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SOLAR UV-B AND UV-A/B EXCLUSION AFFECTS GROWTH AND ANTIOXIDANT ENZYMES IN CUCUMBER AND WHEAT

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ABSTRACT

The solar UV-B background level is often high and possessing an environmental challenge in most of the tropical region of the world, mainly India. A field experiment was conducted to study the effects of ambient solar ultraviolet (280-400 nm) radiation on growth parameters and activity of antioxidant enzymes in wheat (*Triticum aestivum*) and cucumber (*Cucumis sativum*). Plants grown under ambient UV radiation were compared with those grown without UV-B and UV-A/B by excluding ambient UV-B and UV-A/B radiation. To exclude ambient UV components, the sunlight was filtered through a polyester film that selectively absorbed UV-B or UV-A/B. For ambient UV-B effects, plants were grown under polyethylene filters that transmitted the complete solar light spectrum. The results indicate increased shoot length, leaf area, dry matter accumulation and fresh weight of plants of both the crop species grown without UV compared with those grown under ambient UV. The antioxidant enzymes like superoxide dismutase, ascorbic acid peroxidase, peroxidase, glutathione peroxidase and UV-B absorbing compounds were reduced after exclusion of solar UV components in both the crops. Reduction in the antioxidant enzyme activities after UV exclusion indicated that ambient UV components exert a significant stress on these crop plants. Thus solar UV components exerted a limitation on the potential growth of cucumber and wheat plants. The sensitivity index (SI) was calculated for ambient solar UV induced changes in plant height, biomass accumulation and leaf area; according to UV-SI, we conclude that monocot species (wheat) may be less sensitive to current solar UV-B compared with dicots (cucumber).

Key Words: Antioxidant, Biomass, Growth, UV Exclusion, UV Sensitivity Index

Abbreviations

APX	Ascorbic acid peroxidase
ASA	Ascorbic acid
CAT	Catalase
DAE	Days after emergence
EDTA	Ethylenediaminetetraacetic acid
FC	Filter control
GPX	Glutathione peroxidase
GR	Glutathione reductase
H ₂ O ₂	Hydrogen peroxide
NBT	Nitroblue tetrazolium chloride
OC	Open control
PVP	Polyvinylpyrrolidone
POD	Peroxidase
ROS	Reactive oxygen species
SOD	Superoxide dismutase
UAS	UV absorbing substances
-UV-B	UV-B excluded plant
-UV-B/A	UV-B and UV-A excluded plant
UV-SI	UV sensitivity index

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INTRODUCTION

Plants are affected by different kind of stresses which are often species or location specific. They include drought, high salinity, extremes temperatures, water logging, mineral nutrient deficiency, metal toxicity, pollutants and ultraviolet-B (UV-B) radiation (Gupta *et al.*, 2011). Depletion of the stratospheric ozone layer is leading to an increase in solar UV-B radiation (280-320 nm) reaching the earth's surface (McKenzie *et al.*, 2011). Enhanced UV-B radiation produces deleterious effects on physiological and morphological traits of plants and thus, posing a severe threat to the existence and survival of organisms (Frohnmeier and Staiger, 2003; Prasad *et al.*, 2005; Klem *et al.*, 2012). The susceptibility to elevated UV-B irradiation is dictated by a complex interplay between protection, repair and other factors that may lead to highly variable UV-B susceptibility among the species. Some plant species are tolerant or even show stimulation, when exposed to UV-B radiation, while some are highly susceptible (Lesser *et al.*, 1994; Xiong *et al.*, 1995, 1996).

Many studies have shown deleterious UV-B effects on plants including reduced photosynthesis, biomass reduction, decreased protein synthesis, impaired chloroplast function, damage to DNA, etc. which are extensively review (Jenkins, 2009; Kakani *et al.*, 2003). Exposure of plant tissue to UV-B (280-315 nm) radiation accelerates the level of reactive oxygen species (ROS), such as $^1\text{O}_2$, O_2^- , H_2O_2 and OH and can cause oxidative damage to proteins, lipids and nucleic acids. Enhanced production of ROS in plant tissues exposed to supplemental level of UV-B (sUV-B) has detrimental effects on enzyme activities and gene expression, which ultimately leads to cellular damage and programmed cell death (Mackerness *et al.*, 1998). The key factor for UV-B tolerance may be considered as UV-B absorbing pigments, regulation of active oxygen species levels and activity of antioxidants, and the effective repair mechanism for PS II, one of the important components of photosynthetic electron transport chain (Xiong *et al.*, 1995; Adhikary and Sahu, 1998; Mackerness *et al.*, 2001).

Plant have developed a complex biochemical defense system that including carotenoids and flavonoids. Flavonoid compounds, as secondary metabolites are considered to play a major role in protecting plants from UV-B damage (Liang *et al.*, 2006). These flavonoids generally absorb the light in the region of 280-320 nm and thus are capable of acting as a UV filter, thereby protecting the photosynthetic tissues from damage (Siefertmann, 1987). These pigments play an important role against UV-B damage in higher plants (Kumari *et al.*, 2009; Balouchi *et al.*, 2009; Hassan *et al.*, 2013).

An efficient antioxidant defense system is present in plants to counteract oxidative stress. It is composed by enzymatic and non-enzymatic mechanisms. The main enzymatic antioxidants are superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), ascorbate peroxidase (APX) and glutathione reductase (GR), whereas non-enzymatic portion comprised of low molecular weight antioxidants i.e. proline, thiol, ascorbic acid and glutathione (Gill and Tuteja, 2010). The information concerned plants respond to UV-B stress by activating antioxidant enzymes like Superoxide dismutase, Ascorbic acid peroxidase, Glutathione reductase (Takeuchi *et al.*, 1995; Rao *et al.*, 1996; Tekchandani and Guruprasad, 1998; Jain *et al.*, 2003; Kataria *et al.*, 2007).

Much of the early work concerning the effects of UV-B radiation on terrestrial plants was conducted indoors using growth chambers or green-houses. By the 1990s, consensus was that many of these reports of UV-B effect were exaggerated and that extrapolation of these results to field responses was not appropriate (Caldwell and Flint 1996). Since then, there has been emphasis on field studies either by supplementing natural UV-B or by lowering ambient UV-B by means of UV-B absorbing filters. There have been only few studies regarding exclusion of UV-A and UV-B from solar radiation in tropical conditions like India (Pal *et al.*, 2006; Guruprasad *et al.*, 2007; Dehariya *et al.*, 2012; Kataria *et al.*, 2013; Baroniya *et al.*, 2013). Two crops, wheat and cucumber, were studied in the present investigation to evaluate their response to UV-B/UV-A radiation in the Central region of India, Indore. In the present study, we used the exclusion method, to assess the influence of current solar UV-B and UV-A/B radiation on the growth and antioxidant system of two crop species wheat (monocot) and cucumber (dicot).

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MATERIALS AND METHODS

Plant Material and Experiment Design

All the field experiments were conducted in the Botanical garden of School of Life Sciences, Devi Ahilya University, Indore, and M.P. (Latitude -22.4° N) India under natural sunlight. Seeds of cucumber (*Cucumis sativus* var; Long green) were obtained from Sutton and Sons Pvt. Ltd. Calcutta, India and wheat seeds (*Triticum aestivum* var. Purna) were collected from Regional Wheat Research Station, Indian Agriculture Research Institute, Indore. Seeds were treated with recommended fungicides viz. bavistin and diathane M at 2 g/kg seeds. Plants were irrigated and fertilized (NPK) at regular intervals to avoid nutritional deficiencies. Seeds were sown inside iron mesh cages (120 cm L \times 90 cm W \times 150 cm H) in 3 feet row length and 30 cm space between the rows. The cages were wrapped with UV-B, and UV-A/B cutoff filters (Garware Polyester Ltd., Mumbai) that specifically eliminate UV-B (<300 nm) and UV-A/B (<400 nm) radiation and the control plants were grown under an ordinary polythene filter permissible to UV (280-400 nm) radiation. The transmission of the filters was measured by Shimadzu (UV-1601) as described in Kataria *et al.*, (2013). The seedlings were exposed to solar UV radiation from the time of germination. Growth data; plant height, leaf area, fresh weight and dry weight has been taken after 30 days after emergence (DAE) of seedlings, leaves of the same seedlings have been used for biochemical analysis.

Growth Parameters

The plants were grown for 30 days under UV-B and UV-A excluded conditions. Plant height was measured from apex to the starting part of the stem and the mean height of 15 plants was taken. Leaf area was measured in primary leaves of seedling after 30 DAE. Area of leaves was taken by pressing the blotted dry leaf on a graph paper (mm) and tracing the exact outline. The area was measured by weighing the graph cuttings of leaves (Kataria and Guruprasad, 2012a). The mean of five leaves was taken as the average value.

Total plant fresh weight was taken after removing the plants and washing the roots thoroughly with water. Dry weight was obtained after oven-drying of the plants at 60°C for 72 h and weighing on an analytical balance.

Antioxidant Enzymes

All operations were performed at 4°C . The enzyme extract was prepared by homogenizing 0.5g leaves with 10% (w/v) polyvinylpyrrolidone and 10 ml of 0.1 mol/L phosphate buffer (pH 7.0) for SOD, APX, GR and GPX. The homogenate was filtered through four layers of cheesecloth, centrifuged at 15,000 rpm for 30 minutes and the supernatant obtained was used to determine the activity of those enzymes described.

Superoxide dismutase (SOD) [EC 1.15.1.1] activity was assayed as described previously by Beauchamp and Fridovich (1971). The reaction mixture contained 0.24 mM riboflavin, 2.1 mM methionine, 1% Triton-X 100, 1.72 mM nitroblue tetrazolium chloride (NBT) in 50 mM sodium phosphate buffer (pH 7.8) and 200 μl of enzyme extract (in 50 mM Tris-HCl buffer, pH 7.8). The activity was expressed as Units/mg protein. One unit of SOD was defined as the amount of enzyme required to cause 50% inhibition in the rate of NBT photo reduction.

Ascorbic acid peroxidase (APX) [EC 1.11.1.11] activity was measured by the method of Nakano and Asada (1987). The 3 ml reaction mixture contained 2.5 ml sodium phosphate buffer (pH 7.4, 50 mM), 0.3 mM ascorbate and 0.06 mM EDTA, 300 μl enzyme extract (in 50 mM sodium phosphate buffer, pH 7.4) and 200 μl of 2 mM H_2O_2 . The decrease in absorbance at 290 nm (extinction coefficient $2.8 \text{ mM}^{-1} \text{ cm}^{-1}$) was recorded at 25°C for 1 min. The activity was expressed as m mole AA oxidized/min/mg protein.

Guaiacol peroxidase (GPX) [EC 1.11.1.7] was assayed as described by Maehly (1955). The reaction mixture contained 0.5 ml enzyme extract (in 0.02M, phosphate buffer, pH 6.4), 1 ml 20 mM guaiacol and 3 ml 0.02 M phosphate buffer. The reaction was started by the addition of 0.03 ml of H_2O_2 (88.2 mM). The initial and final absorbance was recorded at 470 nm for 2 min. The activity was calculated as the change in OD/min/mg protein.

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Protein was estimated by the method of Lowry *et al.*, (1951) using BSA as the standard.

UV-B Absorbing Compounds (UAS)

UAS was measured in primary leaves by the method of Mazza *et al.*, (2000). For spectrophotometric determination, UAS content were sampled from four leaves (each from a different plant) per plot (youngest fully expanded leaf). Each sample (one 1.0 cm diameter leaf disc) was placed in 5 ml of 99:1 (methanol: HCl) and allowed to extract for 48 h at -4°C . Absorbance of the extracts was read at 305 nm for determination of total UV-B absorbing compounds. Absorbance was expressed on leaf fresh weight basis.

UV Sensitivity Index (UV-SI)

The sensitivity index (SI) was used to evaluate the overall response of wheat and cucumber (at 30 DAE) to ambient UV radiation by removing of UV-B and UV-A/B from the solar spectrum. Differences in the UV-sensitivity of both the crops were ascertained by a UV sensitivity index (UV-SI) which was calculated according to the following equation (Kataria and Guruprasad, 2012a):

$$\text{UV-SI} = \frac{\text{Plant height} + \text{UV}}{\text{Plant height} - \text{UV}} + \frac{\text{Dry weight} + \text{UV}}{\text{Dry weight} - \text{UV}} + \frac{\text{Leaf area} + \text{UV}}{\text{Leaf area} - \text{UV}}$$

An UV-tolerant plant has an UV-SI of 3, whereas UV-SI values below 3 indicate an UV-sensitive plant, where (+UV) means filter control; (-UV) means after UV-B exclusion or UV-A/B exclusion from solar spectrum.

RESULTS AND DISCUSSION

Results

Growth Parameters

Exclusion of UV enhanced plant height, leaf area, fresh and dry weight of plants of both the crops wheat and cucumber (Figure 1). Exclusion of UV-A/B enhanced the growth parameters to a greater extent compared to exclusion of UV-B in cucumber whereas in wheat enhancement was more after UV-B exclusion. Plant height was enhanced by 46% and 115%; area of primary leaf was enhanced by 74% and 38% respectively by excluding UV-B and UV- A/B (Figure 1 A, B) in cucumber. Whereas in wheat there was enhancement of 85% and 15% in plant height; area of primary leaf enhanced by 49% and 10% by excluding UV-B and UV- A/B (Figure 1 A, B).

Exclusion of UV-B and UV- A/B significantly enhanced the fresh weight and dry weight of plants in both the crops, but the magnitude of the response was more in cucumber than in wheat (Figure 1 C, D).

Antioxidant Enzymes

The activity of SOD, APX, POD and GR were lowered by exclusion of UV-B and UV-A/B in both the crops; wheat and cucumber (Figure 2 A, B, C, D). The difference between the control and UV excluded plants was maximum with respect to SOD (61% and 87% by -UV-B and -UV-A/B respectively) in case of cucumber. Whereas there was a reduction of only 45% and 43% by -UV-B and -UV-A/B respectively in wheat (Figure 2A). APX, POD and GR activities were also reduced to a greater extent by exclusion of UV-B and UV-A/B in cucumber than in wheat (Figure 2 B, C, D).

UV-B Absorbing Compounds (UAS)

One mechanism that could protect the sensitive tissue is an alteration in leaf transmittance properties. Epidermal UV-B absorbing compounds are synthesized in most plant species in response to UV radiation. These compounds absorb UV radiation strongly, but do not absorb PAR. In this experiment, plants methanolic extracts of both the crops grown under UV-B and UV-A/B exclusion had a significantly lower absorbance of extract (presumably flavonoids) at 305 nm than those of plants grown in the presence of UV-B and UV-A (Figure 3). But the magnitude of the reduction in UAS by the exclusion of solar UV was more in cucumber than wheat.

UV Sensitivity Index (UV-SI)

UV Sensitivity Index (UV-SI) varied for both the crops tested in the present study. The sensitivity index was numerically lower for cucumber var. long green (1.78) and higher for wheat var. Purna (2.25) for

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ambient level of UV-B. Wheat showed SI of (2.5) and cucumber showed an SI of (1.5) for ambient level of UV-A/B (Figure 4).

Discussion

The present study showed that the current level of ambient UV-B radiation in Indore (22°44'N), India had negative effect on growth and dry matter accumulation of wheat and cucumber. The activities of antioxidant enzymes SOD, APX, GR and POX increased in filter control plants of both the crops. Filter control plants are grown under polyethylene filter which is transmissible to ambient UV-B and UV-A (Figure 2). The observed trend was in agreement of earlier studies, reporting induction of the activities of these enzymes under UV-B to detoxify excess ROS as reported in *Cucumis sativus* (Jain et al., 2004), *Triticum aestivum* and *Vigna radiata* (Agrawal and Rathore, 2007) and *Cassia auriculata* (Agarwal, 2007). Activation of antioxidant enzymes in response to supplemental UV-B has been recorded in several plants like *Arabidopsis thaliana* (Rao et al., 1996), wheat (Sharma et al., 1998), cucumber (Sunita and Guruprasad, 1998; Jain et al., 2003, 2004; Kataria et al., 2007), pea nut (Tang et al., 2010), *Aeschynomene aspera* L. (Ramya and Balakrishnan, 2013), *Hordeum vulgare* (Zancan et al., 2008), *Glycine max* (Xu et al., 2008), *Vigna unguiculata* *Crotalaria juncea* (Selvakumar, 2008) and *Vicia Faba* (Hassan et al., 2013).

Increasing trend of GR activity was also consistent with other studies performed under UV-B stress (Costa et al., 2002; Jain et al., 2004; Xu et al., 2008). Induction of APX and GR due to sUV-B indicates a preferential synthesis/activation of these enzymes, playing a crucial role in scavenging of H₂O₂ via the ascorbate-glutathione cycle (Noctor and Foyer, 1998).

The response of antioxidant enzymes in wheat and cucumber to ambient UV was not tested earlier. The data presented here indicates that the response of wheat and cucumber in terms of reduction in the activity of antioxidant enzymes by exclusion of UV components signifies a common mechanism of signal transduction in plants. Baroniya et al., (2013) also found that the activities of antioxidant enzymes, SOD, APX, GPX and GR and the level of ASA were decreased, while α -tocopherol increased after the exclusion of UV-B and UV-A/B in eight varieties of soybean.

Our results also suggest that the ambient level of UV-B and UV-A radiation evoked some active oxygen species to accumulate, which in turn retarded the growth and development in cucumber and wheat. Enhancement in APX activity and ascorbic acid level under ambient UV-B and its reduction by the exclusion of UV-B was demonstrated in soybean leaves (Xu et al., 2008).

When the UV-B and UV-A are removed from the solar radiation, the synthesis of UV absorbing substances is expected to decrease.

The data presented also showed synthesis of UAS is decreased in the plants grown under UV-B exclusion and reduction is more pronounced after excluding the UV-A/B. This is in agreement with the earlier finding on other plants with similar exclusion experiments (Dehariya et al., 2011; Kataria et al., 2012b; Kataria et al., 2013). UV absorbing compounds frequently increase in response to UV-B and can perform important UV-B protective functions (Mazza et al., 2000). In addition to this, synthesis of UV absorbing substances like flavonoids and other phenolic compounds are enhanced in response to supplemental UV-B (Searles et al., 2001; Day and Neale, 2002).

Sensitivity indices or response indices have been established as useful indicators of plant sensitivity to UV-B radiation (Saile-Mark and Tevini, 1997). In the present study, sensitivity indices of both the crops relative to plant height, total dry weight accumulation and leaf area could reflect the overall sensitivity of wheat and cucumber to current level of UV radiation. The UV sensitivity index (SI) of both the crop species was significantly less than 3, which means both of them are UV (280-400 nm) sensitive to some extent. UV-SI calculated after exclusion of both UV-A and UV-B from solar radiation indicated wheat var. Purna is least sensitive (SI- 2.50) and cucumber var. long green is most sensitive (SI- 1.50) to current UV radiation. UV-SI after exclusion of only UV-B showed similar results, wheat had an UV-SI (2.25) and cucumber showed UV-SI's (1.77). Thus cucumber (a C₃ dicot) is more sensitive than wheat (a C₃ monocot) to ambient level of UV (280-400 nm) radiation at Indore (22°44'N), India.

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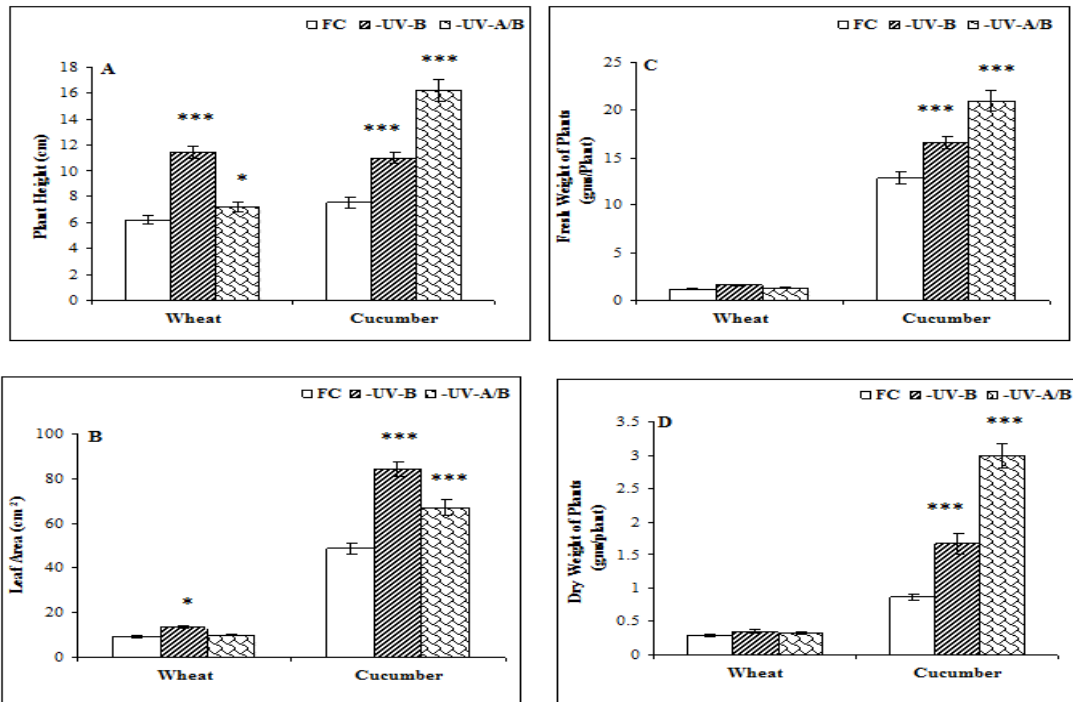


Figure 1: Effect of exclusion of solar UV-B and UV-A/B on (a) Plant height (b) Leaf area and (c) Fresh weight of plants and (d) Dry weight accumulation of wheat and cucumber at 30 days after emergence of the seedlings (DAE). The vertical bar indicates \pm SE for mean. Values are significantly different at ($P^* < 0.05$, $*P < 0.001$) from filter control (Newman-Keulis Multiple Comparison Test).**

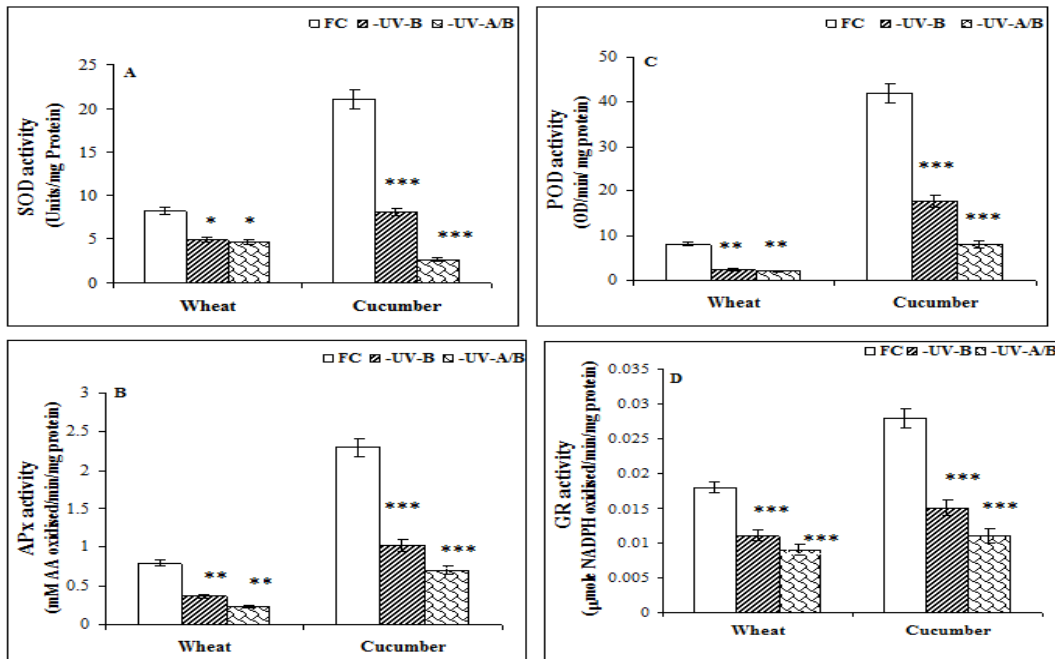


Figure 2: Effect of exclusion of solar UV-B and UV-A/B on (a) SOD, (b) APX, (c) POD and (d) GR activity in primary leaves of wheat and cucumber at 30 DAE. The vertical bar indicates \pm SE for mean. Values are significantly different at ($P^* < 0.05$, $P < 0.01$, $***P < 0.001$) from filter control (Newman-Keulis Multiple Comparison Test).**

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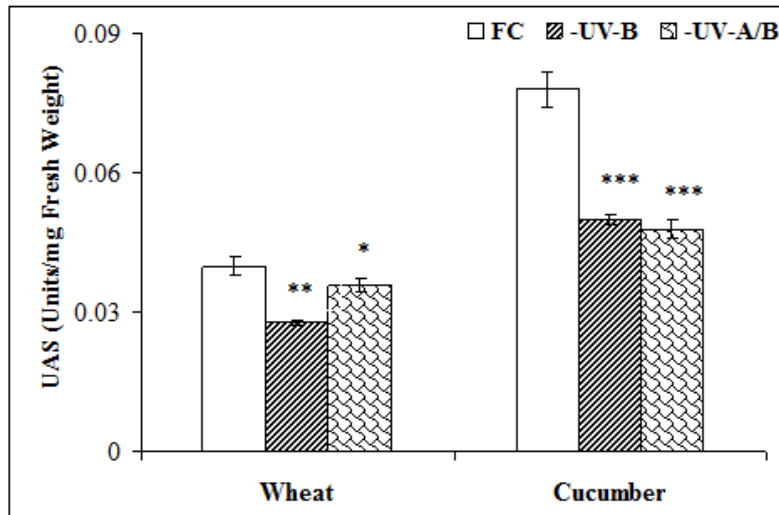


Figure 3: Effect of exclusion of solar UV-B and UV-A/B on UV-B absorbing substances (UAS) content in primary leaves of a wheat and cucumber at 30 DAE. The vertical bar indicates \pm SE for mean. Values are significantly different at ($P^* < 0.05$, $**P < 0.01$, $***P < 0.001$) from filter control (Newman-Keulis Multiple Comparison Test).

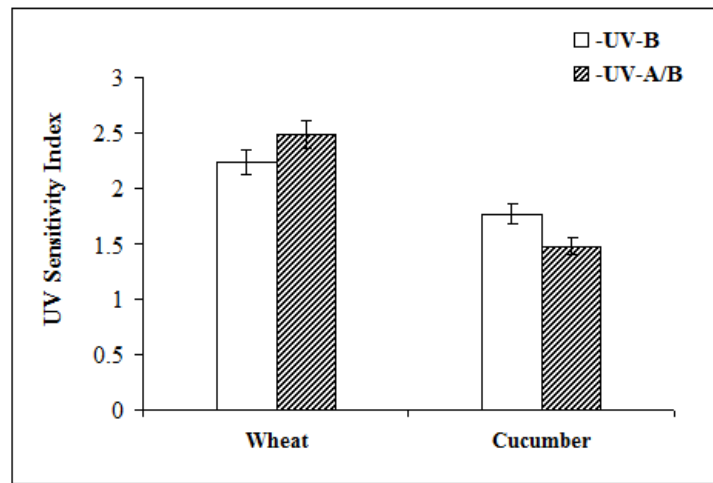


Figure 4: UV sensitive index for sensitivity of wheat and cucumber to ambient level of UV radiation by the exclusion of solar UV-B and UV-A/B at 30 DAE. The vertical bar indicates \pm SE for mean.

Finally, it suggests that antioxidant enzymes provide protection during oxidative injury caused by UV-B stress. Exclusion of UV removes this stress and alters the metabolism of plants to favour primary metabolism resulting in enhanced plant height, leaf area and biomass in wheat and cucumber. As it is clear that these oxygen-scavenging systems play an important role in the response of wheat and cucumber to UV-B exposure, the examination of these two systems could provide important insight into how these C_3 monocot and dicot plants, and possibly other plants as well, are being affected by current global climate change.

Conclusion

In conclusion, an altered the pattern of activity of antioxidant enzymes and UAS is observed in the absence of ambient UV as a result of absence of stress. Thus exclusion of solar UV eliminates the defense against UV-B stress and leads to enhance the growth and biomass accumulation of both the crop plants. It

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indicates that the ambient levels of UV-A along with UV-B are significantly high to accumulate active oxygen species which evoke the antioxidant defense systems, which in turn retards the growth and development of wheat and cucumber plants. Exclusion of UV components is advantageous from the agricultural point to enhance the growth of these plants.

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