a significant antioxidant impact due to its lipophilic nature, inhibits phospholipid peroxidation and cell membrane damage (Gey et al. 1991; McNeil et al. 2004). α-Tocopherol protects cell membranes by reducing the damaging effects of ROS and polyunsaturated fatty acids in membrane phospholipids. α-Tocopherol scavenges lipid peroxyl radicals produced during stress and stops lipid peroxidation chain events (Asthir 2015).

Plant tissue culture is a widely used technology to facilitate and support plant breeding programs. Plant cells are cultured in vitro to create suitable environments, desired characteristics of tissues and organs are determined, and new plants are created (Aydin et al. 2011). During plant growth, in vitro selection is a technique used to select plant genotypes that are resistant to biotic and abiotic challenges such as UV radiation, drought, excessive salt, and disease. It is a natural method for the production of stress-resistant plants that combines traditional and technological aspects. Plant cells, tissues, or organs can be cultured in vitro on a medium containing selective chemicals, allowing for the selection and regeneration of plants with desirable traits (Rai et al. 2011).

Some UV-B light does reach the Earth's surface, although the stratospheric ozone layer absorbs most of it (Sharma and Kumar 2022). Plants are injured by UV-B stress, which is caused by exposure to excessive levels of continuous full-wavelength UV-B radiation (Chen et al. 2022). This has necessitated research into the effects of UV-B radiation, particularly on plants. In this study, the negative effects of UV-B stress on the plant were investigated in vitro in mature embryo culture of Kırik wheat cultivar, and the effects of α-tocopherol application were determined in order to eliminate the negative effects, and the role of α-tocopherol in tolerance to UV-B stress was explained.

Materials and methods

Plant material was acquired from mature seeds of the Kırik bread wheat variety that was supported with endosperm. Endosperm-supported embryo culture was conducted based on methods descripted by Aydin et al. (2011). Mature seeds were cleaned under sterile circumstances for 30 min with industrial-strength bleach (5% sodium hypochlorite) and two drops of Tween 80 after being submerged in 70% ethanol for 5 min. Afterward, sterilized seeds were rinsed with sterile distilled water several times and kept on +4 °C for 14–16 h in dark conditions. Mature embryos of surface sterilized seeds were divided into 6 parts without detaching from the seed. Endosperm-supported embryos were grown for 10 days at 25 °C in the dark with 12 mg/l dicamba, 0.5 mg/l IAA, 20 g/l sucrose, 2 g/l phthalate, and 1.95 g/l MES hydrate added to the callus formation media. Under sterile conditions, 10-day-old calli were exposed to UV-B stress (300 $\mu W\ cm^{-2}$) using a Philips Special 20W/Narrowband tube (311 nm), as previously mentioned (Manaf et al. 2016; Zhao et al. 2021), positioned directly above cultures for 2, 4, and 6 h at a distance of 30 cm under photoperiod (62 $\mu mol\ m^{-2}\ s^{-1}$) and 25 ± 1 °C (Manaf et al. 2016).

The calli exposed to UV-B stress were incubated in a callus formation medium containing different concentrations of α-tocopherol (0, 50, and 100 mg/l) (Sadiq et al. 2019) in the same conditions for 20 days. The relative growth rate of callus (%) (CRGR) and embryogenic callus formation rate (%) (ECF) were determined before calli were transferred plant regeneration. The calli for plant regeneration were kept on plant regeneration medium I (hormone-free callus formation medium) for 2 weeks at 25 ± 1 °C under 16-h photoperiod (62 $\mu mol\ m^{-2}\ s^{-1}$) and then transferred to plant regeneration medium II (plant regeneration medium I contain 0.5 mg/l TDZ). At the end of this period, the rate of responding embryogenic callus (REC) (%) and plant number per explant (PN) (number) were determined. Responding embryogenic callus is a callus that occurs in plantlets with roots and shoots. Regenerated plants were grown in glass jars containing hormone-free callus formation medium until they were 10–12 cm. All media were adjusted to pH 5.7 ± 0.1 before autoclaving for 20 min at 121 °C. MS vitamins and plant growth regulators (dicamba, IAA, TDZ, and α-tocopherol) were added to the autoclaved medium (50–60 °C) after sterilized with cellulose nitrate filters (Milipor®) with 0.22 µm.

Data were analyzed variance analysis (ANOVA) based on a completely randomized factorial design. Every petri dish was approved as a replicate and 10 endosperm-supported embryos were used in each petri dish. Five petri dishes were used for each application. The means were compared using the LSD test at the 0.05 level. Statistical analysis was performed using SAS (v 9.3) computer program.

Results

In this study, the effect of UV-B and α-tocopherol on plant growth activity was looked at by measuring callus relative growth, which is measured by changes in size, fresh/dry

biomass, and the rate at which cells divide. In addition, to determine their effect of them on plant morphogenesis, ECF rate (%), REC rate, and PN (number) parameters, which are widely used in wheat somatic embryogenesis, were investigated.

The main effect of UV-B exposure time and α-tocopherol concentration on callus relative growth rate was very significant ($p < 0.01$) (Table 1). When compared to a 0-h exposure period, the results indicated that all exposure times in this parameter reduced dramatically. The highest CRGR with a % of 7.0 was recorded in an exposure time of 0 h, whereas the lowest value was determined in a 6 h exposure time of 2.4%. Moreover, a decrease in the CRGR was observed depending on the increase in exposure time (Table 2). As for the effect of α-tocopherol concentration on CRGR, there is a very significant difference among the α-tocopherol concentrations. The CRGR increased in tandem with the α-tocopherol concentration; additionally, the highest CRGR was detected in 100 mg/l α-tocopherol. UV-B stress had a different effect on CRGR depending on α-tocopherol application, making the UV-B × α-tocopherol interaction (U×T) very significant ($p < 0.01$). According to the U×T interaction, α-tocopherol increased RGR during all UV-B exposure times (Table 2) (Fig. 1a).

Based on a meaningful comparison of different UV-B exposure times, the ECF rate (%) ranged from 60.7% under 6 h to 87.3% under 0 h, and the main effect of UV-B exposure time was determined very significant ($p < 0.01$) (Table 1). The highest ECF was observed at 0 h of UV-B exposure, while the lowest was observed at 0 h of UV-B exposure time. Furthermore, the main effect of α-tocopherol on embryogenic callus formation rate was very significant (Table 1), and the ECF rate ranged from 52.0 to 60.7 for 0 and 100 α-tocopherol concentrations, respectively (Table 2). The results of the research indicate that the application of α-tocopherol concentrations affects the ECF rate under UV-B stress (Tables 1 and 2). Although the effect of U×T interaction on ECF rate was not significant ($p > 0.05$), all α-tocopherol concentrations increased ECF rate in all UV-B exposure times. The highest ECF rate (88.0%) was recorded in calli exposed to both 50 and 100 mg/l concentrations of α-tocopherol and the 0 h UV-B exposure time while the lowest rate (52%) was observed at 0 mg/l concentration of α-tocopherol and the 6 h UV-B exposure time (Table 2) (Fig. 1b).

Table 1 Variance analysis results for parameters

Variance resources	DF	MS			
		CRGR (%)	ECF (%)	REC	PN
UV-B (U)	3	56.277**	2075.556**	3330.556**	5.009**
α-Tocopherol (T)	2	31.172**	245.000**	131.667*	0.183**
U×T	6	2.551**	40.556^{ns}	60.556*	0.066^{ns}
Error	48	0.195	30.833	29.167	0.029

** and *Significant at 0.01 and 0.05 levels, respectively

^{ns}Non-significant at 0.05 level

The main effect of UV-B exposure time and α-tocopherol concentration on REC rate was very significant ($p < 0.01$) (Table 1). The REC rate increased with 50 mg/l and 100 mg/l α-tocopherol concentrations compared to 0 mg/l α-tocopherol (Fig. 2a-c). In addition to this, with the increase in UV-B application time, an increase in the REC rate was observed (Table 2). UV-B stress had a different effect on REC rate depending on α-tocopherol application, making the U×T interaction not significant ($p < 0.05$). α-Tocopherol generally increased REC rate in UV-B exposure times. The highest REC rate (74.0%) was recorded in calli exposed to 50 mg/l α-tocopherol and the 0 h UV-B exposure time while the lowest rate (28%) was observed at 0 mg/l concentration of α-tocopherol and the 6 h UV-B exposure time (Table 2) (Fig. 1c).

UV-B exposure time and α-tocopherol concentration affected PN and their main effects were very significant ($p < 0.01$), as was the effect of the other parameters (Table 1). When the main effect of UV-B stress was evaluated, a decrease in EBBS was determined in parallel with the increase in UV-B exposure time. However, parallel to the increase in α-tocopherol application concentration, an increase in PN was identified (Table 2) (Fig. 2d–f). UV-B stress had a different effect on PN depending on α-tocopherol exposure time, making the U×T not significant ($p < 0.05$). The highest PN (3.02) was recorded in calli exposed to 100 mg/l α-tocopherol and the 0 h UV-B exposure time while the lowest (1.44) was observed at 0 mg/l concentration of α-tocopherol and the 6 h UV-B exposure time (Table 2) (Fig. 1d).

Discussion

Numerous biotic and abiotic stress factors that plants are subjected to have an adverse effect on their growth and development. Light provides plants with the energy required for photosynthesis and is an essential environmental cue for regulating plant survival and growth. However, light such as high light and UV-B radiation can also be an abiotic stressor for plants (Shi and Liu 2021). Exposure to elevated levels of UV-B radiation induces UV-B stress, which in turn leads to modifications in plant growth, development, morphology, and photosynthesis, as well as damage to DNA, proteins, and membranes (Chen et al. 2022).

The utilization of in vitro culture techniques enables the examination of morphogenesis and its regulatory mechanisms within a controlled experimental setting. The utilization of these models is founded on the fundamental significance of the cell in all morphogenetic occurrences in plants, both in vivo and in vitro. Additionally, the similarity of plant responses in vivo, calli in vitro, and callus regenerants in vitro and ex vitro is based on the universality of

Table 2 Effect of UV-B exposure time and α-tocopherol concentration on tissue culture parameters

UV-B (hour)	α-Tocopherol (mg/l)	CRGR (%)[1]	ECF (%)[2]	REC (%)[3]	PN (number)[4]
0	0	6.5	86.0	70.0	2.56
	50	7.2	88.0	74.0	3.00
	100	7.5	88.0	72.0	3.02
	Mean	7.0	87.3	72.0	2.86
2	0	3.9	80.0	58.0	1.92
	50	6.4	84.0	58.0	1.96
	100	6.6	84.0	54.0	1.96
	Mean	5.6	82.7	56.7	1.95
4	0	2.7	70.0	48.0	1.76
	50	5.6	74.0	52.0	1.76
	100	6.6	76.0	52.0	1.80
	Mean	5.0	73.3	50.7	1.77
6	0	1.4	52.0	28.0	1.44
	50	2.4	64.0	40.0	1.58
	100	3.4	66.0	40.0	1.60
	Mean	2.4	60.7	36.0	1.54
Mean	0	3.6	72.0	51.0	1.92
	50	5.4	77.5	56.0	2.08
	100	6.0	78.5	54.5	2.10
Mean		5.0	76.0	53.8	2.03
$LSD_{(0.05)}$ (UV-B stress) (U)		0.3	4.1	4.0	0.13
$LSD_{(0.05)}$ (α-tocopherol) (T)		0.3	3.5	3.4	0.11
$LSD_{(0.05)}$ (U×T)		0.6	–	–	–
Coefficient variance (%)		8.8	7.3	10.0	8.40

[1] [(Fresh weigh at the end of the culture − initial fresh weight of callus)/initial fresh weight of callus] × 100

[2] (Number of embryogenic callus/number of explants) × 100

[3] (Number of responding embryogenic callus/number of explants) × 100

[4] Total plant number/number of explants

plant morphogenesis pathways (Kruglova et al. 2018). In addition, callus cultures are viable models for investigating the responses of plant cells and tissues to various stressors such as salt stress, drought, and UV radiation (Efferth 2019). UV-B radiation has a wide variety of effects on various metabolic processes in the cell (Correia et al. 1999; An et al. 2000; Láposi et al. 2009; Zu et al. 2010). In this study, the increase in UV-B exposure time resulted in a decrease in the relative callus growth rate. Growth inhibition is one of the most common reactions in plants exposed to UV-B. UV-B radiation on the rate and duration of cell division and elongation can reduce the growth of wheat primary leaves (Hopkins et al. 2002). In our work, the decrease in callus formation rate can be related to the suppression of cell division and slowing of cell expansion in UV-B-exposed calli (Searles et al. 2001; Zavala et al. 2001; Flint et al. 2004). The decrease in growth rate can be attributed to the inhibition of cell division and slowing down of cell expansion in calli under UV-B radiation stress. Hopkins et al. (2002) reported that UV-B stress in bread wheat lowered the proportion of mitotically active cells and lengthened the time required for cell division. Furthermore, both cell growth and development are affected by low doses or continual UV-B radiation, both of which are stress-inducing UV-B conditions (Staxén and Bornman 1994; Allen et al. 1998; Laakso et al. 2000; Hofmann et al. 2003; Kakani et al. 2003; Hectors et al. 2007). After exposure to UV-B, the number of mature epidermal cells reduced in several species (Gonzalez et al. 1998; Hopkins et al. 2002). In lettuce (*Lactuca sativa*), UV-B reduced leaf size and cell expansion rate (Wargent et al. 2011). Absorption of UV-B by IAA leads to the degradation of IAA and the generation of growth-inhibiting photoproducts and thus be reduced cell elongation in response to UV-B (Tevini and Iwanzik 1986). Li et al. (2010) reported that because UV-B lowered the IAA concentration in wheat cultivars, it had a significant impact on the development, morphology, and biomass of wheat plants. UV-B radiation damages DNA, causes cell cycle arrest, inhibits growth, and causes cell death. Pyrimidine dimers, such as cyclobutane pyrimidine dimers and pyrimidine (6-4) photopyrimidone

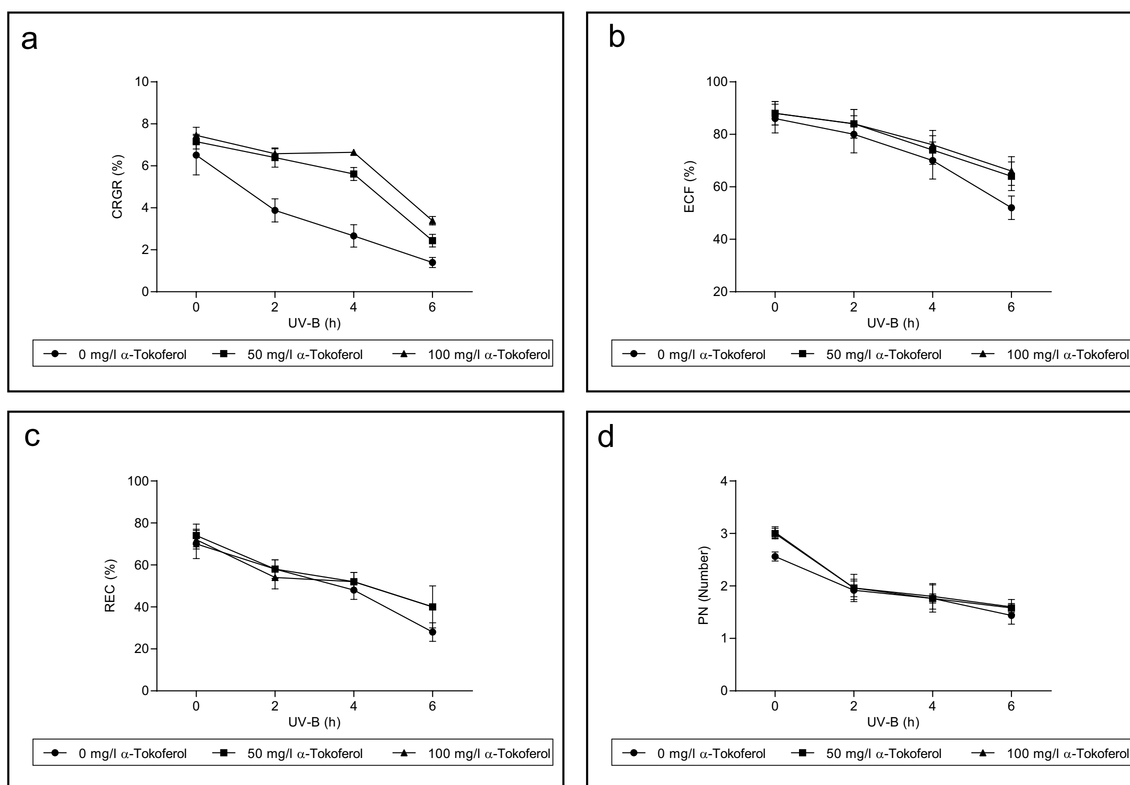

Fig. 1 Effect of U×T interaction on tissue culture parameters. **a** Relative growth rate of callus (%) (CRGR), **b** embryogenic callus formation rate (%) (ECF), **c** rate of responding embryogenic callus (REC) (%), **d** plant number per explant (PN) (number). Data are presented as means ± SE ($n = 4$)

products, are produced as a result of UV-B exposure. As a result, DNA replication and transcription are inhibited, resulting in a rise in mutations, cell death, and cell cycle arrest (Lo et al. 2005; de Lima-Bessa et al. 2008). Moreover, plant cell size regulation is controlled by cell division and cell expansion (Sugimoto-Shirasu and Roberts 2003). Endoreduplication, on the other hand, is a cell size determinant associated with larger cells and greater ploidy levels. UV-B inhibits cell cycle progression by lowering cell count and replication. All of these elements are detrimental to growth. Another reason for decreased growth could be cell membrane damage caused by ROS produced in response to UV-B exposure. ROS accumulate in the cell as a result of severe UV-B stress, causing damage to diverse cellular components such as membrane lipids and disrupting metabolism (Foyer and Noctor 2009). Chen et al. (2019) found that increased UV-B radiation intensified lipid peroxidation in wheat seedlings and changed the activities of antioxidant enzymes involved in scavenging ROSs. Jansen et al. (1998) found that UV-B stress damages membranes and impairs photosynthesis, growth, and development. Moreover, it was determined that watercress (Steinmetz and Wellmann 1986) and tomato seedlings (Ballaré et al. 1995) showed a comparable drop in leaf growth under UV-B stress. Zlatev et al. (2012) determined that plant growth, development, and morphology changed depending on the increase in UV-B, and in addition, the yield of crops decreased, especially in sensitive agricultural plants. A study conducted with 34 plant species showed that there was a decrease in the growth and development of plants due to UV-B stress and 10–15% reductions depending on the plant type, severely limiting crop yield and quality (Torabinejad et al. 1998; Conner and Neumeier 2002; Koti et al. 2004).

In this study, the effect of UV-B exposure time on the rate of formation of embryogenic callus (%), response rate of embryogenic callus (%), and plant number (number) was statistically significant, and it has been determined that these parameters decrease depending on the increase in UV-B exposure time. The reason for the decrease in ECF rate due to UV-B stress in our study may be because of UV-B stress on plant growth regulators, especially auxins, which are important in the formation of somatic embryos. According to the degree of embryo differentiation, somatic embryogenesis is classified into three stages: promoting embryogenesis, growing and developing somatic embryos, and turning mature embryos into whole plants (Malá et al. 2009). Auxins are one of the most important regulators of plant growth in stimulating

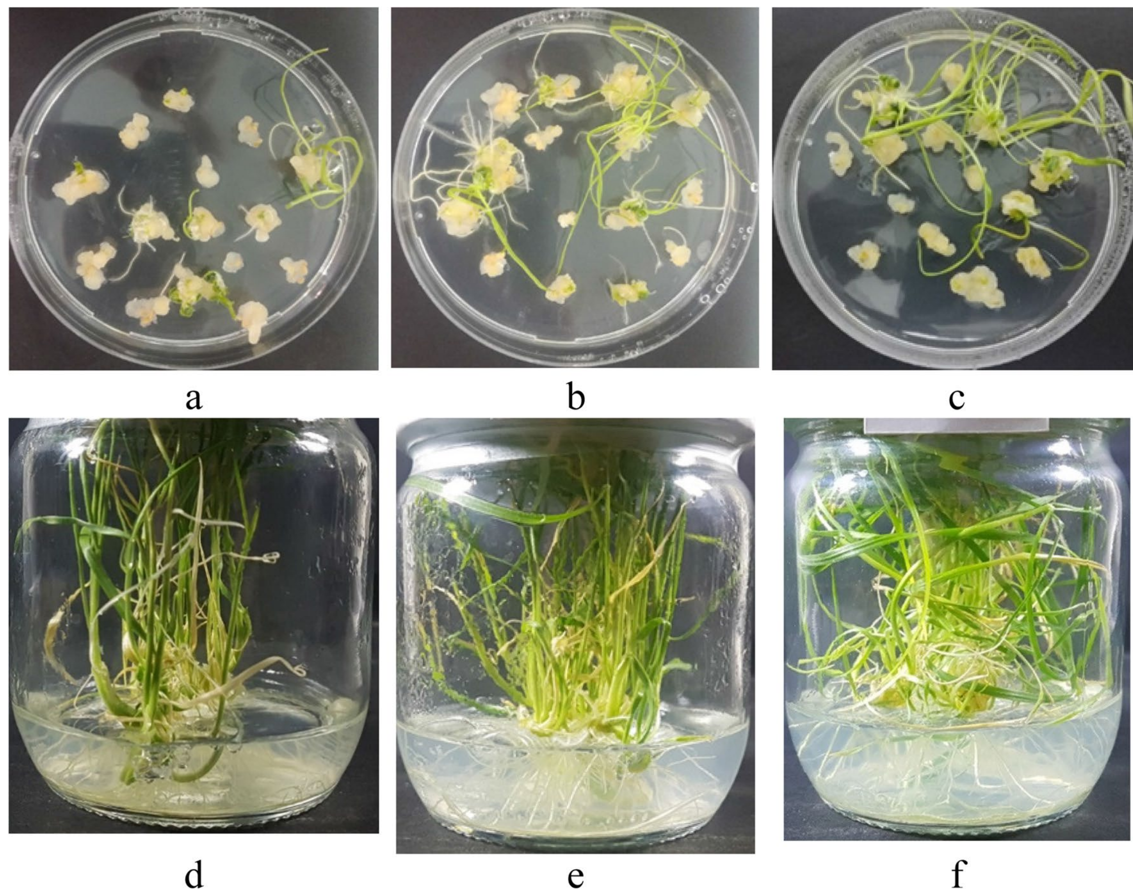

Fig. 2 Effects of α-tocopherol and UV-B exposure on responding embryogenic callus and plant regeneration. **a** Responding embryogenic callus under 4 h UV-B exposure time and 0 mg/l α-tocopherol treatment, **b** responding embryogenic callus under 4 h UV-B exposure time and 50 mg/l α-tocopherol treatment, **c** responding embryogenic callus under 4 h UV-B exposure time and 100 mg/l α-tocopherol treatment, **d** regenerated plants under 4 h UV-B exposure time and 0 mg/l α-tocopherol treatment, **e** regenerated plants under 4 h UV-B exposure time and 50 mg/l α-tocopherol treatment, **f** regenerated plants under 4 h UV-B exposure time and 100 mg/l α-tocopherol treatment

embryogenesis and somatic reproduction. It is known that UV-B stress affects auxins indirectly. Normally, flavonoids accumulate in tissues and organelles exposed to UV-B (Agati and Tattini 2010). Auxin homeostasis is impacted by flavonoid aglycones either by modifying auxin catabolism or by adversely influencing polar transport through oxidation transporters (Peer and Murphy 2007). Changes in auxin distribution and plant shape have been seen in certain flavonoid mutants of *Arabidopsis* (Peer et al. 2004; Ringli et al. 2008). Two *Arabidopsis* auxin mutants demonstrated flavonoid accumulation and a different morphogenic response to UV-B exposure (Hectors et al. 2012). This indicates that the interaction between auxin homeostasis and flavonoid accumulation can influence the morphological responses to UV exposure in a favorable way. UVR8 signaling is responsible for the crosstalk between auxins and flavonoids because it regulates the expression of numerous flavonoid biosynthesis genes (Brown et al. 2005). Furthermore, one of the negative effects of UV-B stress on tissue culture parameters may be due to its effect on polyamines (PA), which are crucial for cell differentiation during somatic embryogenesis as well (Chi et al. 1994; Bajaj and Rajam 1996; Kevers et al. 2000). Stress can cause a decrease in PA synthesis (Smith et al. 2001; Aydin et al. 2016b; Eliášová et al. 2018); in addition, Smith et al. (2001) observed that severe UV-B stress decrease PA levels. These findings suggest that this may be the cause of our study's decreased embryogenic callus production and embryogenic callus rates. Aydin et al. (2016b) reported that the endosperm-supported mature embryo in wheat plays a key role in somatic embryogenesis and plant regeneration. The somaclonal variation caused by UV-B stress may be one of the explanations for its detrimental influence on the tissue culture parameters examined in this study. ROS formed under UV-B stress cause somaclonal variation by causing base deletion and addition at the DNA level, changes in chromosome level, chromosome number and

structure (Czene and Harms-Ringdahl 1995), and hyper- or hypomethylation of DNA (Wacksman 1997).

Stress-tolerant plants contain more tocopherol (Szarka et al. 2012). Tocopherol is essential for several processes, including the transfer of photoassimilates and plant defense (Falk and Munne-Bosch 2010). It also regulates gene expression in signal transduction pathways. Plants usually contain the antioxidant tocopherol, which eliminates additional ROS and singlet oxygen species (Foyer et al. 2005). While tocopherol has an important role in severe stress conditions, other antioxidants play a role in moderate stress conditions (Havaux et al. 2005). Tocopherol's capacity to transfer phenolic hydrogen to free radicals underlies its antioxidant action. Among tocopherol isomers, the most powerful antioxidants α-tocopherol and δ-tocopherol have the least antioxidant activity. Other β- and γ-tocopherols have moderate antioxidant capacity (Kamal-Eldin and Appelqvist 1996; Evans et al. 2002). Tocopherol provides the stability of the structure of cell membranes by removing lipid peroxyl radicals from the plant (Liebler 1993). In our research, it was discovered that α-tocopherol lessens the harmful effects of UV-B on the parameters of the tissue culture that were examined. Munné-Bosch et al. (1999) reported that α-tocopherol reduces the negative effects of stress factors. It is thought that this effect of α-tocopherol is due to its ion balance and cell membrane stability, as well as its antioxidant properties against ROS that damage DNA, protein, and membrane lipids. There are many studies showing that α-tocopherol inhibits lipid peroxidation (Kapoor et al. 2015). Abbasi et al. (2009) determined that tocopherol deficiency increases peroxidation of lipids in transgenic tobacco leaves. Carletti et al. (2003) reported that α-tocopherol in maize exposed to UV-B stress reduced the production of ROS resulting from this stress. On the other hand, Sattler et al. (2006) also reported that tocopherol regulates the expression of genes involved in lipid peroxidation.

Conclusion

UV-B radiation plays a crucial role in plant growth and development, but excessive exposure can have negative impacts on plants and ecosystems. While plants need UV-B radiation for essential processes like photosynthesis and pigment synthesis, high levels of UV-B radiation can cause damage to DNA, reduce plant growth and productivity, and even lead to plant death. Development of UV-resistant crop varieties can help to mitigate the negative impacts of UV-B radiation on plants. Therefore, it is vital to understand and manage the ecological and global impacts of UV-B radiation on plants. Plant tissue culture is useful for investigating the multiple products of plants, as well as for monitoring their reaction to stress conditions and selecting tolerant species. The effect of UV-B stress on some tissue culture parameters (CRGR, ECF, REC, and PN) related to mature embryo-induced somatic embryogenesis in wheat was evaluated. These parameters decreased with increasing UV-B exposure time. Furthermore, α-tocopherol concentrations of 50 and 100 mg/l have an adaptive effect on plants growing under UV-B stress, and its use can be advised to prevent the detrimental effects of UV-B. The results of the study have shown that in vitro conditions may also be a guide as an alternative to traditional methods in determining UV-B-tolerant genotypes in wheat.

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Author contribution All authors contributed to the understanding and design of the study. Laboratory studies and organization of the studies were carried out by Sedat Karaca and Mahmut Sinan Taspinar. In vitro studies were carried out by Murat Aydin in the laboratory. The first draft of the article was written by Güleray Agar and all authors commented on previous versions of the article. All authors have read and approved the final article.

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Data availability This article has all the data that were created or evaluated during this study.

Declarations

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

References

Abbasi AR, Saur A, Hennig P, Tschiersch H, Hajirezaei M, Hofius D, Voll LM (2009) Tocopherol deficiency in transgenic tobacco (*Nicotiana tabacum* L.) plants leads to accelerated senescence. Plant Cell Environ 32(2):144–157. https://doi.org/10.1111/j.1365-3040.2008.01907.x

Agati G, Tattini M (2010) Multiple functional roles of flavonoids in photoprotection. New Phytol 186(4):786–793. https://doi.org/10.1111/j.1469-8137.2010.03269.x

Allen DJ, Nogués S, Baker NR (1998) Ozone depletion and increased UV-B radiation: is there a real threat to photosynthesis? *J Exp Bot* 49(328):1775–1788. https://doi.org/10.1093/jexbot/49.328.1775

An L, Feng H, Tang WX (2000) Changes of microsomal membrane properties in spring wheat leaves (*Triticum aestivum* L.) exposed to enhanced ultraviolet-B radiation. J Photochem Photobiol B Biol 57(1):60–65. https://doi.org/10.1016/s1011-1344(00)00077-4

Asthir B (2015) Protective mechanisms of heat tolerance in crop plants. J Plant Interact 10(1):202–210. https://doi.org/10.1080/17429145.2015.1067726

Aydin M, Pour AH, Haliloğlu K, Tosun M (2016b) Effect of polyamines on somatic embryogenesis via mature embryo in wheat. Turk J Biol 40(6):1178–1184. https://doi.org/10.3906/biy-1601-21

Aydin M, Taspinar MS, Cakmak ZE, Dumlupinar R, Agar G (2016a) Static magnetic field induced epigenetic changes in wheat callus. Bioelectromagnetics 37(7):504–511. https://doi.org/10.1002/bem.21997

Aydin M, Tosun M, Haliloglu K (2011) Plant regeneration in wheat mature embryo culture. Afr J Biotechnol 10(70):15749–15755. https://doi.org/10.5897/ajb11.1495

Bajaj S, Rajam MV (1996) Polyamine accumulation and near loss of morphogenesis in long-term callus cultures of rice (restoration of plant regeneration by manipulation of cellular polyamine levels). Plant Physiol 112(3):1343–1348. https://doi.org/10.1104/pp.112.3.1343

Ballaré CL, Barnes PW, Flint SD (1995) Inhibition of hypocotyl elongation by ultraviolet-B radiation in de-etiolating tomato seedlings. I. The photoreceptor. Physiol Plant 93(4):584–592. https://doi.org/10.1034/j.1399-3054.1995.930402.x

Brown BA, Cloix C, Jiang GH, Kaiserli E, Herzyk P, Kliebenstein DJ, Jenkins GI (2005) A UV-B-specific signaling component orchestrates plant UV protection. Proc Natl Acad Sci U S A 102(50):18225–18230. https://doi.org/10.1073/pnas.0507187102

Carletti P, Masi A, Wonisch A, Grill D, Tausz M, Ferretti M (2003) Changes in antioxidant and pigment pool dimensions in UV-B irradiated maize seedlings. Environ Exp Bot 50(2):149–157. https://doi.org/10.1016/s0098-8472(03)00020-0

Chen Z, Dong Y, Huang X (2022) Plant responses to UV-B radiation: signaling, acclimation and stress tolerance. Stress Biology 2(1):51. https://doi.org/10.1007/s44154-022-00076-9

Chen Z, Ma Y, Weng Y, Yang R, Gu Z, Wang P (2019) Effects of UV-B radiation on phenolic accumulation, antioxidant activity and physiological changes in wheat (*Triticum aestivum* L.) seedlings. Food Biosci 30:100409. https://doi.org/10.1016/j.fbio.2019.04.010

Chi GL, Lin WS, Lee JE, Pua EC (1994) Role of polyamines on de novo shoot morphogenesis from cotyledons of *Brassica campestris* ssp. pekinensis (Lour) Olsson in vitro. Plant Cell Rep 13(6):323–329. https://doi.org/10.1007/bf00232630

Conner JK, Neumeier R (2002) The effects of ultraviolet-B radiation and intraspecific competition on growth, pollination success, and lifetime female fitness in *Phacelia campanularia* and *P. purshii* (Hydrophyllaceae). Am J Bot 89(1):103–110. https://doi.org/10.3732/ajb.89.1.103

Correia CM, Torres-Pereira MS, Torres-Pereira JMG (1999) Growth, photosynthesis and UV-B absorbing compounds of Portuguese Barbela wheat exposed to ultraviolet-B radiation. Environ Pollut 104(3):383–388. https://doi.org/10.1016/s0269-7491(98)00191-2

Czene M, Harms-Ringdahl M (1995) Detection of single-strand breaks and formamidoprymidine-DNA glycosylase-sensitive sites in DNA of cultured human fibroblasts. Mutat Res DNA Repair Rep 336(3):235–242. https://doi.org/10.1016/0921-8777(94)00058-e

de Lima-Bessa KM, Armelini MG, Chiganças V, Jacysyn JF, Amarante-Mendes GP, Sarasin A, Menck CFM (2008) CPDs and 6-4PPs play different roles in UV-induced cell death in normal and NER-deficient human cells. DNA repair (Amst) 7(2):303–312. https://doi.org/10.1016/j.dnarep.2007.11.003

Efferth T (2019) Biotechnology applications of plant callus cultures. Engr 5(1):50–59. https://doi.org/10.1016/j.eng.2018.11.006

Eliášová K, Vondráková Z, Gemperlová L, Neděla V, Runštuk J, Fischerová L, Vágner M (2018) The response of *Picea abies* somatic embryos to UV-B radiation depends on the phase of maturation. Front Plant Sci 9:1736. https://doi.org/10.3389/fpls.2018.01736

Evans J, Kodali D, Addis P (2002) Optimal tocopherol concentrations to inhibit soybean oil oxidation. J Am Oil Chem Soc 79(1):47–51. https://doi.org/10.1007/s11746-002-0433-6

Falk J, Munne-Bosch S (2010) Tocochromanol functions in plants: antioxidation and beyond. J Exp Bot 61(6):1549–1566. https://doi.org/10.1093/jxb/erq030

FAO (2021) Food and Agriculture Organization of the United Nations: home. http://www.fao.org/. Accessed 06 December 2021

Flint SD, Searles PS, Caldwell MM (2004) Field testing of biological spectral weighting functions for induction of UV-absorbing compounds in higher plants. Photochem Photobiol 79(5):399–403. https://doi.org/10.1562/0031-8655(2004)79<399:sftobs>2.0.co;2

Foyer CH, Noctor G (2009) Redox regulation in photosynthetic organisms: signaling, acclimation, and practical implications. Antioxid Redox Signal 11(4):861–905

Foyer CH, Trebst A, Noctor G (2005) Signaling and integration of defense functions of tocopherol, ascorbate, and glutathione. In: Demmig-Adams B, Adams WW III, Mattoo AK (eds) Photoprotection, photoinhibition, gene regulation, and environment. Springer, Dordrecht, pp 241–268. https://doi.org/10.1007/1-4020-3579-9_16

Gey KF, Paska P, Jordan P, Moser UK (1991) Inverse correlation between plasma vitamin E and mortality from ischemic heart disease in cross-cultural epidemiology. Am J Clin Nutr 53(1):326–334. https://doi.org/10.1093/ajcn/53.1.326s

Gonzalez R, Mepsted R, Wellburn AR, Paul ND (1998) Non-photosynthetic mechanisms of growth reduction in pea (*Pisum sativum* L.) exposed to UV-B radiation. Plant Cell Environ 21(1):23–32. https://doi.org/10.1046/j.1365-3040.1998.00243.x

Havaux M, Eymery F, Porfirova S, Rey P, Dörmann P (2005) Vitamin E protects against photoinhibition and photooxidative stress in *Arabidopsis thaliana*. Plant Cell 17(12):3451–3469. https://doi.org/10.1105/tpc.105.037036

Hectors K, Prinsen E, De Coen W, Jansen MA, Guisez Y (2007) *Arabidopsis thaliana* plants acclimated to low dose rates of ultraviolet B radiation show specific changes in morphology and gene expression in the absence of stress symptoms. New Phytol 175(2):255–270. https://doi.org/10.1111/j.1469-8137.2007.02092.x

Hectors K, van Oevelen S, Guisez Y, Prinsen E, Jansen MA (2012) The phytohormone auxin is a component of the regulatory system that controls UV-mediated accumulation of flavonoids and UV-induced morphogenesis. Physiol Plant 145(4):594–603. https://doi.org/10.1111/j.1399-3054.2012.01590.x

Hofmann RW, Campbell BD, Bloor SJ, Swinny EE, Markham KR, Ryan KG, Fountain DW (2003) Responses to UV-B radiation in *Trifolium repens* L.–physiological links to plant productivity and water availability. Plant Cell Environ 26(4):603–612. https://doi.org/10.1111/j.1438-8677.2011.00458.x

Hopkins L, Bond MA, Tobin AK (2002) Ultraviolet-B radiation reduces the rates of cell division and elongation in the primary leaf of wheat (*Triticum aestivum* L. cv Maris Huntsman). Plant Cell Environ 25(5):617–624. https://doi.org/10.1046/j.1365-3040.2002.00834.x

Jansen MA, Gaba V, Greenberg BM (1998) Higher plants and UV-B radiation: balancing damage, repair and acclimation. Trends Plant Sci 3(4):131–135. https://doi.org/10.1016/s1360-1385(98)01215-1

Kakani VG, Reddy KR, Zhao D, Mohammed AR (2003) Effects of ultraviolet-B radiation on cotton (*Gossypium hirsutum* L.) morphology and anatomy. Ann Bot 91(7):817–826. https://doi.org/10.1093/aob/mcg086

Kamal-Eldin A, Appelqvist LA (1996) The chemistry and antioxidant properties of tocopherols and tocotrienols. Lipids 31(7):671–701. https://doi.org/10.1007/bf02522884

Kanungo M, Raipuria RK, Fatima A, Shukla S, Jain M, Kataria S (2022) Plant responses: UV-B avoidance strategies. In: Kataria S, Singh VP (eds) UV-B radiation and crop growth, plant life and environment dynamics. Springer, Singapore, pp 109–127. https://doi.org/10.1007/978-981-19-3620-3_7

Kapoor D, Sharma R, Handa N, Kaur H, Rattan A, Yadav P, Bhardwaj R (2015) Redox homeostasis in plants under abiotic stress: role of electron carriers, energy metabolism mediators and proteinaceous thiols. Front Environ Sci 3:13. https://doi.org/10.3389/fenvs.2015.00013

Kevers C, Le Gal N, Monteiro M, Dommes J, Gaspar T (2000) Somatic embryogenesis of *Panax ginseng* in liquid cultures: a role for polyamines and their metabolic pathways. Plant Growth Regul 31(3):209–214. https://doi.org/10.1023/A:1006344316683

Koti S, Reddy KR, Kakani VG, Zhao D, Reddy VR (2004) Soybean (*Glycine max*) pollen germination characteristics, flower and pollen morphology in response to enhanced ultraviolet-B radiation. Ann Bot 94(6):855–864. https://doi.org/10.1093/aob/mch212

Kruglova NN, Seldimirova OA, Zinatullina AE (2018) In vitro callus as a model system for the study of plant stress-resistance to abiotic factors (on the example of cereals). Biol Bull Rev 8:518–526. https://doi.org/10.1134/s2079086418060063

Laakso K, Sullivan JH, Huttunen S (2000) The effects of UV-B radiation on epidermal anatomy in loblolly pine (*Pinus taeda* L.) and Scots pine (*Pinus sylvestris* L.). Plant Cell Environ 23(5):461–472

Láposi R, Veres S, Lakatos G, Olah V, Fieldsend A, Mészáros I (2009) Responses of leaf traits of European beech (*Fagus sylvatica* L.) saplings to supplemental UV-B radiation and UV-B exclusion. Agric For meteorol 149(5):745–755. https://doi.org/10.1016/j.agrformet.2008.10.023

Li Y, He LL, Zu YQ (2010) Intraspecific variation in sensitivity to ultraviolet-B radiation in endogenous hormones and photosynthetic characteristics of 10 wheat cultivars grown under field conditions. S Afr J Bot 76:493–498. https://doi.org/10.1016/j.sajb.2010.03.005

Liebler DC (1993) The role of metabolism in the antioxidant function of vitamin E. Crit Rev Toxicol 23(2):147–169. https://doi.org/10.3109/10408449309117115

Lo HL, Nakajima S, Ma L, Walter B, Yasui A, Ethell DW, Owen LB (2005) Differential biologic effects of CPD and 6-4PP UV-induced DNA damage on the induction of apoptosis and cell-cycle arrest. BMC cancer 5(1):1–9. https://doi.org/10.1186/1471-2407-5-135

Mackerness SAH, John CF, Jordan B, Thomas B (2001) Early signaling components in ultraviolet-B responses: distinct roles for different reactive oxygen species and nitric oxide. FEBS Lett 489(2-3):237–242. https://doi.org/10.1016/s0014-5793(01)02103-2

Malá J, Cvikrová M, Máchová P, Martincová O (2009) Polyamines during somatic embryo development in Norway spruce (*Picea abies* [L.]). J For Sci 55(2):75–80

Manaf HH, Rabie KA, Abd El-Aal MS (2016) Impact of UV-B radiation on some biochemical changes and growth parameters in *Echinacea purpurea* callus and suspension culture. Ann Agric Sci 61(2):207–216

Mariotti L, Huarancca Reyes T, Ramos-Diaz JM, Jouppila K, Guglielminetti L (2021) Hormonal regulation in different varieties of *Chenopodium quinoa* Willd. exposed to short acute UV-B irradiation. Plants 10(5):858. https://doi.org/10.3390/plants10050858

McNeil JJ, Robman L, Tikellis G, Sinclair MI, Mc Carty CA, Taylor HR (2004) Vitamin E supplementation and cataract: randomized controlled trial. Ophthalmol 111(1):75–84. https://doi.org/10.1016/j.ophtha.2003.04.009

Munné-Bosch S, Schwarz K, Alegre L (1999) Enhanced formation of αtocopherol and highly oxidized abietane diterpenes in water-stressed rosemary plants. Plant Physiol 121(3):1047–1057. https://doi.org/10.1104/pp.121.3.1047

Peer WA, Bandyopadhyay A, Blakeslee JJ, Makam SN, Chen RJ, Masson PH, Murphy AS (2004) Variation in expression and protein localization of the PIN family of auxin efflux facilitator proteins in flavonoid mutants with altered auxin transport in *Arabidopsis thaliana*. Plant Cell 16(7):1898–1911. https://doi.org/10.1105/tpc.021501

Peer WA, Murphy AS (2007) Flavonoids and auxin transport: modulators or regulators? Trends Plant Sci 12(12):556–563. https://doi.org/10.1016/j.tplants.2007.10.003

Puranik N, Rajput S, Verma SK (2022) UV-B and crop research from past to new age. In: Kataria S, Singh VP (eds) UV-B radiation and crop growth, plant life and environment dynamics. Springer, Singapore, pp 93–107. https://doi.org/10.1007/978-981-19-3620-3_6

Rai K, Jaiswal D, Pandey A, Agrawal M, Agrawal SB (2022) UV-B: boon or curse? In: Kataria S, Singh VP (eds) UV-B radiation and crop growth, plant life and environment dynamics. Springer, Singapore, pp 23–54. https://doi.org/10.1007/978-981-19-3620-3_3

Rai MK, Kalia RK, Singh R, Gangola MP, Dhawan AK (2011) Developing stress tolerant plants through in vitro selection—an overview of the recent progress. Environ Exp Bot 71(1):89–98. https://doi.org/10.1016/j.envexpbot.2010.10.021

Ringli C, Bigler L, Kuhn BM, Leiber RM, Diet A, Santelia D, Klein M (2008) The modified flavonol glycosylation profile in the *Arabidopsis* rol1 mutants results in alterations in plant growth and cell shape formation. Plant Cell 20(6):1470–1481. https://doi.org/10.3410/f.1116431.572450

Sadiq M, Akram NA, Ashraf M, Al-Qurainy F, Ahmad P (2019) Alpha-tocopherol-induced regulation of growth and metabolism in plants under non-stress and stress conditions. J. Plant Growth Regul 38:1325–1340. https://doi.org/10.1007/s00344-019-09936-7

Sattler SE, Mene-Saffrane L, Farmer EE, Krischke M, Muller MJ, DellaPenna D (2006) Non-enzymatic lipid peroxidation reprograms gene expression and activates defense markers in *Arabidopsis* tocopherol-deficient mutants. Plant Cell 18(12):3706–3720. https://doi.org/10.1105/tpc.106.044065

Searles PS, Kropp BR, Flint SD, Caldwell MM (2001) Influence of solar UV-B radiation on peatland microbial communities of southern Argentina. New Phytol 152(2):213–221. https://doi.org/10.1046/j.0028-646x.2001.00254.x

Sharma J, Kumar N, Mittal P, Chakrabarti R (2022) Evaluation of UV–B protective properties of leaves and seeds of *Achyranthes aspera* in Asian catfish *Clarias batrachus* (Linn.). Photochem Photobiol Sci 21(8):1341–1356. https://doi.org/10.1007/s43630-022-00222-2

Shi C, Liu H (2021) How plants protect themselves from ultraviolet-B radiation stress. Plant Physiol 187(3):1096–1103. https://doi.org/10.1093/plphys/kiab245

Sigmaz B, Agar G, Arslan E, Aydin M, Taspinar MS (2015) The role of putrescine against the long terminal repeat (LTR) retrotransposon polymorphisms induced by salinity stress in *Triticum aestivum*. Acta Physiol Plant 37:1–9. https://doi.org/10.1007/s11738-015-2002-9

Smith J, Burrit D, Bannister P (2001) Ultraviolet-B radiation leads to a reduction in free polyamines in *Phaseolus vulgaris* L. Plant Growth Regul 35:289–294. https://doi.org/10.1023/A:1014459232710

Staxén I, Bornman JF (1994) A morphological and cytological study of *Petunia hybrida* exposed to UV-B radiation. Physiol Plant 91(4):735–740. https://doi.org/10.1034/j.1399-3054.1994.910427.x

Steinmetz V, Wellmann E (1986) The role of solar UV-B in growth regulation of cress (*Lepidium sativum* L.) seedlings. Photochem Photobiol 43(2):189–193. https://doi.org/10.1111/j.1751-1097.1986.tb09513.x

Sugimoto-Shirasu K, Roberts K (2003) "Big it up": endoreduplication and cell-size control in plants. Curr Opin Plant Biol 6(6):544–553. https://doi.org/10.1016/j.pbi.2003.09.009

Szarka A, Balint T, Gabor B (2012) The ascorbate-glutathione-α-tocopherol triad in abiotic stress response. Int J Mol Sci 13(4):4458–4483. https://doi.org/10.3390/ijms13044458

Tevini M, Iwanzik W (1986) Effects of UV-B radiation on growth and development of cucumber seedling. In: Worrest RC, Caldwell MM (eds) Stratospheric ozone reduction, solar ultraviolet radiation and plant life. SpringerVerlag, Berlin, Germany, pp 271–285. https://doi.org/10.1007/978-3-642-70090-3_21

Torabinejad J, Caldwell MM, Flint SD, Durham S (1998) Susceptibility of pollen to UV-B radiation: an assay of 34 taxa. Am J Bot 85(3):360–369. https://doi.org/10.2307/2446329

Wacksman JT (1997) DNA methylation and the association between genetic and epigenetic changes: relation to carcinogenesis. Mutat Res-Fund Mol M 375(1):1–8. https://doi.org/10.1016/s0027-5107(97)00003-1

Wargent JJ, Elfadly EM, Moore JP, Paul ND (2011) Increased exposure to UV-B radiation during early development leads to enhanced photoprotection and improved long-term performance in *Lactuca sativa*. Plant Cell Environ 34(8):1401–1413. https://doi.org/10.1111/j.1365-3040.2011.02342.x

Zavala JA, Scopel AL, Ballaré CL (2001) Effects of ambient UV-B radiation on soybean crops: impact on leaf herbivory by *Anticarsia gemmatalis*. Plant Ecol 156(2):121–130 https://www.jstor.org/stable/20051141

Zhao X, Zeng X, Lin N, Yu S, Fernie AR, Zhao J (2021) CsbZIP1-CsMYB12 mediates the production of bitter-tasting flavonols in tea plants (*Camellia sinensis*) through a coordinated activator–repressor network. Hortic Res 8. https://doi.org/10.1038/s41438-021-00545-8

Zlatev ZS, Lidon FJ, Kaimakanova M (2012) Plant physiological responses to UV-B radiation. Emir J Food Agric 24:481–501. https://doi.org/10.9755/ejfa.v24i6.14669

Zu YG, Pang HH, Yu JH, Li DW, Wei XX, Gao YX, Tong L (2010) Responses in the morphology, physiology and biochemistry of *Taxus chinensis* var. mairei grown under supplementary UV-B radiation. J Photochem Photobiol B Biol 98(2):152–158. https://doi.org/10.1016/j.jphotobiol.2009.12.001

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