Emir. J. Food Agric. 2012. 24 (6): 481-501
doi: 10.9755/ejfa.v24i6.14669
http://www.ejfa.info/

REVIEW ARTICLE

Plant physiological responses to UV-B radiation

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Abstract

During the last few decades, there has been considerable concern over the depletion of stratospheric ozone as a result of anthropogenic pollutants. This has resulted in a concomitant increase in solar ultraviolet-B radiation (280–320 nm). High levels of UV-B radiation are responsible for multiple biologically harmful effects in both plants and animals. Many different plant responses to supplemental UV-B radiation have been observed, mostly injurious but sometimes beneficial. UV-B can influence plant processes either through direct damage or via various regulatory effects. In plants, direct effects include DNA damage, membrane changes and protein denaturation, which often cause heritable mutations affecting various physiological processes, including the photosynthetic apparatus. These could adversely affect plant growth, development and morphology, especially the productivity of sensitive crop species. This paper reviews the current knowledge about the plant physiological responses to UV-B stress.

Key words: UV-B radiation, Plant growth, Photosynthesis, Morphology, Oxidative stress

Introduction

Abiotic stresses are serious threats to agriculture and result in the deterioration of the environment and of crop loss worldwide, reducing average yields for most major crop plants by more than 50% (Wang et al., 2003). During the last few decades, there has been considerable concern over the depletion of stratospheric ozone as a result of anthropogenic pollutants such as halogenated hydrocarbons and other ozone depleting chemicals reaching the stratosphere (Molina and Rowland, 1974; Rowland, 1996; Madronich et al., 1998). Also greenhouse gases which cause cooling of the stratospheric ozone layer above the arctic, appear to be an indirect factor leading to ozone depletion (Shindell et al., 1998). A decrease in the ozone layer could lead to a significant increase in Ultraviolet-B (UV-B) radiation (280–320 nm) and shifts in the spectral UV-composition reaching the surface of the Earth (Blumthaler and Amback, 1990; Ajavon et al., 2007). This is predicted to continue in the future (Caldwell et al., 2003; McKenzie et al., 2003).

All living organisms of the biosphere are exposed to UV-B at intensities that vary with the solar angle and the thickness of the stratospheric ozone layer. The amount of increase of UV-B is dependent mainly on latitude, with the greatest increases in arctic and antarctic regions. The ultraviolet radiation that is present in sunlight is divided into three classes: UV-A, UV-B and UV-C. The UV-A, with wavelengths from 320 to 390 nm, is not attenuated by ozone and thus is not affected by depletion of the stratospheric ozone layer. The UV-C, with wavelength shorter than 280 nm, does not reach ground level and this is not expected to change. It is the UV-B radiation that has received most attention because UV-B is absorbed by ozone. The daily fluence at the earth's surface increases as stratospheric ozone decreases (Ormrod and Hale, 1995). Although UV-B is only a minor component of the total solar radiation (less than 0.5%), due to its high energy, its potential for causing biological damage is exceptionally high and even small increases could lead to significant biological damage.

Different plant responses to supplemental UV-B radiation have been established, mostly injurious but sometimes beneficial. UV-B can influence plant processes either through direct damage or via

Received 05 March 2012; Revised 01 April 2012; Accepted 01 May 2012; Published Online 06 October 2012

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various regulatory effects (Rozema et al., 1999; Potters et al., 2009). The injury can be classified into two categories: direct injury to DNA, which can cause heritable mutations, and direct and indirect injury to plant physiological functions (Ormrod and Hale, 1995; Lidon, 2012). The effects of UV-B that ultimately result in changed plant growth and productivity are initially felt at the cellular level, where both general and specific, and direct and indirect effects are found. The direct effects of UV-B can include DNA injury, membrane changes and protein denaturation.

In plants, wide inter- and intraspecific differences have been reported in response to UV-B irradiation with respect to growth, production of dry matter and physiological and biochemical changes (Kramer et al., 1991; Mpoloka, 2008; Fedina et al., 2010). Some plant species are unaffected by UV-B irradiation and several are apparently stimulated in their growth, but most species are sensitive and damage results, such as rice and maize (Teramura, 1983; Teramura and Sullivan, 1994; Hidema et al., 2007; Du et al., 2011; Lidon, 2012). On the other hand, plants have developed protective mechanisms against UV-B stress, such as enhancement of the antioxidant system (Brosché and Strid, 2003) and accumulation of UV-absorbing compounds (Frohnmeyer and Staiger, 2003; Fedina et al., 2007). Furthermore, numerous environmental factors such as water deficit, high temperature, ambient levels of visible radiation and nutrient status have also been shown to weaken or enhance the responses of plants to UV-B radiation (Murali and Teramura, 1985; Balakumar et al., 1993; Takeuchi et al., 1993; Mark and Tevini, 1996). Understanding the mechanism(s) by which physiological processes are damaged, repaired, and/or protected is important for understanding the ecophysiological role of UV-B radiation.

It has now been shown, that a natural balance of UV-B/UV-A/PAR is necessary for the adequate function of UV-B protection mechanisms (Rozema et al., 1997). Recent studies under semi-natural field conditions revealed that UV-B radiation is not as detrimental for plant growth and physiology, as previously believed (Björn et al., 2002). Furtheore, UV-B radiation effects are species specific and depend on interactions with other environmental parameters (Sullivan and Teramura, 1990; Gwynn-Jones, 2001; Kyparissis et al., 2001).

The present review surveys current knowledge about the plant physiological responses to UV-B stress based on physiological, biochemical and biophysical information. The interactions of UV-B stress with other environmental stresses are also discussed.

Photosynthesis and Respiration

Photosynthesis is sensitive to increased UV-B radiation, but the environmental relevance of UV-B effects on photosynthesis is not clear. Many studies have demonstrated detrimental effects of UV-B radiation on photosynthesis under laboratory conditions in both C3 and C4 plants (Krupa and Kickert, 1989; Groth and Krupa, 2000; Reddy et al., 2003), but the action spectrum of the UV-B effect does not suggest a specific target molecule (Renger et al., 1989; Fedina et al., 2010). At the whole-plant level, the effect of UV-B stress is usually perceived as a decrease in photosynthesis and growth, and is associated with alterations in carbon and nitrogen metabolism (Teramura and Sullivan, 1994; Julkunen-Tiitto et al., 2005; Lidon, 2012). Treatment with UV-B can affect stomatal conductance, altering the rate of water loss by transpiration and uptake rate of CO_2 for photosynthesis (Yao and Liu, 2006). Stomatal closure by enhanced UV-B and increased leaf diffusive resistance has been demonstrated with the action spectrum peaking below wavelength of 290 nm (Tevini and Teramura, 1989). It is assumed that stomatal closure is generating by a loss of turgor pressure with ion leakage from the guard cells.

It is demonstrared that transpiration is reduced in some UV-B sensitive seedlings (Tevini and Teramura, 1989; Yao and Liu, 2006). The time course for stomatal closure is rapid even at low UV-B levels. Stomatal opening is slowed by higher UV-B levels.

Direct injuries to the photosynthetic apparatus have been studied extensively. These effects include inactivation of photosystem II (PSII), reduced activity of Rubisco, decreased levels of chlorophylls and carotenoids, down-regulation of transcription of photosynthetic genes, and decreased thylakoid integrity and altered chloroplast ultrastructure (Friso et al., 1994; Strid et al., 1994; Teramura and Sullivan, 1994; Greenberg et al., 1996; Jansen et al., 1996; Vass et al., 1999).

Effects on PSII have drawn considerable attention (Jansen et al., 1996). PSII is a highly structured protein-pigment complex, the reaction center core of which is formed by the D1 and D2 similar proteins (Barber et al., 1997; Mattoo et al., 1999). The D1 and D2 reaction center proteins are extremely UV sensitive and degradation is driven by UV-B fluence rates as low as 1 μmol m^{-2} s^{-1} (Jansen et al., 1996). UV-driven D1-D2 degradation is strongly accelerated in the presence of a

background of visible radiation. The accelerated turnover of D2, as well as D1, under mixtures of UV-B radiation and photosynthetically active radiation (PAR), contrasts with the stability of the D2 protein under excessive flux densities of PAR alone (Jansen et al., 1996; Babu et al., 1999). The UV-B-driven degradation of the D1-D2 proteins may be, but is not necessarily, accompanied by a loss of PSII functionality, i.e. a decrease in oxygen evolution or in variable chlorophyll fluorescence.

The reduction in photosynthetic activity in the UV-B sensitive rice cultivar could be due to a decrease of Rubisco content, Rubisco activation and electron transport rate (Fedina et al., 2010). DNA lesions, such as CPD interfere with DNA replication and transcription (Britt, 1999).

Skórska (2011) established that after 60 min of UV-B irradiation the values of chlorophyll fluorescence parameters for cucumber leaves decreased by 4% to 44% versus the control. There were large decreases in F_v/F_o (20%) and vitality index - Rfd (33%). In the UV-B-treated cucumber leaves the Y value slightly decreased immediately after and especially 24 h after the end of the stress treatment.

Similar changes were observed for electron transport rate (ETR). In peppermint most of the measured parameters remained almost the same or even increased as in the F_v/F_m and F_v/F_o values. According van Rensen et al. (2007) damage caused by UV-B radiation occurs first on the acceptor side of photosystem II and only later on the donor side. The decrease of F_v/F_o, attributed to inhibition of photosynthetic electron transport at the acceptor side, was observed only in the cucumber leaves subjected to UV-B. In peppermint leaves it increased, probably due to the higher tolerance of this species to UV-B. It is worth pointing out that changes indicating recovery were observed 24 h after the end of the UV-B stress treatment, suggesting that the damage to the acceptor side of photosystem II was reversible. On the other hand, damage to the donor side, reflected by the Y, ETR and Rfd parameters, seemed irreversible. Jordan et al. (1994) studying etiolated tissue indicated a strong link between the photosynthetic apparatus and UV-B-induced gene expression. The redox potential of photosystems regulates chloroplast gene expression through the redox state of the plastoquinone pool (Tullberg et al., 2000). This may be connected with its interaction with UV-B signal transduction and gene expression. Mackerness et al. (1996) showed that amelioration of UV-B effects on gene expression by strong irradiation involved photosynthetic electron transport and photophosphorylation. This may, in part, account for the lack of UV-B effect on gene expression in etiolated tissue when photosystems are not functional.

Many of the detrimental UV-B effects on photosynthesis observed under laboratory conditions are not obvious under field conditions (Fiscus and Booker, 1995; Rozema et al., 1997; Jansen et al., 1998). Plants respond to UV-B by balancing reactions that lead to damage, repair, and acclimation. A likely reason underlying the discrepancy between laboratory and field studies is a failure to take into consideration the naturally occurring tolerance mechanisms (Fiscus and Booker, 1995; Gonzalez et al., 1998; Jansen et al., 1998). In a converse manner, the effects of UV-B on photosynthesis offer a convenient means to screen for repair and acclimation responses that can confer UV tolerance. Booij-James et al. (2000) have assessed the role of UV-screening pigments in protecting chloroplast metabolism against UV-B radiation in the presence or absence of a background of PAR using the UV-sensitive D1-D2 protein degradation assay as a sensor for UV penetration. In comparison to the more common measurements of photosynthetic electron flow and/or efficiency of photosynthetic light utilization, this assay has several advantages: (a) it is only to a minor extent affected by non-physiological UV-C wavelengths (Greenberg et al., 1989; Jansen et al., 1996a); (b) in healthy plants, the response is triggered by a low threshold fluence (1 μmol m^{-2} s^{-1}) of UV-B (Jansen et al., 1996b); (c) the degradation response is not diminished by a physiologically relevant background of PAR (Jansen et al., 1996a; Babu et al., 1999); and (d) the measured bonafide *in vivo* pulse-chase response directly reflects damage, i.e. not a steady-state balance comprised of damage and repair reactions. UV-B attenuation is mainly attributed to flavonoids and related phenolic compounds that absorb UV-B radiation effectively while transmitting PAR to the chloroplasts (Caldwell et al., 1983; Li et al., 1993; Reuber et al., 1996). Levels of these complex phenolic compounds vary considerably between plant species, with developmental stage, and with differing environmental conditions such as visible radiation levels, water, and nutrient supply (Caldwell, 1971; Murali and Teramura, 1985). In addition, exposure to UV-B radiation may increase the concentration of UV-B-absorbing compounds in the epidermis, rendering some plants less susceptible to photosynthetic damage due to UV-B exposure. Oilseed rape plants when pre-adapted to grow in

light supplemented with UV-B, developed tolerance to UV-B (Wilson and Greenberg, 1993). These plants, which had elevated levels of epidermal flavonoids, were also observed to have an increased half-life of the UV-B-sensitive PSII D1 protein. Arabidopsis mutants defective in the production of flavonoids have been successfully used in assessing the general effects of UV-B on plant growth, oxidative damage (Landry et al., 1995), and DNA repair (Landry et al., 1997). Although these studies have clearly demonstrated a general relationship between UV tolerance and flavonoid content, questions remain concerning (a) the extrapolation to different species, cultivars or ecotypes; (b) the protection of specific molecular targets; and (c) the relative contribution of specific phenols to the screening capacity.

Increases in the amounts of UV protective compounds have been commonly shown in the literature (Tevini et al., 1991; Ziska and Teramura, 1992; Santos et al., 1993), while stimulation in leaf respiration has previously been observed (Sisson and Caldwell, 1976; Ziska et al., 1991) but not discussed (Gwynn-Jones, 2001).

From this evidence, it is hypothesized that a stimulation of leaf respiration represents increased resource demands for protection and repair (cuticular thickening, flavonoid biosynthesis and photoreactivation). The stimulation of respiration in non-growing mature leaves, as pointed Gwynn-Jones (2001) supports this view as it can be used to reflect maintenance respiration. Maintenance respiration can be closely correlated with plant nitrogen content and may account for stimulation of nitrogen commonly observed in leaf tissue at enhanced UV-B (Gwynn-Jones, 1999). Marked changes in the carbohydrate allocation between root and shoot of *C. purpurea* with UV-B exposure also provide supportive evidence for this hypothesis. The soluble carbohydrate:starch ratio was higher in young leaves, the stem and overall in the shoot, whilst the amount of soluble carbohydrates within the roots was reduced at enhanced UV-B.

The results partially agree with a previous study by Phoenix et al. (2000), a long-term stimulation of soluble leaf carbohydrates was observed in the dwarf shrub *Vaccinium ulginiosum*, although root and rhizome carbohydrates were not measured. The findings of both studies might be explained by increased respiratory demand in the leaves influencing photoassimilate allocation.

Oxidative stress

Under elevated UV-B radiation plant cells produce reactive oxygen species (ROS) that induces oxidative damage to DNA, functional and structural proteins, lipids and other cell compounds (Panagopoulos et al., 1990; Foyer et al., 1994; Smirnoff, 1998; Mahdavian, 2008). As a consequence, this environmental stress often activates similar cell signaling pathways (Knight and Knight, 2001; Zhu, 2001, 2002) and cellular responses, such as the production of stress proteins, up-regulation of antioxidants and accumulation of compatible solutes (Vierling and Kimpel, 1992; Cushman and Bohnert, 2000).

To cope with oxidative stress, various ROS-scavenging systems in plants are involved (Bowler et al., 1992). Enzymatic ones include superoxide dismutase (SOD, EC 1.15.1.1), catalase (CAT, EC 1.11.1.6) and Halliwell/Asada pathway enzymes (Foyer et al., 1994). Non-enzymatic scavenging system includes low molecular mass antioxidants such as ascorbate (ASA), glutathione (GSH), carotenoids (Car), proline and compounds such as phenols (Asada, 1999).

Plants respond to UV-B oxidative stress by activation of antioxidant enzymes or changes in the contents of antioxidants. The activities of antioxidant enzymes such as superoxide dismutase (SOD), ascorbate peroxidases (APX), and glutathione raductase (GR) are enhanced by UV-B treatment in *Arabidopsis* (Rao et al., 1996), cucumber (Tekchandani and Guruprasad, 1998), wheat (Sharma et al., 1998) and cyanobacterium (Prasad and Zeeshan, 2005). Similarly, a significant increase in enzymes such as peroxidase, polyphenol oxidase, ascorbate peroxidase, catalase, and glutathione reductase showed enhanced activity in UV-B and UV-C treated pepper plants (*Capsicum annuum*) (Mahdavian et al., 2008). In addition, the coordination among enzymatic activities, antioxidant substrate flux, and gene expression in roots might be different from that of leaves, even though these two organs share almost the same enzymatic machinery. In leaves of the Landsberg erecta strain of A. *thaliana,* it has been reported that UV-B irradiation enhances guaiacol peroxidase, APX, and SOD activities, but not GR or CAT activity (Landry et al., 1995; Rao et al., 1996).

Santos et al. (2004) have emphasized that UV-B radiation interferes with the SOD similarly as do other stresses and also affects the isoenzymes of SOD differently. Agarwal (2007) established that tolerance of *Cassia auriculata* L. seedlings to UV-B is due to the enhancement of SOD activity and other antioxidative enzymes. The same results were reported by Santos et al., (2004) in potato, Mackerness et al. (1999) in pea, Kondo and Kawashima (2000) in cucumber, and Prasad and

Zeeshan (2005) in *Plectonema boryanum.* Increases in activities of CAT and POX by UV-B radiation have been observed in several species including *Cassia* species (Agarwal and Pandey, 2003), cucumber (Krizek et al., 1993; Jain et al. 2004), sugarbeet (Panagopoulos et al., 1990), potato (Santos et al., 2004), sunflower (Costa et al., 2002; Yannarelli et al., 2006); soybean (Xu et al., 2008) and *Acorus calamus* (Kumari et al., 2010). Increasing trend of GR and APX activity was also consistent with other studies performed under UV-B stress (Selvakumar, 2008). Induction of APX and GR due to UV-B indicates a preferential synthesis/activation of these enzymes, playing a crucial role in scavenging of H_2O_2.

Through these pathways chloroplasts are shielded against oxidative burst, with very little damage being caused to the photosynthetic apparatus (Fiscus and Booker, 1995), which allows synthesis and mobilization of photoassimilates. Moreover, enhanced UV-B irradiation might arrest plant growth (Strid et al., 1994; Tevini, 2004), as it inhibits photosynthesis (Teramura and Sullivan, 1994; Ambasht and Agarwal, 1998; Niyogi, 1999) and suppresses isoprenoid synthesis (Kulandaivelu et al., 1991). Thus, depending on the intensity of UV-B irradiation, the potential primary catabolisms involved in uncontrolled tissues injury are photoxidation and ROS production when the antioxidant systems become inhibited (Lidon and Henriques, 1993; Foyer et al., 1994; Caldwell et al., 2003).

It was found that during the beginning of the vegetative growth supplemental UV-B irradiation becomes lethal in directly exposed leaves of *Oryza sativa* L. cv Safari, but does not limit subsequent growth until the end of the life cycle (Lidon and Silva, 2011; Lidon, 2012). Following the sensitivity and recover of this genotype, the induced damages of ROS amplification by UV-B irradiation were timely followed and compared in leaves directly stressed and grown after irradiation. It is pointed that under UV-B stress the rates of ascorbate peroxidation in the xanthophyll cycle drive the availability of the ascorbate pool for the Asada-Haliwell cycle, concomitantly determining the extent of oxidative burst and thylakoid degradation through proteolysis and lipid peroxidation.

Increased content of non-enzymatic antioxidants was observed in pepper plants (Mahdavian et al., 2008), *Cassia auriculata* (Agarwal, 2007) and medical plant *Acorus calamus* (Kumari et al., 2010) after exposure with UV-B irradiation. Increase in ascorbic acid in plants at early age after UV-B exposure was also manifested in several studies suggesting its induction due to UV-B stress (Costa et al., 2002; Nasibi and Kalantari, 2005). Decline in ascorbic acid under UV-B stress was also reported by Agrawal and Rathore (2007) in wheat and mung bean. The reduction in ascorbic acid at later stages of observations could be explained due to increased activity of APX after UV-B exposure resulting into more consumption of ascorbic acid for effective quenching of oxyradicals. Ascorbic acid is postulated to maintain the stability of plant cell membranes against oxidative damage by scavenging cytotoxic free radicals. Conklin et al. (1996) have shown that an ascorbic acid deficient Arabidopsis mutant was very sensitive to a range of environmental stresses, an observation which demonstrates the key protective role for this molecule in *Arabidopsis* foliar tissues.

Synthesis of phenolic substances such as anthocyanin and flavonoids have been observed in UV-B treated *Arabidopsis thaliana* (L.) Heynh. seedlings (Winkel-Shirley, 2002). A role for flavonoids in UV protection is also supported by isolation of *Arabidopsis* mutant that is tolerant of extremely high UV-B levels (Bieza and Lois, 2001).

In addition, the metabolism of phenolic compounds also includes the action of oxidative enzymes such as POX (EC 1.11.1.7) and PPO (polyphenol oxidase, EC 1.10. 3.1), which catalyze the oxidation of phenols to quinones (Thypyapong et al., 1995). Agarwal (2007) found in *Cassia auriculata* a decrease in total phenol contents as well as the enhanced PPO activity under UV-B radiation. Also, phenol contents decreased with successive growth stage of bean plants after UV-B treatment (Singh et al., 2011). Whereas, Balakumar et al. (1997) reported for increases in phenol content and a decreases in PPO activity in *Licopersicon esculentum* after UV-B treatment. It seems possible that oxidoreductases PPO and POX involved in phenol oxidation may play an important role as defense against UV-B oxidative stress. In addition, phenols can protect DNA from UV-B induced damage (Mazza et al., 2000).

A decrease in photosynthetic pigments has been evident during exposure to enhanced UV-B radiation in most of the crop species (Kakani et al., 2003; Agrawal and Rathore, 2007). Carotenoids play an important role against UV-B damage in higher plants. Carotenoids, the scavengers of singlet oxygen species formed during intense light, are involved in the light harvesting and protection

of chlorophylls from photoxidative destruction. Significant reduction in carotenoid content was observed in UV-B treated bean plants (Singh et al., 2011).

Proline accumulation was also higher under UV-B stress condition, which might protect the plant cells against peroxidative process (Pardha Saradhi et al., 1995). Increment of proline under UV-B stress was observed in maize (Carletti et al., 2003) and pea (Singh et al., 2009).

Sensitivity to UV-B irradiation varies widely among plant species and genotypes (Alexieva et al., 2001; Yanqun et al., 2003; Zu et al., 2004). For instance, Sato and Kumagai (1993) working with Japanese lowland and upland rice groups, examined interactions between UV-B radiation and 198 rice cultivars, concluding that in similar ecotypes and groups the resistance of these genotypes vary broadly. Varying responses in antioxidants under UV-B exposure have been reported, depending on intensity of radiation and duration of irradiation period (Rao et al., 1996; Kubo et al., 1999). For example, increased ascorbate peroxidase activity was reported in *A. thaliana* under enhanced UV-B radiation at the level of 18 KJ m^{-1} d^{-1} (Rao et al., 1996). UV-B induced increment in ascorbic acid at 15 days after germination of bean plants whereas reduction was observed at 30 days after germination (Singh et al., 2011).

Under natural UV-B irradiation the sensitivity of genotypes depends of the activation of protective mechanisms, such as UV-B filters, quenchers of ROS (Bjorn et al., 2002; Caldwell et al., 2003) or antioxidant enzymes and some metabolites of the Asada-Haliwell and xanthophyll cycles (Lidon and Henriques, 1993; Asada, 1999; Mackerness, 2000).

Pigments and UV-B absorbing substances

Plants exhibit a wide range of responses to UV-B, including physiological responses which help to protect them from damaging UV-B wavelengths (Tevini and Teramura, 1989; Stapleton, 1992). The best studied direct UV-B protection mechanism, mediated by a photoreceptors is the differential production of UV-B absorbing compounds, such as phenolic compound, flavonoids, and hydroxycinnamate esters in the leaves, particularly in the epidermis (Fohnmeyer et al., 1997; Meijkamp et al., 2001; Caldwell et al., 2003; Fedina et al., 2007). This type of response is not a damage response and involves the stimulation of expression of particular genes by UV-B, implying specific UV-B light detection systems and signal transduction processes, which lead to the regulation of transcription (Jenkins et al., 1997). The largest concentration of these pigments is located in the epidermal and subepidermal cell layers, absorbing and effectively reducing the penetration of UV-B deeper into the mesophyll cells of the leaf with little effect on the penetration of visible or the photosynthetically active radiation (Bornman et al., 1997; Fedina et al., 2007; Fedina et al., 2010), thus acting to screen out the UV-B. The epidermis blocks transmittance of 95 to 99% of incoming UV radiation (Robberecht and Caldwell, 1986).

lnduction of flavonoids in rye seedlings can prevent UV-B-induced damage to photosynthesis (Tevini et al., 1991), which suggests that UV radiation protection is one of the functions of these pigments. This could be tested directly using mutants that are defective in the accumulation of flavonoids.

Species with higher contents of these compounds prior to the onset of UV-B treatment (Gonzales et al., 1996) or species that can rapidly accumulate these compounds (Murali and Teramura, 1986) are protected against UV-B damage and would be UV-B tolerant. However, such a trend was not observed in many studies. Smith et al. (2000) established that mean contents of UV-B absorbing compounds did not differ significantly between the tolerant and sensitive groups, not did an ability to increase the content of UV-B screening pigments in response to UV-B necessarily reduce sensitivity.

Fedina et al. (2010) established that there were no significant correlation between sensitivity to UV-B and accumulation of UV-absorbing compounds in three rice cultivars. Similar results were observed in rice by Teranishi et al. (2004) and in cucumber by Adamse and Britz (1996). Hada et al. (2003) reported that excess accumulation of anthocyanins reduced the amount of blue and UV-A radiation, which is utilized by cyclobutane pyrimidine dimers photolyase for monomerization of dimers and thus lowered CPD photorepair in purple rice leaves.

Beggs and Wellmann (1994) suggest that the synthesis of isoflavonoids in legumes may be induced by DNA damage because the wavelength dependency of the response is similar to that for DNA absorption and acceleration of DNA repair by photoreactivation. It is hypothesized that DNA damage is the sensory mechanism for the response to short UV wavelength. After UV-B exposure, some flavonoids are selectively produced (Markham et al., 1998). This accumulation does not relate to any enhanced capability to absorb UV-B, but rather reflects a greater potential to dissipate energy or produce greater antioxidant capacity.

Flavonoids absorb specifically in the UV region and not in the PAR region (Ballaré et al., 1992). At higher PAR levels, the interaction between UV-B and PAR effects may lead to compensation of negative UV-B effects (Cen and Bornman, 1990; Ballaré et al., 1992; Adamse and Britz, 1996). Firstly, radiation with a wavelength range between 300 and 500 nm is required for the activity of the enzyme DNA photolyase, repairing DNA dimers induced by UV-B (Jordan, 1993; Taylor et al., 1997). Secondly, some UV-B effects such as reduced plant height, thicker leaves and enhanced concentrations of phenolics, which have a protective function against UV-B, are also observed in response to enhanced PAR levels (Cen and Bornman, 1990; Ballaré et al., 1992). In most cases, PAR levels in the greenhouse and in climate chambers are lower than outside. Also, the light spectrum inside differs from the spectral composition of the light outside. Thus, when results from greenhouse experiments are extrapolated to the field situation, this may lead to an overestimation of UV-B effects on growth in the field (Rozema et al., 1997; Caldwell et al., 2003).

In addition to enhanced antioxidant capacity provided by specific flavonoids, plant cell produces a range of alternative antioxidant systems to protect against free radicals generated by UV-B (Strid, 1993). Thus, increased UV-B induces the rapid synthesis of antioxidant enzymes (SOD, CAT, and GPX) to cope with the free superoxide radicals. It is supposed that peroxidases under UV-B stress can use flavonoids as substrates to detoxify hydrogen peroxide.

Anthocyanins absorb also in the UV region of the spectrum of 270-290 nm. Therefore, they have been empirically implicated in UV-B protection of young leaves (Lee and Lowry, 1980). More recently Burger and Edwards (1996) provided experimental evidence that the anthocyanin-rich red varieties of *Coleus* were less damaged by UV-B radiation, compared to anthocyanin-less green varieties. In addition, Stapleton and Walbot (1994) showed that the DNA of maize varieties containing anthocyanins was better protected against UV-B radiation damage. However, Woodall and Stewart (1998) questioned the above on the basis that anthocyanins do not absorb appreciably in the UV-B (290-315 nm) spectral band, unless they are acylated with aromatic organic acids (Markham, 1982). In this case, their 270-290 nm UV peak is shifted to the UV-B region. However, this shift does not necessarily result in a considerable increase in their specific absorbance in the UV-B region of the spectrum (Woodall and Stewart, 1998). In anthocyanins, the UV and visible absorption coefficients are almost the same (Woodall and Stewart, 1998).

Mendez et al. (1999) assume that if anthocyanins in *Pinguicula vulgaris* are indeed acylated, their normalized absorbance at 300 nm would be as low as 0.20 and 0.44 for the control and UV-B treated plants respectively. Since the corresponding total normalized absorbances at this wavelength are 13.83 and 14.67, the relative contribution of anthocyanins to UV-B attenuation would be 1.4% for the controls and 3% for the UV-B treated plants. Authors therefore assume that the UV-B induced increase in anthocyanins of *Pinguicula vulgaris* cannot afford signifcant protection against UV-B radiation damage since the absorbances of other co-occurring phenolics are much higher. Absorption of visible light by epidermal anthocyanins could reduce the photosynthetically active radiation reaching the mesophyll and, accordingly, suppress the already low (Mendez and Karlsson, 1999) photosynthetic rates of this plant. However, corresponding reductions in growth or reproduction were not observed. On the other hand, anthocyanins may protect against photoinhibition by visible radiation, as suggested by Gould et al. (1995). Although previous attempts to verify this hypothesis were negative (Burger and Edwards, 1996), the results of Mendez et al. (1999) clearly showed that the anthocyanin-rich, UV-B treated leaves were less prone to photoinhibition imposed by high light and low temperature. However, it is possible that the apparent correlation between high anthocyanin and lower photoinhibitory risk found in the present study could be coincidental, and that other processes induced by UV-B could be responsible for the increase in resistance to photoinhibitory stress.

Regardless of this, the differences in the extent of photoinhibition observed in the laboratory did not result in corresponding changes in the above-ground biomass accumulation in the field, nor on dry mass of overwintering buds. In addition, the leaf and plant senescence rates measured during late season, where the slightly above zero temperatures could have enhanced the photoinhibitory risk, were the same in control and UV-B treated plants. Therefore, authors have to accept either that the increase in anthocyanins was of no adaptive significance or that the lower photoinhibitory risk counterbalanced the possible negative effects of UV-B radiation. *In situ*

*fl*uorescence measurements and photosynthetic rates of control and UV-B treated plants could help to express an opinion on the above alternatives.

Anthocyanins could also be induced by nutrient (P and N) limitation. Furthermore, the nitrogen content of the leaves was improved under UV-B supplementation. However, this can be correlated with the increased root mass under UV-B supplementation (Mendez et al., 1999). It is concluded that *P. vulgaris* is very well equipped to cope with the ongoing increase of UV-B radiation reaching the surface of the earth. In addition, the preferential increase in leaf anthocyanins may be beneficial to this plant under certain environmental conditions.

Growth and Development

At the plant level, increased UV-B radiation can result in decreases in biomass or total dry matter production and marketable yield.

A large number of experiments world-wide have addressed the impacts of enhanced UV-B radiation on plant growth (Caldwell, 1971; Krupa and Kickert, 1989; Rozema et al., 1997; Caldwell et al., 1998). Plant species (and groups) vary considerably in their response to UV-B, depending on experimental set up, treatment regimes and duration (Warner and Caldwell, 1983; Middleton and Teramura, 1994; Tevini, 1994; Weih et al., 1998). Regardless of such factors, several published (and unpublished) studies have shown evidence of plant resistance to UV-B radiation (Krupa and Kickert, 1989; Gwynn-Jones et al., 1997; Rozema et al., 1997) possibly via constitutive or induced protection against and/or repair of UV-B damage. Protection against UV-B can involve alterations in cuticle (Drilias et al., 1997) and leaf thickness (Johanson et al., 1995) and/or increased production of UV-B protective pigments (Cen and Bornman, 1990; Van de Staaij et al., 1995). In the event of protective mechanisms failing to shield the genome and photosynthetic machinery against UV-B, repair mechanisms are relied upon (Takeuchi et al., 1993). Most plant species are thought to have adequate repair capacities (photoreactivation–photorepair) to deal with projected increases in UV-B (Taulavuori et al., 1998). Nevertheless, one crucial factor to such tolerance is the duration of exposure, as longer-term studies show evidence of cumulative plant damage.

The experiment of Gwynn-Jones (2001) on *C. purpurea* contrasts with previous indoor study on the same species, as plant dry weight was not inhibited by enhanced UV-B radiation. This species is therefore tolerant to short-term exposure to enhanced UV-B under more realistic outdoor conditions. Measurements of leaf UV-B absorbing pigments and leaf respiration rates (young and mature) suggest induced leaf protection and metabolism at enhanced UV-B.

The growth reduction can be the result of a changed allocation of biomass, increasing amounts of secondary compounds or morphological alterations which lead to lower photosynthetic productivity (Teramura et al. 1990; Fiscus and Booker, 1995; Caldwell et al., 2003; Kakani et al., 2003; Liu et al., 2005;). Responses to UV-B include morphological alterations such as reduced leaf size, thicker leaves (Adamse and Britz, 1996), reduced hypocotyl length (Kim et al., 1998) and curling and bronzing of leaves (Teramura et al., 1984; Allen et al., 1998). These effects are more pronounced at lower PAR levels (Teramura, 1983; Musil, 1996). Morphological UV-B effects could either be interpreted as damaging effects when they are caused by photodestructive processes or as photomorphogenic responses mediated via photoreceptors (Barnes et al., 1990; Kim et al., 1998).

UV-B induces changes of in leaf and plant morphology (Jansen et al., 1998), but the mechanism underlying these alterations is not clear. Leaf curling is a photomorphogenic response, observable at low fluencies of UV-B that helps diminish the leaf area exposed to UV radiation. UV-B increases SLW, but it is not clear whether they represent damage or an adaptive response to elevated UV-B.

Some photomorphogenic effects and the production of flavonoids give mesophyll cells protection against UV-B radiation and thus have a role in adaptation to UV-B radiation (Ballaré et al., 1992; Mpoloka, 2008). When leaves become thicker, UV-B as well as PAR are absorbed in higher amounts in the leaves implying that leaf tissue is exposed to reduced levels of both UV-B and PAR (Ballaré et al., 1992; Adamse and Britz, 1996).

Negative impact of enhanced UV-B radiation on cotton growth included reduction in height, leaf area, total biomass and fiber quality (Gao et al., 2004). Growth reduction is mediated through leaf expansion (Pinto et al., 1999), which is a consequence of the UV-B radiation effects on the rate and duration of both cell division and elongation (Hopkins et al., 2002). In general UV radiation deleteriously affects plant growth, reducing leaf size and limiting the area available for solar energy capture (Zuk-Golaszewska et al., 2003). On the other hand the results of Zancan et al.

(2006) showed that UV-B radiation had no significant effect on plant growth. In addition, exposure of plant to UV-B radiation increased both chlorophyll content and root and leaf iron content. These findings have been achieved mainly through studies in greenhouses and exposure to artificial sources of ultraviolet radiation; extrapolation to changes on crop yield as a result of increases in terrestrial solar UV radiation is difficult (Yao et al., 2007). Salama et al. (2011) suggested that the significant increase in proline content was an important factor for providing higher tolerance to UV radiation treated plant species. In addition, increasing proline content is referred to as protective mechanism due to the generation of reactive oxygen species by UV radiation.

For instance, changes seen after supplemental UV-B radiation include biomass reductions (Lydon et al., 1986; Gwynn-Jones, 2001)**,** decreases in the percentage of pollen germination (Flint and Caldwell, 1984), changes in the ability of crop plants to compete with weeds (Barnes et al., 1990), epidermal deformation and changes in cuticular wax composition (Tevini and Steinmuller, 1987), and increased flavonoid levels (Tevini et al., 1991; Beggs and Wellman, 1985).

Photomorphogenesis is a radiation-induced change in plant form. UV-B enhancement alters the growth of several plant species but does not reduce shoot dry weight (Barnes et al., 1990). An action spectrum of the first positive phototropism (curvature) of the alfalfa hypocotyl has demonstrated that UV-B contributes to the response; plants were kept in red light to isolate this response from the similar response through phytochrome (Baskin and Lino, 1987). A cucumber mutant that lacks light-stable phytochrome (López-Juez et al., 1992) has also been used to measure photomorphogenesis after UV-B treatment. UV-B also inhibits hypocotyl growth (Ballaré et al., 1992).

However, because this mutant has some residual phytochrome function (Whitelam and Smith, 1991), the action of phytochrome in this UV-B response cannot be excluded. In the experiments with cucumber, shielding the actively growing tissues from UV radiation did not affect the magnitude of the decrease in hypocotyl length, so direct effects on cell division or elongation would not explain the UV-B-induced growth inhibition. Recovery after return to uninducing conditions was rapid, again suggesting a true photomorphogenic response to UV-B.

Interactions with other environmental factors

Water stress

Evidence of interaction between UV-B exposure and drought stress in plants has emerged in recent years, but the mechanisms of sensitivity or tolerance to combined stress have received little attention and still remain unknown. Some investigations have been carried out on agricultural or model plants, despite the fact that crops account for only 6% of the plant productivity world-wide (Tevini et al., 1983; Sullivan and Teramura, 1990; Schmidt et al., 2000). Elucidation of the interaction between drought and UV-B stresses would help in understanding the potential impact of partial stratospheric ozone depletion on plant adaptation to changing environmental condition.

Under drought stress plants become less sensitive to UV-B as the applied water stress increases. Several experiments have served to elucidate some of the water stress/UV-B interactions. Well-watered soybean plants grown in the field under enhanced UV-B radiation had reductions in growth, dry weight, and net photosynthesis compared with ambient UV-B, while no UV-B effect could be detected in water-stressed plants (Murali and Teramura, 1986). Photosynthesis recovery after water stress was greater and more rapid in UV-B treated soybeans and associated with UV-B effects on stomatal conductance rather than with internal water relations. Drought-stressed cucumber plants lost their capacity to close stomata at midday with increasing UV-B (Tevini et al., 1983). Radish seedlings were less sensitive to UV-B under water stress than cucumber. Radish had higher leaf flavonoid contents, possibly protecting seedlings by absorbing UV-B in the leaf epidermis.

Plants that endure water deficit stress effectively are also likely to be tolerant of high UV-B flux. Nevertheless the research of the interactions between UV-B and drought led to contradictory results. In field-grown soybean, a decrease in productivity following by UV-B exposure was moderated by soil water deficit (Sullivan and Teramura, 1990). The interaction between soil water deficit and UV-B stresses in cowpeas resulted in benefits from the combined stresses in terms of greater growth and development as compared with exposure to single stresses (Balakumar et al., 1993). It seems that under multiple stresses, each of the stress factors may bring out some adaptive effects to reduce the damage experienced by plants and caused by the other stress. UV-B irradiation could alleviate the negative effects of water stress on

plants or exert an additional inhibitory effect on the functional processes in plants. For example, exposure to both UV-B and water stress led to decreased growth in cucumber and radish, but protein content was increased by the combined stresses (Tevini et al., 1983). Teramura et al. (1984) have obtained similar additional injurious effects of UV-B on net photosynthesis of soybean under drought stress. Teramura et al. (1990) also reported that both genotypic differences and assimilate utilization were involved in the interaction between UV-B and water stress in soybeans. The growth of wheat seedlings (their fresh weight) was significantly inhibited by drought, UV-B irradiation, and the combination of stresses. The content of H_2O_2 increased significantly under stressful conditions. A common drought stress, UV-B radiation, and other environmental stresses could cause the accumulation of ROS and thus result in oxidative damage (Smirnoff, 1998; Alexieva et al., 2003). ROS are highly reactive and, in the absence of effective protective mechanism, they can compromise normal metabolism through oxidative damage to pigments, lipids, proteins, and nucleic acids.

In wheat seedlings, drought stress and UV-B irradiation resulted in the high H_2O_2 accumulation, which caused lipid peroxidation along with the reduction of growth. Moreover, UV-B treatment was found to cause a more severe damage than drought stress on wheat seedlings measured as more obvious reduction in growth and much more strong accumulation of H_2O_2 and increased lipid peroxidation (Tian and Lei, 2007). This data corresponded well to those of Alexieva et al. (2001) who also obtained similar results for pea and wheat seedlings. However, the combination of drought stress and UV-B irradiation was additive, in contrast to the other researcher data suggesting an antagonistic effect (Sullivan and Teramura, 1990; Alexieva et al., 2001). The growth of wheat seedlings under combined stress was much more retarded than when stresses were applied separately. Tian and Lei (2007) inferred that in their study the treatment time (7 days) was too short for wheat seedlings under each kind of stress to form protective responses to other stresses, that is, the interaction between stresses did not display their effects completely. The treatment time was longer in other studies, for example, it was 15 days in the case of cowpea (Balakumar et al., 1993).

Kyparissis et al. (2001) established that there were no significant interactive effects between supplemental UV-B radiation and additional watering on Mediterranean evergreen sclerophyll *Ceratonia siliqua* L. Previous field experiments with other Mediterranean plants, showed that supplementary watering during the summer abolished the negative (Drilias et al., 1997) or positive (Manetas et al., 1997).

Many contradictory results about antioxidant enzyme response to different stresses have emerged due to the fact that the levels of enzyme responses depend on the plant species, the developmental stage, the organs, as well as on the duration and severity of the stress (Rout and Shaw, 2001). In many plants, free proline accumulates in response to biotic and abiotic stresses, including UV-B irradiation (Carletti et al., 2003). In wheat seedlings, proline contents were up to 1.71 times higher under drought, UV-B, and combined stresses as compared with the control, respectively.

Tian and Lei (2007) concluded that drought stress and UV-B irradiation both could cause oxidative damage to plant through excessive ROS generation. UV-B caused more severe stress than drought stress, and the effect of drought and UV-B stress was additive in wheat seedlings. Authors suppose that the mechanism of combined effect of drought stress and UV-B irradiation need further study.

Concerning irrigation, the effects were as expected, with well-watered plants being taller and having more leaves compared to water stressed ones (Kyparissis et al., 2001). These effects were sustained throughout the experiment. Additionally, well-watered plants had significantly higher chlorophyll contents during the dry period. In fact, this was due to chlorophyll loss in water-stressed plants, which was abolished with additional watering. This type of response is considered a common photoprotective adaptation under photooxidative conditions (Kyparissis et al., 1995) and has also been found under water stress situations for several Mediterranean semi-decidual and sclerophyllous species (Stephanou and Manetas, 1998). In all other measured parameters, the effects of additional irrigation were negligible and only non-significant trends for increased total leaf area and above ground drymass were observed.

Kyparidis et al. (2001) assume that the growth of the evergreen sclerophyll, slow-growing plant *C. Siliqua* is not much affected by both UV-B radiation and additional watering, at least under the conditions used in this experiment. However, the subtle, mostly season-specific effects observed on some parameters could have a long-term impact on the fitness of this plant.

Visible light

The level of visible light (400-700 nm) to which experimental plants are exposed has been found to have a very great effect on UV-B injury (Ormrod and Hole, 1995). Growth chamber experiments have demonstrated that UV-B injury is greater with low levels of photosynthetic photon flux (PPF) (less than 200 µmol m^{-2} s^{-1}) than with high (ambient) levels (Tevini and Teramura, 1989). High levels of white light as well as UV-A radiation with blue light mediate photorepair mechanisms and ameliorate the UV-B injury. The relationship of PPF and UV-B effects is further complicated by the fact that a source of UV-B, whether simulated or natural, can exhibit not only different total output energies but also varying spectral composition within the range 280 to 320 nm (Krupa and Krickert, 1989). Growth chamber studies have been criticized because greater negative effects on the plant in response to UV-B exposure have been found in growth chambers than when a similar exposure take place under field conditions (Ormrod and Hole, 1995). It is important to study interaction of UV-B with another environmental variable at normal visible light level.

Nutritional status

Biologically available nitrogen is exceeding historical levels in many regions due to human activities. Studies show that plants well supplied with nitrogen are generally more sensitive to UV-B radiation. Both increases (Wand et al., 1996) and decreases (Dai et al., 1992) of leaf nitrogen content due to increased UV-B radiation have been reported, while in other cases UV-B radiation was ineffective (Wand et al., 1996). Levizou and Manetas (2001) reported that supplemental UV-B radiation improved growth in *Phlomis fruticosa* at high nutrient level, whereas greater growth inhibition by UV-B has been reported in nitrate-replete than nitrate-deficient crop plants (Hunt and McNeil, 1998). Tosserams et al. (2001) reported that photosynthetic rate of *Plantaago lanceolata* with high UV-B was not influenced by differential quantities of multiple mineral supply. Nitrogen supply accelerates some growth parameters of Mono Maple seedlings under ambient UV-B (Yao and Liu, 2006). This agrees well with the results of earlier studies (Deckmyn and Impens, 1997), however, some growth parameters were inhibited by nitrogen supply under enhanced UV-B. This indicated that the effects of high UV-B on growth completely overshadowed effects of nitrogen supply, whereas nitrogen supply increased for growth, morphological and physiological responses of Mono Maple to ambient UV-B. Authors conclude that nitrogen supply makes Mono Maple seedlings more sensitive to enhanced UV-B, though some antioxidant compounds increased. Obviously, nitrogen supply could not ease the harmful effects of high UV-B on plants, but aggravated the harm on plants.

The sensitivity of soybean to UV-B is dependent on phosphorus status (Murali and Teramura, 1985). Deficient plants are less sensitive to UV-B than are plants at optimum P levels, due at least in part to the accumulation flavonoids and to leaf thickening in P-deficient plants.

Conclusions

UV-B radiation effects are of increasing interest in plant physiology as questions are raised about the impact of enhanced UV-B in sunlight resulting from stratospheric ozone depletion. This increase in UV-B has been found to cause both photomorphogenic as well as genetic and physiological changes in plants. Photoreceptors acting through signal transduction pathways are responsible for sensing this ultraviolet radiation. Several components of the photosynthetic apparatus have been found to be affected by UV-B, with nuclear encoded genes being more sensitive to UV-B than chloroplast encoded genes. There have been significant advances in our understanding of the effects of UV-B radiation on terrestrial ecosystems, especially in the description of mechanisms of plant response. Many new developments in understanding the underlying mechanisms mediating plant response to UV-B radiation have emerged. This new information is helpful in understanding common responses of plants to UV-B radiation, such as diminished growth, acclimation responses of plants to UV-B radiation. The response to UV-B radiation involves both the initial stimulus by solar radiation and transmission of signals within the plants. Resulting changes in gene expression induced by these signals may have elements in common with those elicited by other environmental factors, and generate overlapping functional (including acclimation) responses. However, long-term effects of UV-B radiation in plants are still not well understood, therefore, more research need to be carried out over longer time periods and under field conditions, to provide definitive answers to questions such as cumulative effects of UV-B, effects of UV-B at ecosystem level, and interactions of elevated UV-B with other stress factors. Concurrent responses of terrestrial systems to the combination of enhanced UV-B radiation and other global change factors (water

availability, increased temperature, CO_2, available nitrogen and altered precipitation) are less well understood.

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