UV-B Radiation, Its Effects and Defense Mechanisms in Terrestrial Plants

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Abstract

The UV-B is an important component of solar radiation to which all terrestrial and aquatic plants were exposed during the early evolutionary phase of the Earth. Hence the plants, principally terrestrial, have evolved different mechanisms to avoid and repair the UV-B damage; therefore, it is not surprising that photomorphogenic responses to the solar UV-B are erroneously assumed to be adaptations to the harmful UV radiation. The responses to UV-B enhancement include changes in the leaf area, leaf thickness, stomatal density, wax deposition, stem elongation, and branching pattern, as well as in the synthesis of secondary metabolites, alterations in plant–pathogen and plant–predator interactions, and in gene expression. However, under field conditions the ambient solar UV-B provides an important signal for the normal plant development and may be perceived by the plants through nondestructive processes involving both UV-B specific and UV-B nonspecific signaling pathways. The specific signaling pathways include the components UVR8 and COP1 which regulate the expression of a set of genes that are essential for the plants' protection. The nonspecific signaling pathways involve DNA damage, reactive oxygen species (ROS), hormones, and wound/defense signaling molecules. Indeed under the field conditions, the ambient UV-B might more properly be viewed as a photomorphogenic signal than as a stressor. Therefore, it might not be appropriate to evaluate the adaptive roles of plant responses to UV-B cues upon stress tolerance by the simultaneous application of both solar radiation and supplemental UV-B. In this chapter, we analyzed the information regarding

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physiological and morphogenic responses of the terrestrial plants to the UV-B radiation, as well as the events related to UV-B perception, signal transduction, gene expression, and ROS formation from different studies carried out in greenhouses, growth chambers, and field conditions.

Keywords
UV-B radiation • DNA damage • DNA repair • Metabolites • Signaling • Secondary metabolites • Morphogenic responses

1 Introduction: Knowing the Solar UV-B Radiation, a Historical Background

Within the electromagnetic radiation spectrum, the UV radiation describes a spectral range between 200 and 400 nm, which borders on the visible range. The UV radiation is divided into three effective types: UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (200–280 nm). Less than 7% of the sun's radiation reaching the Earth's surface falls approximately in the range between 295 and 400 nm (UV-A and UV-B); the shorter UV wavelengths get filtered out by the stratospheric ozone. Therefore, the lower limit of shorter wavelengths of the solar UV radiation reaching the surface is determined by the stratospheric ozone layer. The stratospheric ozone absorbs virtually all the UV radiation ranging approximately 295 nm and lesser. Although the stratospheric ozone determines the amount of UV-B radiation that reaches the surface of the Earth, its level is significantly affected by variations in latitude and altitude. The level of UV-B radiation over tropical latitudes is higher than in temperate regions due to lesser atmospheric UV-B absorption determined by the solar angle and the ozone layer itself which is thinner in equatorial regions. Thus, the UV-B radiation is relatively high in tropical areas and relatively low in the polar regions. Increases of the UV-B irradiance with increasing elevation above sea level is also known, i.e., measurements of the UV-B irradiance show an average increase between 10 and 19% for every 1,000 m increase in elevation. Besides geographical factors, the atmospheric pollutants (e.g., smoke, aerosols) and especially the weather factors (e.g., clouds, haze) greatly decrease the level of UV-B reaching the Earth's surface. Depending upon the type and height of clouds, liquid water content, and particle distribution, the cover of clouds can attenuate over 70% of the incident UV-B radiation (McKenzie et al. 2007).

Over 35 years ago, it was warned that man-made nitrous oxide and chlorine-containing compounds (e.g., chlorofluorocarbons, CFCs) produce the breakdown of large amounts of ozone in the stratosphere (Crutzen 1972; Molina and Rowland 1974; in Velders et al. 2007). This fact causes the depletion of the stratospheric ozone layer increasing the UV-B radiation at the ground level, especially in Antarctic and Arctic regions as well as in high altitude areas (Ryan and Hunt 2005). By their contributions on chlorine-containing compounds and the depletion of the ozone layer, Crutzen, Molina, and Rowland were awarded with the Nobel Prize for chemistry in 1995. After the Molina and Rowland's work, Farman, Gardiner, and Shanklin, scientists of the British Antarctic Survey, shocked the scientific community during the early middle 1980s by publishing the results of a study showing a springtime ozone *hole* in the Antarctic ozone layer (Farman et al. 1985, in Ryan and Hunt 2005). This fact rang alarm bells worldwide and within the same year, 20 nations including most of the major CFCs producers signed the Vienna Convention, which established a framework for negotiating an international regulation on the ozone-depleting substances. After that, on September 16, 1987 the Montreal Protocol on "Substances that Deplete the Ozone Layer" was opened for nations signature

and entered into force on January 1, 1989 (Velders et al. 2007). At present, after several amendments, all the countries in the United Nations have ratified the Montreal Protocol (http://ozone.unep.org/Meeting_Documents/). However, today the ozone depletion is a global phenomenon and according to the European Ozone Research Coordinating Unit (EORCU) its amount approximately reaches 0.6% per year. The level of UV-B radiation in the biosphere varies, spatially and temporally, quite considerably but the depletion of the stratospheric ozone strongly affects its penetration (Ryan and Hunt 2005). Thus, despite reductions in the production and use of ozone-depleting chemicals, the potential of ozone depletion by anthropogenic emissions or natural causes (e.g., volcanoes) still remains. In this scenario, the level of stratospheric ozone will continue decaying with a severe decline occurring between 2010 and 2019 in the northern hemisphere that may result up to 50–60% increase in the springtime UV-B radiation according to the Global Climate Model (GCM) that is based on the simplified ozone-depletion chemistry (Taalas et al. 2000). Furthermore, the recovery of the stratospheric ozone to early 1980s levels is not predicted until roughly 2050.

2 Solar UV-B Radiation and the Life of Terrestrial Plants

Since the discovery of the ozone layer depletion (~30 years ago) the responses of microorganisms, animals, and terrestrial plants to solar UV-B radiation have been active subjects of many studies (Rozema 2000; Björn et al. 2002; Ryan and Hunt 2005). Prior to building of the atmospheric oxygen and then the stratospheric ozone layer, the UV-C radiation and high levels of both UV-B and UV-A would probably have reached the Earth's surface relatively unattenuated affecting all the living organisms. In this context, the UV radiation seems to be a ubiquitous factor in the course of terrestrial biota? Plant evolution from the early Archean era began as solitary photosynthetic cells (Cockell and Horneck 2001). The UV effects on terrestrial plants, which are principally detrimental, have been demonstrated with some of the most essential components of the biochemical machinery, i.e., DNA molecule and photosystem II (PSII) (Singh et al. 2008). However, when the stratospheric ozone layer developed, the UV-A radiation and a minor portion of the UV-B wavelengths only could reach the Earth's surface due to the atmospheric absorption and scattering of the UV-C radiation. Therefore, how the UV radiation has altered the Earth's environment over geological time periods is essential for understanding the evolutionary history of the earth and also to understand how the UV-B radiation has contributed as selection pressure on the development of terrestrial plants (Björn and McKenzie 2007). In fact, Sagan (Sagan 1973 in Singh et al. 2008) first considered the UV radiation as a selection pressure on the early photosynthetic organisms, when our knowledge on biological effects of the UV radiation on plants was in its infancy. During the evolutionary history of the Earth, the terrestrial plants coevolved under different solar UV-B levels and may have experienced significantly higher UV-B irradiances than the current surface UV-B level (Cockell and Horneck 2001; Rozema et al. 2002). Thereby, the UV-B tolerance acquired earlier probably helps to explain why plants are distributed at lower latitudes or higher elevations, where UV-B irradiances are greater, are less sensitive to high levels of the UV-B radiation than those at higher latitudes and/or lower elevations (Turunen and Latola 2005; Ren et al. 2010). The present rate of atmospheric changes is so rapid that evolution may not keep up with it, particularly in long-living plants like trees. The UV-B environment of terrestrial plants is presently quite variable in both time and space, and thus organisms experience different UV-B doses and adapt to UV-B radiation at different levels (Rozema 2000). In this context it is expected that terrestrial plants respond differentially to increasing solar UV-B. Nevertheless, although studies assessing possible consequences of the ozone depletion have greatly increased our understanding on how living organisms are affected by the UV-B radiation, the focus of these researches may also have distracted the attention from the UV-B radiation as a component of the *ambient light environment* involved in the evolution of life on the Earth's surface (Cockell and Horneck 2001).

3 UV-B Radiation as a Modulator of the Plant Function

Due to their absolute sunlight requirement for survival, the plants are inevitably exposed to solar UV-B radiation. However, from equatorial to the polar regions and from the sea level to high mountains, the terrestrial plants are exposed to greatly different UV-B irradiances, given the geographical differences in UV-B irradiances is much greater than corresponding differences in the total solar radiation (Rozema 2000). The plant chemical photoprocesses respond differently to different UV wavelengths as the biological damage exacerbated as wavelength becomes shorter. Thus, the relative effectiveness of UV-B-ranging wavelengths (effective UV-B irradiance) must be known in order to assess the responses to ozone changes. The effective UV irradiance (E) or dose rate exposure is given by

$$E = \int F(\lambda)W(\lambda)d\lambda,$$

where $W(\lambda)$ is the weighting function (action spectrum) for a specific biological or chemical effect and $F(\lambda)$ is the spectral irradiance, either computed or measured, for a given time (e.g., hour, day, year) and location. As a result, the biological effectiveness of the weighted UV-B irradiances (UV-BBE, biologically effective UV-B radiation) related to different action spectra has different responses to atmospheric ozone changes (Flint and Caldwell 2003). It has been estimated that 1% decrease in the stratospheric ozone concentration would result in nearly 2% increase in the UV-BBE at mid-latitudes. Therefore, the recently projected 15% stratospheric ozone reduction would result in up to 30% increase in the value of UV-BBE in the next three decades (McKenzie et al. 2007).

4 Solar UV-B Radiation: Stress Factor or Beneficial Signal Factor?

From the ozone depletion perspective, the UV-B radiation is considered as an environmental stressor of photosynthetic organisms (Jordan 2002; Rozema et al. 2002; Ballaré 2003; Caldwell et al. 2007). However, from an evolutionary perspective this assumption is questionable. The terrestrial plants have always developed under the solar UV-B and then their genetic machinery coevolved together with the *ambient* UV-B level. Therefore, it can be hypothesized that the metabolic machinery of plants contains all the necessary elements for a *normal coexistence* with the current UV-B level and so the solar UV-B radiation should not be considered as an *environmental stress factor*. In fact, the current level of the ambient UV-B radiation should be considered as a *signal factor* that induces the expression of genes related to the normal plant development (Jenkins 2009). While the UV-B exclusion must be considered as an *anomalous signal factor* that induces the expression and/or repression of another set of genes (Brosché et al. 2002; Stratmann 2003; Hectors et al. 2007). In this context, the solar UV-B radiation appears as a reliable plant effector, but it is not always possible to identify a unique particular reason as explanation of the underlying UV-B effects. In nature, the terrestrial plants are seldom affected by only a single environmental factor; they typically respond to several environmental factors acting in concert (Bruno et al. 2003). Therefore, the influence of changing UV-B in natural ecosystems must be evaluated considering two opposite processes: (a) facilitation; (b) competition. These processes have been recognized as key drivers in a wide range of natural communities and hence, effectiveness of the UV-B radiation will be greatly modified by other environmental factors, in some cases aggravating and in others, ameliorating the overall UV-B effect (Bruno et al. 2003).

5 Responses of Terrestrial Plants to Ambient Solar UV-B

The most extended researches relating to the effects of increasing solar UV-B radiation on terrestrial plants have been performed in both austral and boreal polar regions (Day et al. 2001; Phoenix et al. 2003; Robson et al. 2003; Rozema et al. 2006; Newsham and Robinson 2009). The depletion of the stratospheric ozone is greater in both

Antarctic and Arctic regions than in other nonpolar latitudes where it is less pronounced and subject to other atmospheric factors such as horizontal and vertical ozone transport. In the Antarctic zone, the complete breakdown of the stratospheric ozone occurs only during few springtime days, but the springtime ozone depletion reaches 50–60% on average (Rozema et al. 2005). This event has occurred uninterruptedly for at least 30 years, leading to a marked increase of the solar UV-B irradiance. Since the 1990s frequent occurrence of the springtime ozone hole over the Arctic also occurs resulting in significant ozone depletion and increasing the UV-B irradiance at the ground level (Rex et al. 2004). Similar to the Antarctic area, the ozone loss over the Arctic area is higher in the early springtime than in the growing plant season (late springtime and summer). The Arctic springtime ozone depletion is lower than the Antarctic one and rarely reaches 40–50% on average (Rex et al. 2004). Also, the Arctic ozone loss is extremely sensitive to frequency of sudden stratospheric warming due to the greenhouse effect. Because of the influence of increasing greenhouse gases, the ozone holes may worsen leading to greater ozone depletion over the Arctic and increasing the severity and duration of the Antarctic ozone depletion (Rozema et al. 2005). At present both Antarctic and Arctic polar regions represent one the most extreme UV-B environment and constitute an excellent site to study the responses of terrestrial plants to increased solar UV-B. Although almost all the investigations were carried out in the Antarctic area this ecosystem only has two species of higher plants: *Deschampsia antarctica* and *Colobanthus quitensis* (Convey and Smith 2006). While the terrestrial Arctic ecosystem has more than 160 higher plant species, allowing more species interactions and feedbacks and perhaps providing a more general representative ecosystem response to enhanced UV-B than the more simple two-species Antarctic ecosystem (Rozema et al. 2006). Short- and long-term studies have shown different and controversial effects of both enhanced and excluded solar UV-B radiation on the Antarctic and Arctic flora species (Searles et al. 2002; Phoenix et al. 2003; Robson et al. 2003). However, in three extensive overviews, Dormann and Woodin (2002) and Rozema et al. (2005, 2006) claimed the finding that neither flowering plants nor mosses and lichen species of the polar ecosystems are markedly affected by the enhanced solar UV-B. Almost all the plant parameters related to the growth and photosynthesis were not significantly affected by elevated UV-B simulating 15, 30, or may be higher (e.g., 50%) of the ozone depletion (Rozema et al. 2005). In fact, these overviews contradict many authors who hypothesized that stressful harsh climatic and environmental polar conditions would make the polar plants vulnerable to the enhanced UV-B, and that the repair of UV-B-induced damage could be hampered by the low polar temperatures (Newsham and Robinson 2009; Snell et al. 2009). The absence of significant UV-B effects on polar plants could imply that they are better adapted to high UV-B regimes and capable of preventing and/or effectively repairing the UV-B damage (Rozema et al. 2005). Although this fact may be interpreted that terrestrial plants from polar ecosystems are particularly tolerant to the ozone depletion, in a more generalized way it has been applied to all the plants and ecosystems, especially those located in high UV-B environments (e.g., tropical and subtropical mountain areas). This assumption implies that terrestrial plants occurring naturally in the high UV-B habitats would undoubtedly have evolved specific adaptations that protect them against the deleterious effects of the UV-B radiation. Hence such plants could show a reduced responsiveness mainly due to their reduced sensitivity to UV-B radiation. Similarly, the plants growing in habitats with low UV-B irradiances (e.g., forest underground) could suffer changes even under small variations in the stratospheric ozone layer (Turunen and Latola 2005).

The solar UV-B radiation cannot be regarded as merely an environmental factor causing plant damages because it can also act as an informational signal leading to morphogenic effects on the structure of plants and the overall function of forest ecosystems (Julkunen-Tiitto et al. 2005). For many years both field and laboratory experiments have focused on the UV-B increased scenario, being scarce those on the responses of plants to the current level of solar UV-B (Searles et al. 2001). This lack of information constitutes

an important gap that impedes us to understand the responses of terrestrial plants to solar UV-B changes completely. Many reports consider the solar UV-B as an *environmental stressor* that affects the development of plants (Láposi et al. 2002; Kadur et al. 2007), while others have communicated no detrimental effects of the solar UV-B on the plant growth (Amudha et al. 2010). Some have even reported protective and/or beneficial effects of the solar UV-B radiation (Winter and Rostás 2008). Although there is no conclusive explanation for these contradictory effects, they could obey to variations in the UV-B sensitivity among different species and even among cultivars of the same species (Gilbert et al. 2009; González et al. 2009). In this context, the terrestrial plants have developed different strategies to avoid UV-B radiation reaching the most sensitive cellular targets. A major strategy against penetration of the solar UV-B is based on epidermal screening of the incident radiation (Tattini et al. 2005). The mechanisms that inhibit the penetration of UV-B radiation inside the leaf tissues comprise different leaf structural features such as leaf surface reflectance due to the leaf surface wax and hairs (trichomes) (Liakopoulos et al. 2006; González et al. 2007), epidermal thickness (Hilal et al. 2004), epidermal terpenoids (resin) accumulation (Zavala and Ravetta 2002), and epidermal accumulation of UV-absorbing compounds (Burchard et al. 2000; Agati and Tattini 2010). However, despite largely evolved UV-protection mechanisms, complete UV-B protection is not achieved and a small percentage of the solar UV-B radiation penetrates inside the leaf (Krauss et al. 1997). It is generally accepted that a gradient exists in the ability to screening of UV; the herbaceous plants (being least efficient) towards woody and perennial plants, with the conifers being the most efficient (Krauss et al. 1997). Moreover, the proportion of UV-B radiation reaching the leaf photosynthetic mesophyll is significantly higher in the deciduous broadleaf trees than in the evergreen conifer trees (Julkunen-Tiitto et al. 2005; Turunen and Latola 2005). This indicates a greater susceptibility of the deciduous trees to the enhanced UV-B radiation as well as a greater cost of maintenance (Snell et al. 2009). The reason for the low UV-B transmittance in the conifer needles is that UV-absorbing compounds are located in both vacuoles and epidermal cell walls, whereas in herbaceous plants these are located primarily inside the vacuoles of epidermal cells (Julkunen-Tiitto et al. 2005). Moreover, the soluble flavonoids can be actively and rapidly mediated by the exposure to UV-B radiation whereas the cell-wall bound insoluble phenyl-propanoids represent a more passive UV-screening mechanism (Krauss et al. 1997; Clarke and Robinson 2008). These compounds absorb the UV-B wavelengths effectively, but they also transmit the visible PAR inside the mesophyll cells (Krauss et al. 1997). Interestingly, excess of penetrating UV radiation (UV-A and UV-B) could be converted into visible PAR radiation through both yellow and green fluorescence emission from the epidermal cell-wall bound UV-absorbing compounds (Hoque and Remus 1999). Although the epidermal thickness and concentration of UV-absorbing compounds seems to be the strongest predictors of epidermal transmittance and depth of the UV-B penetration, clear relationships between effectiveness of the accumulation of UV-absorbing compounds and epidermal morphological changes have still not been established, suggesting that other intrinsic plant factors are also important in determining the UV-B screening efficiency. Moreover, the endogenous constitution of plants can affect the chemical composition at both whole and organ level. Even within an individual plant the quality and quantity of secondary metabolites may differ between young and old leaves, as well as between the leaves exposed to the sun and those that remain in the shade (Brenes-Arguedas et al. 2006). Alteration in the accumulation of species-specific UV-absorbing compounds may result in changes in the tissue attractiveness or palatability to insects and herbivores (Izaguirre et al. 2007), pathogen attacks (Stratmann 2003), plant–plant interactions (Sullivan 2005), and changes in litter decomposition processes (Pancotto et al. 2003). Because most of these studies have been conducted on

crop monocultures or isolated pot grown plants, the extrapolation of their responses to natural ecosystems is difficult (Phoenix et al. 2003). One previous ecosystem study found little effect of the ambient solar UV-B on *Sphagnum* bog and *Carex* fen in Tierra del Fuego-Argentina (Searles et al. 2002). Moreover, in related studies the solar UV-B reduced the herbivory, but increased the damage of DNA in the perennial herb *Gunnera magellanica* and reduced both the leaf number and length of the Antarctic species *D. antarctica* and *C. quitensis* (Ballaré et al. 2001). Although overall these studies expand our limited knowledge on how the exposure to natural ambient UV-B can modify the biomass accumulation, population dynamics, and competitive interactions in nonagricultural species and thereby how ecosystems may respond to future UV-B fluctuations. Presently long-time studies are very scarce, only a few studies with more than 4 years under continuous monitoring have been communicated (Robson et al. 2003; Rozema et al. 2006; Trošt-Sedej and Gaberščik 2008). Although the visible radiation can often penetrate dense canopies deeper than the UV-B because of its higher transmittance through leaves, in less dense canopies the situation may be reversed. This implies that the UV-B/PAR ratio should change with the canopy leaf area and leaf architecture (Shulski et al. 2004). In order to understand how the natural ecosystems respond to the ambient solar UV-B radiation, many additional well-designed long-term studies with various plant species are needed in order to understand the different behavior of UV-B and PAR inside the canopy as well as to obtain a complete picture of the gene–environment interactions.

6 Effects of Artificially Enhanced UV-B Radiation

Different to polar studies, earlier researches on nonpolar terrestrial plants were mainly focused on the effects of artificially increased UV-B radiation on crop species rather than ecosystems (Flint et al. 2003). Although, such researches were important to understand the physiological responses and identify possible targets for the UV-B radiation, extensive recent studies have shown that effects of the artificially manipulated UV-B have been often overestimated (Rozema 2000). Moreover, the responses of terrestrial plants to simulated solar UV-B enhancement vary greatly due to artifacts derived from the experimental conditions (Musil et al. 2002a; Flint et al. 2003). A critical point besides the variability of experimental conditions in the evaluation of simulated solar UV-B enhancement is the use of lamps to provide the UV-B radiation. Both UV-fluorescent and broad-spectrum xenon-arc lamps are the most commonly used sources of UV radiation in UV-B enhancement experiments (Flint et al. 2009). In terrestrial studies, the UV-fluorescent lamps are usually used, but in aquatic experiments the xenon-arc lamps are preferred. Although the UV-fluorescent lamps are widely used, they supply more short- than long-wave UV-B radiation compared with the solar spectrum (Musil et al. 2002a). In addition, all the UV lamps emit small but biologically effective UV-C radiation, which is not present in the solar radiation reaching the Earth's surface (Flint et al. 2009). Other debatable question in the studies on UV-B effects is the use of UV filters. The major filters used to exclude either UV-A or UV-B in UV-exclusion studies are: (a) cellulose diacetate, CA, that is commonly used to exclude the UV-C radiation and transmit both UV-A and UV-B; (b) polyester, the generic name for Mylar (trade name of the DuPont Co.) that is used to exclude both UV-C and UV-B and transmit the UV-A only; (c) polychlorotrifluoroethylene, PCTFE (Aclar 22 C) that transmits all the UV radiation (UV-A, UV-B, and UV-C); (d) copolymers of tetrafluoroethylene and hexafluoropropylene, Teflon FEP (trade name of the DuPont Co.) that transmits the radiation at 245 nm and above; (e) polyvinyl fluoride, Tedlar TUT (trade name of the DuPont Co.) that blocks wavelengths in the UV-B region; (f) clear polyethylene, Dura-Film Super 4 (trade name of the AT Plastics Inc.) that blocks the UV radiation up to 380 nm; polymethylmethacrylate, Plexiglas (trade name

of the Arkema): the standard Plexiglas excludes the UV-B wavelengths and a portion of the UV-A region, whereas the UV-T Plexiglas transmits all the wavelengths in both UV-B and UV-A regions (Krizek et al. 2005). Although these filters have been widely used in UV-B studies, their transmittance properties vary leading to erroneous interpretations of the UV effects in long-term experiments (Day et al. 2001). Moreover, CA, the most widely used UV filter produces detrimental effects on plants (Krizek and Mirecki 2004). On the other hand, in greenhouses or growth chambers unrealistic balances frequently occur among the different light spectral regions: UV-B/UV-A/PAR (photosynthetic active radiation (PAR), 400–700 nm) and often levels of PAR lower than in the field conditions are also observed. Low levels of PAR increase the sensitivity of plants to UV-B-induced damages (Pradhan et al. 2006). Additionally, to calculate and compare the doses of UV-B under different spectral regimes the UV-B radiation is weighted (UV-BBE) according to a suitable biological action spectrum or biological weighting function (BWF). To obtain the UV-BBE there are different BWFs available but there is a generalized consensus for the use of the Caldwell's BWF (Flint and Caldwell 2003). Several results, however, have shown that this very steep action spectrum may lead to over- or underestimation of the UV-B effects (Micheletti et al. 2003). Moreover, differences in climatic conditions can also affect the interpretations and comparisons among different studies based on the BWF (Musil et al. 2002b; Flint et al. 2009). Therefore, all the quantitative predictions relating to UV-B enhancement effects could be greatly affected. On the other hand, more recent studies have proposed that increases of the ambient solar UV-B radiation at magnitudes anticipated under the current stratospheric ozone projections will not significantly have large-scale deleterious effects on terrestrial plants even though some species may suffer photosynthesis decreases and growth reductions (Rozema et al. 2006; Xu and Qiu 2007; Newsham and Robinson 2009).

7 Physiological and Morphological Responses to UV-B Enhancement

From indoor and outdoor studies, there is a general consensus that UV-B enhancement produces physiological, biochemical, morphological, and anatomical changes in the plants (Searles et al. 2001). According to the literature, the enhancement of UV-B radiation can affect the terrestrial plants at different functional levels involving conformational changes and damages to different molecules such as DNA, proteins, and lipids (Li et al. 2010). As a result, if damage to macromolecules, that is, DNA is not effectively repaired, the UV-B effect will be translated to the biochemical level with the consequent alteration and/or impairment of the plant functionality (e.g., photosynthetic process, growth, yield). Although it is clear that there is a wide range of both intra- and interspecific sensitivity to UV-B radiation (Gilbert et al. 2009) the terrestrial plants through the evolution have acquired different protective strategies to avoid the adverse effects of UV-B radiation. The two major protective mechanisms are: (a) shielding through the production of soluble phenolics (e.g., flavonoids, anthocyanins, hydroxycinnamic acid derivatives), insoluble polyphenols (e.g., lignin), and cell-wall bound UV-absorbing compounds (Hilal et al. 2004; Clarke and Robinson 2008), as well as by reflection of the UV-B radiation by epicuticular waxes and cuticular structures (Hada et al. 2003; Schmitz-Hoerner and Weissenböck 2003; Agati and Tattini 2010); (b) removal and direct reversion of the DNA lesions induced by UV-B radiation (Tuteja et al. 2001; Britt 2004; Kimura et al. 2004).

7.1 DNA: Damage and Repair

The more important UV-B-induced DNA alterations are the formation of cyclobutane pyrimidine dimers (CPDs) and pyrimidine (6–4) pyrimidine dimers (6–4 photoproducts, 6-4PPs) (Dany et al. 2001). The DNA repair mechanisms operating in

plants include the following processes: (a) direct reversal (DR); (b) photoreactivation that induces photolyases; (c) dark repair (Tuteja et al. 2001; Britt 2004). The DR is a simple mechanism that involves a single-enzyme reaction for the removal of certain types of DNA damage. Alkyltransferases simply extract alkyl groups from the alkylated bases that are transferred to internal cysteine residues and thus inactivate themselves. The best example for DR is the correction of miscoding alkylation lesion O^6-methylguanine, which is generated endogenously in small amounts by the reactive cellular catabolites. This reaction is catalyzed by a specific enzyme, called methylguanine methyltransferase (MGMT), which removes a methyl group from a guanine residue of the DNA molecule and transferring it to one of its own cysteine residues in a rapid and error-free repair process (Tuteja et al. 2001). The photoreactivating enzyme DNA photolyase (PRE) is a DR phenomenon performed by the combined action of one or more photolyases and the visible light (blue, violet, or long-wave UV) (Hidema et al. 2007). Photolyases specifically recognize and bind the pyrimidine dimers to form a complex molecular structure which is stable in absence of the light. After absorbing a blue light photon the pyrimidine dimers are reversed to pyrimidine monomers without excision of the damaged base (Tuteja et al. 2001). The repair reaction is fast and requires about 1 h for completion (Takeuchi et al. 2007). In plants, two specific types of photolyases have been characterized: (a) CPD-photolyase; (b) 6-4PP-photolyase (Tuteja et al. 2001). The dark repair processes include the nucleotide excision repair (NER), base excision repair (BER), mismatch repair (MMR), and other DNA repair pathways. These mechanisms have been observed in several plant species and some of the genes required for the processes were identified (Kimura et al. 2004). The wide class of helix-distorting lesions such as CPDs and 6-4PPs are repaired by the NER process. It is one of the most versatile DNA repair pathway operating in plants. Unlike other DNA repair pathways that are specific repair processes, the NER pathway is capable of removing various DNA damage classes, including those induced by the UV-B radiation (pyrimidine dimers) and chemical agents (bulky DNA adducts) (Kimura et al. 2004). The NER pathway sequentially involves recognition of the DNA damage, incision on the damaged strand, excision of the damage-containing oligonucleotides, and the DNA synthesis and ligation (Liu et al. 2003). Also, the NER pathway is a slow process (about 24 h for completion) and includes several enzymes. There are two subpathways of the NER process that are designated as: (a) global genomic repair (GGR); (b) transcription-coupled repair (TCR). While the GGR pathway repairs the DNA damage over the entire genome, the TCR pathway is selective for the transcribed DNA strand in expressed genes (Kimura et al. 2004). Oxidized or hydrated bases and single-strand breaks are repaired by the BER pathway that is considered an essential process for maintenance of the DNA molecule. The BER mainly removes the DNA damages that are arising spontaneously in the cell from hydrolytic events such as deamination or base loss, fragmented bases resulting from ionizing radiation (e.g., UV-B radiation), and oxidative damage or methylation of the ring nitrogen by endogenous agents. The process that involves the BER mechanism is initiated by DNA glycosylases that release the damaged base by cleavage of the sugarphosphate chain followed by excision of the abasic residue or abasic residue containing oligonucleotides and then the synthesis and ligation of the DNA occurs. The BER pathway involves several enzymatic steps and depends strongly on the presence of nicotinamide adenine dinucleotide (NAD+). Also, the BER process comprises two subpathways that are designated as: (a) BERshort-path; (b) BERlong-path. The BERshort-patch is a DNA polymerase beta-dependent mechanism, while the BERlong-patch is a DNA polymerase delta/epsilon-dependent mechanism (Kimura et al. 2004). The major difference between BER and NER pathways is the way by which the DNA damage is removed. The NER pathway cuts out the damage as a part of an oligonucleotide fragment, while the BER mechanism excises only one nucleotide (Tuteja et al. 2001). The excision repair processes (NER and BER) are very important for maintaining the genome stability

and essential for the survival of plants. The mismatch repair pathway (MMR) is also important in the DNA repair processes when by errors of replication or homologous recombination can be produced mismatched bases. The MMR pathway basically discriminates between correct and incorrect bases and after DNA synthesis the error is corrected (Tuteja et al. 2001). Although most of the present understanding of the eukaryotic MMR has come from studies of the *E. coli* MutS and MutL proteins (Kolodner and Marsischky 1999), recent studies carried out in *Arabidopsis* and rice have reported interesting findings on the MMR pathway operating in plant cells (Tuteja et al. 2001; Kimura et al. 2004). According to the *E. coli* model, the MutS dimer recognizes mispairs and then binds on it followed by the MutL binding, which activates the MutH (endonuclease) that makes a single-strand incision (nick). The MutH incision can be done on either side of the mismatch. Subsequent to incision the excision is initiated and proceeds toward mismatch. To fill the gap (100–1,000 nucleotide gap), the original template strand can then be replicated and finally sealed by ligation. The proteins involved in the last step of eukaryotic MMR are: (a) DNA polymerase δ, RP-A (replication protein); (b) PCNA (proliferating cell nuclear antigen); (c) RFC (replication factor) (Kolodner and Marsischky 1999).

Although the UV-A wavelengths can mediate the photoxidative damage (Turcsányi and Vass 2000) the UV-B radiation is the most important photooxidant agent for terrestrial plants. The DNA damage can also be caused by reactive oxygen species (ROS) and free radicals produced by the UV-B radiation. This damage includes several modifications such as cross-linking, aggregation, denaturation, and degradation (Hidema et al. 2007). The formation of 7,8-dihydro-8-oxoguanine (GO) is a common oxidative DNA lesion generated by a direct modification mediated by ROS. The GO is mutagenic and can mispair with adenine (A) during the DNA replication (Yang et al. 2001). If the resulting A/GO is not repaired before the next round of the DNA replication, a C/G → A/T transversion occurs and the opportunity for repair is lost. The A/GO is repaired via the BER which is initiated by the DNA repair enzyme adenine-DNA glycosylase (Yang et al. 2001). The UV-absorbing compounds (e.g., flavonoids, anthocyanins, hydroxycinnamic acid derivatives, phenolics) accumulating in epidermal and subepidermal cell layers have traditionally been thought to function as UV-B filters, but also play an important role as quenchers of the ROS and free radicals in the amelioration of the UV-B-induced DNA oxidative damage (Agati and Tattini 2010). The UV-absorbing compounds are also effective in reducing the induction of cyclobutane pyrimidine dimers (CPDs) in plants exposed to high UV-B levels (Hidema et al. 2007). The inhibition of CDP formation seems to be high enough to compensate the DNA damage arising even from unusually strong solar irradiations (Tuteja et al. 2001). Other related UV-absorbing compounds, that is, anthocyanins through an anthocyanin-DNA complex could also provide protection against the oxidative damage. Since both anthocyanins and DNA mutually protect each other in vitro, it is likely that such protection mechanism may also operate in vivo (Sarma and Sharma 1999). In the plant cells, anthocyanins are predominantly localized inside the vacuoles and thus their putative role in the protection of DNA should be critically examined. Accepting this fact, it has been demonstrated that the excess accumulation of anthocyanins reduces the amount of blue/UV-A radiation reaching the cell and may sometimes lower the ability to photorepair the damaged DNA. For example, the purple rice is a highly UV-B sensitive species despite possessing an elevated level of anthocyanins in their leaves (Hada et al. 2003). Although significant amounts of flavonoids have been found in the chloroplasts or etioplasts isolated from a wide range of plants growing under both ambient and enhanced UV-B irradiances (Tattini et al. 2005; Agati et al. 2007), it is also likely that some amount of anthocyanins can be present in the nuclei and organelles and then may associate with the DNA molecule, offering to it a certain protection against the oxidative damage (Feucht et al. 2004). In this context, the UV-absorbing compounds seem to have an important protective function against the DNA

damage induced by shorter solar wavelengths (Schmitz-Hoerner and Weissenböck 2003) and so the speculations concerning a great biological risk with regard to increases in solar UV-B radiation after the depletion of the ozone layer are presumably premature.

In the natural populations, both protection and DNA repair are complementary and necessary processes for the plant development. Thereby, it is expected that the plants growing under different UV-B irradiances can exhibit different levels of the DNA protective mechanisms (Turunen and Latola 2005). Under field conditions, the observed DNA damage can often be modified by climatic conditions and then a direct extrapolation of the DNA changes obtained in controlled-environment experiments under artificially enhanced UV-B radiation to plants growing under the ambient solar UV-B is complex and unrealistic. Differences between damage, repair, and defense can be subtle and identification of a particular mechanism does not always occur as the explanation underlying a given phenomenon. For example, the UV-induced degradation of the D1 protein of the PSII can be seen either as damage or as a part of the repair mechanism leading to substitution of the damaged components of the PSII (Turcsányi and Vass 2000). Consequently, understanding these differences and potentially using the DNA repair mechanisms could become very important for producing UV-B-tolerant plants.

7.2 Secondary Metabolites: Flavonoids and Anthocyanins

The increase of secondary metabolites synthesis has been recognized as one of the most frequently observed plant response to UV-B enhancement (Searles et al. 2001; Rozema et al. 2002; Bassman 2004). Considerable attention has been focused, over the past two decades, on the UV-B-induced biosynthesis of phenylpropanoid-derivative compounds, particularly flavonoids and hydroxycinnamic acid derivatives (Jordan 2002; Rozema et al. 2002; Bassman 2004). Although these compounds exhibit important interspecific differences induced by the UV-B radiation, they are often derivatives of the flavonols quercetin and kaempferol (Buer et al. 2010). Quercetin- and kaempferol-derivative flavonoids are usually glycosylated and frequently contain a hydroxycinnamic acid moiety esterified to one of the glycosyl groups (orthodihydroxy B-ring-substituted flavonoids) (Tattini et al. 2004). The flavonoids are ubiquitous molecules occurring in the vacuoles and cell walls of epidermal cells and in nonsecretory and glandular trichomes, and it has been assumed that they primarily have the function of attenuating the shorter solar wavelengths due to their good quantum efficiency (Burchard et al. 2000). In this way, the location of flavonoids in trichomes (Tattini et al. 2004), cuticular wax layers (Fukuda et al. 2008), and epidermal cells (Burchard et al. 2000) may largely prevent that the UV-B radiation reaches sensitive targets within the leaf. However, the flavonoids also have another *protective function* against the shorter solar wavelengths. Considering that the flavonoids with orthodihydroxylated B-ring may efficiently dissipate the excess of energy through tautomeric interconversions (Smith and Markham 1998), scavenge the ROS through the quenching mechanism (Yamasaki et al. 1997; Hilal et al. 2008), and inhibit the formation of free radicals (Neill and Gould 2003; Xu et al. 2008), they can also act as effective antioxidant molecules (Jordan 2002; Tattini et al. 2005; Buer et al. 2010). However, a major criticism regarding functions of the flavonoids is the use of mutants that lack or possess the ability to synthesize flavonoids, which may oversimplify the plant model system for quantifying the UV-B-tolerance/flavonoid-biosynthesis relationships (Bieza and Lois 2001). In this context, contrary to determination of the flavonoid concentration at the whole-leaf level, less attention has been devoted to analyzing the tissue-specific location of individual flavonoids, which may clarify their complex functional roles in both attenuation and antioxidant mechanisms against the high UV-B irradiances (Tattini et al. 2004). Furthermore, the short-term experiments and inappropriate microscopy techniques for visualizing the flavonoids also greatly contributed to this *superficial* conclusion. More recent studies, however, suggest that the biosynthesis of

flavonoids, particularly *internal flavonoid glycosides* may be largely controlled by constitutive morphoanatomical and biochemical features, primarily intended both to prevent the light penetration (Burchard et al. 2000) and to remove the consequent oxidative damage (Apel and Hirt 2004). Agreeing with these findings, Semerdjieva et al. (2003) showed in the *Vaccinium* spp. an inverse relationship between cuticule thickness (primary barrier to UV-B penetration) and the mesophyll accumulation of UV-B-induced flavonoids.

Regarding to ROS scavenging activity of the flavonoids, Yamasaki et al. (1997) proposed a model to address major criticisms on the antioxidant functions of the flavonoids compartmentalized in epidermal vacuoles, and at the same time to explain the preferential UV-B-induced synthesis of flavonoids with effective antioxidant properties in vitro. According to Yamasaki's model, the orthodihydroxy B-ring-substituted flavonoids, not their monohydroxy B-ring-substituted counterparts, are effective substrates for the class III peroxidases, which quench the H_2O_2 freely diffusing from the mesophyll cellular organelles to vacuoles of the epidermal cells. The model was remarkable in calling out the question whether vacuolar flavonoids could be effective in protecting underlying tissues from the damaging shorter solar wavelengths, while not protecting the epidermal cells from the oxidative damage. Epidermal cells and glandular trichomes usually contain much higher concentrations of flavonoids than the mesophyll cells (Burchard et al. 2000), then the H_2O_2 leaked out from the mesophyll cells under high UV-B irradiances can be scavenged by the flavonoid-peroxidase system in the epidermal cells according to the proposal of Yamasaki et al. (1997). Consistent with this idea blackening of the epidermis after a severe light stress is frequently observed in many species under the field conditions. This phenomenon has been ascribed to the polymerization of vacuolar phenolics that result from the penetration of H_2O_2 inside the epidermal cells (Yamasaki et al. 1997). Nevertheless, it cannot be excluded the possibility that other apoplastic flavonoid-depending peroxidases such as guaiacol peroxidase and syringaldazine peroxidase associated with the process of lignification may be involved in the mechanism of ROS scavenging (Hilal et al. 2004). The concept of delocalized scavenging of H_2O_2 by the vacuoles can be applied not only to the organelle–organelle interactions but also to the cell–cell interactions (Yamasaki et al. 1997). It is also acknowledged as a controversy matter whether the ability to accumulate flavonoids, particularly flavonoids with orthodihydroxylated B-rings, and the *tolerance* to UV-B radiation is highly correlated (Dixon et al. 2001; Musil et al. 2002b; Hofmann et al. 2003). The orthodihydroxylated B-ring-derivative flavonoids such as quercetin and luteolin glycosides are accumulated in the vacuoles of the mesophyll cells in *Ligustrum vulgare* leaves exposed to the full sunlight, in presence or absence of the UV-B radiation (Agati and Tattini 2010). This finding, which is consistent with previous reports indicating that the UV-B radiation is not a prerequisite for the synthesis of flavonoids (Tattini et al. 2004, 2005; Jenkins 2009), leads to the conclusion that the light-induced oxidative damage may regulate the biosynthesis of flavonoids, irrespective of the presence of UV-B radiation. The flavonoids and other UV-absorbing phenolics (e.g., hydroxycinnamic acid derivatives) are also synthesized in other abiotic/biotic unfavorable conditions such as drought, salinity, low temperature, heavy metal pollution, pathogen attack, and as feeding deterrent. Besides their antioxidant abilities the flavonoids might exert modulatory effects in the cell through selective actions at different components by cell interactions (Buer et al. 2010). This fact has become increasingly important because attention focuses on the new concept of flavonoids as potential modulators of the intracellular signaling cascades that are vital for the cell functionality (Jenkins 2009).

The anthocyanins, other members of the phenol family, have generally been included into photodamaging-protective compounds (Gould 2004). The anthocyanins show a weak absorption in the shorter UV region (270–290 nm), but their acylated counterparts (hydroxycinnamic acid derivatives) exhibit an increased absorption in the longer UV-B region (310–320 nm) (Neill and

Gould 2003). Because anthocyanins are photoinduced many researchers surmise that they must either have a photoprotective function against the light-induced photooxidation or against the UV-B damage (Hughes et al. 2005). Even without acylation the anthocyanins can significantly attenuate the visible radiation. In fact, the more clear evidences really support the theory of the photooxidative protection, while the role in UV-B protection seems to be much less apparent (Kytridis and Manetas 2006). This assumption, however, contradicts the theory that anthocyanins have a UV-B-filtering role (Neill and Gould 2003). Disagreeing with the last theory the UV-B vulnerability is poorly correlated with the content of anthocyanins. For example, an *Arabidopsis* mutant with enhanced sensitivity to UV-B radiation was found deficient in certain flavonoids, whereas the amount of anthocyanins displayed unchanged. Similarly the responses of a *Brassica rapa* mutant to the supplementary UV-B treatment were mostly independent of the anthocyanin level in leaves (Gould 2004). Agreeing with these findings the anthocyanins often occur in very low concentrations compared to other UV-absorbing compounds, and require a long exposure to the UV-B radiation to be synthesized (Neill and Gould 2003). On the other hand, the red-leafed plants of *Impatiens capensis* and rice displayed significantly worse performances under the UV-B enhancement than their green-leafed counterparts (Dixon et al. 2001). Moreover, it has been communicated that the accumulation of anthocyanins can cause deleterious effects on terrestrial plants after a long-term UV-B exposure (Gould 2004). It has been noted that the DNA damage after a prolonged UV-B treatment was substantially greater in the purple-leafed rice than in the near-isogenic green line. Anthocyanins in the purple rice prevented the photoactivation of photolyases by absorbing some of the incident blue/UV-A light on leaves. Thus, any short-term gain from the absorption of UV-B radiation by anthocyanins would be offset by their property to absorb the visible light and thereby limit the rate of DNA repair (Hada et al. 2003). Furthermore, it has been demonstrated that other abiotic and biotic stresses produce changes in the chemical pattern of anthocyanins (Close and Beadle 2003), then it is obvious that such changes will influence the absorption spectra of anthocyanins under the UV-B enhancement. Also absorptive artifacts due to the dissociation of covalent bonds can occur during the improper isolation of anthocyanins and misread absorption spectra will be generated (Gould 2004).

The accumulation of anthocyanins is usually transient and generally occurs in the vacuoles of peripheral tissues such as palisade and/or spongy mesophyll exposed to high light irradiances, but there are some exceptions (e.g., accumulation in the abaxial leaf tissues and in obligatory shade plants) (Kytridis and Manetas 2006). Perhaps the improved solubility of anthocyanins that in contrast to other flavonoids are nearly always glycosylated allows them to be stored in the vacuole more efficiently than the nonglycosylated flavonoids (Winefield 2002). In fact, the importance of flavonoids should not be overlooked in the discussion of anthocyanin production and UV-B protection. In this context, the flavonoids induced by the UV-B radiation (Agati and Tattini 2010; Buer et al. 2010) are recognized as strong UV-B absorbers, and their UV-B absorption capacity is much stronger than that of anthocyanins (Bieza and Lois 2001). Since the production of anthocyanins represents a conversion of flavonoid precursors that themselves are strong UV-B absorbers, a conundrum appears: if one of the effects of UV-B radiation on plants is to induce the UV-B-protective pigments, why are anthocyanins produced instead of their flavonoid precursors? Characteristics of both flavonoids and anthocyanins absorption spectra must be analyzed to respond this conundrum (Solovchenko and Merzlyak 2008). The flavonoids exhibit two bands in the UV region: (a) short-wave peaking around 280 nm; (b) long-wave situated in the range of 300–360 nm. However, the exact positions of the maxima vary for different flavonoid derivatives. The anthocyanins also have two maxima: one in the UV-B region (270–320 nm) and another in the visible region with a maximum located in the blue-green part of the visible wavelengths (500–540 nm) (Gould 2004). In this way, the UV-B component of the solar spectrum can

be screened by both flavonoids and anthocyanins. However the UV-A radiation, whose proportion in the solar spectrum could be tenfold higher as compared with the UV-B spectrum region also exerts significant effects on plants (Krizek 2004). For example, maximum inhibition of the photosynthesis under natural radiation fluxes is induced by radiation in the UV-A region (Ivanova et al. 2008). Although this fact supports the importance of the UV-protection provided by the flavonoids in the range of 300–360 nm, the high visible fluxes (400–700 nm) also induce a photodamage in plant tissues, especially in the chloroplast (Krizek 2004). The anthocyanins are able to intercept a great proportion of the solar radiation in the range of 500–600 nm, which correspond to the maximum solar energy reaching the Earth's surface (Gould 2004). This finding therefore contributes to support the role that anthocyanins play in the photoprotection of plant tissues (Solovchenko and Merzlyak 2008). In this context, the accumulation of anthocyanins requires visible light and generally coincides with the period of high excitation pressure and the increased potential for the photooxidative damage. The photooxidative damage is produced by an imbalance between the light capture, CO_2 assimilation, and carbohydrate utilization (e.g., greening of developing tissues, senescence, adverse environmental conditions) (Hughes et al. 2005). Thereby, the attenuation of light by anthocyanins may help to reestablish this balance and to reduce the excitation pressure (Kytridis and Manetas 2006). Then, the risk of cellular photooxidative damage is lowered. Also, it would seem that the anthocyanin biosynthesis can enhance under the high light, but it is not usually a prerequisite for the protection against the oxidative stress (Gould 2004).

Like the colorless flavonoids the colored anthocyanins may scavenge the free radicals and ROS (Gould 2004). The anthocyanins diminish the oxidative trend in the leaf simply by filtering out the yellow-green light, because most of the reactive oxygen in plant cells is derived from excitation of the chlorophyll molecule (Neill and Gould 2003). Agreeing with this theory, in juvenile and senescing plants the regulation of photosynthetic apparatus functions is often impaired, making it less efficient in utilization of the absorbed light and therefore prone to the photodamage (Merzlyak et al. 2008a). As a general rule, these situations are accompanied by an increased generation of ROS causing photooxidative damage to the plant and, eventually, its death (Bukhov 2004). Under these conditions, the anthocyanins may afford a detoxifying sink for some ROS when the chloroplast, the first line of the antioxidative defense, is surpassed (Kytridis and Manetas 2006). It is not clear, however, whether the ROS scavenging occurs predominantly through the anthocyanins found inside the vacuole or through their counterparts located in the cytosol. Both anthocyanin forms have impressive antioxidant potentials (Neill and Gould 2003), but due to their proximity to the chloroplastic source of ROS it is more probable that anthocyanins located in the cytosol (mesophyll tissue) than in the vacuole (epidermal tissue) provide the major contribution to antioxidant defense (Kytridis and Manetas 2006). In a similar trend, recent evidences suggest that flavonoids may scavenge the ROS within or near sites of its generation (Schmitz-Hoerner and Weissenböck 2003; Tattini et al. 2005; Agati et al. 2007). Interestingly, equal effectiveness as antioxidant molecules of other colorless phenolics suggests that the putative photooxidative protection afforded by the anthocyanins should be unrelated to their ability to quench oxidants.

Noteworthy the accumulation of anthocyanins in terrestrial plants has always been a contentious issue of the special interest. They often appear in juvenile plants but mature plants usually lack them or display transiently levels under stressful conditions (Merzlyak et al. 2008a). Obviously, upon maturation of the photosynthetic apparatus or its acclimation to stressors the photoprotective *screen* of anthocyanins is no longer required and the juvenile reddish pigmentation disappears. However, unfavorable environmental conditions such as low temperatures, heavy metals, drought, wounding, and pollutants can also predispose the photosynthetic apparatus to photoinhibition and photooxidation, and then the plants may increase, although not necessarily ascribed to, the accumulation of anthocyanins in vegetative organs

(Gould 2004). Accordingly, the production of anthocyanins would fit neatly into the definition of Leshem and Kuiper's (1996) *general adaptation syndrome* (GAS). The GAS indicates that different types of stress evoke similar adaptation responses. In this context, along with compounds such as tocopherols, flavonoids, glutathione, and ascorbate, the anthocyanins may function as general mitigators of the oxidative damage. However, it should be addressed that there is no direct evidence that terrestrial plants benefit from the antioxidant properties of anthocyanins yet (Neill and Gould 2003). Although anthocyanins are of special importance for the photoprotection in senescing leaves, it seems not to be the only function of anthocyanins. It has been suggested, for example, that the red color may also deter aphids from laying their eggs or from feeding on the sugar-rich sap in the phloem. Noteworthy, despite that the autumnal color may be an *extravagancy without a vital function*. This phenomenon that enchants so many tourists each year may hold a vital key to the survival of deciduous trees (Archetti et al. 2009). Also the anthocyanins are involved in the photoprotection of ripening fruits, for example, the chlorophyll in apple fruit peel with high anthocyanin content showed a very high resistance to the photobleaching as compared with the anthocyanin-free zones of the same fruit (Merzlyak et al. 2008b). Despite its function as photoprotective molecules, the anthocyanins may instead serve to decrease the leaf osmotic potential. The resulting depression of leaf water potential could increase the water uptake and/or reduce transpirational losses. This phenomenon may allow to the anthocyanin-containing leaves to tolerate suboptimal water levels. The often transitory nature of the foliar anthocyanin accumulation may allow plants to respond quickly and temporarily to environmental variability rather than through more permanent anatomical or morphological modifications (Chalker-Scott 2002). Interestingly, the anthocyanins also fulfill the less common but important function of avoiding the photodegradation of sensitive molecules. The *Ambrosia chamissonis*, for example, hold strands of laticifers surrounded by an anthocyanin sheath. These laticifers contain thiarubrines, toxic chemicals that are believed to deter herbivory and prevent both fungal and bacterial infections. The thiarubrines are photolabile molecules and are degraded by both visible and UV light giving thiophenes that are less toxic. Page and Towers (2002) have shown that the anthocyanin sheath, by absorbing a proportion of the rays that would otherwise strike the laticifers, protects these light-sensitive defensive chemicals from degradation, and thus provides a mechanism for the antiherbivory under conditions of strong sunlight.

However, although the role of anthocyanins in protecting plant tissues under stress conditions, including the photodamage mediated by both UV-B and visible light, as well as in the pollinator attractiveness and seed dispersion seems to be important, it is clearly evident that the adaptive significance of anthocyanins is still not fully understood (Close and Beadle 2003). Meanwhile two poorly explored areas became interesting: (a) how the increase of anthocyanin production is integrated to tissue responses to UV-B; (b) how the UV-B-induced anthocyanins contribute to the plant survival.

7.3 Morphogenic Responses

Studies carried out in greenhouses or in growth chambers using ultraviolet lamps and filters to simulate different solar UV-B enhancements have been conducted on a variety of terrestrial plants, including economically important crops (Santos et al. 2004) and wild plant species (Zu et al. 2010). Overall these studies showed that the UV-B enhancement besides physiological effects induces a range of morphological changes including: (a) increase/decrease of the leaf area and leaf thickness (González et al. 2002; Hilal et al. 2004); (b) reduction of the plant height (Santos et al. 2004) and increase/decrease of the shoot/root ratio (Furness and Upadhyaya 2002); (c) axillary branching (Kakani et al. 2003); (d) increase of the leaf glandular and uniseriate trichome density (Liakopoulos et al. 2006); (e) deposition of the waxy surface structures (Fukuda et al. 2008); (f) opening of the cotyledon curling (Boccalandro

et al. 2001; Barnes et al. 2005); (g) inhibition of the hypocotyl and stem elongation (Shinkle et al. 2004; Gerhardt et al. 2005); (h) premature leaf senescence (Pradhan et al. 2006). The effects of UV-B also include changes (increase/decrease) in the number and size of flowers as well as in the size of seeds (Kakani et al. 2003; Qaderi and Reid 2005). While some of the UV-B responses constitute a stimulation of the growth (e.g., axillary branching, leaf thickening), others reflect a growth inhibition (e.g., reduced hypocotyl elongation). However, in these experimental setups, frequently unrealistic balances between UV-B/UV-A/PAR are obtained, and in some cases the plants have been exposed to relatively high short-term doses of UV-B, which lack the ecological relevance (Newsham and Robinson 2009). Additionally, the levels of UV-A or PAR as well as other experimental conditions also affect the morphogenic responses, making it difficult to compare the results from different indoor studies. In addition, it is clear that not all the plant species respond in the same way to UV-B exposure (Pliura et al. 2008). In general, the monocots are more morphologically responsive to UV-B than the dicots (Pal et al. 1997). Closely related species or ecotypes, especially when occupy different habitats, also differ with respect to their morphogenic responses (Hofmann et al. 2003). Plant species also differ in the use of PAR and UV-B radiation; while some species use the PAR to trigger responses others use the UV-B radiation. Then the plants responding mainly to PAR radiation will probably be more sensitive to UV-B radiation than the UV-responding ones (Rozema et al. 2005). A critical factor in the UV-B studies is the visible light irradiance, which in growth chambers and greenhouses can be quite different to the natural sunlight (Flint et al. 2009). Indeed, it has been shown that as a result of the insufficient visible wavelengths and, therefore, of unrealistically high UV-B/PAR ratios in indoor studies, the morphogenic effects of the UV-B radiation are magnified (Musil et al. 2002a, b). In fact, even if realistic levels of the UV-B radiation in simulating ozone reductions are used the indoor responses of plants to UV-B radiation may be quite variable and exaggerated in relation to the field. Microclimatic conditions and the interactions of different abiotic and biotic environmental factors additionally contribute to inconsistency between the results obtained in growth chambers or greenhouses with those obtained under the field conditions (Flint et al. 2003; Caldwell et al. 2007). Furthermore, the plant responses to above ambient UV-B radiation (e.g., from stratospheric ozone depletion) have rarely been assessed in the broader context of the possible effects emerging from variations in the UV-B radiation within the *ambient range*. Also there is a significant knowledge gap between field and laboratory studies, which has two major components: (a) the occurrence of certain effects of the UV-B radiation under laboratory conditions has not yet been demonstrated in the field studies; (b) although some indoor responses are known to occur in the field, their functional implications are still unclear. Therefore, the obvious corollary from greenhouses or growth chambers studies is: *study methodologies are as varied as results*. In fact, from the field grown plants, the consensus that effects of artificially changed spectral UV-B irradiances are less pronounced (Searles et al. 2001). While under UV-B enhancement among other changes, leaf thickness, reduced leaf area, decreased plant height, changes in plant architecture, and biomass/yield reduction have been observed (Searles et al. 2001; Flint et al. 2003; Barnes et al. 2005). Nevertheless, the more recent studies have suggested that in the field, primary effects of the most realistic solar UV-B enhancements are subtle morphological and chemical changes with altered carbon partitioning and allocation, but doubt reveals such changes show significant effects on both plant growth and biomass accumulation (Gilbert et al. 2009; González et al. 2009; Morales et al. 2010; Ren et al. 2010; Zu et al. 2010). The morphogenic effects of the realistic UV-B enhancements are not usually considered as primary ecological factors influencing both species abundance and species distribution in relation to other abiotic environmental factors (e.g., drought, temperature, salinity). There are, however, situations where the UV-B-induced morphogenic effects can be ecologically important, giving changes in the

competitive ability with a significant impact on the composition of the plant community (Flint et al. 2003). The UV-B enhancement alters the leaf angle and differential transmission, and absorbance of the UV-B radiation through stands of erectophilous or planophilous plant species may have an important consequence on terrestrial plant responses to the UV-B radiation (Rozema 2000). In a model study, it was predicted that a more planophilous leaf angle in erectophilous species would reduce the UV-B/PAR ratio and therefore the UV-B damage. Of course, this effect may affect the competitive relations among species and also the ecosystem composition (Deckmyn 1996 in Rozema et al. 1997). The morphogenic effects often can be pronounced on different organisms at other trophic levels (Bassman 2004). The UV-B radiation also affects the decomposition of plant materials into ecosystems. Plants grown under the enhanced solar UV-B showed a reduced rate of the litter decomposition when compared to control plants grown under the ambient solar UV-B. The accumulation of UV-B-induced lignin and/or tannin accounts for the reduced litter decomposition rate (Cybulski et al. 2000). Nevertheless, the reduced rate of the litter decomposition can be produced as consequence of detrimental effects of the enhanced UV-B radiation on decomposing fungi and other decomposer organisms (Pancotto et al. 2003). In opposite trend, the plant litter material exposed to the enhanced solar UV-B can be decomposed by photodegradation more rapidly than under the ambient solar UV-B (Gallo et al. 2006). Moreover, it has also been demonstrated that the species growing for several generations under enhanced UV-B radiation show accumulation and exacerbation of the UV-B effects and likelihood they might be heritable (Mpoloka et al. 2007).

Much of the UV-B research on terrestrial plants has concentrated on vegetative plant parts, but fitness of the organisms depend mainly on their successful reproduction. Of particular concern is the detrimental effect of UV-B on the pollen quality observed for some species (Koti et al. 2004; He et al. 2007). This finding suggests that pollination may be an ecologically critical developmental stage vulnerable to the UV-B damage, even in the UV-B-tolerant species. The pollen surface of some species may transmit up to 20% of the incident UV-B radiation (Stadler and Uber 1942 in He et al. 2007), despite the presence of a variety of UV-B-absorbing pigments (Rozema et al. 2001). Thus, the mature pollen grains are potentially susceptible to the UV-B damage during a short period between the dehiscence of anthers and the penetration of the pollen tube into the stigmatic tissue (Koti et al. 2004). This fact may lead to both reduced pollen quality and altered patterns of competition among species affecting the composition of the ecosystem. Furthermore, the UV-B enhancement can alter the production and/or the temporal availability of flowers so as to make the plant a less attractive host for the pollinators and impinge upon competition of plants for the pollinator service, as well as on the reproductive success of the plant/pollinator system (Sampson and Cane 1999).

8 UV-B Radiation and Signaling Pathways

The UV-B radiation triggers diverse responses involving a differential regulation of the genes and participate in several protective pathways including the DNA repair, detoxification of ROS, and production of secondary metabolites as well as in photomorphogenic events (Agrawal et al. 2009). The UV-B responses can be elicited with either high fluence (HF-UV-B, over 15 kJ m^{-2}), intermediate fluence (IF-UV-B, 5–7 kJ m^{-2}), low fluence (LF-UV-B, 1–3 kJ m^{-2}), or very low fluence (VLF-UV-B, less than 1 kJ m^{-2}) (Brosché et al. 2002). However, the exposure of plants to low fluence UV-B promotes the expression of varying genes involved in the UV-B protection, and genes responsible for the production of flavonoids and several phenolic compounds, while as the low fluence photomorphogenic responses seem to be initiated by photoreceptors and no alternative UV-B-absorbing molecules seem to mediate the photomorphogenic UV-B responses (Ulm and Nagy 2005). Also, many components of the protective pathways which lead to the changes of the gene expression in response to

both UV-B radiation and pathogens are similar or identical (upregulation of *PDF1.2*), except the pathways which are distinct (upregulation of *PR-1*), signifies the effects of the high fluence UV-B radiation on the gene expression are unlikely to be due to nonspecific damage and a yet unidentified UV-B photoreceptor (Brosché et al. 2002). The response of plants to UV-B radiation depends upon the adaptation and acclimation to UV-B irradiances, as well as of the interactions with other environmental factors. Moreover, studies carried out with *Arabidopsis* plant suggest that some genes are differentially responsive to UV-B in both 280–290 nm and 300–310 nm ranges, hence could be multiple UV-B photoreception mechanisms (Kalbina et al. 2008). Consequently, the exposure of plants to UV-B radiation can cause multiple responses on the primary and secondary metabolisms as well as different changes on the growth and overall performances. Although other light-dependent photoreceptors (e.g., phytochrome, cryptochrome) have been described (Carvalho et al. 2010), presently a UV-B-specific photoreceptor has still not been described and therefore the basic mechanism of UV-B perception and the signal transduction remain still poorly understood. Nevertheless, the chromophores that could act as photoreceptors to absorb the UV-B radiation exist. Pterins or flavins in their reduced forms are candidates where some experimental work supports the involvement of the perception of UV-B radiation (Galland and Senger 1988a, b in Jenkins 2009). For example, the compounds that antagonize the flavins and pterins impair the UV-B induced anthocyanin synthesis in maize (Jenkins 2009) along with UV-B suppression of the hypocotyl elongation in tomato plants (Ballaré et al. 1995). In addition, other possible chromophore can be a phenolic molecule, with this assumption the *p*-coumaric acid chromophore present in the photoactive yellow protein (PYP), a photoreceptor found in the purple photosynthetic bacteria *Ectothiorhodospira halophila*, enables to absorb in UV-A and blue regions of the solar radiation spectrum (Imamoto and Kataoka 2007). Moreover, an alternative possibility is that the UV-B radiation be sensed through some form of direct activation of a cellular component. Whether or not the UV-B photoreceptor exists the responses to UV-B radiation could be mediated by nonspecific signaling pathways involving the DNA damage, ROS production, hormone synthesis (e.g., salicylic acid, ethylene, jasmonic acid), and wound/defense signaling molecules (e.g., flavonoids, phenolics) (Apel and Hirt 2004; Demkura et al. 2010); or by specific UV-B signaling pathways mediated by the UV-B-specific component UV RESISTANCE LOCUS8 (UVR8) (Cloix and Jenkins 2008.). The UVR8 acts specifically to mediate the UV-B response, together with the expression of genes to establish the UV-B protection (Jenkins 2009). Moreover, the UVR8 also mediates the expression of genes activated at low UV-B fluence level, showing consistency with their involvement in the photomorphogenic UV-B signaling pathway (Brown and Jenkins 2008). No other component is known to act specifically in the photomorphogenic UV-B responses. The transcriptome analysis revealed that a set of approximately 70 indentified genes are stimulated by UV-B under control of the UVR8. Among these several genes are known to have key roles in the UV-B protection mechanism, including those encoding principal enzymes of the flavonoid biosynthetic pathway, as well as DNA photolyases and enzymes involved in amelioration of the photooxidative damage (Jenkins 2009). The findings demonstrate that the *Arabidopsis UVR8* mutant shows severe necrosis under exposure to UV-B levels found in the bright sunlight, whereas it is indistinguishable from the wild type in the absence of UV-B (Brown and Jenkins 2008). The UVR8 regulates the expression of both ELONGATED HYPOCOTYL5 (HY5) and HY5 HOMOLOG (HYH) transcription factors at low UV-B fluence levels. The transcriptome analysis shows approximately the half of genes regulated by the UVR8 is also regulated by the HY5 transcriptor factor, but this is an underestimate and does not take into account the functional redundancy between HY5 and HYH (Brown et al. 2005). Further analysis, however, suggests that the HY5 and HYH transcription factors may regulate all the genes of the UVR8 component, and therefore are pivotal downstream

effectors of the UVR8 signaling pathway. In fact, the HY5 is evidently a very important regulator of the UV-B responses because the *HY5* mutant, similar to the *UVR8* mutant, is very sensitive to UV-B, while the *HYH* mutant is less sensitive indicating that it has a subsidiary role (Brown and Jenkins 2008). These findings demonstrate that the UVR8 is a key regulator of the UV-B protection and therefore helps to promote the survival of terrestrial plants exposed to UV-B radiation (Jenkins 2009).

Another important component of the low UV-B signaling pathway is the CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1) (Oravecz et al. 2006). Contrarily to UVR8, the COP1 represses the expression of photomorphogenic genes and the plant development in the darkness. The COP1 acts as an E3 ubiquitin ligase, destroys HY5 and other positive regulators of the expression of photomorphogenic genes (Yi and Deng 2005). Following illumination, the COP1 is inactivated and moves slowly out of the nucleus, enabling the HY5 and other transcription factors to accumulate and promote the photomorphogenesis. In contrast to this function, the COP1 is a positive regulator of the UV-B responses such as the accumulation of flavonoids. Nevertheless, nearly half of genes regulated by the COP1 are controlled by HY5, indicating HY5 a key effector of the COP1 pathway. Both COP1 and HY5 transcriptor factors must act together in the nucleus to evoke the UV-B responses. Furthermore, the positive role of the COP1 seems not to be specific to UV-B because some evidences show a comparable function in several responses to the red light that require the involvement of the phytochrome B. With regard to this theory, the COP1 is required for the nuclear accumulation of the transcriptor factor PHYTOCHROME INTERACTING FACTOR3 (PIF3) in the darkness, although it does not mediate its destruction following the red and far-red illumination (Oravecz et al. 2006). Moreover, a more recent study showed that exposure to supplemental far-red (FR) light compared to red (R) light under UV-B radiation leads to a fast elongation growth and a phenolic accumulation in leaves of the silver birch seedlings (Tegelberg et al. 2004). Whether the COP1 acts positively in other light responses, however, still remains unknown (Jenkins 2009). On the other hand, both UVR8 and COP1 regulate many of the same genes and are required for the low fluence UV-B induction of the HY5 transcriptor factor expression which plays a central role in the regulation of genes involved in the photomorphogenic UV-B responses (Brown and Jenkins 2008). Although both UVR8 and COP1 seem to function in the same pathway, little information is available to explain their functional relationships. Since UVR8 is a UV-B specific component, it may have a direct action of the COP1 in UV-B responses. To explain this fact one possibility is that the UVR8 regulates the nuclear accumulation of the COP1 or vice versa, while another can be that the UVR8 recruits the COP1 into a complex involved in the regulation of the transcription by UV-B. The last hypothesis is supported by a recent study demonstrating that the UVR8 colocalizes with the COP1 and directly interacts with a UV-B-dependent manner (Favory et al. 2009). Besides these, the expression of some genes at low UV-B fluence levels occurs independently of the action of both UVR8 and COP1 components (Jenkins 2009).

According to data of A-H-Mackerness et al. (2001), the expression of genes by intermediate UV-B fluence levels (IF-UV-B) may be regulated partly by the enzymatic ROS formation after the specific UV-B induction, whereas the changes in mRNA levels of the high fluence (HF-UV-B) genes could be due to the formation of ROS as a result of the nonspecific damage to plant cells. However, it seems unlikely that sufficient ROS would be generated by the exposure of plants to the current ambient solar UV-B to cause the activation of the signaling pathway leading to biosynthetic responses; thus, presumably, the activation by ROS would not be UV-B specific (Jenkins 2009). Nevertheless, evidence exists for the involvement of ROS in some morphological changes and gene expression responses initiated by the UV-B radiation. Furthermore, the *Arabidopsis RADICAL-INDUCED CELL DEATH1* (RCD1) transcriptor factor is also involved in the UV-B signaling pathway. Interestingly, the expression of *RCD1* genes is

not significantly changed by the UV-B radiation. Previous study has shown that the SALT TOLERANCE (STO) protein is interacting with RCD1 in vitro being the mRNA level of the *STO* (*SALT TOLERANCE*) gene greatly increased in the *Arabidopsis rcd1-1* mutant after UV-B irradiation. However, the expression of UV-B-induced *HY5* and *CHS* (CHALCONE SYNTHASE) genes is partially inhibited in the *STO* mutant, subsequently, seems to be the RCD1, together with the STO, involved in the *Arabidopsis* UV-B signaling (Jiang et al. 2009).

The cotyledon curling in *Brassica napus* stimulated by both UV-B and H_2O_2 is also inhibited by ascorbate (Gerhardt et al. 2005). In addition, the exposure to relatively high fluence rates of UV-B decreases the abundance of transcripts of the *Arabidopsis LHCB1* gene that encodes the major chlorophyll binding protein of the chloroplast, and this response is inhibited by ascorbate as well as by a scavenger of superoxide radicals (A-H-Mackerness et al. 1999). Interestingly, supplementation of the ambient UV-B under greenhouse conditions increased the formation of CPDs and reduced the leaf area in *G. magellanica*, however did not cause lipid peroxidation being the modulation of the ascorbate content that counters the oxidative stress (Giordano et al. 2004).

The exposure to UV-B stimulates the expression of a set of genes normally induced in response to the pathogen attack, insect predation, and wounding (Stratmann 2003; Ulm and Nagy 2005). It also reduces the level of insect herbivory in a range of species, probably because of increased production of the secondary metabolites, proteinase inhibitors, and other molecules that deter the herbivorous insects (Ibañez et al. 2008). An explanation for the overlap in responses to UV-B, wounding, and pathogens is that the UV-B stimulates the accumulation of ROS and other signaling molecules (e.g., jasmonic acid, ethylene, salicylic acid) that mediate the wounding defense responses (Izaguirre et al. 2007; Demkura et al. 2010). Molecules mediating the responses of some UV-B-regulated genes have been reported (Izaguirre et al. 2003). Alterations in the induction of defense-related genes by the UV-B radiation have been observed in both ethylene *ETR-1* and jasmonic acid *JAR1 Arabidopsis* insensitive mutants (A-H-Mackerness et al. 1999; Jenkins 2009). Also a transgenic *Arabidopsis* plant expressing the salicylate hydroxylase was unable to accumulate salicylic acid and showed a reduced UV-B induction of the several *PR* genes (Surplus et al. 1998). The expression of genes related to the pathogenesis-related proteins (PR) and class I Endo-β-1,3-glucanases (IβGlus I) are also induced by the UV-B radiation (Kucera et al. 2003). The PR genes have been grouped as: (a) intermediate UV-B level genes (PR-5); (b) high UV-B level genes (like PR-1). The IβGlus I are also assigned to PR proteins and constitute the PR-2 family. In addition, it has been demonstrated that the UV-B-induced DNA damage seems to be related to induction of the IβGlus I genes, but not with the synthesis of flavonoids under high levels of UV-B radiation (Kucera et al. 2003). The involvement of ROS in defense signaling is well established and evidences show that superoxide generated by the plasma membrane NADPH oxidase seems to be involved in UV-B-induced regulation of some defense genes, either directly or through the production of H_2O_2 (A-H-Mackerness et al. 2001). In agreement with this assumption, it has been reported that both redox activity of the plasma membrane and cytosolic-free Ca^{2+} homeostasis are involved in the induction of gene expressions by UV-B and blue/UV-A wavelengths in *Arabidopsis* plants (Long and Jenkins 1998). Although the available data supports that ROS might be used by plants to modulate the expression of different genes in response to varying levels of UV-B, little information is available regarding the scope and nature of the ROS production and function in response to the solar UV-B radiation under natural growth conditions. However, the ROS are very dangerous to the cellular integrity and must be eliminated (Agrawal et al. 2009). Most plants scavenge the excessive amounts of ROS using a combination of enzymatic scavengers such as superoxide dismutase, ascorbate peroxidase and glutathione reductase, and nonenzymatic scavengers such as ascorbate, glutathione, carotenoids, tocopherols, and secondary metabolites (mainly flavonoids, hydroxycinnamic acids derivatives, and anthocyanins) (Xu et al. 2008).

Although it is clear that the UV-B radiation stimulates both defense and wound signaling, there is little information on how the UV-B activates components of the signaling pathways. Experiments in tomato indicate that the UV-B radiation initiates similar signaling processes to systemin, an 18-aminoacid peptide that stimulates the wound responses (Ulm and Nagy 2005). Although data suggests that the tomato systemin receptor might also function as a brassinosteroid receptor (Wang and He 2004), more recent evidences indicate otherwise (Holton et al. 2007). In fact, a better knowledge of the mechanisms involved in the signaling pathways can help to understand the functional roles of the solar UV-B radiation in the resistance of plants to environmental factors into the terrestrial ecosystems.

9 Reduced Solar UV-B: A Future Scenario?

Despite the influence that the ambient level of solar UV-B radiation can exert on the plant life, recent findings have shown that the increases of UV-absorbing tropospheric gases (e.g., ozone, SO_2, NO_2) and aerosols can reduce the amount of solar UV-B radiation reaching the Earth's surface (McKenzie et al. 2001). Thus, a further attention is needed to understand how the reduced solar UV-B can have an effect on the dynamics of ecosystems. Similar cues can occur when species originated from highland regions such as mountains (Ren et al. 2010), the Bolivian Altiplano (González et al. 2009) and the Tibet Plateau (Yang et al. 2008) or those from the equatorial regions that naturally receive high UV-B irradiances, are grown in lowland areas and/or high latitudes (Turunen and Latola 2005).

So far the ecological cost of terrestrial plant responses to the solar UV-B radiation has not been studied in detail. Clearly, some morphological and physiological responses must have a cost in terms of resources that in absence of the UV-B could have been allocated elsewhere (Snell et al. 2009). Under this perspective seems to be an interesting point to study the question *how the terrestrial plants respond to the solar UV-B radiation growing under UV-B-reduced irradiances*, because till now data on this topic are very scarce. Like morphological features, emerging findings revealed that the UV-absorbing compounds could be affected by the reduced solar UV-B (Ibañez et al. 2008; González et al. 2009). In this context, the removal of UV-B from the natural solar radiation causes large increases of the growth in *Glycine max* and *Cyamopsis* plants and a marginal increase in the *Vigna radiata* but did not affect the growth of *Vigna mungo* plants (Varalakshmi et al. 2003; Amudha et al. 2010). In addition, it has also been demonstrated that the photomorphogenic regulatory mechanisms, rather than the photosynthesis seems to play key roles in the observed metabolic changes upon exposure to the reduced solar UV-B (Kadur et al. 2007). In agreement with these findings, the prolonged treatment with chronic low doses of UV-B caused changes in the morphology, gene expression, and biomass redistribution without cessation of the growth and in absence of the stress symptoms (Hectors et al. 2007). In fact, the reduced solar UV-B induces probably a plethora of key enzymes into the metabolic pathways transmitting a general plant response, which under a future long-time solar UV-B-reduced scenario will probably affect the plant productivity, species competition, trophic interactions, and ultimately the structure of ecosystems.

10 Conclusion and Future Perspective

The enhanced UV-B radiation produced important physiological and morphological effects on the terrestrial plants, but most of these studies were carried out in greenhouses and growth chambers. Then the extrapolation and quantification of the observed indoor effects to field experiments is very complex, because they can reflect exacerbated responses of the plants and confuse the interpretation of physiological and morphogenic responses, as well as the molecular analysis at both individual species and ecosystem composition. In fact, much remains to be done to define and establish the effects of both increased and

reduced solar UV-B, as well as the signaling pathways to understand how they may be integrated to terrestrial plants growing in the natural environment. *However, although in the solar UV-B alchemy, each successive understanding produces a larger doubt, God does not play dice with the universe! (Einstein).*

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