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REVIEW ARTICLE

UV-B radiation effects on terrestrial plants – A perspective

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Abstract

Both terrestrial and aquatic plants, the primary producers supporting life on earth, can be threatened by global climate change and particularly by UV-B radiation due to the depletion of the ozone layer in both Poles. The injurious effects of UV-B have been assessed mainly through in vitro studies and vary greatly according the dose received, the exposition period and the sensitivity of the species. Adaptive responses can include for example, synthesis of new compounds, increases of UV-B absorbing compounds or anti-oxidant enzymes. Morphological consequences are also documented such as reduced growth and thickening of leaves and cuticule. The main response of UV-B irradiation in indoor experiments is the formation of UV-B absorbing compounds such as phenolic compounds and flavonoids which function as protective screens, although in the natural habitat plants living at higher altitudes and latitudes are tolerant to UV-B due to the natural selection. The main conclusion derived from studies with terrestrial plants is that photosynthesis is not significantly affected by changes in UV-B radiation when plants grow under natural conditions. Moreover, due to the successful implementation of the Montreal Protocol the increase of UV-B radiation in most populated regions of the world (i.e., outside the regions affected by the Antarctic ozone hole) has been modest.

Key words: UV-B radiation, Terrestrial plants, Effects on photosynthesis, Effects on genetic material, Effects on UV-B absorbing compounds

Introduction

The stratospheric ozone layer protects life on Earth by absorbing ultraviolet light, which damages DNA in plants and animals, including humans. Prior to 1979, scientists had not observed ozone concentrations below 220 Dobson Units (DU), but the measurements made by NASA from 1979–2003 and by the Royal Netherlands Meteorological Institute from 2004 to the present, showed a continuous decline of DU values, reaching concentrations below 100, generally (NASA, http://earthobservatory.nasa.gov).

The ozone hole does not mean that the area monitored by satellite is free of ozone but rather it is an area in which ozone concentrations drop below the historical threshold of 220 Dobson Units. The amount of UV radiation reaching the Earth's surface varies widely around the globe and through time and depends mainly of cloud cover, concentrations of ozone in the stratosphere, oblique angle of sunlight reaching the surface, aerosol particles, sun elevation, reflectivity of the Earth's surface and depth in the water column in the case of aquatic environments.

Both aquatic and terrestrial ecosystems (including agricultural lands, and agro-ecosystems), could potentially be affected by increased solar UV-B radiation with consequences ranging from a decrease in biomass production, morphologic and metabolic changes, genetic damages, to a shift in species composition and diversity, although it must be recognized that some species are more vulnerable than others.

A comparison of the growth and physiological responses to various levels of solar UV-B in plant groups from marine, freshwater and terrestrial ecosystems was done by Rozema et al. (2002). Also a comparison of the induction of UV-absorbing compounds in plant groups and its chemical characterization and location, as well as a comparative assessment of the physiological functioning of UV-absorbing compounds as protective UV screens for plants, was performed.

According to the UNEP Report, in terrestrial areas where substantial ozone depletion has occurred, results from a wide range of field studies

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suggest that increased UV-B radiation reduces terrestrial plant productivity by about 6% (UNEP, 2010).

From the effects of UV radiation on plants, probably the most important one is related to genetic damages because the cell macromolecules such as DNA, RNA and proteins have strong absorption at 280-315 nm. However, in the natural habitat, plants are seldom affected by a single stress factor but by a multiplicity of interacting factors, such as water stress, increased atmospheric CO_2, mineral nutrient availability, heavy metals, temperature and the troposphere air pollutants (Caldwell et al., 1998) indicating that the effectiveness of UV-B radiation can be greatly increased or decreased by such factors. Elucidating the mechanisms that mediate plant responses to solar UV-B radiation is important for understanding the effects of radiation on the organism itself, on the whole community and lastly on the ecological interactions that may occur such as plant-herbivore interactions. Although we recognized that aquatic environment and particularly phytoplankton is crucial in the sea life and some areas of Antarctic sea are just below the ozone hole our discussion will be focused in terrestrial environments.

Crop plants – the target of UV-B study effects

Overexposure to UV-B may well reduce the productivity and quality of the main crop plant species to humans with serious economic and even demographic consequences. In that sense, several species and their varieties have been used to assess the effects of UV-B, such as corn (Zancan et al., 2006; de Britto et al., 2011, Campi et al., 2012), rice (Takeuchi et al., 2002), barley (Mazza et al., 1999; Bandurska et al., 2012), wheat (Correia et al., 1999; Agrawal and Rathore, 2007) and soybean (Galatro et al., 2001; Gitz et al. 2005; Chimphango et al., 2007).

In greenhouse experiments, the different doses of UV-B radiation applied (0 - control, 4, 8, 12 KJ $m^{-2}\ d^{-1}$) to *Avena fatua* and *Setaria viridis* induced changes in leaf and plant morphology. A decrease of plant height, fresh biomass of leaves, shoots and roots, leaf area and a leaf curling of both species was observed (Zuk-Golaszewska et al., 2003). In barley, a decrease in dry matter yield and water content of leaves and roots was observed after water deficit and UV-B plus water deficit, while no changes were found after treating barley plants with UV-B alone (Bandurska et al., 2012) indicating that other factors can be more injurious than the UV-B radiation itself.

The effects of UV-B (60 μmol $m^{-2}\ s^{-1}$) on primary leaves of wheat seedlings during different phases of leaf growth and development were assessed. UV-B induced an enhancement in accumulation of flavonoids during all phases of development while it caused a decline in anthocyanin content during senescence (Pradhan et al., 2008). UV-B exposure induced maximum damage to the photosynthetic apparatus during senescence phase of development although the damages were partially alleviated when UV-B exposure was accompanied by photosynthetically active radiation (PAR).

No beneficial interactions between the CO_2, temperature, and UV-B radiation on the reproductive processes of soybean were noted (Koti et al., 2005). Flower morphology, pollen production, pollen germination, pollen tube lengths, and pollen morphology were all negatively affected by CO_2, temperature and UV-B treatments alone or in combination compared with controls using the same parameters but at much lower doses.

Gao et al. (2004) studied the growth and yield responses of a maize crop exposed to enhanced UV-B radiation and the effects on seed quality under field conditions, concluding that enhanced UV-B radiation caused a significant reduction in the dry matter accumulation thus affecting the maize yield.

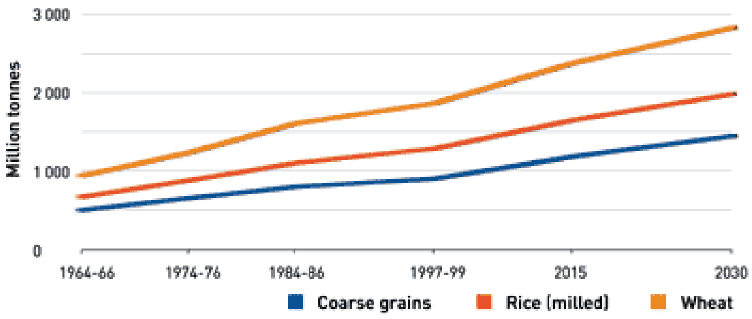

Figure 1. World demand for cereals, 1965 to 2030.
Source: FAO data and projections.

A large program research to assess the effects of UV-B on two rice cultivars was developed at the International Rice Research Institute (IRRI) located in the Philippines. The main conclusions indicated that rice yields likely will not be affected by increases in UV-B predicted from stratospheric ozone depletion under realistic tropical-field conditions based on extensive and intensive field experiments (Dai et al., 1997). This finding is extremely important since food production is a critical issue for human expansion worldwide as can be seen by the FAO demand projections for 2030 (FAO, 2002) and rice is the most important source of calories in the world (Figure 1).

Forestry species

Forestry research has focused attention on the effects of UV-B on the main species used in fast wood forestry such as poplar and eucalyptus, since decreases in productivity reduced the incomes of farmers and the efficiency of pulp and paper industry. Ren et al. (2007) studied the effects of drought and enhanced UV-B radiation and a combination of both stress factors on growth and physiology of *Populus kangdingensis* and *Populus cathayana* originating from high and low altitudes in south-west China and observed a significant reduction in plant height and total leaf area.

Solar UV-B radiation seemed to delay plant growth in all species examined (four *Acacia* and two *Eucalyptus* species) although it did not affect photosynthetic activity significantly. However, a reduced specific leaf area (SLA), and an increased leaf thickness and size of epidermis were observed in plants (Liu et al., 2005).

Other genera of particular interest in forestry are *Pinus, Salix, Betula, Picea* and *Abies.* For example, *Abies faxoniana* a key species in reforestation in the southeast of the Qinghai-Tibetan Plateau of China (Yao and Liu, 2009) when exposed to enhanced UV-B (14.33 KJ m^{-2} d^{-1}) showed a marked decline in growth parameters, net photosynthetic rate, photosynthetic pigments and the maximum quantum efficiency of PSII (Fv/Fm) compared with plants receiving ambient UV-B (11.02 KJ m^{-2} d^{-1}). The same authors (Yao and Liu, 2007) when studying the effects of similar UV-B levels on 3 and 6-year-old dragon spruce seedlings (*Picea asperata*) concluded that enhanced UV-B significantly decreased growth, needle and root nitrogen concentration, needle nitrate reductase activity and increased UV-B absorbing compounds and malondialdehyde (MDA) content in both 3 and 6-year old seedlings, while glutamine synthetase activity was not affected.

Morales et al. (2010) observed that UV-B induces the synthesis and accumulation of the flavonols myricetin-3-galactoside, quercetin-3-galactoside, quercetin-3-rhamnoside and kaempferol-3-rhamnoside in birch (*Betula pendula*) at early stages of leaf development, before the leaves are fully expanded, suggesting that individual compounds might be differentially regulated by UV-B at different stages of leaf development and that their contributions to UV protection might also vary.

Effects on photosynthesis

UV-B impairs photosynthesis in many species although the mechanisms vary greatly. For example, Greenberg et al. (1996) observed that Rubisco from *Brassica napus* exhibited changes in its large subunit. Also the biosynthesis of flavonoids and other UV-absorbing pigments occurred at UV-B levels that caused cotyledon curling.

Wheat plants (*Triticum aestivum* L.) exposed for 4 months to high UV-B levels (simulating a 20% reduction in the ozone layer) showed a decrease in total plant biomass of 18% compared to control plants (ambient UV-B). High UV-B also induces decreases in leaf area, net photosynthesis rate, transpiration rate and water use efficiency; leaf extracts showed increases in chlorophyll content and no effect on accumulation of UV-B absorbing pigments (Correia et al., 1999).

Chlorophyll content decreased but leaf soluble protein content increased in plants under solar UV-B radiation. Solar UV-B radiation apparently had a strong effect on chlorophyll degradation rather than the size of the xanthophyll cycle pool, in both acacia and eucalyptus species (Liu et al., 2005). Sangtarash et al. (2009) observed that seedlings of *Brassica napus* produced more dry matter under ambient UV-B (5 KJ m^{-2} d^{-1}) than under zero UV-B, but 10 KJ m^{-2} d^{-1} caused a decrease in dry mass, indicating that some adaptive mechanisms to the ambient UV-B exists. The highest level of UV-B irradiation also decreased stem height, leaf area, plant dry matter, water use efficiency and wax content.

Neither photosynthesis nor pigment levels of *Zea mays* leaves were affected significantly by UV-B levels (Casati and Walbot, 2004) although damage to leaf ribosomes by crosslinking three different cytosolic ribosomal proteins and chloroplast ribosomal protein L29 to RNA were observed. Hao et al. (2000) also verified that the exposure to enhanced UV-B increased leaf chlorophyll concentration and UV-absorbing compounds in *Lycopersicon esculentum*, but decreased leaf area and root/shoot ratio.

The large spectra of plant responses are mainly due to the different sensitivity of species and cultivars and differences in experimental protocols which are responsible for the diversity of dose-effect relationships. Nevertheless, a large number of studies with terrestrial plants point out that photosynthesis (CO_2 fixation per unit leaf area) is not significantly affected by changes in UV-B radiation when plants are grown under natural conditions (Caldwell et al., 2003; Caldwell et al., 2007) although UV-B radiation may have subtle inhibitory effects on biomass accumulation, often correlated with a reduction in the rate of leaf area expansion.

Effects on genetic material

In response to UV-B exposure, plants have evolved mechanisms of protection and repair such as the accumulation of UV absorbing pigments, phosphorylation of particular ribosome proteins, or for example, histone acetylation. Due to the complete knowledge of *Arabidopsis thaliana* genome, this species is also commonly used in laboratory experiments to evaluate the effects of UV-B radiation on genes (Tong et al., 2008; Campi et al., 2012), indicating that this plant is useful as a comprehensive model.

Using microarray hybridization techniques to study the *Zea mays* acclimation responses to UV-B Casati and Walbot (2003) observed that genes encoding protein translation components were the largest functional group up-regulated by UV-B. Despite the significant ribosome damage and a decrease in translation in RNA of maize (Casati and Walbot, 2004) it has been suggested that new synthesis of ribosomes occur as a response to UV-B damage, thus indicating restoration of the capacity of protein synthesis.

Chromatin remodeling and histone acetylation are important during DNA repair by UV-B in both *Zea mays* and *Arabidopsis thaliana* (Campi et al., 2012) showing that both genetic and epigenetic effects control DNA repair in plants.

Marked differences in genetic response to UV-B of three different ecotypes of *Arabidopsis thaliana* (Kalbina and Strid, 2006) were also observed. The C24 ecotype exhibited the highest expression level of *PR-5* gene (pathogenesis-related protein gene) while the induction of hypersensitive response (HR) like spots, which resulted in necrotic lesions is rapid. Conversely, the Ws ecotype showed the lowest levels of *PR-5* transcripts and its growth rate was the lowest one.

The effects of UV-B on *Mesembryanthemum crystallinum* may be ameliorated by UV-A through the activation of DNA repair mechanisms mainly due to the action of the enzyme photolyase (Ibdah et al., 2002). However, laboratory studies with plants suggest that the effects of ozone depletion (measured by the formation of cyclobutane pyrimidine dimers in DNA) is likely to be less marked than previously thought, because UV-A (315–400 nm) may also cause significant damage by penetrating deeper into plant leaves and it is not affected by ozone shield *i.e.,* it passes almost unaltered through the atmosphere (Rousseaux et al., 1999).

Effects on UV-absorbing pigments

Increased accumulation of phenolic compounds and flavonoids is one of the main responses to UV-B radiation contributing by this way to filter out UV-B photons before they reach sensitive molecules. In *Brassica napus,* approximately 20 distinct UV-absorbing pigments were produced in response to UV-B radiation (flavonoids and other UV-absorbing pigments), their synthesis occurring mainly in the epidermal cell layer (Greenberg et al., 1996).

As a result of UV-B radiation leaves of potato plants increased constitutive flavonoids. Also, the activity of the antioxidant enzymes catalase, ascorbate peroxidase and guaiacol peroxidase increased associated with the induction of a new catalase isoform and three new guaiacol isoperoxidases (Santos et al., 2004) showing that potato plants activate several defense systems.

Xu et al. (2008) observed that solar UV-B caused oxidative stress in both isolines of soybean grown in the field (one with moderate levels of flavonoids and the other with reduced levels) and altered the antioxidant defenses mainly by decreasing superoxide dismutase activity. The greater oxidative stress was observed in the line with very low levels of flavonoids. These protective compounds (phenolic compounds and flavonoids) also influence leaf development, water relations, trophic responses (plant-herbivore interactions) and decomposition process (Xu and Sullivan, 2010).

In *Indigofera tinctoria* (L.) seedlings, the supplementary UV-B radiation significantly decreased the growth, development and changes in UV-B absorbing compounds such as anthocyanin and flavonoids. The antioxidant enzymes were unaffected and showed enhanced activities of peroxidase, superoxide dismutase, polyphenoloxidase and phenylalanine ammonia-lyase, but not catalase (Ravindran et al., 2010), indicating in this particular case that the activation defense mechanisms were mainly based on anti-oxidant enzymes, instead of UV-B absorbing compounds.

Another important approach derived from experimental studies indicates that the enrichment of plant tissues in phenolic compounds or flavonoids as a protective response to UV-B irradiance induces a resistance to herbivores (Izaguirre et al., 2007; Kuhlmann and Muller, 2009). Moreover, the interaction of biotic and abiotic environment factors with UV-B radiation can produce cross-tolerance (*i.e.*, tolerance to one stress induced by another stress), as well as resilience to subsequent stress due to the establishment of a level of protection (Kalbin et al., 2001).

Conjugated effects of UV-B plus CO$_2$, UV-B plus ABA, UV-B plus drought

As previously stated, plants in their natural habitat are seldom affected by a single stress factor. In that sense several interactions of UV-B plus CO$_2$, UV-B plus ABA, UV-B plus drought, have been studied in laboratory conditions. The effects of UV-B radiation on tomato plants growing in a controlled environment were small even if significant alone or interacting with CO$_2$ or O$_3$, (Table 1) suggesting that substantial increases in UV-B may not have strong deleterious effects on productivity (Hao et al., 2000). *Populus kangdingensis* and *Populus cathayana* originating from high and low altitudes from south-west China, respectively (Ren et al., 2007) exhibited significant reductions in plant height and total leaf area when exposed to drought, enhanced UV-B radiation or a combination of both stress factors, indicating that the addition of another negative factor influences decisively the performance of both plants. For example in *Populus kangdingensis* plant height (in cm) decreased from 105.04 in drought-stressed regimes to 83.8 in UV-B plus drought-stressed regimes. The same occurs for the total area (dm^2), from 18.03 to 8.48. When the plant was not submitted to drought the height was 148.9 cm and the total area 32.06 dm^2. Similar results were observed for *Populus cathayana.*

Populus cathayana originating from high and low altitudes from south-west China (Lu et al., 2009) was exposed to exogenous ABA (abscisic acid), enhanced UV-B radiation or a combination of both. The results from plant height (cm), total leaf area (dm^2) and total biomass (g) were shown in Table 1.

Concluding Remarks

Despite the huge number of studies mainly in the laboratory and glasshouse conditions and the variety of responses of plants when exposed to UV-B irradiation the understanding of the complex interactions between UV-B and biota will be always limited by the incapacity to reproduce natural conditions. Even when plants are exposed to conjugated effects of UV-B plus CO$_2$ for example, what is seen is a partial response despite the importance of the data and the relevance of the conclusions.

Table 1. Physiological data of *Populus cathayana*[1] and *Lycopersicon esculentum*[2] exposed to UV-B plus other ambient factors.

		Plant height	Total leaf area	Total biomass
Low altitude[1]	ABA	173.2	27.59	56.33
	UV-B	164.2	20.98	40.64
	UV-B+ABA	169.0	21.56	43.97
	Control	184.0	37.14	66.13
High altitude[1]	ABA	200.8	28.77	65.33
	UV-B	174.6	24.87	58.89
	UV-B+ABA	176.2	22.74	54.69
	Control	199.6	29.50	73.79
Tomato	CO$_2$	73.5	2850	20.52
	UV-B	65.6	2449	14.02
	CO$_2$+UV-B	67.8	2729	18.55
	Ambient	66.6	2591	14.98

(1) Data from Lu et al. (2009); (2) Hao et al. (2000) – leaf area was expressed in cm2 instead dm2 in the case of *Populus*.

Moreover, several authors consider that the observed effects of UV-B on plants on indoor experiments were exaggerated and extrapolations to field conditions must questioned (Caldwell and Flint, 1997; Krizek, 2004).

In glasshouse conditions we do not have rainy days, or clouds, nor do we have aerosol particles or variations in temperature. In that sense, field studies in areas where the ozone hole is high is a priority, such as those undertaken in Antarctica. Others must be done in mountain populations since these species have natural adaptive mechanisms to tolerate to high UV-B irradiation levels. Plant data from the same Genus or Family living in different altitudes or plants from the same species along a gradient in altitude, will be extremely useful when compared with laboratory data.

The perception that UV-B radiation may trigger the synthesis of new compounds, the increase of anti-oxidant activity or the increase of known compounds such as flavonoids and phenolics, can be used to improve the quality of food although it is also suggested that the synthesis of these molecules can be used as biomarkers for the identification of stressed plants (de Britto et al., 2011).

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