Journal of Plant Biology, September 2005, 48(3) : 284-291

Impacts of Ambient Solar UV (280-400 nm) Radiation on Three Tropical Legumes

Paulraj Amudha, Muthukrishnan Jayakumar*†, and Govindaswamy Kulandaivelu
School of Biological Sciences, Madurai Kamaraj University, Madurai 625 021, India

Tropical regions receive the highest level of global solar ultraviolet (UV) radiation especially UV-B (280-320 nm). The average daily dose of the UV-B radiation in Madurai, South India (10° N) is 10 kJ m^{-2}. This is approximately 50% more than the average daily UV-B radiation in many European countries. A field study was conducted using selective filters to remove either the UV-B (< 320 nm) or UV-B/A (<400 nm) of the solar spectrum, and the effects were followed in *Cyamopsis tetragonoloba, Vigna mungo,* and *Vigna radiata* to determine their sensitivity to UV. When compared to ambient radiation, exclusion of solar UV-B increased the seedling height, leaf area, fresh weight and dry weight and the crop yield by 50% in the case of *Cyamopsis*, and the extent of such increase was slightly less under UV-B/A exclusion. In *V. mungo* a significant reduction was seen in solar UV excluded plants while *V. radiata* was found to be unaffected.

Keywords: ambient, *Cyamopsis tetragonoloba*, UV-B/A exclusion, UV-B exclusion, *Vigna mungo, Vigna radiata*

The reduction in the stratospheric ozone column thickness by chlorofluocarbons (CFCs) and other trace gases has generated significant increase in the amount of incident UV-B (280-320 nm) radiation on the earth surface. Recent analyses show that ozone has declined globally by 4-5% since 1979 (Madronich et al., 1995; Pyle, 1997). Numerous studies have been conducted to assess the effects of enhanced UV-B radiation on higher plants (Tevini, 1993; Caldwell and Flint, 1994) but relatively little is known about UV-B exclusion (Sharma et al., 1991; Hasimoto et al., 1993; Tezuka et al., 1993; Searles et al., 1995). The increasing food demands of ever growing population will require increases in agricultural yields. Approximately 90% of the legume species interact symbiotically with *Rhizobium* to fix nitrogen and thus supply themselves with a costly biofertilizer. Increase in the UV-B radiation is known to reduce biomass, leaf area, plant height, and photosynthesis (Tevini and Teramura, 1989; Tevini et al., 1990; Jayakumar et al., 2004). A worldwide decrease of 25-30% in crop yield has also been predicted by UV-B radiation. But the results of UV-B enhancement studies are often difficult to interpret, because of the unrealistically high UV irradiation levels, inadequate levels of UV-A, low photosynthetic photons flux density (PPFD) or other technical difficulties (Edwards, 1992; Adamse et al., 1997; Ryan and Ireland, 1997).

To overcome all these limitations, recent investigations are aimed at using systems that attenuate or exclude the UV components of natural solar radiation (Adamse et al., 1997; Krizek et al., 1997; Pal et al., 1997; Krizek and Mirecki, 2004)). Till now only a few species or cultivars have been investigated under UV exclusion conditions. The results of UV exclusion studies indicate that the plants vary greatly in their response to ambient UV-B. It has been already reported that in some species (cucumber, mung bean, and New Zealand spinach) the growth is inhibited by the solar UV-B and in few crops (tomato) growth is stimulated, while in others (cotton and oats) it is unaffected (Adamse et al., 1997; Krizek et al., 1997).

The primary objective of our study was to determine the changes in vegetative growth, the level of UV-B absorbing compounds, photosystem II activity and fruit yield in tropical legumes by the exclusion of either UV-B radiation or UV-A and B in the natural sunlight.

MATERIALS AND METHODS

Site Description

All the field experiments under the natural sunlight were conducted in the University Botanical garden, Madurai Kamaraj University, Madurai, India. In the

*Corresponding author; fax +91-4562-281338
e-mail ayakuma_99@yahoo.com
†Present address; Research Department of Botany, VHNSN College, Virudhunagar G26 001, India

garden, he average annual day and night temperature was 33/23°C and the maximum and the minimum humidity was 80% and 39%, respectively. The natural photoperiod varied between 10 and 12 h and the total rainfall was 56 mm. The experiments were carried out in summer (February 2003 to May 2003) and pre-winter months (August 2003 to October 2003) when the average daily solar UV-B dose is around 10 kJ m^{-2} which is approximately 50% higher than the average daily dose in the temperate regions. Plants grown directly on soil were covered with polyester film mounted on metal mesh cages (180 cm long, 90 cm wide, 90 cm high). All sides of the frames up to 30 cm from ground were left uncovered to allow normal ventilation. The frames received full solar radiation for most period of the day without any shading.

Plant Material

The certified seeds of *Cyamopsis tetragonoloba* var. Pusa navbagar, *Vigna mungo* var. T9 and *Vigna radiata* var. KM2 obtained from Farm Aids, Madurai, India were used in all the experiments.

Plant Growth and Treatments

Seedlings were exposed to solar UV radiation from the time of germination. One of the cages was covered with 0.12 mm polyester transparent film (Mylar type) to exclude UV-B and the other was covered with 0.3 mm polyester film to exclude both UV-B and UV-A radiation. The cage covered with polyethylene film was used for ambient light treatment. The spectral characteristics of these filers (films) are shown in Figure 1.

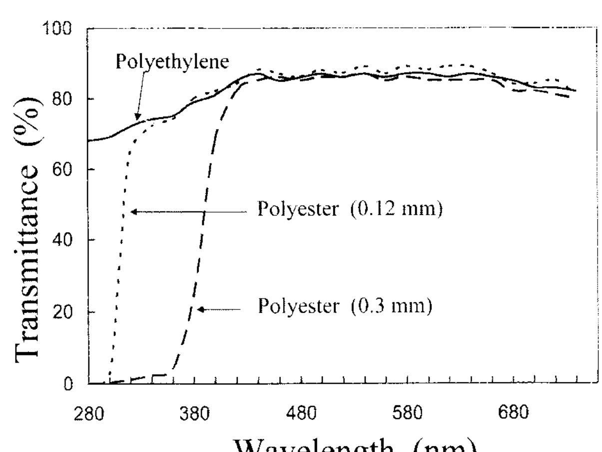

Figure 1. Transmission spectra of polyester [0.12 mm for (–)UV-B and 0.3 mm for (–)UV-B/A] and polyethylene (for ambient) films in UV-visible regions.

Radiation Measurements

Absolute solar irradiance with and without UV-B was measured using a double monochromatic spectroradiometer system (IL–700/760/790, International Lights, USA). The average level of ambient UV-B during the experimental period was 10 kJ m^{-2} d^{-1}. Under (–)UV-B radiation conditions the dosage was 1.5 kJ m^{-2} d^{-1}. The daily average photosynthetic photon flux density (PPFD) inside the filter cages was 54 mol m^{-2}.

Growth Analysis

After the initiation of the 3rd trifoliate leaves, seedlings were harvested for analyses. The growth parameters such as shoot length, leaf area, fresh and dry weight of the shoots were analyzed immediately after harvest. Only plant materials above ground were considered for fresh and dry weight determination in which the latter involved drying the plant parts at 60°C for 72 h.

Pigment Analysis

Fresh leaf tissue was extracted with 80% acetone for the complete release of chlorophylls and carotenoids. The chlorophyll and carotenoid contents were quantified using the formulae of Wellburn and Lichtenthaler (1984).

Crop Yield

Yield parameters including pod fresh weight, pod dry weight, number of pods per plant and their size were measured.

RESULTS

Effects of UV-B and UV-B/A Filtered Solar Radiation on Growth Characteristics

Cyamopsis seedlings grown under (–)UV-B and (–)UV-B/A radiation showed a significant increase in various growth parameters as compared to those under ambient light. In contrast to this, a marginal increase in *V. radiata* and reduction in the case of *V. mungo* was observed. Changes in various growth parameters are shown in Figure 2. Both *Cyamopsis*

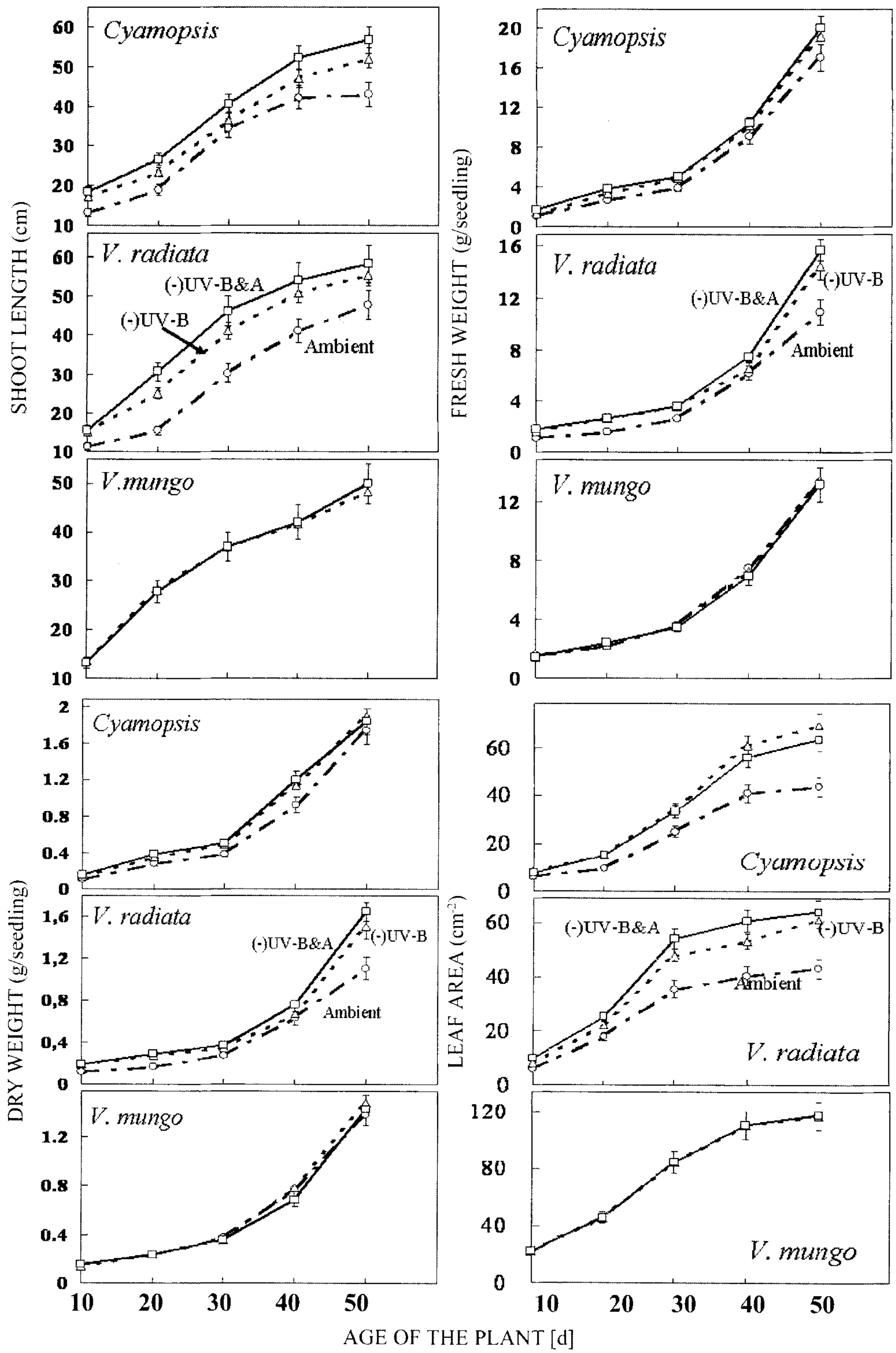

Figure 2. Changes in the shoot length, shoot fresh weight, dry weight, and leaf area of *Cyamopsis, V. radiata* and *V. mungo* seedlings grown under ambient, (–)UV-B and (–)UV-B/A solar radiation at different time intervals.

and *V. radiata* showed a large increase in the shoot length under (–)UV-B. Such increase was more in the case of *V. radiata* than that of *Cyamopsis* during the early growth period and at full maturity. Both the species showed more or less similar enhancement in both UV-B and UV-B/A exclusion. In these plants UV-

Table 1. Changes in the level of total chlorophyll and carotenoid in *Cyamopsis*, *V. radiata* and *V. mungo* seedlings grown under ambient, (–)UV-B and (–)UV-B/A conditions at different time intervals. Values given are in mg g^{-1} leaf fresh weight. Mean±SE, n=5.

Treatment Period (Days)		*Cyamopsis* Total Chl	*Cyamopsis* Carotenoid	*V. radiata* Total Chl	*V. radiata* Carotenoid	*V. mungo* Total Chl	*V. mungo* Carotenoid
10	Ambient	1.22 ± 0.09	0.31 ± 0.01	1.09 ± 0.09	0.252 ± 0.02	1.11 ± 0.10	0.23 ± 0.01
	(–)UV-B	1.45 ± 0.11	0.36 ± 0.02	1.20 ± 0.10	0.260 ± 0.02	1.42 ± 0.13	0.29 ± 0.02
	(–)UV-B/A	1.42 ± 0.13	0.36 ± 0.02	1.34 ± 0.09	0.293 ± 0.03	1.49 ± 0.12	0.29 ± 0.02
20	Ambient	1.87 ± 0.15	0.45 ± 0.03	1.93 ± 0.11	0.352 ± 0.03	1.81 ± 0.16	0.33 ± 0.03
	(–)UV-B	2.22 ± 0.20	0.46 ± 0.04	1.93 ± 0.13	0.371 ± 0.02	1.88 ± 0.17	0.35 ± 0.02
	(–)UV-B/A	2.49 ± 0.22	0.58 ± 0.05	2.04 ± 0.16	0.396 ± 0.03	1.89 ± 0.15	0.36 ± 0.03
30	Ambient	2.63 ± 0.23	0.52 ± 0.04	2.76 ± 0.23	0.482 ± 0.04	2.73 ± 0.24	0.58 ± 0.04
	(–)UV-B	2.90 ± 0.24	0.57 ± 0.05	2.81 ± 0.25	0.502 ± 0.05	2.59 ± 0.21	0.58 ± 0.05
	(–)UV-B/A	3.36 ± 0.31	0.63 ± 0.05	2.87 ± 0.26	0.588 ± 0.05	2.65 ± 0.25	0.58 ± 0.05
40	Ambient	2.82 ± 0.25	0.63 ± 0.06	3.26 ± 0.29	0.541 ± 0.05	3.08 ± 0.29	0.61 ± 0.05
	(–)UV-B	3.04 ± 0.29	0.69 ± 0.07	3.22 ± 0.30	0.589 ± 0.04	3.09 ± 0.31	0.62 ± 0.06
	(–)UV-B/A	3.60 ± 0.31	0.70 ± 0.06	3.54 ± 0.33	0.658 ± 0.05	3.05 ± 0.29	0.61 ± 0.05
50	Ambient	2.66 ± 0.24	0.67 ± 0.06	2.23 ± 0.18	0.523 ± 0.05	2.97 ± 0.25	0.50 ± 0.04
	(–)UV-B	2.67 ± 0.23	0.70 ± 0.05	2.26 ± 0.19	0.544 ± 0.05	2.83 ± 0.25	0.48 ± 0.03
	(–)UV-B/A	2.83 ± 0.25	0.71 ± 0.06	2.53 ± 0.21	0.635 ± 0.06	2.68 ± 0.24	0.50 ± 0.04

B exclusion produced an intermediate level of enhancement. In *V. mungo* none of these treatment conditions produced any significant effect. An increase in shoot fresh weight was observed in *Cyamopsis* under UV exclusion. A 26% increase under (–)UV-B and an additional 3% increase was observed at 30 days when UV-A along with UV-B was excluded. In *V. radiata*, 33% increase in both (–)UV-B and (–)UV-B/A was observed when compared to the ambient grown seedlings, whereas *V. mungo* seedlings showed a 3% decrease when both radiations were excluded. As far as the shoot dry weight is concerned, as much as 29% and 34% increase was observed in (–)UV-B and (–)UV-B/A grown *Cyamopsis* seedlings, respectively. In *V. radiata* seedlings, 25% and 36% increase was observed in (–)UV-B and (–)UV-B/A over the ambient grown ones, respectively. Similar trend was observed in dry weight and in fresh weight in the case of *V. mungo.*

Changes in the leaf area showed a different trend in *Cyamopsis*, where UV-B exclusion produced more increase than UV-B/A exclusion. A significant increase of 40% and 20% was observed in (–)UV-B and (–)UV-B/A filtered seedlings, respectively. In contrast to this 36% and 70% increase was seen in (–)UV-B and (–)UV-B/A grown *V. radiata* seedlings, respectively. No marked reduction or increase had occurred in *V. mungo*. Seedlings grown under ambient radiation produced small and thick leaves in the case of *Cyamopsis* when compared to the plants grown under (–)UV-B and (–)UV-B/A radiation.

Many nodules were noticed under (–)UV-B and much higher number under (–)UV-B/A radiation in *Cyamopsis* but almost same number in the case of *V. mungo* and *V. radiata* under all treatment conditions (data not shown).

Pigment Analysis

Changes in the photosynthetic pigment composition of *Cyamopsis*, *V. radiata* and *V. mungo* seedlings grown under ambient, UV-B and UV-B/A filtered radiation are given in Table 1. Photosynthetic pigments showed an increase on UV-B and UV-B/A exclusion in *Cyamopsis*, when compared to *V. mungo* and *V. radiata*. A 19% and 33% increase in total chlorophyll (Chl) in (–)UV-B and (–)UV-B/A grown seedlings, respectively, when compared to ambient grown seedlings was observed. Such increase was due to changes in both Chl a and Chl b. Increase in the amount of Chl was observed in the initial stages and there was a marked reduction in the level of total Chl after 30

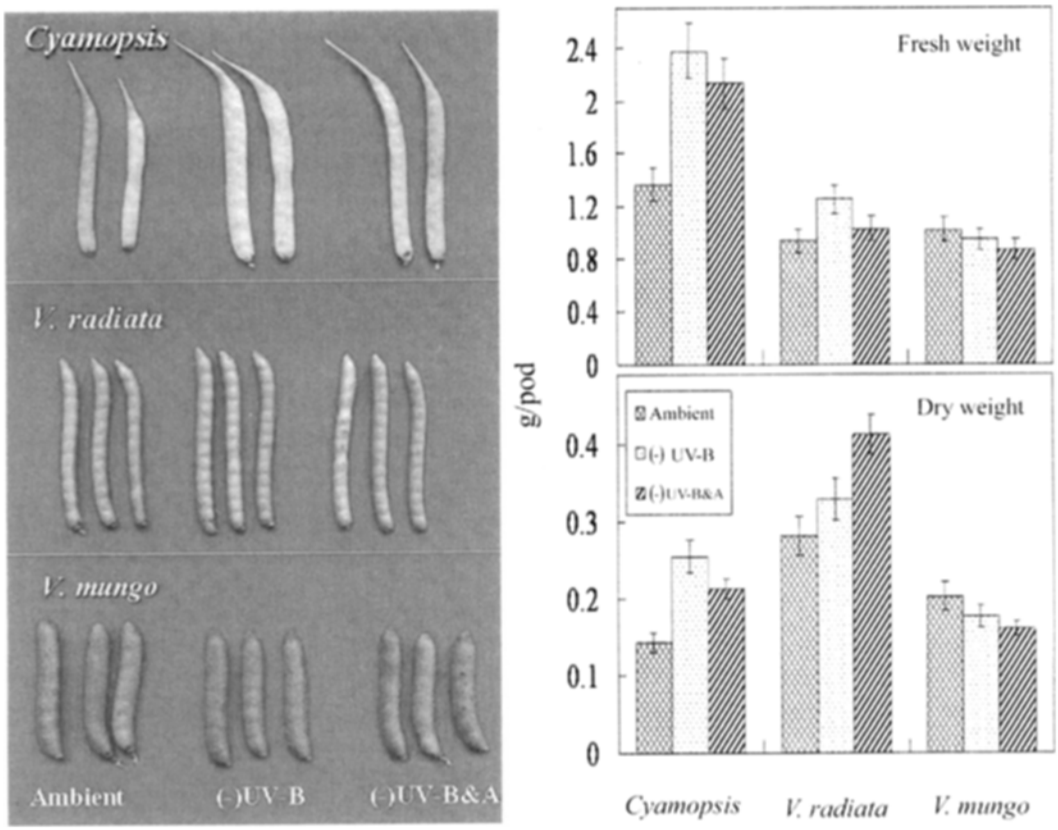

Figure 3. Changes in pod size, pod fresh, and dry weight in *Cyamopsis*, *V. radiata* and *V. mungo* seedlings grown under ambient, (–)UV-B and (–)UV-B/A radiation.

days. A similar trend was observed in the carotenoid levels. The percentage of increase was higher when both the UV-B/A radiations were excluded than that of UV-B exclusion alone.

In *V. radiata,* there was no significant increase or decrease in all the pigments. In *V. mungo*, there was a reduction in the level of pigments under UV filtered seedlings when compared to the ambient radiation grown plants. Such a decrease was more in the case of UV-B filtered seedlings than those under (–)UV-B/A. Both the *Vigna* species showed a high Chl a/b ratio due to reduced level of Chl b (results not shown).

Crop yield

There was a 60% increase in the size of the pod in (–)UV-B grown *Cyamopsis* plants when compared to those grown under ambient radiation, however the increase was reduced to 50% under (–)UV-B/A radiation. There was no change in the size of the pod in *V. radiata*. In contrast to these plants, *V. mungo* showed negative changes (Fig. 3). As far as the pod fresh weight is concerned, there was a 74% and 56% increase in (–)UV-B and (–)UV-B/A plants when compared to the ambient light grown plants, respectively. In *V. radiata*, a 33% and 10% increase was noticed under (–)UV-B and (–)UV-B/A radiation, respectively. In contrast to these plants, pod fresh weight of *V. mungo* showed a 8% and 15% reduction in (–)UV-B and (–)UV-B/A plants, respectively. Similar trend was also reflected in the changes in pod dry weight which are shown in Figure 3.

DISCUSSION

The inhibitory effects of solar UV-B radiation on the growth and various photosynthetic responses have been well investigated in field and green house experiments where plants were either grown under ambient or artificially UV-B supplemented radiation. Since the level of ambient UV-B radiation in sunlight varies with reference to latitude and is relatively higher in tropical regions than in temperate regions, a true assessment of UV radiation effects is possible by the UV exclusion studies. This study provides evidence that these tropical legumes respond to the exclusion of solar UV radiation both positively and negatively and such responses vary with plant species. The inhibitory effects of ambient solar UV radiation on the growth of phytoplankton (Jeffrey et al., 1996; Santaz et al., 1996) and microalgae (Döhler et al., 1995) are well documented. Till date, there are only a few reports on the response of plants to the natural solar UV-B radiation (Latimer and Mitchell, 1987; Ballaré et al., 1991; Sharma et al., 1991; Tezuka et al., 1993; He et al., 1994; Searles et al., 1995; Mark et al., 1996). Little research has been focused on the woody pines (Kossuth and Biggs, 1981; Sullivan and Teramura, 1992, 1994; Naidu et al., 1993).

In this study we have shown that the removal of UV-B and UV-B/A from natural solar radiation caused a large increase in the vegetative growth of *Cyamopsis* as compared to *Vigna* species. These results correspond to the earlier field studies (Ziska et al., 1991; Nouchi et al., 1995; Lingakumar et al., 1999). A significant increase in the shoot length also had occurred in *Cyamopsis* when the UV-B and UV-B/A components in sunlight were removed. This suggests that the level of UV-B present in solar radiation produced a strong effect on the shoot elongation in plants like *Cyamopsis*, but not in *V. mungo*. Reduction in plant height in response to supplementary UV-B radiation has been reported for soybean (Biggs et al., 1981), cucumber (Murali and Teramura, 1985) and cotton (Ambler et al., 1975). Tevini et al. (1981) found that IAA absorbs in the UV-B range and the UV radiation-modified product may be the cause for the reduction in shoot growth. Ambler et al. (1975) found no effect on the plant height in sorghum and corn at high UV irradiance from unfiltered lamps under field conditions. Among the parameters studied, changes in the leaf expansion were prominent. The increase in shoot length of (–)UV-B and (–)UV-B/A grown *Cyamopsis* appears to be due to an overall enhancement growth of the plant as evidenced by the accumulation of more dry matter (55%) than ambient UV-B grown plants.

The results of the growth analysis of *Cyamopsis* used in our study showed an increase in the shoot length, leaf size and biomass production when the solar UV-B radiation was excluded and an additional increase in growth was observed when UV-A radiation also was excluded. These findings suggest that even small changes in ozone depletion may have important biological consequences for certain plant species.

The Chl and carotenoid content in seedlings grown under UV-B and UV-B/A filtered radiation showed a significant increase in *Cyamopsis* and slight increase in *V. mungo* and *V. radiata*. Such increase was found to be due to the enhanced synthesis of Chl a rather than Chl b. Enhanced UV has been shown to cause damage to chl b rather than chl a which could be due to its direct absorption (Lingakumar and Kulandaivelu, 1993) or due to inhibition in Chl biosynthesis (El-Mansy and Salisbury, 1997). On the other hand, on removal of the stress, the inhibition is overcome or degradation processes might have been stopped, resulting in an accumulation of these pigments. Significant reduction in total Chl and carotenoids found in *Cyamopsis* exposed to ambient UV radiation is in agreement with El-Mansy and Salisbury (1997). In the present investigation, high Chl a/b ratio was obtained in both the *Vigna* species (results not shown). UV-B radiation resulted in a greater reduction in the amount of Chl b as opposed to Chl a and may point to more selective destructions of Chl b biosynthesis or degradation of precursors.

High level of UV-B radiation delays flowering and thereby reducing the yield. In the case of *Cyamopsis*, a delay in the onset of flowering was observed in the ambient light grown plants. The reason for the delay is probably the impact of solar UV radiation on the biosynthesis of gibberellins as described by Saile-Mark (1993) in *Hyoscyamas niger*. The reason for yield reduction may be due to alterations in the reproductive phase, e.g. flower suppression and /or delay of flowering as well as morphological changes. As far as the pod fresh weight is concerned, *Cyamopsis* and *V. radiata* plants showed a remarkable increase, whereas *V. mungo* showed a negative change.

Our results show that the exclusion of UV-B or UV-B/A from the solar radiation brings about a larger increase in the vegetative growth, pigments as well as in crop yield in certain tropical crops. However, these changes are species specific.

ACKNOWLEDGEMENTS

We thank the University Grants Commission and Department of Science and Technology, Government of India for financial assistance and Mr. S. Balakrishnan for his technical assistance.

Received March 28, 2005; accepted May 2, 2005.

LITERATURE CITED

Adamse P, Reed HE, Krizek DT, Britz SJ, Mirecki RM (1997) An inexpensive set up for assessing the impact of ambient solar ultraviolet radiation on seedlings. J Nat Res Life Sci Edu 26: 139-144

Ambler JE, Krizek DT, Semeniuk P (1975) Influence of UV-B radiation on early seedling growth and translocation of Zn from cotyledons in cotton. Physiol Plant 34: 177-181

Ballaré CL, Casal JJ, Kendrick RE (1991) Responses of light growth wild type and long hypocotyls mutant cucumber seedlings to natural and simulated shade light. Photochem Photobiol 54: 819-826

Biggs RH, Kossuth SV, Teramura AH (1981) Response of 19 cultivars of soybeans to ultraviolet-B irradiance. Physiol Plant 53: 19-26

Caldwell MM, Flint SD (1994) Solar ultraviolet radiation and ozone layer change: Implications for crop plants. *In* KJ Boote, JM Bennett, TR Sinclair, GM Paulsen, eds, Physiology and Determination of Crop Yield. ASA – CCSA-SSSA, Madison, West Indies, pp 487-507

Döhler G, Hagmeier E, David C (1995) Effects of solar and artificial UV irradiation on pigments and assimilation of ^{15}N ammonium and ^{15}N nitrate by macroalgae. J Photochem Photobiol B 30: 179-187

Edwards NT (1992) State of the-art field-exposure techniques do not qualitatively simulate expected global increases in UV-B irradiance. Bull Ecol Soc America 73: 165

El-Mansy HI, Salisbury FB (1997) Biochemical responses of *Xanthium* leaves to ultraviolet radiation. Radiat Bot 11: 325-328

Hashimoto T, Kondo N, Tezuka T (1993) Harmful and beneficial effects of solar UV light on plant growth. *In* A Shima, M Ichahashi, Y Fujiwara, H Takebe, eds, Frontiers of Photobiology, Elsevier, Amsterdam, pp 551-554

He J, Huang LK, Chow WS, Whitecross MI, Anderson JM (1994) Responses of rice and pea plants to hardening with low doses of ultraviolet-B radiation. Aust J Plant Physiol 21: 563-574

Jayakumar M, Amudha P, Kulandaivelu G (2004) Effect of low doses of UV-A and UV-B radiation on photosynthetic activities in *Phaseolus mungo* L. J Plant Biol 47: 105-110

Jeffrey WX, Aas P, Lyons MM, Coffin RB, Pledger RJ, Mitchell DL (1996) Ambient solar radiation induced photodamage in marine phytoplankton. Photochem Photobiol 64: 419-427

Kossuth SV, Biggs RH (1981) Ultraviolet-B radiation effects on early seedlings growth of Pinaceae species. Can J Forest Res 11: 243-248

Krizek DT, Mirecki RM (2004) Evidence for phytotoxic effects of cellulose acetate in UV exclusion studies. Environ Exp Bot 51: 33-43

Krizek DT, Mirecki RM, Britz SJ (1997) Inhibitory effects of ambient levels of solar UV-A and UV-B radiation on growth of cucumber. Physiol Plant 100: 886-893

Latimer JG, Mitchell CA (1987) UV-B radiation and photosynthetic irradiance acclimate eggplant for outdoor exposure. Hort Sci 22: 426-429

Lingakumar K, Amudha P, Kulandaivelu G (1999) Exclusion of solar UV-B (280-315 nm) radiation in vegetative growth and photosynthetic activities in *Vigna aunguicualta* L. Plant Sci 148: 97-103

Lingakumar K, Kulandaivelu G (1993) Changes induced by ultraviolet-B (280-320 nm) radiation in vegetative growth, foliar characteristics and photosynthetic activities in *Vigna unguiculata* L. Aus J Plant Physiol 20: 299-308

Madronich S, McKenzie RL, Caldwell MM, Björn LO (1995) Changes in ultraviolet radiation reaching the Earth's surface. Ambio 24: 143-152

Mark U, Saile-Mark M, Tevini M (1996) Effects of solar UV radiation on growth, flowering and yield of Central and Southern European maize cultivars (*Zea mays* L). Photochem Photobiol 64: 457-463

Murali NS, Teramura AH (1986) Intraspecific differences in *Cucumis sativus* to ultraviolet-B radiation. Physiol Plant 68: 673-677

Naidu SL, Sullivan JH, Teramura AH, Delucia EH (1993) The effects of ultraviolet B radiation in isolated chloroplasts and intact leaves. Tree Physiol 12: 151-162

Nouchi I, Hobayashi K (1995) Effects of enhanced ultraviolet-B radiation with modulated lamp control system on growth of 17 rice cultivars in the field. J Agric Mateorol 51: 110-120

Pal M, Sharma A, Arbol YP, Sengupta UK (1997) Exclusion of UV-B radiation from normal solar spectrum on the growth of mung bean and maize. Agric Ecosys Environ 61: 29-34

Pyle JA (1997) Global Ozone depletion: Observations and theory, *In* P Lumsden, ed, Plants and UV-B Responses to Environmental Change. Society for Experimental Biology Seminar Series: 64. Cambridge University Press, Cambridge, pp 3-11

Ryan KJ, Ireland W (1997) A small-scale outdoor plant growth chamber with modulator enhancement of solar UV-B radiation. J Environ Qual 26: 866-871

Saile-Mark M (1993) Zur beteiligung von phytohormone an wachstum und blutenbildung verschiedener bohnenkulturvarietaten (*Vigna vulgaris* L) in abhangigkeit von artifizeller und solarer UV-B strahlung. Karlsruher Beiträge zur Entwicklungs-und Ökophysiologie der Pflanzen 13: 1-152

Sandaz R, Häder DP, Lianou C (1996) Effects of solar UV radiation on diatom assemblages of the Mediterranean. Photochem Photobiol 64: 435-439

Searles PS, Caldwell MM, Winter K (1995) The response of five tropical dicotyledonous species to solar ultraviolet-B radiation. Am J Bot 82: 445-453

Sharma A, Abrol YP, Sengupta UK (1991) Effect of solar UV-B radiation on growth of mung bean (*Vigna radiata* L Wilczek) plants, *In* YP Abrol, ed, Impact of Global Climatic Changes on Photosynthesis and Plant Productivity. Oxford & IBH Publishing, New Delhi, pp 175-180

Sullivan JH, Teramura AH (1992) Effects of ultraviolet-B radiation on loblolly pines. II. Growth of field grown seedlings. Trees 6: 115-120

Sullivan JH, Teramura AH (1994) Effects of ultraviolet-B radiation on loblolly pines. III. Interaction with carbon dioxide enhancement. Plant 4Cell Environ 17: 311-317

Tevini M (1993) Effects of enhanced UV-B radiation on terrestrial plants, *In* M Tevini, ed, UV-B radiation and ozone depletion. Effects on Humans, Animals, Plants, Microorganisms, Materials. Lewis Publishers, Boca Raton, pp 125-153

Tevini M, Iwanzik W, Thoma U (1981) Some effects of of enhanced UV-B radiation on the growth and composition of plants. Planta 153: 388-394

Tevini M, Mark U, Saile-Mark M (1990) Plant experiments in growth chambers illuminated with natural sunlight, *In* HD Payer, T Pfirrmann, P Mathy, eds, Environmental Research with Plant in Closed Chambers, Air Pollution Research Report, No 26. Commission of the European Communities, Belgium, pp 242-251

Tevini M, Teramura AH (1989) UV-B effects on terrestrial plants. Photochem Photobiol 50: 479-487

Tezuka T, Hotta T, Watanabe I (1993) Growth promotion of tomato and radish plants by solar UV irradiation reaching the Earth's surface. J Photochem Photobiol B 19: 61-66

Wellburn AR, Litchenthaler HK (1984) Formulae and programme to determine carotenoids and total chlorophylls a and *b* of leaf extracts in different solvents, *In* C Sybesma, ed, Advances in Research. Martinus Nijhoff/ Dr. W. Junk Publisher, Hague, pp 9-12

Ziska LH, Hogan KP, Smith AP, Drake BG (1991) Growth and photosynthetic responses of nine tropical species with long term exposure to elevated carbon dioxide. Oecology 86: 383-389