

## Effects of supplemental ultraviolet-B and mineral nutrients on growth, biomass allocation and yield of wheat (*Triticum aestivum* L.)

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**Abstract:** A field study was conducted to investigate the effects of supplemental ultraviolet-B radiation (280-320 nm) on the growth, biomass allocation and yield of two tropical cultivars (HD 2329 and HUW 234) of wheat (*Triticum aestivum* L.) at four different combinations of mineral nutrients (N, P and K). Supplemental UV-B caused reductions in biomass, shoot length, root length, yield and harvest index. Plants grown without fertilizers exhibited maximum inhibitory response. Plants grown under additional nutrient dose were less affected at enhanced UV-B. The study suggests that use of 1.5 times the recommended dose of N, P and K provided maximum protection against UV-B damage in both cultivars. Cultivar HD 2329 was more responsive than cultivar HUW 234 to the additional dose of mineral nutrients.

**Resumen:** Se llevó a cabo un estudio de campo para investigar los efectos del incremento de radiación ultravioleta-B (280-320 nm) sobre el crecimiento, la asignación de biomasa y el rendimiento de dos cultivares tropicales (HD 2329 y HUW 234) de trigo (*Triticum aestivum* L.) en cuatro combinaciones diferentes de nutrientes minerales (N, P y K). La UV-B adicional causó reducciones en la biomasa, la longitud del tallo, la longitud de la raíz, el rendimiento y el índice de cosecha. Las plantas que crecieron sin fertilizantes mostraron la máxima respuesta inhibitoria. Las plantas que crecieron con dosis adicionales de nutrientes fueron menos afectadas por el aumento de la UV-B. El estudio sugiere que el uso de 1.5 veces la dosis recomendada de N, P y K ofreció la máxima protección contra el daño por UV-B en ambos cultivares. El cultivar HD 2329 respondió más fuertemente que el cultivar HUW 234 a la dosis adicional de nutrientes minerales.

**Resumo:** Para investigar os efeitos de uma suplementação de radiação ultravioleta-B (280-320 nm) no crescimento, distribuição de biomassa e rendimento em duas cultivares tropicais de trigo (*Triticum aestivum* L.) (HD 2329 e HUW 234) sob quatro combinações diferentes de nutrientes minerais (N, P e K) realizou-se um ensaio de campo. A suplementação de UV-B causou uma redução na biomassa, no crescimento do lançamento terminal, comprimento das raízes, rendimento e índice de colheita. As plantas crescendo sem fertilizantes exibiram uma resposta inibitória máxima. As plantas crescendo sob um suplemento adicional de nutrientes foram menos afetadas à maior exposição de UV-B. O estudo sugere que para ambas as cultivares, o uso de 1,5 vezes mais do que a dose recomendada de N, P e K proporcionou a proteção máxima contra os danos provocados pelo UV-B. A cultivar HD 2329 respondeu melhor do que a HUW 234 à adição suplementar de nutrientes minerais.

**Key words:** Biomass allocation, harvest index, mineral nutrients, plant growth, *Triticum aestivum*, ultraviolet-B, yield.

## Introduction

Increase in penetration of UV-B (280-320 nm) to terrestrial surface as a consequence of depletion of the stratospheric ozone layer has received much global concern. A 10% depletion in stratospheric ozone corresponds to a 20% increase in the fluence of biologically damaging UV-B, which is likely to increase in future, if ozone damage is not checked (Baker & Allen 1994). Enhanced UV-B radiation can deleteriously affect overall growth and biomass accumulation in plant species (Tevini 2000). Plants contain a large number of UV-B sensitive targets, including nucleic acids, lipids, proteins and quinines (Jordan 1996), which must be protected to ensure the normal growth and development of plants. Failure to do so may lead to alterations in the overall morphology and physiology of many plants exposed to UV-B.

Earlier studies have focused mainly on the independent effects of UV-B radiation on plants (Ambasht & Agrawal 1995; Demchik & Day 1996; Smith *et al.* 2000). However, several abiotic factors altered and/or modified the responses of plants to UV-B, because of their interactions. The interactions between UV-B radiation and other environmental stresses, such as herbicides (Kulandaivelu & Annamalainathan 1991), high temperature (Nedunchenzhian *et al.* 1995), freezing (Dunning *et al.* 1994), drought (Petropoulou *et al.* 1995) and mineral deficiency (Murali & Teramura 1985a,b; 1987), have reduced the UV-B damage to plants as compared to non-treated control plants. The UV-B damage to plants has been correlated to the nitrogen status of the given plants (Hunt & McNeil 1998); plant growth increases at a high nutrient availability (Levizou & Manetas 2001).

Interaction of UV-B at varying fertility levels of tropical plants is little understood now. In the present field study, therefore, two tropical cultivars HD 2329 and HUW 234 of wheat (*Triticum aestivum* L.) were exposed to supplemental UV-B radiation at varying levels of nutrients (N, P and K) to evaluate their interactive effects on sensitivity of the cultivars.

## Materials and methods

Wheat seeds of cultivars HD 2329 and HUW 234 were grown in 24 plots of 1.0 m<sup>2</sup> each following standard agronomical practices. The experimental

design was a split plot with UV-treatment as whole plot and fertilizer treatment as sub plots randomized within the whole plots. Plots were earlier prepared at four combinations of N, P and K: (I) without additional nutrients, (II) recommended dose (RD) (120, 80 and 60 kg ha<sup>-1</sup> N, P and K, respectively) of nutrients, (III) 1.5 times the recommended dose (RD), and (IV) double the RD. For convenience, these treatments were referred as F<sub>0</sub>C, F<sub>1</sub>C, F<sub>2</sub>C and F<sub>3</sub>C, respectively and corresponding UV-B treated plants were designated as F<sub>0</sub>T, F<sub>1</sub>T, F<sub>2</sub>T and F<sub>3</sub>T. Half of the N and full dose of P and K were provided as basal dose and remaining N was provided as top dressing. After emergence of seedlings, planted rows were thinned to maintain equality. Plots were irrigated evenly as and when required.

UV-B treatment was started just after the emergence of seedlings for 5 h day<sup>-1</sup> in the middle of the photoperiod (10 A.M. to 3 P.M.), and continued until the plants attained maturity. Supplemental UV-B radiation was provided by Q-Panel UV-B 313 fluorescent lamps (Q-Panel Inc., Cleveland, Ohio, USA). UV-B lamps were covered by 0.13 mm thick cellulose diacetate film to absorb the radiations emitted below 280 nm for enhanced treatment, and by 0.13 mm thick polyester film to absorb radiation below 320 nm for control (without UV-B). Four lamps per bed were suspended above and perpendicular to the planted rows on adjustable steel frame. A bank of four lamps was fitted 30 cm apart to the planted rows. A distance of 30 cm was kept constant between the top of the plant canopy and UV-B lamps by altering the distance of the lamps.

Intensity of UV-B was measured at the top of the plant canopy by an ultraviolet intensity meter (UV P Inc. San Gabriel, (A), USA). The readings were converted to UV-B<sub>BE</sub> values by comparing with the Spectro Power Meter (Scientech, Boulder, USA). The plants beneath cellulose diacetate film received UV-B<sub>BE</sub> (ambient + 7.1 KJ m<sup>-2</sup>) that mimicked 20% reduction in the stratospheric ozone at Allahabad (20° 47' N) during clear sky condition on the summer solstice (Green *et al.* 1980) normalized at 300 nm. The ozone column thickness was assumed at 3.0 mm, the albedo 0 and the scatter 1.0. Filters were changed frequently to avoid aging effects on the spectral transmission of UV-B.

Plants were harvested randomly in triplicate for each treatment 35, 55, 75 and 120 days after



sowing (DAS). Different plant parts were separated and then oven dried at 80°C until constant weights had been achieved. Plant parts were weighed separately and values were used for calculating root-shoot ratio (RSR), crop-growth rate (CGR) and harvest index (HI) as given by Hunt (1982). The length of shoot and root was measured in cm and the value was used for measuring absolute growth rate (AGR). Yield per plant was recorded and expressed as g plant<sup>-1</sup>.

Statistical analysis was carried out through SPSS software (SPSS Inc., version 10.0). Multivariate analysis was done for (i) sampling time, (ii) UV-B treatment, and (iii) mineral nutrients and their interactions.

## Results and discussion

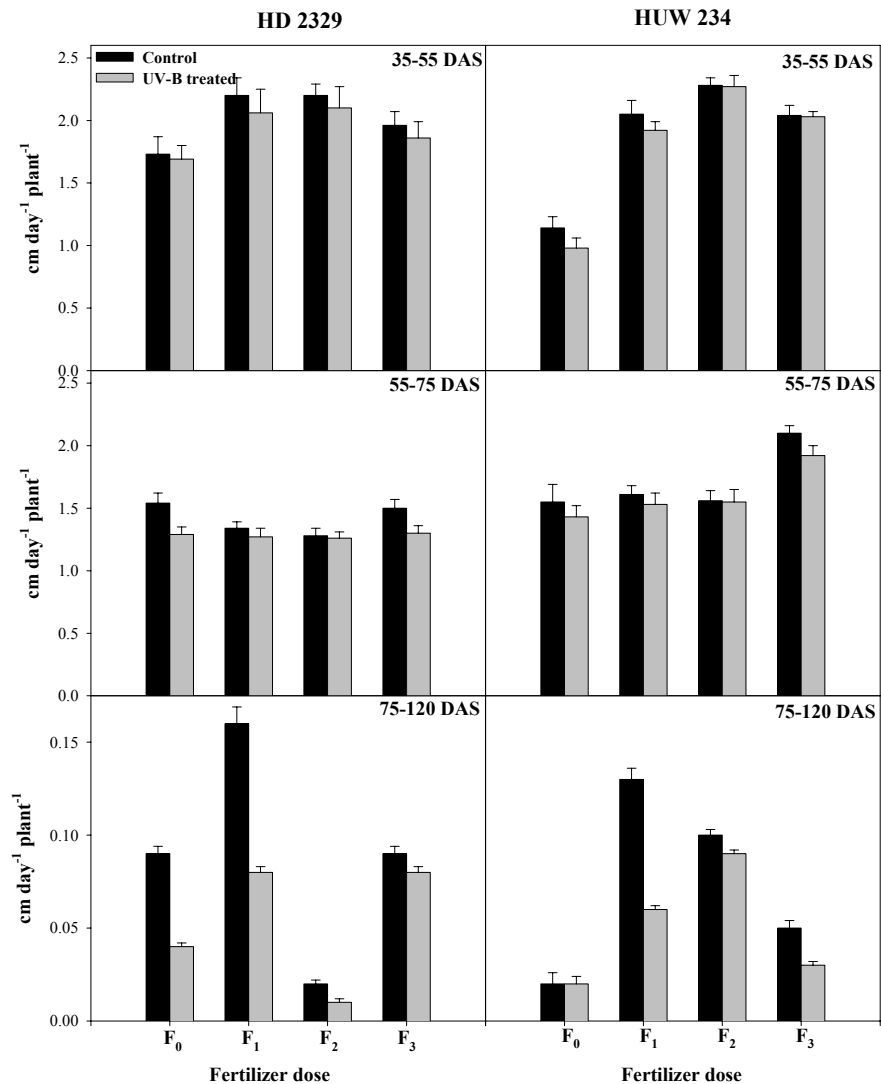
UV-B exposure caused reductions in shoot and root lengths. Reduction in shoot length was 8.7%, 5.2%, 2.9% and 7.0% in cultivar HD 2329 and 7.0%, 7.7%, 2.3% and 5.7% in HUW 234 at final harvest (120 DAS) for F<sub>0</sub>T, F<sub>1</sub>T, F<sub>2</sub>T and F<sub>3</sub>T treatments, respectively. Reductions in root length for these treatments were 19.7%, 35.6%, 2.8%, 13.4% in HD 2329 and 18.3%, 16.2%, 15.2%, 20.1% in HUW 234, as observed at 120 DAS (Table 1). Minimum reductions in shoot and root lengths, taking into account all samplings and both the cultivars, were observed at F<sub>2</sub>T treatment. Multivariate analysis showed that differences in shoot length were significant due to plant age, UV-B treatment and fertilizer dose in both the cultivars (Table 3). Root length showed significant variations due to all the factors and their interactions in HUW 234 whereas only due to plant age and UV-B treatment in HD 2329 (Table 3). Absolute growth rate (AGR) for plant height declined due to UV-B treatment in both the cultivars, and minimum reduction was observed in F<sub>2</sub>T treatment (Fig. 1).

Total biomass increased by addition of fertilizers with maximum value at F<sub>1</sub>C treatment of both the cultivars (Table 2). UV-B exposure led to a decrease in total biomass with the maximum decrease at F<sub>0</sub>T treatment (52.8% in HD 2329 and 55.6% in HUW 234). Root biomass showed higher reductions relative to the above ground biomass. The reductions in root biomass were 59.4 %, 30.2 %, 16.7 % and 42.2% in HD 2329 and 65.1 %, 39.3 %, 28.7 % and 43.4% in HUW 234 at treatments F<sub>0</sub>T, F<sub>1</sub>T, F<sub>2</sub>T and F<sub>3</sub>T, respectively.

Root-shoot ratio (RSR) was lower under UV-B treatment with a minimum reduction at F<sub>2</sub>T treatment (6.4% in HD 2329 and 3.7% in HUW 234). Biomass of stem, leaf and spike also declined in UV-B treated plants all at fertility regimes in both the cultivars. For F<sub>0</sub>T treatment, the reduction was maximum in dry stem weight, while for treatments F<sub>1</sub>T, F<sub>2</sub>T and F<sub>3</sub>T, reduction was maximum in dry leaf weight in both the cultivars. Reductions in dry stem weight for these treatments were 60.3 %, 27.7 %, 11.4 % and 33.3% in HD 2329 and 60.3 %, 35.8 %, 19.1% and 27.6 % in HUW 234, in dry leaf weight 51.4 %, 44.3 %, 34.1 % and 51.0 % in cultivar HD 2329 and 54.8 %, 37.9 %, 32.9 % and 51.2 % in HUW 234, and in dry spike weight 41.3 %, 13.3 %, 5.7 % and 31.2 % in HD 2329 and 46.7 %, 31.3 %, 29.1 % and 34.6% in HUW 234 as observed at 120 DAS. Statistically, the variations in stem, leaf and spike weight were significant due to UV-B treatment and fertilizers in both the cultivars (Table 3). CGR value showed that the crop productivity was lower under supplemental UV-B treatment as compared to their respective controls in both the cultivars (Fig. 2). Minimum reduction in CGR was observed in F<sub>2</sub>T treatment. Statistically, variations in CGR were significant due to plant age, UV-B treatment, fertilizers and interaction between plant age and fertilizer dose in HD 2329 and plant age, UV-B treatment, fertilizers and their interactions in HUW 234 (Table 3).

Grain yield was higher under nutrient amended plants. Supplemental UV-B exposure reduced grain yield at all the treatments in both the cultivars (Fig. 3). Reduction in grain yield was 66.5%, 34.1%, 17.1% and 47.8% in HD 2329 and 69.1%, 53.0%, 34.8% and 49.4% in HUW 234 at F<sub>0</sub>T, F<sub>1</sub>T, F<sub>2</sub>T and F<sub>3</sub>T treatments, respectively. HI was also lowered down due to UV-B treatment (Fig. 4). The variations in yield were significant due to UV-B treatment and fertilizers and their interactions in both the cultivars (Table 3).

Reduction in plant height reflects a specific photomorphogenic response of plants to UV-B, mediated by a UV-B photoreceptor (Ballare *et al.* 1995; Leracari *et al.* 1990). Tevini *et al.* (1989) have suggested that reductions in plant height are characteristic of UV-B sensitive plants. The reduced stem height may be due to shorter internodes rather than reduced number of nodes, as observed in *Pisum sativum* L cv. JI 1289 (Gonzalez *et al.* 1998).



**Fig 1.** Effect of enhanced UV-B radiation on AGR (cm day<sup>-1</sup> plant<sup>-1</sup>) of two wheat cultivars at different growth stages and with different levels of applied fertilizer.

Reduction in total biomass is a consequence of decreased plant height. Alexieva *et al.* (2001) have reported reduction in fresh and dry biomass of wheat and pea seedlings after exposure to enhanced UV-B. Reductions in dry matter and yield have been found associated with reduced photosynthetic rate (Strid *et al.* 1990), stunted growth and changed morphology at supplemental UV-B radiation (Barnes *et al.* 1990; Bond *et al.* 1996; Sharma *et al.* 1998; Teramura 1980). However, the reduction showed no correlation with decline in photosynthesis rate in barley plants (Ghisi *et al.* 2002). Ambasht & Agrawal (1995) found an in-

creased biomass in UV-B treated *Zea mays*, as compared to the control.

Effect of UV-B on roots is indirect and interacted by several other co-occurring factors (Deckmyn & Impens 1995). The results of the present study suggest that UV-B had a more negative effect on roots than on shoot, resulting in a lower RSR. Tosserams *et al.* (2001) reported low root-shoot ratio at low nutrient level, which increased with increasing supply of nutrients in *Plantago lanceolata*. Deckmyn & Impens (1995) reported a variable RSR at different ages of *Phaseolus vulgaris* under high UV-B flux.



**Table 3.** Variance ratio of *Triticum aestivum* L. cultivars HD 2329 & HUW 234 with and without enhanced UV-B at varying fertility levels.

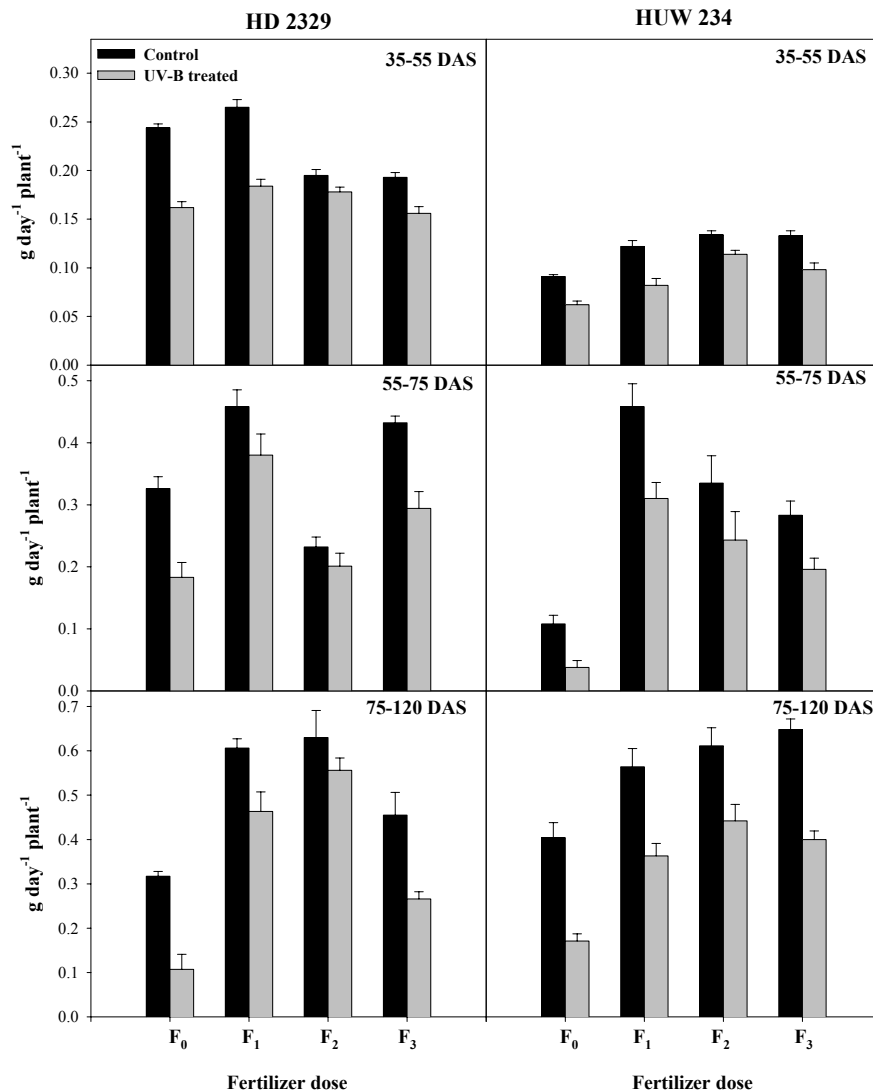
Cultivars	Parameters	Factor						
		Plant age (A)	UV-B treatment (T)	Fertilizer dose (F)	A x T	A x F	T x F	A x T x F
HD 2329	Shoot length	***	***	***	*	***	NS	NS
	Root length	***	**	NS	NS	NS	NS	NS
	Biomass	-	***	***	-	-	***	-
	Dry root weight	-	***	***	-	-	***	-
	Dry leaf weight	-	***	**	-	-	NS	-
	Dry stem weight	-	**	**	-	-	NS	-
	Spike weight	-	***	***	-	-	***	-
	AGR	***	**	*	NS	***	NS	NS
	CGR	***	***	***	NS	***	NS	NS
	RSR	-	***	***	-	-	NS	-
	HI	-	***	***	-	-	***	-
	Yield	-	***	***	-	-	***	-
HUW 234	Shoot length	***	***	***	**	***	**	NS
	Root length	***	***	*	***	***	***	***
	Biomass	-	***	***	-	-	***	-
	Dry shoot weight	-	***	***	-	-	*	-
	Dry leaf weight	-	***	***	-	-	NS	-
	Dry stem weight	-	**	**	-	-	NS	-
	Spike weight	-	***	***	-	-	**	-
	AGR	***	*	***	***	***	NS	NS
	CGR	***	***	***	NS	***	***	***
	RSR	-	***	***	-	-	**	-
	HI	-	***	***	-	-	**	-
	Yield	-	***	***	-	-	***	-

\*\*\*= p < 0.001, \*\* = p < 0.01, \* = p < 0.05, NS= Not significant

Leaf growth is very sensitive to environmental stress (Dillenburg *et al.* 1995). Hence, rapid changes in leaf growth in response to stress may enable plants to alter allocation patterns before a severe imbalance of carbon and nitrogen containing metabolites develops (Chapin 1991). Barsig & Malz (2000) found drastic changes in starch and sucrose partitioning in *Zea mays* due to leaf exposure to UV-B. The present study also showed higher reductions in leaf weight in comparison to dry stem and spike weights even under fertilizer-amended plants after exposure to supplemental UV-B. Normally, leaves are exposed directly for longer time than stem and spikes, which are also

shaded by the leaves. Yue *et al.* (1998) reported a higher reduction in the biomass of leaves than that of stem or spikes in *T. aestivum*, due to enhanced UV-B.

CGR is a measure of productivity and expresses the efficiency of the plant as a producer of new material (Hunt 1982). Lower levels of AGR and CGR under UV-B treatment further establish the relative influence of supplemental UV-B on productivity. Reductions in AGR have also been reported due to UV-B in wheat and maize plants (Rozema *et al.* 1990). UV-B induced growth inhibition was correlated to the reduction or destruction of auxin and the formation of growth inhibiting



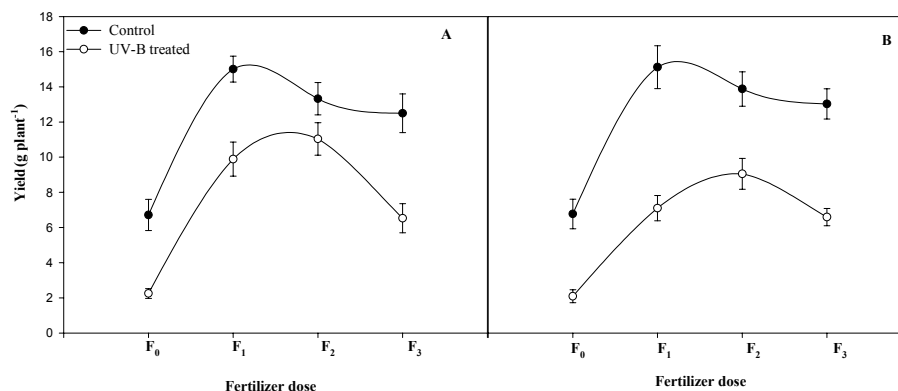
**Fig 2.** Effect of enhanced UV-B radiation on CGR ( $\text{g day}^{-1} \text{ plant}^{-1}$ ) of two wheat cultivars at different growth stages and with different levels of applied fertilizer.

IAA photoproducts (Ros & Tevini 1995). Fertilizer amendments had a beneficial effect on maintaining a high value of growth indices in UV-B treated plants.

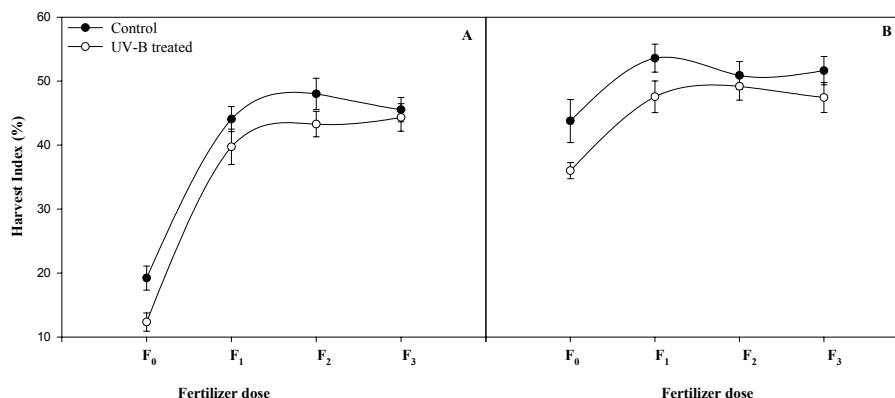
Reductions in the spike and grain weights reflect alteration of photosynthetic allocation due to UV-B. The adverse effect could be due to reduction of photosynthesis in flag leaves of exposed plants responsible for photosynthate allocation to economically important parts. Demchik & Day (1996) reported reduction in seed weight of *Brassica rapa* under 16 and 32% ozone depleted UV-B flux. Re-

ductions in quantity of pollen grains *vis-à-vis* their viability under enhanced UV-B radiation might also contribute to reduction in grain yield (Demchik & Day 1996). In the present field study, the plants were also exposed to UV-B between anthesis and the end of grain filling, so this penetration of UV-B might be more effective in reducing grain set/yield.

Small value of HI under UV-B exposure may be due to reduction in the weight of grains (economic yield) leading to a reduction in biological (dry matter) yield. Yue *et al.* (1998) reported a re-



**Fig. 3.** Effect of enhanced UV-B radiation on grain yield ( $\text{g plant}^{-1}$ ) of HD 2329 (A) and HUW 234 (B) at varying fertility regimes.



**Fig. 4.** Effect of enhanced UV-B radiation on harvest index (%) of HD 2329 (A) and HUW 234 (B) at varying fertility regimes.

duced assimilate allocation to grains due to enhanced UV-B. However, contrasting results have been reported by Deckmyn & Impens (1995) in *Phaseolus vulgaris*, where total yield slightly increased owing to changes in allocation.

Levizou & Manetas (2001) noticed that at a higher nutrient levels, supplemental UV-B improved growth of *Phlomis fruticosa* indicating a strong interactions between the treatments. Studies of Murali & Teramura (1985b) on *Glycine max* and Weih *et al.* (1998) on *Betula pubescens* have shown that changes in nutrient concentrations in combination of UV-B not only affect the dry matter production but also its allocation to different parts of the plants. Contrary to this, Gonzalez *et al.* (1998) postulated that growth inhibition by UV-B is simply a photomorphogenic response, rather

than a function of assimilate limitation. The present study showed a positive response of mineral nutrients (N, P and K) to minimize damaging effects of supplemental UV-B radiation. The effects of UV-B and relative nutrient addition rate were mostly additive rather than synergistic growth of *Betula pendula* seedlings (Rosa *et al.* 2001). Nitrogen metabolism is not influenced by UV-B (Ghisi *et al.* 2002). Leaf thickness increased with increasing N supply (Hunt & McNeil 1998), which protects the plant from damaging effects of UV-B radiation to assimilatory surface. Increase in specific leaf weight ratio (data not given) observed in the present study, is also indicative of increase in leaf thickness.

Another protection mechanism in plants against UV-B damage is accumulation of phenolic

compounds. Changing nutrient availability might be manipulating the level of internal phenolic compounds (Levizou & Manetas 2001). Recently, Agrawal *et al.* (2004) showed that significant increase in proline contents was an important factor for providing higher tolerance to UV-B treated wheat plants grown at higher nutrient level. In conclusion, both the cultivars (HD 2329 and HUW 234) of wheat were sensitive to supplemental level of UV-B. Cultivar HD 2329 showed a higher tolerance to UV-B in comparison to cultivar HUW 234. Additional supply of mineral nutrients (N, P and K), especially 1.5 times of recommended dose (F<sub>2</sub>C), was best to overcome the injurious effects of supplemental UV-B.

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### References

- Agrawal, S.B., D. Rathore & A. Singh. 2004. Combined effects of enhanced UV-B radiation and additional nutrients on two cultivars of wheat (*Triticum aestivum* L.), *Physiology & Molecular Biology of Plants* **10**: 99-108.
- Alexieva, V., I. Sergiev, S. Mapelli & E. Karanov. 2001. The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. *Plant, Cell and Environment* **24**: 1337-1344.
- Ambasht, N. K. & M. Agrawal. 1995. Physiological responses of field grown *Zea mays* L. plants to enhanced UV-B radiation. *International Journal of Biotronics* **24**: 15-23.
- Baker, J.T. & L.H. Allen, Jr. 1994. Assessment of the impact of rising carbon dioxide and other potential climate changes on vegetation. *Environmental Pollution* **83**: 223-235.
- Ballare, C.L., P.W. Barnes & S.D. Flint. 1995. Inhibition of hypocotyle elongation by ultraviolet-B radiation in de-etiolating. I. The photoreceptor. *Physiologia Plantarum* **93**: 584-592.
- Barnes, J.D., D. Velissariou, A.W. Davison & C.D. Holevas. 1990. Comparative ozone sensitivity of old and modern Greek cultivars of spring wheat. *New Phytologist* **116**: 707-714.
- Barsig, M. & R. Malz. 2000. Fine structure, carbohydrates and photosynthetic pigments of sugar maize leaves under UV-B radiation. *Environmental and Experimental Botany* **43**: 121-130.
- Bond, M.A., L. Hopkins & A.K. Tobin. 1996. The effects of UV-B (280-320 nm) and elevated CO<sub>2</sub> on the growth and development of the primary leaf of wheat (*Triticum aestivum*). *Journal of Experimental Botany* **47**: 19.
- Chapin, F.S., III. 1991. Integrated responses of plants to stress. *Bioscience* **41**: 29-36.
- Deckmyn, G. & I. Impens. 1995. UV-B increases the harvest index of bean (*Phaseolus vulgaris* L.). *Plant, Cell and Environment* **18**: 1426-1433.
- Demchik, S.M. & T.A. Day. 1996. Effect of enhanced UV-B radiation on pollen quantity, quality and seed yield in *Brassica rapa* (Brassicaceae). *American Journal of Botany* **83**: 573-579.
- Dillenburg, L.R., J.H. Sullivan & A.H. Teramura. 1995. Leaf expansion and development of photosynthetic capacity and pigments in *Liquidamber styraciflua* (Hamamelidaceae)- effects of UV-B radiation. *American Journal of Botany* **82**: 878-885.
- Dunning, C.A., L. Chalker-Scott & J.D. Scott. 1994. Exposure to ultraviolet-B radiation increases cold hardiness in *Rhododendron*. *Physiologia Plantarum* **92**: 516-520.
- Ghisi, R., A.R. Trentin, A. Musi & M. Ferretti. 2002. Carbon and nitrogen metabolism in barley plants exposed to UV-B radiation. *Physiologia Plantarum* **116**: 200-205.
- Gonzalez, R., A.R. Wellburn & N.D. Paul. 1998. Dose responses of two pea lines to ultraviolet-B radiation (280-320 nm). *Physiologia Plantarum* **104**: 373-378.
- Green, A.E.S., K.R. Cross & L.A. Smith. 1980. Improved analytical characterization of ultraviolet skylight. *Photochemistry and Photobiology* **31**: 59-65.
- Hunt, J.E. & D.L. McNeil. 1998. Nitrogen status affects UV-B sensitivity of cucumber. *Australian Journal of Plant Physiology* **25**: 79-86.
- Hunt, R. 1982. *Plant Growth Analysis*. University Park Press, Baltimore, USA.
- Jorden, B.R. 1996. The effects of ultraviolet-B radiation on plants: A molecular perspective. *Advances in Botanical Research* **22**: 97-161.
- Kulandaivelu, G. & K. Annamalaiathan. 1991. Interaction of herbicide and ultraviolet-B radiation on the photosynthetic apparatus. pp 59-75. In: Y.P. Abrol, P.N. Wattal, A. Gnanam, Ort. D.R. Govindjee & A.H. Teramura (eds.) *Impact of Global Climatic Changes on Photosynthesis and Plant Productivity*. Oxford and IBH Publication, New Delhi.

- Leracari, B., F. Sodi & M.P.D. Lipucci. 1990. Photomorphogenic responses to UV-B radiation: Involvement of phytochrome and UV photoreceptors in the control of hypocotyl elongation in *Lycopersicon esculentum*. *Physiologia Plantarum* **79**: 668-672.
- Levizou, E. & Y. Manetas. 2001. Combined effects of enhanced UV-B radiation and additional nutrients on growth of two Mediterranean plant species. *Plant Ecology* **154**: 181-186.
- Murali, N.S. & A.H. Teramura. 1985a. Effects of Ultraviolet-B irradiance on soybean VI. Influence of phosphorus nutrition on growth and flavonoid content. *Physiologia Plantarum* **63**: 413-416.
- Murali, N.S. & A.H. Teramura. 1985b. Effects of Ultraviolet-B irradiance on soybean VI. Biomass & concentration and uptake of nutrient at varying P supply. *Journal of Plant Nutrition* **8**: 177-192.
- Murali, N.S. & A.H. Teramura. 1987. Insensitivity of soybean photosynthesis to ultraviolet-B radiation under phosphorus deficiency. *Journal of Plant Nutrition* **10**: 501-515.
- Nedunchezian, N, K. Annamalaiathanand & G. Kulandaivelu. 1995. Ultraviolet-B (280-320 nm) enhanced radiation induced changes in chlorophyll protein complexes and polypeptide composition of chloroplasts in *Vigna unguiculata* seedlings grown at various temperatures. *Photosynthetica* **31**: 21-29.
- Petropoulou, Y., A. Kyparissis, D. Nikolopoulos & Y. Manetas. 1995. Enhanced UV-B radiation alleviates the adverse effects of summer drought in two Mediterranean *Pinus* under field conditions. *Physiologia Plantarum* **94**: 37-44.
- Ros, J. & M. Tevini. 1995. Interaction of UV-radiation and IAA during growth of seedlings and hypocotyl segments of sunflower. *Journal of Plant Physiology* **146**: 295-302.
- Rosa, T.M. De La, R.J. Tiitto, T. Lehto & P.J. Aphalo. 2001. Secondary metabolites and nutrients concentration in silver birch seedlings under five levels of daily UV-B exposure and two relative nutrient addition rates. *New Phytologist* **150**: 121-131.
- Rozema, J., G.M. Lenssen & J.W.M. Van de Staay. 1990. The combined effect of increased atmospheric CO<sub>2</sub> and UV-B radiation on some agricultural and salt marsh species. pp. 68-71. In: J. Goudrian, H. VanKeulen & H.H. van Laar (eds.) *The Green House Effect and Primary Productivity in European Agroecosystems*. Pudoc, Wageningen.
- Sharma, P.K., P. Ananad, S. Sankhalkar & R. Shetye. 1998. Photochemical and biochemical changes in wheat seedlings exposed to supplementary ultraviolet-B radiation. *Plant Science* **132**: 21-30.
- Smith, J.L., D.J. Burritt & P. Bannister. 2000. Shoot dry weight, chlorophyll and UV-B absorbing compounds as indicators of plant sensitivity to UV-B radiation. *Annals of Botany* **86**: 1057-1063.
- Strid, A., W.S. Chow & J.M. Anderson. 1990. Effect of supplementary ultraviolet-B radiation on photosynthesis in *Pisum sativum*. *Biochimica et Biophysica Acta* **1020**: 260-268.
- Teramura, A.H. 1980. Effects of ultraviolet-B irradiances on soybean. I. Importance of photosynthetically active radiation in evaluating ultraviolet-B irradiance effects on soybean and wheat growth. *Physiologia Plantarum* **48**: 333-339.
- Tevini, M. 2000. UV-B effects on plant. pp 83-97. In: S.B. Agrawal & M. Agrawal (eds.) *Environmental Pollution and Plant Responses*. Lewis Publishers, Boca Raton, USA.
- Tevini, M., A.H. Teramura, G. Kulandaivelu, M.M. Caldwell & L.O. Bjorn. 1989. Terrestrial Plants. pp. 25-37. In: *Environmental Effects Panel Report*. Pursuant to article 6 of the Montreal protocol on substances that deplete the ozone layer under the auspices of the United Nations Environment Programme.
- Tosserams, M., J. Smet, E. Magendans & J. Rozema. 2001. Nutrient availability influences UV-B sensitivity of *Plantago lanceolata*. *Plant Ecology* **154**: 159-168.
- Weih, M., U. Johanson & D. Gwynn-Jones. 1998. Growth and nitrogen utilization in seedlings of mountain birch (*Betula pubescens* sp. *tortuosa*) as affected by ultraviolet radiation (UV-A and UV-B) under laboratory and outdoor conditions. *Trees* **12**: 201-207.
- Yue, M., Y. Li & X. Wang. 1998. Effects of enhanced ultraviolet-B radiation on plant nutrients and decomposition of spring wheat under field conditions. *Environmental and Experimental Botany* **40**: 187-196.