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REVIEW ARTICLE

Response of Plants to Ultraviolet-B Radiation: Impact on Photosynthesis and Productivity

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The changes in climate as a result of growing imbalance between atmospheric carbon emission and absorption, depletion of ozone in stratosphere, increase in the earth's temperature, etc. are affecting physiological, biochemical and molecular processes of green plants. Research is essential to anticipate the potential impact of these factors on photosynthesis and productivity to provide food security to large population. In this review I discuss the impact of UV-B radiation on plants, with reference to damage and protection to photosynthesis and related processes.

Keywords: Ultraviolet-B radiation, chlorophyll, photosynthesis, productivity.

Introduction

Photosynthesis is the process by which chlorophyll containing plants convert solar energy into photochemical energy and fix atmospheric CO_2 into carbohydrate, providing food for all heterotrophic organism, including human being. During the process plants use sunlight and as a consequence are exposed to UV radiation (190–380 nm) present in the solar energy spectrum. Though the photosynthetic pigments absorb radiation in the range of 400–700 nm called photosynthetically active radiation (PAR), UV-B radiation (280–320 nm) can also activate the photosynthetic process. Electromagnetic radiation from the sun contains a small proportion of UV, about 7% of the radiation striking the earth's surface and an even smaller proportion penetrating the atmosphere, yet energy level of UV photon is high, which makes this a very photochemically active form of radiation. Thus the biological significance of UV-B radiation far outweigh its small contribution to the total solar energy reaching the earth.

UV-radiation (190–380 nm) is part of solar spectrum, however ozone in stratosphere (a layer from 10 km to 45 km above earth surface) is able to absorb large part of UV radiation in the range of 280 nm to 320 nm known as UV-B region. It is widely agreed that a portion of this protective stratospheric ozone layer is being depleted (Jordan, 2002). The major effect of this ozone loss is an increase in the amount of UV-B reaching the biosphere. This increase is largely contained within the UV-B (280–320 nm) region. It was the advent of 'ozone hole' that convinced public, government agencies and skeptical scientists that ozone layer was indeed being reduced by as much as 50% and this loss is mainly attributed to human activities.

Although the list of chemical pollutants responsible for the loss of stratospheric ozone is long and includes CCl_4, methyl chloroform, methyl bromide, bromochloromethane, etc., chlorofluorocarbons (CFCs) are the main one. CFCs invented in 1930 are widely used for manufacturing a variety of goods because of their stability, inertness and long life. Many coolants, electronic solvents, foams, etc. contain CFCs, which are slowly released into the atmosphere where they can exist for up to one hundred years. About 30 years after release the CFCs percolate into the stratosphere where in a reaction involving short wavelength ultraviolet radiation, it is broken down into chlorine. This reacts with ozone and metabolizes it into oxygen, thereby destroying the ozone layer. This is a chain reaction and each CFC molecule can destroy as many as 100,000s of ozone molecules (Coohil, 1991).

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$$2O_3 + 2Cl \rightarrow 2ClO + 2O_2 \quad (1)$$

$$O_2 + UV\text{-}B \rightarrow 2O \quad (2)$$

$$2ClO + 2O \rightarrow 2Cl + 2O_2 \quad (3)$$

Net reaction:

$$2O_3 \rightarrow 3O_2 \quad (4)$$

Ozone is also produced as a result of a natural process as shown here,

$$O_2 + UV \rightarrow O + O \quad (5)$$

$$O + O_2 \rightarrow O_3 \quad (6)$$

but it is largely destroyed by CFCs in the earth atmosphere before it could diffuse to stratospheres to replenish the affected ozone. Therefore, to replenish the ozone layer in the stratosphere, it will require considerable time even after a complete ban on the ozone-depleting substances.

During the Montreal protocol in 1985 a concern about ozone depletion and limiting the use of CFCs was proposed. This will necessarily occur at different rates in different countries across the world. Moreover, the only alternative to CFCs present today is hydrogenated CFCs (HCFCs) which have relatively shorter life span (i.e. about 30 years). Therefore, even if all CFCs usage were to stop, the CFCs already released in the atmosphere will continue to affect the ozone layer for a considerable period of time to come. However, the disturbances of the ozone layer in the stratosphere are not dependent solely on these chemicals and therefore, it is unlikely that the problem of ozone depletion will disappear. It is almost impossible to predict future scenarios given the interaction effects of other global change factors with ozone chemistry, since the mechanisms of which are far from understood.

In this review I discuss how UV-B radiation influences plants at a physiological and biochemical level, with particular emphasis on photosynthesis.

Increase in the UV-B radiation and its consequences

Why should we worry about the increase in the UV-B radiation in the earth's atmosphere? The reason is that UV-B in addition of UV-A and UV-C is biologically effective (however, in this review I discuss impact of UV-B alone) and absorbed by various biological compounds such as DNA, pigments, proteins, chromophores, plastoquinol, etc. The adverse effect includes skin cancers, eye cataract, loss of immune system, etc. in animal and loss of crop productivity in plants with severe consequences to human being (Table 1). Though UV-B radiation comprise only a small portion of electromagnetic spectrum, it has a disproportionately large photobiological effects since the energy content of the UV-B radiation is greater than visual radiation and it is largely absorbed by the two most

Table 1. Biological consequences of increased UV-B radiation.

	Plants	
Human	System likely to get affected	Protective processes
More skin cancer (25%)	Net CO_2 fixation (enzymes)	Flavonoids
More eye cataract (15%)	Stomatal conductance	Carotenoids
Loss of immunity system (10%)	Photosynthetic electron transport	
	Chlorophyll fluorescence	Anatomical and morphological
	Membrane peroxidation	Antioxidant system
	Thylakoid protein and	Enzymatic
	Light harvesting complexes	Superoxide dismutase
		Ascorbate peroxidase
		Catalse
		Glutathione reductase
		Non-enzymatic
		Ascorbate
		Glutathione
		α-Tocopherol

The UV-B is absorbed by DNA, protein, chromophores, pigments, plastoquinones and plastoquinol.

important biological molecules – protein and DNA (Ravanat *et al.*, 2001; Tanaka *et al.*, 2002; van de Poll *et al.*, 2002).

UV-B radiation and photosynthesis

Photosynthesis is one of the most important processes influencing plant productivity. Chromophore, protein, DNA, quinone and pigments all absorb photon in the UV region. Long wave UV-A (320–400 nm) can actually drive photosynthesis to a limited extent if the epidermis of a leaf is removed (Caldwell *et al.*, 1989). Photosynthesis is readily inhibited by UV-C (190–280 nm), which can kill the leaves. UV-B radiation is less effective than UV-C but sufficient energy exists in sunlight to reduce photosynthesis of sensitive species.

The vulnerable targets in the photosynthetic system have not been identified but it may interfere directly with the basic photochemistry of PS II, disruption of electron transport or may be an indirect result of photosynthetic membrane damage (Caldwell *et al.*, 1998). Enzymes of carbon metabolism may also be inactivated (Xiong and Day, 2001) but probably would require higher dosages of UV radiation. Potential consequence of increase in solar UV-B radiation is its potential effect on global agriculture. However, we cannot make quantitative predictions of anticipated effects resulting from stratospheric ozone depletion, this is mainly due to the limitation in controlled environment studies. Plants in nature are seldom affected by only a single stress factor, instead they typically respond to several factors acting in concert such as water stress, increased atmospheric CO_2, mineral nutrients availability, heavy metals air pollutants and temperature and effectiveness of UV-B radiation can be greatly increased or decreased by such factors.

UV-B radiation affects plants in several ways. Chloroplast's function is impaired (Bornman, 1989), protein synthesis is decreased (Jordan *et al.*, 1994) and mRNA levels of photosynthesis genes are lowered (Mackerness *et al.*, 1998). UV-B exposure also results in upregulation of genes involved in the synthesis of phenolic compounds such as PAL, 4Cl and CHS (Strid, 1993; Strid *et al.*, 1996).

Numerous investigations have demonstrated that the photosynthetic system is a sensitive component to exposure to UV-B and can cause damage to both carbon metabolism as well as electron transport. Studies have shown large variability among plant species in their sensitivity to UV-B radiation such as due to quantum efficiency, RUPB (substrate) regeneration capacity (Strid *et al.*, 1990; Sullivan and Teramura, 1990; Ziska *et al.*, 1992; 1993), enzymes metabolism, pigment degradation, cell division, partial stomatal closure (Negash and Bjorn, 1986; Sharma *et al.*, 1998a), anatomical changes (leaf thickness and cutin deposition; Sharma *et al.*, 1997; 1998b), etc.

The decrease in CO_2 assimilation due to UV-B exposure could be explained on three factors, viz. down regulation or inhibition of enzymes of carbon metabolism resulting in direct effect on the rate of CO_2 assimilation, decrease in stomatal conductance resulting in CO_2 limitation and anatomical and morphological changes resulting in limitation of light indirectly related to CO_2 assimilation.

However, there are contrasting reports on the effect of UV-B on the photochemistry of photosynthesis. Several studies have demonstrated that PS II is the most sensitive component of the photosynthetic apparatus to the increased UV-B radiation (Renger *et al.*, 1989; Melis *et al.*, 1992; He *et al.*, 1993; Jansen *et al.*, 1996; Herrmann *et al.*, 1997) while others suggest that UV-B radiation inhibits photosynthesis without an appreciable effect on PS II photochemistry (Ziska and Teramura, 1992; Nogues and Baker, 1995; Allen *et al.*, 1997; Sharma *et al.*, 1997; 1998a). This is probably through the effect on enzymes of carbon metabolism or by photodegradation of photosynthetic pigments (Strid and Porra, 1992) while still others show no effect on photosynthesis (Germ *et al.*, 2002; Rozema *et al.*, 2002).

These differences in apparent photosynthesis response can be explained due to contrasting sensitivities of individual species (Teramura *et al.*, 1990; Ziska *et al.*, 1992; Teramura and Sullivan, 1994), differences in growth and irradiation protocols (Kramer *et al.*, 1992), leaf age (Naidu *et al.*, 1993) and UV-B penetration into leaf mesophyll (Delucia *et al.*, 1992).

UV-B treatment decreased net photosynthesis and dry weight of root, leaf, shoot in cucumber (Tevini and Teramura, 1989; Krizek *et al.*, 1993) and in brassica (Fagerberg and Bornman, 1997). Others have also

reported similar results (Gehrke *et al.*, 1995; Tosserams and Rozema, 1995), however, data on plant biomass and rates of net primary productivity expressed as g/dry weight/unit area are lacking to relate the decrease in CO_2 assimilation to primary productivity (Zepp *et al.*, 1998; Nogues *et al.*, 1998). Musil *et al.* (2002) studied 17 herbs, shrubs and tree species of southern Africa and reported that there was no pattern of response to UV-B related to growth form. Leaves of tree had altered chlorophyll *a* and *b*, carotenoids and flavonoids concentration but those of shrubs and herbs did not. Non-structural carbohydrates were unaffected and smaller canopy area were observed. Only five species have significantly altered leaf biochemical and morphological properties. It seems from the study that a large number of tree plants may not be economically affected by the increase level of UV-B. Smith *et al.* (2002) studied the response of a number of vegetable crops to UV-B exposure and reported that a rapid growth renders plants more sensitive to injurious effect of UV-B radiation. Rozema *et al.* (2002) reported that growth of lower land organisms like lichens and club moss was not significantly affected. Of the terrestrial higher plants studied for UV-B, response results showed variable effect. Gaberscik *et al.* (2002) reported lower level of chlorophyll *a*, *b* and carotenoids in response to UV-B treatment to high altitude crop buckwheat. Photosynthesis was also decreased while the transpiration rate was increased, consequently the decrease in water use efficiency. The production of seeds was decreased by 20% in response to UV-B treatment. However, germination of seeds, produced under UV-B radiation, was not affected and interestingly the time taken in germination of the seeds was decreased. However, Grammatikopoulous *et al.* (2003) reported improved seed yield in *Mentha spiculata* due to UV-B radiation. Day and Neale (2003) reported that photosynthesis was more sensitive to UV-B in phytoplankton than in terrestrial plants. Kakani *et al.* (2003) observed that vegetative parameters such as epidermal cells, stomatal density and leaf thickness were affected at higher level of UV-B radiation but reproductive parameters such as length and area of petals and bracts and number of anthers present were affected even at lower level of UV-B radiation in cotton. Reports also suggested decrease in chlorophyll and carotenoids content in plants exposed to UV-B radiation (Tevini and Teramura, 1989; Beychlang *et al.*, 1988; Strid and Porra, 1992; Tekeuchri *et al.*, 1996; Sprotova *et al.*, 1999). Decrease in chlorophyll *a* content was relatively more than that observed in chlorophyll *b* and carotenoids. However, there are a few reports suggesting increase in the chlorophyll content (Murali *et al.*, 1988; Panagopoulous *et al.*, 1992; Middleton and Teramura, 1993). Growth of cotyledons was also reported to decrease as a result of UV-B exposure, which may be due to accumulation of anthocyanin (Takeuchi *et al.*, 1996). Middleton and Teramura (1993) and Sharma *et al.* (1998a) have shown that UV-B exposure resulted in stomatal limitation, thereby reducing CO_2 assimilation rate. The action spectra for stomatal closure is reported to peak below 290 nm, whereas radiation above 313 nm is nearly ineffective (Negash and Bjorn, 1986). Stomatal closure may also be caused by a loss of turgor pressure mediated through ion leakage from guard cell under UV-B radiation (Nogues *et al.*, 1998). Transpiration rate was also reduced (Teramura *et al.*, 1983). The decrease in net CO_2 assimilation could be explained as a result of any of these factors individually or in combination with each other.

Proteins are vulnerable to UV-B because aromatic amino acids, particularly tryptophan, absorbs in 280–320 spectrum region. Exposure of UV-B has shown to affect RUBP carboxylase (Rubisco), the main CO_2 assimilation enzyme. Strid *et al.* (1990) demonstrated that exposure to UV-B resulted in decrease in both Rubisco activity as well as its content. Allen *et al.* (1997) also reported limitation of CO_2 assimilation as a result of UV-B exposure to *Brassica* due to decrease in carboxylation velocity and Rubisco content and activity. Wilson *et al.* (1995) and Ferreira *et al.* (1996) have shown that UV-B impacts on Rubisco resulting in breakdown products of 66 kDa and this is result of tryptophan photolysis under UV-B exposure. Both subunits of Rubisco contain tryptophan (Jordan *et al.*, 1992; Hartman and Harpel, 1994; Greenberg *et al.*, 1996). However, it is not known whether loss of Rubisco activity is entirely due to tryptophan photolysis (Gerhardt *et al.*, 1999). Decreased activity of Rubisco could also be due to lower mRNA transcript for Rubisco subunit (Jordan *et al.*, 1992) or reduction in quantum efficiency and RUBP regeneration (Ziska *et al.*, 1992; 1993).

Exposure to UV-B has also shown to affect other enzymes of carbon metabolism (Baker *et al.*, 1997; Nogues *et al.*, 1998). Drincovich *et al.* (1998) reported that UV-B exposure when supplemented with visual

induced NADP-malic enzyme in maize. NADP malic enzyme activity also increases in plants under various concentrations of nitrogen and exposed to UV-B radiation (Pinto *et al.*, 1999). Casati *et al.* 2003 reported increase in NADP–Me enzyme content activity and its mRNA due to UV-B radiation in maize. Kumar *et al.* (2003) reported inactivation of nitrogenase in cyanobacteria. Tevini *et al.* (1991) reported that a low dose of UV-B also stimulates the synthesis of water soluble proteins. However, exact composition of these water soluble protein is not known.

Photochemical reaction (light reaction)

PS II is also reported to be site of UV-B radiation damage (Bornman, 1989; Sullivan and Teramura, 1992). Results suggest effect on photosynthetic electron transport could be affected due to damage to D1 and D2 protein or due to oxidative damage to protein and lipids (membrane) as well as photosynthetic pigments in the LHC and reaction center. Occasionally UV-B effects are also reported in PSI (Van *et al.*, 1977; Brandle *et al.*, 1977) and when UV-B was supplemented with low visual radiation (Sharma *et al.*, 1998a). UV-B in combination with visual radiation resulted in increased degradation of D1 and D2 protein in PS II, photosynthetic active radiation degrade D1 while UV-B damages D2, combination of visible and UV-B radiation is far greater on degradation of D2 protein. Post *et al.* (1996) showed that donor side of PS II was affected due to UV-B exposure indicating slow reduction of $P680^+$ by tyrZ. However, Trebst and Depka (1990) have reported that UV-B treatment resulted in degradation of D1 protein under both aerobic as well as anaerobic condition. Germ *et al.* (2002) however, reported no effect of UV-B radiation on photosynthetic electron transport, chlorophyll *a* and carotenoids, while Bergo *et al.* (2003) reported degradation of D1 protein and found a 20 kDa C-terminal fragment. PS I and cytochrome *f* content decreased by 55% and PS II by 80% on a leaf area basis. Damage to PS II may be due to changes in reaction centre itself or function of oxygen evolving complex (Renger *et al.* 1989). Damage to reducing side of the PS II has also been suggested (Greenburg *et al.*, 1989) who demonstrated that a photoreceptor, possibly a semiquinone radical was involved in the process. Melis *et al.* (1992) also reported similar findings (semiquinone anion radicals and quinol have absorbency in the UV-B region and represent potential targets for UV-B radiation). It appears likely that both the oxidising and reducing sides of the PS II complex are targeted by UV-B. Renger *et al.* (1989) reported that water oxidation is the prime target for UV-B, whereas Melis *et al.* (1992) suggest that the quinones in PS II and within thylakoid membrane are likely to be main targets of UV-B treatment. Jordan *et al.* (1994) reported *de novo* synthesis of D1 protein, to replace the damage D1 protein, does not occur in the UV-B irradiated samples. However, Greenberg *et al.* (1989) showed that partial reactions leading to both the synthesis and degradation of D1 protein are enhanced by irradiation with UV-B. They concluded that degradation of D1 protein in UV radiation is mainly sensitized by plastoquinone. Liu and White (1998) showed decreased level of mRNA of two nuclear genes mediating LHC protein AB80 and Cab, by UV-B treatment. Following UV-B treatment mRNA transcript for genes encoding cytochrome *b* and subunit IV of the cytochrome *b/f* complex (pet B and pet D respectively) decreased as in mRNA for subunit β and α of the ATP synthase (atp B and atp E respectively; Zhang *et al.*, 1994). Other photosynthesis genes *psb*A (D1), *rbc*L, *cab*, *rbc*S, *SOD*, *atp*C, etc. also decreased. Integrity of thylakoid membrane seems to be much more sensitive than the activities of the photosynthetic components bound within (Strid *et al.*, 1994). This could be due to changes in the lipid environment of thylakoid membrane as reported by Tevini and Steinmuller (1987), who showed that UV-B resulted in lipids becoming shorter chain length. This shift was due to a direct UV-B impact on their biosynthesis rather due to photooxidation of lipid molecules.

While UV-B radiation may directly alter the function of PS II, photosynthesis may also be indirectly affected due to changes in leaf thickness or anatomy due to massive deposition of cutin and formation of hypodermal cells (Sharma *et al.*, 1997). This may alter penetration of visible irradiance into the leaf and thus indirectly impair photosynthesis. UV-B may also indirectly affect photosynthesis by photodegradation of photosynthetic pigments (Strid and Porra, 1992). One of the earlier consequences of exposure to UV-B is an increase in ion permeability of the thylakoid membrane which affect photochemical reactions (Chow *et al.*, 1992). This phenomenon results in accelerated discharge of the thylakoid transmembrane electric potential difference, which result in an increase in the rate of relaxation of the flash-induced absorption change (electrochromatic shift), suggesting that membrane per-

meability to ions was increased. The effect was highly responsive to UV-B: the dose of UV-B required by the pea plants to affect a 50% increase in ion permeability of the thylakoid membrane was only about one tenth of needed to inhibit other photosynthetic components by 50% (Strid *et al.*, 1994).

The functionality of PS II is most readily impaired (Strid *et al.*, 1990), because several thylakoid membrane components are adversely affected by supplementary UV-B. There is a marked decline in the amount and activity of ATP synthase (Zhang *et al.*, 1994). In contrast, PS I and cytochrome *b/f* complex are affected to a much lesser extent (Strid *et al.*, 1990). As a consequence of the sharp decline in several of the activities carrying out different partial reactions of photosynthesis, both maximum photosynthetic capacity and the light limited quantum yields are even more severely affected by UV-B than each components on its own.

The work presented shows that it is difficult to generalize the effect of UV-B radiation on plants. The extent of damage depends on susceptibility of plants, its genetic potential to adapt to UV-B radiation, morphological and physiological adaptation, the duration and extent of UV-B exposure, age of the tissue, etc. are important factors which influence the effect of UV-B on photosynthesis and productivity. This may also explain contrasting results of the effect of UV-B radiation on various parameters studied.

UV-B and oxidative damage

UV-B radiation can also affect the photochemical reaction indirectly through generation of active oxygen species. The active oxygen species such as H_2O_2, O_2^-, $OH^\bullet$ and $^1O_2$ are present in all plants in varying degree as a result of normal aerobic metabolism. However, there are reports suggesting that UV-B exposure causes accumulation of these active oxygen species (Doke *et al.*, 1994; Landry *et al.*, 1995; Hideg and Vass, 1996). Cellular UV-B chromophores such as aromatic amino acids, NADH and phenolic compounds could be activated by absorption of UV-B light which could react with oxygen to form singlet molecular oxygen and superoxide radicals (Rao *et al.*, 1995; Rao *et al.*, 1996; Hasselt *et al.*, 1996; Hideg and Vass, 1996). UV-B exposure preferentially induces peroxidase-related enzymes and generate activated oxygen species by increasing NADH oxidase activity (Rao *et al.*, 1996). These ROS can cause damage to membrane protein and lipids thereby causing damage to photochemical reaction (Sharma and Singhal, 1992a, b). Cellular UV-B chromatophores such as aromatic amino acids, NADH and phenolic compounds can be activated by the absorption of UV-B light which react with oxygen to form singlet molecular oxygen and superoxide radicals. For example, tryptophan strongly absorbs 290 nm light and is degraded into the photosensitizing compound N-formylkynurenine creating superoxide radicals in the process (Landry *et al.*, 1995). UV-B can sensitize protein damage and is also absorbed by quinone (Spetea *et al.*, 1996).

Reactive oxygen species act as signal transduction leading to down regulation of photosynthetic genes in response to UV-B radiation in green organs. UV-B exposure to rice for 28 days resulted in increased level of reactive oxygen species, hydrogen peroxide, MDA formation (lipid peroxidation) and membrane permeability and decrease in superoxide dismutase, ascorbate peroxidase and catalase (Dai *et al.*, 1997). UV exposure resulted in accumulation of heat shock protein 70 and P53 (Chen *et al.*, 1999) and proline in rice and mung bean. Also, MDA formation was seen (Pardha Saradhi *et al.*, 1995; Sharma *et al.*, 1998b). Formation of both proline as well as MDA is indicative of oxidative damage as a result of the UV-B exposure.

How plants can avoid UV radiation

Except some form of plant life which are motile and show negative phototaxis in response to UV radiation (Caldwell, 1981), the avoidance of UV radiation for most plant life does not include escape movements. Avoidance of UV is mainly achieved by two means, viz. synthesis of UV-B absorbing compounds such as flavonoids and phenolic compounds and anatomical changes such as formation of thick cuticle, massive synthesis of wax/cutin and deformation of epidermal cells, number of trichome and hypodermal cells in response to UV-B radiation (Hahlbrock and Scheel, 1989; Tevini *et al.*, 1991; Sharma *et al.*, 1997). These changes mainly take place in order to prevent UV-B radiation reaching the sensitive site. It is reported that up to 95–98% of incoming UV-B radiation can be reflected or blocked by such mechanism. Such changes may also result in less visible radiation reaching the photosynthesis site or becoming limited and thus resulting in decreased rate of photosynthesis.

When discussing the effect of UV-B on photosynthesis it is important to understand the adaptive defense mechanisms plants can muster to confer protection. UV-B-induced morphological changes include increasing the length of epidermis cells and thus thickening the epidermis (Haupt and Scheuerlein, 1990), formation of hypodermal cells (Sharma *et al.*, 1997). In general, this elongation of cells and formation of hypodermal cells result in attenuation of UV-B as well as visual radiation. However, accumulation of UV-B absorbing flavonoid compounds such as isoflavonoids, anthocyanin (Sharma *et al.*, 1998a) in the vacuole of the epidermal and hypodermal cells provide selective attenuation of UV-B radiation (Sharma *et al.*, 1997; Bhandari and Sharma, 2001). Changes in various phenolic compounds such as flavonoids (Kaempferol), caumarin, flavone and anthocyanin and cinnamic acid (Sharma *et al.*; 1997; 1998a) (Figure 1), product of shikimic acid pathway such as furanocoumarins (Zangerl and Berenbaum, 1987), polyketides and terpenes (canabinoids; Lydon *et al.*, 1986) were observed in response to supplementary UV-B radiation. This also indicates that flavonoids are synthesized in response to UV-B treatment and accumulated in the epidermal layer to provide protection by absorbing UV-B radiation and thus preventing it reaching more sensitive sites such as DNA and protein in mesophyll tissue. However, Nedunchezhian and Kulandaivelu (1997) in higher plants and Germ *et al.* (2002) in amphibious plant species reported no change in UV-B absorbing compounds as a result of UV-B exposure. These adverse results indicate that generalization of effect of UV-B radiation on plants could be misleading.

Lois and Buchannan (1994), Cullen and Neale (1994), Landry *et al.* (1995) and Strid *et al.* (1996) have all suggested that flavonoids and phenyl derivatives are involved in protection against UV-B in higher plants. Gorton and Vogelmann (1996) and Krauss *et al.* (1997) suggested that UV-B induces morphological and anatomical changes in order to accumulate increasing amount of flavonoids such as flavones, isoflavonoids and anthocyanin which provide selective attenuation of UV-B radiation. Sarma *et al.* (1997) reported that anthocyanin not only chelates metal ions but also forms ascorbic acid (co-pigment)–metal–anthocyanin complex, which could scavenge hydro-peroxy radicals. Lois and Buchannan (1994) working with an *Arabidopsis* mutant deficient in flavonoid accumulation found that the mutant displayed a dramatic increase in the sensitivity to UV-B radiation compared with wild type, suggesting a protective role for flavonoids against UV-B radiation. Similarly, Landry *et al.* (1995) and Li *et al.* (1993) also showed that *Arabidopsis tha-*

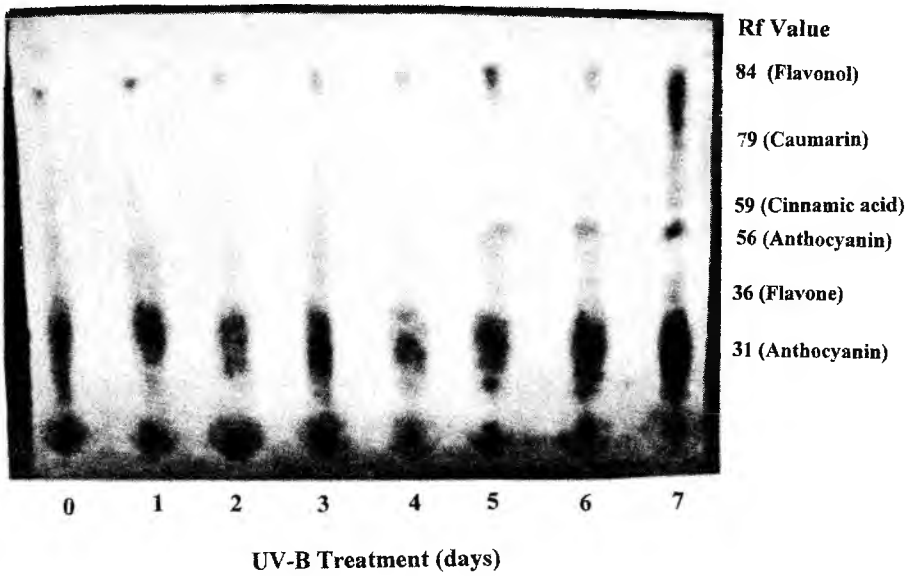

Figure 1. Effect of supplementary UV-B radiation (1 mW cm^{-2}) on phenolic content in wheat seedlings. Solvent system was *n* butanol : Galcial acetic acid: Water (6 : 1 : 2). The compounds were identified based on Rf value, colour changes under UV transilluminator with or without NH_3 fumes, their λ-max and by HPLC analysis.

liana mutants defective in ability to synthesize UV-B absorbing compounds (flavonoids and sinnapic esters) were more sensitive to UV-B than wild type. Plants with low anthocyanin (mutant) resulted in greater damage (Klaper *et al.*, 1996). Three genotypes of *Brassica rapa* with different levels of anthocyanin content showed that plants having low content showed decrease in flower number by half (Klaper *et al.*, 1996). Cen and Bornman (1990) reported overall 20% more UV-B absorbing pigments in leaves as a result of UV-B treatment. They showed 30% more UV screening pigments, including flavonoids, in the adaxial epidermal layer compared to 12% in abaxial epidermis. Also hydroxy cinnamatic was more effective UV-B protectants than flavonoids. Non-glandular leaf hair in *Quercus ilex* accumulated acetylated kaempferil and provides considerable protection to PS II against UV-B (Skaltsa *et al.*, 1994). Warren *et al.* (2003) reported increased levels of quercetin and kaempferol glycosides in populus leaves.

There are several reports in a variety of plants resulting in higher phenolic content in response to UV-B exposure. Xiong and Day (2002) showed higher level of UV-B absorbing phenolic compounds in *Colobanthum quitensis* and *Deshchampsia antarctica*. Sinha and Hader (2001) and Groniger *et al.* (2000) have reported amino acid-like compounds such as mycosporine, scytanemin, polythine, asterine, polythinol, shinorine, polythene, scytonemin, etc. in cyanobacteria. Day and Neale (2003) reported increased level of UV-B screening compounds in both terrestrial and aquatic primary producers. Hada *et al.* (2001) reported accumulation of phenolics in spinach in response to UV-B. Booij-James *et al.* (2000) reported effect of phenolics compounds on protection against UV-B exposure. They indicated that relative contribution of particular phenolics to the total screening capacity varies with the genetic background. Mazza *et al.* (2000) found significant differences in UV penetration among cultivars with different levels of leaf phenolics. They concluded that phenolics sunscreens in soybean are highly responsive to the wavelength that are most affected by variation in ozone levels and phenolic compounds play an important role in protection against UV in field. Rozema *et al.* (2002) reported appearance of various flavonoids (orientin, luteolin, tricin, apigenin, aglycons, gerercitin, Kaempferol, etc. in response to UV-B treatment). Similar results were also reported by Hall *et al.* (2002) in *Cladonia arbuscula* (lichens), Staaij *et al.* (2002) in grass species, Gaberscik *et al.* (2002) in buckwheat and Solovchenko *et al.* (2003) in apple.

Short UV-B exposure induces an increase in a rapid and coordinated expression of genes encoding certain enzymes in the flavonoid biosynthetic pathway. Expression of genes encoding enzymes of flavonoid biosynthetic pathway was increased. Enzymes such as phenylalanine ammonia lyase (PAL; Kuhn *et al.*, 1984), chalcone synthase (CHS; Kreuzaler *et al.*, 1983) and 4-coumarate CoA ligase (4Cl; Kuhn *et al.*, 1984) appeared within hours after UV-exposure. The increase in the amount of the mRNA transcripts for these three enzymes was actually due to an increase in transcription rates (Chappell and Hahlbrock, 1984). While the overall rate of synthesis of mRNA peaked about 4 h after the onset of irradiation, the accumulation of CHS mRNA peaked after 9 h, increase in the CHS activity after 15 h and formation of flavonoids after 50 h (Chappell and Hahlbrock, 1984). The accumulation of CHS mRNA and enzyme molecules occurred only in epidermal cells (Schmelzer *et al.*, 1988). Increase in the activities of several other enzymes in the phenyl propanoid and flavonoid biosynthetic pathways following UV irradiation has also been demonstrated (Chappell and Hahlbrock, 1984).

Another but less specific UV-B excluding response is the production of a waxy cuticle. Cuticle strongly attenuated UV-B radiation at λ below 400 nm (Krauss *et al.*, 1997). Mulroy (1979) showed that glaucesscence, a powdery wax on the leaf surface, is predominantly responsible for a very high reflectance of UV-B (approx. 80%), visible (approx. 65%) and near infrared (40–50%) radiation in *Dudleya brittonii*. In addition to the above-mentioned defense mechanisms, enzymatic and non-enzymatic scavenging of secondary toxic substances occurs.

Other defense mechanisms

As reported earlier UV-B exposure resulted in oxidative damage. In order to overcome oxidizing damage plants exposed to UV-B showed an increase in SOD, APX and GR without measurably affecting transcript levels in pea buds (Sharma *et al.*, 1998b; Mackerness *et al.*, 1999). Plant cells and particularly chloroplasts have multiple protective mechanisms against highly reactive oxygen species with glutathione and ascorbate

being the main stromal antioxidants (Krause, 1994). Raimondi *et al.* (2003) have shown accumulation of viscosizing agent TS-polysaccharides in corneal-derived cells exposed to UV-B radiation. Probably similar substances may also be present in plants to protect against UV-B radiation.

Plant metabolize activated oxygen species by invoking the antioxidant defense system of low molecular weight antioxidants (Alscher and Hess, 1993; Kangasjarvi *et al.*, 1994; Rao *et al.*, 1996) such as ascorbate, glutathione, α-tocopherol and carotenoids (Alscher and Hess, 1993) as well as enzymes such as SOD, GSH and catalase, ascorbate peroxidase, glutathione reductase, POD, etc. (Creissen *et al.*, 1994; Sankhalkar and Sharma, 2002). Flavonoids, apart from protecting plants by absorbing UV-B radiation also possess antioxidant properties (Sarma *et al.*, 1997). The protective properties of flavonoids were time and concentration-dependent (Devasagayam *et al.*, 1995).

Conclusion

It is too early to predict whether UV-B damage to plants would threaten yield of agricultural plants and further studies in the field conditions are needed to correlate the observed changes to photosynthesis under laboratory conditions to normal conditions in order to understand why certain species can better withstand enhanced UV-B. Further studies are also needed to provide a basis for genetically engineered plants which can sustain itself under enhanced UV-B conditions.

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