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Review

Effects of UV irradiation on plants

Eissa Piri[1], Mahdi Babaeian[2]*, Abolfazl Tavassoli[2] and Yasser Esmaeilian[2]

[1]Departmant of Agriculture, Payame noor University, P. O. Box 19395-4697, Tehran, I. R. of Iran.
[2]Department of Agriculture, Shirvan Branch, Islamic Azad University, Shirvan, Iran.

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Global change will definitely introduce changes in agricultural ecosystems that will affect plant productivity. However, the effects on plants will be different for each region depending on the pre-existing climatic conditions and the adaptation potential of local cultivated species. The solar energy from the sun is essential to support the life on our plant, via the process of photosynthesis. However a small proportion of solar spectrum contains short-wavelength ultraviolet-B light (280 to 320 nm), which is deleterious to life. The depletion of stratospheric ozone layer by manmade pollution has substantially increased UV-B light impinging on the earth surface. UV-B affects living organisms by damaging cellular metabolism in several ways, such as dimmers formation in the genetic material DNA, disruption of membrane structure, inactivation of enzymes and generation of highly reactive free radicals. Elevated UV exposure also causes temporary or irreversible damage to the process of photosynthesis. Therefore, increased UV-B radiation would affect the stability of ecosystems and genetic health of living organisms. Many species of plants have evolved mechanisms for protection against deleterious effects of UV-B radiation. Accumulation of the UV-B absorbing pigments such as flavonoids is one of the ways by which plants alleviate the harmful effects of UV-B light.

Key words: Global change, agriculture, UV radiation, absorbing compounds.

INTRODUCTION

The sun is essential for sustaining life on the earth; however, sunlight also contains a small amount of short wavelength ultraviolet (UV) light irradiation, which is harmful to life on planet earth. Fortunately, most of this harmful UV irradiation is filtered out by the stratospheric ozone layer, which strongly absorbs UV light. Unfortunately, this protective shield is being continually damaged by human activities. During the past eighty years the ozone layer has been damaged by the release of ozone depleting substances (ODSs) such as chlorofluorocarbons (CFCs), hydro chlorofluorocarbons (HCFCs), methyl bromide (MeBr) and other industrial compounds containing halogens (Krizek, 1998; Laposi and Mesezaros, 2005). These ODSs which are stable molecules are carried up to the stratosphere where they decompose under UV light and set a chemical chain reaction leading to ozone layer destruction (Sharma, 2001) . The shortest UV waves are most detrimental to living organisms. Usually, UV radiation is divided into; UV-A (315 to 400 nm), UV-B (280 to 315 nm) and UV-C (100 to 280 nm) spectral ranges. UV-C radiation is completely absorbed by the ozone layer while UV-A radiation is unaffected, though, such radiation does no harm to plants. However, the UV-B radiation intensity is mostly affected by the thickness of the stratospheric ozone layer and exactly this type of radiation is most harmful to plants. Recently, research on UV-A radiation also showed some adverse effect on plants (Helsper et al., 2003; Krizek, 2004). UV- B radiation is an important stress factor for plants which may result in damage to the genetic system, cell membranes and several metabolic processes (Bjorn, 1996; Csintalan et al., 2001). Stratospheric ozone depletion resulting from continual anthropogenic release of chlorofluorocarbons and other pollutants has led to an increase in the amount of ultraviolet radiation reaching the earth's surface (Sharma

*Corresponding author. E-mail: mahdi_bbn@yahoo.com.

et al., 1998). UV radiation causes damage to living organisms (Costa et al., 2002). Terrestrial plants are especially vulnerable due to their requirement of sunlight for photosynthesis (Greenberg et al., 1996; Sharma et al., 1998).

Higher than normal levels of UV-B causes various damages to plant such as DNA and 180 membrane injuries and photosynthetic or hormone systems disorders (Rozema et al., 1997; Jansen et al., 1998; Hollosy, 2002). Molecular -level changes affect other processes including gene activity, metabolism, photo-synthesis intensity and consequently, the growth of the whole plant. Some genes are identified as UV-B dependent genes and are responsible for the synthesis of UV screening compounds, DNA repairs and activation of oxidative enzymes (Brosche and Strid, 2003). UV can affect ecosystems directly and indirectly. Direct effects can be physiological damage to plants, consumers and microorganisms (Caldwell et al., 1998; Rozema, 1999). Indirect effects are feedbacks on ecosystem structure and function through many pathways which include altered competitive relationships among species, biogeo-chemical cycles and carbon budgets. The direct effect of UV on plant production is generally negative and small (Searles et al., 2001). However, ecosystems are complex and positive production responses to UV have been reported. Different species have different response to the level of UV-B irradiation (Matthew et al., 1996; and Skorska, 1996). Cline and Salisbury (1966) proposed that monocotyledons might be less affected by UV-C radiation than dicotyledons because of their vertical leaf orientation, protective basal sheath and concealed apical meristem. Many studies have shown deleterious UV effects such as reduced photosynthesis, biomass reduction, decreased proteins, impaired chloroplast function and damage to DNA (Agrawal, 1992). UV radiation also produces oxidative stress (Costa et al., 2002) arising from the deleterious effects of active oxygen species (AOS) which reacts with lipids, pigment, proteins and nucleic acid (Dai et al., 1997).

EFFECT ON PLANT MORPHOLOGY

Plant sensitivity to UV exposure might be determined by direct damage to cell structural and functional elements or by ineffective acclimatization process (Smith et al., 2000). UV-B radiation may induce leaf differentiation and senescence processes via modification of leaf structure (Kakani et al., 2003). Exposure to UV-B decreased plant height, leaf area and plant dry weight increased auxiliary branching and leaf curling (Greenberg et al., 1997; Furness et al., 1999) . Dai et al. (1995) reports that after a few weeks of UV-B exposure, leaf area and plant dry weight of rice were significantly reduced. Weigh et al. (1998) stated that enhanced UV-A decreased leaf area per unit plant biomass but increased biomass productivity both per unit leaf area and per unit leaf nitrogen. High levels of UV-B clearly decreased the relative growth rate and nitrogen productivity, as leaf area ratio, leaf area productivity and leaf nitrogen productivity were all decreased. Zuk-Golaszewska et al. (2003) stated the species *Avena fatua* and *Setaria viridis* grown in the greenhouse under the UV-B radiation had different growth habit and different reaction to UV-B radiation. Plants are capable to accommodate to certain UV-B radiation as well as to light intensity, though tolerance range are determined by plant species, age, duration of exposure and other factors. If the UV-B dosage exceeds the limits of tolerance, plant leaf anatomy is changed and biomass is decreased (Coleman and Day., 2004; Kakani et al., 2003; Zhao et al., 2003).

EFFECT ON CROP GROWTH AND YIELD

UV radiation induces crop growth and productivity in different ways. The main reason for decreased crop production with ultraviolet radiation is damage to organ membranes such as chloroplasts which make other stresses such as oxidative stress affect plant growth indirectly. However latest studies show significant UV-B radiation effect on barley growth parameters including stem height, sprout count, leaf area and biomass (Correia et al., 1999; Nasser, 2001). Hakala et al. (2002) determined sensitivity of various agricultural plant species including barley, wheat, oat, clover, timothy, fescue and potato to UV-B radiation exposure (as if ozone layer would be decreased by 30%) and found no significant variation of biomass accumulation or yield. Increased solar UV-B lead to reduction in photosynthesis (Jansen et al., 1996) and production of some crop species (Teramura and Murali, 1986). Teramura et al. (1991) showed that increased UV-B radiation induces a significant reduction in total biomass in a number of rice cultivars, accompanied by a reduction in tiller number and photosynthetic capacity of the plants. Ziska and Teramura (1992) and Dai et al. (1992) reported that prolonged exposure to UV-B light affects plant height, leaf area, dry weight, net assimilation rate and relative growth rate in some rice cultivars. Nevertheless, other authors (Liu et al., 1995; Stephen et al., 1999; Schmitz-Hoerner and Weissenbock, 2003; Valkama et al., 2003) showed that biomass or photosynthetic pigment content does not change under exposure to UV-B radiation and such variation is insignificant.

UV IRRADIATION AND OXIDATIVE STRESS

Plants are well adapted to minimizing damage that could be induced by AOS under natural growth conditions. However, oxygen toxicity emerges when the production of these AOS exceed the quenching capacity of protective systems due to environmentally adverse conditions such as drought, high light, water logging, high salinity, air pollutants, heavy metal toxicity and UV radiation (Costa et al., 2002; Dai et al., 1997). Recent studies have shown that enhanced UV radiation alters membranes. This can be seen by the increase in malondialdehyde concentration (MDA), reduced monogalagtosyl diacylglycerol (MGDG), as well as an increase in ethylene and ethane concentration (Dai et al., 1996).

Protein degradation occurs under conditions of induced oxidative stress (Palma et al., 2002). Some plants are more tolerant to UV than others because they produce a variety of secondary metabolites including flavonoids and anthocyanins. These compounds often accumulate in the upper epidermis cells of leaves and effectively absorb UV radiation thus preventing it from penetrating the leaf mesophyll cells (Sharma et al., 1998). Plants have developed a complex antioxidant system that includes reduced glutathione (GSH), ascorbic acid (ASA), -tocopherol, carotenoids and enzymes that protect plants against oxidative damage (Costa et al., 2002). ASA is an ubiquitous soluble antioxidant in both plants and animals (Sakihama et al., 2002) and is an important compound in plant cells, as well as being one of the most important reducing substrates for H_2O_2 detoxification (Costa et al., 2002).

The stresses imposed by UV-light (Shibata et al., 1991) irradiation can cause reactive oxygen species generation (ROS) such as O_2^- and H_2O_2. Though H_2O_2 is an innocuous metabolite present in cells, irradiation with UV-light breaks it down to extremely deleterious hydroxyl free radicals (OH^-). Since H_2O_2 can easily diffuse through cell membranes, it is extremely deleterious to cellular constituents such as DNA. Several studies have indicated that *in vitro* anthocyanins could act as effective antioxidants (Sarma et al., 1997).

EFFECT ON PHOTOSYNTHETIC EFFICIENCY

Since photo system II (PSII) has been perceived as being especially vulnerable to UV-B damage (Bornman, 1989) and has thus been considered a key target in determining the possible effects of ozone depletion on crop production, its integrity was studied using chlorophyll fluorescence. The efficiency of open reaction centers of PSII was estimated by Fv/Fm, while the other variables are indicators of the state of the electron transport system (Bolhar-Nordenkampf and Quist, 1993).

No significant UV-B treatment effect on any chlorophyll fluorescence variable was found in the barley experiment while significant UV-B effects on chlorophyll fluorescence variables (Fv/Fm) were observed in pea. The lack of consistent effects of enhanced UV-B on fluorescence characteristics corroborates previous data for pea obtained in the field (Mepsted et al., 1996) and under high PAR in CE conditions (Gonzalez et al., 1996; 1998). A similar absence of detected UV-B effects on chlorophyll fluorescence is reported from other crops in the field, e.g. soybean (Caldwell et al., 1994; Fiscus and Booker, 1995) and in CE conditions where a high PAR irradiance was provided (Cen and Bornman, 1990). Some scientists stated that plant height has been reported to be unaffected by increased UV-B in cassava (Ziska et al., 1993), rice (Kim et al., 1996), pea (Day et al., 1996) and soybean (Sullivan and Teramura, 1990).

UV-ABSORBING COMPOUNDS

The responses to enhanced UV-B radiation vary among species and also cultivars in the same species. Accumulation of the UV- B- absorbing pigments is one of the ways by which plants alleviate the harmful effect of UV-B light (Beggs et al., 1986). Plants are considered to employ a variety of UV-B protective mechanisms, including enhanced accumulation of UV-absorbing compounds in the epidermis have been found to be involved in the protector of sensitive targets in leaves from the inhibitory effects of UV-B radiation (Caldwell et al., 1983; Tevini and Teramura, 1989). A significant and positive correlation among the increase in the amount of UV-absorbing pigment with UV-B exposure and the degree of UV-B sensitivity in five cucumber cultivars was reported by Murali and Teramura (1986). Enhanced UV-B-treat-ment typically induces an increase in UV-B-absorbing compounds in leaf tissues (Tevini, 1993; Caldwell and Flint, 1994). Also, a few investigators have reported that the accumulation of UV-absorbing pigments was genetically controlled as a protection mechanism against UV- B radiation in arabidopsis plants (Li et al., 1993; Lois and Buchanan, 1994). Although cultivars of many crops have already been found to exhibit various degree of resistance to increased UV -B radiation, few studies have demonstrated a genetic relationship between this protective mechanism and the resistance to UV-B radiation in cultivated plants. A few investigations have reported that UV-B treatment increases the amount of UV-absorbing pigments in some rice cultivars (Ziska and Teramura, 1992; Dai et al., 1992).

Flavonoids are implicated as protective pigments in shoots and leaves exposed to UV-B light and their specific location in epidermal layer protects internal cell layers by attenuating the impinging UV- B radiation at the epidermis (Tevini et al*.,* 1991; Braun et al*.,* 1993). Other studies showed flavonoids are the largest UV-B-absorbing compounds produced by barley (Liu et al., 1995). It has been shown that the photo-induced accumulation of these flavonoids is preceded by an induction of several enzymes of phenylpropanoid biosynthetic pathway such as phenylalanine ammonia lyase and chalcone synthase of flavonoid biosynthetic pathway (Hahlbrock et al*.,* 1989; Schmelzer et al*.,* 1989). Some scientists stated that the content of chlorophyll a and carotenoids remain unchanged under the exposure to UV-B, while the amount of chlorophyll b decreases (Barsig and Malz, 2000).

UV IRRADIATION AND STRESS TOLERANCE

Most studies on the effects of UV-B radiation on plants have focused on the potential adverse effects of high doses, photo inhibition, degradation of DNA or increased oxidative stress (Stapleton, 1992; Jordan, 1996). Exposure to lower doses of UV-B radiation, however, it may not impair growth or productivity in many plant species (Allen et al., 1998). There is evidence that exposure of plants to near- ambient doses of UV-B radiation can impart high-light and drought tolerance in woody species, including *Pinus pinea* L. and *Pinus halepensis*. (Petropoulou et al., 1995; Björn et al., 1997; Manetas et al., 1997). UV can in some cases reduce drought stress in plants and increase plant production through several potential water conservation and stress tolerance mechanisms (Manetas et al., 1997; Schmidt et al., 2000), although the interactive effects of the two stresses have also been reported to be neutral (Sullivan and Teramura, 1990; Nogues and Baker, 2000). Drought tolerant species may sometimes also be more tolerant of UV radiation (Al-Oudat et al., 1998; Campbell et al., 1999).

EFFECT OF UV–B IRRADIATION ON FREE AND BOUND POLYAMINES

Putrescine, spermidine and spermine are the main polyamines found in all living cells. They are organic polycations displaying a high biological activity. PAs are present in all compartments of the plant cell and participate in diverse fundamental processes in the cell. The total PA concentration and the ratio between individual PAs vary markedly in dependence of plant species and developmental stage (Kuznetsov et al., 2006). The free PAs level depends not only on their synthesis, but also on their transport, degradation and conjugation. Putrescine degradation is catalysed by diamine oxidase, whereas Spd and Spm are oxidized by polyamine oxidase (Flores and Filner, 1985). PAs can be bound to low or high-weight molecules (phenolic acids, proteins, nucleic acids and membrane structures) (Martin-Tanguy, 2001). In the last years, PAs have been extensively studied due to their participation in the reaction of plants against several environmental stresses (Bouchereau et al., 1999; Kuznetsov et al., 2006; Groppa and Benavides, 2008). Several reports indicate that ambient levels of solar UV-B can present an environmental stress to ecosystems. UV-B radiation produces several detrimental effects on plant cells such as damage to proteins, membrane lipids, DNA (Teramura et al., 1994; Quaite et al., 1992) and an increase in ROS (Brosche and Strid, 2003). UV radiation also triggers protective responses in plants, including changes in antioxidant enzyme activities as well as PAs content. In *Phaseolus vulgaris* free PAs showed a marked decrease in response to UV-B radiation (Smith et al., 2001). In tobacco cultivars Lutz et al. (2005) described increase of total PAs as one of the primary protective mechanisms of the photosynthetic apparatus against UV- B. Ultraviolet radiation penetration varies among different plant species and may be reflected in the sensitivity of these species (Day et al., 1992; DeLucia et al., 1992).

PLANT PROTECTION AGAINST UV-B

Several protective mechanisms against UV-B damage have been described for plants, ranging from repair functions (Barabas et al., 1998; Britt, 1999) to preventive measures (Hoque and Remus, 1999). A particularly important role in this regard has been attributed to phenylpropanoids, including hydroxycinnamic acid derivatives and flavonoids with effective absorption in the UV-B spectral region (Reuber et al., 1996a; Sheahan, 1996; Hoque and Remus, 1999). In addition to UV-screening, other important UV-B protective properties ascribed to flavonoids include antioxidant activities (Dawar et al., 1998) and energy dissipation via intermolecular proton transfer (Smith and Markham, 1998). Flavonoids can increase rapidly in response to UV-B radiation (Jordan, 1996) and are frequently found in or on epidermal layers where they have been shown to increase markedly following UV-B treatment (Reuber et al., 1996b). Studies with flavonoid mutants further highlight the importance of flavonoids for UV-B tolerance (Lois and Buchanan, 1994; Reuber et al., 1996a). Recent reports show that highly specific differential UV-B responses among closely related flavonoids are well conserved in the plant kingdom. Such differential responses were demonstrated in a liverwort (Markham et al., 1998a), in gymnosperms (Schnitzler et al., 1997; Fischbach et al., 1999) and monocotyledons (Liu et al., 1995; Reuber et al., 1996a; Markham et al., 1998b), as well as in several dicotyledons, both herbaceous (Olsson et al., 1998; Ryan et al., 1998; Wilson et al., 1998) and trees (Lavola, 1998). Several of these reports indicate a shift from B-ring mono-hydroxylated flavonoids towards their orthodihydroxylated equivalents under UV-B. The dihydroxylated flavonoids are seen to confer additional UV-B protection, which could, for instance, be mediated by higher relative antioxidant capacity (Montesinos et al., 1995; Cooper Driver and Bhattacharya, 1998).

CONCLUSION

Climate change is going to differently affect crop productivity in different areas of the world, although regional climatic variations and differences in availability of natural resources make difficult the assessment of crop response at a local level based on global models. The depletion of the stratospheric ozone layer by manmade pollution has substantially increased UV-B light impinging on the earth surface. UV-B radiation has negative effects on plant growth. Higher than normal levels of UV-B causes various damages to plants such as DNA and membrane injuries, photosynthetic or hormone systems disorders. In sensitive plants, UV-B has been shown to inhibit photosynthetic electron transport, with PSII as the major site of damage. Increased UV-B radiation would affect the stability of ecosystems and genetic health of living organisms. Increased UV-B radiation can lead to altered food supply, as many crops including staple crops. Many species of plants have evolved mechanisms for protection against the deleterious effects of UV-B radiation. There are several protective mechanisms against UV-B damage in plants that is dependent on plant species. The main mechanisms are accumulation of UV-B absorbing pigments such as flavonoids and polyamines, ways by which plants alleviate the harmful effects of UV-B irradiation.

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