Plant Life and Environment Dynamics

Sunita Kataria
Vijay Pratap Singh *Editors*

UV-B Radiation and

Plant Life and Environment Dynamics

This book series aims to publish volumes focusing on plant responses to changing environmental conditions. The series is cenrted on the theme of plant-environmnet interaction, ecosystem changes, plant physiology, various physio-biochemical and molecular mechanism of adpatation wokring within the plants. The book series also provides knowledge and understanding of plant's stess tolerance strategies such as ionomic transcriptomic, proteomic, phytohaormoes, cellular redox regulation, energy mentabolism, nanomateiral in plant protection and genomics of plants under environmnetal stress metabolomic approaches which are currently being used in order to protect plant life against adverse effects of changing environment. This series will cover book ideas focusing on all aspects of plant's responses to the change in the respective environment. The books published in this series are a useful source of information for academicians and researchers working in the field of agriculture, botany, agronomy, biotechnology, plant science, crop physiology, plant stress physiology, plant and environment interactions related courses.

Series plans to cover dynamics of plant-environment interaction via following broad themes:

(a) Abiotic stress and plant development

(b) Photosynthesis and energy metabolism

(c) Bio-stimulants and plant life

(d) Phytohormones in stress tolerance

(e) Cellular redox regulation (ROS, RNS and RSS), oxidative stress and antioxidant defense system

(f) Transcriptomics, Proteomics and Functional Genomics

(g) Ionomics: Uptake and Assimilation

(h) Nanomaterials and plant life

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UV-B Radiation and Crop Growth

Springer

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Preface

Recent measurements of ozone levels have led to concern that the stratospheric ozone layer is being depleted as a result of contamination with man-made chlorofluorocarbons. Consequently, the amount of solar UV-B radiation reaching on the Earth's surface is increasing. UV-B radiation has been shown to be harmful to living organisms, damaging DNA, proteins, lipids and membranes. Plants are at risk, which use sunlight for photosynthesis and are incapable of avoiding exposure to enhanced UV-B radiation. Thus, mechanisms by which plants may protect themselves from UV-B radiation are of particular interest. UV-B radiation can induce injuries to DNA, causes DNA mutations, inhibits photosynthetic processes, impairs membrane function and can cause lethal cell damage. Living organisms developed photoreceptors in order to respond to light and optimize growth. Photoreceptors absorb specific wavelengths of radiation, triggering a cascade of events, leading to biological responses. Some of the known photoreceptors absorb in the ultraviolet region. UV responses are ascribed to the sensing by cryptochromes (CRYs), phototropins (PHOTs), phytochrome A (PHYA) and UVB-RESISTANCE 8 (UVR8) as a UV-B-specific sensor. This book summarizes the main aspects of UV-B radiation on the plants at morphological, physiological and biochemical level, with particular emphasis on protective structures and defence mechanisms.

Total 16 chapters have been compiled in this book. The contents of chapters range from introduction to UV-B and their impacts on plant system in Chap. 1. For instance, topics ranging from regulation of seed germination under UV-B stress to response of whole plant are covered in this book. Chapter 2 discusses the UV-B radiations and its climatology. Although the emphasis on the regulatory role of UV radiation is less than its damaging nature, in Chap. 3 we have discussed the UV-B: Boon or Curse? UV radiation can play a harmful and regulatory role according to the environmental conditions. In this book, special emphasis has also been given to the photosynthetic performance of the crop plants in Chaps. 4, 11 and 12. Solar UV-B that affects primary producers in Aquatic Ecosystems is discussed in Chap. 5. Chapter 6 is about the effect of UV-B stress on crop research from past to new age. This book also presents the recent development in UVR8 discovery in Chap. 9 and the UVR8 signalling, its mechanism and integration with other pathways are discussed in Chap. 10. We have also mentioned the strategies in use to mitigate the adverse effects of UV-B stress by incorporating various approaches such as

exclusion of solar UV-B, seed pre-treatment with magnetic field or melatonin, in Chaps. 7 and 15. Chapter 8 discusses the alleviating role of phytohormones like salicylate and jasmonate on UV-B-induced inhibition of various physiological and biochemical parameters in higher plants.

The book also highlights the mechanism of action of these stress busters in order to increase their usefulness as a value-added product for stressed agriculture. The role of antioxidant enzyme machinery as a defensive feature has been broadly explained in Chap. 13 of this book. Moreover, one of the most significant consequences of an increase in the level of solar UV radiation is associated with the impact on the reproductive function of plants. Unexpectedly, little interest has been paid to the effect of UV-B on embryonic processes in plants. In Chap. 14, the effect of UV-B on sexual reproduction in the plants is discussed. Chapter 16 discusses both the direct and indirect effects of UV-B on terrestrial ecosystems and also on all the aspects of UV-B research, including the fundamentals of how UV-B's shorter wavelength radiation from the sun reaches the Earth's surface, along with its impact on the environment's biotic components and on human biological systems. Overall, we believe that this book will serve as an important repository for students and researchers for understanding the effects of UV-B radiations on the morphology, physiology of the plants and their potential use in agriculture. We also thank Springer International team for their generous cooperation at every stage of the book production. We believe researchers who work on plants tolerance to abiotic stress will find this book an essential reference.

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About the Editors

Sunita Kataria is working as women scientist in DST WOS-A Scheme in School of Biochemistry, Devi Ahilya Vishwavidyalaya, Indore, Madhya Pradesh, India. She has authored 58 papers in reputed international journals and 16 book chapters. Her H-index is 26; i10-index is 42 and has been serving as editor and reviewer of reputed international journals. Her area of research interest is management of UV-B stress in plants using physiological, biochemical and molecular approach with emphasis on antioxidant defence system, photosynthetic performance, nitrogen metabolism, reactive oxygen (ROS) and nitric oxide (NO) signalling and yield attributes. She has also worked on the alleviation of adverse effects of UV-B stress via exclusion of UV-B radiation from solar spectrum and magnetopriming of seeds in various crop plants. She has also identified the role of ROS NO and growth hormones in the signal transduction of magnetic field pre-treatment under abiotic stresses such as salt, water, heavy metal toxicity and UV-B stress.

Vijay Pratap Singh is working as an Assistant Professor, Department of Botany, C.M.P. Post Graduate College, University of Allahabad, India. Dr. Singh has obtained his D. Phil. degree from the University of Allahabad. He has authored 160 publications including book chapters and editorials in reputed journals. He has edited several books with Elsevier, Wiley, CRC Press, Nova Publisher, Studium Press, etc. His area of research interest is regulation of abiotic stress in plants with special emphasis on nitric oxide, hydrogen sulphide, reactive oxygen species and phytohormonal signalling. Dr. Singh is also serving as editor and reviewer of reputed international journals.

Introduction to UV-B Radiation

1

Renuka Sharma and Namita Singh

Abstract

Ozone is a gas that exists in the Earth's atmosphere. It protects all living things on Earth's surface from the sun's UV-B and UV-C radiations. The majority of UV-B light is absorbed by stratospheric ozone layer, although some of it does reach at the Earth's surface. Human activities may cause significant decrease in stratospheric ozone. Increased UV-B radiation can lower plant growth, photosynthesis, biomass or total dry matter output as well as marketable yield. A decrease in phytoplankton production has been linked to an increase in UV-B exposure. So, in this chapter, we will look at how UV radiation affects terrestrial and aquatic life.

Keywords

Solar radiations · UV-B · Ozone · Plants · Photosynthesis · Phytoplanktons · Zooplanktons

1.1 Introduction

The Sun is responsible for the evolution of life on Earth as well as its continuing existence. Sun produces a lot of radiation of various wavelengths. The amount and nature of electromagnetic radiation received from Earth are completely reliant on the sun. The amount of energy obtained from the sun affects all physicochemical processes in the environment, in the oceans and at the Earth's surface. The Sun's infrared rays burn us, and we see through eyes that react to the visible portion of the

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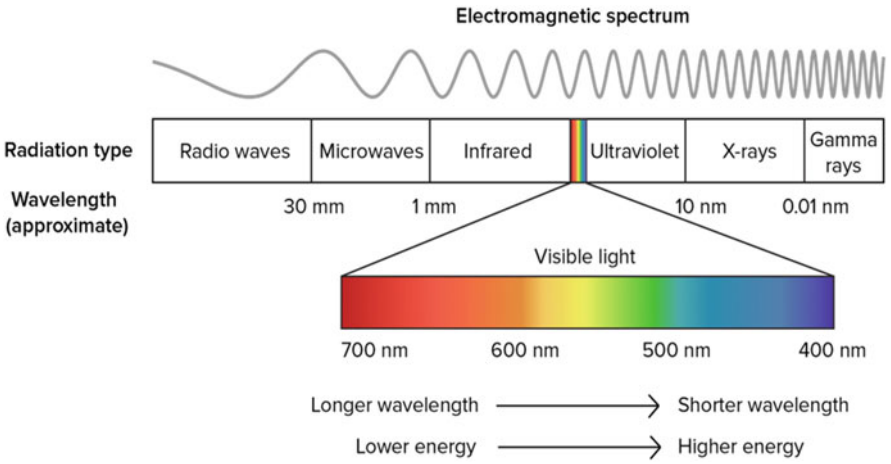

Fig. 1.1 The figure showing the electromagnetic spectrum (Adopted with permission from—electromagnetic spectrum png highres—REDjuvenator Light Therapy by World Leading Expert, Leanne Venier (catalyticcolor.com)

solar spectrum. More specifically, visible light is a required constituent of photosynthesis, the mechanism through which plants receive their energy and provide food for humans. The adverse effects of sunshine on biological processes, on the other hand, were almost exclusively attributed to exposure from the Sun's ultraviolet radiations (Diffey 1991).

Outside the Earth's atmosphere, the solar spectrum includes rays of a broad variety of wavelengths. The Earth absorbs a large portion of it. Just visible light and a portion of ultraviolet (UV) and infrared (IR) radiations pass into the atmosphere. In addition, the harmful effect of radiation increases as the wavelength decreases. Radiation is a form of energy that is often opaque to the naked eye. The electromagnetic spectrum varies from radio waves to gamma waves. The part of the electromagnetic spectrum ranging from the violet, or short-wavelength, end of the visible light continuum to the X-ray field is known as ultraviolet radiation as shown in Fig. 1.1. Ultraviolet (UV) radiation is invisible to the naked eye, but it may cause some objects to fluoresce, or release lower-energy electromagnetic radiations such as visible light, as it hits them. Many insects, on the other hand, can detect ultraviolet radiation. Ultraviolet radiation has wavelengths ranging from 100 to 400 nm (Lisle Punch and Wilkinson 1927).

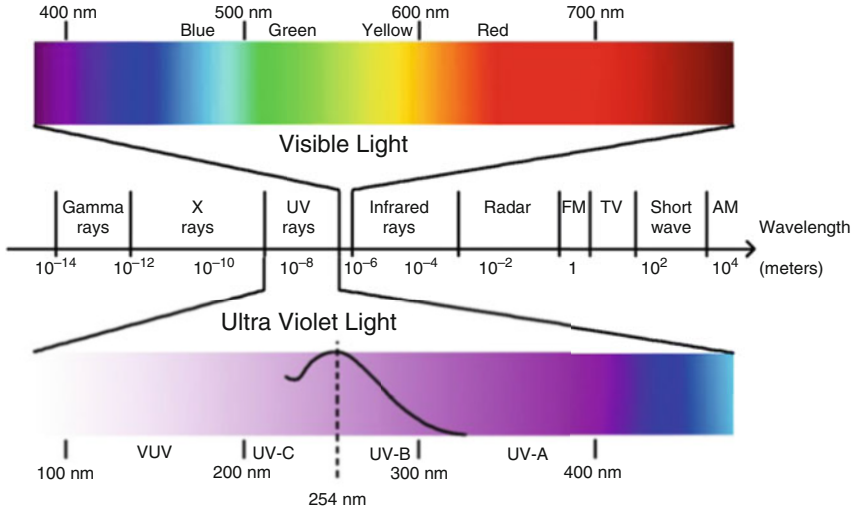

Fig. 1.2 Illustrated view of Electromagnetic wave Spectrum showing respective wavelength range in nm (source:Photoaging causes, prevention, signs, diagnosis & treatment (healthjade.net))

1.2 Types of UV Radiations

UV radiation is a type of non-ionizing radiation (NIR). Non-ionizing radiation is a type of radiative energy that, instead of generating charged ions as it passes through matter, has enough energy to excite it (Ng 2003). Ultraviolet (UV) radiation is traditionally classified into three bands:

UV-A (315–400 nm)—UV-A radiations are less energetic and less harmful as compared to other types of UVR. UV-A is not absorbed by the oxygen and ozone present in the atmosphere so reaches the Earth un-interrupted.

UV-B (280–320 nm). Most of the UV-B radiations are absorbed by the stratospheric ozone but some percent of UV-B is able to reach at the Earth surface.

UV-C (200–280 nm)—UV-C radiations are most energetic and most harmful that is why these are completely absorbed by the atmospheric ozone so does not pass through the atmosphere (Paul and Gwynn-Jones 2003).

Since important biological macromolecules, such as proteins and nucleic acids, absorb effectively in the UV-B region, any rise in this portion of solar radiation poses a possible danger to living organisms (Dean et al. 1993) (Fig. 1.2).

1.3 History of UV-B Radiation

For centuries, ancient civilizations believed that the sun was the source of illumination, vitality, health, and good fortune. However, their later generations felt unenlightened by the explanations, so they started to look for fresh thoughts, concepts,

and a search for comprehension. At the start of the ninth century, newer understanding and principles contributed to the recognition that sunshine is a multitude of wavelengths. Discovery of UV radiation took place before 1920 in that order. First of all, Sala (1614) discovered that silver nitrate crystals reacted to sunlight and become blackish when exposed to sunlight. Scheele (1777) discovered out as well, when he illuminated a sheet of paper with a prism and often saw a spectrum in the same as a different color appear. Ritter (1801) observed the unseen portion of the violet-to-red spectrum and named it chemical rays. Becquerel and Draper (1842) found that 240–400 nm produces a photochemical reaction. This was the first traceable UV radiation to be used spectrally. Electromagnetic waves, in 1865, were postulated by Maxwell. During the 1920s, a breakthrough in the field of solar spectrum studies developed the concepts of UV radiation, its properties, and its contribution to sunlight (Hockberger 2002; Rai and Agrawal 2017).

1.4 Ozone

Before going to discuss UV-B radiation, let us have a look at how ozone affects solar radiation and plant's nature. Ozone is extremely essential in our atmosphere since it shields all living creatures on Earth's surface from damaging solar UV-B and UV-C rays. However, it absorbs both terrestrial IR and solar UV radiations (Staehelin et al. 2001). The ozone layer is a critical component of the stratosphere, which is the portion of the Earth's atmosphere between 10 and 50 kilometers above sea level where temperature rises with altitude (Cicerone 1986). Ozone (O_3) is a gas found in the Earth's atmosphere, with 90% of ozone found in the stratosphere. The remaining 10% is present in the troposphere, although at a lesser concentration, and is referred to as the natural background. The increase in tropospheric ozone is mostly owing to the previous century's fast industrialization and usage of fossil fuels, which have resulted in greater emissions of ozone precursors such as volatile organic compounds or nitrogen oxide (Jimenez-Montenegro et al. 2021).

Ozone (O_3) may penetrate leaves via stomatal holes and cause plant damage. It can cause oxidative stress by producing reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2), which can actively engage in stomatal closure or opening in plants. The phytotoxic effects of ozone are discussed in detail, with a focus on secondary plant metabolism. For herbaceous plants and forest tree species, many ozone-induced genes, enzymes, and stress metabolites of antioxidative and phytopathological defensive responses have been identified. Ozone causes responses similar to those produced by viral and microbiological diseases (Hasan et al. 2021), (Sandermann 1996).

1.5 Effect of UV-B on Terrestrial Ecosystem

Terrestrial ecosystems include agricultural areas, agroecosystems, and less intensively managed lands such as forests, grasslands, savannahs, deserts, tundra, and so on (Caldwell et al. 1998). Terrestrial ecosystems contain the most active organic carbon in the biosphere and comprise biomes with widely varying climatic regimes and a varied collection of species suited to these environments (Ballaré et al. 2011). Although impacts on photosynthesis of higher plants and mosses are seldom observed in most field investigations, influences on growth and morphology (shape) of higher plants and mosses are frequently observed. Fungi and bacteria are usually more vulnerable to UV-B radiation damage than higher plants. However, the species range in their vulnerability to UV-B radiation damage, with some being harmed while others being extremely resistant (Caldwell et al. 2007).

1.5.1 Plants

Human activities can alter some atmospheric trace gases, which can have a direct impact on terrestrial plant systems. Increases in anthropogenically generated chlorofluorocarbons (CFCs), for example, can cause a decrease in stratospheric ozone and, as a result, an increase in ultraviolet-B radiation reaching the Earth's surface (Teramura et al. 1991; Kumar et al. 2016). Reduced stratospheric ozone concentrations enhance UV-B radiation. In contrast, ozone depletion has no impact on surface UVA radiation. Because ozone absorbs shorter UV-B wavelengths more efficiently than longer ones, ozone concentration influences not only total UVR but also the spectral makeup of the UVBR band. As stratospheric ozone decreases, more of the shorter UVBR wave lengths will reach the Earth's surface. Because shorter wavelengths inflict more biological harm than longer wavelengths, ozone depletion causes the atmosphere to become more transparent to biologically active radiation (Buma et al. 1997).

UV-B radiation has a wide range of direct and indirect effects on plants, including DNA and protein destruction, changes in transpiration and photosynthesis, and changes in growth, development, and morphology (Jansen et al. 1998). All the plants respond differently to UV-B; some are tolerant of the stress, while others become sensitive and cannot withstand it. To protect themselves from such environmental stresses, these plants will develop various defense mechanisms such as increased leaf thickness, increased flavonoids synthesis, stimulation of antioxidant formation, activation of reactive species to quench free radicals, and so on (Rai and Agrawal 2017).

1.5.1.1 Photosynthesis

UV-B must reach the leaf and be absorbed by chromophores associated with the photosynthetic machinery in order to have any direct or developmental impact on photosynthetic production (Allen et al. 1998). Some plant species' photosynthetic apparatus appears to be well protected from direct UV-B radiation exposure. The

optical properties of these species leaves seem to reduce the sensitivity of vulnerable objects to UV-B radiation. However, UV-B radiation has been confirmed to cause harm to Photosystem II and Rubisco (Kataria et al. 2014). Reduced photosynthetic power, RuBP regeneration, and quantum yield may be the secondary effects of this injury (Teramura and Sullivan 1994). In another studies, it also have been found that UV-B has a negative impact on several thylakoid membrane components. Photosystem II's functioning is most easily harmed. The quantity and activity of ATP synthase and 1,5-ribulose bisphosphate carboxylase have also decreased significantly (Kataria et al. 2014). Photosystem I and the cytochrome b/f complex, on the other hand, are significantly less impacted. Furthermore, after UV-B treatment, the chlorophyll content of leaves may decrease. Because of the abrupt reduction in numerous activities that carry out various partial reactions of photosynthesis, UV-B has a greater impact on both maximal photosynthetic capacity and light-limited quantum yields than each component on its own (Strid et al. 1994).

1.5.1.2 Growth and Development

UV-B-sensitive plants' growth properties, such as plant height and leaf area, are decreased to varying degrees, depending on plant type and cultivar (Tevini and Teramura 1989). Increased UV-B radiation can reduce biomass or total dry matter production, as well as marketable yield, at the plant level. A vast number of studies have been conducted across the world to investigate the effects of increased UV-B radiation on plant development (Zlatev et al. 2012). Plant height, leaf volume, flowering pattern, etc., are the growth parameters which are also affected by the UV-B radiation exposure (Bornman and Teramura 1993; Caldwell et al. 2007).

1.5.1.3 Nucleic Acid

UV-B photon absorption by DNA results in the production of cyclobutane pyrimidine dimers (CPDs) and, to a smaller extent, pyrimidine (6–4)-pyrimidinone dimers [(6–4) photoproducts]. DNA alterations, in addition to being mutagenic, affect cellular metabolism. Both RNA-and DNA-polymerase are inadequate to read through unrepaired dimers, causing gene transcription and DNA replication to be halted. Repair of UV-B-damaged DNA is mostly accomplished by light-dependent photoreactivation (Britt 1996). UV sensitivity is seen in Arabidopsis mutants defective in light-dependent repair of CPDs (Landry et al. 1997) or (6–4) photoproducts (Jiang et al. 1997). Photolyases reverse dimerization, returning the bases to their original state (Sancar 1996).

1.6 Effect of UV-B on Skin

Daily sun exposure offers numerous health advantages. Excessive solar UV radiation exposure (including UVA and UV-B) can, however, have negative health consequences, including skin cancer (Huang and Chalmers 2021), erythema (sunburn), and tanning (Karentz and Lutze 1990). UV radiation is a potentially hazardous physical element that can cause skin tissue damage. UV rays alter skin cells'

intracellular redox balance, increase inflammation, limit cell growth, and can even cause cell death (Atalay et al. 2021).

There is compelling evidence that sunlight causes each of the three major forms of skin cancer: melanoma, basal cell carcinoma (BCC), and squamous cell carcinoma (SCC) (Armstrong and Kricker 2001).

When UV light penetrates into DNA, it can produce cross-linking of the pyrimidine bases, thymine, and cytosine. Uracil dimers can also be formed by double-stranded RNA. 6,4-pryimidine-pyrimidones and Cyclo-butane pyrimidine dimers and are the two most frequent UV-B products. These premutagenic lesions change the structure of DNA, inhibiting DNA polymerases and halting cell replication (Holick 2016; Pfeifer and Besaratinia 2012).

The synthesis of vitamin D is the only well-established positive impact of solar ultraviolet radiation on the skin (Diffey 1991). Because vitamin D is vitally necessary for the formation and maintenance of a healthy skeletal structure in humans, people who do not receive enough vitamin D nourishment from their food must obtain this important hormone through skin exposure to ambient sunshine (Maclaughlin and Holick 1985). Provitamin D in the skin is photolyzed to previtamin D, a thermally labile intermediate that progressively transforms into vitamin D when exposed to sunshine. Once produced, vitamin D enters the bloodstream and is hydroxylated in the liver to create 25-hydroxyvitamin D and subsequently in the kidney to form the physiologically active form, 1,25-dihydroxyvitamin. It is 1,25-dihydroxyvitamin D that is responsible for increasing the efficiency of dietary phosphorus and calcium absorption in the intestines. Furthermore, this hormone mobilizes stem cells to become osteoclasts, which are bone cells essential for mobilizing and remodeling calcium reserves from bone (Webb and Holick 1988).

The acute effects of UV on the eyes include the development of photoconjunctivitis and photokeratitis, both of which are disagreeable but typically reversible and easily avoided by wearing proper eyewear. Chronic eye effects include the development of pterygium and squamous cell carcinoma of the conjunctiva, as well as cataracts. A review of many research shows that there is enough proof to support acute ocular stimulation to photokeratitis, but we know less about the consequences of chronic exposure. While there is adequate evidence that UV-B can develop cortical and posterior subcapsular cataracts (PSC) in laboratory animals, there is insufficient evidence to correlate cortical and PSC cataracts in people to chronic ocular UV-B exposure (World Health Organization 1994).

1.7 Effect of UV-B on Aquatic System

Marine waters encompass 71% of the Earth's surface and account for one-third of global production. Swimmers (nekton), bottom-dwellers (benthos), and drifters are the three categories of creatures that live in fresh water or the seas (plankton). Plankton can be phytoplankton (plants) or zooplankton (animals). Icthyoplankton,

which are the floating eggs and larvae of many fish species, are included in zooplankton (Diffey 1991).

Phytoplankton receives their energy from sunshine and, as a result, dwell in the upper 100 meters of water, where enough sunlight may enter (termed as the euphotic zone). Since zooplankton relies heavily on phytoplankton for nourishment, they, too, live in the euphotic zone (Diffey 1991).

In aquatic environments, solar radiation is an important ecological element. It regulates water column mixing, thermal stratification, and, as a consequence, the vertical distributions of respiration gases, nutrients, and phytoplankton production (Williamson et al. 1994).

1.7.1 Phytoplanktons

Human activities may result in a 16% drop in stratospheric ozone. The concurrent rise in solar UV-B radiation accessing the Earth's surface may have a negative impact on phytoplankton, which constitute the foundation of the food web in marine and estuarine environments (Worrest et al. 1981). The impact of UV-B radiation on phytoplankton will receive special attention since they are the principal producers in most aquatic ecosystems and hence create a majority of the organic carbon stores that support the whole food chain plants (Holm-Hansen et al. 1993). A rise in UV-B radiation is linked to a drop in phytoplankton production. UV-B light influences a variety of biological activities, including photosynthesis, nitrogen metabolism, growth rate, motility, and phytoplankton direction (Nielsen et al. 1995).

Phytoplanktons are affected by UV-B in the same manner as like terrestrial plants. One of the most well-studied impacts of solar UV-B on phytoplanktonic organisms is the reduction of photosynthetic rates, which has been found in a variety of settings, including temperate, tropical, and polar region conditions. Another impact of UV-B that has received special attention in phytoplanktonic organisms is the disruption of genetic material caused by the production of cyclobutane pyrimidine dimers (CPDs), primarily thymine dimers – T< > T (Helbling et al. 2001).

A number of the study show that natural UV-B sunlight could only be detected down to around 1–2 m, and there was no influence on phytoplankton motility at this level. These findings suggest that plankton at depths greater than around 1 m are less impacted by UV-B radiation than species that are continually near to the water column's surface (Nielsen et al. 1995).

1.7.2 Zooplanktons

A previous research on zooplankton has found that excessive levels of UV-B exposure can result in significant mortality (Al-Aidaroos et al. 2015). The mortality rate of zooplankton is frequently lower in zooplankton that contains photoprotective chemicals. These molecules may include pigments like astaxanthin generated from dietary plant carotenoids, melanin, and mycosporine-like amino acids with UV-A

and UV-B absorption peaks. The existence of these photoprotective chemicals shows that regardless of recent anthropogenic increases in UV-B, aquatic species appear to have adapted in nature to the negative selection pressures connected with harmful short-wavelength ultraviolet irradiance (Williamson et al. 1994).

1.8 Conclusion

The amount and nature of the electromagnetic radiation received by the Earth are entirely dependent on the Sun. We are burned by the Sun's infrared radiation, and we see via eyes that respond to the visible section of the solar spectrum. The wavelengths of ultraviolet light range from 100 to 400 nm. Ozone is a gas that exists in the Earth's atmosphere. It protects all living things on Earth's surface from the sun's UV-B and UV-C radiations. Troposphere ozone may enter leaves through stomatal pores and cause plant harm. By generating reactive oxygen species (ROS) such as hydrogen peroxide, it can induce oxidative stress. The majority of UV-B light is absorbed by stratospheric ozone, although some of it does reach the Earth's surface. Increased UV-B radiation can lower photosynthesis, plant biomass or total dry matter output, as well as marketable yield. Some plants will evolve a variety of defensive strategies, including increased leaf thickness and flavonoid production. Human activities may cause a 16% decrease in stratospheric ozone. A decrease in phytoplankton production has been linked to an increase in UV-B exposure.

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UV-B and Its Climatology

2

Anshu Rastogi, Saurabh Yadav, Pragati Kumari, and Rakesh Kumar Sinha

Abstract

The UV-B radiations are an important part of electromagnetic radiations that penetrate the Earth surface and thus the life forms on Earth are adapted to it. For some physiological processes, it is necessary in certain amounts such as vitamin D synthesis in animals and some of the plants have shown higher photosynthetic activities under certain amount of UV radiations, but excess of it is harmful for plants or animals. To understand the amount of UV-B radiations reaching Earth's surface, understanding of its climatology is important, the information about climatology is also used for the estimation of UV-B radiations. Thus, this chapter discusses the UV-B radiations and its climatology.

Keywords

UV-B radiations · Zenith angle · Albedo · Reflectance · Scattering · Ozone

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2.1 Introduction

Atmosphere is a major factor for the existence of the life on Earth. Atmosphere protects the living being on Earth from high-energy-containing electromagnetic waves by stopping them before it reaches the Earth. Most of the ultraviolet (UV) radiations are stopped by atmosphere before it reaches the surface of the Earth. According to wavelength, the UV radiations are grouped in three clusters such as UV-C (ranging from 100 to 280 nm), UV-B (ranging from 280 to 315 nm), and UV-A (ranging from 315 to 400 nm). The UV-C region is strongly absorbed by ozone and molecular oxygen (at shorter wavelengths) and does not reach the Earth surface, whereas a very small part of UV-B and a large portion of UV-A reaches to the Earth surface (Fig. 2.1). The UV-B part of the electromagnetic radiation is proved to be an important environment concern, as it has shown to be significantly harmful to plants and animals. The other materials such as plastics and paints react adversely to the high energy from UV-B (Gallagher et al. 1997). An increases in the

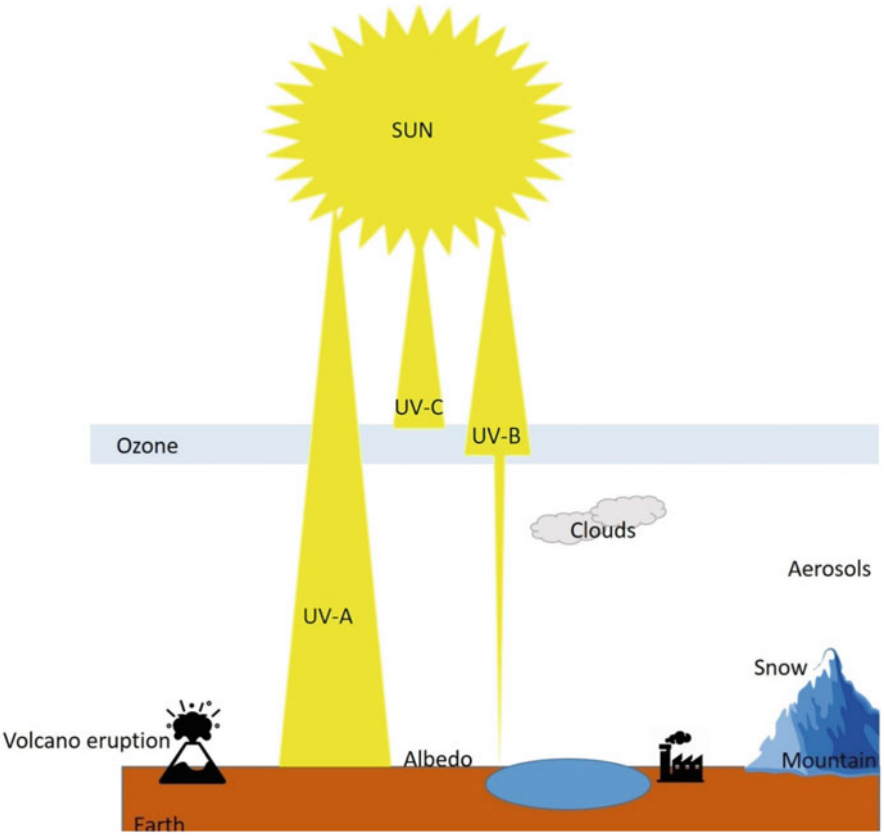

Fig. 2.1 Some of the atmospheric factors influencing the surface ultraviolet radiations

proportion of UV-B irradiance due to ozone depletion is a serious environmental concern, as the higher proportion of UV-B may adversely impact several land species, such as the phytoplankton in the oceans (Cullen and Neale 1997), nitrogen-fixing bacteria in rice field (Banerjee and Hader 1996), food crops (Fatima et al. 2021; Kataria et al. 2021a, b), forests (Laakso and Huttunen 1998), weeds (Rastogi and Pospisil 2013), and aquatic ecosystems (Pienitz and Vincent 2000; Clair et al. 2001). Thus, due to the increasing impact of UV-B radiation on Earth surface, it is very much needed to understand its climatology. In this chapter, our focus will be on the measurement and modeling of surface UV-B along with the climate variables that control the UV-B radiations.

2.2 UV-B Measurements

For several years, measurement of UV radiations was carried out through the spectroradiometers, but with time, the need for the more easy and frequent requirement of UV radiation measurements leads to simpler instrument development (Schmalwieser et al. 2017). In order to provide information to general public, different UV index were developed around the world, but to have a common understanding, a standard UV index was established in 1995 with an effort from World Health Center (WHO), World Meteorological Organization (WMO), and International Commission on Non-Ionizing Radiation Protection (NCNIRP). The standard UV index is calculated by measuring solar spectrum (in W $(m^2\ nm)^{-1}$) which is integrated from 250 to 400 nm and then divided by 0.025 W m^{-2} to get a unit-less number. Since 1988, the World Ozone and Ultraviolet Radiation Data Centre (WOUDC) started to keep the records of UV index from different data stations around the world. Figure 2.2 shows the location of meteorological stations collecting UV dataset around the world.

The simplified instruments such as broadband UV-B filter radiometers are distributed around the world and collected the data for decades now (Weatherhead et al. 1997). There are several multichannel filter instruments that are also being used to estimate biologically effective UV irradiance (Dahlback 1996). Usually, in instruments, the detectors are programmed to match a particular action spectrum, typically the erythemal spectrum (Fig. 2.3). Total Ozone Mapping Spectrometer (TOMS) and UV-A reflectivity at 380 nm are being used for the measurements of total atmospheric ozone as well as the backscattered and reflected radiations at several wavelengths are also being used to infer surface UV-B irradiances (Lubin et al. 1998; Herman et al. 1999). The advantage of the use of satellite data sources is the possibilities of the estimation of UV radiations where it is not possible to directly measure it.

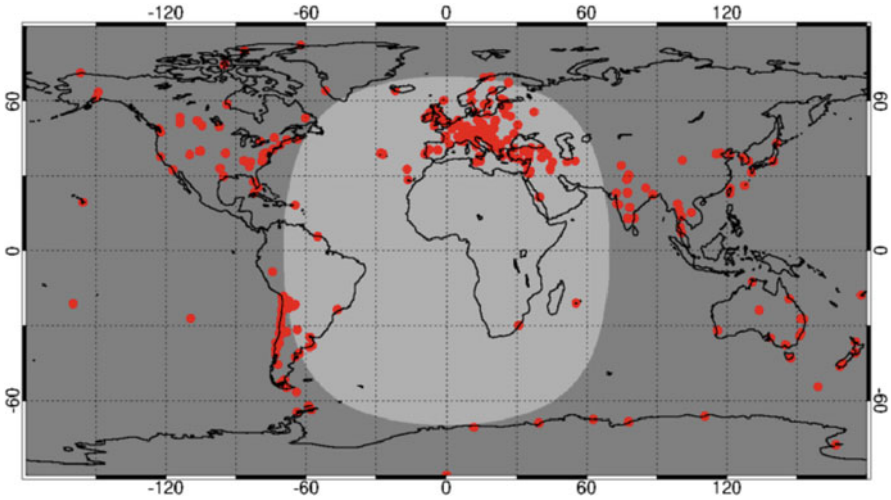

Fig. 2.2 Map showing the Meteosat second-generation data collection area in light gray and the locations of meteorological stations measuring UV-B radiations in red dots. Map taken from https://www.temis.nl/ (accessed on 28 August 2021)

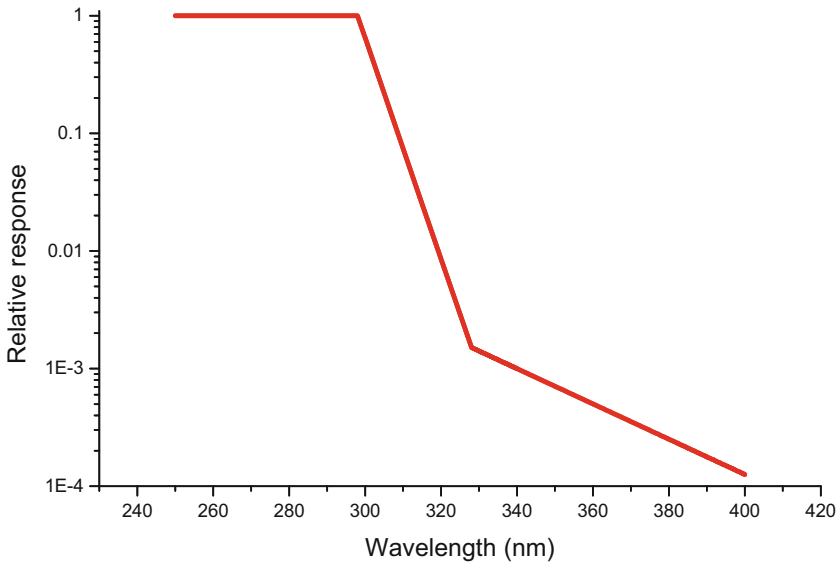

Fig. 2.3 The erythema action spectrum

2.3 UV Irradiations and Its Dependency on Ozone and Other Climate Variables

Outside the Earth's atmosphere, the UV radiations are found to be relatively constant with time, except some variation (less than 1%) due to solar rotation period (27 days) and solar cycle (11 years) (Lean et al. 1997). However, the UV radiations reaching the Earth's surface are impacted by numerous factors such as solar zenith angle, ozone, and other atmospheric particle absorptions, clouds aerosols, and scatterings. Among all, ozone is the most important UV radiation absorber that absorbs about 99% of the UV radiation below 298 nm, whereas the absorption and scattering by aerosol and other air molecules are independent of wavelength (Tarasick et al. 2003). Although several other atmospheric gases such as HNO_3, SO_2, CH_2O, and NO_2 absorb in UV spectral region, only SO_2 from volcanoes or smokestacks is able to be sufficiently quantified by UV spectroradiometers (Kern et al. 2012).

The ozone attenuates most of the UV-B radiations, but the solar zenith angle is also an important factor which determines at large scale the UV-B irradiance reaching the Earth surface. As the solar zenith angle determines the length of the path of the solar radiations passing through the ozone layer along with other particles in Earth's atmosphere, this indicates that the average UV-B irradiance reaching the Earth's surface is much less at mid-latitude and polar sites than at the tropical regions. The position of sun during different seasons influences the UV-B irradiation, where due to longer path length of solar radiations, the variation in UV-B is more in winter than in summer.

The another important factor influencing the UV-B irradiation is the cloud cover. The clouds reduce the UV-B radiations almost uniformly across the spectrum. This is due to cloud droplet sizes which are large for the UV and visible wavelengths. In fact, the Rayleigh-scattered back by the atmosphere to the ground is greater in UV-B region than the scatter light above the cloud, in respect to the visible radiations (Josefsson and Landelius 2000). With very heavy cloud covers an attenuation at shorter wavelengths can be observed, due to multiple scattering which significantly increases the path length of the UV-B radiations through the clouds due it the aerosols and ozone present in clouds deck become more important in reducing the UV-B radiations reaching the Earth's surface (Mayer et al. 1998). But when the clouds get broken, an increase in UV-B radiation can be observed which is due to a high proportion of total radiations reaching to the Earth's surface due to non-uniform scattering and reflections, which may lead to higher irradiations at certain locations than the clear sky conditions (Calbó et al. 2005).

As may be expected, UV irradiance increases with an increase in altitude. This increase is significant because of reduction in scattering and aerosol absorption phenomena, whereas the snow cover also impacts it. With high altitude, the direct flux increases, while the diffuse flux decreases, which results in the increase of net flux (Krotov et al. 1998). However, due to the variability of influencing factor such as aerosols, snow cover, ozone, etc., the variation of UV irradiance with altitude is complex and varies from site to site (Seckmeyer et al. 1997).

The aerosols are a general term that consists of several molecules which may vary and lead to complex relationship with UV-B radiations. For example, the erythemal UV irradiance was observed to be reduced by 5% in the presence of volcanic aerosols (Tsitas and Yung 1996). The dust and smokes are one of the largest influencer in Africa and South America, which restrict the total irradiance and may exceed 50% reduction (Herman et al. 1999). The percentage of UV irradiance reduction is dependent on the absorption properties of the aerosols. The aerosols present in industrial areas such as India, China, and North America where a lot of sulfates or other industrial pollutants are present are able to absorb the UV radiations and thus reduce the total UV-B radiations reaching the Earth's surface.

The ground albedo is another factor which influences the total surface UV-B irradiance, due to the fact that the Earth atmosphere reflects back some of the radiations which tends to reach the Earth's surface. The Earth atmosphere that consists of air molecules, cloud droplets, and aerosols reflects radiation by scattering. The snow cover greatly influences the total UV-B radiations, as the reflectivity from snow-free surfaces ranges from 0.02 to 0.08 (which is considerably very low), while in the presence of snow and ice, the Earth surface reflectivity increases to 0.2 and may reach even more than 0.95 (i.e., considered to be very high). An increases in downwelling UV irradiances over snow-covered surfaces may clearly lead to an increase in total irradiance. However, the major influencing factor is upwelling radiation which is far more higher than the snow-free surface. In snow-free surface, the upwelling radiation is only 1–2% of the downwelling irradiation, whereas over snow-covered surfaces, it may increase to 50% or more. This results in a higher percentage of UV-B radiation on Earth which can be perceived by animals or plants of the locality (Mckenzie et al. 1999). The albedo at Antarctic snow was observed to be the highest with 0.96–0.98 value, with a flat spectral reason between 300 and 400 nm (Grenfell et al. 1994), where the overall effect is wavelength-dependent. The diffused component of atmosphere in the UV region varies also with surface orientation and wavelength (Grant and Heisler 2000).

2.4 Models for UV-B Radiation Estimations and Predictions

Montreal Protocol is an environmental agreement between 198 UN member states to regulate the manufacturing and consumptions of several chemical substances which may result in the depletion of ozone layer. After the implementation of the Montreal Protocol, a significant decrease in ozone-depleting compound was observed resulting in some improvement of ozone layer (Solomon et al. 2016). To have the idea about the global integrity of ozone layer and UV radiations reaching the Earth, some estimations are necessary as it is not physically possible to measure the UV radiations from every places. The physical processes which may impact the surface UV-B irradiance through the scattering and/or absorption of radiation by different atmospheric factors are complex but at the same time understandable as mentioned in the previous section. Thus, through the models, the surface irradiance may be calculated with some accuracy, if required input parameters are available. Due to this

fact, several atmospheric radiative transfer models have been developed for the purpose to estimate the UV-B radiations reaching Earth surface (Lipponen et al. 2020; Stamnes et al. 2010; VoPham et al. 2016). A number of the scripts related to different radiative transfer models are available in open sources. The input parameters are generally the environmental factors which influence UV-B radiations such as ozone layer depth, percentage and type of cloud covers, aerosols, surface albedo, etc. Direction of solar radiation is also an important factor in accuracy of UV-B prediction and it is usually through the zenith angle, whereas some of the models are azimuthal-dependent and therefore its accuracy depends on azimuthal angle.

The estimation of the diffused and direct irradiance is necessary for the accurate estimation of UV-B irradiance. The direct component allows for the atmospheric attenuation of the extraterrestrial solar flux, by $e^{-\tau(\lambda)\sec\vartheta}$, where ϑ is the solar zenith angle and τ is the vertically integrated optical depth. After the estimation of total surface irradiance through the model, the model integrates it over wavelength to provide a spectral weighting term, $w(\lambda)$, that is used to calculate the erythemal action spectrum or a filter response of UV-B radiation. The ozone absorption cross-sections, extra-terrestrial solar flux, Rayleigh cross-sections are the important parameters for the estimation of UV-B radiations. The accurate input of some environmental parameters, such as SO_2 content, ozone vertical distribution, or albedo has an smaller impact for most of the surface area, except some reasons like volcano-erupted area, or for certain wavelength where additional input may help to correctly estimate the UV-B radiations. The information about ice cover area or clouds is also important as it may make a significant impact on final output. The broken or non-homogenous clouds create a significant problem. If the ozone layer distribution is not known or correctly filled, the Umkehr effect may cause a significant error in UV-B estimation. Thus, the information about climatology is important for UV-B prediction.

2.5 Conclusion

The UV-B radiations are an important part of electromagnetic radiations that penetrate the Earth surface, and thus the life forms on Earth are adapted to it. For some physiological processes, it is necessary in certain amounts such as vitamin D synthesis in animals and some of the plants have shown higher photosynthetic activities under certain amount of UV radiations, but excess of it is harmful for plants or animals. To understand the amount of UV-B radiations reaching Earth's surface, understanding of its climatology is important, and the information about climatology is also used for the estimation of UV-B radiations. The UV radiations reaching the Earth's surface are impacted by numerous factors such as solar zenith angle, ozone and other atmospheric particle's absorptions, clouds aerosols, and scatterings. The measurements/estimations of different environmental factors ultimately help to better estimate the UV-B radiations reaching Earth. Thus, the ground

measurements are the necessary process for the validation of the data and estimation of the impact of different concentrations of UV-B on plants and animals.

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UV-B: Boon or Curse?

3

Kshama Rai, Deepanshi Jaiswal, Avantika Pandey, Madhoolika Agrawal, and S. B. Agrawal

Abstract

The origin of life was manifested by the regulatory role of ultraviolet (UV) radiation. UV radiation is a small portion of the solar spectrum possessing the ability to regulate the life forms on the Earth. The plants are inevitably bound to perceive all the incoming radiation. Excessive exposure to UV radiation causes significant changes in the overall performances of the plants. Initially, at the time of the emergence of life, UV radiation was meant to the cue for shaping the life forms as well as plants. Later with the wake of evidence related to ozone layer depletion, most of the studies quickly centred on the damaging effects of UV radiation on plants. The responses showed by the plants under higher UV radiation were also very convincing and vast (negative alterations in growth, morphology, physiology, biochemistry, genetics, and productivity of the plants). The depletion in the ozone layer poses a threat to life processes, including a reduction in plant height, root length, leaf size, internodes length, crop yield losses, and change in the quality of products and several genetic aberrations. However, the trend is reversing, and studies based on UV radiation's multi-faceted role have now been increased. More information regarding the acclimatory and regulatory roles of UV-B radiation has been demonstrated through mechanistic studies of the plants. These studies showed that apart from UV-B radiation's damaging and harmful nature, it can also induce certain changes in the plants' biochemistry, which causes tolerance against pathogens and herbivory. Earlier, UV radiation-induced synthesis of phenolic compounds led to the emergence of life from aquatic to terrestrial ecosystems. Later these polyphenolics, along with flavonoids, also act as antioxidative compounds and play a crucial role in

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secondary metabolite synthesis, which can be commercially extracted and used as drugs against several diseases. Excess exposure to UV-B radiation induces adverse effects such as malignant and/or non-malignant eye and skin tumours, cataracts, and other skin diseases. However, some studies advocate the beneficial role of UV radiation, including the biosynthesis of vitamin D and phytotherapy.

Although the emphasis on the regulatory role of UV radiation is less than its damaging nature, UV radiation can play a harmful and regulatory role according to the environmental conditions. UV-B effects also vary with species, altitude, latitude, time of the day, day of the year, cloud cover, and other meteorological conditions. Here, we review the regulatory, acclimatory, and damaging responses of plants against UV radiation, which could help understand the variable behaviour of UV radiation and could pave new insights related to the function of UV radiation and its exploitation for the benefits of the humankind and biosphere.

Keywords

Ultraviolet-B radiation · Solar spectrum · Reactive oxygen species · Signalling · Secondary metabolites · Medicinal compounds

3.1 Introduction

Solar light is a key environmental factor for all the ecosystems and plays a crucial role in regulating life on Earth. Ultraviolet radiation (UV) is an integral part of the total solar electromagnetic spectrum. It is also known for its role in the evolution of life on Earth (Rai and Agrawal 2017; Singh et al. 2019). It constitutes about 10% of the total solar spectrum. UV radiation is conventionally categorized into UV-C (200–280 nm), UV-B (280–315 nm), and UV-A (315–400 nm) (Fig. 3.1), but this categorization is arbitrary, and their properties show overlapping. UV-C is the most energetic, extremely harmful for life forms, and is strongly absorbed by oxygen and ozone (O_3). Hence, it is unable to penetrate through atmospheric barriers. In contrast, UV-A is the least energetic and can penetrate the atmosphere and reach up to Earth's surface. However, UV-B is comparatively less energetic than UV-C; therefore, it can penetrate through the biosphere and is also very deleterious. But, the stratospheric O_3 layer has UV-B absorbing capabilities, and ~95% of incoming UV-B radiation is absorbed by the O_3 layer (Takshak and Agrawal 2016; Rai and Agrawal 2017) (Fig. 3.1).

Beyond this, the O_3 layer is susceptible to many chemical compounds such as chlorofluorocarbons (CFCs), oxides of nitrogen (NOx), halogens, and other ozone-depleting substances (ODSs), which are involved in the depletion of the stratospheric O_3 layer. The anthropogenically emitted CFC-induced O_3 depletion was first observed by Molina and Rowland (1974), but first documentation related to O_3 layer depletion and the Antarctic ozone hole was put forward by Farman et al. (1985). McKenzie et al. (2007) suggested that 1% depletion in the O_3 layer causes

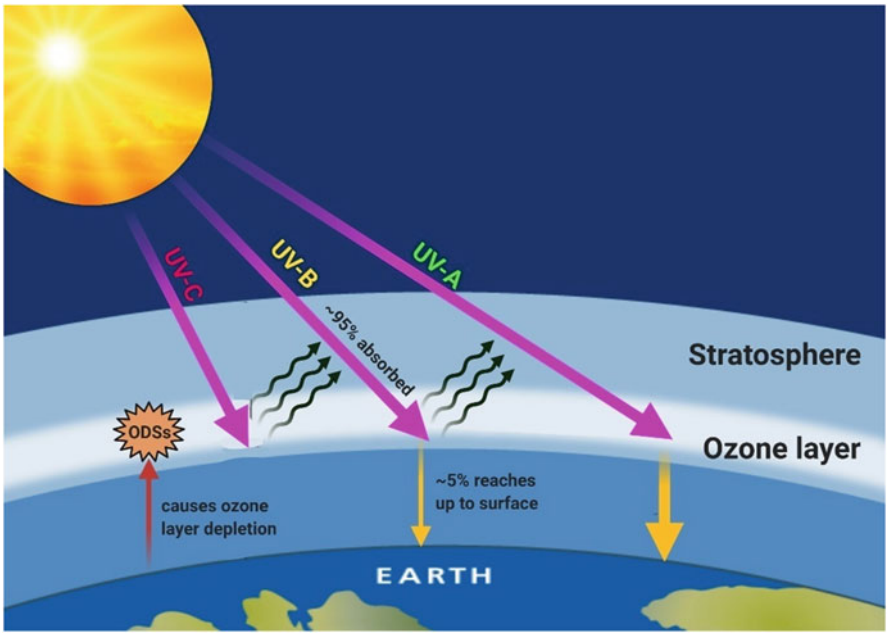

Fig. 3.1 The incoming ultraviolet radiation and status of ozone-related phenomenon

approximately 2% increase in biologically effective UV-B radiation reaching the Earth's surface. Soon after this discovery, the Vienna Convention (1985) was put forward, and the Montreal Protocol (1987) related to limit the emission of ODSs was signed. Chipperfield et al. (2015) in their studies up to 2013 reported the effective control in ODS's emissions and successful implementation of the Montreal Protocol. But, the implementation of the Montreal Protocol was not enough to heal the O_3 hole instantly. Despite the restrictions on ODSs, O_3 hole will take far more time in its full recovery. However, recently in 2015, scientists from the National Aeronautical Space Administration (NASA) predicted the full recovery in an ozone hole size to pre-1980s levels by 2075 (Takshak and Agrawal 2018). UV-B penetration and O_3 layer depletion are directly related to each other, UV-B radiation could be considered a peril to all life forms.

The awareness regarding the depletion in the stratospheric O_3 layer triggers the concerns associated with the incoming harmful radiations, including UV-B. An increase in surface-level UV-B radiation showed potential harmful impacts on life forms up to the ecosystem level. Plants are inevitably bound to entertain all the incoming harmful UV-B radiation. However, the plants of tropical areas receive higher UV-B due to lower solar zenith angle and comparatively thin O_3 layer (Paul and Gwynn-Jones 2003). Thus, they have orchestrated various mechanisms and structure to withstand, improve, acclimatize, and adapt to the stress created by surplus UV-B radiation. Plant responses to UV-B stress vary widely from species to species depending upon several factors such as the amount of UV-B doses, plant

species' characteristics, and environmental factors. Moreover, the amount/dose of UV-B is also affected by various governing factors such as the thickness of the O_3 layer, cloud cover, latitude, altitude, time of the year, and time of the day, as well as meteorological conditions (Takshak and Agrawal 2016). Similarly, plant characteristics also vary with family, genotype, cultivar, and variety.

Considering the stratospheric O_3 layer depletion and damages related to the photosynthetic organism's point of view caused by UV-B radiation, it is considered as an environmental stressor (Kumari et al. 2009b; Singh et al. 2012; Choudhary and Agrawal 2014; Takshak and Agrawal 2016). However, from the evolutionary perspective, UV-B radiation is considered regulatory in function; an assumption related to 'environmental stressor' is questionable (Hideg et al. 2013). It is known that prior to the formation of the O_3 layer, terrestrial plants inevitably perceived high solar radiation, including UV-B and may be UV-C. Therefore, the plant's genetic setup and responses have co-evolved with the ambient UV-B level (Prado et al. 2012). So it could be assumed that plants have evolved themselves with all necessary factors required for survival under the current UV-B level. Hence, UV- radiation would not be considered as an environmental stressor. Rather, lower UV-B radiation could be considered as regulatory in nature involved in several plants development and defence-related signalling. (Jenkins 2009). Several UV-B exclusion-based studies suggested that UV radiation could be considered as signalling factor which can express and/or repress several genes (Takshak and Agrawal 2016). But it is not always possible to identify a plausible reason to explain the underlying effects of UV-B radiation. Under natural conditions, terrestrial plants respond to several biotic and abiotic factors, including UV-B. Consequently, the effects of UV-B radiation on plants will be greatly influenced by these factors, which could be either aggravating or ameliorating the effects of UV-B on plants (Bruno et al. 2003). Here, we are focusing on both the harmful and regulatory roles of UV-B radiation on plants and mankind.

3.2 Why UV-B Is a Curse?

UV-B radiation exposure causes modifications in plant morphology, physiology, cellular organelles, pigments, metabolites, and phytochemical composition, which in turn indirectly induces alterations in other cellular processes, and consequently, growth and development of the plant (Fig. 3.2). Modifications in cell division and cell expansion cause changes in plant architecture and height; it may also accompany reduced leaf area and increase in leaf thickness. It is, therefore, also associated with changes in stomatal and trichome densities. Ultrastructural and anatomical studies revealed the UV-B radiation-induced changes in stomatal and trichome densities (Rai and Agrawal 2020), along with changes in epidermal cells, palisade, and spongy tissues (Hamid et al. 2019). Some studies advocate that UV-B exposure causes elongation in palisade cells and an increase in spongy mesophyll cells (Bornman and Teramura 1993). However, swelling of endoplasmic reticulum and

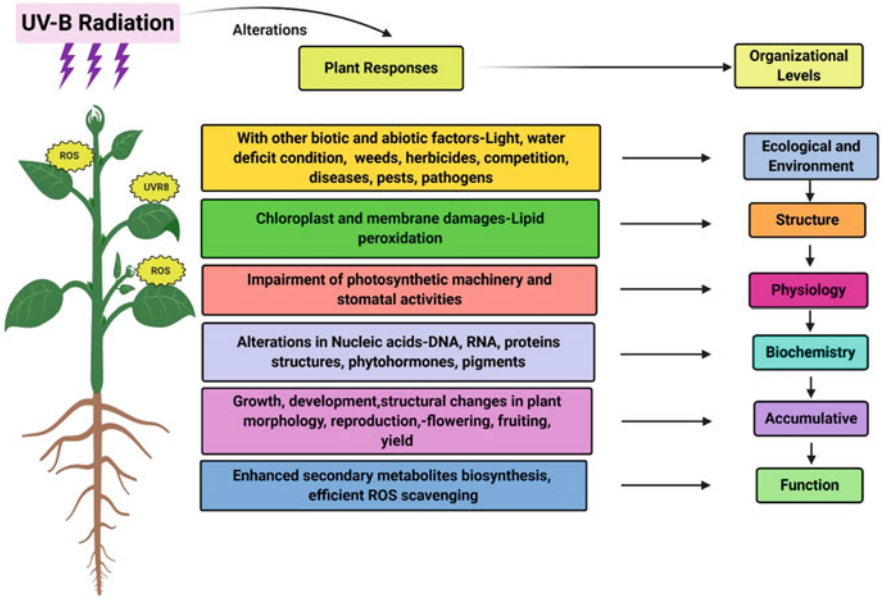

Fig. 3.2 Alterations caused by UV-B radiation on various organizational levels and the responses posed by the plant against these alterations (modified from Runeckles and Krupa 1994). *ROS* (reactive oxygen species)

thylakoid membrane was also observed in plants irradiated with UV-B radiation (Bornman and Teramura 1993) (Fig. 3.2).

Various studies revealed that UV-B causes damage to DNA, proteins, membrane lipids, and photosynthetic machinery, which further lead to photosynthetic impairment, disturbed photosynthate's assimilation and allocation, causing poor growth, development, and functioning of the plants (Fig. 3.2). UV-B radiation is also known to trigger the enhancement in reactive oxygen species (ROS) production creating oxidative stress. Several studies also reported yield losses associated with increased UV-B radiation (Table 3.1). These studies also advocate the degradation of photosynthetic pigments, negative alterations in the plants' structure, and overall morphology.

UV-B radiation induces pyrimidine-dimer formation, genetic mutation, alterations in total protein content, and membrane lipid (changes in chloroplast membranes reflect alterations in photosynthesis). UV-B exposure is likely to induce conformational changes in tubulin dimer and indirectly targets architecture and cell functioning. UV-B radiation is known to be deleterious for both photosystems (PS) I and II. But the effects of UV-B radiation are more prominent in PS-II. PS-II consists of two polypeptides (D1 and D2). UV-B radiation induces modification of D1 and D2 polypeptides and alterations in the number and activity of quinone-binding sites as well (Takshak and Agrawal 2016). Disturbances in these reactions might reflect subtle changes in the plant's net photosynthetic activities, which are associated with

Table. 3.1 Percent change (increase ↑ and decrease ↓) in yield attributes analyzed in several plants under the influence of UV-B

Plants	Cultivar/ Variety	UV-B dose	Yield parameters	% Change	References
Glycine max (L.) Merr.	Essex William	–	Seed yield	20% ↓ 10% ↑	Teramura et al. (1990)
Glycine max (L.)	Hai339 (H339) Heinong35 (HN35) Kennong18 (KN18)	13 kJ $m^{-2}day^{-1}$	Seed yield	5.5%, ↓ 16.9% ↓ 43.7% ↓	Liu et al. (2013)
Oryza sativa (L.)	Sasanishiki Norin 1	0.21 Wm^{-2}	Panicle number	12.6% ↓ 26.5% ↓	Kumagai et al. (2001)
Vigna radiata (L.) Wilczek	–	12.2 kJ $m^{-2}day^{-1}$	Potential yield	18% ↓	Rajendiran and Ramanujam (2004)
Brassica rapa (L.)	–	5.1 kJ m^{-2} 7.4 kJ m^{-2}	Seed yield	No change	Demchik and Day (1996)
Triticum durum (Desf.)	Horani	1.34 Jcm^{-2} to 6.33 Jcm^{-2}	Grain mass	15% ↑	Al-Oudat et al. (1998)
Lactuca sativa (L.)	–	UV-transparent	Harvestable fresh weight	31.5% ↑	Wargent et al. (2011)
Fagopyrum esculentum (Moench.)	–	–	Number of seeds	68% ↓	Gaberščik et al. (2002)
Fagopyrum tataricum (Gaertn.)	–	Spring 5.3 kJ 8.5 kJ Autumn 5.3 kJ 8.5 kJ	Seed yield	27%↓ 47% ↓ 18% ↓ 44% ↓	Yao et al. (2006)
Hordeum vulgare (L.)	Maris Mink RPr 79/4	–	Grain weight	17% ↓ 39% ↓	Mazza et al. (1999)
Triticum aestivum (L.)	Shimai 15	2.54 kJ $m^{-2}day^{-1}$	Grain yield (whole growth stage)	9.6% ↓	Yao et al. (2014)
Phaseolus mungo (L.)	–	0.5 Wm^{-2}	Pod number/ plant	40% ↓	Jayakumar et al. (2003)
			Seed number/pod	50% ↓	
			Seed weight	35.7% ↓	
Pisum sativum (L.)	–	7.1 kJ $m^{-2}day^{-1}$	Yield (g/plant)	18.9% ↓	Agrawal and Mishra (2009)
Gossypium hirsutum (L.)	–	4.8% 9.5%	Economic yield (g/plant)	69.3% ↓ 27.6% ↓	Gao et al. (2003)

(continued)

Table. 3.1 (continued)

Plants	Cultivar/ Variety	UV-B dose	Yield parameters	% Change	References
Zea mays (L.)	–	3.16 kJ $m^{-2}day^{-1}$	Grain yield	Reduced	Correia et al. (2000)
Raphanus sativus (L.)	PusaHimani	7.2 kJ $m^{-2}day^{-1}$	Yield (g/plant)	Reduced	Singh et al. (2012)
Vigna radiata (L.)	HUM 1 HUM 12	7.2 kJ $m^{-2}day^{-1}$	Yield (q/ha)	18.5% ↓ 10.6% ↓	Choudhary and Agrawal (2014)
Eclipta alba (L.) Hassk.	–	7.2 kJ $m^{-2}day^{-1}$	Achenes (no/plant)	43% ↓	Rai and Agrawal (2020)

CO_2 assimilation rate, and changes of sufficient magnitude can affect the productivity and yield of the test plant. Both the oxidizing as well as reducing sides of PS-II could be affected by enhanced UV-B radiation. The oxidizing side of PS-II involves the water-splitting complex (WSC)/oxygen-evolving complex (OEC) and P680. UV-B radiation induces the impairment of the reaction centre as well as the functional connection between OEC and P680(Hideg and Vass 1996).

UV-B radiation-induced plant growth responses could be either inhibitory or stimulatory, and it differs both quantitatively as well as qualitatively among species and cultivars. The decline in photosynthesis at the early stages showed the sensitive nature of the plant. UV-B exposure alters the photosynthates' allocation, which induces changes in biomass and biomass partitioning, flowering patterns, canopy height, and leaf characteristics. Sometimes the reduction in internodal length and increased epicuticular wax deposition was also observed in plants exposed to UV-B radiation.

UV-B radiation can also influence the reproductive processes of plants in many ways. Seed germination and seedling stages are particularly sensitive towards UV-B. This sensitivity is partially due to ontogeny and adaptive mechanisms adapted by the plants against elevated UV-B radiations. Llorens et al. (2015) suggested that anther dehiscence and pollen tube germination and penetration in stigma are also the few most vulnerable stages of flowering and pollination, which suffers UV-B stress. They also reported that UV-B radiation tends to delay the commencement of flowering in annual plants, which might be due to UV-B stress. Floral visits by bees and other pollinators also showed a reduction under elevated UV-B. Enhanced UV-B radiation exposure causes a decline in floral size, pollen viability, and fruit/seed set among several species (Hideg et al. 2013; Llorens et al. 2015). One of the most notable changes observed with respect to pollination and pollinators is alterations in the flowering time caused by UV-B exposure, which is responsible for the changes in fruiting and yield of the plants (Table 3.1).

3.3 Why UV-B Is a Boon?

Higher UV-B radiation has been reported creating stress to the plants and has long been recognized as a stressor. Conversely, recent studies based on plant-UV-B radiation research has experienced major overwhelming evidence and a paradigm shift from being a stressor to an environmental regulator (Jenkins 2009; Hideg et al. 2013; Llorens et al. 2015) (Fig. 3.2). Hideg et al. (2013) suggested that oxidative stress induced by UV-B exposure surely mediates ROS generation, DNA damage, and membrane degradation, but their products also play a major role in facilitating UV-B protection and considerably not hamper plant growth (Paul and Gwynn-Jones 2003). Prominent stress responses have been orchestrated by signalling and adjusting related genes (Fig. 3.3). The ROS-mediated signalling is associated with the actual stress and its acclimation processes. Several studies also reported that UV-B radiation-based responses can control gene expression, cellular functioning, growth, and development of plants. It has been observed that plants growing in ambient or near-ambient UV-B radiation is well adapted in many studies (Rai and Agrawal 2020). The lower doses of stress sometimes provided regulatory mechanisms to the plants to acclimatize against the prevailing stress. This low level of stress is termed as 'eustress' or 'good stress' (Hideg et al. 2013; Llorens et al. 2015). Conversely, the conditions in which the negative impacts of UV-B radiation dominate are termed 'distress' conditions. The scenario leading to eustress or distress responses of plants against UV-B radiation depends upon factors such as specific UV-dose, ambient photosynthetically active radiation (PAR), meteorological conditions, as well as the genetic setup of the plants. Plants exposed to higher doses of UV-B radiation or any other such factors show impairment in proper functioning. However, exposure to the stress for a smaller time period or in lower doses strengthens the plant and amplifies its tolerance abilities against the respective stress (Singh et al. 2020). Several studies have shown that UV-B exposure induces the enhanced biosynthesis of several primary and secondary metabolites such as phenols, flavonoids, anthocyanin, ascorbic acid, alkaloids, lignins, terpenes, fatty acids, stilbenes, and sterols (Fig. 3.3). It was evident that the emergence of plants from the aquatic to the terrestrial ecosystem was possible only because of the secondary metabolites synthesis and metabolites-mediated protection of the plants from harsh environmental conditions (Singh et al. 2020). UV-B radiation exposure has long been known as a potent elicitor of the phenylpropanoid pathway, which is one of the secondary metabolites biosynthetic pathways (Takshak and Agrawal 2016) UV-B exposed plants showed alterations in the enzymes and products associated with the phenylpropanoid pathway. This pathway is known to synthesize a vast array of phenolic compounds too. Exposure to UV-B radiation induces the enhanced production of various compounds, and the first enzyme involved in this pathway is phenylalanine ammonia-lyase (PAL). PAL is involved in catalyzing the conversion of phenylalanine to *trans*-cinnamic acid. Chalcone synthase (CHS) utilizes malonyl CoA and 4-coumaroyl CoA to produce chalcones. Isoflavone synthase (IFS) plays a role in root nodulation and plant defence. Isoflavone reductase (IFR) catalyzes the phytoalexin biosynthesis associated with plant defence;

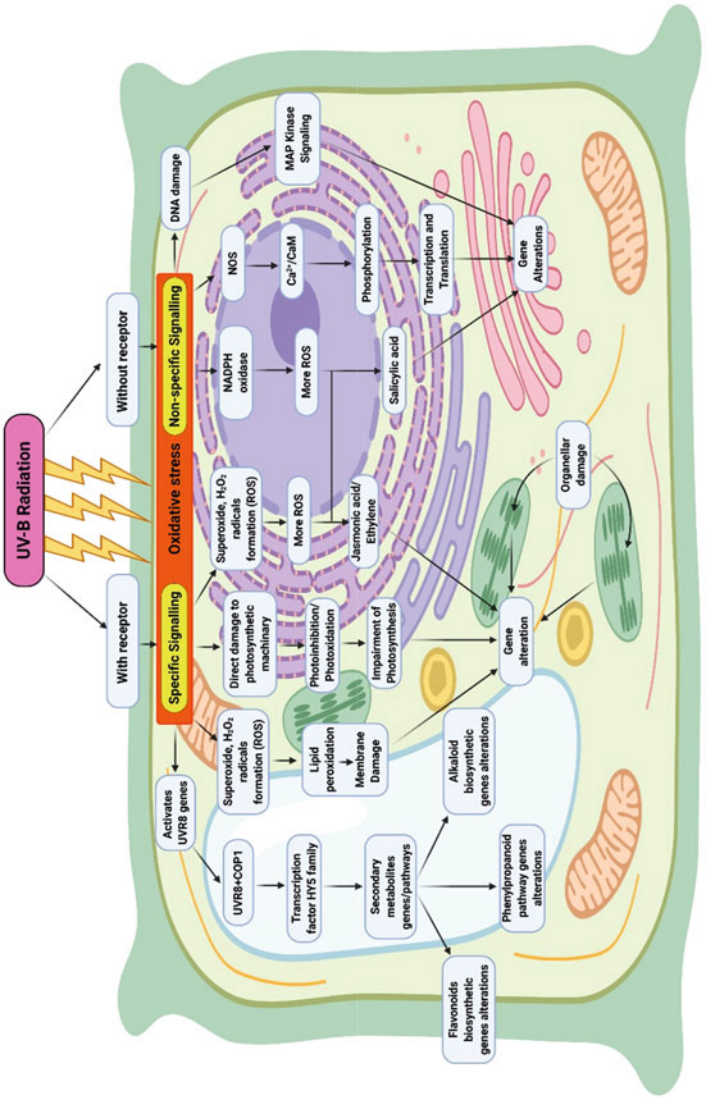

Fig. 3.3 A schematic diagram of UV-B radiation-induced oxidative stress and related signalling pathways involved in plant functioning modified from the processes explained by Mackerness et al. (2001). *UV-B* Ultraviolet-B, *ROS* reactive oxygen species, *NOS* nitric oxide synthase, Ca^{2+} Calcium ion, *CaM* calmodulin, *MAP* mitogen-activated protein, *UVR8* UV Resistance Locus8, *COP1* Constitutively Photomorphogenic1, *HY5* Elongated Hypocotyl5

dihydroflavonol (DFR) is the first enzyme involved in anthocyanin biosynthesis, and flavanone-3-hydroxylase (F3H) plays a crucial role in anthocyanin as well as flavonol biosyntheses. Besides these, many other enzymes are widely studied against various artificially supplemented UV-B exposure-based studies and found mostly

upregulated in plants (Ravindran et al. 2010; Agati et al. 2012; Takshak and Agrawal 2014a, b, 2015a, b, 2018; Jaiswal et al. 2020) (Fig. 3.3).

Beyond metabolites, the production of various enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), few peroxidases (POX), and glutathione reductases (GR) was also enhanced in order to scavenge excess ROS formed under UV-B stress. Many plants scavenge excessive ROS using enzymatic as well as non-enzymatic scavengers such as ascorbate, glutathione, carotenoids, tocopherols, and secondary metabolites.

Apart from damaging effects, ROS is also involved in many signalling processes. The ROS-mediated signalling plays a plausible role in eustress, which is associated with the acclimation of plants against UV-B radiation. The processes involved in ROS-mediated signalling are complicated processes that could be affected by UV-B fluence rate, individual ROS, ROS production, and scavenging enzymes, as well as by various antioxidants oxidation–reduction states which are vital for cellular redox regulation. Brosché and Strid (2003) categorized the UV-B fluence into high (over 15 kJ m^{-2}), intermediate (5–7 kJ m^{-2}), low (1–3 kJ m^{-2}), and very low fluence (less than 1 kJ m^{-2}). They also reported some genes influenced by specific fluence rates, i.e. high fluence; *PR-1* and *PDF1.2*; intermediate fluence: *PR-5;* low fluence: *PYROA, CHS, UBQ3, LHCB,6* and *F5D21.10*; and very low fluence: *MEB5.2*. Studies suggested that low fluence of UV-B to plants promotes the expression of various genes involved in plant defence and phenolic-flavonoid production (Ulm and Nagy 2005; Kumari et al. 2009a, b) (Fig. 3.3). During UV-B stress, the plants' intracellular redox status could be an important factor for UV-B induced signal transduction. The ROS formation could follow either non-specific or specific routes. Under non-specific ROS formation routes, aromatic amino acids and phenolic compounds facilitate the transfer of energy to nearby oxygen molecules. ROS, DNA damage, and hormones' (salicylic acid, ethylene, and jasmonic acid) biosynthesis mediate the non-specific signalling (Demkura et al. 2010). However, specific UV-B signalling requires specific receptors and facilitated by UV RESISTANCE LOCUS8 (UVR8) and also via oxidative stress (Cloix and Jenkins 2008) (Fig. 3.3). UVR8 is associated with gene expression activated by low UV-B radiation fluence levels (Brown and Jenkins 2008). UVR8 also regulates the expression of ELONGATED HYPOCOTYL5(HY5) and HY5 HOMOLOG (HYH) transcription factors (Fig. 3.3). Moreover, UVR8 is known to regulate the expression of more than 70 genes stimulated under UV-B radiation, so it is a key regulator of defence mechanism in the survival of terrestrial plants exposed to ambient UV radiation (Jenkins 2009). Another signalling pathway is CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1), which represses photomorphogenic genes' expression (Fig. 3.3). It acts as an E3 ubiquitin ligase, which degrades HY5 and other photomorphogenic positive regulator genes (Prado et al. 2012). But due to lack of information, the exact role, and mechanism of action of COP1, its negative or positive expressions under UV-B radiation are still debatable.

Better knowledge about the genetic setup, variety, cultivar of the test plant, amount of UV-B radiation, environmental factors, and mechanism of action

involved in various pathways can help understand the exact effects of UV-B radiation on the plants and their response towards prevailing UV-B radiation.

3.4 UV-B and Terrestrial and Aquatic Ecosystem

Excess UV-B radiation adversely affects the Earth's ecosystem. Besides the ozone layer, absorption and scattering of the radiation through several gases, clouds, and particles present in the environment profoundly altered the radiation, leading to very little penetration of UV radiation on the Earth's surface (Madronich 1993). UV-B has direct and indirect effects on both terrestrial and aquatic ecosystems. Through affecting the plants, animals, and microbes, UV-B imposes its impact on the Earth ecosystem.

3.4.1 Effects of UV-B Radiation on Terrestrial Ecosystem

The terrestrial ecosystem includes agro-ecosystems and less intensively managed lands (forests, grasslands, savannahs, deserts, tundra, etc.), which are the most vulnerable exposed against UV-B radiation as compared to the aquatic ecosystem. UV-B sensitivity in plants varies among species. Several studies on plants that were conducted with supplemental UV-B doses showed variable responses. Sensitive plants exhibit reduced growth and photosynthesis; however, resistant plants showed a very low level of damage or no damage to even enhanced level of UV-B radiation (Teramura and Sullivan 1994). UV-B radiation affects plants' systems either through affecting the physiological processes that can influence the growth and yield or via the disruption or alterations at the molecular level, which can cause heritable changes (Zlatev et al. 2012). Plants exposed to UV-B varied with time and space; in accordance with that, plants respond differently and developed acclimation strategies (Rozema et al. 2009). In ozone-depleted terrestrial areas, UV-B reduces the plant's productivity by 6% (UNEP 2011). Exposure to UV-B radiation reduced the crop quality and productivity, leading to serious economic consequences (Reboredo and Lidon 2012).

Experiments with enhanced UV-B radiation suggest alterations in morphological architecture or phenotype, which varied among plants due to the varied genotypic and experimental conditions (Robson et al. 2015). Most reported phenotypic changes under UV-B stress include reduced leaf area, increased leaf thickness, reduced plant height (due to the reduction in nodes and internodes), enhanced branching, reduced size of flower and fruit, altered root-shoot ratio (due to the changes in the pattern of biomass allocation), and the biomass of plants (Kakani et al. 2003; Choudhary and Agrawal 2014; Robson et al. 2015; Takshak and Agrawal 2015a, b; Rai and Agrawal 2017; Václavík et al. 2017; Mariz-Ponte et al. 2019; Rodríguez-Calzada et al. 2019; Tripathi et al. 2019). The response differs between the dicot and monocot species; some reports revealed that the numbers of tillers were generally increased in monocots; however, dicots had not shown this

trend (Barnes et al. 1990; Jaiswal et al. 2020). Some studies reported UV-B's positive effect on morphological characters such as plant height and biomass (Jaiswal et al. 2020). The changes in morphological characters were mostly dependent on productions of photosynthates, which are generally impaired or altered under the stressful environment.

Physiological processes are the key mechanisms upon which the whole plant's life is dependent. Studies with an enhanced UV-B level showed that photosynthetic processes are sensitive to UV-B radiation (Zlatev et al. 2012). UV-B affects the photosynthetic mechanisms through the generation of ROS, which can degrade photosynthetic pigments or activate the UVR8 pathway, which alters the turgidity of guard cell, proceeding through a set of mechanisms to stomatal closure (Tossi et al. 2014). Qaderi and Reid (2005) observed the reduced photosynthetic pigment (Chl b) in *Brassica napus* under UV-B and CO_2 treatments. In *Vitis vinifera,* both short-term and long-term UV-B exposures lead to a reduction in photosynthetic machinery with a higher reduction in long-term exposures were observed (Martínez-Lüscher et al. 2013). According to Chen et al. (2016), photosynthesis was reduced in both male and female plants of *Morus alba*, without objecting to any changes in stomatal conductance. A study in Korean pine (*Pinus koraiensis*) also suggests the detrimental effect of UV-B on physiological mechanisms and photosynthetic pigments. It showed the reductions were increased with increasing UV-B doses and exposure (Zu et al. 2011). Dias et al. (2018) reported that the activity of the major photosynthetic enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) was also reduced under the two different levels of UV-B exposures. A study conducted on two varieties of *Olea europaea* (Giarraffa and Olivastraseggeianese) showed that Giarraffa showed higher photosynthetic stability under the UV-B stress, so it showed the different responses between the varieties (Piccini et al. 2020). Several studies showed that impairment of chlorophyll and other pigments, photosynthetic rate, stomatal conductance, and enzymatic activities lead to lower photosynthates assimilation and thus hamper the overall yield of the plants (Table 3.1).

The plants' sensitive targets are pigments, plasma membrane chloroplasts, mitochondria, peroxisomes, ER, and the cell wall, which generate ROS under the stressful environment. Chloroplasts and peroxisomes are the important components for ROS production in the presence of light (Cassia et al. 2019). ROS functions as signal molecules or produces oxidative damage depends on the severity of the stress and the plant's ability to scavenge it (Sharma et al. 2012; Petrov et al. 2015). In chloroplasts, photosynthetic reaction centres are the most sensitive targets for UV-B, leading to the generation of ROS through inhibiting PS II. Reduced CO_2 assimilation through decreased carboxylation velocity and Ribulose-1,5-bisphosphate carboxylase/oxygenase (RUBISCO) under UV-B could lead to the formation of superoxide radicals (Strid et al. 1994; Han et al. 2009).

3.4.2 Effects of UV-B Radiation on Aquatic Ecosystem

Enhanced level of UV-B also had effects on the aquatic system, but there is a reduction in UV-B strength with depth (Rozema et al. 2002). The UV-B sensitivity varies among individuals, populations, and species at different trophic levels (Williamson 1995). Aquatic ecosystems are mostly populated with phytoplankton; therefore, they receive a high amount of solar UV radiation. According to Day and Neale (2002), photosynthetic sensitivity is higher in phytoplankton than in terrestrial plants. The productivity in aquatic plants is even compromised under short-term exposure. The long-term assessments on aquatic producers are complicated because of difficulties in accounting for the horizontal and vertical mixing and the nonlinear nature of responses. Vertical migration is adopted by the motile biomass producers and consumers to avoid excessive radiation, whereas sessile (attached) organisms depend on habitat selection to reduce the exposure (Häder et al. 2011). The major biomass producers (macroalga and seagrasses) showed a marked sensitivity to UV-B. Reduced biomass production in the aquatic ecosystem complicates the food web resulting in reduced food production (Häder 2000).

The reduced photosynthetic rate was observed in brown alga *Laminaria digitata* (Forster and Lüning 1996). Impaired photosynthesis and respiration were observed in some aquatic plants, such as *Ceratophyllum*. Some species revealed that photosynthesis was often more decreased when UV radiation was filtered out. UV-B screening in aquatic alga was generally provided by UV screening pigments such as carotenoids and UV-absorbing mycosporine such as amino acids. These simple UV screening compounds are as efficient as the complex flavonoids of higher plants. Experiments with liverworts and mosses showed that UV screening compounds and antioxidants were more striking in liverworts than in mosses (Häder et al. 2011).

The negative effects of UV-B radiation have been shown in the growth and survival of a wide range of aquatic organisms. Even the eggs and larvae of many aquatic animals are sensitive to UV-B radiation (Häder 2000). UV radiation also influences the interactions of zooplankton with other components of aquatic ecosystems. An experiment with a freshwater aquatic plant *Nymphoides humboldtiana* showed enhanced photosynthetic performance and antioxidant production under UV-B exposure (Nocchi et al. 2020). Algal communities exposed to UV-B radiation showed an enhanced concentration of ROS-scavenging enzymes (Li et al. 2010). The experiments or aquatic species were generally conducted in laboratories provides very little information as interspecific interactions, self-protective behaviour, and chemical interactions with naturally occurring organic matter found in the natural aquatic system are not provided here (Fernanda Pessoa 2012). However, the several studies advocating the evolution of plants from aquatic to terrestrial ecosystems suggest that it was only possible because of the elicitation provided by UV-B radiation to biosynthesize secondary metabolites to adapt to the prevailing harsh conditions.

3.4.3 Effects of UV-B Radiation on Secondary Metabolites

Initially, secondary metabolites were considered as the by-products of primary metabolisms, but increasing research in this area revealed that they were generated through an independent pathway that is connected with primary metabolism. Its production was generally enhanced under stressful environmental conditions as they also serve an important role in the plant's defence mechanisms. UV-B activates a signalling cascade in plants through UVR8, the photoreceptor in plants, which is further involved in the production of several secondary metabolites. Activation of UVR8 photoreceptors also leads to localization of UVR8 into the nucleus and activates the UV-B responsive genes involved in the production of secondary metabolites. They provide both active and passive resistance to plants. Passive resistance is provided by the constitutive one, while the active resistance is provided by the metabolites which are induced or newly synthesized under a specific environmental condition (Korkina 2007; Takshak and Agrawal 2019). The effects of UV-B radiation are further described under different classes of secondary metabolites.

3.4.3.1 Effects of UV-B Radiation on Alkaloids

Alkaloid forms a diverse array of natural compounds having a wide range of biological activities. They are biologically active heterocyclic chemical compounds having nitrogen with pharmacological properties and important ecological functions (O'Connor 2010). The most studied alkaloid group under UV-B stress is terpene indole alkaloids in *Catharanthus roseus*, which showed the upregulation of an alkaloid biosynthetic gene, strictosidine synthase (*Str*), and also the enhanced production of catharanthine in cell cultures (Ramani and Chelliah 2007). A high level of UV-B-induced production of another indole alkaloid, 6-hydroxyl-1H-indol-3-yl, was reported in *Clematis terniflora* by Gao et al. (2016). Increased production of vindoline and catharanthine was observed in the initial exposure of UV-B but reduced upon prolonged UV-B exposure; however, vinblastine content increased up to 15 days (Liu et al. 2011).

Qin et al. (2014) reported that enhanced gene expression (PMT, TRI, CYP80F1, and H6H) leads to higher accumulation of alkaloid scopolamine and lower accumulation of hyoscyamine in hairy root cultures of *Anisodus luridus* under UV-B treatment. Enhanced production of artemisinin in *Artemisia annua* under UV-B and UV-C treatments was reported by Rai et al. (2011). Increased content of total alkaloids both in the leaves and roots of *Withania somnifera* was observed; however, examination of individual alkaloids showed an adverse effect of UV-B on withanolide A, whereas positive effects on withaferin A content (Takshak and Agrawal 2014a). A sharp increase in total alkaloid content was found in leaves and roots of *Coleus forskohlii* under the UV-B stress (Takshak and Agrawal 2015b). A study by Do Nascimento et al. (2013) showed an increased content of brachycerine, which also acts as ROS scavenger and UV shield under UV-B stress. Contrary to the positive effects of UV-B radiation on alkaloid accumulation, a study by (Larson et al. 1990) reported the negative effect of UV-B radiation on alkaloid content in *Aquilegia caerulea*. From most of the studies, it can be concluded that

UV-B enhanced the expression of alkaloid biosynthetic genes and alkaloid content in most of the plant species; however, only a few showed reduced content under the UV-B stress.

3.4.3.2 Effects of UV-B Radiation on Terpenes/Terpenoids

Terpenes are the largest single class of compounds and constituent of essential oil. They are also called isoprenoids, as they are made up of isoprene units. Based on the number of isoprene units, different types of terpenes are classified as monoterpenes, sesquiterpenes, diterpenes, triterpenes, and tetraterpenes. Most of the plant's essential oil was contributed by mono-, sesqui-, and diterpenes, and they were also studied under the UV-B treatments. A study by Jaiswal and Agrawal (2021)showed enhanced monoterpenes in two species of *Curcuma* (C. *caesia and C. longa*); however, sesquiterpenes were enhanced only in *C. longa*. This enhanced content of terpenes contributed to the increased essential oil content in both species. A study by Zavala and Ravetta (2002) reported the importance of UV-B in a specific class of terpene (resins), as an exclusion study of ambient UV-B leads to a reduction in the resin content in *Grindelia chiloensis*. Loreto and Schnitzler (2010) also discussed the induction of isoprene under the UV-B stress in European oak.

As terpenoid/s played an important role in defence in pines, a study in indoor-grown *Picea abies* showed that terpene (bornyl acetate, borneol, myrcene, and limonene) contents were enhanced in the initial day of exposure; however, their content becomes same as control plants after the prolonged exposure (Ohlsson et al. 2013). Enhanced essential oil content was reported in *Mentha piperita* under two different growth conditions (natural field and growth chamber) with a higher content in growth chambers under UV-B exposure, which is mainly because of (−)-menthone, (+)-menthofuran, and (+)-pulegone. Other compounds such as 1,8-cineole, linalool, (+)-menthofuran, (+)-pulegone, (E)-β-caryophyllene, and germacrene-D, whereas reductions for piperitone, (−)-menthol, and menthyl acetate were observed. A significant difference in the chemical profile of terpenes that has been observed under different growth conditions was reported in *Mentha piperita* under UV-B stress (Dolzhenko et al. 2010). Kumari et al. (2009a) reported the enhanced essential oil content under UV-B in *Acorus calamus*; however, the chemical profiling was altered. The major component of the oil, i.e. t beta-asarone, was reduced; however, p-cymene and carvacrol contents were induced under UV-B. So, we can say that most of the studies revealed enhanced essential oil (terpenes) content in plants; however, the variations found in the individual terpene compounds could vary with dose and growth conditions.

3.4.3.3 Effects of UV-B Radiation on Phenolic Compounds

The compounds with hydroxylated aromatic rings, in which the hydroxyl group is attached directly to the phenyl, substituted phenyl, or other aryl group, come under the category of phenolic compounds. They are synthesized through shikimic acid and phenylpropanoid pathways. Most of the phenolic studies mainly focused on the model plant *Arabidopsis*, and later on, crop plants were mostly studied (Takshak and Agrawal 2019). Flavonoids form the largest subcategory of phenolics, and it also

serves as UV screening compounds under UV stress. Flavonols, flavones, and anthocyanin provide protection by working as ROS scavengers under UV-B. Kumari et al. (2009a) reported the significant increase in total phenolics under the UV-B treatment in *A. calamus*. Enhanced anthocyanin contents were reported in the leaves and roots of *C. forskohlii* under UV-B stress. The importance of UV-B for the phenolics, especially anthocyanin was reported by an exclusion experiment of UV-B, which depicted the reduced content in red-leafed lettuce plants (Chalker-Scott 1999). Müller-Xing et al. (2014)showed the induction of flavonoids under high light and UV radiation in *Arabidopsis*. Induction of flavonoid content in *Cymbopogon citratus* under the enhanced UV-B exposure was reported by Kumari and Agrawal (2010).

Enhanced activities of flavonols and anthocyanin biosynthetic enzymes (CHI and DFR) of phenylpropanoid pathway were reported in *W. somnifera* (Takshak and Agrawal 2014a). Nguyen et al. (2020) reported that UV-B radiation induced enhancement in the phenolic content as well as phenolic compound resveratrol in peanut sprouts, which is generally present in very low concentrations. A slight increase in phenolic compounds in broccoli sprouts under UV-A treatment was reported by Moreira-Rodríguez et al. (2017). A study by Nascimento et al. (2015) also showed that UV-B radiation enhanced the flavonoid and quercetin contents in *Kalanchoe pinnata*. Most of the studies showed enhancement of phenolics under UV exposure.

3.4.3.4 Effects of UV-B Radiation on Glucosinolates

Glucosinolates are anionic, hydrophilic β-thioglucoside N-hydroxysulfates, which are abundant plant secondary metabolites reported primarily throughout 15 botanical families of the order Capparales, e.g. the Brassicaceae, Capparaceae, and Resedaceae in Brassicaceae family; however, more than 80% of glucosinolates reported from Brassicaceae. As reviewed by Kumari et al. (2013), *Arabidopsis* showed the induced production only under the 1 h of exposure, whereas its contents reduced over prolonged exposure. Enhanced accumulation of glucosinolates was found after the 24 h exposure of UV-B radiation in broccoli sprouts (Moreira-Rodríguez et al. 2017). Glucosinolates, which are expressed as glucotropaeolin in *Tropaeolum majus,* were found to be increased after UV-B exposure. As there were few studies conducted on UV-B radiation with glucosinolates, we infer from the studies conducted that UV-B radiation is also used as a stimulator for its production.

Apart from the enhanced biosynthesis of different classes of secondary metabolites induced by elevated UV-B radiation, some major medicinally important compounds such as withanolides, withaferin A, wedelolactone, glycyrrhizin, vinblastine, vindoline, and catharanthine, etc. were also studied under various UV-B doses. These individual compounds and their respective plants showed differential roles against UV-B radiation and were highly exploited for their usage and benefit of mankind.

3.4.3.5 Effects of UV-B on Fatty Acid and Amino Acid Metabolic Profile

Lipids are the important components of the cell and its content play a major role in maintaining the membrane structure in a stressful environment. It is important for insulation, energy storage, protection, and cellular communication. Lipid profiling of *Olea europea* showed that palmitic acid and oleic acid were enhanced under high doses of UV-B exposure, whereas the ratio of unsaturated to saturated fatty acids remains unchanged (Dias et al. 2018) (Table 3.2). The reduction in saturated fatty acids and increased unsaturated fatty acids was reported in *Spirulina platensis* exposed to UV-B (Gupta et al. 2008) (Table 3.2). In *G. max* (cultivars JS-335, PS-1042), the total oil content was reduced in eUV-B. The profiling of fatty acid showed that saturated fatty acids such as stearic and palmitic acids in JS-335 and only palmitic acid in PS-1042 were reduced, whereas total unsaturated fatty acids were enhanced under UV-B radiation. Among mono-unsaturated fatty acids (MUFA), oleic acid was reduced in both the cultivars, whereas in poly-monounsaturated fatty acids, linoleic acids and linolenic acids were increased in cultivars JS-335; however, only linolenic acid was enhanced in PS-1042 (Choudhary and Agrawal 2015) (Table 3.2). Tripathi et al. (2019) reported the reduced oil content in sunflower under UV-B radiation. Sunflower contains four major fatty acids (palmitic, stearic, oleic, and linoleic acids), among which palmitic acid was

Table 3.2 Variations (increase ↑ or decrease ↓) in fatty acid and amino acid profiles of different plants under UV-B exposure

Plants	UV-B dose	Fatty acid profile		References
		Saturated	Unsaturated	
Olea europea L.	12.4 kJ $m^{-2}day^{-1}$	Palmitic acid ↑	Oleic acid ↑	Dias et al. (2018)
Glycine max L.	7.2 kJ $m^{-2}day^{-1}$	Palmitic acid ↓ Stearic acid ↓	Oleic acids ↓ Linoleic acid ↑ Linolenic acid ↑	Choudhary and Agrawal (2015)
Helianthus annus L.	7.2 kJ $m^{-2}day^{-1}$	Palmitic acid ↓ Stearic acid ↓	Oleic acids ↓ Linoleic acid ↑	Tripathi et al. (2019)
		Amino acids profile		
Vitis vinifera L.	9.66 kJ $m^{-2}day^{-1}$	Threonine, methionine, isoleucine, serine and glycine content ↓ Gamma-amino butyric acid (GABA) ↑		Martínez-Lüscher et al. (2014)
Helianthus annus L.	7.2 kJ $m^{-2}day^{-1}$	Total amino acids ↓		Tripathi et al. (2019)
Populus cathayana Rehd.		Aspartic acid, leucine, arginine, and proline content ↓		Zhang et al. (2017)

reduced in DSRF 108 variety, and stearic acid was reduced in Sungold variety of sunflower under UV-B exposure (Table 3.2).

Amino acids are the building blocks of proteins, utilized as enzyme and precursors of different pathways. Martínez-Lüscher et al. (2014) reported that total free amino acid concentration remains unaffected under UV-B radiation in grape berries (Table 3.2). Analysis of amino acids profile revealed that threonine, methionine, isoleucine, serine, and glycine contents were reduced, whereas 61% enhancement in gamma-amino butyric acid (GABA) was reported in grape berries (Table 3.2). Tripathi et al. (2019) reported 18% reduction in amino acid content in sunflower under UV-B exposure. Amino acid profiling of *Populus cathayana* exposed to UV-B radiation showed reduced content of aspartic acid, leucine, arginine, and proline, whereas cystine content showed slight variations under UV-B exposure (Zhang et al. 2017).

3.5 Some Medicinal Compounds Under UV-B

Withanolides are a group of C-28 steroidal lactones commonly occur in *Withania somnifera* (Ashwagandha) of Solanaceae family. Withanolides have a wide range of pharmaceutical applications, including anti-tumour, antioxidant, and anti-stress properties. Two withanolides, namely Withaferin A and Withanolide A, have been reported to possess anti-cancerous and immunomodulatory properties, respectively. Takshak and Agrawal (2014b) reported that in leaves of *W. somnifera*, withanolide A and withaferin A were more than roots. Due to elevated UV-B exposure (eUV-B), the overall content of withanolide A in leaves was reduced by 41.2%, whereas withaferin A increased by 12.4% in above-ground plant parts as compared to control. They concluded that exposure of *W. somnifera* to UV-B radiation could act as a better source for the exploitation of these medicinally important compounds (Table 3.3).

Eclipta alba (Asteraceae) is traditionally used in Ayurveda for the treatment of several diseases such as hepatitis, liver cirrhosis, and baldness. It contains an important compound wedelolactone, which is a coumarin derivative. When *E. alba* is exposed to intermittent and continuous exposure of eUV-B wedelolactone, content increases by 74.5 and 8.3%, respectively, compared to control (Rai and Agrawal 2020) (Table 3.3).

A triterpenoid saponin compound, namely glycyrrhizin, is believed to be 50 times sweeter than sugar. It is the major active compound of the medicinal plant *Glycyrrhiza uralensis* and generally present in this plant's roots and rhizomes. Its antitumour activity has been reported in several malignant human cell lines, and it is also found to be highly active in inhibiting the replication of HIV-1 and SARS-associated virus. Furthermore, glycyrrhizin also exhibits anti-ulcer, anti-coagulative, anti-inflammatory, and antioxidant properties (Afreen et al. 2005). Following *G. uralensis* (three-month-old pot grown plant) *exposure* to the low and high UV-B intensities, the content of glycyrrhizin increased in root tissue by nearly 1.5 fold as compared to control (Afreen et al. 2005). Afreen et al. (2005) also suggested

Table 3.3 Effect of UV-B on medicinally active compounds

Plants	Active compounds	Effects of UV-B	References
Psychotria brachyceras Müll. Arg.	Brachycerine	100% increase	Gregianini et al. (2007)
Centella asiatica L.	Saponins (asiaticoside and madecassoside) and centellosides	No significant changes	Müller et al. (2013)
Astragalus membranaceus Fisch.	Isoflavonoids	2.29-fold increase	Jiao et al. (2015)
Rosmarinus officinalis L.	Carnosic acid	50% increase at lower UV-B dose	Luis et al. (2007)
Glycyrrhiza uralensis Fisch.	Glycyrrhizin	1.5-fold increase	Afreen et al. (2005)
Artemisia annua L.	Artimisin	20% increase in inflorescence and 3% increase in leaves at full-bloom stage	Rai et al. (2011)
Prunella vulgaris L.	Rosmarinic acid, caffeic acid and hyperoside	Rosmarinic acid, caffeic acid, and hyperoside increase by 53.4%, 22.5%, and 121%, respectively	Zhang et al. (2017)
Catharanthus roseus L.	Catharanthine and vindoline	Vindoline and catharanthine contents increase by 12 and three-fold, respectively. With 5-minute UV-B treatment	Ramani and Jayabaskaran (2008)
Eclipta alba L. (Hassk)	Wedelolactone	Wedelolactone content increase by 74.5% and 8.3%, respectively, at intermittent and continuous exposure	Rai and Agrawal (2020)
Withania somnifera Dunal	Withanolide A and withaferin	Withanolide decrease by 41.2%, whereas withaferin A increase by 12.4%	Takshak and Agrawal (2014a, b)
Acorus calamus L.	β-Asarone	8.46% decrease	Kumari et al. (2009a, b)

that growing *G. uralensis* in controlled environmental conditions can be seen as a good alternative to the wild collection and for obtaining a high concentration of glycyrrhizin in a 3-month old plant. Appropriate dose and duration of UV-B radiation can be considered as a tool for enriching plants with valuable secondary metabolites.

Exposure of *Rosmarinus officinalis* to two different doses (5.4 and 31 kJ m^{-2} day^{-1}) of UV-B radiation was found to increase the concentration of two major metabolites, such as rosmarinic acid (polyphenols) and carnosic acid (diterpenes). However, such an increase was more at a higher dose than the lower dose of UV-B radiation (Luis et al. 2007).

Prunella vulgaris is a medicinally important plant of the family Lamiaceae and a rich source of phenolics, namely rosmarinic acid, caffeic acid, and hyperoside

(Table 3.3). It exhibits a wide range of activities such as antioxidant, anti-inflammatory, and antifungal. UV-B radiation at a dose of 35 μW cm^{-2} nm^{-1} showed enhancement in the content of rosmarinic acid, caffeic acid, and hyperoside by 53.4%, 22.5%, and 121%, respectively, as compared to control (Zhang et al. 2017). Flavonoids (quercetin, kaemperol, and isorhamnetin) of *G. biloba* have been known to possess neuroprotective, antimicrobial, and anticancer properties (Sun et al. 2010). In a study by Sun et al. (2010) on *G. biloba* showed that treatment of UV-B radiation enriched these health-promoting flavonoids of *G. biloba*.

Kalanchoe pinnata is a medicinal plant of the family Crassulaceae that is traditionally used to treat inflammation and wound healing in Brazil. It is a rich source of phenolic compounds, mainly flavonoids, which could account for its pharmaceutical activities, including anti-hypertensive, anti-cancer, analgesic, and anti-inflammatory. Quercetin, which is an important bioactive flavonoid of this plant, showed higher concentration when plants were provided with white and UV-B light. Nascimento et al. (2015) suggested that UV-B radiation can be used as a supplemental light source to improve the flavonoid's content and composition in *K. pinnata*.

The flavones' metabolites namely cynaroside and graveobioside A have been reported in bell pepper and possess several pharmaceutical properties such as anti-apoptotic, insecticidal, and reduce the side effect of anti-cancerous chemotherapeutic drugs. Exposure of bell pepper plants to UV radiation leads to the enhancement in the content of these two important metabolites under greenhouse conditions (Ellenberger et al. 2020).

Catharanthus roseus plant of the family Apocynaceae contains important terpenoid indole alkaloid (vinblastine, vindoline, and catharanthine) and exhibits anti-tumour, anti-diabetic, and anti-hypertensive properties. Ramani and Jayabaskaran (2008) reported that exposure of cell suspension culture to UV-B irradiation was found to enhance the content of catharanthine and vindoline in *C. roseus*.

The medicinally important plant *Centella asiatica* has flavonoids and saponins as its major bioactive compounds. The saponins of *C. asiatica* are widely used in food, cosmetic, and pharmaceutical industries and are known as centellosides. In a study by Müller et al. (2013), UV-B radiation showed no significant alterations in the two saponins such as asiaticoside and madecassoside and the total centellosides of *C. asiatica*.

Artemisinin, a major bioactive compound of *Artemisia annua,* is widely used against malaria-causing strains of *Plasmodium falciparum* and other infectious diseases such as leishmaniasis, schistosomiasis, and hepatitis B. Rai et al. (2011) reported that short-term UV-B radiation (14 days) pre-treatment at a dose of 4.2 kJ m^{-2} day^{-1} enhanced the artemisinin content in *Artemisia annua* at all developmental stages as compared to control plants.

Astragalus membranaceus is a perennial herb of the family Leguminoseae. Its root contains important isoflavonoids namely Astraisoflavan-7-O-β-D-glucoside (ASG), Calycosin-7-O-β-D glucoside (CAG), Formononetin (FO), Calycosin (CA), and Ononin (ON), which are responsible for its properties, including cardio-protective, antioxidant, anti-viral, anti-inflammatory, immunomodulatory,

hematopoietic, neuroprotective, hypolipidemic, estrogenic, and anti-tumourigenic activities. Elicitation of *A. membranaceus* hairy root culture with different doses (5.4–172.8 kJ m^{-2} day^{-1}) of UV-B radiation was found to increase the content of these important isoflavonoids with maximum enhancement in the content of total isoflavonoids by 2.29-fold at 86.4 kJ m^{-2} day^{-1} elicitation dose (Jiao et al. 2015).

The genus *Genista* L. of the family Fabaceae consists of 87 species that are widely grown in the Mediterranean region and are characterized by the presence of a high concentration of isoflavones, mainly Genistein and Daidzein. Many *Genista* species exhibit important biological activities such as anti-inflammatory, hypoglycemic, antioxidant, anti-ulcer, estrogenic, and cytotoxic activity. Tůmová and Tůma (2011) reported a higher level of daidzein, genistein genistin, and biochanin A after UV irradiation compared to control in the callus culture of *Genista tinctoria*.

Curcuma caesia, a perennial herb of Zingiberaceae family, showed anxiolytic, antifungal, central nervous system (CNS) depressant, and anti-cancerous activities. Treatment of *C. caesia* with elevated dose (9.6 kJ m^{-2} day^{-1}) of UV-B leads to an increase in the content of important metabolite 1,8- cineole, whereas a decrease in level D-camphor (Jaiswal et al. 2020) (Table 3.3).

The monoterpene-indole alkaloid brachycerine obtained from plant *Psychotria brachyceras* is known to possess analgesic, antioxidant, and anti-inflammatory activities (Table 3.3). Gregianini et al. (2007) reported that exposure *of P. brachyceras* to UV-B radiation doubled the yield of brachycerine and suggested that UV-B radiation may enhance the yield of brachycerine, which is of pharmaceutical interest.

The rhizome and leaves of *Acorus calamus* contain aromatic oil, due to which it is highly valued and commercially cultivated in Asia (Table 3.3). *A. calamus* is known to exhibit carminative, anti-spasmodic, hypotensive, anthelminthic, and anti-depressant activities. The main component of the essential oil of *A. calamus* is β-asarone, which is toxic for human health. So in the herbal medicinal products, the low content of β-asarone would be preferential due to the known toxicity of β-asarone. Kumari et al. (2010)revealed that exposure of *A. calamus* to an elevated level of UV-B leads to a decrease in the content of β-asarone of essential oil, which is of prime importance and the significant finding of investigation as per the human health perspectives (Table 3.3).

In addition to plants and their differential responses, UV-B radiation impacts on animals and human health is also widely studied. Similar to plants, the animal also showed differential responses against UV-B radiation.

3.6 Effect on Human Health

UV-B radiation of the solar spectrum has been known to cause deleterious effects on human health since for a long time. This includes the negative effects on the skin (sunburn, hyper-pigmentation, photo-aging, skin cancers including squamous cell carcinoma, basal cell carcinoma, and cutaneous malignant melanoma), eye (cataract, pterygium, and eye cancer), and the immune system (Fig. 3.4). However, some

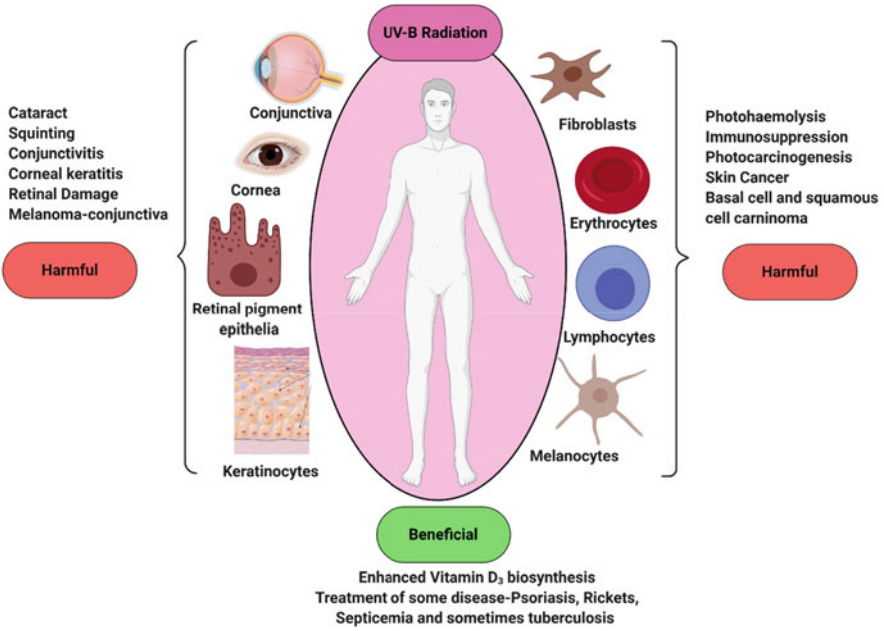

Fig. 3.4 The harmful and beneficial effects of UV-B radiation on human body

beneficial effects of UV-B radiation have also been reported, including its role in the cutaneous synthesis of vitamin D and phototherapy (Fig. 3.4). The following sections deal in detail with the negative and the positive effects of UV-B on human health.

3.6.1 Harmful Effects of UV-B Radiation on Human Health

UV-B radiation affects the various biomolecules and cells' processes, including DNA, lipids, proteins, extracellular matrix (ECM), and the molecules involved in the cell cycle and signalling processes. UV-B radiation directly damages the DNA molecules by the formation of DNA photoproducts such as pyrimidine-pyrimidone (6–4) photoproduct (6–4PP) and cyclobutane pyrimidine dimer (CPD) or indirect damages due to ROS production. These photoproducts inhibit the process of replication, transcription and generate permanent mutation, which consequently leads to photo-aging and skin cancers (Karapetsas et al. 2020). The mutation in the p53 gene occurs via C → T and CC → TT base substitution, which is recognized as the 'UV-B signature' or 'UV-B fingerprint' mutations. In approximately 50% of basal cell carcinoma cases and 90% of cases of squamous cell carcinoma, p53 mutations have been reported (Takshak and Agrawal 2019) (Fig. 3.4).

Exposure to UV-B radiation causes increased production of ROS in cells, due to which level of antioxidants present in cells affected and the redox status of cells get

disturbed which ultimately leads to oxidative stress. Larsson et al. (2006) reported that UV-B radiation decreased the level of reduced glutathione (GSH; a non-enzymatic antioxidant) and activated the transcription factor nuclear factor kappa beta (NF-κB), which affect the redox status and enhanced the frequency of apoptosis in *in -vitro* human melanocytes (Fig. 3.4). Lymphocytes are also sensitive to UV-B irradiation and go through apoptosis. Prasad et al. (2009) found increased DNA damage, lipid peroxidation, and reduced level of antioxidants when human lymphocytes were exposed to UV-B radiation. UV-B radiation was found to inhibit the membrane-bound acetylcholinesterase and ATPase, altered the content of GSH, and increased the lipid peroxidation, and thus damages the constituents of RBC membrane, which were responsible for the normal structure and functions of RBC membrane. Misra et al. (2005) reported that UV-B radiation leads to photo-haemolysis in RBC and induced toxicity in human erythrocytes in vitro in a dose-dependent manner (Fig. 3.4). Exposure of human dermal fibroblast to UV-B radiation leads to oxidative stress, which further leads to photo-aging by accelerating matrix metalloproteinase (MMP; zinc-dependent endoproteinases) production, which degrades the collagens in the extracellular matrix (Sun et al. 2015).

Inflammation is a prominent mediator of UV-B radiation-induced skin cancers and skin aging (Bosch et al. 2015) (Fig. 3.4). In the skin, numerous mast cells are present, which play an important role in UV-B radiation-induced inflammation of the skin by inducing several pro-inflammatory mediators (Endoh et al. 2007). The inflammatory mediators are also released from fibroblasts, keratinocytes, tumour cells, and blood vessels' endothelial lining. These inflammatory mediators include lipid-mediators such as leukotrienes, prostaglandins, and platelet-activating factor, plasma-derived molecules such as plasmin, fibrin, bradykinin, and various cytokines such as interleukin-1 (IL-1), IL-2, IL-4, IL-6, IL-8, IL-10, IL-12, IL-13, IL-1β, and tumour necrosis factor-α (TNF-α). In general, UV radiation stimulates an inflammatory response and activates the immune system components by the following mechanisms: (1) activation of keratinocytes, fibroblast, and other cells to release inflammatory mediators; (2) enhancing the immunogenicity of externally provided substances; (3) alteration of self-proteins due to which it becomes more immunogenic; and (4) sequestered auto antigens release by the UV-damaged cells and its subsequent identification (Maverakis et al. 2010). The exposure of UV-B nuclear factor kappa beta (NF-kB) was activated, stimulating the secretion of several inflammatory mediators such as TNF-α, IL-1, and IL-6 (Maverakis et al. 2010).

At the transcriptional and translational levels, UV-B radiation increased the lipid-derived mediators, interleukins, and TNF-α (Takshak and Agrawal 2019). Hawk et al. (1988) suggested that accumulation of neutrophils and mononuclear cells in the skin dermis after short-term exposure to UV-B irradiation to the skin causes acute inflammatory reactions in the skin.

There are several signalling pathways that are activated by UV-B radiation, including Mitogen-activated protein kinase (MAPK) (Fig. 3.2), the nuclear factor-kappa beta (NF-κB), nuclear factor erythroid 2-related factor 2 (Nrf2), and p53 signal transduction pathways. Exposure of fibroblast cells to UV-B irradiation in human activates the components of mitogen-activated protein kinase (MAPK)

signalling pathways such as Jun N-terminal kinase (JNK), extracellular-regulated protein kinase (ERK), and p38 kinase, which induce the activity of activator protein-1 (AP-1). In addition, AP-1, by inducing MMP-1 and by blocking the transforming growth factor-b1 (TGF-b1), inhibits the synthesis of type I procollagen. In UV-irradiated photo-aged skin, mostly enhanced level of MMP-1 and reduced levels of type I procollagen were found (Sun et al. 2015).

UV-B radiation has been known to influence the immune system at both the local and systemic levels. Langerhans cells are one of the major antigen-presenting cells (APCs). UV-B radiation affects the Langerhans cells by decreasing their number and functions (Schwarz 2005). Weiss et al. (1995) reported that a low dose of UV-B radiation suppresses the APC function of human Langerhans cells due to inhibition of the expression of co-stimulatory molecules B7.1 and B7.2. Dendritic cells derived from the human peripheral blood system and spleen are other APCs. Its ability to stimulate T cells is disturbed upon exposure to UV-B radiation, leading to immunosuppressive effects (Young et al. 1993). Further, it was reported that suppression of immune responses due to UV-B exposure plays an important role in activating bacterial, viral, and protozoan infections, reducing vaccination efficacy and developing skin cancers (Lucas et al. 2019).

Acute or chronic exposure to UV-B radiation also imparts adverse effects on the eyes. The effects of UV-B on eyes are mostly from indirect sunlight, such as those passes natural barriers (brows and squinting) or those reflected from surfaces and scattered by environmental components. UV-B radiation has been known to cause several diseases of the eyes, including cataracts and age-related macular degeneration (AMD) (Solomon 2008). Exposure of conjunctiva or cornea to UV radiation of high-intensity causes photo-conjunctivitis and photo-keratitis, respectively. Long-term exposure of these structures over the lifetime can lead to squamous neoplasia, pterygium, and melanoma of the conjunctiva (Lucas et al. 2019). ROS is generated in retinal pigment epithelial (RPE) cells under UV-B radiation, resulting in oxidative stress and damage to the retina. Oxidative stress induced due to exposure to UV-B radiation leads to DNA damage in RPE cells, which might play an important role in the generation of AMD in RPE cells (Xu et al. 2010).

3.6.2 Beneficial Effects of UV-B on Human Health

The most important beneficial role of UV-B radiation is the cutaneous synthesis of vitamin D, which in turn plays a vital role in the treatment of several diseases such as rickets, psoriasis, and hypertension (Takshak and Agrawal 2019) (Fig. 3.4). UV-B radiation synthesizes vitamin D in the skin through the conversion of 7-dehydrocholestrol (a cholesterol derivative) to 25- hydroxyvitamin-D (25 (OH) D, also known as pre-vitamin D_3 and an inactive form of vitamin D_3), which is further converted into cholecalciferol (vitamin D_3) (Fig. 3.4). Osmancevic et al. (2015) reported that exposure of Caucasian volunteers to broadband UV-B increased the serum level of vitamin D, i.e. cholecalciferol. Further, they reported an increase in vitamin D depending on several factors, including exposed skin area, age,

and UV-B flux. Exposure of skin to narrowband UV-B was found to increase the diversity of alpha and beta microbiome in the human intestinal microenvironment, which might provide potential health benefits in chronic inflammatory diseases such as inflammatory bowel disease and multiple sclerosis (Bosman et al. 2019).

In phototherapy, UV radiation is used for the treatment of skin diseases. Several studies suggested that broadband and narrowband UV-B phototherapies were used to treat vitiligo, psoriasis, and atopic dermatitis (Juzeniene and Moan 2012) (Fig. 3.4). Wu et al. (2016) reviewed the use and significance of ultraviolet blood irradiation (UBI), which was used to treat several diseases such as septicemia, asthma, pneumonia arthritis, and tuberculosis.

3.7 Conclusions and Future Perspectives

From the above discussion, it can be said that higher levels of UV-B radiation exposure could cause stress in plants. Stressed plants may undergo oxidative stress by elevated production of ROS as higher UV-B radiation, ROS, and oxidative stress are highly interlinked to each other. The plant experiencing higher UV-B and unfavourable meteorological conditions can also suffer from stress conditions. Conversely, the lower levels of UV-B radiation and other favourable environmental conditions could lead to better acclimation and adaptive strategies in plants. However, the role of ROS in plant adaptive responses under low UV-B exposure is still debatable. Since the enhanced generation of ROS is evident in plants exposed to lower and higher UV-B radiation, both lower and higher UV-B exposures have the capabilities to alter the antioxidative activities, cellular redox maintenance, accumulation of secondary metabolites, and expression of various genes. UV-B radiation-induced alterations in secondary metabolites profile may synergistically or antagonistically affect the related primary and secondary metabolites. At the same time, the bioavailability of individual compounds and related pathways should be thoroughly investigated along with specific environmental factors. UV-B radiation-induced various signalling pathways associated with UVR8, HY5, and COP1 could be considered as major regulatory pathways that are still not fully explored; hence, it requires detailed study.

From the experimental point of view, damages caused by UV-B radiation on several aspects of plants emphasize the deleterious nature of UV-B radiation, pointing it as a curse to life forms and the ecosystem. Contrary, the evolution point of view focuses on UV-B-induced defensive strategies, enhanced secondary metabolites biosynthesis in plants, and its utilization in treating several human diseases; hence, it is considered as a boon for living beings and the biosphere. The beneficial or harmful impacts of UV-B radiation could be decided by overall interaction resulting from UV-B doses, environmental conditions, and the plants' genetic setup. So, it can be concluded that environmental factors are the major driving factors behind overall impacts imposed by UV-B radiation on plants.

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Major Influence on Photosynthetic Apparatus Under UV-B Exposure

4

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Abstract

Depletion of stratospheric ozone has appeared to be the main cause behind the prominent enhancement in UV-B radiation. Enhanced UV-B exposure causes adverse effects on plant growth viz., reduced plant height, diminished leaf area, delayed fruit ripening, chlorosis, curling of leaves, necrosis, decreased leaf photosynthesis, and reduction in root development and biomass which finally resulted in lower crop yield. This chapter reveals harmful effects of UV-B radiation on phytochrome and photosynthetic machinery of plants at various sites. The sites of damage include light-harvesting complex II, oxygen evolving complex, and D1/D2 proteins components. UV-B stress primarily targets Mn cluster, whereas consequent targets are D1 and D2 proteins, quinone molecules, and cytochrome b. Furthermore, reduction in carbon is vulnerable towards UV-B, which has a direct impact on Rubisco activity. Alterations in photosynthetic pigments, leaf morphology, and stomatal conductance are some of the indirect effects of UV-B stress. UV-B-mediated responses in plants include reactive oxygen species as both signaling and damaging agents. It can be concluded that an increase in UV-B radiation in the future will have substantial influence on the efficiency of photosynthesis in plants.

Keywords

Chlorophyll · Oxygen evolving complex · Photosynthesis · Phytochrome · Rubisco · Ultraviolet radiation

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4.1 Introduction

The ultraviolet region is subdivided into three bands termed as UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (200–280 nm). Reduced stratospheric ozone has appeared to be the most important reason for the prominent increase in solar UV-B radiation (Ballaré et al. 2011; McKenzie et al. 2011). Many reports have shown that higher levels of UV-B affect morphological, physiological, and biochemical aspects of many crops (Hectors et al. 2007; Caldwell et al. 2007). The morphological effects of UV-B include reduction of leaf area, plant height, increased auxiliary branching, delayed fruit ripening, chlorosis, curling of leaves, necrosis, root and rhizome development, lower biomass accumulation which is ultimately reflected in reduced crop yield (Searles et al. 2001; Meijkamp et al. 2001; Golaszewska et al. 2003; Ruhland et al. 2005; Zinser et al. 2007; Li et al. 2010; Wang et al. 2012; Reddy et al. 2013). The physiological effects caused by UV-B include destruction of carotenoids and chlorophyll, disruption of stomatal functions, reduction in photosynthesis, degradation of PS II proteins, and reduced Rubisco activity (Cooley et al. 2000; Sullivan et al. 2003; Surabhi et al. 2009; Yu et al. 2013). The biochemical effects of UV-B include accumulation of flavonoids, production of reactive oxygen species (ROS), which may cause lipid peroxidation, protein, and DNA damage (Hollosy 2002; Kliebenstein et al. 2002). The plants respond to UV-B stress by activating antioxidant enzymes such as guaiacol peroxidase (POD), superoxide dismutase (SOD), ascorbic acid peroxidase (APX), and glutathione reductase (GR) (Xu and Sullivan 2010; Hassan et al. 2013). In this chapter, we have made a significant effort to review the harmful effects of UV-B radiation at multiple sites of photosynthetic machinery (Fig. 4.1) in green plants.

4.2 Effect of UV-B on Phytochrome

Phytochromes play a significant role in regulating growth and development of plants. Two photo-reversible forms of phytochrome such as “Pr” and “Pfr” change back and forth upon absorption of light in the red/far-red region to facilitate photomorphogenic responses such as seed germination, chloroplast development, leaf expansion, and flowering (Jansen 2002; Jenkins 2009). Several studies reported UV-B-induced photomorphogenic responses (Jiang et al. 2012; Heijde and Ulm 2012). Kim et al. (1998) observed that UV-B radiation at low doses produced photomorphogenic responses, i.e., hypocotyl inhibition and stem elongation, while higher doses had detrimental effects.

4.3 Effect of UV-B on Ultra-Structure of Leaves

Higher UV-B radiation changes the ultra-structure of leaves which alters the light attenuation and affects photosynthesis. Crops differ in their structural responses towards UV-B, though increased leaf thickness because of UV-B was common in

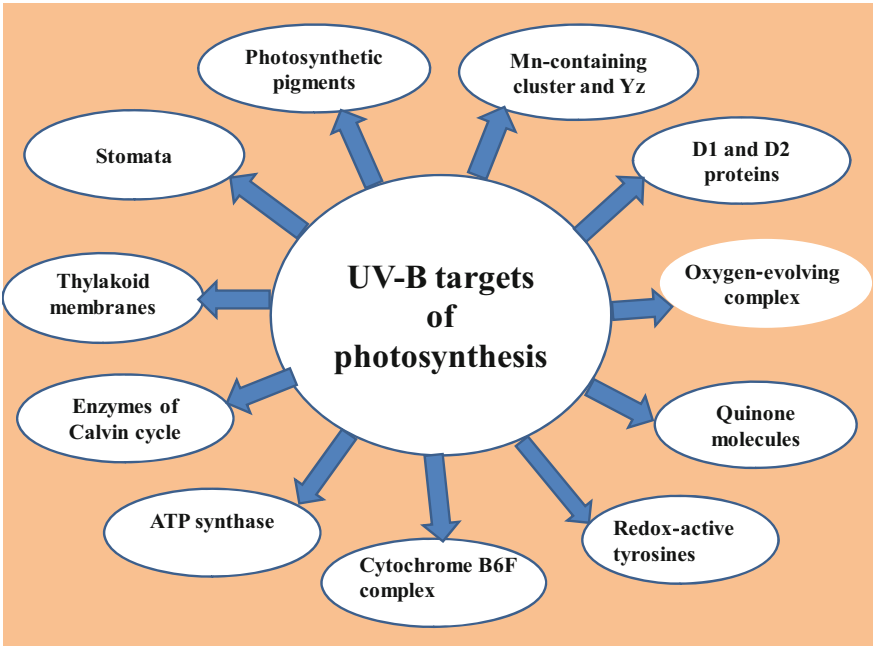

Fig. 4.1 UV-B targets of photosynthesis

many plant species, a decrease in leaf thickness was recorded in cotton (Kakani et al. 2003). The enhancement in leaf thickness was mainly due to the accumulation of spongy mesophyll cells, and the palisade cells were wider and shorter after UV-B irradiation. These harmful effects of UV-B on anatomical structure would hinder the CO_2 uptake and sequentially photosynthesis. Under increased UV-B, trichomes density enhanced on the abaxial leaf surface and there was a decrease in stomatal frequency and number of xylem tubes (Lingakumar and Kulandaivelu 1993; Barnes et al. 1996).

4.4 Effect of UV-B on Photosynthetic Pigments

For light attenuation of a specific wavelength, plants have developed superb sensory systems called as photoreceptors. These photoreceptors can be "photosynthetic" (chlorophylls and carotenoids), driving photosynthesis by absorption of light, or "photomorphogenic" (phytochromes), initiating the developmental shift from dark to light growth.

4.4.1 Chlorophylls, Carotenoids, and Other Pigments

UV-B affects the pigments, either through inhibiting their synthesis or affecting the enzymes involved in their synthesis. A significant decrease in chlorophyll a, b and total chlorophyll content has been observed due to UV-B radiation in barley, corn, bean, radish (Tevini et al. 1981), sweet almond (Ranjbarfordoei et al. 2011), and pepper (Hoffmann et al. 2015). Carotenoids protects chlorophyll from photo-oxidative damage; therefore, a decrease in carotenoids could have deleterious effect on chlorophyll content under UV-B stress (Agrawal and Rathore 2007; Mishra et al. 2008). UV-B generates free radicals that causes degradation of photosynthetic pigments and causes damage of photosynthetic apparatus (Hideg et al. 2013). Other leaf pigments, such as anthocyanin, flavonols, and flavones, are also affected by UV-B (Stafford 1990; Tevini et al. 1991). These pigments act as a protective cover for the photosynthetic machinery against UV-B injury (Feng et al. 2007).

4.4.2 Photosystem II

PS II is a multifunctional protein complex present in the thylakoid membrane and its main function is the splitting of water to molecular oxygen in presence of light (Kulandaivelu et al. 1991; Chaturvedi et al. 1998; Mattoo et al. 1999). Other targets of UV-B in PS II are quinine electron acceptors, tyrosine electron donors and the D1 and D2 protein reaction centers (Lidon and Ramalho 2011). D1 and D2 are most sensitive, whereas only minor or no effects are observed for CP43 and the extrinsic proteins of 17, 23 and 33 kDa (Ihle 1997; Sass et al. 1997). UV-B stress degrades D1 and D2 proteins, leading to deterioration of PS II, which can be calculated in terms of variable chlorophyll florescence or reduced oxygen evolution (Bolink et al. 2001; Savitch et al. 2001). UV-B stress damages first the acceptor side and then the donor side of PS II (Van Rensen et al. 2007). UV-B generate ROS which leads to decreased PS II activity (Prasad and Zeeshan 2004; Gerhardt et al. 2005; Prasad et al. 2005; Szilard et al. 2007). In the PS II complex, UV-B-sensitive sites are redox-active tyrosines, Mn cluster (donor side), and quinone electron acceptors QA and QB (acceptor side) (Vass 2012). The main reason behind inhibition of the PS II function by UV-B is the inactivated electron transport between the Mn cluster and the redox-active tyrosines (Tyr-Z, Tyr-D), on the donor side (Larkum et al. 2001; Szilard et al. 2007), or it can be quinone electron acceptors (Melis et al. 1992).

PS II components which are the main targets of UV-B radiation in chronological order are as follows: (1) oxygen-evolving complex, (2) plastoquinone (electron acceptor), (3) tyrosine residues (electron donor), and (4) light-harvesting system.

4.4.3 Oxygen-Evolving Complex

The oxygen-evolving complex (OEC) appears to be UV-sensitive, and the main effect of UV-B is the inhibition of the Mn cluster of the OEC which inactivates the

electron transport chain (Lidon et al. 2012). Direct absorption of UV-B by Mn ions in Mn (III) and Mn (IV) oxidation states causes inhibition of oxygen evolution and damages quinone electron acceptors and tyrosine donors which ultimately lead to the degradation of D1 and D2 reaction center (Vass et al. 2005; Tyystjärvi 2008). Rodrigues et al. (2006) observed that QA^- (semiquinone radical) is photosensitized by UV-B, initiates the reactions, disrupts the D2 protein, and obstructs the electron transport of PS II. Damaging effect of UV-B may produce a structural or functional change making the entire complex inactive (Szilard et al. 2007; Ivanov et al. 2008; Albert et al. 2011).

4.4.4 Plastoquinones and Redox-Active Tyrosines

Followed by the OEC impairment, the subsequent targets of UV-B are quinone electron acceptors and tyrosine donors. Loss of EPR signals indicates deterioration to the redox function of Tyr Z and Tyr D (Vass et al. 1995, 1996). UV-B influences the QB quinone acceptors more as compared to QA, due to structural changes in QB-binding site or specific destruction of the reduced quinone (Dobrikova et al. 2013). This indicates high sensitivity of the PS II acceptor side towards UV-B as it is associated with damage to the QB quinone acceptor (Vass et al. 2005). Water oxidation is catalyzed by a cluster of four Mn ions which undergo light-induced changes in their oxidation states, called S-states. The complex cycles through five S-states denoted as S0, S1, S2, S3, and S4 and oxygen is released during the S3→S4→S0 transition, in which S4 is a short-lived intermediate. UV-B induced damage of oxygen evolution is S-state dependent, exhibiting higher sensitivity in the higher (S3, S2) than in the lower (S1, S0) S-states, which is likely to be related to UV-B absorption either directly by the Mn cluster or by intermediates of the water oxidizing process (Szilard et al. 2007). Higher sensitivity of S2 and S3 to UV-B indicates that Mn (III) and Mn (IV) are main sensors involved in UV-B-induced damage (Vass et al. 2001; Tyystjärvi 2008). Also, it has been reported that UV-B induces splitting of disulfide bridges in the 33 kDa water-soluble protein subunit of the water-oxidizing complex which implies inactivation of Mn site (Ferreira et al. 2004).

4.4.5 D1 and D2 Proteins

One of the major impacts of UV-B radiation is the damage to the PS II reaction center protein complex, mainly the D1 and D2 subunits (Jansen et al. 1993; Barbato et al. 1995; Friso et al. 1995; Spetea et al. 1996). The UV-B prone damage site at D1 is probably located at the center, or near the lumenal end, of the second transmembrane helix, which is closely associated with the assumed binding site of the catalytic cluster of water oxidation (Zouni et al. 2001; Kamiya and Shen 2003).

4.4.6 Photosystem I

Various reports have been demonstrated that the impact of UV-B radiation has a minor or no effects on PS I as compared to PS II (Turcsányi and Vass 2000), which is probably because of the absence of a water-oxidizing complex in PS I and redox active tyrosine. However, UV-B induced changes in linear electron transport (Lidon and Ramalho 2011) and cyclic phosphorylation (Pang and Hays 1991) of PS I have also been recorded. The main target within PS I is contributed to the production of ROS, damage of protein structure, generation of lipid peroxidation of thylakoids, and proteolysis of PS II (Lidon et al. 2011). Damage to PS I has been mainly related to electron transfer components X and centers A and B associated with 18/16 kDa polypeptides (Lidon and Henriques 1993).

4.4.7 Cytochrome B6F Complex

The cytochrome B6F complex (Cyt B6F) along with PS II and PS I is a main membrane protein complex comprising the electron transport chain in thylakoid membrane (Sang et al. 2010). The cytochrome B6/F complex consists of two quinone binding sites: one where quinol is oxidized and the other where quinine is reduced. Cyt B6F seems to be resistant to UV-B, and quinones mediate UV-B induced damage to the photosynthetic apparatus (Eichhorn et al. 1993).

4.4.8 ATP Synthase

Cytochrome B6F complex is the least affected thylakoid component by UV-B irradiation (Strid et al. 1990), while most affected are ATP synthase and Rubisco. The reaction of photophosphorylation is catalyzed by ATP-synthase in chloroplast. Lower photophosphorylation and ATPase activities were observed under enhanced UV-B radiation possibly due to alteration in the transformation efficiency of electrical energy into chemical energy, causing reduction in the photochemical capacity and CO_2 assimilation (Yang et al. 2013).

4.4.9 Rubisco

Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) is the most abundant leaf protein, which is also susceptible towards UV-B (Yu et al. 2013). In the Calvin cycle, it assimilates carbon di-oxide into carbohydrates (Jordan 1993; Hartman and Harpel 1994). Rubisco composed of eight large subunits (53 kDa) and eight small subunits (14 kDa). UV-B radiation reduces Rubisco content, activity, and as well as the mRNA levels. Under the influence of UV-B, large subunit (54 kDa) of Rubisco could change into a 66 kDa protein (Gerhardt et al. 1999; Savitch et al. 2001) which impairs its catalytic capacity (Jordan et al. 1992a, b). Rubisco contains tryptophans

that are the probable sites for UV-B damage. Rubisco could be inactivated under UV-B possibly due to degradation of the protein, modification of the peptide chain, or reduced gene transcription (Jordan et al. 1994; Takeuchi et al. 2002; Bouchard et al. 2008). UV-B generates ROS which causes proteolytic degradation of the Rubisco (Caldwell 1993; Desimone et al. 1998; Ishida et al. 1999; Bischof et al. 2002; Pedro et al. 2009).

4.5 Effect of UV-B on Photosynthesis

UV-B acts as a physiological factor with the prospective to alter growth, photosynthesis, and crop yield (Ballaré et al. 2011; Kataria et al. 2013; Sharma et al. 2019; Joshi-Paneri et al. 2020). Photosynthesis is the most sensitive plant process, as it is unswervingly related to growth, biomass production, and seed yield, it becomes obligatory to study the effect of UV-B on photosynthesis (Strid et al. 1994; Tevini 1994; Teramura and Sullivan 1994; Fiscus and Booker 1995; Lidon and Ramalho 2011; Lidon et al. 2012). Many reports have shown that UV-B under high irradiance inhibits photosynthesis in pea (Nogués and Baker 1995), soybean (Middleton and Teramura 1993), rice (Teramura et al. 1991), oilseed rape (Allen et al. 1997), and algae (Lesser 1996). There are both direct and indirect effects of UV-B radiation on photosynthesis (Kataria et al. 2014). Under the direct influence of UV-B, starch and chlorophyll contents are decreased (Ines et al. 2007; Surabhi et al. 2009), there is loss in integrity of the thylakoid membranes (Swarna et al. 2012), photodamage of PS II (Hollosy 2002; Hideg et al. 2006; Tyystjärvi 2008; Dobrikova et al. 2013), activity loss of enzyme sedoheptulose 1,7-biphosphatase (Allen et al. 1998), diminished RuBisCO activity (Allen et al. 1997), and reduced fixation of CO_2 and O_2 evolution (Kakani et al. 2003; Cicek et al. 2012). Under high UV-B radiation, there is a breakdown of the structural integrity of chloroplasts which ultimately leads to the reduction of chlorophyll content and photosynthesis (Sullivan and Rozema 1999). Primary carbon metabolism is also sensitive to UV-B which can be seen from the reduction in O_2 evolution, organic acids, and soluble sugars. In UV-B exposed seedlings, glucose, fructose, and sucrose were the extensively affected soluble sugars, while glycerate, fumarate, and succinate were the considerably reduced organic acids. Indirect effects of UV-B on photosynthesis include changes in gas exchange efficiency, stomatal closure (Nogues et al. 1999), leaf anatomy (Bornman and Vogelmann 1991), canopy morphology (Zhao et al. 2004), and leaf color which ultimately results in desiccation, chlorosis, and necrosis of the leaves (Visser et al. 1997).

4.6 Effect of UV-B on Photosynthetic Gene Expression

UV-B exposure can inhibit photosynthesis by altering gene expression of photosynthetic process (Caldwell et al. 2007) which ultimately causes reduction in synthesis and expression of photosynthetic proteins such as Rubisco (Jordan et al. 1994;

MacKemess et al. 1997) and the Chl a/b-binding proteins (Lhcb) of the photosystem II (psb A). Nuclear-encoded genes are more susceptible to UV-B, for example, atpc-g subunit of ATP synthase, ca—chl a/b binding protein of PS II and rbcs—small subunit of Rubisco as compared to chloroplast-encoded genes such as psb A3—D1, D2 protein, atpB, and atpE- B and E subunit of ATP synthase, pet B—cyt-b, pet D—subunit IV of cyt b/f complex and rbcL–large subunit of Rubisco (Jenkins 2009). Contrary to this gene down-regulation, UV-B causes gene up-regulation of gene-encoding antioxidant enzymes and the enzymes involved in the synthesis of pigments (Jordan et al. 1994; Rao et al. 1996; MacKerness et al. 1998).

4.7 Stomatal Regulation

Stomatal regulation is another crucial process restraining leaf photosynthesis. UV-B affects stomata both directly and indirectly. Direct effect of UV-B on stomata is by controlling the mechanisms of opening of the guard cells, whereas indirect effect is by changing the mesophyll photosynthesis (Nogues et al. 1999) which ultimately causes damage to PS II in the guard cells, inhibits photophosphorylation, and affects ATPase proton pump and ion transport (Allen et al. 1998). Under the UV-B exposure, stomata are unable to readjust their aperture. UV-B causes reduction in photosynthesis which can also be caused by reduction in stomatal conductance, stomatal density, and opening of stomata (Dai et al. 1995; Jansen and Van Den Noort 2000; Feng et al. 2003; Duan et al. 2008; Reddy et al. 2013).

4.8 Effect of UV-B on Plant Productivity

Increase in UV-B radiation level can lead to deleterious effects on crop photosynthesis and productivity (Robson et al. 2015). UV-B radiation alters the protein content and enzyme activity, damages the plant photosynthetic apparatus, membrane, DNA and transforms the leaf chemistry. This damage ultimately causes reductions in vegetative biomass and grain yield. Flowering delay was the most important negative aspect, it is directly connected to yield reduction in crop plants (Mark et al. 1996). Decrease in photosynthetic rates due to decline in enzyme activity, PS II efficiency, and stomatal conductance leads to the reduction in the total biomass production and ultimately yield (Strid et al. 1990; Jordan et al. 1992a, b; Searles et al. 2001; Kakani et al. 2003; Ruhland et al. 2005).

4.9 UV-B-Induced Plant Responses

UV-B can induce stress responses or photomorphogenic responses in plants. The kind of responses that are tempted by UV-B mainly depends on the level of exposure. High UV-B level causes stress-related processes including cellular damage, DNA damage, production of ROS, and oxidative stress, and thus activates a

signal transduction pathway. Low levels of UV-B occur via a UV-B which activates special signaling pathways such as kinases, calcium, and the formation of ROS. High UV-B radiation mainly controls the genes which encode for photosynthetic genes, DNA repair, cell cycle genes, proteins involved in the synthesis of antioxidative enzymes, and protective pigments. However, low UV-B encourages photo-morphogenic responses like inhibition of hypocotyls growth, cotyledon expansion, opening of stomata, synthesis of anthocyanins, and flavonoids (Ulm and Nagy 2005; Jenkins et al. 2009). These responses are facilitated by photoreceptor UV RESISTANCE LOCUS8 (UVR8), which are required by plants to adjust to UV-B stress (Rizzini et al. 2011; Li et al. 2013). UVR8 is required for the induction of genes in UV protection (flavonoid and alkaloid pathways). UVR8 is a photoreceptor of UV-B in plants which exists in the form of dimers, while UV-B acts unswervingly on the protein to promote its monomerization. This photoconversion is particular to UV-B and requires only low levels of UV-B that initiates changes in transcription. UV-B exposure kindles rapid nuclear accumulation of UVR8 and its interface with the E3 ubiquitin ligase. Photomorphogenic 1 (COP1) protein and elongated Hypocotyl 5 (HY5) is required for the UV-B photomorphogenic response (Favory et al. 2009).

4.10 Protection, Adaptation, and Repair

Plants acquire diverse defense mechanisms which alter the kindliness of the photosynthetic machinery to UV-B. These defensive mechanisms include production of a waxy cuticle, increased length of epidermal cells, increase of UV-B absorbing compounds (flavonoids and phenolic components), and formation of ROS (Haupt and Scheuerlein 1990). Plants can reduce the effect of UV-B on the photosynthesis apparatus by developing a set of repair mechanisms like photoreactivation, excision, and recombination repair. DNA is predominantly susceptible to UV-B radiation because UV-B causes phototransformations, which results in the production of cyclobutane pyrimidine dimers (CPDs) and pyrimidine (6–4) pyrimidinone dimers (6–4 PPs) (Caldwell et al. 2003). CPDs can be repaired by all of these repair mechanisms. In addition, plants under UV-B also repair by homologous recombination (Ries et al. 2000).

4.11 Conclusion and Future Perspective

Enhanced UV-B exposure causes several primary effects on plant growth. These include decreased vegetative growth, damaged photosynthetic system, and up regulation of pathways which produce defense compounds which subsequently result in diminished growth and development of plants, which in turn declines photosynthesis, reduces biomass, and yield. The major targets of UV-B induced damage in plants are the Calvin cycle enzymes, PS II complex, and the nucleic acid molecules. PS II is more susceptible to UV-B and in PS II, D1/D2 proteins; OEC, LHCII, quinone

electron acceptors, the catalytic Mn4Ca cluster, and the tyrosine electron donors are the main target sites. However, further damage occurs at the QA and QB quinone electron acceptors and the TyrD and Tyr-Z electron donors. UV-B-induced ROS production which causes oxidative stress to membrane lipids, proteins, and nucleic acids. This results in decline of photosynthetic pigments which leads reduced photosynthetic efficiency of PS II and Rubisco activity hence ultimately alters the crop growth and yield. To overcome this damage under UV-B stress, plants increases the activity of antioxidant enzymes like peroxidase, ascorbic acid peroxidase, superoxide dismutase, glutathione reductase, and non-enzymatic antioxidants like carotenoids, phenolics, ascorbate, glutathione, and tocopherols.

Despite extensive reports on UV-B, the actual impact of natural UV-B is not fully unstated because most studies involved exposing plants to quixotically high UV-B in growth chambers or greenhouses. Further exploration is necessary to apprehend these possibilities. An emerging field of UV research concerns the revelation of the connection between UV damage caused on the photosynthetic machinery to that at the nucleic acid level. Another important research topic will be studying the role of UV radiation in signal transduction pathways in cells of photosynthetic organisms. It will be extremely crucial to investigate the relation of these signaling pathways with the adjustment and accustoming processes occurring in plants under UV-B exposure. Also, with a distinct perceptive of the interaction among UV-B, phytohormones and responses to environmental factors, UVR8 signaling may prove a means to control plant tolerance to abiotic and biotic stress. Future challenge will include alteration in UV radiation in amalgamation with other globally changing factors such as increased carbon dioxide, temperature, and drought which will influence the defensive repair systems under present-day conditions and future UV-B levels.

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Solar UV-B and Primary Producers in Aquatic Ecosystems

5

Donat-Peter Häder

Abstract

Primary producers in aquatic ecosystems are bound to dwell in the photic zone since exposure to solar visible radiation is a requirement for energy harvesting in photosynthesis. The physical depth of the photic zone depends on the penetration of solar radiation through the water column. Simultaneously the organisms are exposed to detrimental solar UV radiation. While moderate levels of UV-A radiation can be useful in photosynthesis and for repair mechanisms, UV-B radiation is detrimental for structural integrity and physiological functions. In addition to damaging proteins, accessory pigments and membranes, the main targets for short-wavelength photons are the cellular DNA and the photosynthetic apparatus. Having been exposed to solar UV radiation during evolution resulted in the development of several protective mechanisms to avoid the challenge. These include vertical migration, effective repair mechanisms and protective pigments to mitigate the damage.

Keywords

Aquatic ecosystems · UV-A · UV-B · Radiation damage and mitigation · Protective pigments

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5.1 Introduction

About 71% of the Earth is covered by water. Freshwater habitats represent less than 1% of this, while the large majority is contributed by marine ecosystems. The productivity of aquatic habitats rivals that of all terrestrial ecosystems taken together even though the standing crop is only 1% of that of their terrestrial counterparts (Falkowski 2013). In accordance, aquatic primary producers absorb the same amount of atmospheric CO_2 as all terrestrial plants, which correspond to 50–60 Pg carbon (Fig. 5.1).

Among the primary producers, macroalgae are restricted to rocky shores of the continental shelves, with the notable exception of the brown floating *Sargassum* species in the mid-Atlantic Ocean east of the Gulf of Mexico (Dierssen et al. 2015) as well as in the western Yellow Sea off China as seen by high-resolution satellite observations (Xing et al. 2017). The lion's share of the primary producers is represented by prokaryotic and eukaryotic unicellular or multicellular phytoplankton. The phytoplankton is not evenly distributed in the oceans. The highest concentrations are found in the polar waters and along the equator and consequently most fish are harvested in these regions (Fig. 5.2). In contrast, the mid-latitude areas of both hemispheres are almost deserts (Häder and Gao 2018a).

Approximately, 90% of the biomass enters the food web and is taken up by primary and secondary consumers, while the rest sediments to the deep sea in the form of fecal pellets and dead organisms. The sedimenting particles can be observed as "marine snow" (Turner 2002); the removal of carbon originating from the atmosphere is called "biological pump" (Basu and Mackey 2018).

Because the primary producers need solar radiation for their photosynthetic energy conversion, they are restricted to the photic zone (also euphotic, epipelagic or sunlit zone) which extends from the surface to a depth where the surface irradiance is attenuated to 10% (Falkowski and Knoll 2011). This is the compensation point below which respiration exceeds photosynthesis and no net positive biomass

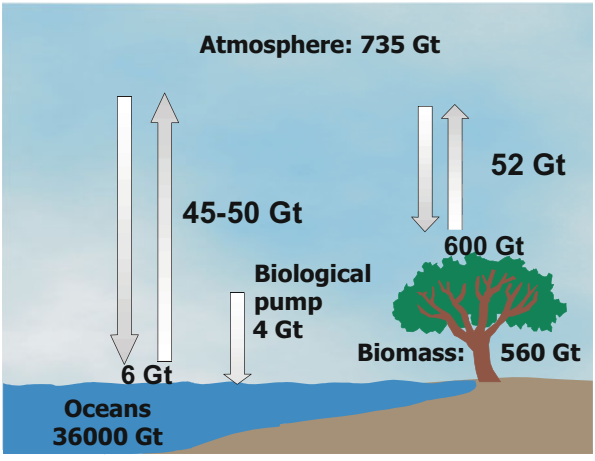

Fig. 5.1 Standing crop and carbon uptake of terrestrial and aquatic ecosystems (in gigatonnes)

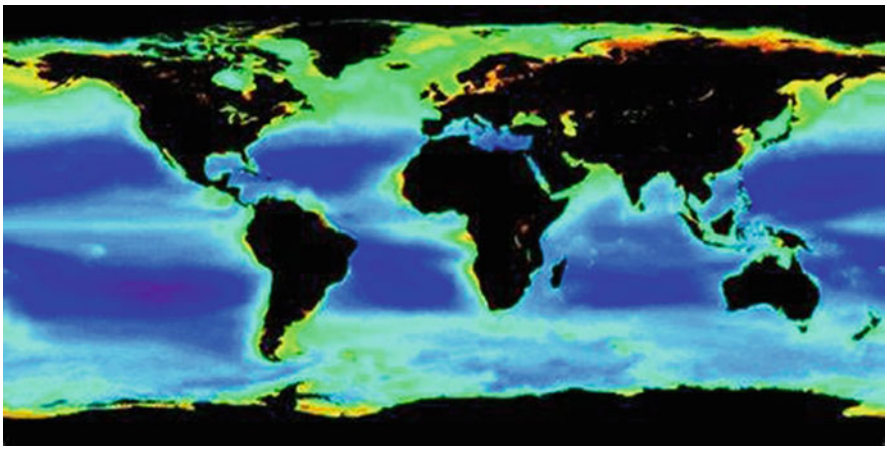

Fig. 5.2 Chlorophyll fluorescence in the oceans as seen by satellite imaging in pseudocolors (high concentrations green to orange; low concentrations blue to purple). (Courtesy https://www.nasa.gov/vision/earth/livingthings/glowing_algae.html)

production is possible. The physical depth of the photic zone depends on the transparency of the water: in clear open ocean waters, it can be 200 m, and in turbid coastal waters, it may be limited to a few meters or even less. Another definition relates to the upper mixed layer (UML) in which most of the phytoplankton and their predators dwell (Tett 1990). The lower boundary of the UML is the thermocline which marks a sharp decrease in temperature which a diver notices when he descends below the warm surface layer. The UML is characterized by wind-generated turbulence to which the organisms are exposed (D'Asaro 2014).

5.2 Stress Factors for Aquatic Primary Producers

Productivity of primary aquatic producers is controlled by a number of environmental stress factors. Temperature, salinity, availability of nutrients, solar irradiance, and pollution are the major drivers of growth and development in phytoplankton and macroalgae.

Due to clime change, the temperature in the ocean surface waters has increased by about 0.23 °C per decade since the late 1970s while the atmosphere became warmer by about double that value (Ishii et al. 2017). This does not seem much, but has resulted in major shifts in the biota as seen by changes in the habitat selection and species composition of phytoplankton assemblages (Thomas et al. 2012), such as cyanobacteria (Pittera et al. 2014), dinoflagellates (Fu et al. 2012), coccolithophorids, and diatoms (Mericoa et al. 2004; Hare et al. 2007). The temperature increase in Arctic waters is almost double that of mid-latitude waters with the result that tropical radiolaria have been found in Arctic waters (Bjørklund et al. 2012). The permissive temperature for corals is about 28 °C which has been

exceeding in a number of tropical habitats such as the Gulf of Mexico and the Great Barrier Reef resulting in massive bleaching and break down of reef communities (Lough et al. 2018; Häder 2018a).

The rising temperature increases the stratification in the top layers of the oceans and causes a shoaling of the UML (Häder and Gao 2017, 2018b; Gao et al. 2018). This exposes the organisms in the UML to higher solar visible and UV radiation even though the irradiance at the surface does not change (Gao and Häder 2020). In addition, it inhibits the penetration of nutrients from deep water layers into the UML resulting in reduced growth and productivity (Häder and Gao 2018c).

Another consequence of global climate change is ocean acidification. The increasing atmospheric CO_2 concentrations—from 270 ppm in 1880 to more than 400 ppm today—are reflected by decreasing pH values in ocean surface waters since the absorbed CO_2 forms carbonic acid. The proton concentration has increased by about 40% (Häder and Gao 2015; Gao and Häder 2017).

5.3 UV Penetration into the Water Column

Primary producers have to be close to the water surface in the photic zone in order to harvest solar radiation for their photosynthetic energy conversion. Simultaneously, they cannot avoid being exposed to solar UV radiation. Macroalgae and seagrasses are (mostly) attached to the substratum and have no means to escape the UV stress. In addition to the daily variation in solar radiation and changes due to cloud cover, they are subject to strongly varying irradiances due to the non-circadian tidal rhythm. Depending on their resilience or sensitivity, different species choose habitats close to the surface where at times they are exposed to unfiltered solar radiation in the intertidal zone, while others prefer to dwell deeper in the water column in the subtidal zone. Some chlorophytes such as *Ulva* or *Enteromorpha* belong to the first group (Häder et al. 1999, 2001), while many Rhodophytes such as *Peyssonnelia* or *Callithamnion* are found at a depth of several meters or tens of meters (Häder et al. 1998, 2004).

In coastal waters, the penetration of solar visible and UV radiation is affected by many factors. Depending on the solar zenith angle, more or less radiation is reflected from the water surface. In the water column, particulate and dissolved organic and inorganic substances attenuate the impinging radiation (Snyder et al. 2008; Feister and Häder 2019). Particulate inorganic matter (PIM) is composed of sand and silt, while particulate organic material (POM) includes bacteria, plankton, and decaying organic particles and debris carried into coastal waters by terrestrial runoff (Ittekkot and Laane 1991; Nakatsuka et al. 1992). Rivers transport large amounts of debris which can be detected in their plumes hundreds of kilometers from the coast which can be visualized by satellite imaging (Warrick et al. 2004). With global climate change and increasing temperatures as well as changing precipitation patterns, the concentrations of absorbing materials in coastal waters will change (Larsen et al. 2011; Wilson et al. 2013). On the other hand, melting of ice and snow increases

penetration of solar radiation in polar waters due to the influx of clear freshwater (Light et al. 2008).

The dissolved materials are either inorganic (DIM, mainly minerals) or organic (DOM). The latter are degradation products from decaying biological material which can be either of terrigenous substances entering coastal ecosystems by runoff (Frigstad et al. 2020) or derived from dead phytoplankton, macroalgae, and seagrasses (Bai et al. 2018). While PIM and DIM attenuate the impinging solar radiation neutrally at all wavelengths by absorption and refraction, DOM absorbs stronger in the UV than in the visible range and is therefore called colored DOM (cDOM) (Webb et al. 2019). UV breaks down cDOM which allows bacteria to metabolize the fragments which in turn reduces the attenuation (Boreen et al. 2008). Jerlov (1976) has classified water systems according to their optical properties. Clear open oceans have a higher transmission than murky coastal waters. Super oligotrophic waters in the South Pacific Gyre allow 1% of the impinging solar radiation at the surface to penetrate to a depth of 84 m (Tedetti et al. 2007). In contrast, penetration of solar radiation can be as low as a few centimeters or meters in inland and coastal habitats (Bukata et al. 1995). Global climate change will alter the optical properties of aquatic ecosystems and the exposure of organisms to solar UV and visible radiation due to shoaling of the UML (Jankowski et al. 2006). Different wavelengths are absorbed to a different degree (Fig. 5.3).

5.4 UV-B Effects on Aquatic Primary Producers

UV-B photons have the highest energy in the solar spectrum reaching the Earth's surface. They are effectively absorbed by vital biomolecules such as proteins, lipids, and nucleic acids such as DNA and RNA which are mutilated and destroyed (Park et al. 2018). In addition, UV radiation can be absorbed by a number of biomolecules such as chlorophyll which transfer the excitation energy to a nearby oxygen molecule forming a reactive oxygen species (ROS) such as singlet oxygen ($^1O_2$), peroxides, superoxide hydroxyl radicals, and alpha-oxygen (Diaz and Plummer 2018). Since these ROS species can have highly detrimental effects of cellular biomolecules and structures, they are eliminated by either antioxidant enzymes such as superoxide dismutase, peroxidase, catalase, or glutathione reductase (Cheng et al. 2016) or by non-enzymatic antioxidants such as carotenoids, tocopherol, ascorbic acid, glutathione, flavonoids, and phenolic compounds (Rezayian et al. 2019).

5.4.1 UV-B Effects on Photosynthesis

One of the main targets of solar UV-B radiation is photosynthesis (Gao et al. 2018). Photosynthetic bacteria were the first prokaryotes to utilize sunlight to produce organic substances using one of two possible photosystems. The Gram-negative cyanobacteria were the first oxygenic prokaryotes to employ two photosystems in

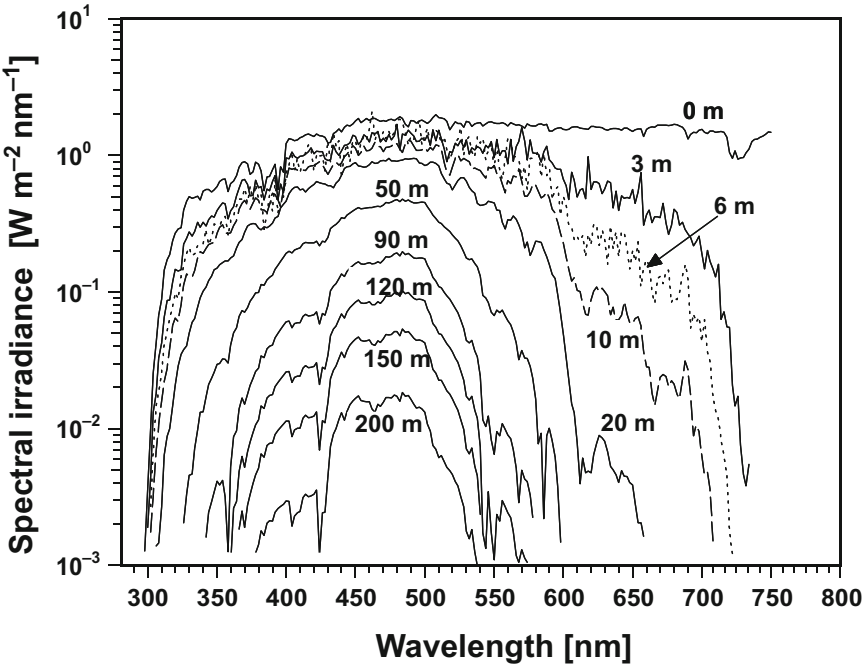

Fig. 5.3 Spectral solar scalar irradiance measured between 0 and 6 m depth in the central Atlantic Ocean and calculated for 10–200 m based on the spectral attenuation coefficient for oceanic water (Jerlov type 1). (Redrawn after data from (Piazena et al. 2002))

tandem to produce reduction equivalents utilized to reduce CO_2 in the synthesis of sugar (Pathak et al. 2018). The overall equation for the endergonic photosynthetic reaction is.

$$6CO_2 + 12H_2O \rightarrow C_6H_{12}O_6 + 6H_2O + 6O_2 \tag{5.1}$$

Light is absorbed by a special pair of chlorophyll *a* molecules (P680) in the reaction center to release electrons that are taken up by a plastoquinone in photosystem II (PSII). From there, they follow a chain of redox components until they reach P700 in the reaction center of photosystem I where they are again activated to a higher energy level until they are used to reduce nicotinamide dinucleotide phosphate (NADP) (Häder and Tevini 1987). The missing electrons in PSII are replaced by the photosynthetic splitting of water in a manganese complex.

$$2H_2O \rightarrow O_2 + 4e^- + 4H^+ \tag{5.2}$$

Oxygen is a waste product in this process and has accumulated in the previously anoxic atmosphere of our planet starting about 2.8–3.5 billion years ago in the Precambrian era (Pathak et al. 2019a).

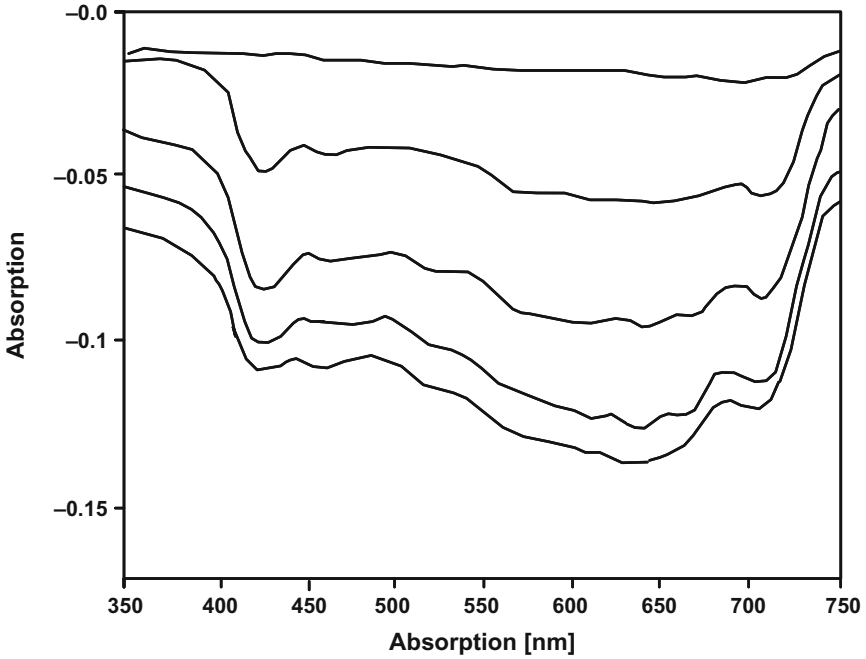

Fig. 5.4 Absorption difference spectra of *Peridinium gatunense* measured after increasing exposure times to solar radiation in Portugal (from top to bottom: 15, 30, 60, 90, and 120 min during noon). (Redrawn after (Häder et al. 1990))

Light is harvested by antenna pigments such as carotenoids, phycobilins, and other chlorophylls and then funneled to the reaction centers PSI and PSII. These accessory pigments also absorb in the UV-B region and are bleached by excessive short-wavelength radiation (Fig. 5.4). Cyanobacteria possess phycobilisomes as antenna structures attached to the thylakoid membrane; they are composed of several phycobiliproteins. The absorbed photons are passed from one pigment to the next (MacColl 1998):

$$\text{Phycoerythrin} \rightarrow \text{Phycocyanin} \rightarrow \text{Allophycocyanin} \rightarrow \text{Chlorophyll } a$$

When exposed to excessive solar UV radiation, the transport of the harvested energy is reduced by the disruption of the phycobilisomes and released as fluorescence from the phycobiliproteins (Fig. 5.5). Initially, the fluorescence increased after exposure to UV radiation indicating a reduced transport of photosynthetic energy to chlorophyll; later on, the fluorescence emission decreased and the maximum shifted to a shorter wavelength indicating that the phycobilisome structure was affected and the phycobiliproteins bleached.

The D1 protein is an essential 32 kDa component in the electron transport chain within PSII of terrestrial and aquatic primary producers (Han et al. 2000). This

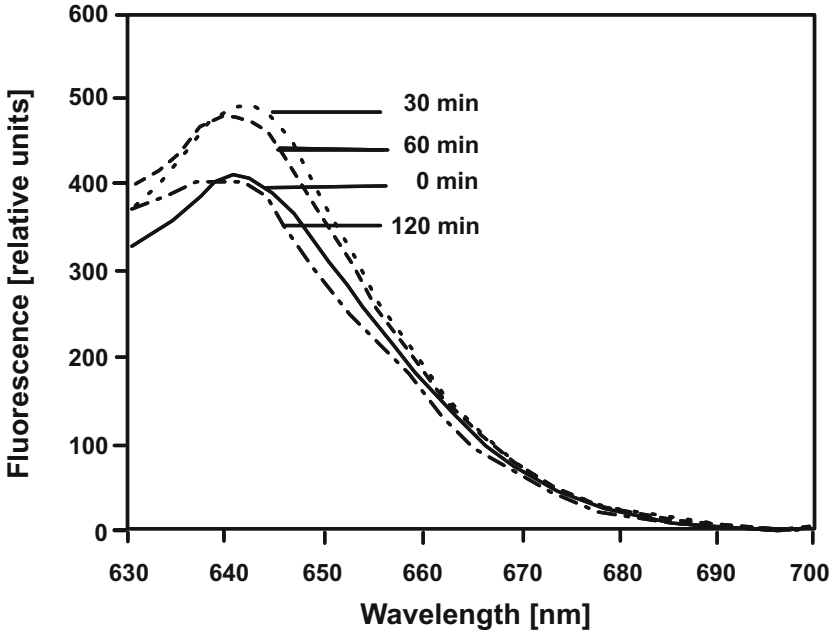

Fig. 5.5 Fluorescence emission spectra of phycocyanin from *Nostoc* spec. excited at 620 nm after increasing exposure times to UV-B radiation (5 Wm^{-2}). (Redrawn after data from (Sinha and Häder 1998))

protein is a prominent target of solar UV-B radiation which kinks the structure of the protein (Nina Bouchard et al. 2005). This damage is detected by the cell and the mutilated protein is removed by a protease and replaced by a de novo-synthesized molecule (Sass et al. 1997; Mate et al. 1998).

Any damage of the photosynthetic apparatus by solar UV-B radiation results in a reduction of the quantum yield and performance. Principally, this can be quantified by determining the amount of CO_2 incorporated or the amount of sugar produced (Eq. 5.1). In the field, it is easier to measure the amount of oxygen produced. The oxygen concentration can be determined with a Clark electrode (Li and Graham 2012). The change in the O_2 concentration over time indicates the photosynthetic production or respiratory consumption of oxygen. We have built a box in which thalli are confined in a quartz cuvette exposed to solar radiation at the surface or a desired depth in the water column. Figure 5.6 shows the change in oxygen concentration in the green alga *Caulerpa prolifera* harvested from 5-m depth on the coast of Korinthos, Greece (Häder et al. 1997). Initially, the thalli were kept in darkness for adaptation which resulted in respiratory oxygen consumption. Subsequently, they were exposed to unfiltered solar radiation inducing photosynthetic oxygen production which decreased over time by photoinhibition until respiration exceeded production following 20 min of exposure.

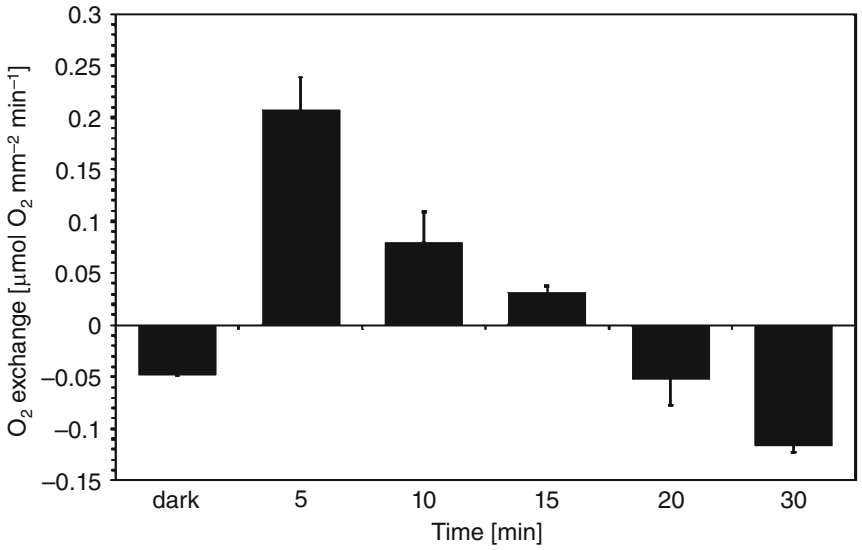

Fig. 5.6 Photosynthetic oxygen exchange (±S.D.) of *Caulerpa prolifera* harvested from 5 m depth and exposed to solar radiation at the surface. Dark respiration was measured before exposure in darkness and then over subsequent 5-min intervals. (Redrawn after data from (Häder et al. 1997))

The damage of the photosynthetic electron transport chain results in reduced quantum efficiency. This can be measured easily and noninvasively by pulse amplitude-modulated (PAM) fluorescence (Consalvey et al. 2005). When photons are absorbed by the photosynthetic apparatus, their energy can be utilized for energy harvesting as described above. However, some of the excitation energy is lost by conversion to heat or by fluorescence emission (Häder 2018b). From the fluorescence signal after a short light pulse, the photochemical quantum yield (efficiency of photosynthetic quantum conversion) can be calculated. After exposure to excessive visible or UV radiation, a part of the excitation energy is lost as non-photochemical quenching reducing the quantum yield. We collected thalli of the green macroalgae *Acetabularia mediterranea* during the summer in the Mediterranean Sea (Korinthos, Greece) from their position at 5-m depth, exposed them to solar radiation at the surface and determined the quantum yield during exposure (Fig. 5.7). Thalli exposed to only PAR (photosynthetic active radiation, 400–700 nm) showed a slight reduction of the quantum yield over time, addition of UV-A worsened the inhibition and even more so unfiltered radiation (including the full UV component), which resulted in maximal inhibition (Porst et al. 1997). Also the recovery in dim light was less effective in thalli exposed to unfiltered solar radiation.

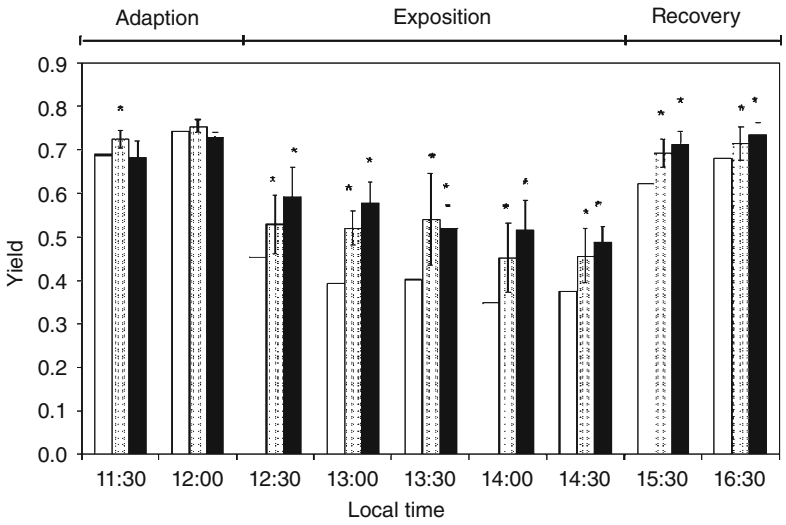

Fig. 5.7 Photosynthetic quantum yield of *Acetabularia mediterranea* harvested from 5 m depth measured after collection (11.30 h), after 30-min dark adaptation and after 30-min intervals exposed to unfiltered solar radiation (open bars), visible plus UV-A (dotted bars), or PAR-only radiation (solid bars). The last two data points were measured after 1 and 2 h of recovery in darkness. Each data point has been averaged from 8 measurements and standard deviation was calculated. Asterisks indicated values which significantly deviate from the values obtained for thalli exposed to unfiltered radiation at each exposure time. (Redrawn after data from (Porst et al. 1997))

5.4.2 DNA Damage by UV-B

The DNA is a vital biomolecule of all living organisms. It has a strong absorption in the UV-B region and absorbs short-wavelength, highly energetic photons. This may lead to various forms of damage, mutations, and death if not repaired on short notice. Depending on the wavelength of the absorbed photons, a number of different damages have been found (Pathak et al. 2019c). The most frequent damage is the formation of cyclobutane pyrimidine dimers (CPD) in which adjacent pyrimidines such as cytosine or thymine form a dimer which results in a local change in the conformation of the DNA structure (Fig. 5.8). This block stops the replication mechanism and thus protein biosynthesis (Tommasi et al. 1996). During sun exposure, hundreds of such dimerization events can occur in each cell which would be detrimental for the organisms if not repaired immediately. In most organisms, this is done by a photolyase, an enzyme which splits the dimer by using the energy of a UV-A or blue photon, a process which is called photoreactivation (Zhang et al. 2013). Because of their vital importance, photolyases have been invented by the earliest life forms during evolution on Earth and are found in bacteria, algae, plants, fungi, invertebrates, and vertebrates, but are lacking in placental mammals such as mice and humans (Essen and Klar 2006). Shorter wavelengths (UV-C) predominantly result in the formation of pyrimidine-pyrimidone (6–4) photoproducts (6–4

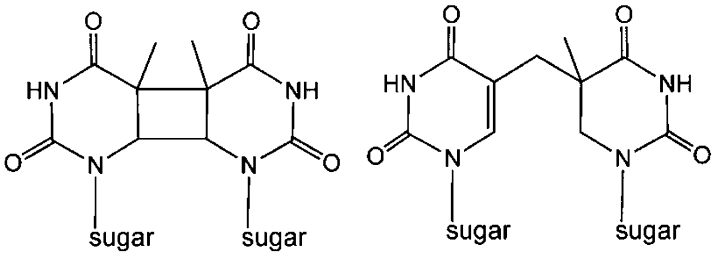

Fig. 5.8 Cyclobutane pyrimidine dimer (left) and 6–4 photoproduct (right)

PP) (Fig. 5.8) (Richa et al. 2015; Rajneesh et al. 2018). Also this lesion is repaired by a specific (6–4) photolyase (Jepsen and Solov'yov 2017). In addition to the main types of damage by UV radiation, other lesions are known including 8-oxo-7, 8-dihydroguanyl, (8-oxoGua), 8-oxo-Ade, 2, 6-diamino-4-hydroxy-5-formamidoguanine, (FapyGua), FapyAde, and oxazolone (Pathak et al. 2019c).

Since DNA repair is a serious task, several other mechanisms have been developed during the evolution to make sure that (almost) every lesion is corrected. Excision repair aims at removal of interstrand cross-links. The mechanism removes a single nucleotide (base excision repair) or a small number of bases and subsequent resynthesis of the original strand (Fleming et al. 2017). DNA glycosylases and AP nucleases are the major enzymes involved in base excision repair (Sinha and Häder 2002b). Single- and double-strand DNA breaks are repaired by recombinational repair. This mechanism is based on filling the gap in one DNA strand by using the complementary strand as matrix (Ranjha et al. 2018). The final resort is SOS repair which is employed after a large accumulation of DNA lesions. This complex pathway has been studied extensively in the bacterium *Escherichia coli* (Maslowska et al. 2019).

5.4.3 Motility and Orientation

Many planktontic primary producers use motility to optimize their position in the habitat to ensure that they receive sufficient solar energy for photosynthesis and to avoid exposure to excessive radiation. However, these mitigating strategies are thwarted by UV-B radiation. For example, motility in the freshwater *Cryptomonas* spec. was found to be completely abolished within 100 min when exposed to solar radiation in an open container during a sunny summer day in Portugal (Häder and Häder 1989a). When the container was covered with a flat cuvette filled with ozone to filter out solar UV-B radiation, the percentage of motile cells decreased much slower (Fig. 5.9). Similarly, motility was impaired by solar or simulated UV-B radiation in the marine flagellate *Cryptomonas maculata*, the slime mold *Dictyostelium discoideum* (Häder 1983), the cyanobacterium *Phormidium uncinatum* (Häder 1984), the green flagellate *Euglena gracilis* (Häder 1985), the desmid *Cosmarium cucumis* (Häder 1987a), and many others.

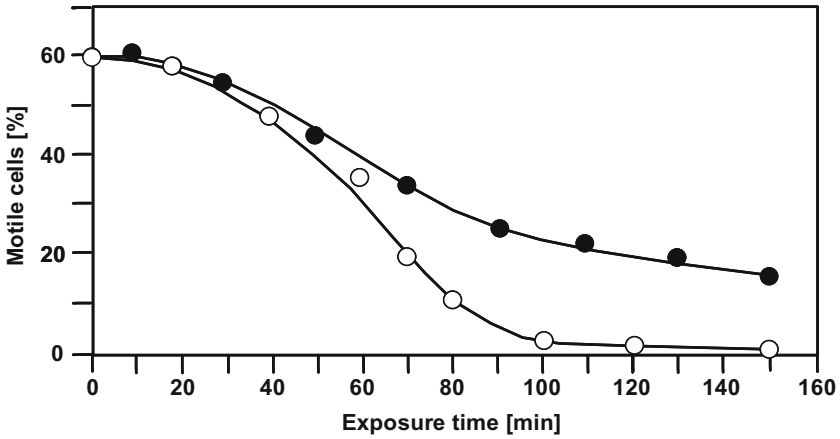

Fig. 5.9 Motility in *Cryptomonas* spec. was completely blocked within 100 min when exposed to unfiltered solar radiation during a sunny summer day in Portugal (open circles). The percentage of motile cells decreased much slower when the radiation was filtered through a cuvette filled with artificially produced ozone (closed circles). (Redrawn after data from (Häder and Häder 1989a))

Motile microorganisms use light and gravity as external clues to find an optimal position in the water column for survival, growth, and reproduction. Many respond to light by moving toward a light source (positive phototaxis) at low irradiances, but move in the opposite direction (negative phototaxis) at excessive irradiances (Häder 1979; Lenci et al. 1984). The precision of orientation is impaired by exposure to solar and artificial UV-B radiation (Häder 1986, 1996). For example, short wavelength radiation deteriorates the precision of negative phototaxis in the green flagellate *Euglena gracilis*, while radiation $\geq$310 nm had no significant effect (Häder 1985). Likewise, photoorientation was found to be impaired by solar and artificial UV-B radiation in the cyanobacterium *Phormidium* (Häder et al. 1986; Häder 1987b), green and colorless flagellates (Häder and Häder 1989b), and many other motile phytoplankton organisms (Häder 1993). Further analysis revealed that the impaired photoorientation is due to damage of the paraflagellar body in *Euglena gracilis*, the photoreceptor in this flagellate (Brodhun and Häder 1993, 1995).

Another important external factor for motile microorganism to find a suitable niche in the habitat is gravity (Häder et al. 2017). The organisms can respond by swimming upwards (negative gravitaxis), downwards (positive gravitaxis), or perpendicular to the gravity vector of the Earth (diagravitaxis) (Häder 1987c; Eggersdorfer and Häder 1991). In contrast to earlier hypotheses, gravitaxis in *Euglena* has been found to be mediated by a physiologically active gravireceptor which induces a sensory transduction chain involving several enzymatic amplification steps which eventually result in a gradual reorientation keeping the cells on course (Lebert and Häder 1996; Häder and Hemmersbach 2017). Also in the case of graviorientation, UV-B has been found to deteriorate the precision of orientation (Sebastian 1993; Häder 1989). Many motile organisms have been found to be impaired in their gravitactic orientation mechanisms, such as the freshwater

dinoflagellates *Peridinium gatunense* (Häder and Liu 1990a), and the green flagellate *Euglena gracilis* (Häder and Liu 1990b).

5.5 Mitigating Strategies Against Solar UV Radiation

Because of the obvious collision of interest between harvesting solar energy for photosynthesis and protection from detrimental ultraviolet radiation, primary producers—and also consumers living in the same habitat—have developed strategies to mitigate UV-induced damage (Häder and Gao 2018a, c). As detailed above, motile organisms can undergo vertical migrations in the water column to adapt to the ambient photoclimate using external clues such as light, temperature, and gravity for steering (Eggersdorfer and Häder 1991; Leach et al. 2015). In dinoflagellates and other microorganisms, vertical migrations of up to 30 m are governed by an endogenous rhythm (Enright and Hamner 1967). Some cyanobacteria form microbial mats in which the individual organism in the top layer may be sacrificed to protect those below; but in some cases, it was observed that the trichomes undergo vertical migration in the mat (Bebout and Garcia-Pichel 1995).

Other mitigating strategies have also been mentioned above which include efficient repair mechanisms. In the UML, phytoplankton are passively moved by the forces of wind and waves which induce Langmuir waves which transport the organisms between the surface and the thermocline (Polton et al. 2008). When exposed to high irradiances near the surface, the cells suffer from excessive UV radiation that induces damage to vital cellular biomolecules and functions such as the DNA and the photosynthetic apparatus. These lesions can be repaired when the organisms are passively moved to deeper layers with lower irradiances (Helbling et al. 2003).

5.5.1 UV-Absorbing Pigments

Because of the vital problem of damaging ultraviolet radiation, sun-exposed organisms have started producing UV-screening substances early during evolution (Sinha and Häder 2002a, 2008) both in motile prokaryotic and eukaryotic phytoplankton as well as in sedentary macroalgae (Gröniger and Häder 2001; Sinha et al. 2008). A database lists numerous organisms in many taxa such as cyanobacteria, phytoplankton, macroalgae, fungi, and animals possessing UV-screening substances (Gröniger et al. 2000; Sinha et al. 2007). Animals do not produce these substances because they lack the Shikimate pathway, but they take up these pigments with their diet, incorporate them in their tissues, and use it for the purpose of UV protection as has been found, e.g., in copepods (Moeller et al. 2005; Carroll and Shick 1996).

5.5.2 Scytonemin

The Precambrian Earth was anoxic and consequently did not have ozone in the stratosphere, and solar UV-C could reach the surface of the planet. Therefore, it is no wonder that the early organisms developed UV-screening substances which absorb UV-C in addition to UV-B and UV-A (Mloszewska et al. 2018). Scytonemin is a dimeric heterocyclic molecule (Fig. 5.10) with a major absorption at 386 nm, but also strong maxima at 252, 278, and 300 nm (Pathak et al. 2019a). In addition to reduced and oxidized scytonemin, other molecular structures have been found such as scytonin, scytonemin-3a-imine, dimethoxyscytonemin, tetramethoxyscytonemin, and scytonemin A (Pathak et al. 2019b). Scytonemins are exclusively produced by cyanobacteria; they are brown, lipophilic molecules which are excreted by the cells into the cell wall where they can optimally screen UV radiation from entering the cells and harming vital biomolecules and structures (Rastogi et al. 2014). Their synthesis is induced by exposure to UV radiation (Rastogi et al. 2013). In addition to its role as passive UV absorber, scytonemin has radical scavenging activity (Matsui et al. 2012).

5.5.3 Mycosporine-Like Amino Acids

Mycosporine-like amino acids (MAAs) are produced by many aquatic photosynthetic organisms including prokaryotic and eukaryotic phytoplankton and macroalgae in many orders and families (Gröniger et al. 2000; Sinha et al. 2007). In contrast to scytonemin, they are usually found inside the cell but in the outer cytoplasm layer, so that they can protect the central DNA region. MAAs are small (less than 400 Da) hydrophilic, colorless molecules based on an amino acid or its amino alcohol attached to an cyclohexenone or cyclohexylamine chromophore (Fig. 5.11) (Pathak et al. 2017; Singh et al. 2010). More than 20 MAAs are known

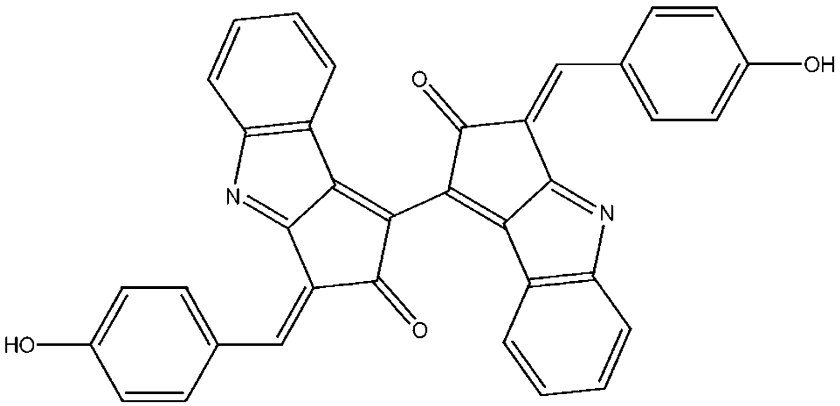

Fig. 5.10 Molecular structure of oxidized scytonemin. (Redrawn after (Pathak et al. 2019a))

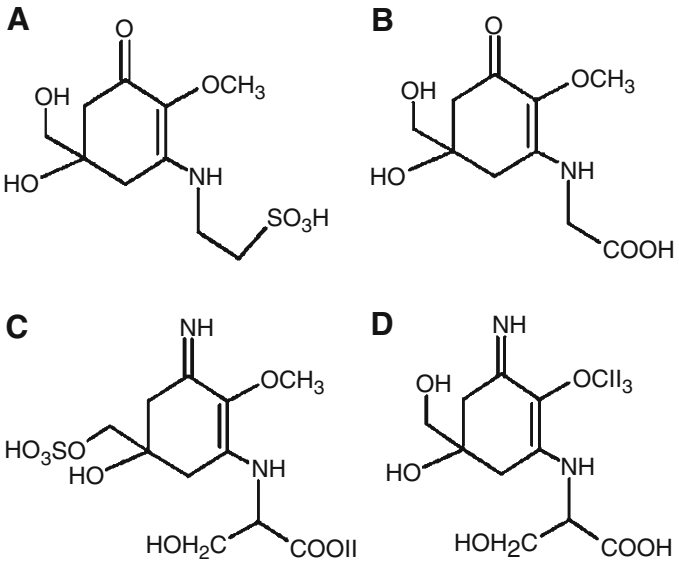

Fig. 5.11 Molecular structures of some mycosporine-like amino acids. (**a**) Mycosporine-taurine, (**b**) mycosporine-glycine, (**c**) palythine-serine-sulfate, (**d**) palythine-serine. (Redrawn after (Sinha and Häder 2008))

by now characterized by high molar extinction coefficients (28,100–-50,000 M^{-1} cm^{-1}) with absorption maxima between 310 and 362 nm (Sinha and Häder 2008). Their synthesis occurs in the Shikimate pathway via deoxygadusol and is induced by exposure to UV radiation as shown for the freshwater cyanobacterium *Anabaena* spec. and three marine *Nodularia* species (Sinha et al. 1999, 2003). Also in the macroalgae *Prasiola stipitata*, MAA synthesis is induced by UV radiation (Gröniger and Häder 2002) while in *Chondrus crispus* also photosynthetically active radiation was found to induce MAA synthesis (Karsten et al. 1998). Some MAAs have been found to also operate as antioxidants (Rastogi et al. 2016; De la Coba et al. 2009b).

MAAs are very stable molecules even at extreme temperatures and pH values (Gröniger and Häder 2000), and due to their high extinction coefficients, MAAs are very effective in preventing UV photons from causing havoc in the cell. For this reason, they have a high potential as UV-absorbing compounds in humans preventing photoaging and skin cancer (De la Coba et al. 2009a). They are a potent substitute for synthetic organochemicals in suntan lotions and cremes such as oxybenzone, octinoxate, or octocrylene which have toxic effects on marine organisms such as corals and their larvae and are or will be phased out in some areas such as Hawaii (Narla and Lim 2020).

5.6 Conclusions and Future Perspectives

Primary aquatic producers utilize solar energy and are simultaneously exposed to detrimental short-wavelength UV-B radiation. In order to avoid damage of vital biomolecules and cellular structures, prokaryotic and eukaryotic organisms such as bacteria, phytoplankton, and macroalgae use a number of strategies to mitigate damage. Motile organisms rely on vertical migration to minimize exposure to excessive UV radiation; but both motility and orientation mechanisms may be affected by the same radiation. Another mechanism is repair and replacement of damaged molecules as found in DNA and the photosynthetic apparatus. Many organisms utilize UV-absorbing pigments such as scytonemin and mycosporine-like amino acids. Environmental changes in the aquatic ecosystems due to the results of global climate change and stratospheric ozone depletion require close analysis of the life conditions of the vital aquatic producers.

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UV-B and Crop Research from Past to New Age

6

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Abstract

UV-B is electromagnetic radiation from the sun with medium waves, most of which is absorbed by the ozone layer. It covers only a small part of the electromagnetic spectrum, but has a disproportionately large photobiological effect. The biological effects of UV light are greater than the simple heating effects, and many practical uses of UV light result from their interaction with organic molecules. UV-B radiation that interacts with biological systems has several specific cellular targets that result in adverse reactions. Both plants and animals are severely affected by increased UV-B radiation, but the susceptibility of plant species to UV-B radiation varies greatly. Plants adapt to changing environmental conditions and seek to develop some adaptive response. A large understanding about the effects of UV-B radiation on plants was established from research on economically important crops. The effectiveness of UV-B radiation was strongly influenced by common microclimate factors such as precipitation patterns and temperature. Ongoing field research suggests that they respond to UV-B radiation by increasing the levels of needle flavonoids, even under the full solar spectrum. Plants have developed natural adaptations such as anatomical, morphological, and biochemical changes that protect them from UV-B radiation. The degree of these natural adaptations may be related to the geographic origin of the species. This chapter describes the basics of UV-B, how it reaches the surface of the Earth, and its impact on the biological elements of the environment. So far, "UV-B" has been perceived as purely harmful to the environment. However, recent technological advances have changed the perceptions in UV-B research. It is now

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focused on how UV-B is beneficial to crop productivity and agriculture. This chapter provides comprehensive insights into the current status of UV-B research and deals with progress from past to present.

Keywords

Ultraviolet radiation · Plant production · Growth and development · Plant hormones · DNA damage

6.1 Introduction

There are many spectrums of radiation generated from the Sun light which reaches the Earth. Ultraviolet radiations have already been defined in the previous chapters as invisible spectrum of solar radiation that is determined as an electromagnetic measurement. There are three types of this UVR, of which UV-A and UV-B are the center of research attraction. About 5% of the terrestrial radiation of the midday sun is UVR, of which 95% accounts for UV-A and 5% for UV-B and UV-C. Out of this, most of the UV-B and UV-C are expelled from extraterrestrial radiations by stratospheric zone. The three types of radiation mentioned above have wavelengths: UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (100–280 nm), respectively (Gueymard 2012). Although the maximum UVR of sunlight is filtered by the ozone layer of the stratosphere, so that only UV-A spectrum reaches the Earth. Studies done in the last few years revealed that in addition to UV-A some amount of UV-B also reaches the Earth and this UV-B is the main source of interference in terrestrial and aquatic ecosystems (Schmalwieser et al. 2018).

Although the UV-B and UV-C spectrum is taken up by the ozone surface and other gases present in the stratosphere, a very small amount of UV-B reaches the Earth. But for the last few years, due to the degradation of the ozone layer in the stratosphere, the amount of UV-B reaching the Earth has also increased (Molina and Rowland 1974). Since the minimum amount of UV-B is capable of interfering with biological systems, increasing amounts of UV-B can puts serious effects on biological systems.

Human population spread throughout the world depends on agricultural products for its nutrition and livelihood. Cereals, pulses, fruits, and flowers prominently figure these agricultural products. Due to direct contact with the surrounding, various biotic and abiotic components affect the crops directly or indirectly (Satterthwaite et al. 2010; Pandey et al. 2017; Capstaff and Miller 2018; Gull et al. 2019). Abiotic components are mainly physical factors such as temperature, air, water vapor, exposure, light and radiation, etc. All these factors play an important role in affecting the physiology of the crop species (Charrier et al. 2015). UVR affects all three of the plants, animals, and microorganisms; since plants are a major component of terrestrial ecosystem and are also the principle absorbers of sunlight, UVR has a maximum effect on their genetic makeup and physiology (Bais et al. 2018; Bornman et al. 2019).The importance of plants in UVR research also increases manifold because

the phenomena of converting light energy into chemical energy can only be achieved by plants. As we know, a large population of the world depends on plants for food and economic support; hence, successive efforts for crop improvement and crop-related research need to be done continuously so that the availability of crop products is maintained sustainably. In the last few years, a lot of progress has been seen in scientific research related to plant products of agricultural importance, and along with this, the effects of UV-B on crops have also been observed in many species like rice, maize, soybean, chickpea, etc. (Raza et al. 2019; Begum et al. 2019).

Since this is an important aspect, it is necessary to know what exactly UV-B does to the plant physiology, or which physiological process of plants was mostly affected due to UV-B exposure?

We know that the process of photosynthesis in plants depends on light, and UV-B is a type of light radiation, so basically the center of focus for most researches is to study the effects of UV-B on photosynthesis and its subsequent metabolic fate (White and Jahnke 2002; Suchar and Robberecht 2016). In past years, many important scientific studies and research related to UV-B-mediated alteration in photosynthetic physiology of plants, molecular genetics, plant ecology, primary and secondary metabolism, etc., have been done specially focusing on crop production and stability (Bita and Gerats 2013; Kumar et al. 2017; Durairaj et al. 2018). **Presented chapter includes the report of past, present work done, and future studies to be conducted in relation to UV-B and plant responses as well as future researches in this field.**

6.2 UV-B, Plant Growth, and Development

Plant growth and development not only depend on the intrinsic and biotic factors, but it is also affected very much by abiotic factors too. Solar UV-B can potentially affect plant growth parameters such as seed germination, morphological characteristics of root, shoot, leaf, and its area, etc. UV-B doses behave differentially in plants species to species. Furness et al. (1999) demonstrated dose-dependent effects of UV-B on three weed species as decrease in leaf, stem, and root fresh weights, leaf area, and leaf: shoot ratio, while increase in shoot dry matter content, specific leaf weight, and leaf greenness of Cynoglossum officinale seedlings, in Centaurea diffusa Lam., leaf, stem, and root fresh weights, leaf area, and leaf: shoot ratio was increased, and no effects were observed in shoot dry matter content, specific leaf weight, and leaf greenness, and change in Trichome abundance and orientation was observed in Tragopogon pratensis L. A decrease of plant height, fresh mass of leaves, shoots and roots as well as leaf area with the curving of leaves was also observed in *Avena fatua* and *Setaria viridis* while exposing to different doses of UV-B radiations (Golaszewska et al. 2003). Similarly, dose-dependent effect of biologically effective UV-B was also reported for alteration in in chlorophyll content in Dwarf shrubs Bilberry (*Vaccinium myrtillus L.*) and cowberry (*Vaccinium vitis-idaea L.*), while *Vaccinium myrtillus* was found less sensitive than *Vaccinium vitis-idaea* as permanent discoloration was seen in later species

(Ştefănescu et al. 2020). Zhang et al. (2019) demonstrated the inhibition of root growth and related parameters (total root length, root surface area, root volume, average diameter, root tip number, and root dry weight) in soybean seedlings due to elevated levels of UV-B radiations. Shaukat et al. (2013) reported reducing effects of UV-B exposure on germination, seedling growth, and biochemical responses of *Vigna mungo (L.)* Hepper with increase in germination velocity, decrease in final germination, decrease in seedling growth and chlorophyll content. Kakani et al. (2003) stated the altering effects of UV-B on vegetative and reproductive morphology of field crops, and later on Raja Reddy et al. (2003) reported that enhanced UV-B exposure affects cotton plant at the level of morphology and anatomy both. Similar observation were made by Jansen et al. (2012) stated that UV-B exposure decreases the plant biomass as shorter petioles and shorter, narrower, and/or thicker leaf blades were formed in Arabidopsis thaliana. UV-B-mediated alteration in three cultivars of soybean was reported by Liu et al. (2013) at the level of pod number per plant and seed numbers per pod, while seed numbers were not affected by exposure. Despite being negatively impacted on plant growth and development, UV-B can positively influence the growth in some plant species as described by Bernado et al. (2021) in *Coffea arabica and C. canephora* cultivars which showed anatomic adjustments at the leaf scale such as increases in stomatal density at the abaxial and adaxial cuticles and abaxial epidermal thickening. Effect of UV-mediated plant morphological alteration also leads to the change in insect herbivory. Caputo et al. (2006) reported alteration of attractiveness in Arabidopsis plants to diamondback moths oviposition and changes in jasmonic acid pathways. Metwally et al. (2019) reported significantly increased vegetative morphology in in vitro cultivation of Spathiphyllum plant under increased UV radiation treatment. Farokh et al. (2010) reported the impact of UV-B on the seed germination and root morphology of Safflower plant. Pre-treatment of Cantaloupe type melon seeds of cultivar "Topmark" with UV-B impacts on the morphological characteristics after cultivation reported by Sosa-Flores et al. (2014). All of the above evidences indicate that UV-B exposure differentially affects the morphological characteristics of different species of plants.

6.3 UV-B and Plant Biochemistry

Solar UV-B affects the biochemical levels of plants upon irradiation and it causes changes in different biochemicals and secondary metabolites. As a biologically active radiation, UV-B is absorbed at an extent of 90% by leaves and subsequently puts deleterious impacts over biochemical responses in plants (Miller et al. 1994; Rao et al. 1996; Ambasht and Agrawal 2003). The experiments conducted on field-grown soybean crops by Mazza et al. (2000) revealed that there is an increase in phenylpropanoid content in leaves pretreated with solar UV-B in reference to the UV-B-induced cyclobutane pyrimidine dimer formation in leaf tissues. Similarly, combined yield decreased, and biomass production effect of increased UV-B and nitrogen fortification was seen in the simulation experiment on maize plants at a 20%

stratospheric ozone depletion over Portugal (Correia et al. 2000, 2012). Enhancement of differential flavonol glycosides content in nine populations of white clover (*Trifolium repens* L.) under the influence of increased UV-B exposures was recorded by Hofmann et al. (2000) through methane water extraction followed by high-throughput HPLC. In similar experiments, Pal et al. (1999) also reported the enhancement of flavonoid content in field crops under UV-B exposures and concluded that monocots are more protected against UV-B-induced alterations. Kakani et al. (2003) enlisted 128 studies on 35 field crop responses against photosynthetically active UV-B on various parameters like visual symptoms, leaf ultrastructure and anatomy, photosynthetic pigments, UV-B absorbing compounds, photosynthesis, growth and development, and yield, genotypic differences. Enhanced exposure of UV-B radiations alter leaf ultrastructure and biochemical accumulation in potato plants was reported (Santos et al. 2004) with increase in flavonoid content end elevation in Antioxidant enzyme levels. Biochemical sensitivity of rice plants under UV-B irradiation was reported (Dai et al. 1992; Hidema and Kumagai 2006; Yu et al. 2013). Differentially, UV-B-irradiated coriander *Coriandrum sativum L* plantlet showed an increased proline content while decreased photosynthetic pigments (chlorophyll a, chlorophyll b, and carotenoid) and total carbohydrate contents (Kumar and Pandey 2017). Choudhary and Agrawal (2014) reported negative effects of UV-B on the growth, biomass, yield, and its quality by generating oxidative stress directly or due to elevation of salicylic acid in two cultivars of Pea plant (Pisum sativum) with increased accumulation of flavonoids (quercetin and kaempferol) while neither protecting photosynthetic machinery nor helping in the elevation of biological nitrogen fixation. Biochemical alteration due to UV-B exposure also reported in some other species like two species of Vigna; *Vigna mungo (L.)* and *Vigna aconitifolia* (Jacq.) seedlings were tested at ambient and supplemental 280–320 nm dose of enhanced UV-B (Dwivedi et al. 2014) and shown accelerated generation of reactive oxygen species with increased positive response on antioxidants: superoxide dismutase (SOD) and guaiacol peroxidase (GPX) activity, and contents of proline, ascorbic acid, total phenolic contents (TPCs), and total flavonoid contents (TFCs) in leaves of both species. Schreiner et al. (2012) mentioned that low, ecologically relevant UV-B levels trigger distinct changes in the accumulation of, among others, phenolic compounds, carotenoids, and glucosinolates. Kataria and Guruprasad (2015) excluded solar UV-B in field experiments and observed improved photosynthetic performance and yield in four varieties of wheat *Triticum aestivum* with a remarkable increase in carbonic anhydrase, Rubisco, and nitrate reductase activities. The effect of biologically active UV-B was also investigated in highbush blueberry [*Vaccinium corymbosum L. cv.* Brigitta and Bluegold] (Inostroza-Blancheteau et al. 2014), and subsequent alterations were observed in leaf thickness, anthocyanin, and total phenolic contents with an increased accumulation of chlorogenic acid. Oxidative stress-mediated inhibition in physiology of *B. napus* L. due to the exposure of ambient UV-B was also reported by Zhu and Yang (2015). So, UV-B acts as the eustressor in horticulture and agriculture crops (Neugart and Schreiner 2018). Several ethnopharmacological constituents like alkaloids, terpenoids, and phenolics etc.,

are present in various medicinal plants which are important from the therapeutic point of view. Medicinal plants were also tested for the biochemical and metabolic responses under UV-B exposures, UV-mediated generation, enhancement and accumulation of bioactive compounds and new phytochemicals, UV-B influenced enhanced antioxidant activities and also evaluated as filters of UV radiations (Kumari and Prasad 2013; Mejia et al. 2015; Takshak and Agrawal 2019; Zhang et al. 2017; Chen et al. 2018; Klein et al. 2018; Vanhaelewyn et al. 2020; Pandey et al. 2021). In the current scenario, experiments are conducted on crops like peach, cucumber, pigeon pea, rice, wheat, tomatoes, and holy Basil, etc., with a special focus on the metabolomics, genomics, and proteomics-based studies to evaluate the potential of UV-B exposure on plant physiology and biochemistry at molecular level like alterations in secondary metabolite such as terpenoids, phenylpropanoids, phytoalexins, and fatty acids (Lv et al. 2020; Santin et al. 2021; Yang et al. 2021; Palma et al. 2021; Gupta and Prasad 2021; Phuong et al. 2021; Fernández et al. 2021; Sakalauskaitė et al. 2013; Al Hamedi et al. 2021).

6.4 UV-B and Plant Hormones

There are two classes of UV exposure effects on plants: (a) photomorphogenic effects and (b) stress effects. Both of these effects depend on the control and interaction between hormone pathways. Discovery of UV-B-specific photoreceptor UV RESISTANT LOCUS 8 enables to understand the effect of UV-B on different hormonal pathways in different ways such as photochemical, affecting biosynthesis, transport, and/or signaling. The possible mechanism of action for the UV-B-mediated regulation of hormone is either by inhibition of growth-promoting hormone and enhancement of environmental stress-induced defense hormone (Vanhaelewyn et al. 2016). Yang et al. (2004) reported UV-B-influenced changes in the hormonal levels in the vegetative and reproductive tissues and subsequent alteration in morphological characteristics of Tomato plants. Fina et al. (2017) evaluated the impact of UV-B on the hormonal changes in Maize crop and reported the altered growth regulating factor with Gibberellin levels with inhibition in leaf growth. Effect of UV-B exposure on plant hormones was investigated for the different species of crops such as tomato, soybean, rice, wheat, Quinoa, and some medicinal plants, etc., at their different parts like roots and shoots (Mannucci et al. 2020; Mao et al. 2017; Pan et al. 2014; Mariotti et al. 2021).

6.5 UV-B and Photosynthesis

Plants use sunlight to drive the mechanism of photosynthesis. In some past recent years, the approach of UV-B to the Earth surface is increased and since UV-B is a biologically significant radiation, it affects the photosynthetic machinery of the different species of plants differentially. Since 1996, expansion of ozone hole is being a serious and alarming issue and for the same duration many plant species have

been undertaken to understand the effect of increasing UV radiations on photosynthesis. Comparative study on different plant species in response to the UV-B exposure was reported by Tevini et al. (1981, 1983, 1991), Tevini and Teramura (1989) for the alterations in physiological functions, photosynthetic response, and pigment contents. As a model to understood the long- term effects of UV-B on photosynthesis, members of Chlorophyceae (Macroalgae) were studied (Altamirano et al. 2000) under in situ conditions. Although UV-B causes deleterious effects on plants but some intrinsic mechanisms can also able to protect the plant from damage such as Cuadra and Harborne (1996) showed in the experiment conducted on *Gnaphalium luteo-album* and revealed that surface increase in leaf surface flavonol content in response to the UV-B exposure, acts as a protective shield for plant against damage and subsequently increases the photosynthetic pigment content. Mishra et al. (2008) evaluated the combined effects of UV-B and dimethoate on the photosynthetic response and pigment content of Cowpea seedlings stage. Being biologically active radiation, UV-B causes alterations in the mechanism as well as the content of photosynthetic pigments in different species of terrestrial, desert, and aquatic plants at their different tissue levels like leaves and even in shoots (Cen and Bornman 1990; Panagopoulos et al. 1990; Buma et al. 1996; Sarghein et al. 2008; Ibañez et al. 2008; Juozaitytė et al. 2008; Salama et al. 2011; Abney et al. 2013; Sztatelman et al. 2015; Piccini et al. 2020). Presently, some targeted studies are under progress to ameliorate the effect of UV-B on photosynthetic pigments using nanoparticle- based systems (Kataria et al. 2019; Azadi et al. 2021).

UV-B directly affects the photosystem performances of different species of plants by decreasing the penetration of PAR, reduction in photosynthetic and accessory pigments, impairing in stomatal function and altering canopy morphology, and thus reduces the photosynthetic carbon assimilation indirectly. UV-B may incorporate to alter the cytochrome *f* content in Photosystem I with decreased ribulose-1,5-bisphosphate carboxylase (Rubisco) activity hydrolysis of ATP synthase photosystem II. Strid et al. (1990) reported altered physiology of Photosystem I and Photosystem II in Pea plants under UV-B exposure. Similar studies were reported by Sinclair et al. (1990) on soybean plants. Sicora et al. (2006) investigated the effects of UV-B on Photosystem II at molecular level and reported the primary UV damage at the catalytic Mn cluster of water oxidation and de novo synthesis of the D1 and D2 reaction center protein subunits to repair UV- induced damage in PS II. UV-B-induced photoinhibition of Photosystem II was demonstrated in winter wheat *Triticum aestivum L.* which is associated with the altered PS II photochemistry with subsequent antioxidants profiles and xanthophylls cycle (Yang et al. 2007). Many studies have been conducted to evaluate the effect of UV-B on the photosystems in different species of plants (Bouchard et al. 2008; Guruprasad et al. 2007; Pescheck et al. 2014; Kataria et al. 2020; Sen and Puthur 2020; Maher et al. 2021; Xue et al. 2021). Since, evaluation of UV-B as the damaging agent of photosystems is established and it was already known that UV-B causes decrease in crop productivity, so now it is a necessity to develop approaches to protect crops from UV-B- induced damage. The overall criteria by which plant protect themselves from UV-B-mediated damage, mainly by plant flavonoids, which are synthesized

due to the activation of UV RESISTANT LOCUS 8 which is a UV-B receptor in plant genome. Currently, focus is being made on the strategies to protect the crop and enhancement of product yield by using some shielding techniques and evaluation of intrinsic factors for crop growth (Podolec et al. 2021a, b).

6.6 UV-B and DNA Damage

UV-B is known as an ionizing radiation, and upon exposure, it causes serious alterations in the genetic content of any organism which results in form of mutation that reflects in the traits and phenotypes of the affected organism (Gill et al. 2015). Since the biochemical and physiological constituents of cell are actually the products of gene expression, UV-B exposure causes gene-mediated alterations in the crops (Casati and Walbot 2003). UV-B damages nuclear and orgenellar DNA by inducing various DNA lesions like cyclobutane pyrimidine dimers (CPDs) generation and other photoproducts, as the major lesions pyrimidine pyrimidone dimmers are produced by UV-B, while oxidized or hydrated bases, single-strand breaks, and others are minor lesions (Ballaré et al. 2001; Takahashi et al. 2012). Ries et al. (2000) demonstrated the reduction in genome stability in plant using *Arabidopsis thaliana and Nicotiana tabacum* as a model system with increase in somatic DNA rearrangements' recombination by a strong induction of photolyase and Rad51 gene expression.

6.7 Conclusion and Future Prospective

Sustainable availability of crops is a key issue for current and future point of view. Day-by-day increase in pollution is leading the increased reach of UV radiations to the Earth which accounts damage to not only in animals but a major damage also causes in the crop-producing plants. In context to the increasing population, assured availability of adequate quantity of edible food for each and every individual is a crucial point in present scenario. Past studies suggested the damaging effect of UV-B on crops such as decrease in nutritional contents, low yield, etc.; in developing world, more advance practices like targeted crop breeding, transgenic, and UV-resistant plant production must be undertaken to cope with the UV-B exposure to assure the crop survival and yield enhancement.

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Plant Responses: UV-B Avoidance Strategies

7

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Abstract

Solar radiation is the major source of energy in the universe and critical for the plant growth and development. The UV-B radiations, the small fraction of solar radiation affect the plant growth via altering various morphological, physiological, and molecular responses. However, plants cope UV-B stress using their defense system which is not strong enough to recover the damage and yield losses caused by enhanced or ambient UV-B exposure. Hence, various strategies have been developed by plant scientists in the past years to circumvent or mitigate the UV-B stress. In the present chapter, we have discussed the impact of UV-B stress upon overall performance of plants including yield. In addition, various available UV-B-avoiding strategies have been addressed such as exclusion of solar UV-B by UV-B cutoff filters and seed priming with magnetic field which are useful to provide UV-B stress tolerance to the plants.

Keywords

UV-B exclusion · Growth · Photosynthesis · UV-B · Magneto-priming · Crop yield

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7.1 Introduction

The solar radiation affects all living organisms on the earth directly or indirectly, and it is the major source of energy essential for the growth and development of the plants. In general, solar radiation reaches to the Earth surface is mainly composed of ultraviolet (UV), visible, and infrared rays. Among these rays, particularly, UV radiations are composed of three types of wavelengths: UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (200–280 nm). The UV-B radiation constitutes a small fraction of total solar radiation which reaches to the Earth's surface due to stratospheric ozone depletion (Kataria et al. 2014a, b; Bornman et al. 2019) and it is currently reached to its maximum level which is a serious concern to the world. Towards controlling the ozone depletion, Montreal protocol (an international agreement to protect ozone depletion) suggested that ozone layer can be revert to the pre-1980 levels at the mid-latitudes by 2040–2070, if it is followed properly by participating countries (Mohammed and Tarpley 2010; Bais et al. 2018, 2019). However, the rise in the levels of greenhouse gases could delay this return (Newman et al. 2001; Bais et al. 2019). UV-B radiation plays an imperative role in terrestrial ecosystems but, it can represent a risk for plants in excess. The excess UV-B exposure induces various negative effects to which plants can respond with defense and adaptive mechanisms (Kataria et al. 2014a; Rácz et al. 2018). Photoexcitation of biomolecules like nucleic acids, proteins and lipids via absorbing UV-B can cause alteration in the various biological processes (Caldwell et al. 2007; Jenkins 2009; Tian and Yu 2009; Kataria et al. 2014a). The UV-B exposure is known to delay seedling emergence, reduce leaf area, leaf length, leaf thickness and midrib thickness. Furthermore, curling of cotyledons/leaves, bronzing/glazing of leaves, leaf chlorosis with necrosis, reduced internode length with overall plant height, and delayed flowering are the symptoms shown by various crop plants (Caldwell et al. 1995, 2007; Robson et al. 2015; Suchar and Robberecht 2015). It has been suggested that these variety of symptoms are the result of perturbed hormone metabolism and cell wall loosening due to UV-B rays (Hectors et al. 2007; Casati and Walbot 2003). In spite of morphological changes, physiological parameters are also known to be affected via UV-B exposure. The photosynthetic machinery of plants is very sensitive to excess UV-B exposure which leads to hamper the carbon, nitrogen metabolism, photosynthetic efficiency and ultimately reduces the biomass accumulation and crop yield (Kataria et al. 2013, 2014a; Dotto and Casati 2017). Earlier, various indoor studies have shown that UV-B exposure can impair three major processes of photosynthesis: CO_2 fixation, photophosphorylation, and stomatal movement to regulate the CO_2 supply (Allen et al. 1998; Teramura and Sullivan 1994; Kataria et al. 2014a). The prolonged exposure of UV-B rays destruct the carotenoids and chlorophyll which ultimately reduces the photosynthetic performance of plants (Nogues and Baker 1995; Baker et al. 1997; Allen et al. 1998; Wilson et al. 1995; Yu et al. 2013). It has been reported that photosystem-II (PS-II) is very sensitive to UV-B exposure due to their chemical organization of D1 and D2 proteins along with oxygen-evolving complex (Kataria et al. 2014a, b; Faseela and Puthur 2018; Schultze and Bilger 2019; Çiçek et al. 2020). The chlorophyll *a* (chl *a*) fluorescence

parameters such as polyphasic fluorescence transients (OJIP transients) show lower fluorescence yield particularly at I to P-phase in leaves of plants grown under UV-B stress (Kalaji et al. 2018; Kataria et al. 2020a, 2021).

In addition, prolonged exposure of UV-B rays triggers oxidative stress due to increased production of reactive oxygen species (ROS) in plants (Jain et al. 2004; Kataria et al. 2017a, b). However, increased ROS production can be neutralized through enzymatic and non-enzymatic defense mechanisms (Jain et al. 2004; Kataria et al. 2007; Dias et al. 2020). The enzymatic defense system includes antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), and enzymes of Halliwell/Asada pathway, whereas non-enzymatic defense system includes molecules like ascorbate, tocopherol, glutathione, carotenoids, and phenolics (Jain et al. 2004; Hideg et al. 2013; Kataria et al. 2007; Dias et al. 2020). Although plants have evolved with these defense systems, these are not enough to recover the damage and yield loss caused by prolonged UV-B exposure. In this scenario, UV-B rays reaching on the Earth could not be avoided and so it becomes crucial to find out the ways which can protect the plants from the UV-B exposure. However, various methods are available to avoid or mitigate UV-B stress, but exclusion of solar UV component from natural solar radiation and magneto-priming is most commonly used methods found in the literatures (Krizek and Mirecki 2004; Kataria et al. 2013, 2017a, 2020a, 2021; Prajapati et al. 2020; Raipuria et al. 2021). Therefore, present chapter is aimed to provide an overview about avoiding strategies used to improve the plant tolerance towards UV-B stress by circumvent the harmful effects of UV-B radiations.

7.2 Solar UV Exclusion as a Strategy to Avoid the Effects of UV-B Stress

It is difficult to get the place devoid of UV-B rays, therefore, UV-B stress related studies were conducted under growth chambers and green houses equipped with UV-B lamps. Later by 1990s, the scientific community questioned the usage of this strategy, as UV-B lamps could not provide the natural ratios of UV-B/UV-A and UV-B/PAR radiations (Caldwell and Flint 1994, 1997; Krizek and Mirecki 2004). Further, it was suggested that outdoor studies should be carried out under ambient solar radiations to evaluate the actual impact of solar UV-B radiation on the plant growth and development. Now, there are two widely preferred ways of conducting outdoor studies aiming to see the effect of UV-B exposure: (1) UV-B enhancement and (2) UV-B attenuation approach (Rousseaux et al. 2004). In UV-B enhancement approach, solar radiations are supplemented with UV-B lamps to mimic the condition of increased UV-B incidence due to ozone depletion. On the other hand, UV-B attenuation is performed using solar UV-B exclusion filters to mimic the (–UV-B) conditions (Lingakumar et al. 1999; Phoenix et al. 2000; Krizek and Chalker 2005; Zhang et al. 2014; Kataria et al. 2013, 2014b; Kataria and Guruprasad 2012a, b, 2014, 2015). The plastic screens or polyester filters can reduce the ambient UV-B levels and can be used to provide the sub-ambient and near-

ambient UV-B treatment conditions. These two outdoor approaches are simple, reliable, and cost-effective which can be used to see the actual impact of ambient or enhanced UV-B on the plants performance.

7.2.1 Plant Growth, Photosynthesis, Antioxidant Defense, and Yield Under Solar UV-B Exclusion

In the natural environment, plants are exposed to combined stresses which in turn cause several changes in gene expression, plant metabolism, and morphology. Enhancing the crop productivity under variable climate has been a major challenge to the entire agricultural scientific community. One of the unavoidable stresses, UV-B radiations, hamper the plant growth and development by damaging the cell membranes, DNA, RNA, cell organelles like mitochondria, chloroplasts, etc. (Hollosy 2002; Jain et al. 2003, 2004; Kataria et al. 2014a; Vanhaelewyn et al. 2020). However, the extent of damage depends on the intensity with duration of UV-B irradiance and most importantly the plant developmental stage getting exposed. In regard to overcoming UV-B stress, ambient UV-B exclusion is a potential strategy to obtain higher growth and biomass/yield. Several reports have revealed that plants grown under solar UV-B exclusion conditions showed increased growth in both aboveground and belowground parts of the plants. For example, various plant species like radish, barley, mung bean, pea, pumpkin, soybean, Cyamopsis, Vigna, wheat, cucumber, cotton, sorghum, amaranthus, and trigonella showed increased growth in terms of plant height, leaf area, specific leaf weight, leaf weight ratio, overall biomass accumulation, efficiency of PSII, photosynthesis, and yield under solar UV-B exclusion conditions (Pal et al. 1997; Mazza et al. 1999; Zavalla and Botto 2002; Krizek and Mirecki 2004; Amudha et al. 2005; Guruprasad et al. 2007; Pal et al. 2006; Kanungo et al. 2013; Kataria and Guruprasad 2012a, b, 2014, 2015; Kataria et al. 2013; Sharma et al. 2019). Similarly, ambient UV-B exclusion allowed plants to produce more tillers and branches in monocots and dicots, respectively (Mazza et al. 1999; Coleman and Day 2004; Kataria and Guruprasad 2012a). In *Vaccinium uliginosum*, it was reported that ambient UV-B exclusion increases the biomass of belowground tissues (Rinnan et al. 2005). The UV-B-free environment improved the photosynthetic capacity up to 33% over normal condition grown common beans plant which suggested that UV-B rays primarily reduces the photosynthetic rate and CO_2 fixation (Moussa and Khodary 2008). A number of reports have shown the enhanced net photosynthetic rate and stomatal conductance upon UV-B exclusion in Populus (Schumaker et al. 1997), maize, and mung bean (Pal et al. 1997), wheat and pea (Pal et al. 2006), *Vaccinium uliginosum* (Albert et al. 2008), sorghum (Kataria and Guruprasad 2012b), *Amaranthus tricolor* (Kataria and Guruprasad 2014), and wheat (Kataria and Guruprasad 2015). In another reports, it was shown that the UV-B exclusion via polyester filters increased the root biomass, number of nodules, and nodule fresh weight along with increased nitrogenase activity (by 120%) and leghemoglobin content (by 63%) in fenugreek (Sharma and Guruprasad 2012). Other reports

showed the higher levels of α-tocopherol in UV-B-excluded plants which are important for translocation of photosynthates from leaves to root (Chouhan et al. 2008; Baroniya et al. 2014; Kataria et al. 2014b). Secondary metabolites are the byproducts of various metabolic pathways which are known to help the plants in the adaptation to its surrounding climate (Alvarez 2014). The saponins are the triterpene glycosides known to have antimicrobial, antitermitic properties, and their concentration in the plants increased under higher light intensities (Mathur et al. 2000; Maulidiani et al. 2012). In cotton, UV-B-excluded plants showed increased plant height due to increased number of elongated nodes. These increased elongated nodes showed the lower amount of saponins as compared to plants grown under ambient UV-B conditions. This study proved that saponins act as growth inhibitor in ambient UV-B conditions (Dehariya et al. 2018).

The plants grown under solar UV-B exclusion conditions showed enhanced photosynthetic performance due to higher photosynthetic pigments, efficiency of PSII, electron transport rate, photosynthetic rate, and stomatal conductance with increased activity of photosynthetic enzymes such as carbonic anhydrase (CA), Ribulose-1,5 bisphosphate carboxylase/oxygenase (Rubisco), and phosphoenolpyruvate carboxylase (PEPC) over the plants grown under ambient solar UV-B conditions (Solanki et al. 2006; Kataria et al. 2013, 2014a; Kataria and Guruprasad 2012b, 2014, 2015). In a recent study, UV-B exposed scot pine seedlings showed decreased quantum yields and electron transport at both donor and acceptor sides of photosystems and the performance indexes (Çiçek et al. 2020). However, chlorophyll fluorescence parameters such as quantum efficiencies, phenomenological fluxes, and performance indices were enhanced by UV-B exclusion which suggests the adverse impact of ambient UV-B on these parameters (Kataria et al. 2013; Kataria and Guruprasad 2014, 2015). On the other side, solar UV-B exclusion has been observed to significantly increase the RuBisco activity and protein in the in microalgae and higher plants; it indicates that the ambient or enhanced UV-B lowers the Rubisco activity and protein content (Bischof et al. 2000, 2002; Pedro et al. 2009). The reduced activity of Rubisco could be due to suppression of genes encoding subunits of Rubisco and damage from the ROS generated under UV-B radiations (Jordan et al. 1992; Mackerness et al. 1999; Dehariya et al. 2012; Shine and Guruprasad 2012a, b; Kataria et al. 2013).

The soluble sugars, polysaccharides, secondary metabolite, and total flavonoid contents were also increased in the medicinal plant *Prunella vulgaris* upon UV-B exclusion (Chen et al. 2019). In another report, cumulative impact of altitude, cultivar, and solar radiation on the growth, physiology, and yield was analyzed. The exclusion of UV-B rays from solar radiation prompted the photosynthetic rate, stomatal number, and conductance with dry matter of Boloso-1 cultivar of *Colocasia esculenta* (L.) species (Derebe et al. 2019). In a recent report, UV-B exposed plants of *Silene littorea* showed increased concentration of anthocyanin (20–30%) and UV-B-absorbing compounds (12–25%) over UV-B-excluded plants which gave a clue of their involvement in photoprotection (Del Valle et al. 2020).

Overall solar UV-B exclusion can alter various morphological and physiological parameters leading to the improved plant performance (Fig. 7.1). For instance, UV-B

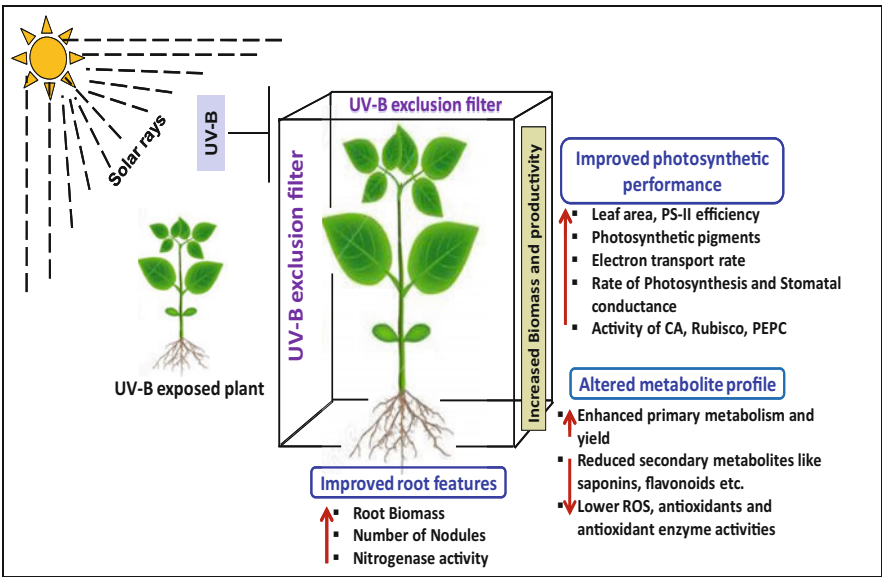

Fig. 7.1 The impact of solar UV-B exclusion upon various parameters determining overall performance the plants

exclusion increases photosynthesis, reduces the content of UV-B-absorbing substances, ROS and antioxidants (ascorbic acid and α-tocopherol); and lower activities of antioxidant enzymes such as SOD, peroxidase (POD), ascorbic acid peroxidase (APX), and glutatione reductase (GR) (Baroniya et al. 2013; Dehariya et al. 2011, 2012; Kataria et al. 2013, Kataria and Guruprasad 2012a, b, 2014, 2015; Sharma et al. 2019). Also, several others reports claim that solar UV-B exclusion improve the metabolism pattern that leads to enhanced primary metabolism and reduced synthesis of secondary products, like saponins, flavonoids, and phenolics compounds (Alemu and Gebre 2020; Dehariya et al. 2018; Kataria et al. 2013, 2014b).

The crop productivity depends on the overall performance of plants grown in the field under dynamic climate. The plant performance is proportionally related to yield and may vary due to their environmental interaction. The incidence of damaging effects caused by UV-B exposure varies according to the locations around the globe (Teramura et al. 1990). Several research groups have suggested that impact of UV-B radiation is high in tropical regions including India due to longer exposure of sunlight (Agrawal and Rathore 2007; Amudha et al. 2005; Guruprasad et al. 2007; Kataria and Guruprasad 2012a, b, 2014, 2015). Therefore, ambient solar UV-B radiation causes significant yield loss on terrestrial plants of tropical regions (Kataria et al. 2013; Kataria and Guruprasad 2014; Zhu and Yang 2015). Primarily, enhanced UV-B exposure alters the leaf ultrastructure and damages the photosynthetic apparatus, PS-II efficiency, and hence affects the net photosynthesis and ultimately reduces the yield of plants (Kakani et al. 2003; Kataria et al. 2014a). There are several reports which have been proved to enhance the yield in various crops. In

pumpkin (*Cucurbita pepo* L.), the UV-B filtration from solar radiation doubled the yield (Germ et al. 2005). In a field study, the effect of UV-A/UV-B exclusion showed up to 50% increased yield of *Cyamopsis tetragonoloba* among three tested tropical legumes (Amudha et al. 2005). In another greenhouse study conducted by using UV absorbing films showed that UV-B exclusion enhanced the fruit size and yield by 20% in eggplant (Kittas et al. 2006). Similarly, two strawberry cultivars named Camarosa and Ventana showed enhanced productivity of 30% and 20%, respectively, when grown in the absence of UV radiation (Casal et al. 2009); however, the ripening of fruits was delayed and no nutritional parameters were improved in both cultivars. In a field study, four different varieties of wheat (Purna, Vidisha, Naveen Chandausi, and Swarna) grown under UV-B cutoff filters showed the significant enhancement in grain yield (44%) of wheat variety of Purna; Vidisha showed 65% increase after the exclusion of UV-B. However, other two varieties Swarna and N. Chandausi did not showed significant enhancement (Kataria and Guruprasad 2015). The solar UV-A + UV-B and UV-B exclusion showed enhanced yield parameters in terms of weight of total bolls and fibers (cotton), fresh weight of leaves (amaranthus), number of ears/panicles, grain yield per plant (wheat and sorghum), and number of seeds and seed weight (soybean) (Baroniya et al. 2011, 2014;Kataria and Guruprasad 2014, 2015; Kataria et al. 2013, 2014b). However, the extent of improved yield parameters was more in UV-B exclusion rather than UV-A + UV-B exclusion (Kataria et al. 2013). In *Curcuma longa*, UV-B exclusion grown plants showed significant increment in the photosynthetic rate, biomass accumulation, curcuminoid, and curcumin yield (Ferreira et al. 2016). To check the performance of monocots and dicots under ambient UV-B stress, Kataria et al. (2013) and Kataria and Guruprasad (2012a, b, 2014, 2015) research group conducted a comparative study and concluded that UV-B stress in the tropical environment lowers the PS-II efficiency, assimilation of nitrogen and carbon dioxide, which ultimately leads to reduced plant growth and productivity. They also showed that dicots are more sensitive than monocots for UV-B radiations. In addition, several reports have witnessed the improved crop yield under solar UV-B exclusion conditions when compared with ambient UV-B stressed conditions (Guruprasad et al. 2007; Kataria and Guruprasad 2012a, b; Roro et al. 2016; Sharma et al. 2019). On the basis of discussed literatures, solar UV-B rays considerably hamper the plant growth, development, and productivity, and if ozone depletion continues, it will allow more UV-B rays reaching to the Earth's surface which will further have more biological sequences to the plant growth and development.

7.3 Magneto-priming as a Strategy to Avoid UV-B Stress

Magneto-priming is a method of seed priming, where dry seeds are treated with magnetic field (MF). For improved performance of seeds, exposure timing and intensity of MF always need to be optimized according to the species (Sarraf et al. 2020, 2021). For example, the treatment of soybean seeds with static magnetic field (SMF) strength of 200 mT for 1 h has been used to improve its performance and for

the alleviation of adverse effects caused by ambient or supplemental UV-B stress (Fatima et al. 2021b; Kataria et al. 2017a, 2020a, 2021; Raipuria et al. 2021). In last decade, several scientific reports have been published showing magneto-priming based improved seed germination, seed vigor, seedling emergence, seedling growth, increased biomass accumulation, photosynthesis, and yield (Shine et al. 2011, 2012; Bhardwaj et al. 2012; Sarraf et al. 2020, 2021). Besides improved seed performance, magneto-priming of seeds have been shown to provide the tolerance against various abiotic stresses such as drought, salinity, heavy metal, and UV-B stress during seed germination and subsequent developmental stages of plants (Anand et al. 2012; Fatima et al. 2021a, b; Baghel et al. 2016, 2018, 2019; Kataria et al. 2015, 2017a, b, 2019, 2020a, b; Raipuria et al. 2021; Sarraf et al. 2020, 2021).

These improved performances of seeds after magneto-priming raise the question that how does SMF interacts with biological systems and improves their growth and performance. The answer of this question lies in the magneto-reception theory which accounts for the reaction of plants to DC/static fields and alternating magnetic fields (Camps-Raga et al. 2009; Shine et al. 2011; Shine and Guruprasad 2012a, b). As per this theory, there are two mechanisms named as ion cyclotron-resonance (ICR) and radical pair model to understand the influence of magneto-priming on plants (Galland and Pazur 2005; Fatima et al. 2021b). As per radical pair model, the biochemical reaction involving spin-correlated radical pairs should be sensitive to external magnetic fields. The biological reaction involving the spin selectivity and thus the sensitivity to magnetic field are the emission intensity of the photosynthetic reaction center and the triplet yield. As evidenced from the experimental and theoretical studies, the application of magnetic fields increases the radical lifetime and average radical concentration and shoot up the probability of radical reactions with the cellular components. These examinations apply also to the enzymatic systems entailing the radical pair formation and recombination (Galland and Pazur 2005). The external magnetic field can also modulate the emission intensity and the radical pair intermediates and triplet yields that occur in photosystems I and II of green plants. The increased water uptake in SMF-treated seeds as compared to untreated seeds is explained by the assumption that the magnetic field interacts with ionic currents in the cell membrane of the plant embryo (García-Reina and Arza-Pascual 2001).

When the magnetic field is applied, the chemical reaction rates modulate according to the radical pair mechanism. There is also a modulation of transport rates and binding by the ICR mechanism. Liboff in the ICR model explains the acceleration of Ca^{+2} by cyclotron resonance which is generated by the acceleration of extremely low-magnetic field and there is increased flux Ca^{+2} ion (Liboff 1985). The formula by ICR model states the frequency and ion specificity and also explains the frequency-specific absorption of electromagnetic fields by the ions (Del Giudice et al. 2002). In addition to these mechanisms, the interaction between environmental impacts such as ionizing radiation (ultraviolet–UV) and the magnetic field influence as a repair mechanism has also been discussed by Galland- Pazur (Dicarlo et al. 1999).

UV-B and MF are the two aspects of radiation biology, and both have contradictory effects; UV-B irradiation has damaging effects while MF priming has beneficial effects on plant growth and development (Shine et al. 2011, 2012; Kataria et al. 2013, 2014a, 2017a, 2020a, 2021). The UV-B radiation and magnetic treatments caused alteration in the cell membrane, seed germination, plant photosynthetic efficiency, enzyme activities, and yield of the crop plants (Yinan et al. 2005; Shine et al. 2011, 2012; Kataria et al. 2014a, b, 2015, 2017a, 2020a, 2021).

7.3.1 Effect of Magneto-priming on Seed Germination, Growth, Photosynthesis, Nitrogen Fixation, Antioxidant Defense, and Yield under UV-B Stress

Once the seed has sown in the soil, faster germination and vigorous seedling growth are very important for seedling establishment and their ability to cope with continuously changing environment (Prajapati et al. 2020; Sarraf et al. 2020). The faster seed germination is very well documented as the primitive effect of magneto-priming. In a recent report, UV-B exposure for 1 h caused severe reduction in seed germination and early seedling growth parameters of soybean possibly due to reduced activities of total amylase, nitric oxide synthase (NOS), and nitrate reductase (NR). At the same time, they have also proved that magneto-priming of soybean seeds promotes the nitric oxide (NO) production via NOS and alleviates the UV-B stress in soybean seedlings (Raipuria et al. 2021). Further, perusal of literature also revealed that stimulation from magneto-priming exists in the plants till its maturity; thus, the magneto-priming (200 mT, SMF for 1 h) of soybean seeds increased the growth parameters such as plant height, leaf area, specific leaf weight, thickness of the midrib of trifoliate leaves, biomass accumulation, nitrogen fixation, photosynthetic performance, and crop yield in the presence of ambient and supplemental/enhanced UV-B stress (Fatima et al. 2021b; Kataria et al. 2017a, 2020a, 2021). Magneto-priming with SMF pretreatment and exclusion of solar UV-B components are the methods that put an end to the defense against the stress caused by ambient UV-B stress (Fatima et al. 2021b; Kataria et al. 2015, 2017a, 2020a, 2021). The comparison of soybean plants from magneto-primed groups with the respective unprimed ones even in the presence of ambient UV-B as well as enhanced or supplemental UV-B irradiations found that the rectifying effects of SMF were distinctive on overall growth of the plants (Fatima et al. 2021b; Kataria et al. 2015, 2017a, 2020a, 2021). The magneto-priming and solar UV-B exclusion have shown to accumulate higher biomass and increased leaf thickness in sorghum and amaranthus (Kataria and Guruprasad 2012b, 2014). The reduction in nitrogenase, nitrate reductase, nitrite reductase, and leghemoglobin (contents in the nodulated mung bean cultivars) confirmed that there is a negative impact of UV-B elevation on nitrogen fixation and assimilation (Choudhary and Agrawal 2014). Similarly, UV-B supplementation also reduced N_2 fixation in the two tropical leguminous crops *Phaselous mungo* and *Vigna radiate* (Singh 1997). However, the number and size of nodules, total protein, and Lb content was found to be reduced in soybean plants

grown under ambient UV-B stress after exclusion of solar UV-B (Chouhan et al. 2008; Baroniya et al. 2014). Earlier studies on individual effects of SMF priming and solar UV exclusion in several crops indicated the stimulations in the activities of CA, NR, nitrogenase, and Rubisco along with the enhancement of plant growth, leaf area, biomass accumulation, and photosynthetic efficiency (Kataria et al. 2013, 2015, 2017a, 2020a; Kataria and Guruprasad 2012b, 2014, 2015). The SMF treatment has also shown the positive effect on the activity of nitrogen fixation under ambient UV-B stress as it enhances the leghemoglobin and heme-chrome content and also nitrogenase activity in the soybean root nodules (Kataria et al., 2017a, 2020a).

Ambient and supplemental UV-B were observed to increase the synthesis of UV-B-absorbing substances (UAS), reactive oxygen species (ROS) like superoxide radical ($O_2^{\bullet -}$) and hydrogen peroxide (H_2O_2), antioxidants like ascorbic acid and α-Tocopherol, and decrease the NR activity; subsequently, it results in a decreased rate of photosynthesis, biomass accumulation, and yield of the plants (Kataria et al. 2017a, 2020a, 2021). The SMF pretreatment caused reduction in the amount of ROS, MDA, proline, and UV-B-absorbing substances and the antioxidant enzymes such as SOD, GR, and POD activities similar to solar UV-B exclusion (Kataria et al. 2017a, 2020a, 2021). It indicates that the presence of UV-B stress caused the oxidative stress, and the exclusion of solar UV-B and SMF pretreatment to the seeds eradicates the requirement for the defense against harmful UV-B stress and leads to augmentation of primary metabolism and improves the crop yield (Kataria et al. 2017a, 2020a, 2021). Thus, crop yield is enhanced by SMF pretreatment and solar UV exclusion due to better leaf growth, leaf biomass, and higher efficiency of PSII, carbon and nitrogen fixation, higher DNA, RNA and protein content in the plants as compared to the plants receiving ambient UV-B and also supplemental or enhanced UV-B radiation (Kataria et al. 2017a, 2020a, 2021). Kataria et al. (2021) also found that SMF pretreatment increased the NO content and NR activity, higher efficiency of PSII, higher values of quantum yield of electron transport, relative amplitude of the I–P phase of Chl *a* fluorescence, performance indices, decreased intercellular CO_2 concentration, lower amount of UAS, ROS, and antioxidants that consequently improve the yield of soybean plants under ambient UV-B as well as supplemental UV-B stress. The recent reports on SMF pretreatment on yield of soybean plants in the presence of ambient or supplemental UV-B stress showed the enhancement in all the yield parameters namely number of pods, number of seeds/pods, pod and seed weight per plant and harvest index in the plants emerged from SMF-treated seeds as compared to the plants emerging from untreated seeds (Kataria et al. 2017a, 2020a, 2021).

7.4 Synchrotron Radiation and Its Use for Leaf Venation Imaging After Solar UV Exclusion and SMF Pretreatment

Synchrotron light sources are the scientific tools for basic and applied research in variety of fields ranging from material science, physics, chemistry, life science to archeological applications (Margaritondo 1988; Margaritondo and Meuli 2003).

During the past five decades, synchrotron source has evolved from first to fourth generation. The synchrotron light sources are composed of a storage ring which emits electromagnetic radiation (EMR) when the relativistic electron moves on a curved path with speed of light (Margaritondo 1988). The highly coherent radiation emitted from the synchrotron source can be used for phase sensitive imaging. Synchrotron radiation has been successfully used to observe the structural variations in leaf venation mainly the major conducting vein and adjoining minor veins of soybean plant under the influence of external environmental effects; the images of middle region of leaf midrib were obtained in intact third trifoliate leaves without any staining or sectioning (Fatima et al. 2016, 2017).

The morphological changes in leaf venation after exclusion of UV-B radiation and its impact on the leaf hydraulic activity of soybean plant have been studied using synchrotron-based X-ray imaging technique (Fatima et al. 2016). These authors reported that exclusion of solar UV-B caused 98% and 117% increase, respectively, in width of the mid-rib and minor veins of soybean third trifoliate leaves as compared to the leaves of plant grown under ambient UV-B stress. The novel phase contrast imaging technique with synchrotron source has also been applied to investigate the morphological changes in venation of leaves grown from soybean seeds pretreated with static magnetic field of different strengths from 50 to 300 mT (Fatima et al. 2017). The SMF strength of 200 mT for 1 h that caused considerable increase of 20% in thickness of the midrib was observed in soybean leaves (Fatima et al. 2017). These results encouraged the combined effect studies, involving soybean leaf midrib imaging grown from magneto-primed seeds in UV-exclusion conditions also; this study also showed the higher thickness of midrib and minor veins in soybean leaves as compared to the plants grown under ambient UV-B stress (Fatima et al. 2021b).

Leaf venation consists of the midrib or the major conducting vein and the associated minor veins which form a network for transporting water and nutrients to the plants from the roots. To understand the distribution of nutrient resources in plants, leaf venation is visualized and quantified using high-resolution X-ray Phase-Contrast Imaging (PCI) (Fatima et al. 2016). Compared to the conventional methods, X-ray PCI is a fast and novel method to image the leaf venation in intact leaves as plant leaves are thin weakly absorbing samples (Fatima et al. 2016). The leaf venation network is linked to the rate of photosynthesis in plants through the leaf hydraulic mechanism. Water transportation is the vital leaf growth parameter and shows an increment with the SMF pretreatment of the seeds which are also indicated by the midrib enhancement. X-ray PCI has been used to image the midrib and the associated higher order minor veins to indicate the enhancement in these veins in soybean with the SMF treatment, UV exclusion from the solar radiation and in the combination of these two phenomena (Fatima et al. 2016, 2017, 2021b). In order to visualize and quantify the leaf venation from the PCI images obtained at the synchrotron, single-distance phase retrieval has also been applied for soybean leaves which are comprised of light-absorbing element. These structural changes in leaves obtained from X-ray PCI are associated with the photosynthetic rate and stomatal conductance which thus showed and improved plant productivity after the SMF

treatment and UV exclusion (Fatima et al. 2016, 2017). Detailed investigation has been performed to correlate leaf venation and leaf hydraulic mechanisms by imaging major and minor vein up to 3°. These studies conducted with synchrotron-based X-ray PCI showed that the two parts of radiation biology namely magnetic field treatment with low flux densities and solar UV exclusion have positive effects on leaf venation and plant growth parameters such as leaf biomass and thickness of midrib and minor veins of third trifoliate leaves of soybean along with higher rate of photosynthesis under both individually and in the combination (Fatima et al. 2016, 2017, 2021b).

7.5 Conclusion and Future Perspectives

Current projected elevated levels of UV-B rays and its impact on agricultural crops have become a major concern to the plant biologists. The enhanced UV-B rays hamper the crop productivity by altering the developmental rates, leaf photosynthesis (photosystems, thylakoid, and grana membrane integrity), defense compounds like flavonoids, phenolic compounds, or waxes. In other direction, current UV-B levels are strong enough to induce ROS generation which triggers the antioxidant defense systems which also results in retarded growth and development of crop plants. In order to cope with UV-B stress, growing the plants under solar UV exclusion and SMF pretreatment of seeds, both improve the performance under ambient UV-B or enhanced UV-B stress. Both strategies improve the plant growth, biomass accumulation, nitrogen fixation through higher leghemoglobin, hemechrome content, nitrogenase activity in the root nodules, higher efficiency of PSII, and rate of photosynthesis which eventually results in higher crop yield. Thus, SMF pre-sowing treatment and solar UV-B exclusion alter the plant metabolism and provide protection to the plants from UV-B stress. As per the available reports, increased crop yield by SMF and solar UV exclusion is due to the better leaf growth, leaf biomass, efficiency of PS II, higher carbon and nitrogen fixation, higher the nucleic acid and protein content in the plants in comparison to untreated ones grown under UV-B stress conditions. Hence, magneto-priming of seeds before sowing and exclusion of solar UV-B can be used as potential strategies for the protection of plants to provide the tolerance against ambient UV-B stress. However, molecular mechanisms involved in magneto-priming-based or UV-B exclusion-based improved performance of the plants, are not fully understood. Detailed studies in this direction need to be conducted which can shed the light upon hidden molecular mechanism proving UV-B stress tolerance in both cases. Also, genes regulating the leaf growth, photosynthesis, nitrogen fixation in model plants and crops can be explored and characterized to be involved in the UV-B stress tolerance.

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8 Interaction of Salicylate and Jasmonate on the UV-B Induced Changes in Physiological and Biochemical Activities of Crop Plants

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Abstract

As far as plant systems are concerned, numerous physiological and biochemical mechanisms exist in order to cope with the fluctuating abiotic stresses. Their life cycle is completed only with the help of phytohormones, which act as endogenous signaling molecules regulating growth and metabolism. Recent studies indicate that exogenous application of phytohormones, especially salicylate and jasmonate, is considered to be an eco-friendly and effective means of chemical control against pathogen attack and abiotic stresses. Among the types of abiotic stresses, UV-B effects and amelioration of the negative effects using phytohormones were not reviewed in detail. This study is aimed to discuss the alleviating role of phytohormones like salicylate and jasmonate in UV-B induced inhibition of various physiological and biochemical parameters in higher plants.

Keywords

Amelioration · Salicylic acid · Jasmonic acid · MeJA

8.1 Introduction

Ultraviolet radiation (UV) is a part of the nonionizing region of the electromagnetic spectrum, which comprises approximately 8–9% of the total solar radiation (Coohill 1989; Frederick 1993). The UV radiation reaches the Earth's surface along with the visible light. It comprises shorter and longer wavelengths. The shorter wavelength ranges from 200 to 400 nm in the UV region. The longer wavelength ranging from

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400 to 700 nm constitutes the visible light. UV range is classified into three regions: UV-A, UV-B, and UV-C. The UV-A, with wavelengths from 320 to 400 nm, is not attenuated by ozone and thus not affected by depletion of the stratospheric ozone layer. The UV-C, with wavelength shorter than 280 nm, does not reach ground level, and this is not expected to change. UV-B radiation comprises wavelengths from 280 to 320 nm. Among UV wavelengths, UV-B radiation has received most attention because UV-B is absorbed by ozone. The daily fluence at the Earth's surface increases with a decrease in stratospheric ozone (Ormord and Hale 1995). Although UV-B is only a minor component of the total solar radiation (less than 0.5%), due to its high energy, its potential for causing biological damage is exceptionally high and even small increases could lead to significant biological damage. Current stratospheric ozone levels are at the lowest point since measurements began in 1970s and global terrestrial UV-B radiation levels range between 0 and 12 $kJ.m^{-2}$ on a given day with near-equator and midlatitudes receiving higher doses. The changes in ozone and UV-B are not uniform over the Earth's surface. The ozone concentrations in the high latitudes (comprising Antarctic and Arctic regions) are 40–50% lower than the pre-1980 values; in the midlatitudes (35–60°N and 35–60°S), these are 3–6% lower than pre-1980 values; and it shows minimum changes at the equator (UNEP 2002). Due to the ozone depletion, UV-B radiation on the Earth's surface has increased since early 1980s by 6–14% (UNEP 2002). The amount of UV-B received at a location depends on several atmospheric factors like the amount of ozone, position of the sun, and cloud cover. Land factors such as sand, snow, and water also influence the total amount of UV-B. Relative to the 1979–1992 conditions, in the 2010–2020 time period, the GISS model results indicate a springtime enhancement of erythemal UV doses of up to 14% in the Northern Hemisphere and 40% in the Southern Hemisphere (Taalas et al. 2000). Spectral studies on UV-B radiation indicated a 35% increase in intensity at 300 nm wavelengths, while there was no change in intensity at 320 and 325 nm wavelengths due to wavelength dependence of absorption coefficient of ozone (Kerr and McElroy 1993). Although the UV-B radiation comprises only a small portion of the electromagnetic spectrum, it has a disproportionately large photobiological effect on both plants and animals due to its absorption by important biological molecules such as proteins and nucleic acids (Jansen et al. 1998). The effect of UV light on plants has been investigated only after 1900s. Earlier studies were carried out on microbes. Arnold (1993) first studied the effects of UV light on the morphological and physiological aspects of plants. Effects of UV-B on different aspects of plant life have been reported to an extent (Caldwell et al. 1989; Teramura 1983; Tevini and Teramura 1989). UV radiation can be regarded as a stress factor, which is capable of significantly affecting plant growth characteristics. Plant height, leaf area, and leaf length have been showed to decrease, whereas leaf thickness was increased in response to UV-B radiation (Teramura 1983; Tevini and Teramura 1989; Rozema et al. 1997a). In addition, photosystem II was adversely affected by UV-B radiation (Teramura 1983; Caldwell et al. 1989; Tevini et al. 1991; Rozema et al. 1997a). Chlorophyll fluorescence has been shown to be a simple and reliable technique for measuring the performance of photosystem II and the extent to which environmental stress can impair photosynthetic efficiency

(Maxwell and Johnson 2000), e.g., temperature (Lu and Zhang 2000; Daymond and Hadley 2004), UV light (Kolb et al. 2001; Reddy et al. 2004), salinity (Chen et al. 2004; Jiang et al. 2006), and water (Saccardy et al. 1998). Plants produce a wide range of flavonoids and related phenolic compounds, which tend to accumulate in the leaves of higher plants in response to UV radiation (Tevini and Teramura 1989; Rozema et al. 1997b). It has been suggested that plants have developed UV-absorbing compounds to protect them from damage to DNA or to physiological processes caused by UV radiation (Stapleton and Walbot 1992). These UV-absorbing compounds accumulate in the epidermis, preventing UV radiation from reaching the photosynthetic mesophyll tissue (Stapleton and Walbot 1992; Braun and Tevini 1993).

UV radiation causes an increase in the peroxidase, catalase, pyruvate kinase, and polyphenol oxidase and IAA oxidase activity (El-Mansy and Salisbury 1971). Visual symptoms consisting of chlorotic or necrotic patches on leaves exposed to UV-B were not unique. Both vegetative and reproductive morphology were altered by UV-B radiation. Leaf anatomy was altered due to changes in the thickness of epidermal, palisade, and mesophyll layers. Enhanced UV-B generally decreased chlorophyll content (10–70%), but increased UV-B absorbing compounds (10–300%) in many crops. Decrease in photosynthesis particularly at higher UV-B doses was due to both direct (effect on photosystem) and indirect (decrease in pigments and leaf area) effects. The decrease in chlorophyll pigments and photosynthesis resulted in lower biomass and yield of most crop plants. Genotypes of crop species exhibited variability in leaf wax layer thickness, loss of chlorophyll, and increase in phenolics as mechanisms of tolerance to enhanced UV-B radiation resulting in changes in biomass/yield. Results from the few studies on the interaction of UV-B with other abiotic and biotic factors did not lead to useful conclusions. Studies are needed to quantify the effects of UV-B radiation on crops in order to develop dose–response functions that can facilitate the development of dynamic simulation models for use in UV-B and other environmental impact assessments. Phytohormones are chemical messengers that coordinate the activity of organs with each other. Phytohormones regulate cellular activities, pattern formation, vegetative and reproductive development, and stress responses. The five classic plant hormones, discovered by the mid-twentieth century, are auxins, cytokinins, gibberellins, ethylene, and ABA. The recently characterized hormones are jasmonates, salicylates, and brassinosteroids. An attempt was made to understand the influence of salicylate and jasmonate on short-term UV-B-induced changes on growth, biochemical constituents, and enzyme activity in two pulse crops, *viz.*, *Vigna radiata* (L.) Wilczek and *Vigna mungo* (L.) Hepper. The current study is aimed to discuss the alleviating role of phytohormones like salicylate and jasmonate in UV-B-induced inhibition of various parameters in higher plants. To achieve this, short-term UV-B treatment was given for 15 min/day for 3 days in ambient light-grown green gram and black gram seedlings. The dosage of UV-B at the plant surface was 400 $Wm^{-2}s^{-1}$. The UV treatment was initiated only in 7-day grown seedlings so as to enable photoreactivation. Soon after UV-B treatment, the seedlings were shifted to ambient daylight. UV-B-treated seedlings were sprayed

with different concentrations of SA (50–250 ppm) and JA (2–10 ppm), and the changes occurring thereafter were analyzed after 7, 15, and 30 days of plant growth.

8.2 Role of UV-B in Plant Defense

UV-B (280–315 nm) comprises one of the three classes of ultraviolet radiation and is positioned between UV-A (315–400 nm) and UV-C (100–280 nm) in the electromagnetic spectrum. The permeability of the atmospheric ozone layer to UV radiation begins within the UV-B range of wavelengths. Hence, natural sunlight contains UV-A, a part of UV-B but undetectable levels of UV-C and UV-B below 290 nm. However, the impinging measurable radiation at the ground surface starts from 295 nm. UV-mediated induction of phenolic compounds is one of the most common described plant responses that can directly alter the feeding of herbivorous insects. For instance, solar UV-B-mediated induction of the isoflavonoid glycosides daidzin and genistin in soybean pods was reported to be negatively correlated with the percentage of damaged seeds by the stink bugs *Nezara viridula* and *Piezodorus guildinii* (Zavala et al. 2015). This was explained by the fact that isoflavonoids restricted to Fabaceae members are one of the main chemical defenses against herbivorous arthropods in soybeans. Oxidation of chlorogenic acid by plant polyphenol oxidases and peroxidases occurs after disruption of plant tissues caused by herbivory. This results in the production of highly reactive quinones that can covalently bind to leaf proteins and inhibit their digestion by the herbivore (War et al. 2012). Interestingly, the authors demonstrated that the UV-B-mediated induction of a specific diterpene glycoside plays a major role in *N. attenuata* defense against the *Tupiocoris notatus*. Hence, UV-B can modulate the production of different plant chemicals varying in their effects on plant resistance. Likewise, Mewis et al. (2012) described the UV-B-mediated induction of two different plant defense-related metabolites, flavonoids and glucosinolates, in *Brassica oleracea* sprouts. This induction was positively correlated with higher levels of resistance against the caterpillar *Pieris brassicae* and the aphid *Myzus persicae*. Glucosinolates produced by Brassicales are nitrogen- and sulfur-containing glucosides that are hydrolyzed by myrosinases upon tissue disruption. The resulting hydrolyzed compounds, mainly isothiocyanates and nitriles, possess high toxicity against some herbivorous arthropods (Jeschke et al. 2015). However, whether this is due to UV-B-mediated induction of glucosinolates alone or in combination with flavonoids, responsible for the enhanced resistance, has not been fully addressed. These examples highlight the complexity of the interactions between the UV-B-induced chemical defense and herbivorous arthropods. Nevertheless, we can speculate that the overlapping plant responses to UV-B and herbivore's attack might have a similar impact on plant defenses. For instance, this would be the case of common UV-B- and herbivory-mediated induction of chlorogenic acid in *Nicotiana attenuata* (Izaguirre et al. 2007).

8.3 UV-Induced Expression of Pathogen Defense

Induced defense against plant pathogens involves metabolic pathways that produce structural and toxic metabolites to effectively limit the spread of the pathogen. Protection of plant cells and tissues from UV light by the production of flavonoids also uses the phenylpropanoid pathway, for which PAL is the key entry-point enzyme. The protective and repair responses outlined in earlier sections feature examples of UV-induced increases in transcript levels. Similarly, exposure to UV-B has been shown to stimulate the expression of genes important for pathogen resistance in plants, including those encoding chalcone synthase, chitinase, ß-1,3-glucanase, lipoxygenase, pathogenesis-related (PR) proteins, PAL, and stilbene synthase (Savenstrand et al. 2000). Profiling of plant transcriptomes has revealed that UV enhanced the expression of these genes after 30 min of treatment (Molinier et al. 2005). The nature of the inducing signal remains to be established, but photoreversible damage, presumably photoproducts, was associated with enhanced transcription of the β-1,3-glucanase gene (Kucera et al. 2003). However, no correlation between UV photoproduct levels and induced expression of several other pathogen defense genes was observed (Kalbin et al. 2001). Alternatively, damage responses may have very low thresholds potentially accounting for the absence of change when larger UV doses were applied. Whatever the nature of the primary photoreceptor, UV-B is known to act through downstream signaling pathways, the components of which closely resemble those for pathogen defense. Thus, plant responses to UV radiation and pathogens might also be linked through ubiquitin-mediated signaling. UV-induced changes in gene expression were reported in unexposed tissues of maize and tobacco (Casati and Walbot 2004). Such upregulation of defensive genes by UV treatment or out of plant-pathogen interaction was also expected. Although UV radiation and pathogen infection may activate common sets of genes in this pathway, there can be great variability between individual plants and pathogen-host interactions, and moreover UV may induce completely distinct responses also (Glombitza et al. 2004). The effect of UV radiation on defense gene expression strongly suggested that UV could modulate plant diseases (Stevens et al. 2005). However, because they involve either concurrent or postinoculation UV exposure, the possibility of direct effects or postharvest infection could also exist rather than the response of plant host. Nonetheless, there is evidence consistent with UV indirectly enhancing plant resistance to pathogens. UV-C irradiation of tobacco increased resistance to subsequent infection with TMV (Yalpani et al. 1994). Several groups demonstrated that postharvest treatment of various fruits with UV-C activated resistance against *Botrytis cinerea, Colletotrichum gloeosporioides, Monilinia fructicola, Penicillium digitatum, P. expansum,* and *Rhizopus stolonifer* (Stevens et al. 2005). Exposure of leaves of normally susceptible ecotype of *Arabidopsis* to sublethal doses of UV-C radiation induced resistance to subsequent challenges with virulent isolates of the biotrophic pathogen *Hyaloperonospora parasitica*. Although UV-B induction of many defense genes may not be attributable to UV photoproducts, there are indications that DNA damage may provoke the development of resistance to pathogens. The induced

resistance to *Monilinia fructicola* in postharvest UV-C-treated peaches was reported to be photoreversible (Stevens et al. 1998). Collectively, these observations suggest that UV-induced pyrimidine dimers may be important factors in activating pathogen resistance in response to UV-C treatment. Flavonoids are free radical scavengers and *tt5* mutants, which are sensitive to ROS, exhibited a high incidence of DNA strand breaks, and showed enhanced spontaneous recombination frequency as compared to the wild species (Filkowski et al. 2004). Therefore, in addition to UV photoproducts, an accumulation of endogenous DNA damage caused by ROS also triggered resistance to the pathogen.

8.4 Role of Hormones in Plants Under Stress

Plant hormones are involved in responses to abiotic (e.g., heat and cold, drought, and flooding) and biotic stresses (e.g., herbivory). During the normal processes of growth and development, plants are subjected to different types of stresses, such as drought, UV light, air pollution, and pathogen attack. Most of the plants suffer from both physiological and biochemical damage by exposure to high temperature or low temperature. Added to the established phytohormones like auxins, gibberellins, cytokinins, ethylene, ABA, and brassinosteroids, the recently added salicylic acid and jasmonic acid contribute much to the plant defense.

8.4.1 Salicylates

Salicylic acid (SA) named after Salix plant (willow) was first discovered as a major component in the extracts of willow tree bark that had been used as a natural anti-inflammatory drug from the ancient time to the eighteenth century (Rainsford 1984; Weissman 1991). Acetylsalicylic acid, which is widely known as aspirin, was the world's first synthetic drug that had been produced by Bayer company as an anti-inflammatory agent in 1897 (Weissman 1991). Since then, aspirin became one of the most popular drugs among the people and has been widely used for over 100 years; pharmacological actions of aspirin and related salicylates in animal system have been intensively studied, while only little about the action of SA in plants has been elucidated. White (1979) paid attention to salicylates as disease resistance-inducing chemicals. Injection of aspirin into tobacco leaves enhanced the resistance to subsequent infection by TMV (White 1979; Antoniw and White 1980). Later, it has been shown that this treatment induces the accumulation of PR proteins (Kessmann and Ryals 1993; Malamy et al. 1990; Metraux et al. 1990). SA is an endogenous plant growth regulator of phenolic nature that possesses an aromatic ring with a hydroxyl group or its functional derivative. SA was found as a crystalline powder having a melting point of 157–159 °C with a pH of 2.4 (Raskin 1992a). SA plays a key role in the regulation of plant growth, development, and interaction with other organisms and in the responses to environmental stresses (Raskin 1992b; Yalpani et al. 1994; Senaratna et al. 2000). Further, its role in seed germination, fruit yield, glycolysis, flowering in thermogenic plants (Klessig and Malamy 1994),

ion uptake and transport (Harper and Balke 1981), photosynthetic rate, stomatal conductance, and transpiration (Khan et al. 2003) was evident.

During the last 30 years, SA drew the attention of researchers due to its ability to induce systemic acquired resistance in plants to different pathogens. This is manifested in the appearance of pathogenesis-related proteins (PR), while SA is considered to serve as a signal in the induction of expression of these genes (Metraux 2001). The important role of SA is probably played by its ability to induce the expression of not only genes coding for PR proteins but also the extension genes in *Arabidopsis* (Merkouropoulos et al. 1999). SA has been identified as a signaling molecule in numerous plant responses to biotic and abiotic stresses, including UV-B, exposure to O_3 and pathogen attack. SA has been involved in activation of the stress induced antioxidant system, stimulates flowering in many plants, increase flower life, control ion uptake by roots and stomatal conductivity (Muthulakshmi and Lingakumar 2017). Data are available on SA-induced synthesis of HSPs in tobacco (Burkhanova et al. 1997) and fast activation of 48 kDa protein kinase in suspension cell culture of tobacco during osmotic stress (Mikolajczyk et al. 2000). SA could be actively transported, metabolized, or conjugated and translocated rapidly from the point of initial application to different plant tissues. Using modern analytical techniques, it was found that salicylates are distributed in many important agricultural plant species. In many plants, such as rice, crabgrass, barley, and soybean, the levels of SA have been found to be approximately in micro quantities. A survey of SA in leaves and reproductive structures of non-thermogenic angiosperms confirmed the ubiquitous distribution of SA in plants. The highest levels of SA were determined in the inflorescence with necrotizing pathogens (Raskin 1992a). SA stimulated flowering in a range of plants, increased flower life, and regulated ion uptake by roots and stomatal conductivity (Bhupinder and Usha 2003). It acts as an endogenous signal molecule responsible for inducing abiotic stress tolerance in plants (Einhellig 1989). SA decreased the inhibitory effect of water stress in wheat seedlings, low and high temperatures in tomato and bean, and chilling injury in maize and alleviated heavy metal toxicity in *Cassia* (Bhupinder and Usha 2003; Janda et al. 1999; Senaratna et al. 2000). The role of SA in plant growth and development, flowering, ion uptake, stomatal regulation, and photosynthesis has been thoroughly investigated. The intracellular SA concentration and SA signaling pathways are associated with the functions controlling cell growth, cell death, and defense. Exogenous application of SA resulted in a wide range of physiological responses, viz., inhibition of ethylene biosynthesis and seed germination, interference with ion transportation and absorption in the membrane of root cells, reversal of ABA effects in leaf abscission, and inhibition of plant growth. SA is most importantly considered as a signal molecule in the induction of systemic acquired resistance (Cutt and Klessig 1992; Klessig and Malamy 1994). Despite its presence in plants, exogenous application was shown to influence the yield performance, stomatal closure, seedling growth, and seed germination (Raskin 1992a). Additionally, it also affects the NO_3/NO_2 reductase and other enzyme activities involved in nitrogen metabolism without deleterious effects on the environment (Jain and Srivastava 1981; Negi and Prasad 2001). Some of the effects of SA may have been caused by its general chemical properties (as an iron chelator or acid) (Raskin 1992a).

The enhanced activity of peroxidase and increased synthesis of PR were some of the responses of SA which correlated with the fundamental responses involved in hypersensitive reactions that restricted the pathogen growth and caused tissue necrosis. Decline in catalase activity along with the significant reduction in diseased area was reported by Chandra et al. (2001). SA is involved in a broad range of physiological and metabolic responses in plants (Hayat et al. 2010). SA has been reported to play a vital role in abiotic stresses like drought, low and high temperatures, heavy metals, and osmotic stress (Janda et al. 1999; Rao and Davis 1999; Molina et al. 2002; Nemeth et al. 2002; Munne-Bosch and Penuelas 2003; Shi and Zhu 2008; Rivas-San Vicente and Plasencia 2011). Salicylic acid was extensively used to regulate the physiological, metabolic, and biochemical activities of plants, thereby affecting their growth (López-Orenes et al. 2013; Khan et al. 2015). SA stimulatory effects on callus and plant development have been reported in *Calendula officinalis* (Bayat et al. 2012), *Ziziphus spina-christi* (Galal 2012), and *Vigna mungo* (Lingakumar et al. 2014). SA enhanced both the primary and secondary metabolites in plants (Babel et al. 2014). It induced pathogen resistance protein and was successful in providing systemic acquired resistance to pathogens. SA potentially altered the metabolic pathways, leading to the accumulation of phytoconstituents during *in vitro* culture (Ram et al. 2013), since SA directly or indirectly affects the synthesis and signaling pathways of auxins, ethylene, and JA (Vlot et al. 2009). SA supplementation elicited different metabolite contents in several plant species such as *Andrographis paniculata* (Zaheer and Giri 2015), *Bacopa monnieri* (Largia et al. 2015), and *Achillea millefolium* (Gorni and Pacheco 2016).

8.4.1.1 Interaction of UV-B and SA on Morphological Parameters

Changes in the morphology of *V. radiata* and *V. mungo* seedlings to UV-B and posttreatment with SA at various concentrations (50–250 ppm) are shown in Figs. 8.1 and 8.2. UV-B treatment alone caused a 15–34% reduction in *V. radiata* and 20–22% reduction in *V. mungo*. Supplementation of those UV-B-treated seedlings with various concentrations of SA proved to be effective in relieving the UV-B inhibition to 4–8%. The relieving of UV-induced inhibition was noticed at 100 ppm of SA. High concentrations of SA such as 250 ppm were not helpful in alleviating UV-B-induced response. Root length was also found to be influenced under short-term UV-B and hormonal posttreatment as shown in Fig. 8.1c. UV-B treatment caused a 5–15% reduction and 11–18% reduction in the root length of green gram and black gram, respectively. SA supplementation to UV-B-irradiated seedlings proved to be effective in controlling the UV-B inhibition. There was not much difference in the reduction of inhibition within these species of *Vigna.* Shoot fresh weight got significantly decreased under short-term UV-B treatment to a level of 17–23% in *V. radiata* and 13–18% reduction in *V. mungo.* Both green gram and black gram seedlings that were exposed to UV-B and subsequent hormonal posttreatments brought in significant changes in fresh weights of both the crops (Fig. 8.2).

In both the cases, 100 ppm of SA was found to be effective. Similar to shoot fresh weights, root fresh and dry weights were found to be reduced under UV-B treatment,

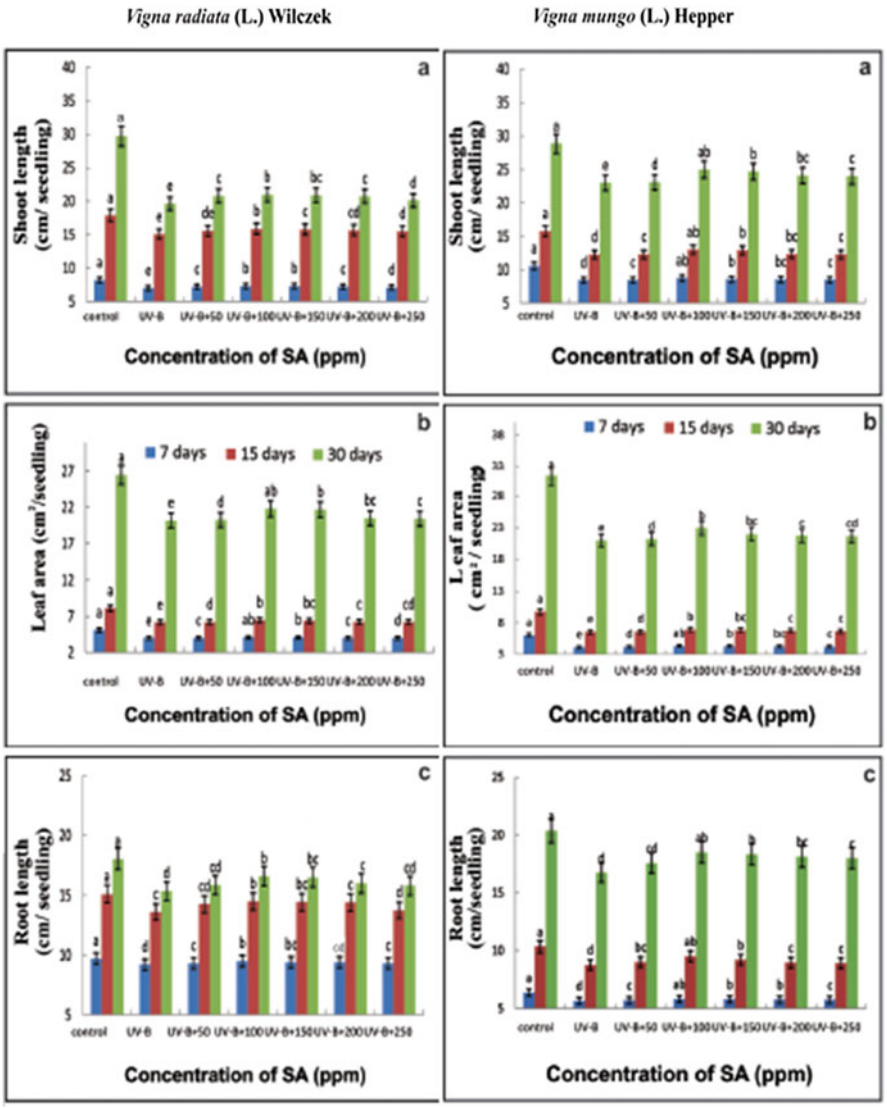

Fig. 8.1 Typical morphology of *Vigna radiata* and *Vigna mungo* seedlings exposed to short-term UV-B (15 min/day) and SA foliar spray. Each value represents the mean of six independent measurements (mean ± SE, $n = 6$). Bars carrying different letters are significantly different at $p < 0.05$

whereas foliar spray of SA was more effective in reducing the loss. Alleviation of UV-B by the exogenous application of SA was not much evident during the early stages of growth. SA has been reported to improve *in vitro* regeneration as well as abiotic stress tolerance in plants. The effect of various concentrations of SA on *in vitro* propagation of shoot apices of *Hibiscus* confirmed the regenerating potential

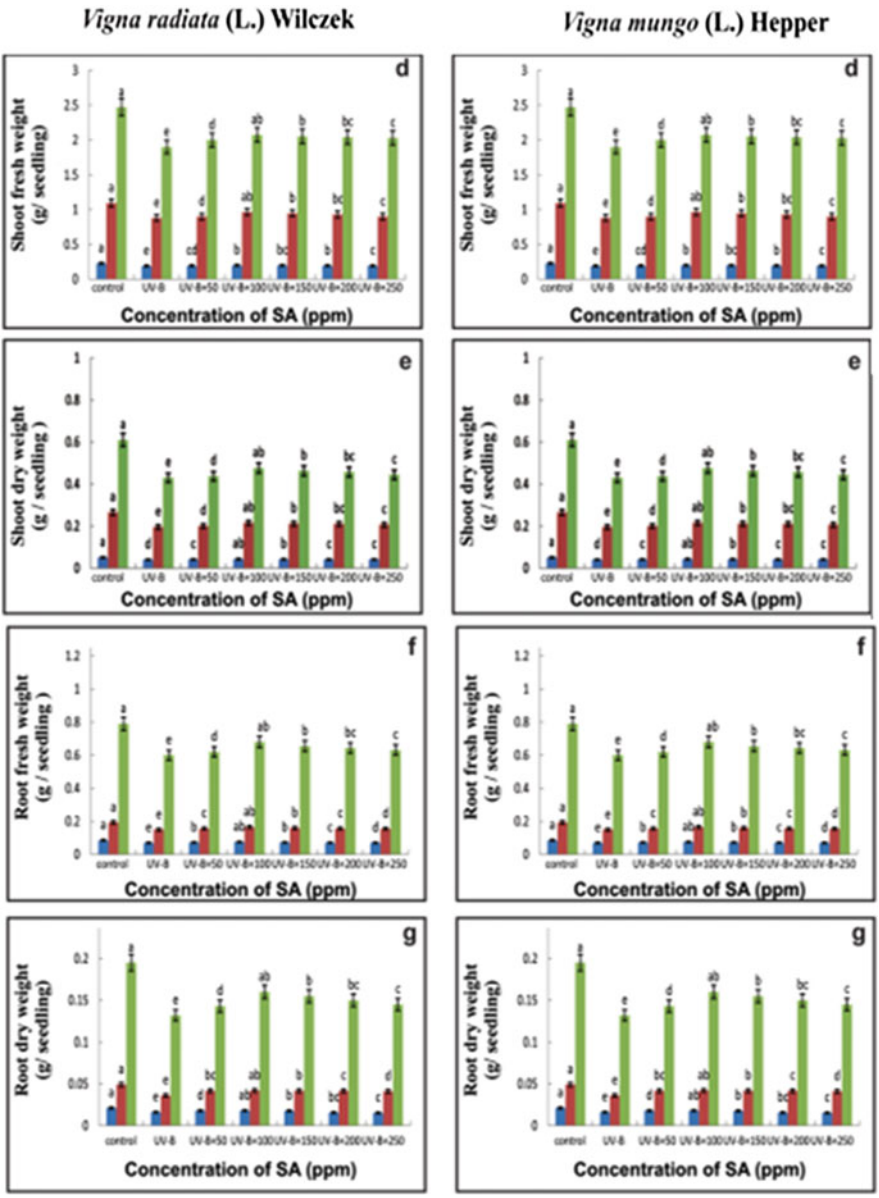

Fig. 8.2 Typical changes in growth parameters of *Vigna radiata* and *Vigna mungo* seedlings exposed to short-term UV-B (15 min/day) and SA foliar spray

of SA (Sakhanokho and Kelley 2009). Furthermore, SA has been used to enhance *in vitro* regeneration in several other plant species (Quiroz-Figueroa and Mendez-Zeel 2001; Lu et al. 2001; Hao et al. 2006). More of root formation than shoot

initiation was seen at all concentrations of SA (Lingakumar et al. 2014) in tissue culture.

8.4.1.2 Interaction of UV-B and SA on Pigment Content

The photosynthetic pigment changes in *V. radiata* and *V. mungo* seedlings that were exposed to short-term UV-B treatment and hormonal posttreatments are shown in Fig. 8.3. UV-B treatment significantly reduced the amounts of Chl *a* and *b* and total Chl and carotenoids as compared to untreated control. The changes in Chl *a* content upon UV-B treatment alone showed an appreciable decrease in both the species. Supplementation with various concentrations of SA proved to be effective in relieving the inhibition of Chl *a* synthesis (Fig. 8.3a). Regarding Chl *b* content, SA was more helpful in relieving the UV-B inhibition. Total Chl content got decreased under UV-B treatment around 23–31% in *V. radiata* and *V. mungo*. SA at high doses inhibited plant growth and Chl contents in tomato (Kord and Hathout 1992). However, a reduction in Chl content was observed in plants pre-treated with SA (Pancheva et al. 1996; Anandhi and Ramanujam 1997; Shehata et al. 2001). Besides seed-soaking treatment, foliar application of SA increased the pigment content in *Brassica napus* (Ghai et al. 2002). Similar increase was observed when *B. juncea* was sprayed with lower concentrations of SA only (Fariduddin et al. 2003). Moharekar et al. (2003) reported that SA activated the synthesis of carotenoids and xanthophylls and also enhanced the rate of de-epoxidation with a concomitant decrease in Chl pigments and Chl *a*/*b* ratios. Exogenous application of SA was found to enhance the net photosynthetic rate, internal CO_2 concentration, water-use efficiency, stomatal conductance, and transpiration rate (Fariduddin et al. 2003). Khan et al. (2003) found that foliar spray of SA and ASA led to an increase in the overall photosynthetic yield of soybean and corn. Canakci (2003) was of the opinion that Chl *a* and *b* decreased without affecting carotenoid content, whereas Khodary (2004) observed a significant increase in growth, pigment content, and photosynthetic rate in maize seedlings upon SA spray. There are reports wherein SA induced not only photosynthetic pigment content but also Rubisco activity and net photosynthetic rate and increased production of photosynthates (carbohydrates). Foliar spray of SA caused an increase of Rubisco and PEP case activity (Singh and Usha 2003). The improvement of all these characteristics ultimately increased the net photosynthesis. Foliar application of SA and L-trp regulated stomatal opening and reduced water loss under drought conditions enabling the plants to maintain turgor to carry out photosynthesis even under water-deficit conditions.

He et al. (2005) and Sakhabutdinova et al. (2003) postulated that SA increased the production of photosynthates. The enhanced photosynthetic activity led to increased sap production, which resulted in the maintenance of relatively high leaf water content for better growth. Enhancement of carotenoid pigments, photosynthetic rate, and CO_2 fixation and modification of the activity were some of the roles assigned to SA (Hayat and Ahmad 2007). Application of SA increased Chl *a* content of maize (Khodary 2004), barely (El-Tayeb 2005), wheat (Agarwal et al. 2005), and *Brassica napus* (Ghai et al. 2002). Exogenous application of SA also increased the net photosynthetic rate by increasing the stomatal conductance and

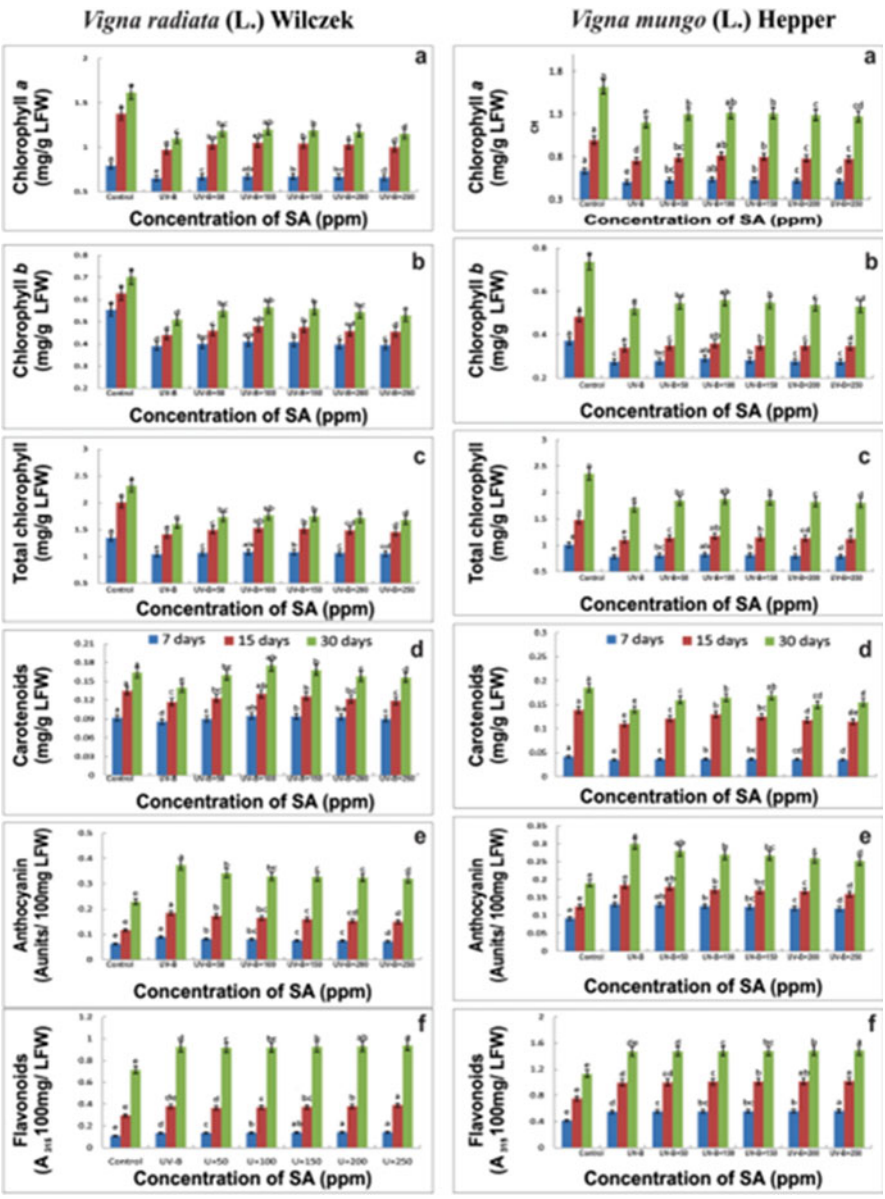

Fig. 8.3 Changes in photosynthetic and non-photosynthetic pigment composition of *V. radiata* and *V. mungo* seedlings exposed to UV-B and SA treatments

carbonic anhydrase activity (Hayat et al. 2010, 2012). The changes in anthocyanin content upon short-term UV-band hormonal posttreatment are shown in Fig. 8.3e. UV-B treatment caused 42% reduction in both the species of *Vigna*. Foliar spray of

SA at 100 ppm to UV-B treated species was more effective in reducing the UV-B inhibition to 16–19% in *V. radiata* and 10% in *V. mungo* seedlings. Irrespective of the growth stage, anthocyanin content was found to increase under SA treatment. As reported earlier, anthocyanin synthesis was more under UV-B and after SA treatment. Combined treatment further stimulated the anthocyanin synthesis to a greater extent. The results indicate that both UV-B and SA act as stress signals. Previous reports have demonstrated that SA induced anthocyanin content in *Capsicum* (Mahdavian et al. 2008) and *Zingiber officinale* (Ghasemzadeh and Jaafar 2012). On the contrary, Chashmi et al. (2010) reported that total anthocyanin was not affected by SA treatment in *Atropa belladonna*. Moreover, an insignificantly increased amount of anthocyanin was reported in *Coriandrum sativum* treated with SA (Rahimi et al. 2013). Saw et al. (2010) noticed that the anthocyanin concentration in SA-treated sample was not increased during the initial days of growth but increased thereafter in cell suspension cultures of *Vitis vinifera*.

Flavonoid content was also found to be increased under short-term UV-B treatment in both the species (Fig. 8.3f). In contrast to anthocyanin, the flavonoid content declined in both species of *Vigna* after SA treatment. UV-B plus SA treatment failed to induce significant changes in *Vigna*. According to Kim et al. (2009), the total flavonoid content in *Taraxacum officinale* also increased significantly in response to the application of SA, cytokinin, and GA3, demonstrating the effects on the biosynthesis of secondary metabolites; Klessig and Malamy (1994) observed a significant higher total flavonoid content in marigold in florescence treated with 1 m MSA. Exogenous application of SA also induced the expression of many defense genes, which encode particular enzymes of secondary metabolic pathway to form bioactive compounds such as phenolics (Ali et al. 2007). A significant increase in the synthesis of flavonoids in response to the application of SA was observed in various plant species like *Matricaria chamomilla* (Kovacik et al. 2009), *Zingiber officinale* (Ghasemzadeh and Jaafar 2012), and *Silybum marianum* (Khalili et al. 2009). Kovacik et al. (2009) pointed out that SA concentrations proved to be growth promoting (50 μM) and growth inhibiting (250 mM) when tested in *M. chamomilla*. Bandurska and Cieslak (2013) have shown accumulation of SA under drought and UV-B stress due to increased activity of enzymes like PAL and benzoic acid hydroxylase.

8.4.1.3 Interaction of UV-B and SA on Biochemical Constituents

The quantification of biochemical constituents such as total soluble protein, sugar, starch, free amino acid level, and proline under stress conditions could be considered as a direct measure of the damage caused by biotic, physical, or chemical agents. The changes in total soluble protein content of *V. radiata* and *V. mungo* seedlings that were exposed to short-term UV-B and hormonal posttreatment are shown in Figs. 8.4 and 8.5. UV-B treatment alone caused ~36% and 29–32% decrease in *V. radiata* and *V. mungo*, respectively. Compared to *V. radiata*, there was a greater reduction in the total soluble protein content in *V. mungo*. Supplementation of UV-B-treated seedlings with various concentrations of SA proved to be effective in relieving the UV-B inhibition of protein content (Fig. 8.4a). In *V. radiata*, SA at

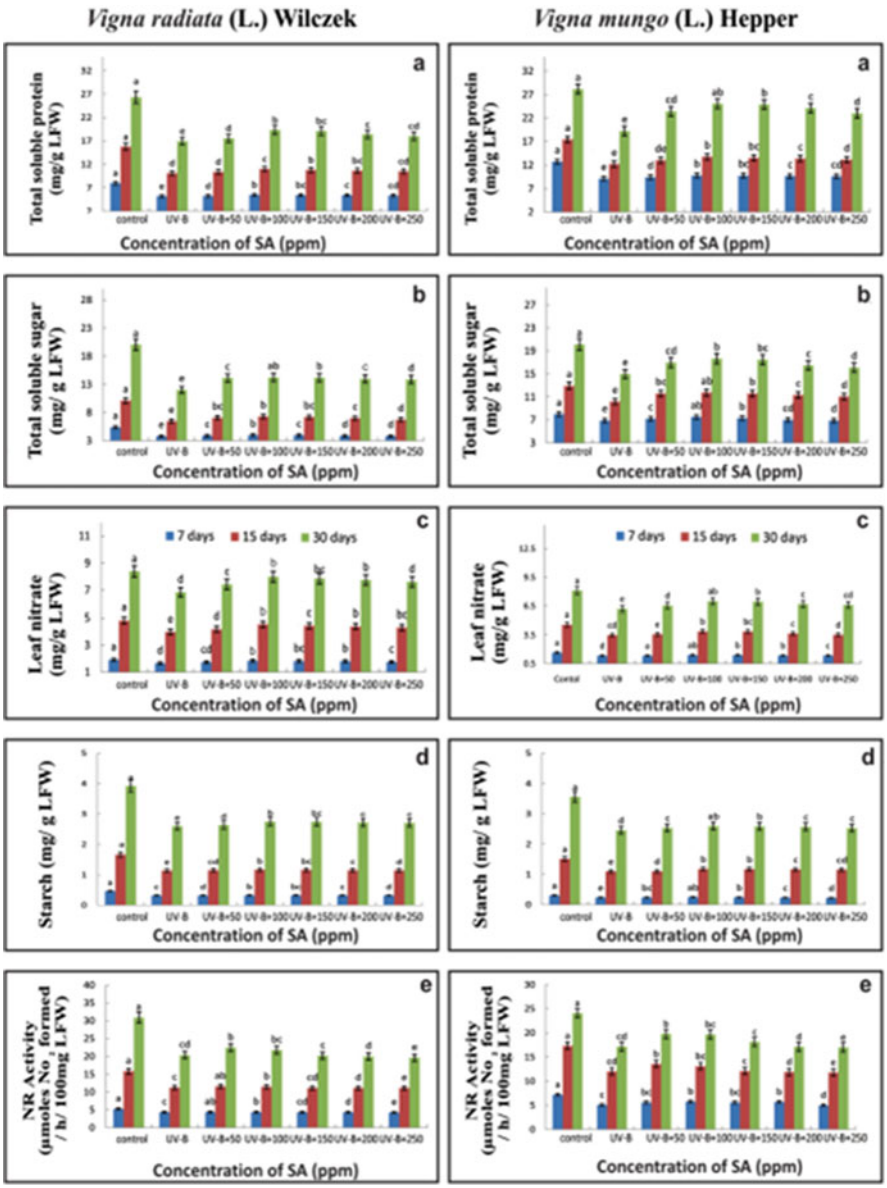

Fig. 8.4 Biochemical constituents of *V. radiata* and *V. mungo* seedlings exposed to UV-B and SA treatments

100 ppm was found to bring down the inhibition of protein level to 4–9% throughout the stages of growth, whereas it was 3–7% in *V. mungo*. Chandra et al. (2007) reported that the application of SA increased total soluble protein content of cowpea. SA induced the formation of defensive types of proteins such as protein kinase and

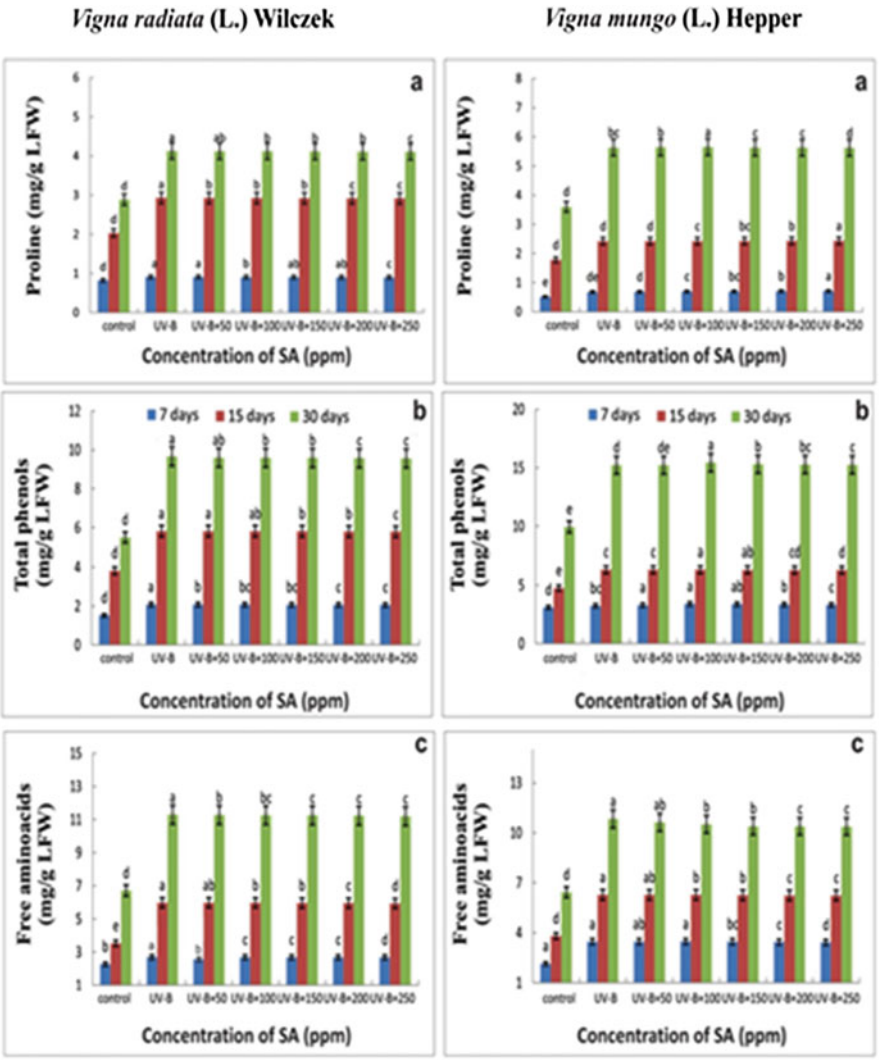

Fig. 8.5 Biochemical constituents of *V. radiata* and *V. mungo* seedlings exposed to UV-B and SA treatments

Rubisco, indicating the accumulation of plant proteases (Raskin 1992b). Under SA treatment, a high amount of PR proteins was produced and those proteins got decreased under salt stress. UV-B treatment alone caused a decrease of sugar level to 30–42% and 14–33% in *V. radiata* and *V. mungo*, respectively (Fig. 8.4b). When compared to *V. radiata*, there was a greater reduction in the total soluble sugar content in *V. mungo*, which could be due to the composition of the species itself. SA supplementation to UV-B-treated seedlings showed relief of UV-B inhibition. The UV-B-induced inhibition of sugar content was relieved to 4–13% and 8–21% in

green gram and black gram, respectively. Kiddle et al. (1994) reported that SA significantly induced nearly all glucosinolates, especially 2-phenylethyl glucosinolate in *Brassica napus* leaves. Mikkelsen et al. (2003) reported that SA induced the accumulation of 4-methoxy-glucobrassicin and reduced the content of glucobrassicin and neoglucobrassicin. Plants like tomato and maize, when exposed to salinity treatment, showed a gradual increase of sugars in solutions affecting polysaccharide levels (Khodary 2004). Ali et al. (2007) reported that SA regulated sugar contents (translocation from source to sink) and caused a significant increase in total soluble sugars. Chandra et al. (2007) reported that the application of SA increased total soluble sugar and soluble protein levels. Gunes et al. (2007) reported that the interaction of SA and salinity decreased the sugar content. Gigolashvili et al. (2008) observed that *MYB28*, the major regulator of aliphatic glucosinolate biosynthesis, was regulated by SA treatment. Accumulation of soluble sugars was detected in tomato pre-treated with SA at saline conditions (Gemes et al. 2008).

On the contrary, Baghizadeh et al. (2014) have reported that SA reduced sugar content under various concentrations of salinity. SA application was found to increase the polysaccharide level of soluble sugars and activated the consumption of soluble sugar metabolism by increasing osmotic pressure (Zahra et al. 2010). Keshsvarz et al. (2011) demonstrated that foliar application of SA at 400 μM increased the level of soluble sugars in *Brassica napus*. The changes in leaf nitrate content of *V. radiata* and *V. mungo* seedlings that were exposed to short-term UV-B and SA posttreatments are shown in Fig. 8.4c. UV-B treatment alone caused 14–19% and 20–24% decrease in nitrate content in *V. radiata* and *V. mungo*, respectively. Supplementation of UV-B-treated seedlings with various concentrations of SA proved to be effective in relieving the UV-B inhibition (Fig. 8.4c). 100 ppm of SA was effective enough to reduce the UV-B-induced inhibition to a level of 10–14% throughout the stages of growth. The changes in starch content of *V. radiata* and *V. mungo* seedlings exposed to short-term UV-B and SA posttreatments are shown in Fig. 8.4d. UV-B treatment alone caused 30% and 23% decrease in *V. radiata* and *V. mungo*, respectively, after various times of growth. Supplementation with SA hormone to the irradiated seedlings was found to be helpful in terms of starch content. Alleviation of UV-B by exogenous application of SA was not much evident during the early stages of growth. High concentration of SA such as 250 ppm was not helpful in completely alleviating UV-B-induced inhibitory response. Sugar and starch content showed an increased trend with progressive increase in SA treatment in black gram and green gram due to their role in the enzymatic reaction related to the cycle of carbohydrate catabolism. Kumar et al. (2010) confirmed the effects of SA on seedling growth, development, and nitrogen-use efficiency in cucumber with or without nitrogen nutrient. SA at 50 μM concentration increased starch content appreciably with or without nitrogen. The rate of nitrogen assimilation increased in response to SA with increase in the amounts of soluble sugar and starch. The changes in *in vivo* nitrate reductase activity of *V. radiata* and *V. mungo* seedlings exposed to short-term UV-B pre-treatment and hormonal posttreatment are shown in Fig. 8.4e.

UV-B treatment caused nearly 30% reduction in NR activity, and foliar spray of SA at various concentrations to these seedlings helped to overcome the inhibition as presented in Fig. 8.4e. *In vivo* NR activity decreased under short-term UV-B treatment but increased upon SA treatment. Both leaf nitrate and nitrate reductase activities were found to increase at a low concentration of SA. Application of SA increases the availability of substrate for NR, and NO_2 generated after NO_3 reduction could function as a substrate for NiR activity. The application of SA was beneficial in improving their nitrogen uptake and thereby enzyme synthesis. Decrease in NRA and NiRA under salinity or other stress has been earlier demonstrated by Khan et al. (1990) and Ashraf and Fatima (1995). The process of nitrate reduction is well known for its sensitivity to environmental stresses (Iqbal et al. 2006). Sarangthem and Singh (2003) reported that the levels of nitrogen, protein, and NR activity were increased in *Phaseolus vulgaris* by foliar application of SA. This is possible because of changes in membrane organization at higher SA level or chelation of some important elements of cellular and organelle membranes (Uzunova and Popova 2000). However, internal nitrate may provide an inductive concentration to NR activity at lower concentrations of SA and SA-induced modulation of nitrogen-use efficiency in cucumber cotyledons (Singh et al. 2008). The NO_3 assimilation was dependent on the physiological concentration of SA when NO was absent. The total protein content was increased in soybean plant seedlings sprayed with SA, and this increase might be due to enhanced activity of NR following SA treatment (Kumar et al. 1999). However, at higher concentrations (10^{-3}/10^{-4} M), SA proved to be inhibitory. Treatment of maize with lower concentrations of SA also enhanced the uptake of nitrogen and NR activity, whereas higher concentrations were proved to be inhibitory (Jain and Srivastava 1981; Fariduddin et al. 2003). It can therefore be assumed that SA concentration plays an important role in regulating NR activity, with lower concentrations enhancing nitrate reductase protein and higher concentrations decreasing it. Accumulation of proline in the leaves of *V. radiata* and *V. mungo* seedlings exposed to short-term UV-B and SA foliar spray is shown in Fig. 8.5a. Proline content got increased under UV-B pre-treatment up to 10–44% and 32–56% in *V. radiata* and *V. mungo*, respectively. Even after supplementation with SA, the level of proline remained unchanged.

Proline as an amino acid is known to occur widely in higher plants and accumulates in large quantities in response to environmental stresses. In addition to its role as an osmolyte for osmotic adjustment, proline contributes by stabilizing subcellular structures (e.g., membranes and proteins), scavenging free radicals, and buffering cellular redox potential under stress conditions. The proline content was found to be decreased and unchanged due to SA application. It may also function as a protein-compatible hydrotrope (Srinivas and Balasubramanian 1995), alleviating cytoplasmic acidosis and maintaining appropriate $NADP^+$/NADPH ratios compatible with metabolism (Hare and Cress 1997). Also, rapid breakdown of proline upon relief of stress may provide sufficient reducing agents that support mitochondrial oxidative phosphorylation and generation of ATP for recovery from stress condition and repairing of stress-induced damage (Hare and Cress 1997; Hare et al. 1998). Thus, increasing of proline under drought decreased the adverse effects of stress.

Moreover, Yazdanpanah et al. (2011) reported that SA treatment increased the proline content, and Delavari et al. (2010) showed that SA treatment elevated proline under salinity stress. UV-B treatment caused significant increase in phenol content in both the species (Fig. 8.5b). SA supplementation to UV-B-irradiated *Vigna* species did not cause any change. SA simultaneously increased the accumulation of phenolic compounds and increased the activities of H_2O_2-scavenging enzymes. SA-induced increase of synthesis of cinnamic acid favored an increase of phenol content. The results suggested that some relationships might exist between H_2O_2 and secondary metabolism in the SA-applied *Vigna* seedlings. SA played a role in regulating PAL activity and phenolic compound biosynthesis by bringing about a relationship among SA, PAL, and phenolic compounds (Chen et al. 1993). War et al. (2012) evaluated the biochemical response of *Cicer arietinum* to a range of SA concentrations. Plants responded very quickly to SA with accumulation of phenols. No significant differences were recorded in the phenolic content at 1–2 mM of SA. Mohammed and Tarpley (2013) studied the impacts of α-tocopherol, glycine betaine, and SA applications under UV-B stress conditions. The treated plants showed significant increases in leaf phenolic concentration under UV-B treatment. Application of these compounds increased leaf phenolic content and offered protection against elevated UV-B. Free amino acid content of *Vigna* seedlings exposed to UV-B and SA treatment is shown in Fig. 8.5c. UV-B treatment caused appreciable increase of free amino acid content in both the species of *Vigna*. SA treatment of *Vigna* species showed decreased amount of free amino acid content throughout the stages of growth. The increase in amino acid level in plant organs under UV-B-treated conditions could be due to breakdown into amino acids (or) as a result of decrease in the synthesis due to reduction of NRA, leaf nitrate, and substrate. It is also observed that under stress conditions, some low-molecular-weight compounds such as amino acids, polyamine, polyols, proline, glycine betaine, and organic acids are produced, consequently reducing leaf osmotic potential (Dantas et al. 2005). Reports indicate that under stress conditions, plants produced some stress proteins and some of them are taken by phytohormones such as SA, resulting in decrease of protein content (Hussain et al. 2007). El-Khallal (2007) observed higher free amino acid content in tomato plants treated with JA and SA. Thakur and Sohal (2014) reported different concentrations of elicitors, *viz*., salicylic acid and benzothiadiazole (BTH), in morphological and biochemical parameters of *Brassica juncea* and *B. napus* cultivars under fungicide treatment. Among the treatments, the combination of BTH and SA exhibited maximum free amino acids. Hayat et al. (2005) suggested that the combinations of elicitors act synergistically to promote growth and metabolic activities leading to the induction and regulation of disease resistance.

8.4.1.4 Interaction of UV-Band SA on Antioxidant Enzyme Activities

The activities of enzymes like catalase, polyphenol oxidase, superoxide dismutase, and peroxidase were assessed under UV-B and UV-B plus SA treatments. Catalase activity of *Vigna* seedlings exposed to UV-B and SA treatment is shown in Fig. 8.6a. Like any other antioxidant enzymes, UV-B treatment caused increased CAT activity in both the crops. Supplementation of UV-B-treated seedlings with various

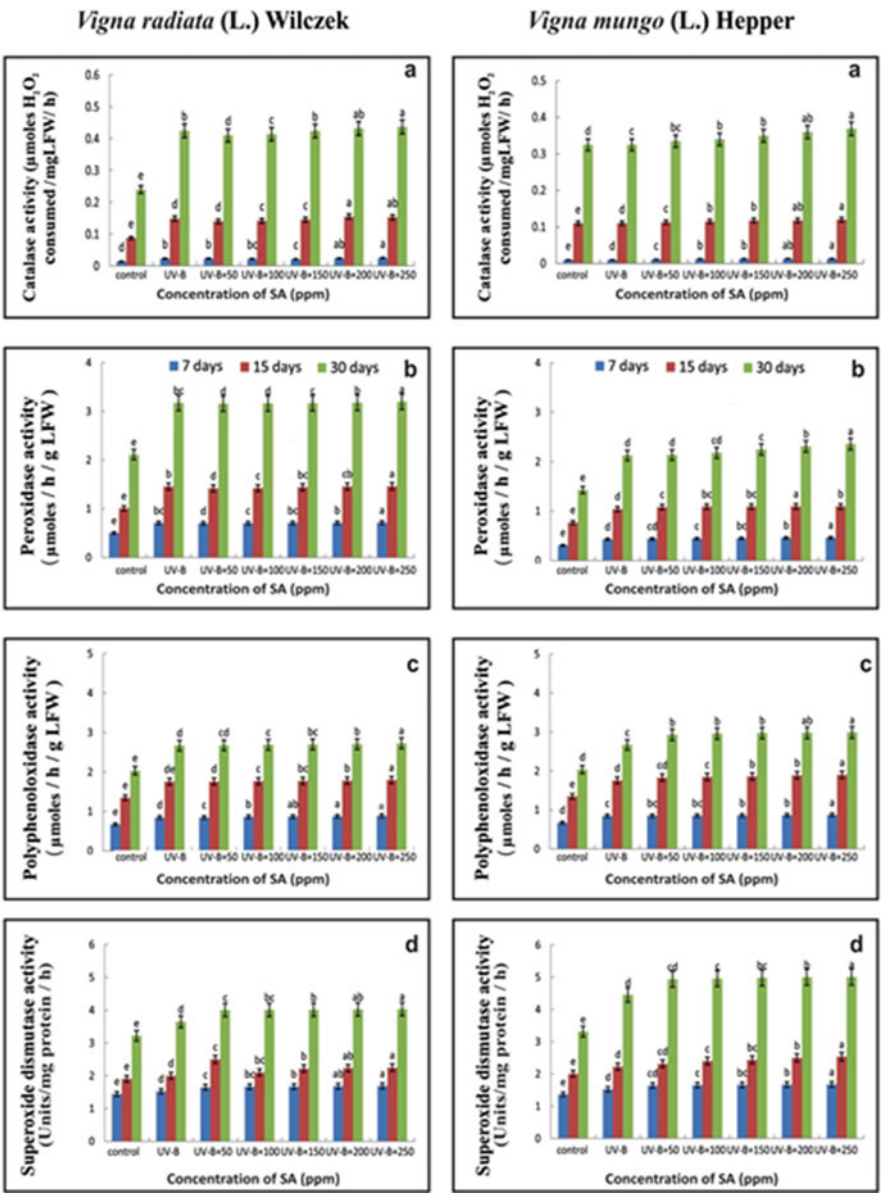

Fig. 8.6 Effect of UV-B and SA spray on antioxidant enzyme activities in *V. radiata* and *V. mungo* seedlings. The measurements were made after 7, 15, and 30 days of growth

concentrations of SA showed increased CAT activity. At 100 ppm of SA treatment, high amount of catalase activity was up to 57–72% in *V. radiata* and 35–59% in *V. mungo*. The CAT activity increased with increase in the concentration of SA. Catalase, which utilizes H_2O_2 as a substrate, also oxidizes a wide range of

hydrogen donors such as phenolics. In addition, salt-induced degradation of CAT protein exceeded its biosynthesis. CAT activity due to SA application might have been due to increased endogenous level, a phenomenon that occurs in many plant species exposed to oxidative stress (Shim et al. 2003). There are evidences to show that SA decreased CAT activity (Dat et al. 2000; Shi et al. 2006; Shi and Zhu 2008; Shim et al. 2003), while some other studies also showed that SA treatment did not inhibit CAT activity (Tenhaken and Rubel 1997). Ding et al. (2007) have reported that treatment with SA decreased the activity of CAT in plants like *Triticum aestivum*, *Lepidium sativum*, and *Oryza*. It seems that response to SA may differ according to the intensity of the stress, plant parts and species, time assayed after stress treatment, and induction of new isozymes (Shim et al. 2003; Hashemi et al. 2010; Mutlu and Atici 2013). Peroxidase activity was assayed in green gram and black gram seedlings exposed to UV-B and SA treatment (Fig. 8.6b). UV-B treatment caused 40–50% and 35–49% increase in *V. radiata* and *V. mungo*, respectively. SA supplementation in UV-B-stressed seedlings decreased and increased in both the species. At higher concentration of SA, both *V. radiata* and *V. mungo* seedlings responded with increased activity of peroxidase, while lower concentrations were not able to bring about any change in peroxidase activity. Peroxidase activity got increased under SA treatment. The increase of peroxidase activity under the influence of SA was shown earlier in cereals (Ruffer et al. 1995, Ananieva et al. 2002; Kolupaev et al. 2010). Polyphenol oxidase activity of *V. radiata* and *V. mungo* seedlings exposed to short-term UV-B pre-treatment and post-hormonal treatment is shown in Fig. 8.6c. UV-B treatment caused 25–31% and 29–48% increase in *Vigna* species. Supplementation of UV-B-treated seedlings with various concentrations of SA caused an increase in PPO activity in both the plants. In *V. radiata*, 250 ppm of SA was found to increase PPO activity to a level of 29–33%, and in black gram the increase was 29–40%. At 100 ppm of SA, the PPO activity was not induced. Regarding polyphenol oxidase, a consistent increase at high concentration of SA was observed in *Vigna* at all ages of plant. The effects of SA on apoplastic enzyme activity in wheat plant leaves were found to increase with SA treatment, while catalase, peroxidase, and polyphenol oxidase activities got increased (Tasgin et al. 2003). SOD activity of *V. radiata* and *V. mungo* seedlings exposed to short-term UV-B treatment and post-hormonal treatment is shown in Fig. 8.6d. UV-B treatment caused 4–18% and 10–54% increase in *V. radiata* and *V. mungo*, respectively, after 7, 15, and 30 days of growth. Supplementation of UV-B-treated seedlings with various concentrations of SA caused an increase in superoxide dismutase activity in both plants. High concentration of SA such as 250 ppm was found to increase enzyme activity to a level of 10–25% in *V. radiata* throughout the stages of growth. With respect to *V. mungo*, the increased SOD activity was 22–51% at 250 ppm concentration of SA. SOD, a key enzyme in cellular defense, catalyzes the dismutation of superoxide radicals to H_2O_2 and O_2 (Foyer and Noctor 2000).

SOD constitutes the first line of defense against AOS and is a major scavenger of the superoxide (Alscher et al. 2002; Takahashi and Asada 1983). POD is known to decompose H_2O_2 by the oxidation of phenolic compounds and prevent lipid peroxidation of the membranes (Chakraborty and Tongden 2005). Evidences showed that

SA increased the SOD and POD activities (Mutlu et al. 2009; Shi and Zhu 2008). Enhanced activities of SOD due to SA application might have been one of the factors contributing to improved growth in *Vigna* under UV-B. Similar to our results, other reports have shown that salt stress induces an increase in SOD activity, which has been correlated with plant salt tolerance (Sreenivasulu et al. 2000; Sudhakar et al. 2001). For example, in a salt-tolerant rice cultivar, SOD activity was high compared to a salt-sensitive cultivar (Dionisio-Sese and Tobita 1998). Although leaf SOD activity and shoot fresh weight bear some degree of positive correlation, net CO_2 assimilation (Noreen and Ashraf 2008) and leaf SOD activity are not positively correlated with each other.

8.5 Jasmonates

Jasmonates are one of the newest plant growth regulators, which cause decrease in damages due to environmental stresses on plant system (Wang 1999). MeJA was discovered as a sweet-smelling compound in *Jasminum grandiflorum* flower extracts (Demole et al. 1962). After this discovery in jasmine flowers, JA was isolated from a pathogenic fungus, *Lasiodiplodia theobromae* (Aldridge et al. 1971). The biological activity of MeJA extracted from *Artemisia absinthium* was reported nearly 10 years later (Ueda and Kato 1980). Since then, JA has been found in many species and considered to be ubiquitous (Meyer et al. 1984; Hamberg and Gardner 1992). JA and its cyclic precursors and derivatives constitute a family of bioactive oxylipins that regulate plant development and responses to environmental cues (Turner et al. 2002; Devoto and Turner 2003). JA exists as methyl jasmonate (MeJA), JA hydroxylated (11-OH-JA and 12-OH-JA), conjugated to some amino acids such as leucine (JA-leucine) and isoleucine (JA-Ile) as well as glucoside and sulfate of 12-OH- JA (12-*O*-Glc-JA, 12-HSO_4-JA), and these collectively receive the name of jasmonates. These molecules are involved in a variety of processes related to plant development and survival, including direct and indirect defense responses (*e.g.*, defense against insects and necrotrophic pathogens), secondary metabolism, reproductive processes (*e.g.*, pollen maturation, anther dehiscence, ovule development), and fruit development (Seo et al. 2001; Wasternack and Hause 2002; Arimura et al. 2005; Liechti and Farmer 2006; Wasternack 2007). In addition, JA-related responses are directly associated with a reset downstream of gene expression in the biosynthetic pathway (Thines et al. 2007). Jasmonate compounds have also been observed in tea, rosemary, mint, and a few fungi (Creelman and Mullet 1995). Pericarps, reproductive structure particularly ovarian and elongation zone of root and stem, have a high amount of JA. According to Creelman and Mullet (1997), jasmonates exist in ferns, mosses, and fungi and more than 206 plant species.

Jasmonates are considered to be phytohormones because they elicit cellular responses at low concentrations distant from their site of synthesis. For instance, long-distance wound signaling is at least partially mediated by the interplay of JA and systemin throughout the vascular system involving H_2O_2 (Browse 2006; Ryan and Moura 2002; Schilmiller and Howe 2005; Stratmann 2003; Wasternack 2006).

On unit fresh weight basis, the quantity of JA in plants typically ranges from few nanograms to micrograms. JA is produced as a signaling molecule in response to external stimulators such as wounding, mechanical force, pathogen attack, and osmotic stress (Molina et al. 2002). Genes responsible for the JA synthesis are expressed in apical parts of a plant. Increase in JA controls biosynthesis of proline and putrescine during environmental stresses, and during fungal pathogen attack, JA encodes proteases and reduces damage. Furthermore, it adjusts proteins of wall like PRP, which may be necessary for barrier synthesis against infection (Gao et al. 2004). JAs are important cellular regulators involved in several developmental processes such as seed germination, root growth, fertility, fruit ripening, and senescence. Most of the plant parts contain JA, and the highest concentration appears to be present in reproductive tissues, whereas much lower levels are found in roots and mature leaves (Lopez et al. 1987; Creelman and Mullet 1995). But these consequences are based mainly on the studies done on excised or intact leaves after exogenous application of JA (Weidhase et al. 1987). Moreover, JA accumulated in actively growing tissues such as hypocotyl hooks, flowers, and developing seed pods.

8.5.1 Effect of JA on Plant Morphology and Growth

Foliar spray of *Vigna radiata* and *Vigna mungo* seedlings with various concentrations of JA (2–10 ppm) resulted in remarkable increase in morphological parameters such as shoot and root length, fresh and dry weight of shoot and root, and leaf area. UV-B treatment caused 15–34% reduction in shoot length of *V. radiata* and 20–22% reduction in *V. mungo* (Figs. 8.7 and 8.8). Supplementation of UV-B-treated seedlings with various concentrations of JA proved to be effective in reducing the UV-B inhibition. JA treatment at 8 ppm to UV-B-irradiated seedlings gave a better response. UV-B treatment caused 23–30% reduction in the leaf area of *Vigna* seedlings. High concentration such as 10 ppm was not effective in completely alleviating UV-B-induced response. Under UV-B irradiation, shoot fresh weight got significantly decreased to 13–23% in both the species of *Vigna*. Similarly, there was also inhibition in shoot fresh and dry weights of the grown samples. UV-B treatment caused 20–30% decrease in *V. radiata* and 11–18% decrease in *V. mungo* after 7, 15, and 30 days of growth. Supplementation of UV-B-treated seedlings with 8 ppm of JA was more effective to cause 8% reversal in *V. radiata* and *V. mungo*. Alleviation of UV-B by the exogenous application of JA was not much evident during the early stages of growth. With regard to root fresh weight, UV-B-induced reduction of up to 18–24% in green gram and 20–30% in black gram seedlings was evident. Heil (2004) reported that shoot growth, fruit number, inflorescence number, and development rate of *Phaseolus lunatus* were enhanced by the application of JA.

Exogenously applied MeJA was transported through phloem and xylem pathways (Thorpe et al. 2007). Through cell membranes, JA-Me is probably transported by the same or a similar carrier as sucrose, due to enhancement of the energy of the plasma membrane (Thorpe et al. 2007). JA accelerated root growth and

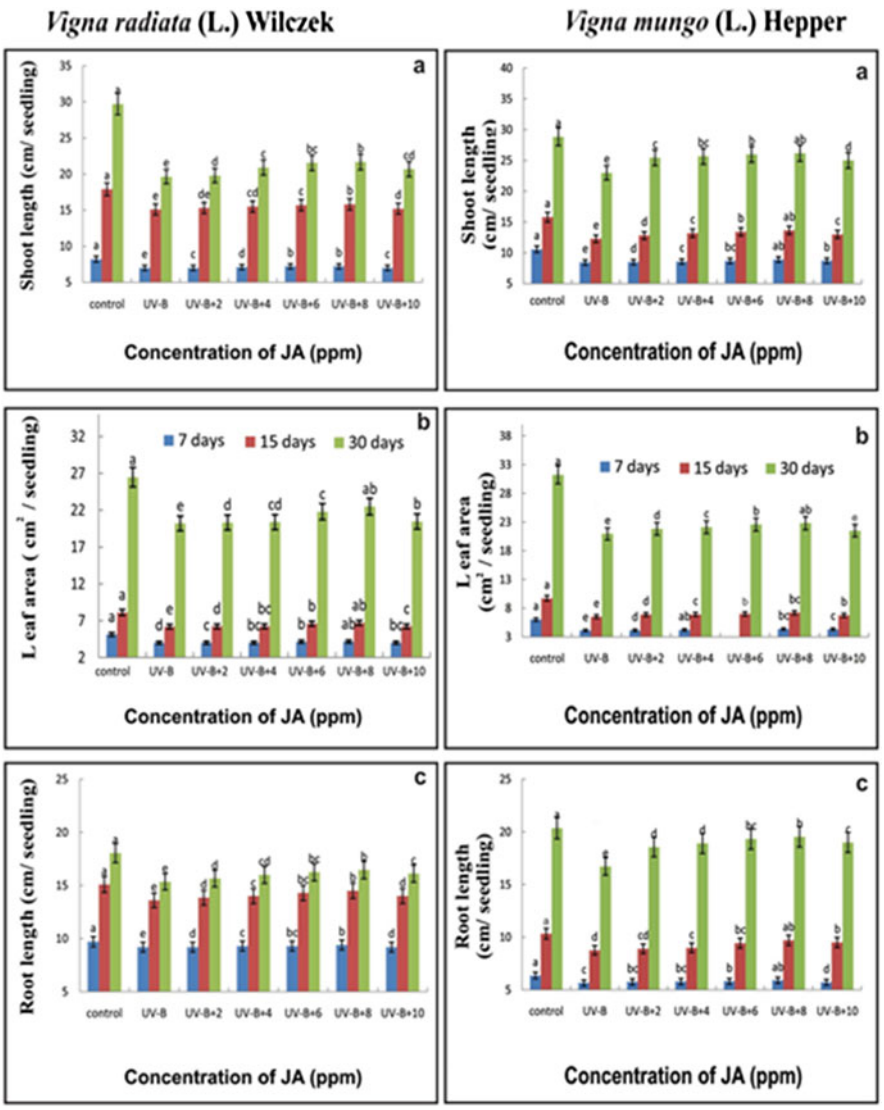

Fig. 8.7 Effect of UV-B and JA spray on growth parameters in intact seedlings of *V. radiata* and *V. mungo*. The measurements were made after 7, 15, and 30 days of growth

enhanced bulb development (Regvar and Gogala 1996). The contribution of jasmonates to morphogenetic events has been well documented. Besides promoting cell expansion, JA controlled cell division and growth direction, supporting the adequate formation of tissues and organs (Koda 1997). Maciejewska and Kopcewicz (2002) ascertained the contribution of JA towards the control of growth and elongation in shoot and root tissues, as well as the formation of floral buds in *Pharbitis nil*.

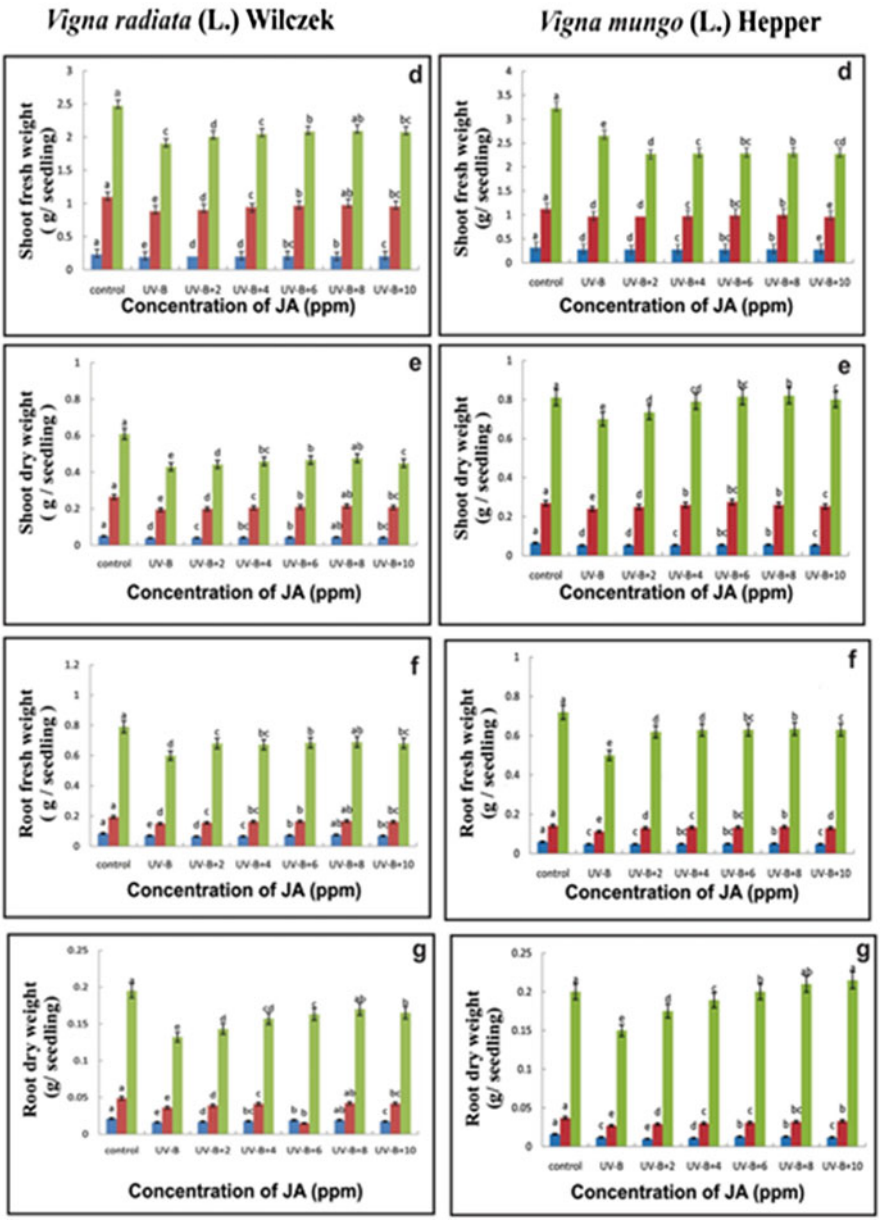

Fig. 8.8 Effect of UV-B and JA spray on growth parameters in intact seedlings of *V. radiata* and *V. mungo*

JA application inhibited root growth (Staswick et al. 1992) and induced tuber formation (Koda 1992) and tendril coiling (Weiler et al. 1993). It is considered that JA, particularly methyl esters of JA, acts as a chemical stress agent mimicking the effects that appear in response to external stress factors inducing senescence (Wasternack and Hause 2002). Sorial et al. (2010) reported increase in the number of stalk, leaf dry weight, shoot dry weight, and Chl content. Abdelgawad et al. (2014) reported a possible role of MeJA treatment in the early vegetative growth stage and chemical constituents of maize subjected to water stress. Presoaking of maize grains in MeJA solution increased growth parameters under different water stress conditions.

8.5.2 Interaction of UV-B and JA on Pigment Composition

On unit fresh weight basis, the contents of Chl *a* and *b* and carotenoids were estimated in *Vigna* seedlings exposed to UV-B and SA treatments (Fig. 8.9). UV-B treatment had significantly reduced the amount of Chl *a* level to 19% and 21% in *V. radiata* and *V. mungo*, respectively, during the initial phase of growth. After a period of 30 days, both species of *Vigna* showed reduction of more than 25%. Supplementation of UV-B-treated seedlings with various concentrations of SA proved to be effective in relieving the inhibition. Generally, Chl *a* content in *V. radiata* at 6 ppm and 8 ppm of JA was found to show UV-B-induced inhibition to the same level of 4–6%. In *V. mungo*, 6–10% and 7–10% relief was noticed at 6 ppm and 8 ppm of JA. Alleviation of UV-B inhibition by exogenous application of JA was more effective. Chl *b* content under UV-B treatment was reduced to 30% in both the species. Total Chl content got decreased by UV-B treatment to 23–31%, and JA at 6ppm was found to bring down the level of inhibition to 5% (Fig. 8.9b and c). Tsonev et al. (1998) reported that pre-treatment with JA reduced the inhibitory effect of high salt concentrations on photosynthesis in barley. JA and its related compounds have been shown to stimulate the accumulation of plant pigments. Induction of Chl accumulation was reported previously in higher plants (Fletcher et al. 1983) and *Chlorella vulgaris* (Czerpak et al. 2006). It seems that the stimulatory effect of JA on photosynthetic pigment accumulation could be due to strong effect on Chl synthetic pathway, specially δ-ALA, which is the rate-limiting step in the biosynthesis of Chl (Beale 1978). Kovac and Ravnikar (1994) reported that JA treatment resulted in an increase in cytokinin concentration, which enhanced Chl accumulation. The contents of Chl *a* and *b* were substantially increased at low concentrations of JA growth regulators or chemicals under different environmental conditions (Ananiev et al. 2004). Previous reports indicated that MeJA treatment inhibited Chl accumulation in dark and it was confirmed by the application of MeJA to the excised cotyledons of *Cucurbita pepo*. JA at concentrations above 50 μM induced senescence in plant cell cultures and excised leaves. The senescence response included loss of Chl, degradation of RuBPCase, and accumulation of new proteins. JA specifically inhibited translation of the LSU by inducing cleavage of the *rbc*L transcript (Reinbothe et al. 1993).

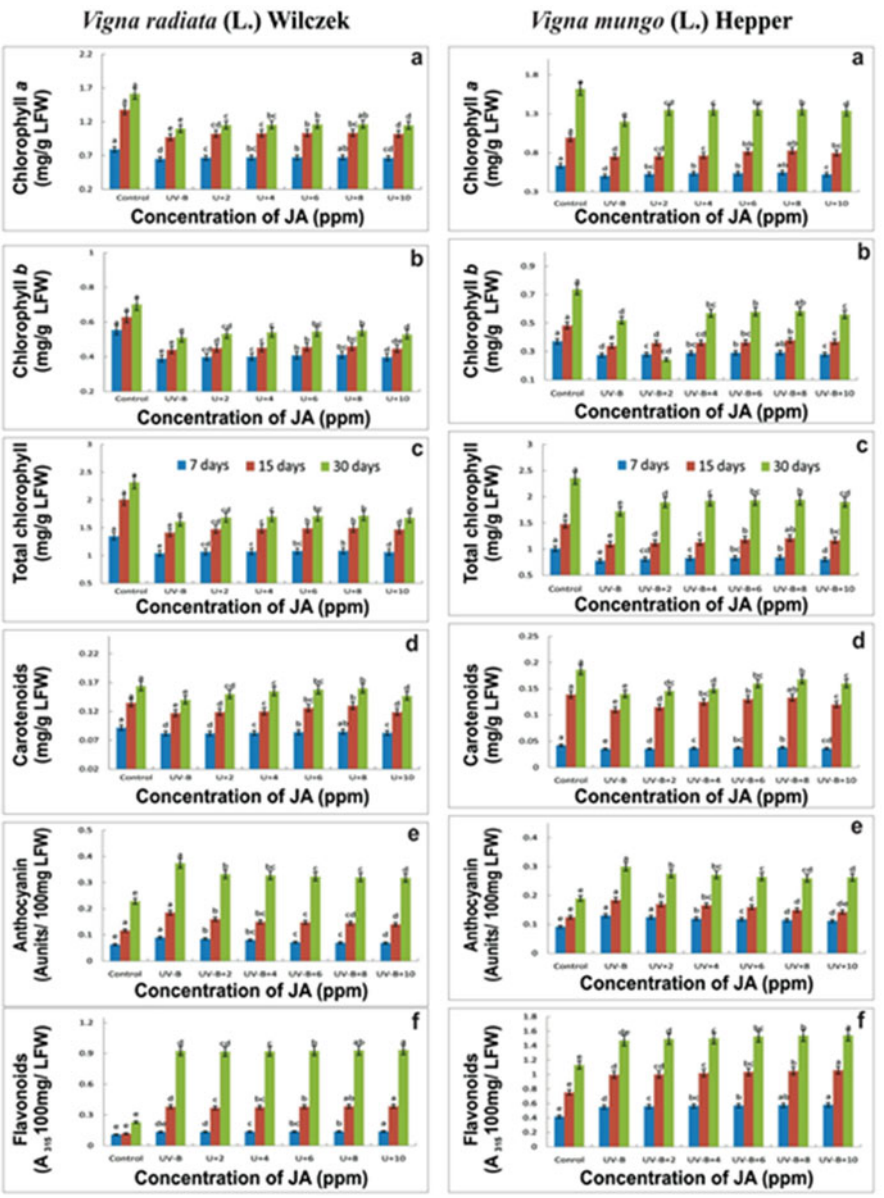

Fig. 8.9 Photosynthetic and non-photosynthetic pigment composition of *V. radiata* and *V. mungo* seedlings exposed to UV-B and JA treatments

Carotenoid pigments have a protective role in the photosynthetic excitation energy transfer to photosynthetic centers. Carotenoids protect chloroplast membrane through dispelling a lot of energy into harmless chemical reactions from PSI and II. Also, carotenoids are oxidized by singlet oxygen and can reduce the oxygen reactive species (Koryo 2006). The changes in carotenoid level under JA treatment were the same as observed for Chl content (Fig. 8.9d).

The foliar application of JA showed maximum results at 8 ppm in *V. radiata* and *V. mungo* seedlings. Similar results were obtained for carotenoid levels under UV-B as well as under SA supplementation. Even though marginal decrease of carotenoid level was noticed under JA posttreatment, the possibility of JA in reversing the UV-B-induced changes holds good potential (Fig. 8.9). Poonam et al. (2013) investigated the exogenous effect of JA at seed level in pigeon pea in the presence and/or absence of copper. Plants were analyzed for photosynthetic pigments like total Chl and carotenoids. Seedlings treated with JA alone showed an increase in Chl and carotenoid accumulation with increase in concentration from picomolar to micromolar. But when JA-primed seeds were grown in copper solution, the trend became opposite; that is, with increase in concentration of JA, the pigment accumulation got decreased.

Anthocyanins are one of the most widespread classes of pigments in higher plants. They are important secondary metabolites produced through the flavonoid biosynthetic pathway in various plant organs (Winkel and Hirley 2001). The anthocyanin biosynthetic pathway is controlled by environmental factors (light and temperature), internal factors (plant hormones), and other secondary metabolites and nutrients (Mol et al. 1996). With regard to non-photosynthetic pigments like anthocyanin and flavonoids, JA treatment was found to have some influence. Shan et al. (2009) showed the molecular mechanism for JA-regulated anthocyanin accumulation. It was found that the F-box protein COI1 was required for JA-specific induced expression of the "late" anthocyanin biosynthetic genes DFR, LDOX, and UF3GT. (1) It is known that JA-induced anthocyanin accumulation is primarily via upregulation of the "late" anthocyanin biosynthetic genes DFR, LDOX, and UF3GT and COI1 is essential for the JA-induced expression of these anthocyanin biosynthetic "late" genes. (2) The expression of anthocyanin biosynthetic regulators, PAP1, PAP2, and GL3, was significantly induced by JA, and COI1 is required for JA-induced PAP1, PAP2, and GL3 transcription. It was speculated that COI1 regulates the expression of the transcription factors, including PAP1, PAP2, and GL3, which mediates the "late" anthocyanin biosynthetic genes and thereby modulates JA-induced anthocyanin biosynthesis. High concentration of MeJA resulted in less accumulation of anthocyanin as compared to lower concentrations. Anthocyanin accumulation in response to MeJA was greater in cooled tulip bulbs (Saniewski et al. 1998). Similar observations have been observed in *Kalanchoe blossfeldiana* (Saniewski et al. 2003). Exogenous application of JA induced anthocyanin accumulation in various plants (Franceschi and Grimes 1991; Tamari et al. 1995; Saniewski et al. 2006). According to Franceschi and Grimes (1991), atmospheric JA-Me induced a five- to sevenfold increase in anthocyanin accumulation in light-grown soybean seedlings but inhibited in etiolated seedlings. Bideshki et al.

(2013) studied the impact of IBA and JA on anthocyanin content, bulb yield, and allicin content in garlic cultivar under drought stress. Although drought stress reduced anthocyanin content, the interaction of drought and MeJA was found to be significant for the regulation of anthocyanin levels. Combination of IBA and MeJA was more effective under drought stress conditions. It was concluded that a combination of MeJA and IBA was effective for the promotion of growth and yield under non-drought stress. Flavonoids are a large group of stress-induced phenylpropanoids that possess antioxidant activity that plays an important role in antimicrobial defense, protection against high light and oxidative stress, and signaling. Flavonoid content was found to increase under UV-B treatment in both the crops (Fig. 8.9f). UV-B treatment caused 24–29% and 30–33% increase in *V. radiata* and *V. mungo*, respectively. When these seedlings were supplemented with JA solutions, it caused significant increase in the level of flavonoid content at 8 and 10 ppm.

8.5.3 Interaction of UV-B and JA on Biochemical Constituents

The biochemical composition of green gram and black gram exposed to various treatments measured in terms of protein, sugar, nitrate, starch, and NR activity is shown in Figs. 8.10 and 8.11.

Changes in total soluble protein content of *V. radiata* and *V. mungo* seedlings exposed to short-term UV-B and JA posttreatment are shown in Fig. 8.10a. UV-B treatment caused 35% and 29% decrease in *V. radiata* and *V. mungo*, respectively, after 7, 15, and 30 days of growth. Compared to *V. radiata*, there was a greater reduction in total soluble protein content in *V. mungo.* Supplementation of UV-B-treated green gram seedlings with 8 ppm of JA was found to relieve UV-B-induced inhibition to a level of 5–10% throughout the stages of growth, whereas 8–26% reduction was observed in black gram seedlings. Earlier studies revealed that JA treatment enhanced the protein concentration of peanut seedlings (Kumari et al. 2006). JA application increased cell division and altered membrane permeability. It is proposed that JA-induced changes are mediated through JA-induced stress proteins (Rakwl and Komatsu 2001). There are reports of JA-induced specific changes in the protein content of soybean, tomato, barley, rice, and tobacco (Mason and Mullet 1990; Staswick et al. 1991; Wasternack et al. 1998). With regard to total soluble sugar content, UV-B treatment alone caused 30–42% and 14–33% decrease in *V. radiata* and *V. mungo* seedlings, respectively (Fig. 8.10). Supplementation of UV-B-treated seedlings with various concentrations of JA proved to be effective in relieving the inhibition (Fig. 8.10b). In *V. radiata* and *V. mungo* seedlings, 6–8 ppm of JA brought down the level of UV-B-induced inhibition to 5–22%. Such responses were reported in sugar beet, pea, and black cumin (El-Khallal 2001; Cherki et al. 2002, Murakeozy et al. 2003). Hajar et al. (1996) suggested that carbohydrate accumulation in *Nigella* increased the ability for water absorption under salt stress. Involvement of soluble sugars in osmotic adjustment has been proposed by Mansour (2000) in alleviating the adverse effect of salt stress.

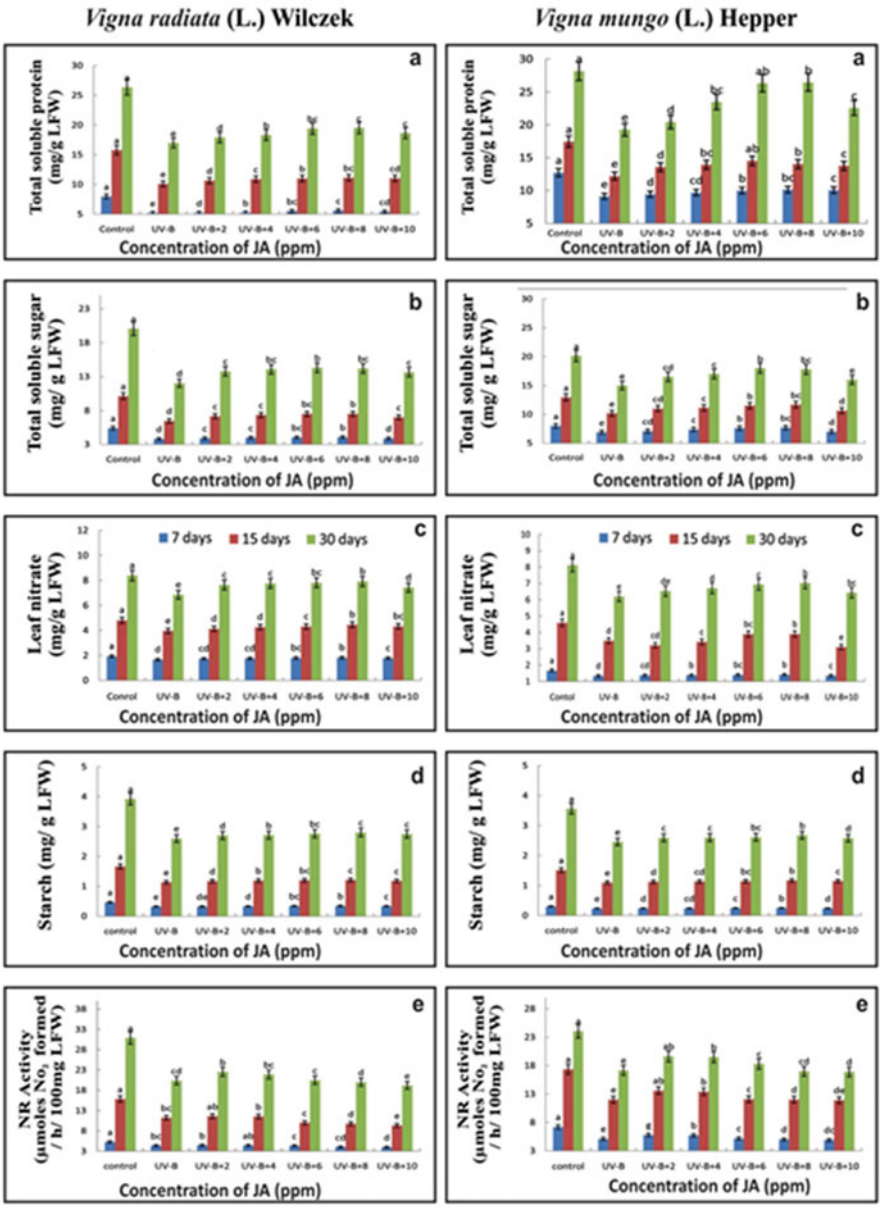

Fig. 8.10 Biochemical constituents of *V. radiata* and *V. mungo* seedlings exposed to UV-B and JA treatments

Exogenous application of JA increased the total soluble sugars, reducing and nonreducing sugar content under NaCl stress (Kaur et al. 2013). The increase in sugar concentration may be a result of the degradation of starch (Fischer and Holl

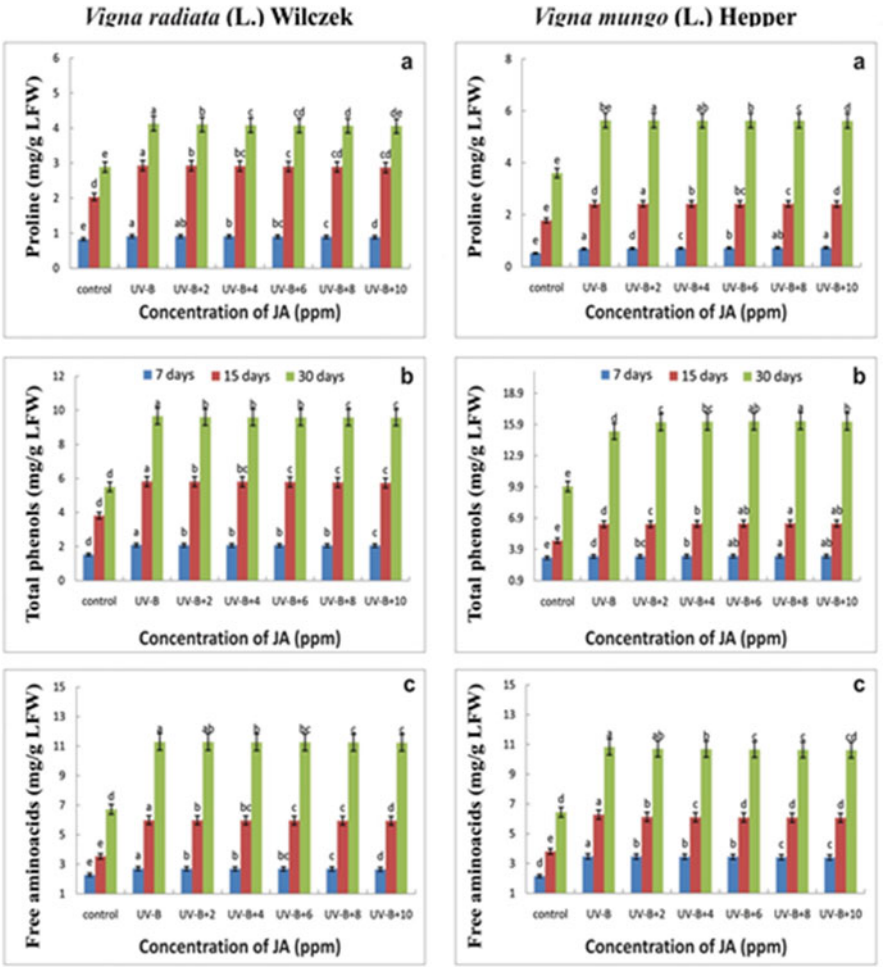

Fig. 8.11 Biochemical constituents of *V. radiata* and *V. mungo* seedlings exposed to UV-B and JA treatments

1991). JA treatment enhanced the accumulation of carbohydrates in the presence of salt stress. Takahashi et al. (1995) have reported the changes in levels of soluble sugars and starch, as well as changes in levels of cell wall polysaccharides during JA-induced expansion of potato tuber disc cells. Nitrate assimilation is energy intensive and occurs preferentially in foliar chloroplasts, where carbon skeletons, energy, and reducing power derived from photosynthesis can be easily accessed. Thus, the direct coupling of nitrate assimilation and photosynthesis in chloroplasts is believed to be energy efficient and is known as nitrate photoassimilation (Searles and Bloom 2003), a process adopted by most herbaceous plants and requiring long-distance root-to-shoot transport of nitrate taken up by plant roots (Smirnoff and Stewart 1985; Andrews 1986). The changes in leaf nitrate content of *Vigna* seedlings exposed to short-term UV-B and JA posttreatment are shown in Fig. 8.10c. UV-B

treatment caused 14–19% and 20–24% decrease in nitrate content in the leaves of *V. radiata* and *V. mungo*, respectively. Supplementation of UV-B-treated seedlings with various concentrations of JA reduced the inhibition of nitrate content to a tune of 4–16%.

Starch is a major storage carbohydrate in plants. Since starch is used for a wide variety of applications including food feed, fuel, and industry, technical developments that increase the starch yield of plants are considered very important (Slattery et al. 2000; Smith 2008). Starch accumulates in both photosynthetic and non-photosynthetic tissues. The chloroplasts of leaves contain transitory starch, which is synthesized in the day and broken down at night. The non-photosynthetic storage organs such as tubers, roots, and seeds have reserve starch. Because the amount of reserve starch in the storage organs is overwhelming, almost all starch applied to end uses is the reserve type (Slattery et al. 2000; Smith 2008; Keeling and Myers 2010). However, leaf biomass containing much transitory starch can be a promising source of biofuel if biorefinery technologies can be developed (Smith 2008). The precursor of starch synthesis is ADP-glucose, which converts glucose-1-phosphate by ADP-glucose pyrophosphorylase (Zeeman et al. 2010; Geigenberger 2011; Stitt and Zeeman 2012). ADP-glucose is used as a substrate of starch synthase, which generates linear α-1,4-glucosyl chains. Starch branching enzyme and debranching enzyme are involved in the formation of starch granules. The changes in starch content of *V. radiata* and *V. mungo* seedlings exposed to various treatments are shown in Fig. 8.10d. UV-B treatment caused nearly 30% decrease in leaf starch content of both the species. Supplementation of JA solutions as foliar spray proved to be effective in relieving the UV-B inhibition. JA at 8 ppm was moderate enough to cause 5–6% reversal of the inhibition. Light-dependent redox signals, metabolic intermediates, and phosphate concentration influenced starch biosynthesis (Geigenberger et al. 2005). These findings show that MeJA promoted starch synthesis rather than inhibiting starch breakdown. To increase the starch contents of forage and silage plants by genetic engineering, downregulation of starch degradation genes like GWD has been conducted. Although this strategy has been successful, plant growth may have been inhibited because of the suppressed starch breakdown and the reduced carbon availability in the dark. Indeed, the *Arabidopsis sex1* mutant deficient in the GWD gene showed a strong growth suppression phenotype (Lloyd et al. 2005). Using the transient RNAi lines showed higher starch content without significant reduction in growth (Weise et al. 2012). Changes on *in vivo* NR activity were followed in the leaves of *V. radiata* and *V. mungo* seedlings, which were exposed to short-term UV-B and JA posttreatment (Fig. 8.10e). UV-B treatment alone had caused inhibition of the enzyme activity to 18–36% and 30% in *V. radiata* and *V. mungo* seedlings, respectively. Supplementation of UV-B-treated *V. radiata* seedlings with 8–10 ppm of JA resulted in reversal of NR activity to 24–35% and 24–38% in green gram and black gram, respectively. Stress tolerance was earlier correlated with nitrate allocation via the *ET/JANRT1.5/NRT1.8* signaling module. Similar results were obtained for the JA-insensitive mutant *coi1-2* and the double mutant *coi1-2 nrt1.5-4*. The positive relationship between nitrate concentration and Na/Cd tolerance was also suppressed in *tri*-2 mutants, which imitate the functional impairment of *NRT1-8*, thus causing stress sensitivity (Li 2010).

Accumulation of proline in the leaves of *V. radiata* and *V. mungo* seedlings exposed to both UV-B and JA treatments is shown in Fig. 8.11a. Proline content increased to 44% in *V. radiata* and 32–56% in *V. mungo* after UV-B irradiation. Application of JA to the irradiated seedlings caused further hike to 10–42%, and 36% remained almost unchanged. In this study, proline content was significantly decreased at various concentrations of JA and UV-B pre-treatment and hormonal posttreatment in both *Vigna* seedlings. Proline content was found to be significantly increased in UV-B-treated *Vigna* seedlings, indicating the stress-causing nature of UV-B. JA application promoted the biosynthesis of proline under environmental stresses (Chen et al. 1993; Gao et al. 2004). Proline content significantly increased in common bean (Khadri et al. 2006), corn (Yoon et al. 2005), and soybean (Chon et al. 2003) under salt stress. Phenolic compounds are the main class of secondary metabolites in plants. Several such compounds have been identified in various plant species. The phenolic compounds are important for plants due to their various biological functions including UV protection, pollen tube growth, antimicrobial activity, and insect resistance (Steyn et al. 2002; Winkel 2002). In this study, total phenol content was remarkably decreased in both *Vigna radiata* and *Vigna mungo* seedlings treated with various concentrations of JA.

Total phenolic content increased after MeJA treatment in *Lactuca sativa* and *Ocimum basilicum* (Kim et al. 2006, 2007), and the increased accumulation of phenolics was due to induction of PAL activity. MeJA added to *Ginkgo biloba* cell suspension cultures showed stimulation of phenolic acids like ferulic, chlorogenic, and syringic acids (Szewczyk 2008). Additionally, MeJA clearly induced the biosynthesis of phenolic acids and flavonoids in root suspension of *Panax ginseng* cultures (Ali et al. 2007). Kim et al. (2006) found that MeJA increased total phenolic content to about 27%. Moglia et al. (2008) reported that MeJA enhanced biosynthesis of flavonoids without affecting the level of dicaffeoylquinic and chlorogenic acids. Ghasemnezhad and Javaherdashti (2008) expressed that MeJA enhanced total phenolics and therefore induced the defense mechanism of raspberry against low temperature stress. Short-term UV-B treatment caused appreciable increase in phenol content in both the species. Even 2–4 ppm of JA was able to cause further increase of phenolics to 63–74% in the species during the later stages of growth. Free amino acids play an especially important role in plant adaption to unfavorable environmental conditions (Kishor et al. 2005) and have previously been involved in the resistance of cereals to aphids (Corcuera 1993; Eleftherianos et al. 2006). Tariq et al. (2011) reported that the activities of CAT, POX, and SOD increased in the leaves on account of MeJA treatment. They also mentioned that the application of MeJA further enhanced the activities of all antioxidant enzymes, both in non-stressed and stressed plants, by supplementing increased content of FAAs in needles of saplings (Canovas et al. 2007). Free amino acid content of *V. radiata* and *V. mungo* seedlings exposed to UV-B and JA posttreatment is shown in Fig. 8.11c. There was an overall increase of free amino acids to 18–68% in the pulse crops under study. Foliar application of JA also increased the concentration in UV-B-exposed species. Even low concentrations of JA such as 2 and 4 ppm enhanced the content of free amino acids.

8.5.4 Interaction of UV-B and JA on Antioxidant Enzyme Activities

The effects of UV-B and JA treatment on functions of enzymes like catalase, peroxidase, polyphenol oxidase, and superoxide dismutase are presented in Fig. 8.12. Catalase is an iron-containing enzyme. Catalase is most notably

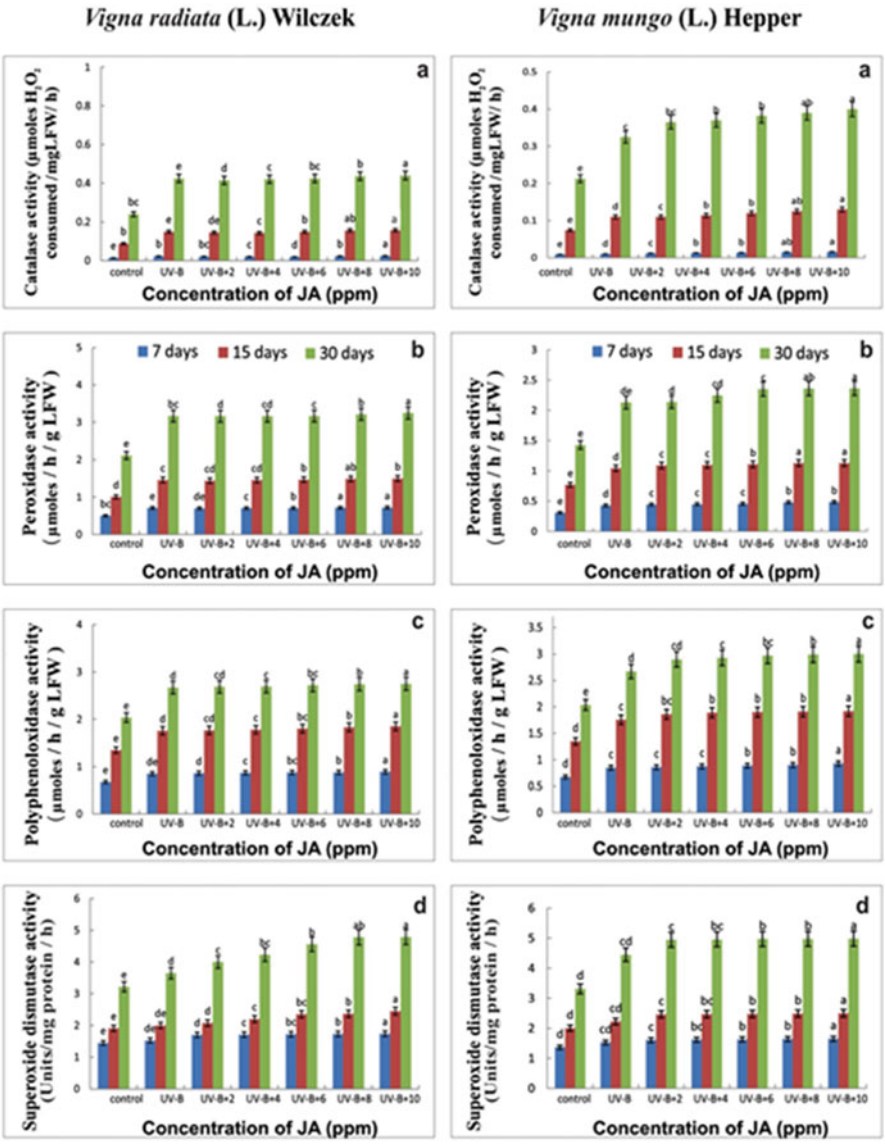

Fig. 8.12 Changes in antioxidant enzyme activities in *V. radiata* and *V. mungo* seedlings exposed to UV-B and JA treatments

distinguished from the other enzymes in not requiring a reductant as they catalyze a dismutation reaction and readily degrade hydrogen peroxide. The rate of catalase activity was determined in *V. radiata* and *V. mungo* seedlings sprayed with five different concentrations of JA and assessed after 7, 15, and 30 days of growth (Fig. 8.12a). The activity of catalase decreased significantly under JA treatment alone. Ali et al. (2005) found that CAT activity declined severely in *Panax ginseng* and *Panax quinquefolium* under MeJA treatment, indicating the inactivation of the enzyme and its isoenzyme expression. Also, Chong et al. (2005) showed that CAT activity was low in JA-treated *Morinda elliptica* cell cultures. On the contrary, MeJA treatment increased the CAT activity in strawberry (Wang 1999). The effects of UV-B and post-JA treatments on catalase activity are shown in Fig. 8.12a. UV-B treatment caused increase in CAT activity in both species amounting to 11–65%. JA at 8 ppm and 10 ppm was found to induce catalase activity significantly to 75% irrespective of the crop species. Peroxidases participate in a variety of defense mechanisms in plants (Liu et al. 2008) to ameliorate oxidative burst (Lamb and Dixon 1997). The rate of peroxidase activity was determined in *V. radiata* and *V. mungo* primed with various concentrations of JA (Fig. 8.12b).

Peroxidase activity was estimated in both the crops, and UV-B treatment caused an increase to 35–50%. With JA supplementation of UV-B-stressed seedlings, the activity got decreased though it increased initially in both plants. With high concentration of JA addition, the activity got increased. In *V. radiata*, at high concentration, it was 40–52%. In the case of high concentrations (8 and 10 ppm), increase of peroxidase activity was noticed to a level of 54–65% and 55–65% in *V. mungo*. The activity of peroxidase increased at high concentrations of JA. High concentrations induced stress response, and the results suggest that JA and its related compounds have differing effects depending on dosage. Jaiti et al. (2009) found that exogenous application of JA at 50 μM increased the activity of peroxidase. The increase of POD activity in the presence of JA was much more obvious than under pathogen infection. Liu et al. (2008) found that cell wall POD activity in JA-treated species was not in parallel to H_2O_2 accumulation. MeJA offered protection against *Blumeria graminis* accompanied by significant increase in PAL and POD activities (Walter et al. 2002). Response of MeJA-treated Norway spruce stems involves tissue-specific differentiation of traumatic resin ducts, terpenoid accumulation, and induction of defense enzyme activities in the developing xylem tissues (Martin et al. 2002). Increase in the activities of various antioxidant enzymes during MeJA treatment was evident as CAT and APX are the most important H_2O_2-scavenging enzymes that can catalyze the direct decomposition of H_2O_2 or the oxidation of H_2O_2 (Comparot et al. 2002). It has been stated that MeJA induced CAT activity in plants subjected to water stress (Li et al. 1998; Wang 1999). Secondary metabolite production is usually associated with rapid, transient increase in activities of key enzymes of the phenylpropanoid/flavonoid pathway such as PAL and chalcone isomerase (Gundlach et al. 1992; Dixon et al. 2002).

Most physiological stresses including UV-B enhancement disturb plant metabolism and cause oxidative injury by enhancing the production of ROS. The metabolism of ROS depends on low-molecular-weight antioxidant systems as well as

enzymes such as catalase, peroxidase, polyphenol oxidase, and superoxide dismutase. In this study, the catalase activity increased under supplemental UV-B radiation treatment. *Vigna radiata* exhibited a high level of catalase activity. Catalase is the most efficient antioxidant enzyme, which protects plants by scavenging free radicals and H_2O_2 (Gao and Zhang 2008). Decreased catalase activity in the *vtc1* mutants of *Arabidopsis thaliana* during the course of the UV-B exposure experiment could be due to destruction of lipid peroxidation (Yannarelli et al. 2006). In this study, the peroxidase activity increased with supplemental UV-B radiation in *Vigna*. The increase in peroxidase activity is correlated with the reduction in fresh weight and biomass accumulation, which in turn is linked with the reduction in Chl and carotenoid level. Balasinha (1982) reported that peroxidase plays a vital role in Chl degradation. Thus, the observed increase in peroxidase activity could be correlated to the reduction in Chl content, fresh weight, and dry weight. Sheen and Calvert (1969) demonstrated that phenol-oxidizing peroxidase unlikely contributes to UV tolerance as a result of their radical scavenging activity. Peroxidase is a metalloenzyme containing porphyrin-bound ion. The enzyme acts on a wide range of substrates including phenols, aromatic amines, amino acids, and inorganic compounds. Peroxidase is known to play a role in IAA destruction and Chl degradation (Van et al. 1977). The reduction in Chl content and IAA degradation may be the reason for the inhibitory effect observed in UV-stressed plants.

UV-B caused significant increase in polyphenol oxidase in *Vigna mungo* than *Vigna radiata* after 7, 15, and 30 days of growth. Polyphenol oxidase is responsible for the oxidation of phenolic compounds (Jansen et al. 2001). Several studies have shown increased polyphenol oxidase due to UV-B irradiation (Balakrishnan et al. 2005; Santos et al. 1999). Enhanced UV-B radiation activated polyphenol oxidase activity and induced polyamines causing leaf damage exemplified by a decrease in Chl concentration. PPO activity of *V. radiata* and *V. mungo* seedlings exposed to short-term UV-B treatment and post-hormonal treatment is shown in Fig. 8.12c. UV-B treatment alone caused 25–31% and 29–48% increase in *V. radiata* and *V. mungo*, respectively, after 7, 15, and 30 days of growth. Supplementation of UV-B-treated seedlings with various concentrations of JA caused increasing PPO activity in both plants (Fig. 8.12c). In green gram, JA was found to cause a slight increase to a level of 30–37. In black gram, the PPO activity was found to be 33–47% at 8 and 10 ppm of JA. PPO has been reported to be strongly induced by MeJA (Constabel et al. 1995). PPO induction occurred by multiple signals in parallel with other anti-herbivore compounds (Bergey et al. 1996; Chen et al. 2005).

In addition, many studies have shown that PPO was induced in response to mechanical wounding, fungal and bacterial infection, and treatment with signaling molecules (Constabel et al. 2000; Stewart et al. 2001). Defense proteins whose expression is dependent on the JA/*coi1* pathway included PPO also (Browse and Howe 2008). Increase in the caffeic and p-coumaric acids was recorded 3 days after JA elicitation. UV-B caused significant increase in SOD activity in *Vigna mungo* than *Vigna radiata*. SOD played an important defensive role by scavenging singlet oxygen or H_2O_2. We noted enhanced H_2O_2 content after enhanced UV-B irradiation with correlated increase in SOD activity. This suggests that under UV-B stress, H_2O_2

was formed intensively as a result of enzymatic superoxide anion dismutation. Similar changes have been reported by Baumbusch et al. (1998), Dai et al. (1997), Kubo et al. (1999), Rybus-Zajac (2005), and Kubis and Rybus-Zajac (2008). Rarely analyzed is the plant response at the seedling stage, especially at a very early stage, which is connected with high oxidative activity and involvement of cotyledons (Jain et al. 2004). There are reports on changes in SOD activity and overproduction of H_2O_2 as a result of exposure to UV-B radiation (Yannarelli et al. 2006) and *Picea asperata* seedlings (Han et al. 2009). Watanabe et al. (2006) detected H_2O_2 accumulation and suggested that UV irradiation caused oxidative damage to DNA in plant cells. UV-B caused a significant increase in SOD activity (Krizek et al. 1993). Similar to SOD, phenylalanine ammonia lyase activity also increased under supplemental UV-B treatment. Singh et al. (2011) evaluated the response of bean plants to supplemental UV-B and found that UV-B stimulated the antioxidant defense system (both enzymatic and nonenzymatic). Superoxide dismutase activity caused an increase in H_2O_2 content that is normally detoxified by CAT in peroxisomes and by APX in cytosol, mitochondria, and chloroplasts (Foyer et al. 1997; Asada 1999). APX reacts with H_2O_2 in the presence of ascorbate to produce water and monodehydroascorbate. Oxidized ascorbate is then regenerated through the ascorbate glutathione cycle (Comparot et al. 2002). In *Arabidopsis thaliana*, the total SOD activity decreased 3 days after MeJA treatment and increased twofold after 7 days of treatment (Jung 2004). The increase in SOD activity may be due to upregulation of the genes or an increased activation of constitutive enzyme pool (Li et al. 1998; Norastehnia and Asghari 2006). SOD activities of *V. radiata* and *V. mungo* seedlings exposed to UV-B treatment and JA hormone treatment are shown in Fig. 8.12d. UV-B treatment alone caused around 4–34% increase of SOD activity in the species of *Vigna.* Supplementation of UV-B-treated seedlings with various concentrations of JA caused an increase in SOD activity. JA at 8 and 10 ppm concentrations increased the enzyme activity. The increase was more than that of UV-B induction.

8.5.5 Role of SA and JA in Resistance to Plant Pathogens

Several lines of evidence have shown that SA is associated with SAR. Cellular levels of SA increased at the onset of pathogen-induced defense reactions, locally in the infected tissues or systemically in noninfected tissues (Malamy et al. 1990). The expression of a number of pathogenesis-related (PR) proteins is highly correlated with acquired resistance (Ward et al. 1991; Uknes et al. 1993). More recently, it has been recognized that SA is required in the signal transduction for inducing systemic acquired resistance against some pathogenic infections (Gaffney et al. 1993). It has been shown that many important functions in a plant can change physiological behavior. Thus, SA could be expected to influence the growth and yield of red amaranth plants. Increased levels of SA are required to activate the transcription of defense genes and to develop an efficient pathogen resistance response (Gaffney et al. 1993; Delaney et al. 1994). Accumulation of SA and activation of defense

genes have also been reported to occur after ozone or UV exposure (Yalpani et al. 1994). Pathogen infection and exposure to ozone or UV radiation are associated with an accumulation of ROS in plants. The appropriate balance in the cellular levels of SA and ROS seems to be crucial for the efficient activation of defense responses against the abovementioned environmental stresses (Draper 1997; Van Camp and Van Montagu 1998; Alvarez 2000; Van Breusegem et al. 2001). Exogenous application of SA is involved in the defense against pathogen attack, and more recently, it has been widely investigated under both biotic and abiotic stresses (Shi et al. 2006). Various chemicals such as osmoprotectants, growth regulators, and stress signaling molecules are being successfully used to induce tolerance against several biotic and abiotic stresses (Farooq et al. 2010). Plants have a variety of defenses against stress. Some of these are physical or morphological in nature, and some are chemical. Constitutive plant defenses include glandular trichomes, cuticular waxes, and other structural and chemical defenses (Wittstock and Gershenzon 2002). Inducible chemical defenses include a wide variety of compounds that are toxic, anti-nutritive, or injurious to attacking organisms, including alkaloids, phenolic compounds, chitinases, and protease inhibitors. As a class, these compounds generally aid in defending a plant and possibly surrounding plants from attack by pests or diseases. PPO activity is induced by volatile or liquid jasmonates in many plants (Doan et al. 2004).

Peroxidases function in numerous biochemical processes, but they may be related to the production of ROS or structural defenses (e.g., lignin, cell wall cross-links). Peroxidase and PPO were induced in tomato plants after a 12-h treatment with gas-phase MeJA. Treating *Cucurbita melo* seeds with gaseous MeJA induced defense against soilborne seedling pathogens but failed to induce peroxidase (Buzi et al. 2004). However, soaking seeds in 45 μM of MeJA induced both lipoxygenase and peroxidase synthesis. PPO and protease inhibitors were induced systemically in *S. lycopersicum* after treatment with JA, and lipoxygenase was induced locally (Thaler et al. 1996). Structural defenses were also shown to be jasmonate inducible or requiring JA signaling. For instance, trichome number and density increased after JA application to *Arabidopsis* (Traw and Bergelson 2003). Vijayan et al. (1998) reported that JA plays a crucial role in protecting *Arabidopsis* from weak fungal pathogens such as *Pythium mastophorum.* The evidences to confirm the role of JA in plant defense include accumulation of JA compounds in wounded plants (Creelman et al. 1992) and in plants or cell cultures treated with elicitors of pathogen defense. Secondly, JA activated genes encoding protease inhibitors that helped plants to protect against insect damage. JA also activated the expression of genes encoding antifungal proteins such as thionin and osmotin (Xu et al. 1994). Creelman et al. (1992) reported that JA modulated the expression of cell wall proteins such as PRP, which are involved in the synthesis of barriers to infection, as suggested by Casati. Furthermore, JA induced induction of genes involved in phytoalexin biosynthesis (Creelman et al. 1992) and phenolics (Doares et al. 1995). The oxylipin pathway that leads to JA was also the source of other volatile aldehydes and alcohols that function in plant defense and wound healing. For example, C_6-aldehyde 2-hexenal completely inhibited the growth of *Pseudomonas syringae* and *E. coli* and

C_6-aldehydes and alcohols reduced aphid fecundity. These compounds are synthesized from 13-hydroperoxylinolenic acid through the action of hydroperoxide-lyase. Treatment of potato with JA increased resistance to *Phytophthora infestans*. Similarly, *JL5* tomato mutant was more susceptible to damage by *Manduca sexta* due to lack of conversion of 13-hydroperoxylinolenic acid to 12-oxo-PDA (Howe et al. 1996). *Arabidopsis* mutants, which were susceptible to fungal gnats, restored resistance to fungal gnat demonstrating the vital role of JA in resistance. The complexity of plant defense responses and JA's role was demonstrated in *Pdf1.1* and *Pdf1.2*, which were involved in fungal resistance in *Arabidopsis*. JAs were also involved in plant defense responses against wounding by insects and pathogen attack (Wasternack and Parthier 1997). Levels of JA and its metabolites increased transiently in plant tissues in response to wounding and pathogens (Reymond and Farmer 1998; Zhang and Turner 2008).

8.6 Conclusion

Phytohormones and plant growth regulators can be classified into long-range compounds (auxins, cytokinins, gibberellins, ethylene), short-range compounds (NO, SA, JA, BRs), and very-short-range chemicals (ROS, H_2O_2). In this study, SA and JA were selected to find out the amelioration potential on UV-B-induced changes in green gram and black gram. At the outset, the seedlings were exposed to short-term UV-B radiation for a brief period. The changes caused by short-term UV irradiation were studied in detail in terms of morphology, growth parameters, foliar characteristics, pigment composition, and antioxidant enzyme activities. Salicylate and jasmonate effectively alleviated the UV-B-induced inhibition effects. Exogenous foliar application of SA and JA at lower concentrations proved to be beneficial in enhancing the growth and various other physiological and biochemical characteristics of *Vigna*. However, at higher concentrations, SA was not beneficial for the crop plants. But exogenous application of SA and JA at high concentration enhanced the activities of antioxidant enzyme systems. In future, the exogenous application of SA and JA could act as a powerful tool in enhancing the growth, biochemical content, and antioxidant enzyme activity, combating the ill effects generated by UV-B exposure. The future applications of these plant hormones hold a great promise as a management tool for providing tolerance to our agricultural crops against the aforesaid constraints, consequently aiding to accelerate potential crop yield in the near future.

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UVR8 Discovery: A New Vision in UV-B Research

9

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Abstract

In spite of being a minor component of the solar spectrum, ultraviolet-B (UV-B) radiation has the ability to significantly affect all the living organisms on Earth's surface. As plants are photoautotrophic sessile organisms, they constantly exposed to high-energy UV-B radiation in their environments that may influence the development, growth, and the overall physiology and metabolisms of plants. Plants are known to possess wide variety of photoreceptors in order to respond against the light environment. However, researchers were unable to find any UV-B-specific photoreceptors from the several decades. In the year 2002, a group of researchers identified the *Arabidopsis thaliana* mutant (*UV resistance locus 8-1)* hypersensitive to UV-B and suggested that UVR8 probably played an important role in UV-B signal transduction pathway. Later in 2011, it was found that UVR8 homodimers perceive UV-B radiation mediated through tryptophan residue that acts as a UV-B chromophore. Absorption of UV-B radiation by UVR8 dimers leads to its monomerization and interaction with COP1 which consequently leads to activation of further downstream-signaling pathway. These findings paved the way toward the UVR8-dependent responses of plants to UV-B radiation. UVR8 has been associated with diverse array of plant responses, including inhibition of hypocotyls extension, flavonoids biosynthesis, phototropism, leaf epinasty, responses to osmotic stress, inhibition of thermo-morphogenesis, stomatal density and stomatal closure. In view of the above, this chapter focuses on facts about the UVR8 discovery and reviews in brief about the structure and UVR8-mediated plants responses.

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Ultraviolet-B · UVR8 · Photomorphogenic responses · UV-B-absorbing compounds · Arabidopsis

9.1 Introduction

Ultraviolet-B (UV-B) radiation shares the minor portion of solar spectrum, but it has the ability to significantly affect all the living organisms on Earth's surface. As being photoautotrophic and sessile organism plants are constantly and inevitably exposed in its environment to high-energy UV-B radiation. UV-B radiation causes damaging effect on the biomolecules such as DNA, protein, and lipids and, thus, imparts the significant effect on the development, growth, and the overall metabolisms of plants. It was found that lower doses of UV-B induce the photomorphogenic responses including inhibition of hypocotyls extension, flavonoids biosynthesis, phototropism, leaf epinasty, and stomatal closure in plants (Jenkins 2017). These observations prompted researchers to find out the specific UV-B photoreceptor. However, researchers were unable to find any UV-B-specific photoreceptors from several decades. In the year 2002, a group of researchers identified the *Arabidopsis thaliana* mutant (*UV resistance locus 8)* hypersensitive to UV-B and suggested that UVR8 probably played a pivotal role in UV-B signal transduction pathway. Later in 2011, subsequent structural and functional characterization affirmed the role of UVR8 as UV-B photoreceptor that mediates the photomorphogenic responses through a specific signaling pathway (Rizzini et al. 2011). In view of the above, this chapter deals with UVR8 discovery, structure, and the UVR8-mediated signaling pathway and also reviews in brief about the UVR8 from diverse species, UVR8-mediated plants responses and interaction of UVR8-signaling pathway with other pathways.

9.2 Discovery of UVR8

Plants have different photoreceptors for the specific wavelength of light that activates specific signaling mechanism. The discovery of UV-B-induced specific photomorphogenic responses recommended the presence of specific UV-B photoreceptors as other photoreceptors in plants. Continuous research in this area led to the discovery of UVR8 mutant which is unable to involve in the signaling mediated through UV-B (Kliebenstein et al. 2002). Initially, it was believed that UVR8 has only some specific role in UV-B signaling (Kliebenstein et al. 2002), with continuous studies but not providing satisfactory results (Cloix and Jenkins 2008; Favory et al. 2009). Till 2010, protein involved in UV-B light perception and signaling was not discovered. Later on, Rizzini et al. (2011) published an article, which reported the presence of UVR8 photoreceptor, involved in the perception of UV-B radiation and activation of the signaling cascade for photo-protection and the flavonoids and anthocyanins production. It was revealed that monomerization of

UVR8 dimers activates UV-B photoreceptors with tryptophan-based mechanism, followed by COP1 interaction. The constitutive expression of UVR8 throughout the plants prepares plant to adapt in the presence of UV-B radiation.

9.3 UVR8 Structure

UVR8 is a peculiar photoreceptor, distinct in structure and mechanism of actions. Analysis of the protein with selenium-based single-wavelength anomalous dispersion (SAD) in Arabidopsis revealed a high-resolution crystal structure of UVR8 core domain having 12–381 residues, representing 84% of the overall protein (Wu et al. 2012). In contrast to the other known photoreceptors, UVR8 does not have any prosthetic cofactor but has specific amino acid residue as chromophore for perception of UV-B.

Most of the studies related with UVR8 conducted on Arabidopsis revealed a 440 amino acid protein (~47 kDa) with highly conserved seven-bladed β-propeller core with short N-terminal extension and 60 amino acid flexible C-terminal region (Jenkins 2014). These seven blades of UVR8 are structurally identical to cell-cycle regulatory protein Regulator of chromatin condensation 1 (RCC1). Each blade constitutes only three β-strands (A, B and C). In each strand, an extended loop CD is present which follows strand C. Their structure shows that loop AB and CD occupy the bottom face, whereas the loop BC is located on the top face of β-propeller. In AB loops of 5–7 blades, a prominent sequence motif GWRHT is present. In the crystal form, two UVR8 domains combined to form a homodimer, through associating the acidic and basic surface patches from one UVR8 core domain combined with the complementarily charged surface patches of another core domain to form a symmetric homodimer. The surface complimentary charges are located on the bottom face of each core domain. At homodimeric interface, a total of 20 intermolecular hydrogen bonds were formed by the two prominent surface patches of core domain. A detailed structure of UVR8 homodimer on the basis of amino acid level was given by Wu et al. (2012).

Two independent scientific groups revealed the crystal structure of UVR8 (Christie et al. 2012; Wu et al. 2012) and explains the mechanism behind UVR8-mediated UV-B perception in plants, i.e., (1) UVR8 dimerization through salt bridge interactions: The interface of UVR8 dimers is the crucial region for monomer interaction which contains charged amino acid residues and creates electrostatic potential on the opposing monomer. The key amino acid present in the interface is basic arginine (Arg) and acidic aspartic (Asp) and glutamic (Glu) acid forming salt bridges holding the UVR8 monomers. Among several amino acids interaction, double-hydrogen-bonded interactions are more critical (Arg 286 with Asp 107). Similarly, the double- hydrogen-bonded salt bridge between R-146 and Glu-182 also contributes for UVR8 dimerization (Christie et al. 2012; Wu et al. 2012). (2) Chromophore and key tryptophan (Trp) residues mediated disruption of dimmers: for light absorption, chromophore requires but UVR8 does not contain any prosthetic cofactor as chromophore but utilizes specific amino acid residues as chromophore

for photoperception. In Arabidopsis, photoperception has been mediated by 14 Trp residues: one in the C-terminal region, six in the β-propeller core, and seven in the dimer interface region. In the β-propeller core, each Trp residue is presented on the different propeller core along with a tyrosine (Tyr) residues forming a ring of aromatic residues. The core structure is maintained by the formation of hydrogen bonds and hydrophobic interactions between adjacent blades. In the dimer interface, three residues are highly conserved which allow overlapping of electronic orbitals. Similarly to core, an aromatic shield is presented in dimer interface, created by the three Trp residues, along with the Tyr residues. Wu et al. (2012) reported that W285 and W233 are the major chromophore. It is clear from several studies that Trp-285 and Trp-233 are key chromophore components involved in UV-B sensing. Dissociation of dimer occurs as a result of destabilization of intermolecular H-bonds, and disruption of cation–pi interaction between Trp-285, Trp-233, and surrounding residues (Yadav and Atri 2017).

9.4 UVR8-Mediated Signaling in Plants

As distinct perception mechanism is needed to discriminate UV-B light from other light qualities. Molecular and biochemical characterization demonstrated that under exposure of UV-B, instant monomerization of UVR8 homodimer is through an intrinsic Trp-dependent mechanism. The monomers and dimer forms of UVR8 are dynamic and reversible, and redimerization is facilitated by WD40-repeat proteins, RUPs (REPRESSOR OF UV-B PHOTOMORPHOGENESIS) (Jenkins 2017). To transduce UV-B signal, UVR8 monomer physically interacted with COP1, WRKY36, BES1, and BIM1 (Favory et al. 2009; Liang et al. 2019). UVR8 monomer first interacts with COP1 (CONSTITUTIVELY PHOTOMORPHOGENIC 1) in an UV-dependent manner, and regulates COP1 activity, and thus induces dissociation of COP1-SPA core complexes from E3 ubiquitin ligase apparatus and forming UVR8-COP1-SPA1 to reduce ubiquitination of HY5 (ELONGATED HYPOCOTYL 5). UVR8-COP1 interaction is also necessary for the nuclear accumulation of UVR8, required for HY5 induction and photo-morphogenesis under UV-B (Liang et al. 2019). Two models were raised for UVR8-COP1-induced nuclear accumulation of UVR8, (1) nuclear co-import model: the interaction of UVR8-COP1 in the cytosol leads to the COP1 containing nuclear localization sequence facilitates the co-import of UVR8 into the nucleus, (2) nuclear retention model: UV-B-induced monomerization and further translocation into nucleus by an unknown mechanism. Figure 9.1 outlines the UVR8-mediated signal transduction pathway in plants. It has also been demonstrated that UVR8 monomer also interacts with several other transcription factors such as WRKY36 (WRKY DNA-BINDING PROTEIN 36), BES1 (BRI1-EMS-SUPPRESSOR 1), and BIM1 (BES1-INTERACTING MYC-LIKE 1) to regulate the gene expression. A downstream regulation of HY5 is crucial for the UV-induced photo-morphogenesis which has been governed by WRKY36. In nucleus, UVR8 interacts with WRKY36 to inhibit its DNA-binding ability, promoting *HY5* transcription and preventing hypocotyl elongation (Yang

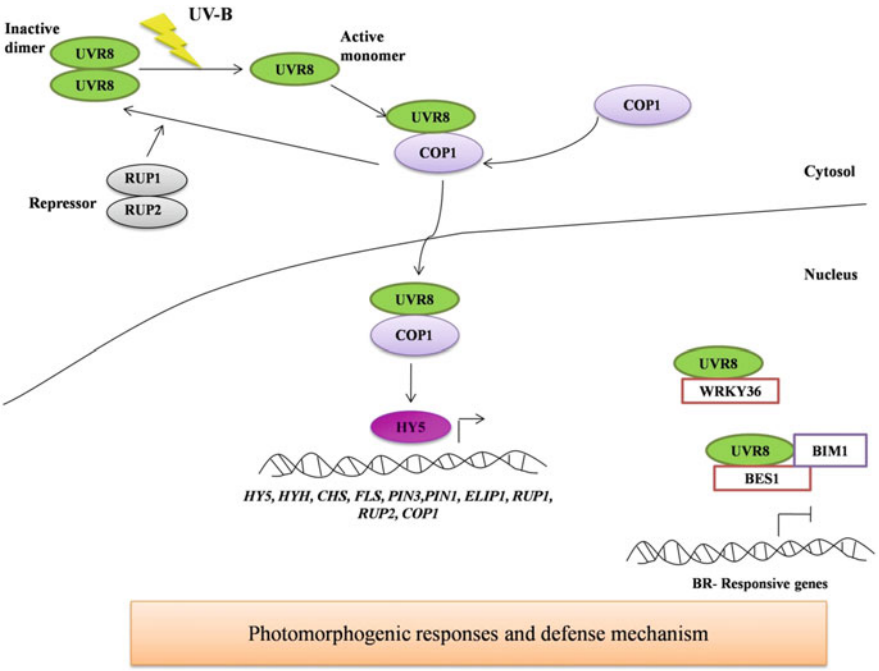

Fig. 9.1 UVR8-mediated signal transduction pathway in response to UV-B radiation in plants (modified from Tossi et al. 2019). *UV-B* ultraviolet-B radiation, *UVR8* UV RESISTANCE LOCUS 8, *COP1* CONSTITUTIVELY PHOTOMORPHOGENIC 1, *HY5* ELONGATED HYPOCOTYL 5, *HYH* HY5 HOMOLOG, *WRKY36* WRKY DNA-BINDING PROTEIN 36, *BES1* BRI1-EMS-SUPPRESSOR1, *BIM1* BES1-INTERACTING MYC-LIKE 1, *BR* Brassinosteroids, *RUP1 and RUP2* REPRESSOR OF UV-B PHOTOMORPHOGENESIS 1 and 2, *FLS* FLAVONOL SYNTHASE, *ELIP1* EARLY LIGHT-INDUCIBLE PROTEIN1, *CHS* CHALCONE SYNTHASE

et al. 2018a). UVR8 also interacts with brassinosteroid signaling transcription factors (BES1 and BIM1) to control its expression under UV-B. UVR8 interacts with BES1 to prevent it from binding to promoters of growth-related genes, ultimately repressing the expression of the respective genes (Fig. 9.1).

9.5 UVR8 in Diverse Plants Species

UVR8 is highly conserved molecule from green algae to higher plants, as evident from the analysis of amino acid sequences and key motif that are responsible for UVR8 function. The higher degree of conserved sequences and the earlier emergence of UVR8 in the evolution of plants emphasized the functional importance of UVR8 (Tossi et al. 2019). In *Chlamydomonas reinhardtii* (Cr) (green algae), dimers of CrUVR8 dissociate following exposure of UV-B and further re-associate under white light. Yeast two-hybrid assays confirmed the interaction between CrCOP1 and CrUVR8. CrUVR8 from *C. reinhardtii* complements the Arabidopsis uvr8 mutant,

which indicates that, the mechanism of action of UVR8 described in Arabidopsis was well conserved (Tossi et al. 2019). Liverwort *Marchantia polymorpha* and the moss species *Physcomitrella patens* had two forms of UVR8 which were derived from alternative splicing and functionally complement the impaired responses in uvr8 mutant of *Arabidopsis thaliana* (Soriano et al. 2018). In angiosperm such as *Malus domestica* (Md), *Populus euphratica* (Pe), and *Chrysanthemum morifolium* (Cm), heterologous expressions of MdUVR8, PeUVR8, and CmUVR8 protect the deficient phenotype of Arabidopsis uvr8 mutant from UV-B radiation. Yeast two-hybrid analysis showed the interaction of MdUVR8-MdCOP1 and CmUVR8-CmCOP1 under UV-B in these angiosperms species (Tossi et al. 2019). Under UV-B exposure overexpression of *Solanum lycopersicum,* UVR8 (SlUVR8) enhances the tolerance toward UV-B through regulation of hypocotyls elongation and the accumulation of anthocyanins at seedling stage. These results suggest the important roles of SlUVR8 in the regulation of UV-B stress tolerance and also in the development of tomato seedling (Liu et al. 2020). Fernández et al. (2020) reported that ZmUVR8 from *Zea mays* (monocotyledons) depicts a conserved structure. UV-B regulates the *ZmUVR8* expression, which further regulates the elongation of hypocotyls and the expressions of *CHS and HY5*, which were the two main UVR8 responsive genes.

9.6 Role of UVR8 in UV-B-Mediated Responses of Plants

From the discovery of UVR8 to now, there are several compelling studies which documented the importance and physiological role of UVR8 in responses of plants against UV-B radiation; however, the function of UVR8 is yet not completely explored. Table 9.1 summarizes the physiological role of UVR8 in plants against UV-B radiation. UV-B inhibits the lateral growth of root in Arabidopsis in UVR8-dependent manner. Yang et al. (2020) reported that after activation of UVR8 by UV-B light, UVR8 monomer is localized to nucleus and represses the DNA-binding activities of downstream MYB73/MYB77 transcription factor which further represses the auxin-responsive genes and thereby lateral root growth. Yang et al. (2018a) identified and characterized the UVR8-interacting protein WRKY DNA-BINDING PROTEIN 36 (WRKY36) from Arabidopsis and reported that, by binding to W-box motif of HY5 promoter, WRKY36 inhibits the transcription of HY5 promoter. Activation of UVR8 by UV-B light and its interaction with WRKY36 repress the binding of WRKY36 to HY5 promoter, which promote the transcription of HY5 and lead to inhibition of hypocotyls elongation. Unlike several studies that reported UVR8 is up-regulated following the exposure of UV-B, Shamala et al. (2020) reported that UVR8 was down regulated under short- and long-term exposure of UV-B radiation with differentially expressed genes of further downstream signal transduction pathway. They also observed enhanced accumulation of terpenoids and flavonoids due to differential expression of genes under UV-B (Shamala et al. 2020). SlUVR8 promotes acclimation to UV-B radiation in *S. lycopersicum* by enhancing the expression of *HY5* and *CHS* (UV-B-responsive

Table 9.1 UVR8-dependent responses of plants to UV-B radiation

S. no.	UV-B responses	Plants	References
1	Inhibition of hypocotyl growth	*Arabidopsis thaliana*	Favory et al. (2009)
		Solanum lycopersicum	Liu et al. (2020)
2	Accumulation of UV-B absorbing compounds	*Chrysanthemum morifolium*	Yang et al. (2018b)
		Vaccinum corymbosum	Inostroza-Blancheteau et al. (2014)
3	Fruit chloroplast development	*S. lycopersicum*	Li et al. (2018a)
4	Phototropism (hypocotyls)	*Arabidopsis thaliana*	Vandenbussche et al. (2014)
5	Phototropism (Inflorescence stem)	*Arabidopsis thaliana*	Vanhaelewyn et al. (2019)
6	Stomatal closure	*Arabidopsis thaliana*	Tossi et al. (2014)
7	Entrainment of circadian clock	*Arabidopsis thaliana*	Feher et al. (2011)
8	Antagonizing shade avoidance	*Arabidopsis thaliana*	Hayes et al. (2014)
9	Acclimation and UV-B tolerance	*S. lycopersicum, Chlamydomonas reinhardtii*	Liu et al. (2020), Tilbrook et al. (2016)
10	Antagonizing thermo-morphogenesis	*Arabidopsis thaliana*	Hayes et al. (2017)

gene) and accumulation of UV-B absorbing compounds. In addition, fruit chloroplast development was also promoted by SlUVR8 using enhanced accumulation of GOLDEN2-LIKE2 (SlGLK2) transcription factor, which determine the level of chloroplast and chlorophyll. Li et al. (2018a) suggest that the manipulation of SlUVR8 level provides a new option to increase the tolerance of *S. lycopersicum* towards UV-B and nutritional value of tomato fruits.

In Arabidopsis, UV-B radiation regulate the closure of stomata in UVR8-dependent manner by involving the signaling components COP1, HY5 and HYH (Tossi et al. 2014). Flavonoids serve as UV-B absorbing compounds and protect plant from harmful effect of UV-B radiation. UV-B radiation is one of the stimuli that regulate the synthesis of fllavonoids through UVR8 pathway. Under UV-B exposure UVR8-COP1 complex stabilizes the HY5 and HYH, which further promote the R2R3MYB transcription factor activity that in turn activates the transcription of flavonoids biosynthesis pathway genes (Zoratti et al. 2014). In *Chrysanthemum morifolium,* CmUVR8, COP1 and HY5 take part in the UV-B-mediated induced expression of flavonoids biosynthesis pathway genes and lead to enhanced accumulation of flavonoids in *C. morifolium* (Yang et al. 2018b).

9.7 Integration of UVR8 Signaling and Other Pathways

In environment, plants are inevitably subjected to multiple stresses simultaneously and the different signal transduction pathways operated in plants are closely related to each other. Several studies documented that there is a cross talk between UV-B and other abiotic stress signal transduction pathways (Li et al. 2018b). In seedlings of Arabidopsis, UV-B via UVR8 neutralizes the shade avoidance phenotype by decreasing the expression of auxin biosynthesis gene (Hayes et al. 2014). Vandenbussche et al. (2014) also reported that the UVR8 pathway through downregulation of auxin-inducible gene differentially affects the growth of Arabidopsis seedlings. Fierro et al. (2015) noticed changes in the shape of Arabidopsis leaf blade under supplemental UV-B light. The wild-type plant showed epinasty of the edges of leaf blade, whereas none of this effect was observed in uvr8 mutant plant. This suggest that the effect of UVR8 mimics the phytochrome (phy) B effect in red light, as phyB and UVR8-signaling pathways had over 70% of gene regulation in common. UVR8 also regulates the phototropic responses in inflorescence stem of *Arabidopsis thaliana*. Exposure of UV-B to one side (i.e., unilateral exposure) of inflorescence stem causes unilateral activation of UVR8 and increase of HY5 and HYH transcript and proteins at UV-B-exposed site. The exposed side also showed accumulation of flavonoids, increased expression of gibberellins (GA) 2-oxidase, diminished level of GA1, diminished auxin signaling which leads to growth inhibition at irradiated side whereas other shaded side elongate and hence allow bending toward exposed side. These suggest that the UVR8-regulated harmonal pathway also played a role in the phototropin-independent phototropism of inflorescence (Vanhaelewyn et al. 2019). Vandenbussche et al. (2014) reported that UVR8 played a prominent role in phototropin-independent phototropic responses to UV-B in Arabidopsis seedlings. Li et al. (2018b) isolated and characterized *UVR8* gene from *Betula pendula* (BpUVR8), which showed enhanced expression under abiotic stress including UV-B stress and abscisic acid (ABA) signal. BpUVR8 acts as a positive regulator in UV-B-induced photomorphogenic responses and also regulates the ABA-responsive gene. This suggests that BpUVR8 has a prominent role in the integration of ABA and plant growth-signaling pathway (Li et al. 2018b).

9.8 Conclusions and Future Perspectives

UVR8 is a seven-bladed β-propeller protein molecule with short N-terminal extension and flexible c-terminal region and the tryptophan residues as chromophore for the perception of UV-B light. The structure and function of UVR8 are highly conserved from algae to higher plants. Absorption of UV-B by UVR8 homodimers leads to its monomerization and subsequent interaction with COP1 which consequently leads to activation of further downstream-signaling pathway and the photomorphogenic responses in plants. There is a crosstalk between UVR8-signaling and other stress-signaling pathways including hormonal pathway. The

discovery of UVR8 as photoreceptor of UV-B radiation increased our understanding of the responses of plant against UV-B radiation. As most of the studies related to UVR8 -mediated plant-UV-B responses are concentrated on model plant Arabidopsis and performed under laboratory condition, the studies need to be further explored by involving different plant species and natural growth condition.

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UVR8 Signaling, Mechanism, and Integration with Other Pathways

10

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Abstract

Ultraviolet (UV) is a part of solar spectrum and has 3 subtypes: UV-A, UV-B, and UV-C. Out of them, UV-B has major impact on biological systems. It acts as an abiotic stress and also informational signal for plant growth and development. The photoreceptor responsible for UV signaling is UVR8, which changes its conformation on UV exposure leading to signaling pathways involving factors, like COP-1, FHY3, HY5, HYH, RUP1, RUP2, BIM1, WRK36, MYB73/MYB77, CRY, and many more. UVR8 signaling has holistic impact on plant, including various physiological effects, such as DNA alteration, defense, morphogenesis, phototropism, circadian clock, and induction of flowering. COP1 with UVR8 affects photomorphogenesis, gene expression, propanoid accumulation, and hypocotyl growth. The later involves HYH and HY5 for action. Cryptochromes and UVR8 lead to change in flavonoid levels aiding UV tolerance. RUP1 and RUP2 along with UVR8 lead to changes in flowering pattern as well as morphogenesis and UV acclimation. On the other hand, MYB, under the effect of UVR8, regulates root growth and development. It also alters expression of auxin-responsive genes, which further leads to multiple effects. BIM1 with UVR8 affect brassinosteroid-responsive genes affecting plant growth. As UVR8 helps multiple factors to link with each other, henceforth, the mode of action, signaling, and impact on plant growth is detailed in the sections ahead.

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Keywords

Ultraviolet-B (UV-B) · UV-resistant locus 8 (UVR8) · Plant signaling · Plant growth · Plant development

10.1 Introduction

10.1.1 UV Radiations

Various environmental stresses affect the development of plants under natural conditions. This triggers them to adapt and evolve copious strategies to exist under such hostile conditions. Ultraviolet (UV) radiations are part of the solar spectrum and have three types: UV-A, UV-B, and UV-C. Less than 0.5% of solar energy reaching the surface of the earth is contributed by UV-B (Blumthaler 1993). Factors, like altitude, latitude, stratospheric ozone, solar angle, and troposphere pollution, play a major role in this (Paul and Gwynn-Jones 2003; McKenzie et al. 2007). Every stress triggers a definite set of signaling factors for the perception of the stimulus, regulators of transcription, and downstream-responsive genes for stress acclimation and its tolerance.

UV-B light of wavelength 280–315 nm is latent stress and signal, which proves to control plant growth and its development (Tilbrook et al. 2013a, b). Its low fluence rate acts as a stimulus that mediates many chief plant physiological responses, such as circadian rhythm, photomorphogenesis, and photoprotection. Plant growth, development, and biochemical composition are well regulated by a low fluence of ambient UV-B (Boccalandro 2001; Suesslin and Frohnmeyer 2003) and mark the gene expression (Casati and Walbot 2003, 2004; Jenkins 2009). In comparison, UV-B at high fluence may trigger both specific as well as non-specific pathways instigating the formation of reactive oxygen species (ROS), inhibition of photosynthetic processes, protein synthesis, and damage to DNA and proteins (Jenkins 2009; Frohnmeyer and Staiger 2003). Subsequently, this leads to a varied range of alterations in morphology as well as at molecular levels (Brown et al. 2005; Kataria et al. 2014; Meegahakumbura et al. 2018). Also, high doses of UV-B mutilate cell membranes, lipids, as well as photosynthetic machinery, leading to changes at the cellular level and viability, posing stunted growth and a decline in crop yield as well as quality (Frohnmeyer and Staiger 2003). Subsequently, various ways had been evolved by plants to dodge UV-B damage (Tilbrook et al. 2013a, b). Primitive organisms, viz., cyanobacteria, and many eukaryotic algae form UV protective substances, like mycosporine-like amino acids (MAAs) (Llewellyn and Airs 2010; Rastogi and Incharoensakdi 2013; Rozema et al. 2002). As the complexity increases from algae to higher plants, there occur changes in the UV-B absorbing with reference to environmental UV-B levels (Rozema et al. 2002; Kataria et al. 2013). There exist an array of very sensitive and intricate photoreceptors for combating changes in light duration, quality, quantity, as well as direction.

10.1.2 UVR8

During the course of evolution, plants have developed different photoreceptors for the light of specific wavelengths: phototropins (phot1 and phot2) for blue light, phytochromes (phyA–E) to detect red/far-red light; cryptochromes (CRY1 and CRY2), Zeitlupe family proteins (ztl, fkf1, and lkp1), and the UV Resistance Locus 8 (UVR8) for ultraviolet (UV)-B (Rizzini et al. 2011; Tilbrook et al. 2013a, b; Jenkins 2014; Galvao and Fankhauser 2015). In higher plants, phytochromes are also involved in the UV-B protection mechanism and it makes UV-B response more complex (Kreslavski et al. 2020). Unlike photosynthetic complexes, a majority of photoreceptors have merely a single chromophore. Therefore, a single site is responsible for photon absorption as well as subsequent photoreactions leading to protein conformational changes with no transfer of excitation energy.

Previous researches proved the role of UVR8 photoreceptor in UV-B-induced responses. It has been observed by the action spectrum of UVR8 that although the major UV absorption occurs around 280 nm, the most important physiological responses occur by absorbing a wavelength of ≈300 nm with a minor absorption peak. UVR8 is a β-propeller protein, containing integral Trp residues that act as the base for the reception of UV-B (Christie et al. 2012; Liu et al. 2014). UVR8 from *Arabidopsis thaliana* is made up of total 440 amino acids containing two discrete domains: a core domain (seven-bladed β-propeller section) and a C-terminal area of 27 amino acids (Cloix et al. 2012; Kliebenstein et al. 2002). Unlike various infrared and visible photoreceptors (Möglich et al. 2010; Rockwell et al. 2006; Spudich et al. 2000), UVR8 has no external chromophore, and rather it utilizes its tryptophan (W or Trp) residues for the perception of light (Christie et al. 2012; O'Hara and Jenkins 2012; Ulm and Jenkins 2015; Wu et al. 2012). Precisely, intrinsic Trp285 and Trp337 play a major role in the absorption of UV-B light directly (Christie et al. 2012; Rizzini et al. 2011; Wu et al. 2012). Intriguingly, UVR8 has highly organized light-harvesting networks for photoreception (Rizzini et al. 2011). As these Trp networks are highly conserved among different species (Tilbrook et al. 2016; Fernández et al. 2016; Soriano et al. 2018), the light-harvesting mechanism possibly could have arisen early during the evolution of UVR8.

It is noteworthy that there exist the homodimer and the monomer states of UVR8, which are transitional, reversible, and dynamic. In the ground or "dark" state, UVR8 exists as a homodimer with its interface being well decorated with numerous intersubunit salt bridges and hydrogen bonds (Rizzini et al. 2011; Christie et al. 2012; Wu et al. 2012). However, in the presence of UV-B, the tryptophan residues of UVR8 undergo structural changes after UV absorption and lead to the immediate formation of active monomer units (Rizzini et al. 2011; Christie et al. 2012; Wu et al. 2012; Zeng et al. 2015). Every monomer of UVR8 consists of 14 tryptophan residues. Apart from the unstructured C-terminal one, the remaining 13 structural Trp residues are generally classified into three different groups, viz., a distal ring ($6W_d$), a peripheral outlier ($3W_{p,}$ viz., W198, W250, and W302), and a pyramidal center ($4W_c$) (Christie et al. 2012; O'Hara and Jenkins 2012; Liu et al. 2014; Wu et al.

2012, 2014, 2015; Voityuk et al. 2014; Zeng et al. 2015). The dimer form of UVR8 consists of two symmetry-related pyramid centers ($4W_c$); each is shaped by van der Waals clustering of $3W_c$ (W285, W233, and W337) from one monomer and a fourth W_c (W94) from the opposing monomer. Moreover, six residues of Trp, $6W_d$, are concealed at the center of the beta-propellers and lead to the formation of a highly symmetrical ring. Out of all the tryptophan residues, only two pyramid center Trp (W285 and W233) of the Wc pyramid play the chief role during light-induced monomerization (Christie et al. 2012; Liu et al. 2014; O'Hara and Jenkins 2012; Wu et al. 2012, 2014, 2015; Voityuk et al. 2014; Zeng et al. 2015).

Li et al. used a site-directed mutagenesis approach and found that there exists a significant difference in absorption spectra longer than 300 nm among the Trp residues. The distal group of $6W_d$ residues has negligible absorbance beyond 310 nm; the absorption spectrum of the $3W_p$ extends to 314 nm, while that of $4W_c$ reaches beyond 320 nm. As a result of differential absorption, there exist differences in selective excitation of W_d, $W_{p,}$ or W_c, leading to diverse emission spectra with peaks at 320 nm, 340 nm, and 350 nm, respectively. Despite UV-B absorption by all the Trp residues, only the interfacial pyramid remains the chief site for the critical reaction leading to dimer dissociation (Christie et al. 2012; O'Hara and Jenkins 2012; Rizzini et al. 2011; Wu et al. 2012; Wu et al. 2014, 2015; Liu et al. 2014; Voityuk et al. 2014; Zeng et al. 2015; Mathes et al. 2015). Conclusively, it can be stated that Trp residues not just play a structural role but also the distal and peripheral tryptophan networks have a chief functional role in harvesting and funneling UV-B energy to $4W_c$ (the pyramid perception centers), which leads to induction of the reaction and unfold the dimer interface resulting in a further signaling cascade.

Moreover, current structural studies propose the importance of the C-terminal tail of UVR8. This includes C27 and C17 domains, making diverse conformational changes for action. For instance, compact and the extended states of their structure have a key role in regulating the activity of UVR8 (Camacho et al. 2019).

UVR8 protein is reported to be present throughout the plant body (Rizzini et al. 2011). Even in the absence of UV-B, it is frequently located in the cytoplasm, whereas a small amount is found in the nucleus. Within minutes of UV-B exposure, UVR8 hoards in the nucleus, whereas its major amount remains in the cytoplasm (Kaiserli and Jenkins 2007; Yin et al. 2016; Qian et al. 2016). This nuclear localization of UVR8, as well as its monomerization, is critical for its role in controlling signal transduction and photomorphogenesis, resulting from changes in expression of genes, followed by acclimation responses (Kaiserli and Jenkins 2007; Rizzini et al. 2011).

10.2 UVR8-Mediated Signaling

UV-B, with the help of UVR8, induces many physiological responses, which lead to growth regulation and developmental changes. It is also a signal which helps modulate photomorphogenesis, which involves accretion of flavonoids and anthocyanins, inhibition of hypocotyl elongation, and increased expression of UV-

B-responsive genes (Jenkins 2009; Ballaré et al. 2012; Heijde and Ulm 2012; Wargent and Jordan 2013). On the perception of UV-B, the UVR8 triggers the signaling pathway and further leads to alteration of gene expression via molecular signaling. UVR8 helps acclimation for low fluence, while promotion of tolerance to high fluence of UV-B light (Kliebenstein et al. 2002; Brown et al. 2005; Favory et al. 2009).

White light can travel through the root tissues through an effect known as light piping and leads to photomorphogenic changes in the roots as that is not directly exposed to light (Lee et al. 2016). It is proven that CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1), Far-Red Elongated Hypocotyl 3 (FHY3), and ELONGATED HYPOCOTYL 5 (HY5) are three common factors playing a chief role in promoting light signaling and inducing photomorphogenesis. Transcription factors viz FHY3, COP1, and HY5 affect positively (Stracke et al. 2010; Huang et al. 2012; Binkert et al. 2014a, b) and the negative regulators RUP1 and RUP2 (Gruber et al. 2010; Heijde and Ulm 2013) ally the signaling pathway mediated by UVR8. Also, UVR8 precisely controls UV-B photomorphogenesis, which includes seedling de-etiolation, leaf development, phototropism, lateral root development, stomatal movements, floral transition, and stress tolerance (Wargent et al. 2009; Demkura and Ballaré 2012; Li et al. 2013; Tossi et al. 2014; Vandenbussche et al. 2014; Jenkins 2017; Yin and Ulm 2017; Arongaus et al. 2018; Liu et al. 2019; Liang et al. 2019; Vanhaelewyn et al. 2019).

Moreover, BES1-INTERACTING MYC-LIKE 1 (BIM1), WRKY36, and MYB DOMAIN PROTEIN 73 and 77 (MYB73/MYB77) also play a role in regulating gene expression (Brown and Jenkins 2008; Favory et al. 2009; Huang et al. 2012; Liang et al. 2018, 2019; Yang et al. 2018, 2020). So, it is established that certain genes are known to be reporters for UVR8 signaling: HY5, CHS, HYH, ELIP1, CRYD, GPX7, SIG5, PHR1, and WAKL8 with the first two as most implemented examples (Ulm et al. 2004a, b; Cloix and Jenkins 2008; Favory et al. 2009; Stracke et al. 2010; Binkert et al. 2014a, b; Yin et al. 2015; Moriconi et al. 2018).

Recently, it has been found that there occur multiple physiological responses that are regulated by UVR8: phototropism, auxin signaling, thermomorphogenesis, entrainment of the circadian clock, defense, salt stress tolerance, shade avoidance, chloroplast development, stomatal density and closure, leaf epinasty, photoprotective flavonoid biosynthesis, inhibition of hypocotyl extension, leaf expansion, endoreduplication, tolerance to Botrytis, and response to osmotic stress (Kliebenstein et al. 2002; Favory et al. 2009; Rizzini et al. 2011; Tilbrook et al. 2013a, b; Hayes et al. 2014; Jenkins 2017; Yin and Ulm 2017). A major hallmark for UV-B sensitivity can be the accumulation of photoprotective pigment. Interestingly, UV-B augments H_2O_2 production, thereby increasing the levels of nitric oxide and subsequently magnifying the expression of UVR8 (Wu et al. 2016).

It has been understood that by microarray and reverse transcription PCR analyses that UVR8 can regulate the expression of genes related to photooxidative damages (ELIP1, SIG5), protection against oxidative stress (PDX1), UV protection (flavonoid, PHR1), a number of genes encoding signaling components, transcription

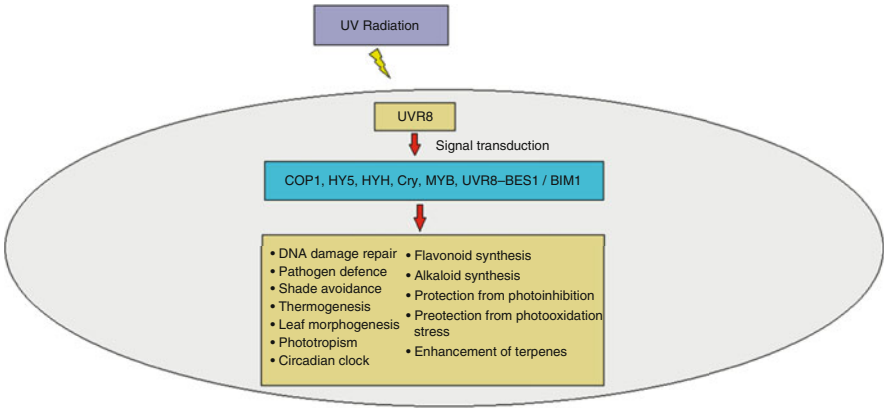

Fig. 10.1 UVR8 signaling, mechanism, and integration with other pathways

factors, transporters, proteases, and several proteins with unknown functions (Brown et al. 2005) (Fig. 10.1).

10.2.1 CONSTITUTIVELY PHOTOMORPHOGENIC 1 and Photomorphogenesis

CONSTITUTIVELY PHOTOMORPHOGENIC 1 is a chief negative regulator of plant photomorphogenesis in the dark and visible light, therefore involved in many light signaling pathways (Lau and Deng 2012; Podolec and Ulm 2018). Intriguingly, being a repressor of photomorphogenesis, COP1 plays a role in protein selection for ubiquitination and degradation (Lau and Deng 2012).

Being an E3 ubiquitin ligase, COP1 interacts directly with the photoactivated UVR8 monomer, proving this association crucial for the UVR8 signal transduction (Tilbrook et al. 2016). As UV-B is needed for UVR8–COP1 association (Rizzini et al. 2011; Cloix et al. 2012), followed by COP1 accumulation in the nucleus, implies that COP1 associates with the UVR8 monomer and UV-B signaling occur inside the nucleus (Oravecz et al. 2006; Favory et al. 2009). The truncated UVR8 has only the C27 domain, which is very critical to interact constitutively with COP1. For the interaction, COP1 utilizes its C-terminal WD40-repeat domain to interact with the two domains (beta-propeller) of UVR8 (Cloix et al. 2012; Yin et al. 2015). The UVR8 C-terminal tail alters to compact and extended conformations (Camacho et al. 2019). Numerous proteins join the C27 domain due to the extended conformation, while the compact version prospectively constrains UV-B signaling. Lin et al. (2020) suggested that C17 of COP1 hinders both the types of associations: the UVR8–COP1 as well as the C27–COP1. Although the interaction of C17 with UVR8 leads to C17 folding back onto full-length UVR8 which further forms more packed C-terminal conformation inhibiting the C27–COP1 association. In the dearth of UV-B treatment, the C27 domain of full-length UVR8, being protected inside the

homodimer interface, is barred from COP1 association (Cloix et al. 2012; Yin et al. 2015).

There are two suggested models for UVR8 and COP1 interaction: (1) The nuclear co-import model, where UV-B induces the formation of UVR8 monomer leading to cytoplasmic COP1 association. The COP1-containing nuclear localization sequence aids in the co-import of UVR8 to the nucleus. So, the UVR8–COP1 association is important for UVR8 transport to the nucleus (Qian et al. 2016; Yin et al. 2016). (2) The nuclear retention model: UV-B-dependent nuclear localization of UVR8 monomer and its transportation into the nucleus by an unidentified mechanism, whereas nuclear COP1 prevents instant nuclear export of UVR8 (Yin and Ulm 2017). Although COP1 is an E3 ubiquitin ligase, the association of UVR8 and COP1 checks the degradation of UVR8 (Favory et al. 2009). Moreover, UV-B radiation upsurges COP1 protein post-transcriptionally in a UVR8-dependent manner, and the probable reason being relegated is autoubiquitination of COP1 (Favory et al. 2009). Additionally, the COP1 transcript gets enhanced due to transcription factors FHY3 and HY5, which work with UVR8 signaling on exposure of UV-B (Huang et al. 2012), and the binding sites for both the transcription factors on the COP1 promoter are adjacent to each other (Huang et al. 2012). It has also been studied that far-red light represses, while UV-B induces the expression of FHY3 (Lin et al. 2007; Huang et al. 2012).

ELONGATED HYPOCOTYL 5 acts as a photomorphogenesis-promoting bZIP transcription factor. COP1 associates with HY5 as well as many other positive regulators of photomorphogenesis for 26S proteasomal degradation (Osterlund et al. 2000). Contrastingly, under UV-B exposure, COP1 guards HY5 from 26S proteasome-mediated degradation (Huang et al. 2013; Ren et al. 2019). The prevention of HY5 ubiquitination can be due to the competition between UVR8 and HY5 for association with COP1 interaction (Yin et al. 2015; Lau et al. 2019). Hence, there occurs the maintenance of HY5 and the upregulation of multiple target genes, which encode proteins for photomorphogenesis (Huang et al. 2012; Binkert et al. 2014a, b). Most likely, this leads to related overlapping photomorphogenic responses, for instance, changes in gene expression, hypocotyl growth inhibition, phenylpropanoid accretion, along with induction of flowering (Galvao and Fankhauser 2015; Jenkins 2017; Yin and Ulm 2017; Podolec and Ulm 2018; Arongaus et al. 2018; Wang et al. 2018).

Moreover, it has also been suggested that COP1 associates with SPA1 (SUPPRESSOR OF PHYA) as well as other components of E3 ubiquitin ligase complexes which stimulate ubiquitination and degradation of transcription factors HY5 and HYH (HY5 HOMOLOG) (Lau and Deng 2012). The interaction of UVR8 and COP1 controls COP1 functioning and likely promotes functional dissociation of the COP1–SPA core complexes. This helps in forming an exceptional association, including UVR8–COP1–SPA1, and thereby controls the ubiquitination of HY5 (Huang et al. 2013). Conclusively, UV-B exposure initiates the association of UVR8 and COP1 and helps HY5 expression as well as protein stabilization, which further induces expression of UV-B-responsive gene leading to photomorphogenesis.

10.2.2 HY5 and HYH

Transcription factor HY5 is one of those genes which are activated upon UV exposure and has a chief role in signaling (Stracke et al. 2010; Huang et al. 2012). It is a bZIP transcription factor that responds to multiple wavelengths of light for directing gene expression involved in UV-B photomorphogenesis along with flavonoid biosynthesis (Lee et al. 2007; Brown and Jenkins 2008; Stracke et al. 2010). The HY5 induction and photomorphogenesis are critically dependent on the photoactivated nuclear UVR8 because cytoplasmic UVR8 is incapable of the same (Qian et al. 2016; Yin et al. 2016).

It has been studied that the expression of HY5 is dependent on UVR8 and COP1 with the exposure of UV-B (Oravecz et al. 2006; Favory et al. 2009). Intriguingly, the chromatin binding site of UVR8 and HY5 genomic locus is adjacent to each other (Brown et al. 2005; Cloix and Jenkins 2008). HY5, along with HYH, is commonly known to regulate many UV-regulated transcription (Brown and Jenkins 2008). It is also true that HY5 associates with HY5 Homolog (HYH), which regulates photomorphogenesis positively. This implies that HYH participates in UVR8-mediated signaling. As a mark of early photomorphogenic UV-B response, HY5 and HYH transcripts upsurge (Vanhaelewyn et al. 2019). HY5 plays an important role for UVR8-mediated UV-B signaling because it is deployed in COP1 and proteasome-mediated degradation in the absence of light (Osterlund et al. 2000). Three cis-regulatory elements (a T/G-box, an ACG-box (ACG), and an E-box) transcriptionally activate HY5, where the ACG-box is a light-induced HY5 repression factor (Binkert et al. 2014a, b). Furthermore, after induction of HY5 expression, one of the three ACGT-containing elements (ACEs) binds to the COP1 promoter leading to its increased expression (Huang et al. 2012). A supplementary characteristic attribute of HY5 is its re-engagement, which helps maintain a functional implication in older seedlings as well as mature plants (Oravecz et al. 2006). Upon UV-B exposure, HY5 and its homolog HYH attach to the T/G-box in the HY5 promoter to alter the expression of HY5 (Binkert et al. 2014a, b). HY5 further controls the expression of several UV-B-responsive genes, like RUPs, COP1, and flavonoid biosynthesis genes (Ulm et al. 2004a, b). WRKY36 is a transcription factor and uses its C-terminal DNA-binding domain for interaction with the C27 domain of UVR8. Under UV absence, UVR8 chiefly limits in the cytosol, whereas WRKY36 confines in the nucleus to negatively impact HY5 transcription and enhance hypocotyl elongation (Yang et al. 2018; Liang et al. 2018). While, on UV-B exposure, UVR8 monomerization leads to its accumulation in the nuclear compartment and associates with the WRKY36 to impede its DNA-binding feature. Additionally, HY5 affects auxin signaling by promoting the expression of its negative regulators, and thereby HY5 acting as a signaling links light and hormone signaling (Cluis et al. 2004).

10.2.3 Cryptochromes (CRYs)

Cryptochromes are a diverse array of flavoproteins, which are sensitive to blue light and have roles in maintaining circadian rhythms and magnetic field sensing. There exist two different genes for coding distinct proteins, viz., CRY1 and CRY2. In the presence of blue light, the monomer (inactive form) of cryptochrome modifies to homodimer (active) (Wang et al. 2016). Blue-light inhibitors of cryptochromes (BIC1) and BIC2 directly bind to cryptochromes and inhibit their dimerization, showing negative feedback regulation (Wang et al. 2016, 2017). Interestingly, there exists an overlapping in the absorption spectra of CRYs and UVR8. The absorption spectra of CRY range from UV-B to green wavelength (Ahmad et al. 2002; Zeugner et al. 2005; Banerjee et al. 2007), whereas those of UVR8 range from UV-C to the violet wavelength. This implied interaction between CRYs and UVR8. Cryptochrome-mediated blue-light signaling exhibit certain fascinating similarities to UVR8 UV-B signaling. Tissot and Ulm (2020) showed that the UVR8 photoequilibrium is responsive to blue-light signaling mediated by cryptochrome, thus identifying a novel photoreceptor co-action mechanism that balances UV-B sensitivity of plants under the polychromatic spectrum of sunlight. Fascinatingly, both non-functional CRYs and UVR8 impede the survival of plants under UV-B (Morales et al. 2013; Rai et al. 2019). In the presence of UV-B, flavonoid levels upsurge with the help of UVR8. When CRYs and UVR8 interact with COP1, it leads to stabilization of HY5 and HYH, further regulating the expression of many blue- and UV-responsive genes. Such genes, like CHALCONE SYNTHASE (CHS), DIHYDROFLAVONOL 4-REDUCTASE (DFR), EARLY LIGHT-INDUCED PROTEIN 2 (ELIP2), CHALCONE ISOMERASE (CHI), and SOLANESYL DIPHOSPHATE SYNTHASE 1 (SPS1), are induced by UV and blue light with the help of UVR8 and CRY (Favory et al. 2009; Yu et al. 2010; Nawkar et al. 2017). Also, active cryptochromes inhibit the COP1 to stabilize HY5 and help its accumulation (Lian et al. 2011; Liu et al. 2011; Zuo et al. 2011; Holtkotte et al. 2017; Lau et al. 2019).

Both photoreceptors CRY and UVR8 require to bind with COP1 for signaling cascade (Mao et al. 2005). Morales et al. (2013) proposed that the survival of the plant in the presence of UV is due to other pathways as well, which are independent of UVR8. Besides Fuglevand et al. (1996), Liu et al. (2018) also studied that CRY1 helps induce CHS in the presence of blue light, while Gruber et al. (2010) studied the RUP2 induction under blue light. Moreover, Rai et al. (2019) showed that together CRYs and UVR8 are essential for transcript accumulation of CHI in the presence of UV-A.

It is noteworthy that CRY1, CRY2, and UVR8 are crucial for survival under natural sunlight (Rai et al. 2019). So, the interactions between phytochrome, cryptochrome, and UVR8 signaling pathways help in UV-B tolerance, which aids plant survival in sunlight in natural conditions (Tissot and Ulm 2020).

10.2.4 Repressor of UV-B Photomorphogenesis 1 (RUP1) and RUP2

RUP1 and RUP2 (REPRESSOR OF UV-B PHOTOMORPHOGENESIS) are two important regulators that affect the UVR8 pathway negatively and are induced by UV-B (Gruber et al. 2010). Under UV-B exposure, UVR8, COP1, and HY5 upsurge the transcription of RUP1 and RUP2. RUPs directly interact with UVR8 and are important for UV responses as well as plant growth. COP1 promotes, while RUPs repress UVR8 accumulation (Qian et al. 2016; Yin et al. 2016). RUPs are vastly homologous to WD40-repeat proteins and both promote UVR8 redimerization (Gruber et al. 2010; Heijde and Ulm 2013). They are also phylogenetically related to COP1 and the SPA proteins and their overexpression leads to early flowering and impedes the inhibition of hypocotyl growth in UV-B absence, irrespective of photoperiods (Wang et al. 2011).

Podolec et al. (2021) suggested that UVR8 redimerization can occur through two stages: First is RUPs outcompete COP1 and other VP-domain interactors, separating them from UVR8, while second is RUPs facilitate UVR8 redimerization. uvr8-17D has been studied to be a UV-B-hypersensitive UVR8 allele allied with a single glycine-101 to serine amino acid alteration. This hypersensitivity is linked with its monomeric conformation *in vivo*, indicating that redimerization facilitated by RUPs is compromised.

Expression RUPs increase due to the interaction of UVR8-RUP1/RUP2 (Gruber et al. 2010). Heijde and Ulm (2013) indicated a significant role of RUPs in UVR8 redimerization, and this is independent of COP1. Under UV-B irradiated conditions RUPs negatively regulate UV-B signaling by mediating UVR8 redimerization, which further interposes the association of UVR8 with COP1. Additionally, RUP proteins hinder UV-B signaling by degradation of HY5 (Ren et al. 2019). C27 domain mediates binding between RUP1 and RUP2 with UVR8 (Cloix et al. 2012; Yin et al. 2015). It is proposed that C17 inhibits the association of C27 to RUP proteins because the binding between C44 and RUP is not as strong as C27 and RUP. Here, the Val-Pro residues within C27 play a major role in the reformation of UVR8 homodimers (Yin et al. 2015). RUP1 and RUP2 are likely to be a part of a CUL4-DDB1-based E3 ubiquitin ligase that aims HY5 for degradation (Ren et al. 2019). It is also likely that many signaling pathways triggered by environmental signals beyond light perception can affect RUP1 and RUP2, thus involved in further cross-regulation of UVR8-mediated photomorphogenesis and UV-B acclimation (Tissot and Ulm 2020).

10.2.5 MYB (Myeloblastosis) Transcription Factors and Regulation of Root Growth and Development

It is known that UVR8 leads to plant growth reduction under drought conditions (Kliebenstein et al. 2002; Brown et al. 2005). Fasano et al. (2014) made a phenotypic analysis of *UVR8*-overexpressing plants and found a negative effect on root growth

on light exposure. This inhibitory action was due to a decrease in cell enlargement than in cell numbers.

MYB is a group of different transcription factors which interact with UVR8 to modulate lateral root growth as well as cotyledon development (Qian et al. 2020). Yang et al. (2020) studied that UVR8 limits lateral root growth with UV-B irradiation. This is due to the downregulation of the diverse auxin-responsive genes. There exists a binding between UVR8 and the two MYB types (MYB73 and MYB77) under UV-B presence. Both the MYB types are positive regulators that aid in the upregulation of auxin-responsive genes. The interaction between UVR8 and MYB73/77 revokes the DNA-binding ability of the two MYBs and consequently controls the expression of auxin-responsive genes (Yang et al. 2020). Qian et al. (2020) has put light onto the global UV-B-responsive transcriptome and found that MYB13 expression level promptly increased by nucleus-localized UVR8. MYB13 is explicitly expressed in cotyledons and is required for UV-B-responsive cotyledon expansion as well as flavonoid biosynthesis. Here, MYB13 associates with UVR8 under the presence of UV-B and further controls MYB13 DNA binding to its target promoters (Qian et al. 2020). Collectively, UV-activated UVR8 binds with either MYB73/77 in roots or MYB13 in cotyledons. This association of UVR8 and MYB transcription factors leads to transcriptional alterations regulating lateral root growth, cotyledon expansion, as well as stress acclimation. MYB13 directly interacts with the promoter sequences of auxin-responsive genes to regulate gene expression. UVR8–MYB interactions indicate the complexity of the UVR8 interactome. MYB73 and MYB77 have a key role in lateral root growth as well as they also partly regulate hypocotyl elongation.

It is noteworthy that the growth of the lateral roots is governed by auxin. Fasano et al. (2014) studied elevated levels of flavonoids and a reduction in IAA conjugates content in UVR8-overexpressing plants. (Casimiro et al. 2001; Bhalerao et al. 2002; De Smet and Jürgens 2007). Conclusively, more flavonoids are related to a decrease in cell expansion, that later alters polar auxin transport. UVR8 can control the flavonoid concentration as well as auxin movements within roots, which is significant for root growth, and hence connect light and hormone signaling pathways together. MYB12 being an explicit transcription factor for FLAVONOL SYNTHASE (FLS) leads to the increase in the concentration of flavonoids with UV-B irradiation. Moreover, its expression is regulated by HY5 (Stracke et al. 2010). MYB4 is another transcription factor, which suppresses C4H, 4CL, LAR, CHS, and ANR2 to arbitrate UV-B-dependent anthocyanin and phenylpropanoid formation (Schenke et al. 2011; Li et al. 2017). Also, bHLH is an alternative group of the transcription factor playing multiple roles extending from regulation of floral development to flavonoids biosynthesis (Sorensen et al. 2003; Ohno et al. 2011). Moreover, MYB4a is a negative regulator of C4H, 4CL, CHS, LAR, and ANR2 which works by binding to target gene promoters (Li et al. 2017).

10.2.6 The UVR8–BES1 (BRI1-EMS Suppressor1)/BIM1 Pathway

Brassinosteroids are phytohormones, which play role in controlling plant growth and development, like photomorphogenesis and skotomorphogenesis, and in combatting abiotic and biotic stresses (Clouse 2011). The surface receptor kinase BRASSINOSTEROID INSENSITIVE 1 (BRI1) responds to Brassinosteroids and leads to activation of BES1 and BZR1 (BRASSINAZOLE RESISTANT 1) (He et al. 2002; Nam and Li 2002). There exist several mechanisms through which the GSK3-like kinase BIN2 (BR-INSENSITIVE 2) leads to inhibition of BES1 and BZR1 by phosphorylation, in the absence of BR (Li and Jin 2007). BIN2 activity gets inhibited in the presence of BR, and as a result, dephosphorylated BES1 and BZR1 get accumulated inside the nucleus (Belkhadir and Jaillais 2015). This promotes the upregulation of BR target genes (Wang et al. 2002; Yin et al. 2002). BIM1 interacts with BES1 for regulation of BR-induced gene as well as hypocotyl elongation (Yin et al. 2005). Also, UVR8 interacts with BIM1 to modulate transcriptional events (Liang et al. 2018). Additionally, UVR8 binds with the dephosphorylated BES1 (active state) to control BR signaling. Dephosphorylated BES1 can bind with DNA under the influence of BR (Vert and Chory 2006). UVR8 can interact with BES1 homolog BZR1 as well as the long isoform of BES1 (BES1-L), that comprises a supplementary N-terminal nuclear localization signal (Jiang et al. 2015). Also, the interaction of UVR8 and BIM1 leads to inhibition of the BR-responsive genes and decreases the hypocotyl elongation (Sun and Zhu 2018). UVR8 interacts with the C-terminus of BIM1 as well as the BIN2 phosphorylation domain of BES1. UVR8 interacts weakly with the basic helix–loop–helix (bHLH) domain of BIM1, whereas the same interacts strongly with the bHLH domain combined with either the N-terminus or C-terminus of BIM1. BIM1 and dephosphorylated BES1, as they are transcriptional factors, are sited mainly in the nuclear compartment, whereas UVR8 is found in the nucleus due to UV stimulus. Conclusively, the UVR8–BES1/BIM1 complex, in the nucleus stimulated by UV exposure, regulates hypocotyl elongation and photomorphogenesis. This is mediated by inhibition of BR signaling and altogether it helps fine-tune plant growth (Liang et al. 2018).

10.3 Molecular Mechanism of Photoreceptor-Mediated Signaling

Christie et al. (2012) suggested that β-propeller subunits constituting a group of tryptophan residues form a dimer interface which gets stabilized with the help of a complex salt-bridge network. UV-B sensing occurs with the help of a UV-B antenna, which is formed by a Trp pyramid, having Trp 233, Trp 285, and Trp 337, along with Trp 94 (integral tryptophans in UVR8). Post UV-B perception, an excited electron gets transferred from the excitonically coupled Trp pyramid that lies adjacent to arginine(s), leading to charge neutralization, subsequent breaking of cross-dimer salt bridges, and hence dimer destabilization and dissociation. The Trp pyramid becomes critical for UVR8 photoperception, where W285 plays a chief role. Correspondingly,

W233 helps maintain excitation coupling for photoreception, while W337 and W94 have secondary roles. For UVR8 photoreception, there exists a conserved sequence of Gly-Trp-Arg-His-Thr repeat forms a "triad" of tryptophan residues: W233, W285, and W337 having a tight packing. The piling of W285 with adjacent R286 is critical for dimerization and connecting UV-B photoreception with salt-bridge formation. To sum up, the extensive packing congregation of the conserved aromatic cluster neighboring the Trp pyramid and the salt bridges zipping the dimer interface imply that UVR8 has evolved a strenuous mechanism for the perception of UV-B and signaling.

Wu et al. (2012) studied and unleashed the mechanism of UVR8-dependent UV-B sensing. The study successfully explained that UV-B perception by UVR8 requires its chromophore with its two tryptophan residues, Trp 285 and Trp 233. These experimental studies and the information on tryptophan fluorescence explain a mechanistic model for UVR8-dependent UV-B perception. The exposure of UV-B leads to excitation of the indole rings of Trp 285 and Trp 233. This excitation is believed to unsettle the P bond over the indole rings and further result to destabilize the intramolecular cation–π interactions. These changes cause distinct conformational alterations to the side chain comprising Arg 286 and Arg 338 that fails to uphold intermolecular hydrogen bonding with Asp or Glu residues from the adjacent UVR8 molecule and leading to UVR8 monomerization. There exists an excited-state proton transfer to the indole rings undergo that makes the indole ring positively charged, leading to destabilization of the cation–π interactions. This results in quenching of intrinsic tryptophan fluorescence and hence results in a slight decrease of fluorescence signal. As proton donors for the same, Trp 233 and Trp 285 lie adjacent to Asp 129, Glu 182, and Arg 234. The reformation of homodimers is possible because there exists no covalent modification of UVR8 on the perception of UV-B.

Voityuk et al. (2014) proposed three steps for the photodissociation mechanism of UVR8 through high-level quantum chemical calculations:

1. On conversion of dimeric UVR8 to monomers, the intrinsic tryptophan residues establish a broad light-harvesting system, where the excited form of Trp 233 undergoes strong electrostatic stabilization by the protein environment.
2. Charge separation leads to fast decay of the locally excited state, which creates the radical ion pair Trp 285(+)-Trp 233(−), with a dipole moment of ≈18 D.
3. The resultant dipole moment destabilizes the salt bridges between the two monomer subunits.

Yin et al. (2015) studied the two distinct domains of UVR8 and suggested that they interact with COP1: the β-propeller domain of UVR8 facilitates association with the WD40-repeats-based predicted β-propeller domain of COP1 on exposure to UV, while the C-terminal C27 domain of UVR8 networks with COP1. UV-B exposure leads to its absorption by Trp residues next to Arg residues and forms salt bridges across the dimer interface. These changes dissociate the UVR8 homodimers by disordering the salt bridges instantly. The resultant UVR8 monomer,

along with its seven-bladed β-propeller domain (C27), joins the WD40 domain (a structurally related seven-bladed β-propeller) of COP1. This UVR8–COP1 complex stabilizes HY5 and upsurges the expression of the two RUP genes, leading to a negative feedback loop. HY5, being a basic leucine zipper transcription factor, has a critical role in the process of de-etiolation (Osterlund et al. 2000; Saijo et al. 2003; Yi and Deng 2005). RUP1 and RUP2 are WD40-repeat proteins and hold phylogenetic and structural similarities with COP1. Their association with the C27 domain disrupts the UVR8–COP1 complex promoting the formation of UVR8 dimers again.

RUP1/RUP2-UVR8–COP1 complex forms briefly when RUPs remain associated with UVR8 by its C27 domain, whereas UVR8 and COP1 still remain associated. Also, the differences in the UVR8–COP1 and UVR8-RUP1/RUP2 associations are because of variances in their modes of interaction. The exposed β-propeller surface of UVR8 monomers has the tendency to bind with COP1 but not with RUP proteins. Also, COP1 and RUPs have a discrete capability to associate with the C-terminal. Moreover, COP1 binding needs UV-B activation and UVR8 monomer formation but RUPs can associate with inactivated homodimers as well.

Zeng et al. (2015) crystallized UVR8 (12–381 residues) and studied light-induced structural alterations. They concluded that the two clusters of strong positive and negative difference densities occur at the dimer interface explicitly linked with Trp 285/Trp 233 and a water molecule. The water molecule establishes hydrogen bond at the dimer interface, which includes Trp 285/Arg 286 in one subunit and Asp 96/Trp 94/Asp 107 in another one. Due to strong attraction, Trp 285 and Trp 233 strike and result in a change in conformations around them. This leads to the breakage of inter-subunit interactions at the dimer interface leading to monomerization.

Heilmann and Jenkins (2013) studied and suggested that the UVR8 monomerization is never *de novo*. Also, redimerization reversal is a complex process and is assisted by numerous factors: occurrence of intact cells, translation due to UV irradiation, and association of UVR8 C-terminal with multiple factors.

10.3.1 DNA Alterations and Damage Repair

UV-B causes harm to DNA by producing two photoproducts, pyrimidine photoproducts (6–4 PP), and, mainly, cyclobutane pyrimidine dimer (CPD). In prokaryotes as well as eukaryotes, the chief repair pathway for CPD and 6–4 PP includes photolyases (Britt 2004). One of the important photolyases being type II photolyase PHR1 can regulate several genes for UV defense as well as damage repair (Brown et al. 2005). On exposure to the wavelength of 350–450 nm, these light-dependent photolyases join with dimers to restore the native DNA by reversal of damage without any error (Jansen et al. 1998).

DNA methylation for gene regulation is known to be a conserved mechanism that can have quintessential roles in transposon silencing, imprinting, development, and environmental responses (Pikaard and Scheid 2014; Schübeler 2015). Jiang et al. (2021) studied that UV-B suppresses DNA methylation through DRM2 and derepresses the dependent reporter genes in UVR8-dependent fashion. UVR8 can

interact with DNA methyltransferase DRM2 within the nucleus, mediated by the ubiquitin-associated (UBA) domains of DRM2. UVR8 impedes DRM2 chromatin association and catalytic activity. Taken together, UVR8 is a negative regulator of DRM2 to begin a mechanistic assembly between light signaling and DNA methylation in plants.

10.3.2 Plant Defense

Sinapate is a precursor for syringyl-type lignin synthesis and helps in cell wall synthesis as well as is capable of preventing fungal hyphae penetration within the plant cell (Kishimoto et al. 2006; Quentin et al. 2009; Lloyd et al. 2011). It is suggested that UV-B radiations provide defense against fungal infections in *Arabidopsis*, and it is most likely that this can be due to increased sinapate levels involving UVR-8 in the process (Demkura and Ballaré 2012).

Jasmonic acid (JA) synthesis, as well as signaling genes transcript buildup, takes place, and that is mediated by UVR8 on UV exposure. The responsible JA biosynthesis genes (Allene Oxide Synthase [AOS], Allene Oxide Cyclase 1 [AOC1], AOC3, and Oxophytodienoate Reductase 3) and JA signaling transcription factors (WRKY70, Jasmonate Zim Domain 1 [JAZ1], Syntaxin-Related Protein 1) play a major role (Morales et al. 2013). This indicates that the UVR8 and JA signaling pathways offer pathogen resistance and defense against herbivores (Izaguirre et al. 2003; Demkura et al. 2010; Demkura and Ballaré 2012).

Volatile terpenoids are biosynthesized through the mevalonate and methylerythritol phosphate (MEP) pathways (Schwab et al. 2008). AACT1 HMGR, HMGS, and DXS, PMK, and MVK from either the MVA or MEP pathway are all boosted by light, jasmonic acid, and ethylene (Hemmerlin et al. 2012). Shamala et al. (2020) studied that all these genes except HGMR-2, PMK-1 DXR, and DXS are upregulated by UV exposure indicating the participation of UVR8. Many volatile terpenoids were found to be greater due to UV exposure (Gil et al. 2012; Liu et al. 2017).

10.4 Inhibition of Plant Shade Avoidance and Thermomorphogenesis

Under scarce sunlight due to neighboring vegetation, plants have evolved shade avoidance responses to compete, enhance growth, and acquire light (Fraser et al. 2016). UVR8 is involved in shade avoidance responses with the help of auxin and gibberellins (GAs). UVR8–COP1 interaction upsurge the levels of HY5 and HYH, leading to augmented GA2ox1 (Gibberellin 2 oxidase) transcript. This decreases GA levels while stabilizing DELLA protein (a negative regulator of GA), and suppresses PIFs (Phytochrome Interacting Factor 4 and Phytochrome Interacting Factor 5) (de Lucas et al. 2008; Feng et al. 2008). DELLAs are repressor proteins of growth and inactivate PIF function (Feng et al. 2008). In a parallel HY5/HYH-independent

pathway, photoactivated UVR8 prevents low R:FR-mediated induction of Indole-3-pyruvate monooxygenase genes YUCCA2, YUCCA5, YUCCA8, and YUCCA9 (genes which are involved in auxin biosynthesis and convert indole-3-pyruvic acid (IPA) into indole-3-acetic acid (IAA)) and the auxin-responsive genes IAA29 and GH3.3, so hindering auxin formation. UV-B is responsible for PIF degradation and stabilizes DELLAs to impede the function of PIF (de Lucas et al. 2008). This inhibits PIF from triggering the expression of auxin biosynthesis genes, therefore leading to inhibition of shade avoidance responses (Hayes et al. 2014). UVR8 regulates PIF4 and controls shade avoidance responses as well as thermomorphogenesis (Hayes et al. 2014, 2017). PIF4 is known to be a key positive regulator for thermomorphogenesis response (Koini et al. 2009; Hayes et al. 2017). The UVR8–COP1 complex inhibits PIF4 transcription and also prevents shade-promoting hypocotyl elongation by regulating the protein stability and function of PIF4 and PIF5, which helps in shade avoidance responses (Lorrain et al. 2008). Hayes et al. (2014) suggested that UVR8 activation is linked to PIF degradation. This decreases auxin activity, and further inhibits elongation and leads to suppression of shade avoidance.

UV-B-stabilized HFR1 (LONG HYPOCOTYL IN FAR RED) forms a competitive complex with PIFs to hinder their DNA-binding ability (Hayes et al. 2017; Yin and Ulm 2017). Tavridou et al. (2020) studied that UVR8-mediated inhibition of the COP1 leads to balance HFR1. This suggests that HFR1 is a molecular effector of UVR8 photoreceptor signaling to regulate plant shade avoidance. The stabilized HFR1 inhibits non-degraded PIF4 and PIF5 under UV-B through heterodimer formation and prevents their binding to DNA (Hornitschek et al. 2009), therefore antagonizing the effect of UVR8 on both thermomorphogenesis and shade responses (Hayes et al. 2017; Tavridou et al. 2020).

Moreover, SAS is also inhibited through phytochrome-, cryptochrome-, and UVR8-mediated induction of the bZIP transcription factors HY5 and HYH (Moriconi et al. 2018).

10.4.1 Regulation of Leaf Morphogenesis

UV-B leads to inhibition of leaf growth and shape (Searles et al. 2001). UVR8 is responsible for mediating photomorphogenesis in response to UV-B (Jenkins 2017). Photomorphogenesis is the result of altered gene expression, which is due to signaling events triggered by the perception of UV-B and blue by UVR8 and CRYs, respectively (Jenkins 2017). The epidermis holds a key role in directing leaf growth and shape (Savaldi-Goldstein et al. 2007). Yet, on UV-B exposure, epidermal cell division has been studied to be mostly independent of UVR8.

The regulation of endopolyploidy, which is correlated with increased cell size, entails UVR8 on exposure to UV-B (Wargent et al. 2009). It has been found that UVR8 has a regulatory role in other developmental events. Hence, UVR8 is a key signaling component in regulating important morphogenetic activity in the leaves.

10.4.2 Phototropism

Positive phototropism is a directional growth of plants toward the light, allowing plants to orient the photosynthetic tissues toward the incoming light (Whippo and Hangarter 2006; Preuten et al. 2013; Vandenbussche et al. 2014). Phototropism is important to optimize photosynthesis, increase pollination efficiency, and reproductive success (Serrano et al. 2018). The epidermis plays an important role in UV-B sensing, signaling, and driving a considerable bending response mediated by UVR8. UVR8 is well related to different signaling pathways, including hormonal cascades (Vanhaelewyn et al. 2016). Auxin is a known plant growth promoter that not just causes cell division and cell elongation but also regulates development. It is also noteworthy that auxin works under the control of UVR8 in seedlings (Hayes et al. 2014; Vandenbussche et al. 2014; Fierro et al. 2015).

Phototropism also decides flower position and hence impacts pollination (Serrano et al. 2018). The action spectrum of phototropism was found to be 280–500 nm, indicating the role of UV-A and blue light for the process (Christie and Murphy 2013). Phototropins can perceive not just blue light but also UV-A and UV-B (Briggs and Christie 2002; Guo et al. 2005; Vandenbussche et al. 2014). The UVR8 requires auxin efflux and functional PINOID (PID; Vandenbussche et al. 2014). UVR8 has a leading role in the UV-B-mediated phototropism and controls hormonal pathways, which results in the bending of the stem toward the UV-B. HY5 plays a central role for UV-B-mediated phototropism in seedlings (Vandenbussche et al. 2014), while it was found outmoded with HYH in inflorescence stems. There occurs disparity in the distribution pattern of HY5 and HYH, with high levels found at the irradiated side of stems and extremely low levels at the shaded side of stems (Vanhaelewyn et al. 2019).

10.4.3 Circadian Clock

There exists an inter-relationship between the circadian clock and photomorphogenic UV-B light. Feher et al. (2011) highlighted the involvement of low-intensity, non-damaging UV-B for the light-mediated entrainment of the circadian clock. This involves UVR8 and COP1 in the process, although HY5 and HYH do not contribute. Responsive clock genes that undergo transcriptional activation are needed for UV-B-mediated photomorphogenic circadian rhythm. It is suggested that temporal restriction of low-intensity UV-B responses by the circadian clock is likely to be utilized for saving resources during acclimation and not for increasing stress tolerance. It is noteworthy that, within the roots, red light travels better than blue light to entrain the circadian clock in unexposed tissues (Nimmo 2018).

10.4.4 Flavonoid and Alkaloid Pathways

UVR8 is required for the induction of genes involved in flavonoid and alkaloid pathways (Brown et al. 2005; González Besteiro et al. 2011; Demkura and Ballaré 2012). These genes help in UV protection, the best studied being the UV-B induction of CHS, while other genes help in flavonoid biosynthesis, which have free radical scavenging action, and also work as a sunscreen by absorbing UV radiation (Jenkins et al. 1997). CHS is the first enzyme in the flavonoid biosynthesis pathway. There are distinct phototransduction pathways for UV-B and UV-A/blue light (CRY1) for CHS regulation (Jenkins et al. 1997). Calmodulin antagonist W-7 is responsible for inhibition of UV-B-mediated induction of CHS, but this does not hold true for UV-A/blue light (CRY1) mediated CHS induction (Christie and Jenkins 1996). CHS, FLS, and several other genes belonging to distinct pathways are target genes for HY5 that undergo upregulation by UV-B. Moreover, UV-B leads to stabilization and transcriptional induction of HY5 (Oravecz et al. 2006; Huang et al. 2013). Radiation-mediated responses, including gene expression and phenolics biosynthesis, can get triggered within a few minutes to a few hours (Morales et al. 2013). However, accumulation is dependent on turnover rate, which is slower for phenolics than for gene transcripts.

On UV-B exposure, UVR8 leads to alterations in the concentrations of phenolic compounds in the leaf epidermis and increases the content of epidermal flavonoids (Demkura and Ballaré 2012; Morales et al. 2013). However, the induction of phenolic compounds was mainly done by the blue component of sunlight (Siipola et al. 2015). UV exposure leads to an increased concentration of flavonoid glycosides and hydroxycinnamic acids (HCAs), which are the two chief groups of phenolic compounds with UV-B absorbing features (Burchard et al. 2000). Moreover, UVR8 is a positive regulator of the UV-B induction of kaempferol-3-glucoside, quercetin, and quercetin-3-glucoside (Morales et al. 2013).

Vanhaelewyn et al. (2019) suggested that UV-B irradiation can penetrate the endodermis and pith of the stem, hence reaching radial cell layers where the UVR8 signal induces flavonoid accumulation. Additionally, the UVR8- dependent flavonoid accumulation is a tissue-independent process, indicating that flavonoid synthesis occurs locally (Buer et al. 2007). Intriguingly, genes for flavonoid biosynthesis overlap with the genes responsible for light signaling as well as abiotic stresses (Vandenbussche et al. 2018; Georgii et al. 2017). Also, UVR8–COP1 can regulate some transcriptional factors, like R2R3-MYB, bHLH, and WD40 (MBW ternary complexes), which further regulate multiple enzymatic processes involved in flavonoid biosynthesis (Mano et al. 2007; Zhao et al. 2013; Shamala et al. 2020).

10.4.5 Protection from Photoinhibition and Photooxidative Stress

Oxidative stress triggers the synthesis of antioxidants, like vitamins C and E, carotenoids, and glutathione (Chen and Xiong 2005). Pyridoxine (vitamin B6) is an essential antioxidant which helps in UV-B protection (Brosché et al. 2002; Ulm

et al. 2004a, b; Kalbina et al. 2008; Ristilä et al. 2011) and makes use of two proteins for its biosynthesis—Pyridoxine Biosynthesis 1 (PDX1) and PDX2. Ristilä et al. (2011) studied that UV-B exposure to *Arabidopsis thaliana* leaves leads to the accumulation of PDX1 and vitamin B6. However, at a low fluence, UV-B can regulate PDX1.3 (homolog of PDX1) transcripts.

ELIPs (Early Light Inducible Proteins), the thylakoid proteins, are encoded by light-responsive nuclear genes and lead to tolerance to photoinhibition and photooxidative stress (Adamska et al. 2001). Brown and Jenkins (2008) proposed that the expression of ELIP1 can be controlled by the HY5 and, therefore, it is regulated by the UVR8-dependent UV-B signaling pathway.

10.4.6 Other Pathways

Photosynthetic competence is modulated by UVR8 by regulating the expression of genes, like chloroplastic proteins (SIG5 and ELIP1), in UV-B-dependent manner (Davey et al. 2012). Among them, SIG5 encoding the plastid RNA polymerase sigma factor regulates PsbD (a transcript of PsbD-BLR-P encoding the PSII D2 proteins) (Kanamaru and Tanaka 2004; Brown and Jenkins 2008).

Gibberellins play an important role in enhancing germination and flowering. Also, they promote growth by deactivating growth inhibitor DELLA proteins (Hauvermale et al. 2012). GA2 oxidases regulate the levels of bioactive GA in *Arabidopsis* by inactivating GA by hydroxylation. GA2 oxidases are target genes for HY5, and hence, UV-B reduces GA levels as well as growth (Ulm et al. 2004a, b; Weller et al. 2009; Hayes et al. 2014). The UVR8-mediated upregulation of the GA signal inhibits DELLA proteins at the irradiated side of the endodermis and cortex. This overlaps with this zone of activity and hence shows a direct control of growth by light.

Increased exposure is not just taken in the context of light capture and photosynthesis but also taken as maximized flower visibility and increased inflorescence temperature, which is considered to be significant factors for plant–pollinator interactions (Serrano et al. 2018). Exposure to UV-B can induce the synthesis of floral volatiles for attracting pollinators (Falara et al. 2013; Amarasinghe et al. 2015) and flavonoid-derived pigments for determining flower color (Khoo et al. 2017; Serrano et al. 2018).

Davey et al. (2012) studied substantial photoinhibition in UVR8, demonstrating that PSII is comparatively more sensitive to UV-B-induced damage. Even low doses of UV-B can also be deleterious for photosynthetic machinery. The defense is offered through UVR8-regulated gene expression. It can be done directly via induction of chloroplastic proteins and indirectly via regulating the phenylpropanoid and other secondary metabolites pathway, photomorphogenesis, and DNA repair. Therefore, UVR8 has a chief role in plant acclimation and distinct responses to UV-B.

Moreover, Raipuria et al. (2021) studied Static Magnetic Field-stimulated tolerance toward UV-B stress during early seedling growth and indicated that nitric oxide could be an important signaling molecule. Also, NOS initiates SMF-triggered NO production in soybean seedlings on exposure to UV-B.

10.5 Conclusion

UV exposure to plants poses several effects on plant growth, development, reproduction, defense, flowering, senescence, and overall metabolism. These effects involve the role of an important photoreceptor called as UVR8. This photoreceptor is a β- propeller protein, which resides in the cytoplasm in its homodimer state. On UV exposure, it monomerizes and moves to the nucleus for various signaling cascades. UVR8 allies with different factors, like COP1, RUP1, RUP2, CRYs, MYB, HY5, HYH, and BES1/BIM1 to give several responses, like photomorphogenesis, circadian rhythms, defense mechanism, flavonoid synthesis, regulation of root growth, flowering induction, and many more. To give the effects, there occur distinct signaling pathways which have been studied very extensively so far, but there are still several areas to explore the detailed mechanism of action.

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Acclimation of Photosynthetic Apparatus to UV-B Radiation

11

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Abstract

The effects of UV-B radiation on photosynthesis and photosynthetic apparatus of higher plants are reviewed. In addition to the regulatory role, the UV-B represents an important stress agent. Results of numerous studies demonstrate the adverse effects of UV-B on different plant structures and components, including those essential for the photosynthetic processes. The plant species and genotypes differ in responses and susceptibility to UV-B stress, highlighting the role and importance of acclimation processes and protective mechanisms, including creating the efficient UV screen in plant epidermis and dynamic regulation of photosynthetic processes toward efficient photoprotection. Presented results demonstrate that the rapid, non-invasive, chlorophyll fluorescence-based methods may provide valuable information on the actual functional state of photosynthetic apparatus related to the processes of light energy conversion in the chloroplast, including monitoring of the UV-sensitive sites of the photosynthetic system. In addition to the damages, the acclimation processes to UV-B can be investigated. The prospects for future applications in crop breeding are proposed. In addition to UV-B crop resistance, the nutritional and health benefits of UV-B-induced accumulation of

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UV-absorbing compounds are discussed, with possible role of screening techniques in fresh vegetables and fruits improvement.

Keywords

UV-B radiation · Stress · Non-invasive methods · Photosynthesis · Chlorophyll fluorescence

11.1 Introduction

Plants are exposed to a very complex light environment characterized by large fluctuations of intensity and spectral characteristics of incident solar radiation. Even though ultraviolet (UV) radiation represents only a marginal fraction of solar radiation on the Earth's surface, contributing by 6% in a case of UV-A (315–400 nm) and less than 0.5% in case of UV-B (280–315 nm) (Favory et al. 2009), the biological effects of the UV, especially of UV-B spectra on the biosphere, are significant, as this fraction of spectra represents an important environmental stressor for photosynthetic organisms (Caldwell et al. 2007).

In similar to visible light, UV intensity is very variable and fluctuating, depending enormously on geographic position, especially the latitude and altitude of the location. As a consequence of ozone depletion, UV levels have increased (Seckmeyer et al. 2008), with adverse effects for all kinds of living organisms, including plants (Vincent and Roy 1993; Ivanov et al. 2000; Herman 2010; Kataria et al. 2014).

Besides, the intensity of UV-B fluctuates over shorter time frames (diurnal or seasonal), following the natural rhythms in solar angles over a year or day, as well as the intra-seasonal fluctuations in the ozone layer (Madronich et al. 2011; Bais et al. 2015). The cycles of UV radiation are commonly disrupted by cloudy weather and plant cover, also generating erratic and unpredictable periodic sunflecks in the understory (Thiel et al. 1996; Heisler et al. 2003; Lopez et al. 2009; Aphalo 2017).

The leaves produced in low PAR environments, such as those in deep shade in canopies or understory environments or glasshouses, are exposed and acclimated to low UV levels (Pollastrini et al. 2011; Barnes et al. 2013). When these plants are exposed to high UV-B levels (e.g., vegetable crops propagated in glasshouses and transplanted to the field), the significant injury of photosynthetic apparatus by UV-B radiation may occur (Wargent 2017), which documents the importance of UV protection and acclimation for plants in a natural environment exposed to a significant intensity and fluctuations of UV radiation. In this chapter, we focused on the main biological effects of UV radiation, especially of UV-B fraction, on the photosynthetic apparatus of plant and crop species and the mechanisms by which plants acclimate to high UV-B levels.

11.2 General Effects of UV-B Radiation on Plants

11.2.1 UV-B as a Regulatory Factor

The effects of UV-B radiation are highly dependent on plant species, the doses of the radiation, and the acclimation level of the plants. Although the UV-B is studied mainly as a stress factor, UV-B plays a significant role in regulating the growth, development, and abiotic/biotic interactions of the plants (Llorens et al. 2020). UV-B radiation can act as a stress-inducing agent or a developmental cue, depending on its intensity and duration of exposure (Yin and Ulm 2017; Yadav et al. 2020). Besides being the source of energy in photosynthesis, light is an important signal regulating plant growth and development. Plants perceive light signals through several protein photoreceptors: phytochromes sensitive to red and far-red light (600–750 nm), cryptochromes, phototropins (and Zeitlupe proteins for blue and UV-A radiation (315–500 nm), and UV Resistance Locus 8 (UVR8) for sensing the UV-B radiation (Jiao et al. 2007; Heijde and Ulm 2012; Tossi et al. 2019). There is strong evidence that UV-B is an environmental regulator controlling gene expression, cellular and metabolic activities, and also the growth and development (Jenkins 2009), and multiple UV-B signaling pathways associated with UVR8 were observed in plants (Wu et al. 2012; Christie et al. 2012; Srivastava et al. 2014). Plants perceive the UV-B signal, leading to modulated growth, development, and metabolism in plant organs. Lower doses of UV-B support the plants by triggering the photomorphogenic responses, for example, downregulation of unnecessary stem elongation, cotyledon expansion, and opening of stomata (Kim et al. 1998; Ulm and Nagy 2005; Jenkins 2009). The most discussed UVR8-dependent responses, including are UV-B-induced photomorphogenesis and the accumulation of UV-B-absorbing flavonols (Tilbrook et al. 2013). The UVR8-mediated pathways are crucial for UV acclimation and plant tolerance (Ballaré et al. 2011; Mannuss et al. 2012; Wargent and Jordan 2013).

In addition to photoprotective responses, UV-B can mitigate the adverse effects of other stresses. The positive effects of UV-B pretreatment on drought tolerance were associated with a higher photosynthetic rate, biomass accumulation, and leaf water content (Manetas et al. 1997; Schmidt et al. 2000; Poulson et al. 2006), as well as enhanced antioxidative capacity of plant tissues under drought (Mátai et al. 2019).

11.2.2 UV-B as a Stress Agent

Besides the regulatory effects, the UV-B is most frequently reported as a stress agent negatively influencing wild and agricultural plants, with direct effects on food supply (Piri et al. 2011; Zuk-Golaszewska et al. 2003). The main reason for the harmful effects is the high energy of short wavelengths leading to initiations of photochemical reactions, including production of reactive oxygen species (ROS), such as superoxide ($O_2^{\bullet -}$) and hydroxyl radicals (•OH), but also hydrogen peroxide (H_2O_2) and singlet oxygen. These ROS can cause oxidative damage to membrane

lipids, nucleic acids, and proteins even at low fluence rates (Hideg and Vass 1996; Jansen et al. 1998; Hideg et al. 2002; Brosche and Strid 2003; Hideg et al. 2013; Hideg and Vass 1996; Foyer et al. 1997). In addition, UV radiation is photochemically absorbed by not only biologically significant molecules, such as nucleic acids, proteins, and lipids, but also carotenoids, porphyrins, and quinones, leading to disruption of the integrity and function of essential macromolecules (DNA, proteins, and lipids), and related deleterious effects at the sub-cellular level (Harm 1980; Zu et al. 2010; Czégény et al. 2016; Strid and Hideg 2017).

Ultraviolet irradiation leads to several biological effects, such as reduction in the cell mitosis and chromosome aberration, and, of course, cell death (Yannarelli et al. 2006; Liu et al. 2015). Crucial effects of UV-B are related to photosynthetic processes, which are summarized in the following sections.

11.3 The Effects of UV-B Radiation on Plant Photosynthesis

Although the UV-B radiation affects multiple physiological processes in plants, the photosynthetic apparatus use to be indicated as the main action target of UV-B (Lidon et al. 2012), and the inhibition of photosynthetic processes are predominantly responsible for UV-B-induced reductions in the biomass of crop plants (Agrawal et al. 2004; Kataria et al. 2012; Kataria et al. 2014).

The downregulation of photosynthesis due to UV-B was observed in *Arabidopsis thaliana* (Coffey and Jansen 2019; Khudyakova et al. 2019; Schultze and Bilger 2019), blueberry (González-Villagra et al. 2020), grapevine (Doupis et al. 2016), sugar beet (Karvansara and Razavi 2019), and soybean (Choudhary and Agrawal 2015), eggplant (Romanatti et al. 2019), pea (Nogues and Baker 1995), cotton (Zhao et al. 2004), and oilseed rape (Allen et al. 1997).

The effects are partly differing depending on the way of examination. UV-B can reduce the CO_2 assimilation rate to one-third of the original in experiments with supplementing UV-B (Bornman and Teramura 1993; Kakani et al. 2003; Lu et al. 2009; Kotilainen et al. 2011; Ranjbarfordoei et al. 2011; Lidon et al. 2012). However, a significant decrease in photosynthesis was also observed in more realistic UV-B exclusion studies (Ruhland et al. 2005; Albert et al. 2011; Berli and Bottini 2013; Gitz et al. 2013). On the other hand, the adverse effects of the natural fluence rates of UV-B radiation on well-acclimated plants of some species were found to be relatively low (Searles et al. 2001; Valkama et al. 2003; Ballaré et al. 2011; Hideg et al. 2013; Comont et al. 2013; Müller et al. 2013a, b; Vidović et al. 2015). The reported variability of the reported results highlights the importance of adaptation and acclimation of plants to UV-B and provides evidence on efficient mechanisms by which some species can resist high doses of UV-B. In the next sub-chapters, we will review the partial effects on different levels of photosynthetic apparatus.

11.4 The Effects on Plant Leaf Area and Leaf Anatomy

The overall photosynthetic performance depends not only on the photosynthetic rate but also on the overall leaf area and canopy structure, which may significantly influence the biomass production and yield of crops. Thus, the regulatory and inhibitory effects leading to reduction of leaf area, plant height, and related growth traits are highly relevant for crop productivity (Gerhardt et al. 2005; Vyšniauskienė and Rančelienė 2014). For example, in cotton plants (*Gossypium hirsutum* L.) exposed to elevated UV-B radiation (up to 10% higher dose of UV-B), the reductions of height (−14%), leaf area (−29%), and total biomass (−34%) were observed when compared with the plants grown under natural conditions (Gao et al. 2003). Reduced growth of leaf area was also observed in *Triticum aestivum* (Kataria and Guruprasad 2015), *Vigna mungo*, *V. radiata*, and *Glycine max* (Mazza et al. 1999; Amudha et al. 2005; Guruprasad et al. 2007), Amaranthus tricolor (Kataria and Guruprasad 2015), and Oryza sativa (Teramura et al. 1991). That leads to alterations in the canopy morphology that were described by different authors (Barnes et al. 1990; Ryel et al. 1990).

Additional effects are related to UV-exposed leaf anatomy and morphology changes, which also influence the photosynthetic functions. The characteristic visual symptoms are the changes in the thickness of epidermal, palisade, and mesophyll layers of leaves (Kakani et al. 2003). Palisade parenchyma being the first barrier against UV-B radiation is getting thicker and more compressed, thus decreasing the adverse UV-B effects on cells of spongy parenchyma, which are crucial for CO_2 assimilation processes (Romanatti et al. 2019).

In addition to UV-B-induced upregulation of leaf thickness (Bornman and Vogelman 1991; Nagel et al. 1998), multiple anatomical and morphological changes were observed, such as a higher density of trichomes on the leaf surface (Barnes et al. 1996) or a decrease in diameter and number of xylem tubes (Lingakumar and Kulandaivelu 1993). Whereas necrosis and reductions of growth may be considered as the direct negative effects of UV-B, the alterations in morphological and anatomical traits represent the first level of acclimation of the photosynthetic apparatus ensuring plant survival, but with possible adverse effects on the photosynthetic capacity of plants and canopies.

11.5 The Effects on Stomata Functions

The stomata closure is responsible for a substantial part of photosynthetic limitation in various stress conditions (Zhao et al. 2004; Zivcak et al. 2013). However, in the case of UV-B stress, the information on the importance of stomatal closure is controversial. Most frequently, UV-B radiations were shown to have adverse effects on stomatal movements (Eisinger et al. 2003; He et al. 2013). The detrimental effects on CO_2 assimilation were particularly severe when combining UV-B stress with other stresses, such as drought or low nutrient stress (Musil and Wand 1994; Nogues et al. 1998; Tian and Lei 2007; Lu et al. 2009; Arroniz-Crespo et al. 2011; Doupis

et al. 2016). On the other hand, the cross-tolerance observed at the stomata closure level was demonstrated when UV-B was combined with high-temperature stress (Ibrahim et al. 2013). In woody plants, the long-term increase of UV-B radiation influenced stomatal closure and the stomatal density, both contributing to changes in canopy transpiration and water use efficiency (WUE) (Keiller and Holmes 2001).

The effects of UV-B on stomata opening strongly depend on doses. At the same time, the low UV-B stimulate stomatal opening, but high levels of UV-B lead to stomata closure (Eisinger et al. 2003; Tossi et al. 2014), with adverse effects on CO_2 assimilation rate (Jansen and Noort 2000; Lu et al. 2009; Reddy et al. 2013).

The stomata on the adaxial part are more sensitive to UV-B than the guard cells located on the abaxial side of the leaf (Nogues et al. 1999). Whereas decreased stomatal conductance represents a typical stress response, the decrease in stomatal density and changes in the distribution of stomata on the leaf surface represent typical acclimation response (Gitz et al. 2013).

11.6 The Effects of UV-B on Chlorophyll and Carotenoid Content

The effects of UV-B radiation are highly dependent on UV-B doses, plant species, and plant acclimation level. Pigment degradation (chlorophylls and carotenoids) and thylakoid disruption were described as typical symptoms of UV-B stress (Strid and Porra 1992; Gaberscik et al. 2002; Kataria et al. 2013; Leon-Felix 2017; Chen et al. 2019). A UV-induced loss of chlorophyll a, b, and total chlorophyll was found in numerous plant species, such as *Zea mays*, *Hordeum vulgare* (Tevini et al. 1981), *Pisum sativum* (Vu et al. 1982, 1983), *Amygdalus dulcis* (Ranjbarfordoei et al. 2011), and *Capsicum annum* (Hoffmann et al. 2015).

Severe damage of assimilation apparatus associated with the chlorophyll breakdown and the decline of biochemical and physiological indicators was observed in *Triticum durum* exposed to UV-A, UV-B, and UV-C radiations. In addition to chlorophylls, the other pigments, such as carotenoids, flavonoids, and anthocyanins, were negatively influenced, and the proline concentration decreased due to excessive values of UV (Balouchi et al. 2009).

Based on the study of Marwood and Greenberg (1996), chlorophyll *a* tends to be more affected by the UV-induced damage than chlorophyll *b*. In similar, Zhang and Chen (2013) showed a lover chlorophyll a/b ratio in *Oryza sativa* exposed to UV-B treatment, supporting the predominant reduction of chlorophyll a.

Carotenoids were shown to be less affected by UV-B treatment than chlorophylls (Pfundel et al. 1992; Sharma et al. 1998; León-Chan et al. 2017). It may be associated with the fact that carotenoids are considered directly associated with the photoprotection of photosynthetic function under UV-B (Middleton and Teramura 1993). However, some studies also reported a significant decrease in some plant species (Muzafarov et al. 1995; Cicek et al. 2012; Hoffmann et al. 2015), and reduction in carotenoids could have a serious impact on pigments (Agrawal and Rathore 2007; Mishra et al. 2003).

Some authors associated the reductions in photosynthetic pigments with the loss of photosynthetic yield (Jordan et al. 1994). However, the effects on photosynthetic functions seem to be the more probable reason for the decrease in photosynthesis than a simple decrease of photosynthetic absorption due to a decrease in photosynthetic pigment concentrations.

11.6.1 The Effects of UV-B on Thylakoid Membrane Complexes

The damaging effects of UV-B on the chloroplast level are associated with a lower chloroplast number and changes in chloroplast ultrastructure (Fagerberg and Bornman 2005; Holzinger et al. 2004). UV-B causes disintegration of the envelope around chloroplasts (He et al. 1994), as well as dilation of thylakoid membranes (He et al. 1994), resulting in leakage of the membrane, which increases ion permeability (Doughty and Hope 1973; Vass et al. 2005). The thylakoid membrane is the main target of UV-B radiation, leading to reduced functioning and alterations in the membrane organization (Petroluleas 2002). Structural and functional effects of UV-B have been predominantly observed at the level of chloroplast structures, especially at the level of thylakoid membranes (Lidon et al. 2012).

11.6.1.1 The Effects of UV-B on PSII Reaction Centers and Oxygen-Evolving Complex

The PSII reaction centers contain the main proteins D1 and D2, which can be damaged by light, but, under normal conditions in light, the repair and synthesis of these proteins, especially of D1, are fast enough to keep the degradation and synthesis in equilibrium. However, under UV-B exposure, their degradation rate of D1 and D2 is fast (Greenberg et al. 1989; Trebst and Depka 1990; Melis et al. 1992; Jansen et al. 1993; Barbato et al. 1995; Friso et al. 1995; Spetea et al. 1996; Vass 1997; Jansen et al. 1998; Kataria et al. 2014; Faseela and Puthur 2018), which disturbs the equilibrium (Friso et al. 1994; Savitch et al. 2001; Vass et al. 2005; Lidon et al. 2012). During photosynthetic electron transport driven by light, tri-molecular oxygen is produced continuously in OEC, producing superoxide radical ($O_2^{\bullet -}$), hydroxyl radical (•OH), and hydrogen peroxide (H_2O_2) (Apel and Hirt 2004). The damage to D1 and D2 proteins can also induce the semiquinone radicals induced by UV (Brosche and Strid 2003; Zvezdanovic et al. 2013). The inactivation of PSII reaction center and specifically oxygen-evolving complex are vital for the decrease of PSII quantum efficiency, leading to a significant decrease of oxygen evolution in UV-B conditions (Renger et al. 1986; Renger et al. 1989; Bornman 1989; Barbato et al. 1995; Jordan 1996; Segui et al. 2000; Vass 2012). The damage of D1 protein by UV-B seems to be located close to the lumenal end or in the middle of the second transmembrane helix (Friso et al. 1993), which may affect catalysis of water oxidation in OEC (Svensson et al. 1990; Kamiya and Shen 2003). Overreduction of Q_A leads to significant damage of D2 protein (Friso et al. 1994; Jansen et al. 1996). However, the damage of D2 protein in conditions of elevated UV-B has not been observed to the extent typical for D1 protein (Friso et al.

1994). In addition to faster damage, UV-B was shown to downregulate the turnover of D1 and D2 proteins (Jordan 1996; Wong et al. 2015).

Nevertheless, other components of the electron transport chain are sensitive to UV-B, as well. For example, the UV-B-mediated impairment of 43 and 47 kDa pigment-protein complexes associated with PSII was clearly demonstrated (Gupta et al. 2008). In addition, changes in quinone binding sites caused by UV were observed (Renger et al. 1989), especially the sensitivity of the Q_B binding site of the electron transport chain between PSII and PSI (Bornman 1989; Jordan 1996; Cai et al. 2016). The acceptor side of PSII may be affected by UV radiation also via the direct damage of molecules of plastoquinone (PQ) electron carriers (Bornman and Teramura 1993).

Analyses of the UV-B effects on PSII membrane fragments demonstrated that the donor side of PSII, the oxygen-evolving system, is one of the major and primary targets of UV-B damage (Renger et al. 1989; Hideg et al. 1993; Vass 1997; Lidon and Ramalho 2011). The resistance of the reaction center of purple bacteria lacking the water-oxidizing complex to UV-B confirms the major contribution of OEC damage in the inactivation of PSII reaction centers (Tandori et al. 1996). Although the exact mechanism of OEC inactivation by UV-B is not fully clear, it was found that the tetra-nuclear Mn complex of OEC is the primary site of the adverse effects (Hideg et al. 1993; Vass 1997; Szilard et al. 2007).

11.6.1.2 The Effects of UV-B on Light-Harvesting Complexes

The light-harvesting complex of PSII (LCH II) is essential to absorb the incident light and transfer the energy to the PSII reaction center. It also influences the organization of thylakoids. The light-harvesting complex of PSII (LCH II) may be adversely affected by UV-B stress associated with changes in the composition of binding proteins. This effect can be ascribed to a decrease of the transcriptional level of cab genes (Vass et al. 2005) and disconnection of LHC II from PSII, which significantly modifies LHC II function (Lidon et al. 2012; Ashraf and Harris 2013). The damage of the light-harvesting complex of PSII (LCH II) is associated with a reduction of chlorophyll a/b ratio in binding proteins. Whereas chlorophyll *a* occurs in the core complex of both photosystems (PSI and PSII), chlorophyll *b* is located in their antenna systems (more in PSI). Thus, the decrease of chlorophyll a to b ratio demonstrates a higher UV-B susceptibility of the core complex compared to the peripheral antenna complexes (Zhang and Chen 2013).

11.6.1.3 The Effects of UV-B on Photosystem I and Cytochrome b6/f

Variability in the effects of UV-B irradiation on photosystem I has been observed, and many studies report only minor or no effects on PSI (Brandle et al. 1977; Kulandaivelu and Noorudeen 1983; Iwanzik et al. 1983; Turcsanyi and Vass 2000). The reason for the lower susceptibility of PSI compared to PSII can be not only the absence of a water-splitting complex in PSI but also the lack of redox-active tyrosine (Hansson and Wydrzynski 1990; Yadav et al. 2017). A slight decline in PSI activity was observed as an acclimation response associated with adjusting the PSI/PSII ratio after UV-B-induced damage of PSII occurred (Yadav et al. 2017).

In high UV-B conditions, the destruction of PSI reaction centers was observed, which was reflected by the decrease of fraction of oxidizable reaction centers of PSI (lower $P700^+$), indicated by lower amplitude of absorption change at 700 nm. Alternatively, this effect was demonstrated by the analyses of OJIP transient, indicating a decrease of the amplitude of the I–P phase (ΔV_{IP}), which was shown to be sensitive to UV-B radiation (Çiçek et al. 2020).

In similar to photosystem I, cytochrome b6/f complex is considered as relatively resistant to UV-B (Bornman et al. 1984; Teramura and Ziska 1996; Biswal et al. 1997; Mishra et al. 2008; Lidon et al. 2012), and recent studies pay minimum attention to cytochrome b6/f activity associated with UV-B stress.

11.6.1.4 The Effects of UV-B on Photosynthetic Enzymes

UV-B radiation has significant adverse effects on the activity as well as the content of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) in plants (Vu et al. 1982; Correia et al. 1998; Takeuchi et al. 2002; Savitch et al. 2001; Fedina et al. 2010; Kataria et al. 2013, 2019; Kataria and Guruprasad 2015). The most abundant leaf protein in plants, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.1.39), was found to be sensitive to UV-B damage. The Rubisco protein contains the aromatic amino acids absorbing the UV-B band efficiently and, hence, it represents a typical target of direct physical impairment of the peptide structures (Yu et al. 2013). The alterations of the molecular chain and UV-induced degradation result in Rubisco inactivation and an overall decrease of photosynthetic activity. The reactive oxygen species present in the chloroplast in UV-B conditions may cause division of the larger Rubisco subunit into two polypeptides (Takeuchi et al. 2002; Bouchard et al. 2008; Singh et al. 2017).

An indirect reason for the Rubisco decrease in UV-B stress conditions may be the expression of senescence-associated genes (SAGs), namely, SAG12, as observed in *Arabidopsis sp*. They serve as encoders of cysteine protease, an enzyme responsible for the upregulation of Rubisco degradation (John et al. 2001).

In conditions of elevated UV radiation, the decline in Rubisco activity correlates with lowering the mRNA level of Rubisco subunits. Diminution is also observed in photosynthetic genes' expressions (Mackerness et al. 1997; Casati and Walbot 2003; Lv et al. 2021). On the other hand, the UV-B activates the genes encoding antioxidative protection (Strid et al. 1994; Singh et al. 2017).

In addition to Rubisco, the following steps of the Calvin cycle, including the stage of RuBP regeneration, were inhibited by excessive UV-B radiation (Allen et al. 1998). Adverse effects on malic dehydrogenase (MDH), phosphoenolpyruvate carboxylase (PEPC), and chlorophyllase were also observed (Kataria et al. 2019). The studies also indicate other enzymes, such as RuBP and sedoheptulose 1,7-bisphosphatase, which are degraded or downregulated by UV-B (Savitch et al. 2001; Lee et al. 2014). A reduction in photosynthetic under UV-B radiation was attributed to the decline of sucrose biosynthesis, regeneration rate of RuBP, and consumption of triose phosphate. Reduced activities were also observed in catalase and nitrate reductase (Kataria and Guruprasad 2015). In turn, the activity of nitrate reductase was stimulated in leaves of wheat, barley, and common bean grown in

experiments, in which the UV-B was excluded (Pal et al. 2006; Moussa and Khodary 2008). In addition to nitrate reductase, the UV-B was found to affect also nitrogen metabolism by inhibiting nitrogenase activity (Dohler et al. 1987).

The chloroplast ATP synthase belongs to the group of components the thylakoid membrane impaired by UV-B radiation. Both reduction of amount (Murphy et al. 1985) and activity of ATP synthase (Zhang et al. 1994; Lee et al. 2014) were reported in response to UV-B irradiation. Analogical results were obtained when the expression level of ATP synthase subunits was investigated (Wang et al. 2015).

11.6.2 Effects of UV-B Radiation on Photosynthetic Apparatus Measured by the Non-invasive Techniques

UV-B exposure of plants influences the emission of chlorophyll fluorescence signals originating from the photosystems and related antenna complexes in thylakoids. As in the case of other stresses, the UV-B-induced photoinhibition of PSII can be indicated according to the values of effective quantum yield ($\Delta F/Fm'$) measured in light-adapted samples (Gómez et al. 1998; Fabón et al. 2012; Inostroza-Blancheteau et al. 2016) or maximum quantum yield of PSII photochemistry (Fv/Fm) measured in dark-adapted samples (Ziska et al. 1993; Šprtová et al. 2000; Ranjbarfordoei et al. 2011; Li et al. 2012; Yoon et al. 2020; Mosadegh et al. 2021). In addition, the UV-induced changes of parameters, such as increase of basal fluorescence(F_0) or decrease variable fluorescence (F_v), were also reported, indicating adverse effects on PSII photochemistry, in addition to the decrease of photosynthetic rate and chlorophyll content upon UV-B exposure (Ranjbarfordoei et al. 2011). The application of modulated fluorescence technique was found to be very efficient in UV-B studies (Tevini et al. 1988; van Rensen et al. 2007; Kalaji et al. 2017) as this method enables to analyze the mechanistic aspects of the regulation of electron transport in stress conditions, applying various protocols and parameters (Brestic and Zivcak 2013; Kalaji et al. 2014). For example, applying this method, van Rensen et al. (2007) indicated a decrease in photosystem II efficiency with increasing intensity and the length of UV-B exposure. Studies of photoprotective responses indicated an increase of NPQ parameter (Li et al. 2011; Liu et al. 2012), representing an acclimating response. On the other hand, exclusion of UV-B may also lead to NPQ rise (Láposi et al. 2009), which may be well explained by an increase of the proton motive force due to enhanced ATP synthase activity.

Despite numerous advantages of modulated fluorescence technique, the measurements are time consuming, which limits its use in screening experiments (Brestic and Zivcak 2013; Kalaji et al. 2017). Therefore, an alternative fluorescence technique represented by the analyses of fast chlorophyll *a* fluorescence transient was proposed (Strasser et al. 1995), which sensitively reflects the damage or modifications in PSII photochemistry. The analysis is based on recordings of polyphasic curves of florescence rise during 1 s light pulse, showing visual changes due to UV-B stress (Fig. 11.1).

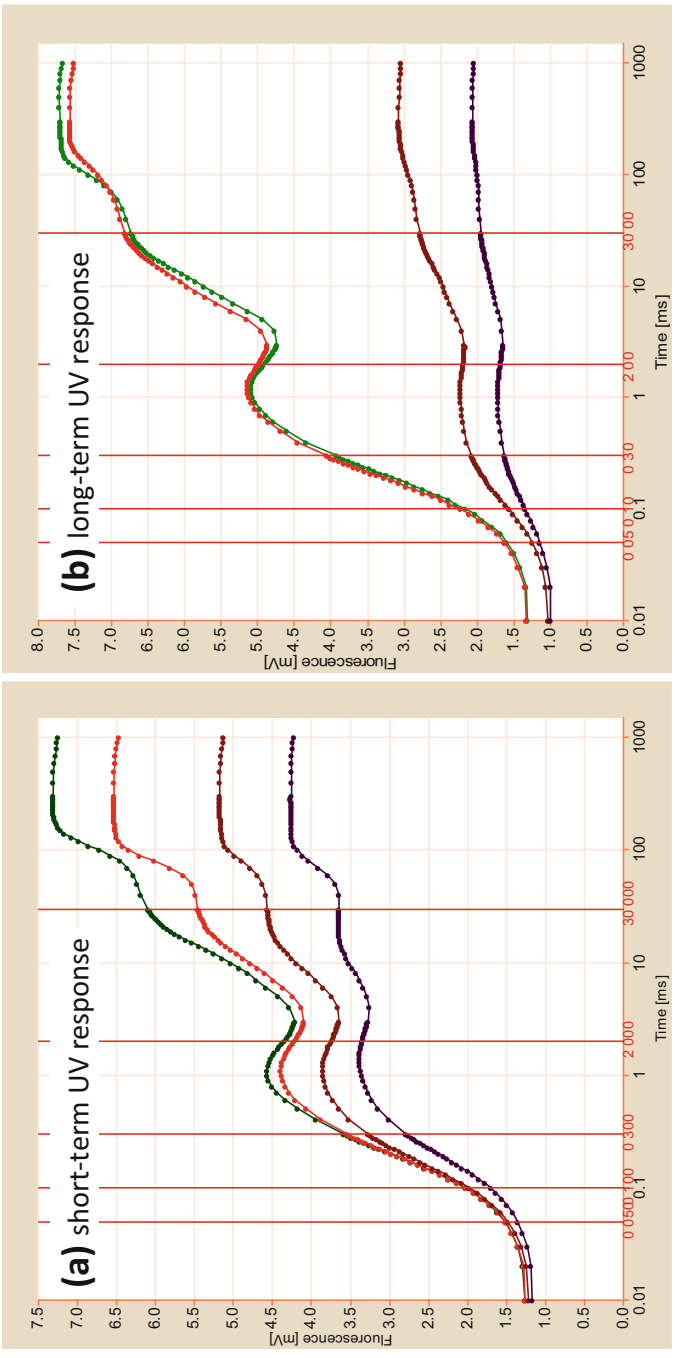

Fig. 11.1 OJIP transient measured in control variant without UV (green), moderate UV (red), high UV (brown), and very high UV (purple). The figure left shows the short-term response (day 1, after 4 h of UV exposure); the figure right shows the long-term effects (after 7 days of treatments). The fluorescence curves were processed and visualized using the Biolyzer Software (version 3.06, R. Rodriguez R. Strasser, University of Geneva, Switzerland). Unpublished data by the authors

The functional changes may be estimated based on proportional changes of variable fluorescence values in particular time threshold levels (O, K, J, I, P steps), as shown in Fig. 11.2.

The numerical analyses of fast chlorophyll kinetics using the model of Strasser et al. (2004) identified the decrease in the number of active reaction centers (Essemine et al. 2012; Mathur and Jajoo 2015), decrease in efficiency of energy trapping per reaction center (TRo/RC) (Albert et al. 2011), the efficiency of light absorption (Yamane et al. 2000; Hollosy 2002; Yu et al. 2013), decrease of quantum efficiency of PSII photochemistry (Guo et al. 2005; Guidi et al. 2007), and inhibition of the electron transfer at the PSII acceptor side (Lidon et al. 2012; Yu et al. 2013; Mathur and Jajoo 2015).

Wang et al. (2010) observed significant inhibition in CO_2 assimilation rate and the contents of chlorophyll and carotenoids. The chlorophyll fluorescence indices, such as quantum yield of primary photochemistry (Φ_{Po}), electron transport (Φ_{Eo}), and efficiency per trapped excitation (Ψo), declined in conditions of a high UV-B. In parallel, the number of active reaction centers of PSII per functional cross-section (RC/CS) and per absorbed light unit (RC/ABS) changed significantly, as well. It indicates that the photosynthetic function at the level of CO_2 assimilation and PSII photochemistry was impaired under the high irradiance of UV-B (Wang et al. 2010).

UV-B causes a reduction in quantum yields and electron transport at both donor and acceptor sides of photosystems, resulting in a decrease of the performance indices, indicating UV-B effects at different levels on the photosynthetic functionality of plants (Çiçek et al. 2020). The values of parameters characterizing the redox state of the PSII acceptor site and the presence of closed reaction centers indicate the transformation of PSII reaction centers into dissipative sinks for excitation energy in the condition of elevated UV radiation (Pan et al. 2011).

The study of Mathur and Jajoo (2015) demonstrated in plants drastically affected by elevated UV radiation the inactivation of oxygen-evolving complex, functional disconnection of light-harvesting complexes from PSII core, and increase of the fraction of inactive reaction centers, all of them contributing to declining of electron transport process indicated by the specific parameters (e.g., ET_0/CS).

In all published studies, the observed effects are dependent on UV-B intensity and the length of the treatment. The interaction of these two factors is demonstrated by the leaf models based on the analysis of OJIP transient chlorophyll fluorescence measured in lettuce leaves cultivated in a growth chamber with supplemental UV-B radiation (Fig. 11.3).

The results indicate that whereas the short-term response is associated mainly with the decrease of electron transport at the PSII acceptor side, the long-term UV-B treatment causes accumulation of inactive PSII reaction centers and decrease of light absorbance per leaf cross-section, which reflects the photooxidation of the photosynthetic structures, altogether leading to the drastic decrease of electron transport at the PSII acceptor side.

The fast fluorescence kinetic analysis also enables detection of a specific limitation of electron transport at the PSII donor side associated with impairment of oxygen-evolving complex. That can be well recognized by the double normalization

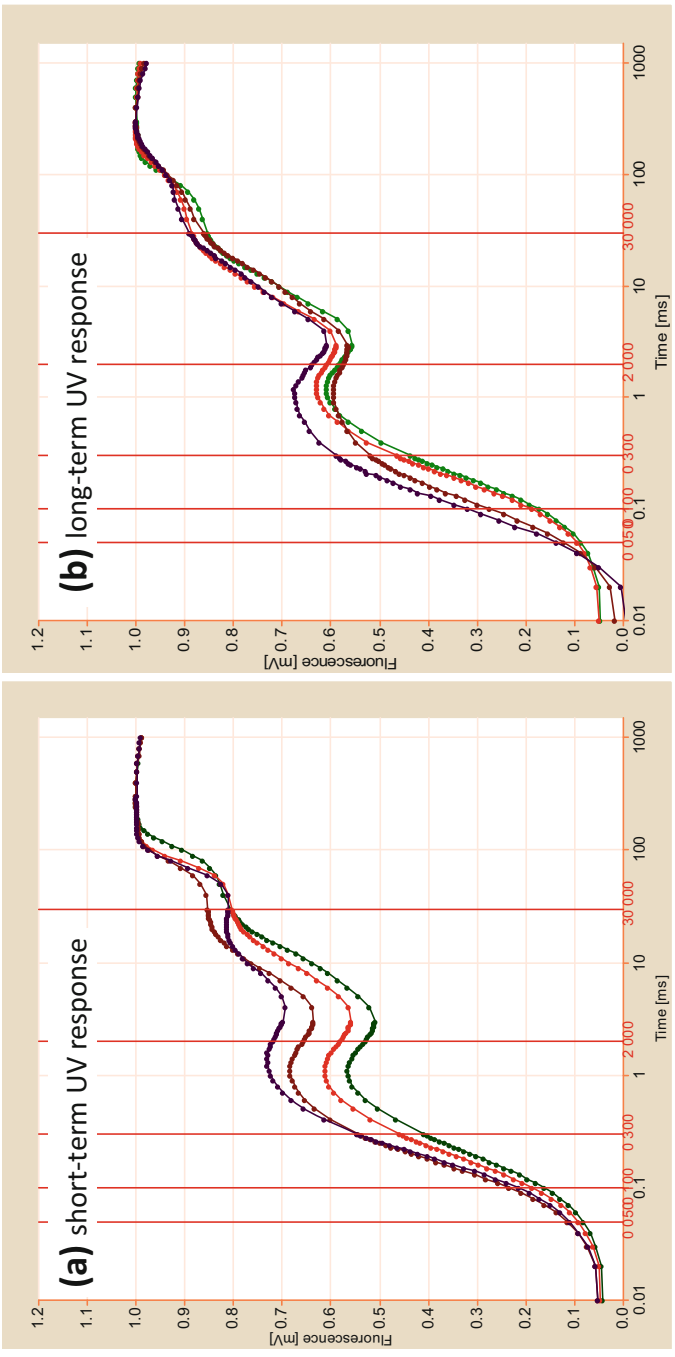

Fig. 11.2 Double normalized OJIP transient (Fo–Fm normalization) measured in control variant without UV (green), moderate UV (red), high UV (brown), and very high UV (purple). The figure left shows the short-term response (day 1, after 4 h of UV exposure); the figure right shows the long-term effects (after 7 days of treatments). The fluorescence curves were processed and visualized using the Biolyzer Software (version 3.06, R. Rodriguez R. Strasser, University of Geneva, Switzerland). Unpublished data by the authors

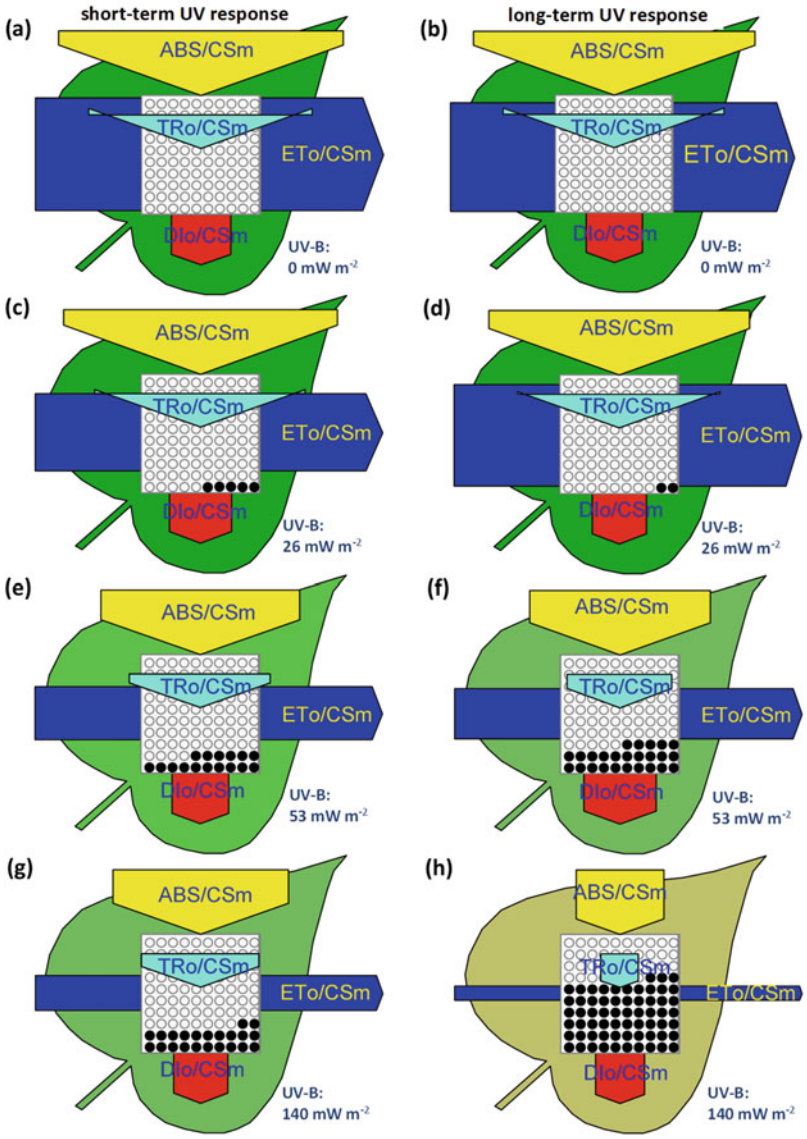

Fig. 11.3 Leaf models showing phenomenological energy fluxes per excited cross-section (CS) of lettuce leaves exposed to a different level of UV-B radiation. The models left (**a**, **c**, **e**, **g**) show the short-term response (day 1, after 4 hours of UV exposure), the models right (**b**, **d**, **f**, **h**) show the long-term effects (after 7 days of treatments). *ABS/CSm* absorption flux per excited CS approximated by Fm, *TR/CSm* trapped energy flux per CS, *ET/CSm* electron transport flux per CS, *DI/CSm* dissipated energy flux per CS. Each relative value is represented by the size of proper parameters (arrow), empty circles represent reducing QA reaction centers (active), full black circles represent non-reducing Q_A reaction centers (inactive or silent). The color intensity of leaves is proportional to its chlorophyll content calculated by Biolyzer software. The models were produced using the Biolyzer Software (version 3.06, R. Rodriguez R. Strasser, University of Geneva, Switzerland). Unpublished data by the authors

of the initial O–J phase (Fig. 11.4), in which an increase of relative variable fluorescence at 0.3 ms (K step of the transient) represents the specific indicator of OEC damage (Strasser 1997).

It is evident that short-term UV-B stress in lettuce was not associated with significant damage of OEC, but the elevated K step observed after several days of elevated UV-B indicated that the damage of OEC might be responsible for a substantial number of inactive PSII reaction centers. A decrease in the fraction of OEC measured by an increase of K step in fluorescence transient after exposure to UV-B in wheat was also observed by Mathur and Jajoo (2015). It corresponds to molecular studies and physical methods identifying the OEC as a major target of UV-B damage (Renger et al. 1989; Vass 1997; Lidon and Ramalho 2011).

The alternative fluorescence method used frequently in UV-B studies is the multispectral analysis of the fluorescence signal obtained after excitation by the different monochromatic lights, followed by calculations of fluorescence excitation ratios (Cerovic et al. 2002; Ghozlen et al. 2010). Based on previous knowledge on UV-induced fluorescence (Bilger et al. 1997; Cerovic et al. 1999; Bilger et al. 2001), the ratio of the fluorescence values measured after excitation by red and UV-B light sources was used as an estimate of UV-absorbing compounds in plant epidermis, mainly belonging to the group of flavonols. Indeed, the epidermis with a low content of flavonols transmits the UV light to the chloroplast, leading to a high fluorescence signal. In turn, the epidermis with a high content of flavonols absorbs most UV-B, and the fluorescence signal is low. The absorbance of red light by flavonols is very low; hence, the flavonols' concentration does not significantly influence the fluorescence signal induced by red light. Therefore, the ratio between the red light-induced fluorescence and UV-light-induced fluorescence is proportional to the flavonol concentration. Analogically, using the green light instead of UV, the anthocyanins with absorption maximum in the green band can be assessed. Due to a non-linear trend of relationships, the logarithms of the ratios were introduced as FLAV and ANTH indices enabling fast and non-invasive estimates of flavonoid and anthocyanin contents in leaves and other aboveground plant organs (Cerovic et al. 2002; Sytar et al. 2016). The most promising were the applications in assessing the quality and maturity level of grapes (Baluja et al. 2012; Tuccio et al. 2020; Agati et al. 2020a, b) or fruits (Lafontaine and Freund 2013; Pinelli et al. 2013; Groher 2019; Agati et al. 2020a, b), but the applications in vegetables (Bruckova et al. 2016; Chaturvedi et al. 2021) or medicinal plants (Müller et al. 2013a, b; Sytar et al. 2015, 2020) were also reported. Thanks to the ability to assess the compounds protecting plants against UV-B stress, the method was successfully used in several studies evaluating the UV-B acclimation responses and co-occurring environmental effects in lettuce (Zivcak et al. 2017; Sytar et al. 2018) or medicinal plant *Centella asiatica* L. (Müller et al. 2013a, b) or tobacco (Mátai et al. 2019). Some examples of the observed trends in conditions of different UV-B doses will be presented in the next chapter as an acclimation response.

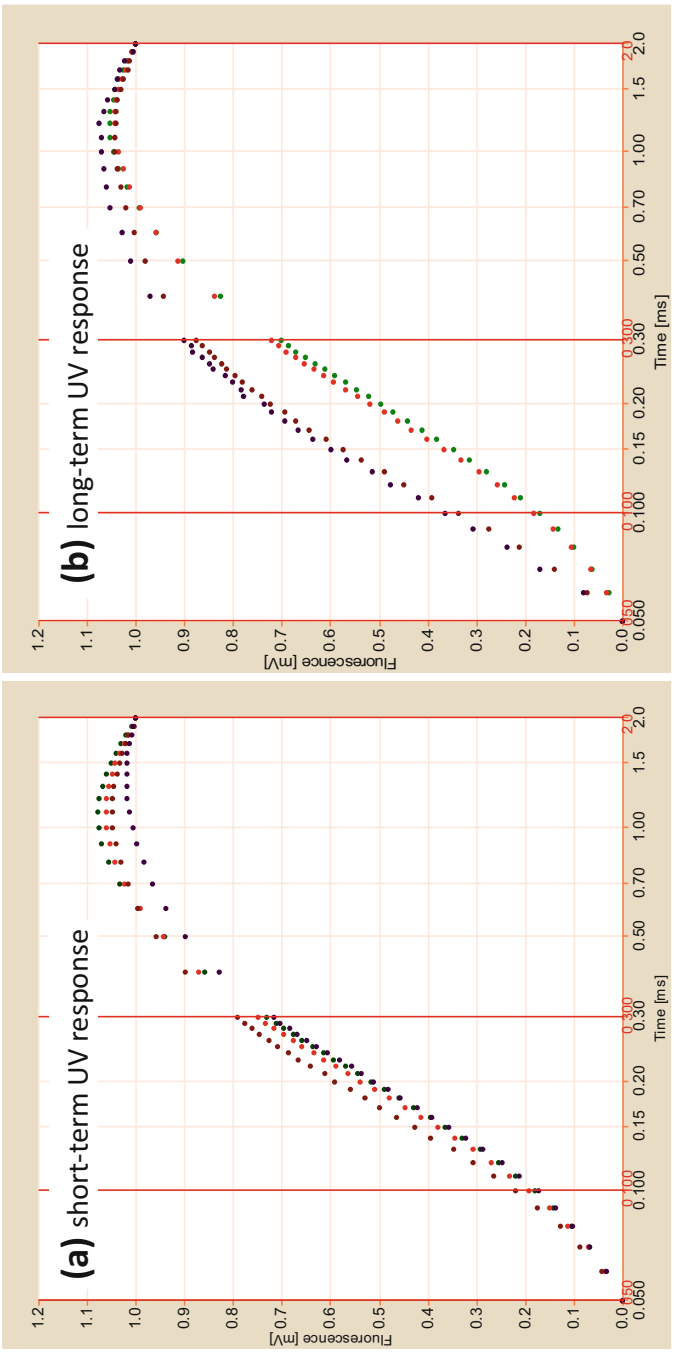

Fig. 11.4 Double normalized O-J step of OJIP transient (Fo–Fj normalization) measured in control variant without UV (green), moderate UV (red), high UV (brown), and very high UV (purple). The figure left shows the short-term response (day 1, after 4 hours of UV exposure); the figure right shows the long-term effects (after 7 days of treatments). The fluorescence curves were processed and visualized using the Biolyzer Software (version 3.06, R. Rodriguez R. Strasser, University of Geneva, Switzerland). Unpublished data by the authors

11.7 Acclimation Responses of Photosynthetic Apparatus to UV-B Radiation

11.7.1 Acclimatory and Protection Mechanisms Against UV-B Stress

Jansen et al. (1998) stated that UV-B tolerance depends on the balance between damage reactions and both repair and regulation of the general stress tolerance pathways.

UV-B radiation represents a significant stress factor affecting the growth and productivity of crop plants. The plants dispose of protective mechanisms that eliminate the UV damages, thus maintaining productivity and yield (Kakani 2003; Ballaré et al. 2011; Wargent and Jordan 2013; Ballaré and Austin 2017). The grasses and other monocots use to resist UV-B radiation more efficiently, as their leaves are better arranged to protect apical meristem and leaf sheath. One of the protective responses is lowering of the leaf area (Caldwell and Flint 1994), which was observed in various crops, such as oat (Skórska and Lewandowski 2003), sugar beet (Panagopoulos et al. 1990), maize, and sunflower (Saile-Mark and Tevini 1997). This acclimation helps the plants survive the UV-B stress by reducing exposure to damaging radiation. Additional acclimation response is represented by the synthesis of UV-absorbing compounds, especially flavonoids. They use to be located in the epidermal layer of leaves, and they protect the sensitive cell structures inside leaves by absorbing the excessive UV-B radiation and thus protecting the photosynthetically active tissues against the harmful effects (Tevini et al. 1991; Braun and Tevini 1993; Solovchenko and Schmitz-Eiberger 2003; Hideg and Strid 2017). Flavonoids act as a UV filter absorbing the radiation in the region of 280–320 nm (Singh et al. 2012; Schaller et al. 2013). There are also other compounds accumulated in conditions of elevated UV-B, protecting the photosynthetic tissues from damage, such as the products of the shikimic acid pathway (furanocoumarins, polyketides) and terpenoids, such as cannabinoids (Treutter 2005). In addition, carotenoids have antioxidant properties protecting against harmful effects of UV-B radiation (Middleton and Teramura 1993; Brosche and Strid 2003; Sandmann 2019).

The antioxidative defense supplements the UV-absorbing protection; these two acclimation responses represent the main two pillars of the defense against UV-B damages in higher plants (Caldwell and Flint 1994; Jordan 1996; Piri et al. 2011; Szwarc and Skórska 2007; Vidović et al. 2017). Multiple experimental studies are supporting the importance of the antioxidant defense by the activity of not only the antioxidant enzymes—superoxide dismutase SOD (EC 1.15.1.1), catalase (CAT; EC 1.11.1.6), APX (EC1.11.1.11), glutathione reductase (GR; EC1.6.4.2), guaiacol peroxidase (POD; EC 1.11.1.7), and dehydroascorbate reductase (DHAR; EC1.8.5.1) (Alexieva et al. 2001; Szwarc and Skórska 2007; Wang et al. 2008; Varga et al. 2012; Mishra et al. 2013; Kong et al. 2014; Tripathi et al. 2016)—but also the phenolic antioxidants (Li et al. 1993; Lois and Buchanan 1994), as well as UV-screening effects of the flavonoids (Ziska et al. 1992; Liu et al. 1995; Ravindran et al. 2010; Agati et al. 2020a, b).

Although there is general agreement in the role of antioxidant enzymes in acclimation against UV-B, the experimental studies provide in equal responses for individual antioxidative enzymes in different crops. For example, Agrawal and Rathore (2007) found an increase of SOD and POD but decreased CAT in a condition of high UV-B in wheat. Singh et al. (2012) found an increase of SOD and APX, suggesting the vital role of APX in controlling endogenous hydrogen peroxide content. In the same crop species, Ibrahim et al. (2013) also observed an increase of GPX. In turn, the inverse trend was observed by Tripathi et al. (2016) in wheat, where SOD and APX activities decreased, whereas CAT and POD were enhanced by elevated UV-B. Comparison of the antioxidative enzyme activity in plants grown under ambient and low UV-B indicated higher SOD, APX, POD, and GR activities in UV-rich environment (Kanungo et al. 2013), whereas CAT was found to be lower (Romanatti et al. 2019).

Non-enzymatic antioxidants, such as phenolic acids, ascorbate, reduced glutathione, or α-tocopherol, also play an essential role in alleviating the oxidative stress in high UV environments (Kataria et al. 2007; Selvakumar 2008). The synthesis of UV-B-protecting compounds strongly depends on UV doses. Moderate UV-B intensity stimulates the expression of genes involved in UV-B protection and, hence, synthesis of compounds from the flavonoid family (Brosche and Strid 2003; Ulm et al. 2004). On the other hand, too high UV-B concentrations are not efficient in increasing the synthesis of UV-protecting compounds, and the damage reaction prevails, leading to a decline in the synthesis of antioxidants (Kliebenstein et al. 2002).

The biosynthesis of secondary metabolites plays a significant role in protecting plants from UV-B damage. The dynamics of flavonoid and anthocyanin synthesis after the onset of UV-B radiation in red lettuce grown under monochromatic LED light are shown in Fig. 11.5.

Whereas the increase in flavonol content was very fast and steep, the anthocyanin content remained low in the absence of blue light. It confirms that the flavonols play a vital role in protection against UV-B (Agati and Tattini 2010), whereas the anthocyanins serve as regulators of spectral light distribution in visible bands, absorbing quanta in the green region of the solar spectrum (Kytridis and Manetas 2006; Lev-Yadun and Gould 2007; Gould et al. 2010; Agati et al. 2020a, b). The accumulation of UV-absorbing compounds, such as flavonoids, eliminates the transmittance of UV-B to the epidermis, with only minimal effect on transmitting photosynthetically active radiation necessary for photosynthesis (Day et al. 1994; Mazza et al. 1999; Bidel et al. 2007).

There is also the hypothesis that the biosynthesis of phenylpropanoids and flavonoid glycosides represents an energy escape valve using excessive electrons from the photosynthetic electron transport in conditions of stress (Grace and Logan 2000; Hernandez and Van Breusegem 2010). Moreover, Dobrikova and Apostolova (2015) suggested that the flavonoid quercetin present in the chloroplast protects photosynthetic structures against UV-B damage. It provides protection by increasing the production of antioxidants, absorbing the UV-B increasing membrane fluidity, and protecting the Mn cluster, thus decreasing the adverse effect of UV-B.

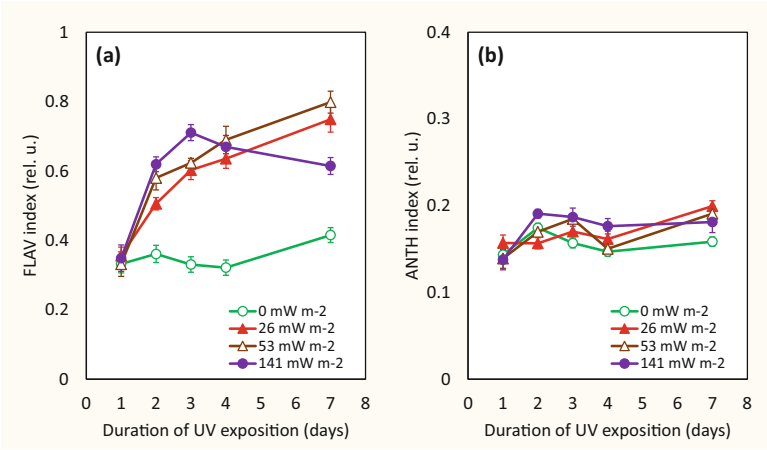

Fig. 11.5 The values of flavonoid index (**a**) and anthocyanin index (**b**) measured in the control variant without UV (green), moderate UV (red), high UV (brown), and very high UV (purple). The figure left shows the short-term response (day 1, after 4 h of UV exposure); the figure right shows the long-term effects (after 7 days of treatments). Unpublished results by the authors

The production of UV-absorbing compounds is an important UV acclimation response, but it is associated with significant energetic expenses (Snell et al. 2009; Guidi et al. 2011; Hofmann and Jahufer 2011), which causes the differences between the species and environments (Day et al. 1992; Qi et al. 2010; Randriamanana et al. 2015). On the other hand, it is crucial to point out that the production of secondary metabolites as a response to UV-B is linked with cross-tolerance to other abiotic and biotic stresses (Mewis et al. 2012; Bandurska et al. 2013; Zavala et al. 2015), providing additional value to this synthesis.

The evidence on the protective role of flavonoids in lettuce leaves is demonstrated in Fig. 11.6.

It is evident that the decrease of Fv/Fm is lowering with an increase of flavonol concentration shown in Fig. 11.5, representing the same experiment with lettuce. Thus, the flavonoid concentration was found to be inversely correlated with the decrease of photochemical efficiency by UV-B. However, it is important to point out that the protection was insufficient at very high UV-B doses, and significant damage occurred despite a very high flavonol accumulation.

In addition to protection, the repair of sensitive targets of UV-B plays an essential role in survival in adverse environments (Favory et al. 2009; Hectors et al. 2009; Schreiner et al. 2017). Moreover, plants possess additional defense mechanisms to protect photosynthetic machinery, such as increased length of epidermal cells, production of a waxy cuticle, and some other morphological and functional adjustments (Hideg et al. 2002).

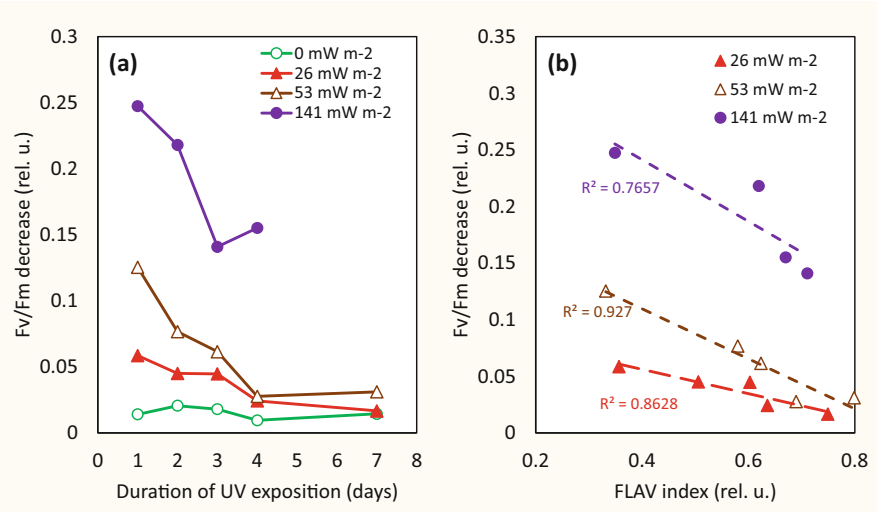

Fig. 11.6 (**a**) The decrease of parameter Fv/Fm parameters after 4 h of UV exposition (difference of Fv/Fm between morning and afternoon measurements) in control variant without UV (green), moderate UV (red), high UV (brown), and very high UV (purple). (**b**) The relationship between the values of flavonoid index (FLAV index) and decrease of parameter Fv/Fm in various levels of UV-B radiation. Unpublished data by the authors

11.7.2 Positive Effects of UV-B on Productivity, Stress Resistance, and Quality of Production

The acclimation to UV-B may also bring some benefits to plants, with consequences on crop production.

Some studies demonstrate the positive effects of ambient UV-B radiation on photosynthetic rate (Musil and Wand 1994; Favory et al. 2009; Davey et al. 2012; Vidović et al. 2015). It may be associated with UV-B signaling pathways and their regulatory role in expressing specific genes directly linked to photosynthesis (Singh et al. 2014). An increase in electron transport rate was also observed, which was explained as an additional energy need for the biosynthesis of UV-absorbing compounds (Vidović et al. 2015). Kumari et al. (2009) observed in the experiments with the sweet flag that appropriate doses of UV-B radiation led to increased photosynthetic rate, stomatal conductance, and WUE, leading to higher productivity and yield. In similar, wheat trials have shown that curtailing UV-B radiation can improve photosynthesis and productivity of wheat varieties (Kataria and Guruprasad 2015). On the other hand, it is needed to note that most studies report decreased productivity and yield due to UV-B. Nevertheless, the existence of variability in UV-B responses provides a good scope for the subsequent research aimed at molecular and physiological studies of relationships between the UV-B signaling and crop yield.

Compared to the positive effects of UV-B on photosynthesis and yield, much more knowledge exists on the indirect effects of UV-B on physiological responses and qualitative traits of plants and crops. For example, UV-B increased the expression of genes related to pathogenesis-related (PR) protein synthesis, directly promoting resistance to pathogens (Barka et al. 2000; Fujibe et al. 2000; Charles et al. 2009).

More frequently reported are the effects of UV-B on the quality and nutritional value of plant products. In a study by Brzozowska et al. (2014), elevated UV-B during germination increased the content of L-ascorbic acid and polyphenols, and it enhanced the antioxidant activity and improved the sensory properties of germs. UV-B stress increased the content of beta-carotene and lycopene in *Cuminum cyminum* L. (Ghasemi et al. 2019). UV-B improves the nutritional quality of fruits, potentially making these fruits more attractive (Mariz-Ponte et al. 2019).

The UV-B-induced oxidative stress initiates protective cascades leading to the increase of phenolic compounds and antioxidants (Lobo et al. 2010; Agati et al. 2012; Ilić and Fallik 2017). Typically, the phenylalanine ammonia-lyase (PAL) (de Oliveira et al. 2016), chalcone synthase (CHS), and flavonol synthase (FLS) (Heijde and Ulm 2012) are stimulated, increasing the levels and proportion of different polyphenols in the crops or fruits (Heijde and Ulm 2012). It may be associated with elevated antioxidant content leading to the nutritional benefits to consumer's health (Lobo et al. 2010). The UV-B may stimulate the production of some volatile organic compounds contributing to fruit flavor and taste (Severo et al. 2016). There are several attempts to apply the UV as a treatment to increase of quality of plant products, especially in the case of vegetables produced in greenhouses (Schreiner et al. 2012; Brazaitytė et al. 2015; Bian et al. 2015; Urban et al. 2016; Dzakovich et al. 2016; Neugart and Schreiner 2018).

11.8 Summary and Conclusions

UV-B radiation represents an important environmental factor. As the photosynthetic apparatus is almost entirely exposed to a dynamic light environment also containing the UV component with its diurnal and seasonal dynamics, the UV-B radiation significantly influences the photosynthetic performance, as well as quantity and quality of crop production. Being an essential regulatory factor, UV-B influences plant morphology and anatomy of photosynthetic organs and structures, with possible effects on leaf area, plant surface structures, including stomatal characteristics. Thus, the UV-B may directly influence the radiation and WUE by plants. In addition to the regulatory role, the UV-B represents an important stress agent. Numerous studies indicate the adverse effects of UV-B on different plant structures, including those essential for the photosynthetic processes. The plant species and genotypes differ in responses and susceptibility to UV-B stress, which highlights the role and importance of acclimation processes and protective mechanisms, such as the building of the efficient antioxidative system, synthesis of UV-absorbing compounds creating the efficient UV screen in plant epidermis, and dynamic regulation of

photosynthetic processes toward efficient photoprotection and high efficiency of solar light conversion and assimilation. Graphical examples proposed in this chapter demonstrate that the rapid, non-invasive, chlorophyll fluorescence-based methods may provide valuable information on the actual functional state of photosynthetic apparatus related to the processes of light energy conversion in the chloroplast, including monitoring of the UV-sensitive sites of the photosynthetic system. In addition to the damages, it is possible to monitor also the acclimation processes to UV-B, such as the accumulation of UV-screening compounds in plant epidermis. Thanks to the rapidity, non-invasiveness, and simple applications of the techniques, the scope for future screening programs aimed at identifying highly UV-resistant genotypes opens, which may lead to higher and more stable yields, especially in crops identified as sensitive to UV-B. Moreover, the accumulation of UV-absorbing compounds may be associated with nutritional and health benefits to consumers, especially in fresh vegetables and fruits. Therefore, the future applications in UV-B research should be aimed not only at eliminating the harmful effects of UV-B radiation on photosynthetic processes and overall plant productivity by enhancing the proper acclimation responses but also at efficient exploitations of benefits related to the positive effects of UV radiation on quality and nutritional value of fresh plant products.

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Role of UV-B in Regulating Performance of Photosystem I and II

12

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Abstract

In this chapter, we discuss the effects of UV-B radiations on plant growth and development, particularly on the process of photosynthesis. Solar UV-B affects photosynthetic performance of plants by reducing photosynthetic efficiency of Photosystem I and II. This may be because of more production of reactive oxygen species (ROS) which has several targets in photosystem II (PS II). Quantum yields of Photosystem II and photosystem I (PS I) were significantly affected by UV exclusion from the solar radiations. This was exhibited in the form of change in electron transport rates of PS II and PS I. At the same time, it has been demonstrated that UV-B exclusion triggered linear electron flow (LEF) as well as cyclic electron flow (CEF), which is directly linked to the activation of two photosystems. Thus, if less UV-B reached the earth's atmosphere, then the growth of the plants will be better.

Keywords

UV-B radiations · Photosynthesis · Electron transport · Photosystem II · Photosystem I · Quantum yield · Cyclic electron flow

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12.1 Introduction

Ultra-violet (UV) radiation is a part of natural sunlight, and photosynthetic organisms are inevitably exposed to UV radiations. Under natural conditions, more UV radiation reaches earth surface simultaneously with more amount of photosynthetic active radiation (PAR) (Klem et al. 2015). UV radiation constitutes three categories of wavelength band ranges: UV-A, 315–400 nm; UV-B, 280–315 nm; and UV-C, 100–280 nm. The ozone layer effectively absorbs the most of the part of UV (some range of UV-B, and all UV-C rays) and only greater than 290 nm part of UV can reach the earth's surface. The depletion of the protective ozone layer (ozone hole) has resulted in an increase of UV-B radiation on the earth's surface, and it will continue to increase in the next few decades, emerging as a serious global environmental problem (Gupta et al. 2017). The elevated levels of UV-B can alter the productivity and reproductive rate of individual species (microorganisms, plants, and animals), and therefore, can affect the whole ecosystem.

Photosynthetic organisms need sunlight and inescapably face UV-B radiations too. Increase in incident UV-B radiation even by a small amount can have substantial biological effects since UV-B radiations are readily absorbed by several important macromolecules including nucleic acids, proteins, lipids, and phytohormones (Hectors et al. 2007). Several studies have shown that enhanced UV-B radiations adversely affect plant growth through alterations in many physiological and biochemical processes such as damage to DNA, photosynthesis, respiration, and antioxidant system of plants (Kataria et al. 2014). High UV-B radiations diminish leaf area, plant height, and shoot growth in various plants (Golaszewska et al. 2003; Wang et al. 2012). Various morphological changes such as thicker leaves, shorter petioles, and early senescence have been reported in plants exposed to increased UV-B radiations (Inostroza-Blancheteau et al. 2014; Robson et al. 2015). In plants, high UV-B radiation also induces cellular damage through alterations in DNA, and protein, and triggering lipo-peroxidation of biomembranes (Luengo-Escobar et al. 2017; Celeste-Dias et al. 2018). In response to UV-B radiation, several cellular enzymatic antioxidant systems e.g., superoxide dismutase, peroxidise, and catalase, develop in plants. At the same time, some non-enzymatic antioxidant systems also develop, e.g., phenolic acids and flavonoids (Kataria et al. 2007). Non-enzymatic antioxidants and secondary metabolites scavenge reactive oxygen species (ROS) and protect against oxidative damage caused by UV-B radiations (Czégény et al. 2016; Coffey et al. 2017; Yang et al. 2018). These compounds were found to accumulate in the leaves to screen out harmful UV radiations (Tsormpatsidis et al. 2008). Flavanoids which absorb in the region 280–340 nm absorb UV and protect the plant by decreasing UV penetration into the tissues (Jansen and van den Noort 2000). Cell membrane characteristics are changed by UV light that may result in altered membrane permeability and ionic balance leading to several physiological and biochemical responses (Jenkins 2017).

The impact of UV-B depends on the species and on the balance between potential damage and self-protective mechanisms (Gaberscik et al. 2001). The study of

possible consequences of increased UV-B on plant growth and development and the mechanisms involved have become a subject of interest for researchers. A systematic and detailed knowledge is essential to understand the effects of levels of UV-B on crop plants. If experiments are performed by removing UV-B rays from the solar radiations (e.g., by using UV-exclusion filters), we can get valuable information related to adaptation of plants to increased UV-B in the atmosphere.

In this chapter, we have explained the effects of UV-B radiations on plants, particularly on the process of photosynthesis. There are at least three major sensitive sites for environmental stress in the photosynthetic apparatus. These are (1) photosystem II (PSII) with its oxygen evolving complex and plastoquionone (PQ), (2) photosystem I (PSI), and (3) carbon assimilation processes. To have optimum photochemistry of both reactions centers, activity of them should be balanced well. The structural and functional coordination between the two photosystems is important for regulating energy utilization and rate of electron transport in thylakoid membrane (Tu et al. 2016). At present, little information is available related to UV exclusion-induced changes in the flow of energy conversion within PSI. In this chapter, we provide an overview of the impact of exclusion of natural UV-B on plant photosynthesis, particularly on the energy flow between photosystem I and II.

12.2 Impact of UV Exclusion on Plant Photosynthesis

Photosynthesis, an important physiological process in plants, is highly sensitive to abiotic stresses (Mathur et al. 2011; Tomar et al. 2012). Photosynthetic organisms get inevitably exposed to solar UV-B radiation. UV-B radiations inhibit plant growth, photosynthesis, and thereby overall yield and biomass as studied in several plant species like wheat, cotton, and soybean (Fina et al. 2017; Suchar and Robberecht 2016). According to Mathur and Jajoo (2015), the photosynthetic machinery undergoes remarkable changes in its structure and function upon exposure to UV radiation. UV radiation can reduce chlorophyll content and inhibit photosynthesis in algae and higher plants (Xue et al. 2005; Suchar and Robberecht 2016). It has been shown that enhanced UV-B irradiation arrests plant growth (Egert and Tevini 2003), suppresses chlorophyll (Chl) synthesis (Sakalauskaitė et al. 2013), and inhibits electron transport (Mathur and Jajoo 2015) and net photosynthesis (Albert et al. 2011). Gao et al. (2009) suggested that under UV-B stress, the pigment content (Chl *a,* Chl *b*, and Chl *a* + *b*) of wheat leaves was reduced. Another study by Yao et al. (2006) demonstrated that enhanced UV-B radiation also damaged the membrane structure of chloroplasts. In photosynthetic apparatus, PSII is the most sensitive component to UV-B radiation (Albert et al. 2011; Kataria et al. 2014; Mathur and Jajoo 2015). The direct effects of enhanced UV-B radiation in the plants include inhibition of PSII activity (Mathur and Jajoo 2015), reduction in Rubisco activity (Choi and Roh 2003), decreased CO_2 fixation, and O_2 evolution (Savitch et al. 2001). Basahi et al. (2014) and Wang et al. (2015) have shown that UV-B radiations reduce carbon dioxide (CO_2) assimilation and stomatal conductance in rice and lettuce, leading to decreased plant growth and crop yields. At high UV-B,

down regulation of photosynthesis is mainly associated with damage to the D1 protein as well as the donor and acceptor sides of PSII. It also disrupts electron transport, reduces CO_2 assimilation, and compromises with plant growth (Lidon and Ramalho 2011; Kataria et al. 2014; Inostroza-Blancheteau et al. 2016; Jordan et al. 2016). On the other hand, reduction of UV-B caused an increase in the rate of various photosynthetic processes in several crops.

The UV-exclusion studies showed that cut-off of the UV-B from ambient light, resulted in a reduction in biosynthesis of UV-B absorbing phenolic compounds which causes lower stress level to plant (Ferreira et al. 2016). Tezuka et al. (1993) used different UV radiation filters to study photosynthetic activity in tomato and radish. They found that the carbon metabolism was always greater under the UV-B exclusion, while dark respiration was not promoted by UV exclusion. Activity as well as concentration of enzymes like carbonic anhydrase (CA), RuBisco, and PEPcase increased when UV radiation was excluded (Bischof et al. 2000; Bischof et al. 2002; Yu et al. 2013) which could be due to degradation of protein subunits (Xu et al. 2008).

Using UV-exclusion films, an increase in photosynthetic activity was found in mung beans (*Vigna radiata* L.) (Pal et al. 1997) and in broccoli (*Brassica oleracea* L.) (Kuhlmann and Muller 2009) where higher C/N ratio values were reported. In another study, gas exchange, carbonic anhydrase, Rubisco, nitrate reductase activities, and total soluble protein content also increased in wheat (*Triticum aestivum* L.) plants (Kataria and Guruprasad 2015). An increase in the net photosynthetic rate of soybean (*Glycine max* L.) plants was observed under UV-B exclusion. González-Villagraa et al. (2020) studied the effects of UV exclusion in five-year-old plants of two high bush blueberry (*Vaccinium corymbosum* L.) cultivars, Legacy, and Bluegold. They reported that Bluegold cultivar showed a significant increase in photosynthesis reaction, such as increase in PSII activity and net photosynthesis in UV-B exclusion, while these reactions did not show any change in Legacy cultivar. Pal et al. (2009) observed an increase in growth parameters, dry matter accumulation, and specific leaf weight in wheat and pea grown without UV-B. The effect of UV-B exclusion was more evident in pea as compared to wheat. Exclusion of UV-B enhanced the yield parameters in terms of fresh and dry weight, number of leaves and foliage yield (fresh weight of leaves), number of ears/panicles, grains, and grain yield per plant although the extent of promotion in yield parameters varied with different species (Kataria et al. 2013). The exclusion of UV brings about a larger increase in the vegetative growth and in crop yield; however, these changes are species specific.

Measurement of Chl *a* fluorescence is among the most important parameters currently used to study plant response to several abiotic and biotic stresses. Chl *a* fluorescence measurements indicate the physiological state of plants, providing insights into photosynthetic apparatus especially of PSII and PSI (Kalaji and Guo 2008). This technique allows the analysis of photosynthetic performance such as the relationship between the absorb energy and their utilization and dissipation. Bredahl et al. (2004) reported higher maximal photochemical efficiency (Fv/Fm) under UV-B reduction. Kataria et al. (2013) reported an increased maximal photochemical

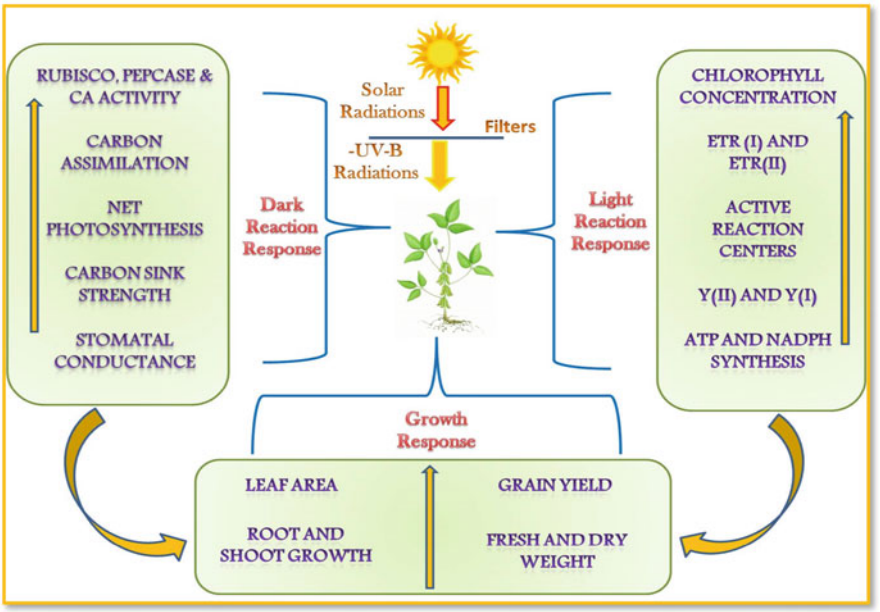

Fig. 12.1 A model to summarize the photosynthetic and growth responses to exclusion of UV-B radiations

efficiency and Performance Index (PI) in C3 and C4 Plants. Moreover, specific energy flux per cross section of leaf sample, the number of active PSII reaction centers (RC/CS), and electron transport rate (ET/CS) and performance index (PI) were increased in reduced UV-B conditions. These data indicated that exclusion of ambient UV-B enhanced photon absorption efficiency and capture of excited energy in PSII, as well as increase in the density of active RC. This points toward an improved overall processing of light energy in UV-excluded plants (Albert et al. 2008; Albert et al. 2010; Kataria et al. 2013). Studies revealed that the leaves of UV-excluded plants had higher reducing capacity of PSII with higher efficiency of electron transport which led to an increase in carbon uptake in these plants (Albert et al. 2010; Shine and Guruprasad 2012; Kataria and Guruprasad 2014). These findings clearly indicate that solar UV-B affects photosynthetic performance of plants by reducing photosynthetic efficiency of PSII (Xiong and Day 2001; Albert et al. 2011; Kataria et al. 2013; Kataria and Guruprasad 2014). This may be because of more production of reactive oxygen species (ROS) which has several targets in PSII (Shine and Guruprasad 2012) (Fig. 12.1).

12.3 Effects of UV-B Exclusion on Energy Conversion Between Photosystem I and II

Optimum performance of photosynthesis in plants requires coordination in the energy conversion processes taking place in PSII and PSI. PSI has been shown to be less sensitive to various environmental stresses as compared to PSII. Here, we present our own unpublished data related to the effect of UV-B exclusion on energy regulation mechanism between PSII and PSI in soybean plants. Simultaneous assessment of energy conversion in PSI and PSII was done using Dual PAM-100. Utilization of absorbed energy in PSII can be measured by Chl *a* fluorescence quantum yield parameters determined by the light-curve response (LCR). At the same time, measurement of absorbance changes between 830–875 nm gives information about the redox state of the PSI (P700) (Tomar and Jajoo 2017). Our experimental results revealed change in energy conversion yield of PSI and PSII following UV-B exclusion.

The light-curve response (LCR) (0–800 μmol m^{-2} s^{-1} PAR) provides valuable information on the efficiency with which PAR is used by plants (Klughammer and Schreiber 2008). Light curves of the quantum yield of different energy conversions parameters were recorded in 55-day-old control and UV-B-excluded soybean plant leaves. Prior to any measurement, the plants were dark adapted for 30 min. Saturation pulses (10,000 μmol photons m^{-2} s^{-1}) were used for the assessment of P700 parameters (Zivcak et al. 2013; Tomar and Jajoo 2017; Tomar and Jajoo 2019; Jain and Jajoo 2020; Mathur et al. 2019).

12.3.1 Effects of UV Exclusion on the Quantum Yield of Energy Conversion of PSII and PSI

Y(II) which corresponds to the fraction of energy that is photochemically converted in PSII increased in UV-B-excluded plants as compared to control plants (Fig. 12.2). Mode of energy dissipation in PSII can be calculated from 1-Y(II) which demonstrates the total quantum yield of all loss processes. Measurements of non-photochemical quenching, Y(NPQ), and Y(NO) give information about the mechanisms that protect plants from damage under biotic and abiotic stress condition (Mathur et al. 2019; Tomar and Jajoo 2015). Y(NPQ) reflects the dissipation of excess excitation energy in the regulated form (NPQ mechanism), and Y (NO) reflects the dissipation of excess excitation energy in the non-regulated form mainly due to closed PSII reaction centers (down regulation of PSII) (Klughammer and Schreiber 1994). An enhancement in the value of Y(II) in UV-B-excluded soybean plants is due to lower energy dissipation in non-regulated form, as reflected by less value of Y(NO) (Fig. 12.2c) and lower regulated non-photochemical energy dissipation as reflected by low value of Y(NPQ) (Fig. 12.2b). Higher Y(II) indicates the presence of a large population of active PSII centers. High chlorophyll concentration in UV-B-excluded plants (Kataria and Guruprasad 2014) might have led to higher Y(II). Higher values of Y(II) along with low values of Y(NO) reflect more

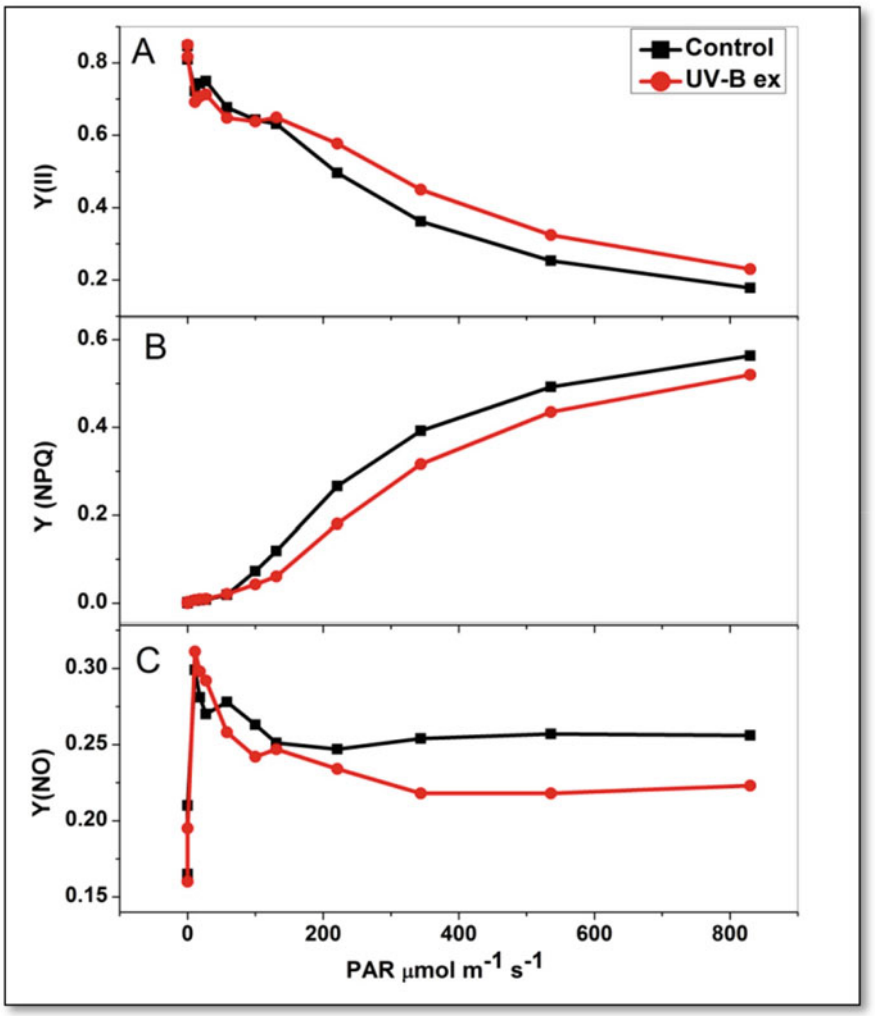

Fig. 12.2 Light-Response Curve of quantum yields of energy conversion in PSII in control and of UV-B-excluded soybean plant leaves where (**a**) Y(II) is the quantum yield of PSII, (**b**) Y(NPQ) is the yield of regulated energy dissipation, and (**c**) Y(NO) is the yield of non-regulated energy dissipation

efficient photosynthetic machinery and less photochemical damage. In UV-B-excluded soybean plants, light is efficiently harvested so that part of the absorbed light energy is utilized in photochemical reactions. In this case, regulated and non-regulated both non-photochemical dissipation of energy pathway were suppressed. In favorable conditions, successful regulation is aimed at maximal values of Y(II), while the remaining loss is aimed at high ratio of Y(NPQ)/Y(NO),

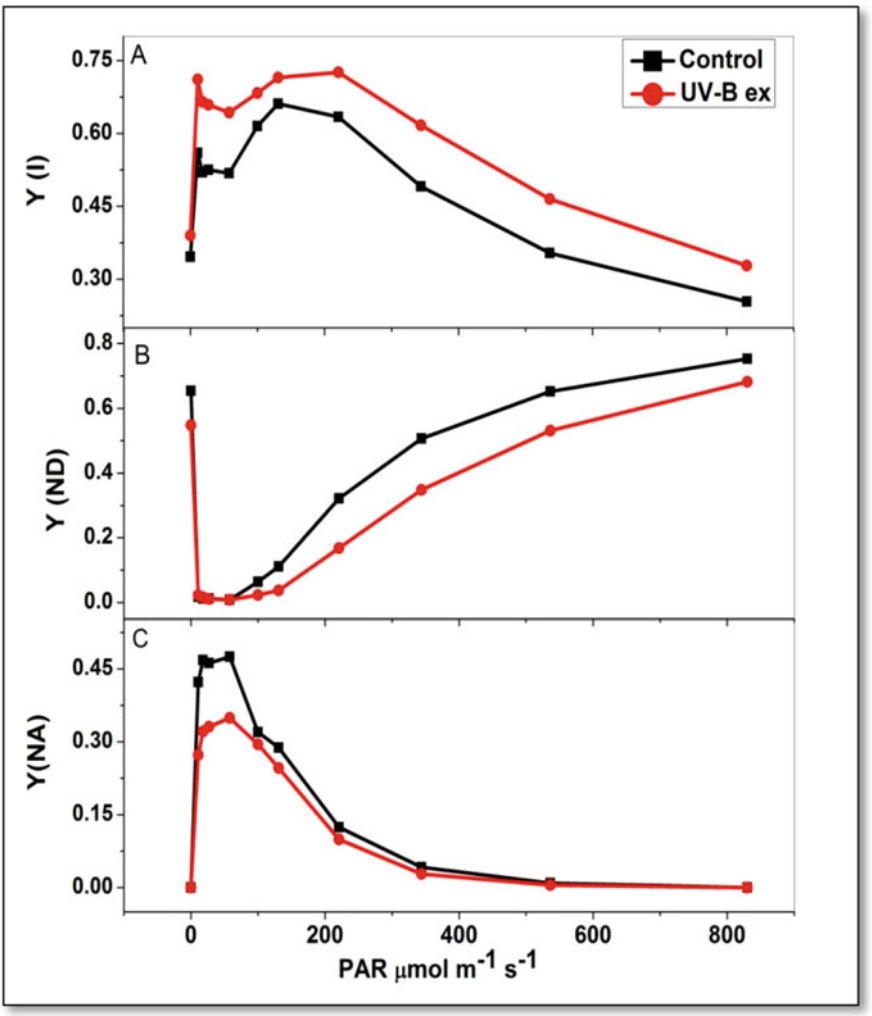

Fig. 12.3 Light-Response Curve of quantum yields of energy conversion in PSI in control and of UV-B-excluded soybean plant leaves where (**a**) Y(I) is the quantum yield of PSI, (**b**) Y(ND) is the quantum yield of non-photochemical energy dissipation caused by donor-side limitation, and (**c**) Y (NA) is the quantum yield of non-photochemical energy dissipation caused by acceptor-side limitation

and it was observed that this loss is minimum with UV-B exclusion, reflecting maximum capacity of photochemical reaction.

Analysis of the quantum yield of energy conversion in PSI in control and UV-B-excluded soybean plants is presented in Fig. 12.3. There are 2 fates of excitation energy that reaches PSI center: (1) photochemical charge separation with quantum yield Y(I) and (2) non-photochemical conversion to heat. PSI is either oxidized due

to donor-side limitation, Y(ND) or reduced due to acceptor-side limitation, Y(NA). Y(I) corresponds to the effective photochemical quantum yield of PS I. Y (ND) corresponds to the quantum yield of non-photochemical energy dissipation in reaction centers. Y(NA) corresponds to quantum yield of non-photochemical energy dissipation of reaction centers (Mathur et al. 2019). The sum of these three quantum yields is 100%. As compared to control, photochemical quantum yield of PSI, Y(I) was higher in UV-B-excluded plant (Fig. 12.3a). This indicated that the fraction of PSI complex, which displayed the capability of charge separation and stabilization, increased in UV-B-excluded plants. It seems likely that in UV-B-excluded plants, higher proportion of PSI complexes may exist in more efficient form which makes the photochemistry more feasible. Increase in value of Y(I) in treated plant is related to decrease in Y(ND) and Y(NA) parameters (Fig. 12.3b, c). Non-photochemical quantum yield Y(ND) (donor-side limitations) represents the fraction of overall P700 that is oxidized in a given state and was found to be higher in control plants as compared to UV-B-excluded plants. Lower Y(ND) in UV-B-excluded plant suggested an increase in photosynthetic efficiency at Cyt b_6f complex and better regulation of PSII reaction centers. Moreover, as compared to control Y (NA), which represents the non-photochemical quantum yield at acceptor-side limitation, also decreased with UV-B exclusion. The lower value of Y (NA) revealed that in UV-B-excluded plants, the fraction of acceptors of P700 was increased as compared to control. The efficient light absorption in PSII caused high rate of PSII charge separation which matched the capacity of PSI (Pfündel et al. 2008). Lower Y(ND) in UV-B-excluded plants is also related with efficient light absorption by the antenna of PSII and PSI (Pfündel et al. 2008).

12.3.2 Effects of UV Exclusion on the Electron Transport Rates of PSII and PSI

Electron transport rates for PSI as well as for PSII were monitored in control and UV-B-excluded soybean plants (Fig. 12.4). The results showed higher rates of ETR (I) and ETR(II) in UV-B-excluded plants as compared to control soybean plants (Fig. 12.4a, b). In other words, electron transport rates were up-regulated due to exclusion of UV-B. A raise in ETR(II) and ETR(I) reflected maximum electron transport for both photosystems (PSII and PSI). Electron transport rate (ETR) is a relative measure of photosynthesis. A higher ETR rate in UV-B-excluded plants is an indicative of better physiological status of these plants as compared to control soybean plants. It is also known that UV-B-excluded plant has less ROS production (Baroniya et al. 2013) which could be a reason for enhanced ETR (II) and ETR (I) rates. It is speculated that in UV-B excluded plants, root growth is better; thus, plant can efficiently absorb nutrient and water from soil which could be a reason for enhanced ETR(II) and ETR(I) rates. Electron transport via PSI was essential for the light-dependent translational elongation of the D1 protein. The data from this study show that exclusion of UV-B radiation from ambient light is beneficial for PSII and as well as PSI. The improved adaptation of plants in UV-B exclusion condition was

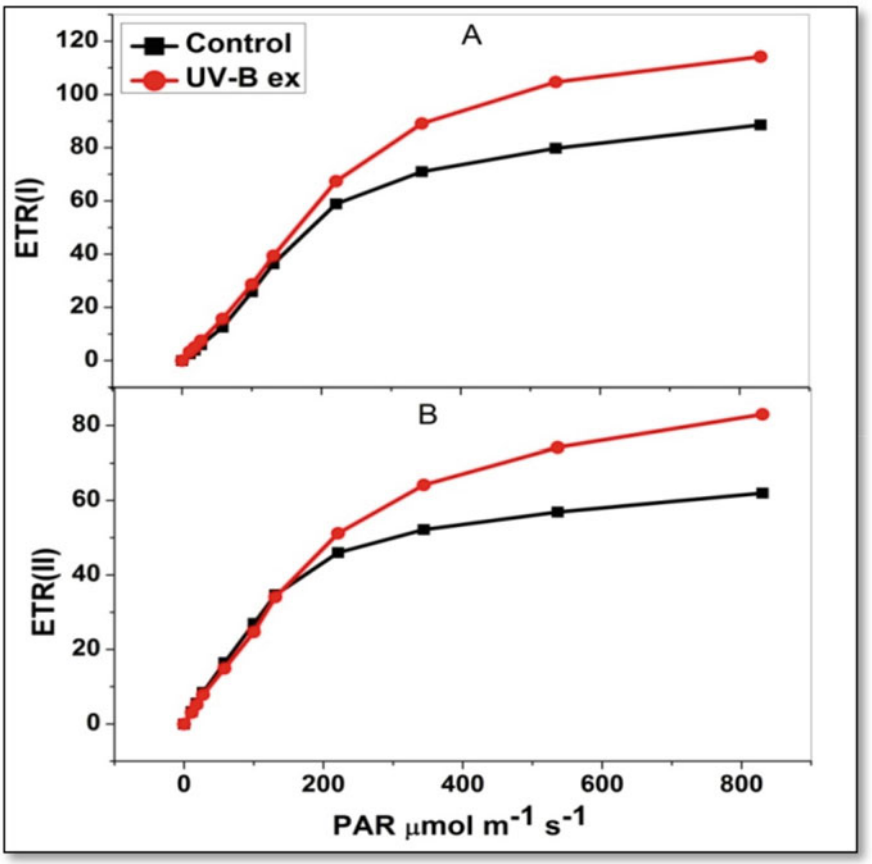

Fig. 12.4 Light-Response Curve of (**a**) ETR(I) relative electron transport rates in PSI and (**b**) ETR (II) relative electron transport rates in PSII, in control and of UV-B-excluded soybean plant leaves

thought to be linked to a combination of physical, physiological, and cellular effects, which commonly include the induction of better electron transport and photosynthetic rate.

12.3.3 Effects of UV Exclusion on the Cyclic Electron Flow (CEF)

The changes in the ratio of Y(II):Y(I), Y(CEF):Y(I), and Y(CEF):Y(II) indicate the change of energy distribution between the photosystems, and the relationship of CEF and LEF (Fig. 12.5). Both Y(I) and Y(II) were increased in UV-B-excluded plants and the change in percentage was almost similar for Y(I) and Y(II) in soybean plants. The ratio of Y(CEF):Y(II) and Y(CEF):Y(I) did not change in UV-B-excluded plants as compared to control plants. The ratio of Y(II):Y(I) did not alter significantly

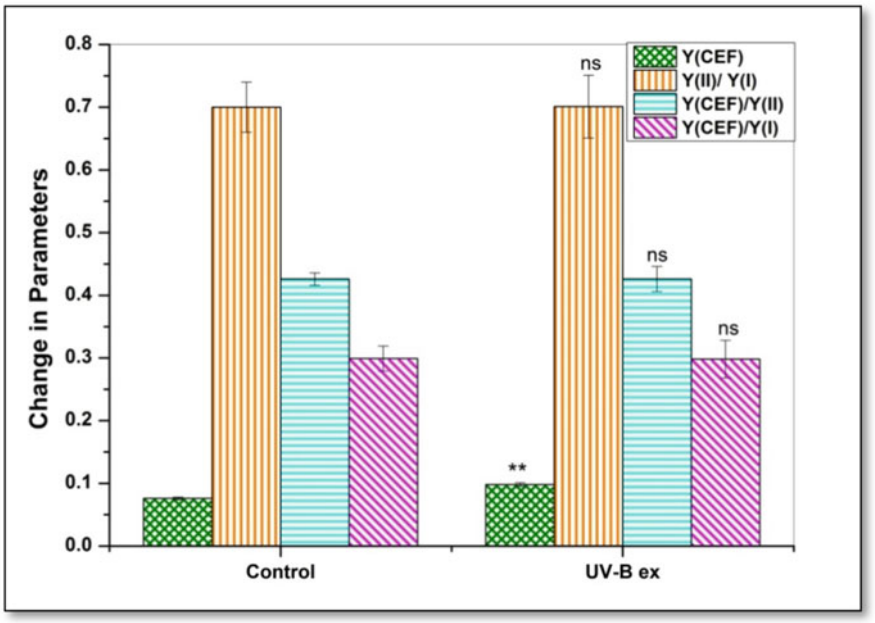

Fig. 12.5 Effect of UV-B exclusion on the various parameters related to cyclic electron flow (CEF) and linear electron flow (LEF) in soybean plant after 55 days

due to UV-B exclusion; however, the value of Y(CEF) was increased in UV-B-excluded plants. These results indicated up-regulation of linear electron flow as well as cyclic electron flow with UV-B exclusion to avoid the excessive reduction of PSI and PSII electron acceptors due to high absorption capacity. Therefore, it is clear that the stimulation of CEF is not associated with inhibition of LEF, suggesting a positive impact of UV-B exclusion on activation of LEF as well as CEF.

Exclusion studies have more significance in tropical environment where the plants receive higher amount of UV-B and would help in the assessment of the adaptability of the plant to a variety to ambient UV-B received. Based on various studies, it is speculated that a strong positive effect emerged on physiological and biochemical processes under UV-B-excluded plants. The plant functions that are most affected by UV-B exclusion are enhancement in photosynthesis performance which stimulates plant growth and enhanced biomass. Improved photosynthetic efficiency under UV-B exclusion may be due to better harvesting of light and overall processing of light energy between two photosystems. The exclusion of UV components from the solar spectrum triggered LEF and CEF, which are directly linked to the activation of two photosystems. Exclusion of UV radiations increases electron transport through PSII and PSI, and as a consequence, higher amounts of ATP and NADPH are produced leading to better carbon assimilation. The results indicated a positive action of exclusion of ambient UV-B on PSII as well as PSI, and no great difference was found in sensitivity of both photosystems.

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Relationships of Oxidative Stress and Ultraviolet-B Radiation in Plants

13

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Abstract

Plant undergoes many different stresses in life. Among the abiotic stress, UV-B radiation is a stress which causes serious threat because plants are photosynthetic and require sunlight. During photosynthesis, exposure to different extreme variations of radiations, including UV radiations, causes damage to the plants. The photosynthetic efficiency gets hindered by solar UV radiations. More than the threshold, UV-B when in excess causes damages to the biological macromolecules inside the plants including, lipids, proteins, and DNA. DNA damage leads to the changes at molecular level including gene expression. There are many UV-B targets in plants, and the main targets of UV-B are the photosynthetic machinery, and its damage is responsible for overall damage caused by the UV-B radiations. It is known that whenever UV-B stress is encountered, ROS is generated in plants that antioxidant machinery gets activated. Responses to UV-B are mediated by both nonspecific signaling pathways and specific signaling pathways. The nonspecific signaling pathways deal with DNA damage, reactive oxygen species, and defense signaling molecules whereas UV-B-specific

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pathways mediate photomorphogenic responses to low levels of UV-B. Under UV-B stress, there is transcriptional programming to induce the defense-related genes, which plays important roles to alleviate stress. The UV-B stress and its alleviation and associated signaling will be helpful for plant biotechnologists to develop UV-B stress-resistant plants.

Keywords

UV stress · Oxidative stress · Photosynthesis · UV-B · Transcriptional reprogramming

13.1 Introduction

When plant is growing in non-ideal conditions, then it faces stress and growth is hindered. Since, plants cannot move here and there, they grow in several harsh environments. There are many stress factors: both biotic and abiotic which reduce growth of plants. The abiotic factor includes, temperature either low or high, less or more water, salinity environment, heavy metals, and ultraviolet radiation (Wang et al. 2003; Ibrahimova et al. 2021; Kumari et al. 2020). Whenever stress is more, it reduces crop growth and yield and can also cause permanent damage or death if stress exceeds the tolerance limits (Mosa et al. 2017).

Earth is surrounded by air, light, and water in addition to many other factors. Life on Earth gets sustained by sunlight and gets exposed to the natural radiation of light spectrum ranging from ultraviolet-B (UV-B) to infrared wavelengths (295–2500 nm). Between X-rays and visible light of the electromagnetic spectrum falls Ultraviolet (UV) radiation. It is categorized into three classes: UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (200–280 nm) (Ulm and Jenkins 2015). But only UV-B and UV-A are reached to the earth's surface (Vanhaelewyn et al. 2020). Ultraviolet-B (UV-B) radiation has the highest energy which reaches the earth's surface and is one of the important sources of environmental stress for plants. This UV-B light causes photochemical DNA damage and triggers other developmental and defense responses at the molecular levels (Herrera-Vásquez et al. 2021). The amount of UV-B which reaches the earth's surface is highly dynamic and dependent upon many factors viz. ozone found in stratosphere, solar angle (latitude dependent, season dependent, timings of day), altitude, pollution in troposphere, and also cloud cover, shading due to plant canopies shading, e.g., in plant canopies. DNA damage is caused when nucleic acids absorb UV-B radiation (Tilbrook et al. 2013).

For the plant biologists, UV-B radiation is a kind of stress which poses serious concern because plants perform photosynthesis and require sunlight. During photosynthesis, plants are exposed to different and extreme variations of solar radiations, including UV radiations. The photosynthetic efficiency gets impaired by solar UV radiations. In plants, few important photochemical reactions in thylakoids, Calvin cycle (enzymatic processes), and stomatal limitations to CO_2 diffusion, by causing

many changes in the chloroplast, can be observed (Sharma et al. 2017). Plants being sessile organisms are highly dependent on sunlight as the primary energy source for photosynthesis. Since sunlight is a mix of many radiations, plants need to exploit radiation which is good for photosynthesis and also to get it protected by UV-B radiation (Ulm and Jenkins 2015). UV-B, in excess to the threshold, causes various damages to the biological macromolecules inside the plants and including, lipids, proteins, and DNA. The damage in DNA leads to changes at molecular level including gene expression, metabolism, photosynthesis, and finally, growth of the whole plant (Piri et al. 2011).

13.2 Reactive Oxygen Species (ROS)

Reactive oxygen species (ROS) production is inevitable in plants and ROS is byproducts of several metabolic reactions like photosynthesis and respiration. This produces oxidative stress due to imbalance between the ROS production and antioxidant response. ROS does cell damage mounting response against reactive damaging species. The cellular system has an elaborate system of antioxidants consisting enzymatic and nonenzymatic systems to scavenge these generated ROS. To understand the roles of many enzymes involved in ROS scavenging, they have been over expressed or downregulated to analyze the response (Ahmad et al. 2010; Yadav et al. 2012). The gene expression is modulated by the stress response and generated ROS by the environmental factors, and signal transduction is initiated in response to it (Szymańska and Strzałka 2010).

13.3 Kinds of ROS

Heterotrophs are dependent on other organisms for food, and phototrophs are the organisms which convert energy from the sunlight into biochemical energy and help in sustaining life on Earth. There are different types of ROS in living organisms like hydroxyl radical ($OH^{\bullet}$), superoxide radical ($O^{\bullet -}{}_2$), singlet oxygen ($^1O_2$), and hydrogen peroxide (H_2O_2). ROSs are necessary evil because they are generated as unwanted byproducts and causes oxidative damages (Das and Roychoudhury 2014).The free radicals damage the biological macromolecules like proteins which gets oxidized, lipids of which peroxidation of membrane's unsaturated fatty acids leads to membrane permeability, oxidation of carbohydrates produces dicarbonyls which reacts with the oxidized proteins by cross-linking reactions and purine and pyrimidine bases of nucleic acids (are potential targets of oxidative damage). ROS gets generated from 1 to 2% of total oxygen consumed by plants, and they are necessary for plants as they are involved in many signaling pathways. ROS production in plants is at many places like mitochondria, chloroplast, glyoxysomes, and cytosol under controlled conditions (Inze and Montagu 2002). When ROS production exceeds capacity to detoxify them, then it leads to a process of leaking ROS in plant cell.

13.4 Antioxidants in Plants

The metabolism in plants is divided into primary and secondary and the compounds produced via primary metabolism are referred to as primary metabolites, are required for maintenance of plant cells, and they are sugars, fatty acids, amino acids, and nucleic acids. (Kliebenstein and Osbourn 2012). The secondary metabolites of plants are essential to the normal growth, development, and defense. Many different types of secondary metabolites were identified in plants (Korkina 2007). The chemical nature of these compounds is either alkaloids or terpenoids and phenolics) (Patra et al. 2013). The flavonoids and phenolic acids are belonged to plant phenolics and are biosynthetically derived from the acetate and shikimate pathways (Dewick 2009). These phytochemicals possessed excellent antioxidant activity and synergistically interact with other physiological antioxidants such as ascorbate or tocopherol (Croft 1998)**.** Antioxidant potential of plant, phenolics, is always linked to reducing power and metal ion-chelating ability (Rice-Evans et al. 1997; Kasote et al. 2015). Flavonoids and phenylopropanoids get oxidized by peroxidase and help in removal of H_2O_2 (Michalak 2006; Sakihama et al. 2002). The antioxidant defense systems found in plants (Blokhina et al. 2003) help in removal of ROS and render protective functions. So it has to be regulated balance between ROS production and their destruction to perform functions under both optimal and stress conditions (Pandhair and Sekhon 2006).

13.5 Targets of UV-B Radiations

The main targets of UV damage are the nucleic acids and proteins. Although the physiological targets' investigation of UV radiation can be seen as a prerequisite for an understanding of effects at the whole organism level, environmental factors such as the interaction of quality and quantity of visible light, temperature, herbicides, and microbial plant systems cannot be excluded in the overall attempt to understand the increasingly important role of UV-B radiation on plant systems and more specifically on the photosynthetic system (Bornman 1989).

13.6 Effects of UV Irradiation on Plants

Whenever plant encounters UV-B radiation, there are many direct and indirect effects on plants (Jansen et al. 1998) as cellular metabolism gets damaged. To name a few, the formation of dimer in the genetic material (DNA), disruption of membrane, and enzymes get inactivated and there are generation of very reactive-free radicals called ROS. Elevated UV exposure also causes irreversible damage to the photosynthesis. So, by increased UV-B radiation on the earth's surface, stability of ecosystems gets disturbed, thereby causing adverse genetic health of organisms (Piri et al. 2011), and there is reduction in biomass accumulation also (Jansen et al. 1998). There are many related ill effects on the plants as shown in Fig. 13.1.

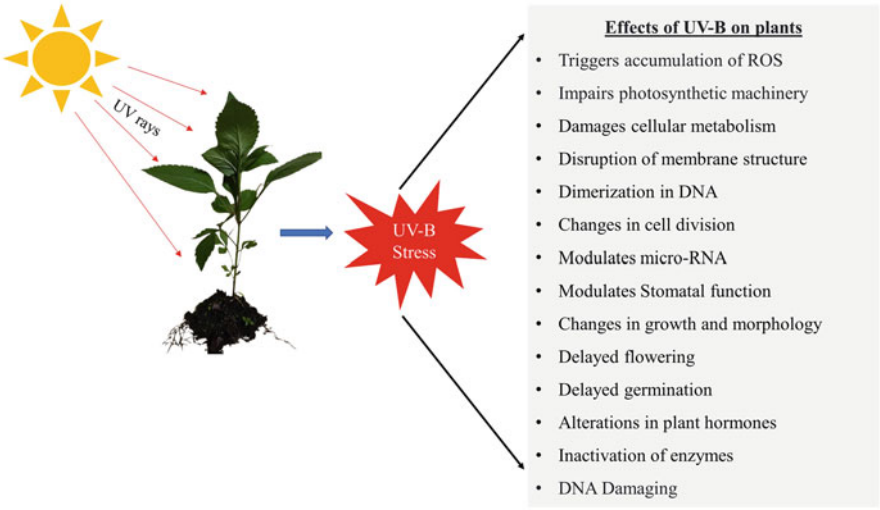

Fig. 13.1 Effects of UV-B stress on plants

13.7 Effect on Morphology of Plants

There are many effects of UV-B radiation which induce effects in plants. These include thickening of leaves, curling of cotyledon, hypocotyl inhibition, elongation of stem and leaf, axillary branching, and others (Jansen 2002). Plants are sensitive to UV exposure and its effects may be observed as direct damage inside cell. Leaves may get differentiated and senescence may be induced by UV-B radiation via some modification of leaf structures. If the UV-B dosage exceeds the tolerance limit, plant leaf anatomy is changed and biomass is decreased (Piri et al. 2011).

13.8 Effect on Crop Growth and Yield

The UV radiation has many impacts and induces crop growth and productivity in several ways. It may also decrease the crop growth and main reason for decreased crop production with ultraviolet radiation may be correlated to the damage of various membranes like chloroplasts which make other stresses such as oxidative stress affect plant growth indirectly (Piri et al. 2011).

13.9 Effect on Photosynthesis

Since photosynthesis is vital to plant's growth and yield production, it is also one of the most sensitive metabolic processes and is directly linked to biomass and yield. So, it becomes necessary to study response of photosynthesis to UV-B stress. In plants among various UV- targets, the main targets of UV-B are the photosynthetic apparatus, and damage to it is responsible for overall damage caused by UV-B (Kataria et al. 2014). Apart from studies on partial reactions of the photosynthetic electron transport chain, the effect of UV-B radiation on different aspects of net photosynthesis has been investigated. The fixation and reduction of CO_2 occur in the chloroplast stroma. The most important stage in CO_2 incorporation in plants involves the carboxylation enzymes, ribulose-1,5-bisphosphate carboxylase (RuBPcase) and phosphoenolpyruvate (PEP) in C3 and C4 plants, respectively. Since RuBPcase may comprise up to 50% of the soluble leaf protein, a reduction in leaf protein may reflect a decrease in RuBPcase (Bornman 1989). Proteins and lipids are not only important membrane constituents but are also part of the photosynthetic system. Therefore, it follows that appreciable reductions in soluble protein content should be correlated to a reduction in RuBPcase activity and, hence, net photosynthesis (Bornman 1989). UV stress has ill effects on photosynthetic efficiency. Decreases in photosynthetic activity may also be due to photodestruction of pigments due to UV light. The photosynthetic pigments get adversely affected by relatively large amounts of UV-B radiation; generally carotenoids are less affected than the chlorophylls (Bornman 1989). Since photosystem II (PSII) has been perceived as being especially vulnerable to UV-B damage (Bornman 1989) and has, thus, been considered a key target in determining the possible effects of ozone depletion on crop production, and its integrity was studied using chlorophyll fluorescence (Piri et al. 2011).

13.10 Effect of UV-B on Polyamines

Polyamines (PAs) have antioxidant properties and their induction in response to stress is well known. Putrescine, spermidine, and spermine are the main polyamines found in all living cells. They are organic polycations displaying a high biological activity. PAs are present in all compartments of the plant cell and participate in diverse fundamental processes in the cell. The role of PAs in augmenting antioxidant-based defense systems to impart tolerance against heavy metals, UV, and other stresses that are potent inducers of superoxide molecules causing oxidative damage to the living cells has been reported in several studies (Mapelli et al. 2008). UV radiation also triggers protective responses in plants, including changes in antioxidant enzyme activities as well as PAs content.

13.11 Signaling During UV-B Radiation

Whenever plants encounter any stress, there is orchestrated signaling and crosstalk which helps in plant defense (Checker et al. 2018). This signaling engages many pivotal players which play the roles of inducing defense. So, whenever UV-B stress is encountered by the plants, ROS is generated and it does help in protection of plants via antioxidant machinery. Responses to UV-B are mediated by both nonspecific signaling pathways, involving DNA damage, reactive oxygen species, and defense signaling molecules, and UV-B-specific pathways that mediate photomorphogenic responses to low levels of UV-B. Importantly, photomorphogenic signaling stimulates the expression of genes involved in UV protection and, hence, promotes plant survival under UV-B stress. Photomorphogenic UV-B signaling is mediated by the UV-B-specific component UV RESISTANCE LOCUS8 (UVR8). Both UVR8 and CONSTITUTIVE PHOTOMORPHOGENESIS1 (COP1) are required for UV-B-induced expression of the ELONGATED HYPOCOTYL5 (HY5) transcription factor, which play a central role in the regulation of genes involved in photomorphogenic UV-B responses (Jenkins 2009).

Plant responses to UV-B are achieved through the regulation of gene expression (Jenkins 2009). Transcriptomics is a tool used to analyze changes in gene expression in plants in a given set of conditions. Transcriptomics profiling has been extensively used in many different plants to study various stresses and genes associated with it (Mulema and Denby 2012; Jaiswal et al. 2012; Zhao et al. 2018). Transcriptome analyses, in particular with maize (Casati and Walbot 2003; Casati et al. 2011) and Arabidopsis (Brosché et al. 2002), have demonstrated that exposure to UV-B differentially regulates the expression of several genes in different functional categories. Low doses of longer wavelength UV-B activate the expression of genes principally via UVR8 (Fig. 13.2). When there is exposure of Arabidopsis seedlings for 1 or 6 h of narrowband UV-B (λmax 312 nm), then mostly the genes which were modulated were regulated by under UVR8 control (Favory et al. 2009). It was also observed by various groups that upon exposure to higher doses and shorter wavelengths of UV-B, many additional sets of genes which are common to those induced by several other stress treatments (Ulm et al. 2004; Brown and Jenkins 2008). So, we may infer that gene expression regulation by UV-B includes activation by UV-B-specific signaling, UVR8-mediated signaling, and also by the activation of pathways, which are not specific to UV-B (Jenkins 2009). Now the pathways that are nonspecific include DNA damage signaling and defense, MAP kinase, ROS related, salicylic acid, nitric oxide, ethylene, and jasmonic acid, and they are all have roles in UV-B-induced gene expression (Mackerness 2000; Jenkins 2009; González Besteiro et al. 2011; Hideg et al. 2013; Vanhaelewyn et al. 2016). In plants, many phytohormones-regulated signaling pathways get involved in both UVR8 responsive and nonspecific UV-B responses (Vanhaelewyn et al. 2016; Jenkins 2017).

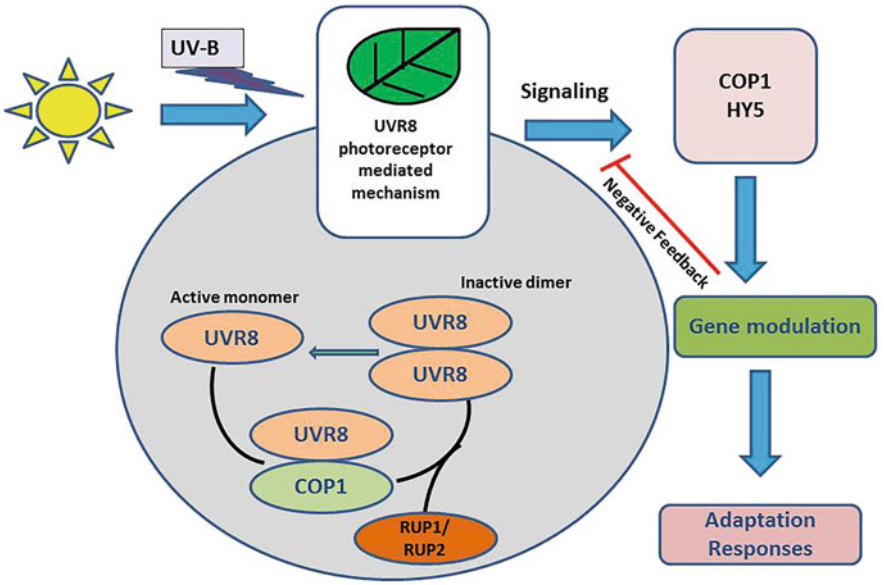

Fig. 13.2 Signaling response of UV-B stress in plants

13.12 UVR8 Action at Molecular Level

Now, how the plants sense UV-B radiation? And the answer is—by the mediation of UVR8 photoreceptor. When there is activation of UVR8, it leads to interaction with the COP1 and stabilization of HY5, and this relays the UV-B signal resulting in gene expression modulation. COP1 is an E3 ubiquitin ligase, and HY5 is a bZIP transcription factor. Out of the many genes which are UV-B-responsive genes, they include proteins having function in UV-B-induced photomorphogenesis and acclimation. To name, a few proteins which are involved in UV protection are phenylpropanoid biosynthesis pathway related, antioxidants, and DNA damage repair (e.g., photolyases). Also, the WD40-repeat proteins RUP1 and RUP2 are induced upon UV-B, which facilitate negative feedback of the UV-B signaling pathway by directly inactivating UVR8 (Tilbrook et al. 2013). RUP 1 and 2 are REPRESSOR OF UV-B PHOTOMORPHOGENESIS 1 (RUP1) and RUP2, and these directly interact with UVR8 and act as repressors of UV-B signaling. In plants, both genes get activated by UV-B COP1-, UVR8-, and HY5-dependent manner. In the rup1 rup2 double mutants, there is an enhanced response to UV-B and gets more tolerance to UV-B after getting acclimated. When RUP2 is overexpressed, there is reduced UV-B-induced photomorphogenesis and plants become hypersensitive to UV-B stress (Gruber et al. 2010). This was observed because RUP1 and RUP2 are located downstream of UVR8-COP1 and act as a negative feedback loop and disturb

UVR8 function. This helps the plants in making balance between UV-B defense response and plant growth (Gruber et al. 2010). So, we can say that there is a negative feedback regulation provided by the WD40-repeat proteins RUP1 and RUP2, which helps in UVR8 redimerization further disrupting the UVR8-COP1 interaction (Tilbrook et al. 2013).

UVR8 was originally identified in Arabidopsis via a genetic screening for searching mutants which were hypersensitive to UV-B (Kliebenstein et al. 2002). One of the mutants, i.e., *uvr8* mutants were sensitive as compared to control plants under simulated sunlight, and thus, role for UVR8 in UV-B tolerance was observed and reported (Favory et al. 2009). The molecular studies have shown homodimerization of UVR8 photoreceptor when devoid of UV-B light. But the monomerization was observed under UV-B exposure, and this is related to tryptophan residue and is dependent on it because it serves as an UV-B chromophore (Tilbrook et al. 2013).

Monomer UVR8 now interacts with COP1, transducing and initiating a molecular signaling pathway leading to gene expression changes which culminates in UVR8-dependent responses like UV-B-induced photomorphogenesis and the accumulation of UV-B-absorbing flavonols.

Upon UV-B irradiation, plant undergoes many metabolic and transcriptional reprogramming. The gene expression of UV-B signaling cascade and proteins, enzymes, and compounds which act as UV-B protectants are transcriptionally regulated and are related to the network coordinating by the UVR/COP/HY5 system. There are many secondary metabolites which are involved in plant defense growth and development. Also some of these metabolites have role in protecting against the detrimental effects of UV-B light damage. Examples of such metabolites are flavonol, phenylpropanoid, anthocyanin, and carotenoids and it was observed that they have a transcriptional association with the UV-B response (Tohge et al. 2011).

13.13 ROS in UV-B-Exposed Plants

Generation of reactive oxygen species (ROS) is one major process for UV-B radiation to cause damage to the plants. It is harmful to plants and affects growth and development of plants. A-regulated balance between ROS production and destruction is required if metabolic efficiency and function are to be maintained in both optimal and stress conditions. The electron transport chains of the chloroplast and mitochondria are two important sources of ROS (Asada 1999).

UV-B stress is more damaging to the chloroplast, and its excessive dose may lead to photoinhibitory damage to the photosynthetic apparatus. When oxidative stress is there, then oxidation increases and many oxidized molecules may be used as ROS reporters. Its example is malondialdehyde (MDA) which gets accumulated after increase in ROS and oxidative stress. In rice cultivars when treated with UV-B, MDA was formed in the leaves. There are many evidences which suggest that several ROSs are involved when UV-B stress is there and damage is caused by mostly lipid peroxidation in plants (Kataria 2017). When UV-B stress is there, then

ROS increases due to disruption of many metabolic activities and also because of increased activity of NADPH-oxidase which is membrane localized. UV-induced ROS generation under in vivo conditions, and its fate helps us to decipher the role of these ROS but due to its reactive and multifarious nature, this does not seem to be technically straightforward. There are many challenges faced by the plant scientists as they are unable to use the full range of tools for ROS. Also identifying the H_2O_2 by its UV absorption capability is hampered since there are many abundant UV-absorbing molecules present in plants (Hideg et al. 2013).

It was observed that when there is UV-B radiation stress, then at the molecular levels, the transcript levels of several defense-related and photosynthetic genes get altered in plants. Exploiting the model plant, *Arabidopsis thaliana*, DNA array technique proved important roles of many genes under UV-B stress. Many genes showed modulation of transcript levels and testing through northern blots with RNA from low-dose UV-B radiation-exposed plants showed few genes (MEB5.2, PyroA, Ubq3, Lhcb6, F5D21.10 and the gene for an RNA polymerase II subunit) to be correlated with stress-specific gene regulation. The results of this analysis identified some genes (PyroA, Ubq3, and the gene for a RNA polymerase II subunit) of which transcript got elevated by UV-B stress One gene PyroA has shown protective role against singlet oxygen in fungi. There were some elements present in the PyroA and MEB5.2 promoters which may be related to or responsible for having role under UV-B responses (Brosché et al. 2002). Ulm et al. (2004) studied and identified *Arabidopsis* genes which were involved in the UV response, and gene expression profile of UV-B-irradiated seedlings was analyzed using microarrays. When low-level UV-B stress was given, then many early responsive genes were identified and mostly UV-B induction was independent of known photoreceptors. It was also seen that HY5 (bZIP transcription factor) was required for UV-B-mediated regulation of few genes.

13.14 UV-B-Dependent Expression of Oxidative Defense Genes

Many groups studied few parameters like daily UV-B doses, spectra, PAR background levels, and durations of UV-B exposure and studied correlation with oxidative stress (Raschke et al. 2011; Favory et al. 2009). One study used low levels of UV-B, and expression of genes like glutathione reductase and pyridoxine biosynthetic protein PDX1.3 was elevated. When oxidized proteins are there after oxidative stress, they get reduced by reducing components inside the cell. So, glutathione reductase reduced glutathione and is part of ascorbate-glutathione antioxidant system and helps in alleviation of oxidative stress (Brosché et al. 2002). Other enzymatic antioxidants like glutathione peroxidase, glutathione transferases, and glutaredoxins also got upregulated when there was exposure of high-intensity UV-B (Ulm et al. 2004; Brown et al. 2005). Redoxins such as thioredoxins (Kumari et al. 2020) and glutaredoxin (Yadav et al. 2012) have been associated with oxidative stress tolerance in plants.

Glutaredoxin expression in plants gets increased initially upon chronic UV-B exposure and later gets downregulated (Hectors et al. 2007). There are alterations in ROS metabolism, whenever UV-B exposure is there and there are numerous evidences that expression of glutathione-related genes gets altered. This alteration depends upon range of UV doses, exposure times, and altered GSH:GSSG ratios (Kalbin et al. 1997). PDX acts as strong antioxidants that neutralize singlet oxygen, superoxide radicals, and hydroxyl radicals (Ristilä et al. 2011). It was observed that PDX1.3 gene gets upregulated upon exposure to both short periods of low (Brosché et al. 2002) or high-intensity UV-B (Brown et al. 2005) but not upon chronic stress suggesting that PDXs are related to initial quick and early response to UV-B stress. In Arabidopsis upon exposure to short periods of low-level UV-B, numerous genes encoding caffeoyl-CoA O-methyltransferase, flavonol synthase, and 4-coumarate-CoA ligase 3 are upregulated (Brosché et al. 2002). The following genes like phenylalanine ammonia lyase, cinnamoyl-CoA reductase, isoflavonereductase, caffeoyl-CoA O-methyltransferase, leucoanthocyanidindioxygenase (Ulm et al. 2004) chalcone synthase, chalconeisomerase, flavanone 3-hydroxylase, flavonol synthase, dihydro-flavonolreductase, and cinnamoyl-CoA reductase in Arabidopsis were induced upon high UV-B levels and short exposures (Brown et al. 2005). When plants get exposed to low and high UV-B doses, there is altered expression of genes involved in the biosynthesis of phenols and may be a common feature. In UV-B-exposed plants, phenolics which are considered to be an important antioxidants (Agati and Tattini 2010), get altered under ROS metabolism (Hideg et al. 2013)

13.15 UV-B Stress, Nanoparticles, etc.

Nanotechnology deals with small nanosize nanoparticles or nanomaterials which find many applications in various fields (Rastogi et al. 2019; Ihtisham et al. 2021). In a hydroponic experiments, silicon nanoparticles were shown to be efficient against UV-B stress. The UV-B radiation on wheat (*Triticum aestivum*) seedlings caused many changes and oxidative stress was increased (Tripathi et al. 2017). UV-B stress caused differential changes to the antioxidants. Silicon nanoparticles application involved the mechanism to enhance antioxidants to counter the oxidative stress caused by the UV-B exposure on plants. This study also compared and deduced that silicon nanoparticles were more effective than silicon alone in reducing UV-B stress (Tripathi et al. 2017). It was also observed that silver nanoparticles (AgNPs) protect thyme *(Thymus vulgaris* L.) when they were exposed to UV-B exposure. AgNPs not only protected the plants but also imparted beneficial effects like growth and development. So, upcoming roles of nanoparticles in alleviation of UV-B-induced cell injury pave the way for application of nanotechnology in agriculture field.

13.16 Conclusions

The environmental concerns related to UV stress are alarming, and apart from other negative effects, it also affects the plants and agriculture per se. The main cause if UV-B increase is related to anthropogenic activities. In plants, UV-B stress affects the biological macromolecules, and DNA, RNA, lipids, and proteins can absorb UV-B radiation directly. This impairs the growth and development of plants as the oxidative stress increases and plants get involved in elevating the repair mechanisms to deal with UV-induced damage. UV-B regulates the signaling by interacting with numerous proteins mediated by UVR8. Under UV-B stress, there is transcriptional programming to induce the defense-related genes, enzymes, and proteins. The future lies to exploit genetic engineering and biotechnology to make UV-B stress-resistant plants.

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UV-B Stress and Plant Sexual Reproduction

14

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Abstract

For decades, effect of ultraviolet radiation on plants and their sexual reproduction has been under focused attention of biological research globally. This work has been conducted to further investigate the response of plants to UV-B radiation as an integrating process of the interaction of the genome with environmental factors through signaling and regulatory mechanisms. UV-B radiation has two main effects: the first is the response to induced damage, and the second is the perception by the UV-B receptor, which leads to UV-B-induced photomorphogenesis and adaptation. The activation of the general stress response is associated with the changes in gene expression. The generative organs of angiosperms are effectively protected from UV-B by integumentary tissues, which accumulate phenolic components, absorb UV radiation, and trap reactive oxygen species. However, pollen and the pollination process are vulnerable to UV radiation. The flower is also exposed to indirect effects of ultraviolet radiation. High exposure to UV-B negatively affects the trophic supply of plants. Depending on the dose, UV radiation can suppress or stimulate flowering, generative organ differentiation, activate cytomixis, and increase the pollen grain (PG) of "low plasma" with signs of autophagy. UV causes genome instability, which can be one of the adaptation mechanisms. With an increase in UV radiation, the importance of cell selection grows; its activation has a threshold character. Accordingly, the "genetic load" on

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the reproductive tissue can be removed more efficiently, since the defense/recovery mechanisms are activated. Meiosis and cytomixis, performing the function of selection, play an important role in maintaining tissue and genetic homeostasis in the male reproductive system.

Keywords

Plant sexual reproduction · Male reproductive system · Cytomixis · Cell selection · Genomic variability · UV-B irradiation

14.1 General Plant Response to UV Radiation

Plants are naturally exposed to UV-B radiation, and, consequently, they have developed effective mechanisms of protection and adaptation to UV-B. The UV-B radiation is believed to cause two main effects in seed plants: the first is seen as a response to the induced damage and the second one is a response to UV-B receptor perception. The latter leads to UV-B-induced photomorphogenesis and acclimatization (Jansen et al. 1998; Frohnmeyer and Staiger 2003; Ulm and Nagy 2005; Jenkins 2009; Yin and Ulm 2017; Benca et al. 2018; Yadav et al. 2020). The development of both responses depends on the dose and duration of the UV exposure, its wavelength, radiation rate, and other factors (Coohill 1989). Activation of a general stress response, triggering changes in gene expression, occurs when UV-B causes damage (Ulm and Nagy 2005). In the case of angiosperms, UV-B radiation is received by the UVR8 and COP1 loci, interaction of which from the first steps of the signaling pathway leads to photomorphogenesis, activation of protective mechanisms, and development of adaptation (Jordan 1996; Rozema et al. 1997; Frohnmeyer and Staiger 2003; Ulm and Nagy 2005; Jenkins 2009; Christie et al. 2012; Wu et al. 2012; Ulm and Jenkins 2015; Yin and Ulm 2017). Plants respond to UV-B radiation by synthesizing protective pigments and UV-absorbing compounds, changing the expression of genes encoding DNA that repairs proteins and activates the enzymes responsible for trapping reactive oxygen species (Hideg and Vass 1996; Agrawal et al. 2009). The protective mechanism against oxidative stress also includes an increase in the expression of genes, which leads to the activation of the phenylpropanoid pathway (Jordan 1996; Bieza and Lois 2001; Ghasemi et al. 2019).

Genome-wide microarray analysis of UV-B-irradiated Arabidopsis seedlings revealed many genes that depend on HY5 and become activated by low UV-B levels (Ulm et al. 2004). Low-energy density UV-B radiation usually induces the expression of cyclobutane pyrimidine dimer photolyase (CPD), which is involved in DNA repair mechanisms and depends on UVR8 (Li et al. 2015). High UV-B energy flux leads to the activation of genes involved in damage and stress responses via the UVR8-independent signaling pathway (Brosché and Strid 2003; Frohnmeyer and Staiger 2003). UV-B radiation induces expression of anthocyanin biosynthetic genes such as chalcone synthase (CHS) and chalcone isomerase (CHI) (Fuglevand et al.

1996). UV-B stress negatively affects the photosynthetic capacity of plants. Many crop species are well known to significantly reduce the photosynthesis and productivity when exposed to UV-B (Kakani 2003). In general, low levels of UV-B radiation act in various ways as a signal for plant development, while high doses of UV-B cause plant resistance. The response of plants to UV-B is an integrating process of the interaction of the genome with environmental factors through signaling and regulatory mechanisms. Transcriptional changes in response to UV-B irradiation play an important role in this process. Below, we will focus on the nature of UV-induced DNA damage that leads to the activation of the general stress response.

14.2 UV-B-Induced DNA Damage, Mechanisms of Resistance, and Repair

One of the most prominent targets of solar UV-radiation is cellular DNA, which absorbs UV-B radiation. UV-B can damage nuclear and chloroplast and mitochondrial DNA, forming the CPDs, (6–4) photoproducts ((6–4) PPs), Inter/intra crosslink (ICL), 8-oxoG or even DNA double-strand breaks (DSBs) (Hutchinson 1987; Ries et al. 2000a; Frohnmeyer and Staiger 2003; Molinier et al. 2008; Esnault et al. 2010; Takahashi et al. 2011; Gill et al. 2015). Repairing of these injuries and elimination of photoproducts are essential for plant survival.

Basically, UV-B effects are known to be realized via mechanisms associated with hormonal and metabolic regulation as well as with changes in the transcription profile (Tevini et al. 1981; Tevini and Teramura 1989; Flint and Caldwell 1984; Caldwell et al. 1989, 2007; Jansen 2002; Mittler 2002; Jansen et al. 2012; Demkura et al. 2010; Keller et al. 2011; Krasylenko et al. 2012; Li et al. 2015; Gill et al. 2015; Yadav et al. 2020). An important role in the mechanisms of resistance to UV is played by the changes in the expression of genes that encode DNA repair proteins (Ries et al. 2000b) and enzymes responsible for the removal of reactive oxygen species (Jordan 1996; Hideg and Vass 1996; De Tullio 2010; Yi and He 2013).

The plants adopt three separate mechanisms to minimize the DNA damage, namely, plant-specific photo reactivation, global genome repair-nucleotide excision repair (GGR-NER), and homologous recombination (Hutchinson 1987; Ries et al. 2000a; Liu et al. 2000; Dubest et al. 2002; Molinier et al. 2008; Boubriak et al. 2008; Gill et al. 2015). Out of the three above types of repair of UV-induced DNA damage, only photoreactivation by photolyase is UV-specific and light-dependent (Jordan 1996; Ries et al. 2000a; Waterworth et al. 2002). The excision and the recombinant network of CPD-dependent repair mechanisms are also effective to remove damaged nucleotides and restore the DNA, but they do not require illumination (Liu et al. 2000, Ries et al. 2000a; Crowley et al. 2006; Gill et al. 2015). UV-B irradiation activates membrane-localized NADPH oxidation (NOX) leading to the production of ROS (Sagi and Fluhr 2006) and increases the expression of senescence-related genes (SAG) (Sagi and Fluhr 2006). UV-B-induced ROS as well as DNA lesions (CPDs and 6–4PPs) may cause primary as well as secondary breaks, respectively.

These lesions are commonly associated with transcription/replication blockage that may lead to the production of DNA double-strand breaks (DSBs) known to be caused by UV-B irradiation (Esnault et al. 2010).

14.3 UV-B-Induced PCD

When repair mechanisms do not work, it can cause irreversible cell cycle arrest and/or programmed cell death (PCD). PCD plays an important role in the organisms' survival by preventing the proliferation of mutated chromosomes, ensuring the removal of damaged cells and maintaining cell and tissue homeostasis. To prevent PCD, high UV-B doses trigger a defense program aiming to alleviate the symptoms of oxidative stress including synthesis of the stress hormones, salicylic acid, jasmonic acid, and ethylene, upregulation of pathogenesis-related proteins, and genes participating in senescence processes (Bandurska et al. 2013). Molecular studies have revealed genes involved in response to UV exposure, with respect to PCD (Nawkar et al. 2013). Plant cell death is described as an apoptotic-like PCD (AL-PCD) (Danon et al. 2000, 2004).

In plants, AL-PCD is a cell-death process that can be defined by the presence of a number of characteristic hallmark features. These defining characteristics include recurring corpse morphology where the protoplast has shrunk from the cell wall, and the degradation of DNA, often, but not always, into DNA "ladders" (Reape and McCabe 2008). The mechanism of execution of AL-PCD is often associated with the activation of caspase-like molecules and the release of mitochondrial proteins, including cytochrome c. The death process is relatively quick, usually 6 h from initiation until the final destruction of the cell (Reape and McCabe 2008). The stress pathway activated under high-fluence UV-B radiation is independent of UVR8 signaling that includes a mitogen-activated protein kinase (MAPK) cascade (González Besteiro et al. 2011). High-fluence UV radiation has been shown to induce AL-PCD (Lam and Pozo 2000). UV-B overexposure has been shown to induce PCD in cell cultures and the tobacco cell line BY-2 (McCabe and Leaver 2000; Lytvyn et al. 2010). Interestingly, plant PCD is inhibited under dark conditions suggesting that light requirement is a plant-specific character of PCD. Caspase-like activity is also required for this type of PCD to emerge, as evidenced by the ability of caspase inhibitors to interfere with this process (Danon et al. 2004; Reape and McCabe 2008).

14.4 Associated Factors Affecting Plant UV Sensitivity

The sensitivity of plants to solar ultraviolet radiation depends significantly on the genotype, ecotype, stage of ontogenesis, as well as on the geographical latitude or altitude above sea level of the places of growth (Jordan 1996; Caldwell 1968; Torabinejad et al. 1998; Li et al. 2010, 2019). For instance, about 66% of the 300 plant genotypes studied proved to be sensitive to UV-B radiation, 25% exhibited medium sensitivity, while only 9% were insensitive (Kanash 2002).

UV-B modifies the influence of other environmental factors, often acting additively (Kanash 2002; Caldwell et al. 2003; Koti et al. 2005, 2007; Bandurska et al. 2013). UV stress often accompanies drought and heat stress. The synergistic or additive effect of UV-B has been observed to inhibit growth under water-scarce conditions (Ren et al. 2007; Ballaré et al. 2011). Similar to UV-B, increase in temperature can act as a developmental as well as a stress factor, depending on the magnitude. Considerable interactions have been established between the temperature and UV-B signaling pathways in plants (Yin and Ulm 2017). It has been shown that plants grown either at enhanced UV-B or high temperature, alone or in combination of these factors, produced smaller flowers with shorter standard petal and staminal column lengths. The damaging effects of high temperature and enhanced UV-B were not ameliorated by high CO_2 conditions (Koti et al. 2005, 2007). The flowers produced under the above test conditions had less pollen, poor pollen germination, and shorter tubes. Resistance of plants, grown in arid conditions, to UV-B radiation can be selectively affected and enhanced in subsequent plant generations (Musil 1996). Accumulated UV-B induced earlier reproductive effort, a substantial (up to 35%) decrease in the production of stems and inflorescences, lower seed productivity, as well as reduction of some physiological parameters (photosynthetic pigments and soluble sugar concentrations, seed germination success) (Musil 1996). Other studies have shown that UV-B can mitigate the negative effects of drought on photosynthetic rate, biomass accumulation, and leaf water content (Manetas et al. 1997; Schmidt et al. 2000; Poulson et al. 2006). It is believed that the selection of optimal conditions for growing plants under UV-B radiation is one of the most important tasks of agronomy. Cross-acclimatization to UV-B has been shown as a result of salt treatment (Çakırlar et al. 2008). Hardening of plants by increasing resistance to heat and drought is the most commonly used approach to increase resistance to UV.

Abscisic acid (ABA) can play a vital role in strengthening the plants to withstand environmental stress, like drought, heat, and cold (Yadav et al. 2020). There is a possibility of ABA and UV-B cross-linking to combat the combinatorial effect of multiple environmental stresses, although the exact molecular mechanism has not been determined yet. It has been suggested that UV-B induces ABA accumulation, which in turn increases the cytosolic Ca2+ levels, activates, through nitric oxide synthase, the nitric oxide signaling (Yadav et al. 2020). The latter results in enhanced antioxidant defense response (Tossi et al. 2012). Indeed, a positive correlation between the intensity of natural UV radiation and the accumulation of antioxidants has been reported (Jordan 1996; Klaper et al. 1996; Li et al. 2018; Ghasemi et al. 2019).

14.5 Influence of UV-B Radiation on Plant Sexual Reproduction

One of the most significant consequences of an increase in the level of solar UV radiation is associated with the impact on the reproductive function of plants. Surprisingly, little attention has been paid to the effect of UV-B on embryonic

processes in plants. In general, it has been shown that most generative tissues are usually effectively protected by epidermal and integumentary tissues with UV-B absorption properties (Flint and Caldwell 1983). However, the indirect effects of UV-B radiation is manifested on the phenology of flowering, morphogenesis of flowers, size and number of flowers and inflorescences, pollination, productivity, and quality of pollen grains and seeds (Demchik and Day 1996; Conner and Neumeier 2002; Koti et al. 2004, 2005; Kravets et al. 2008; Kravets 2011, 2013; Llorens et al. 2015; Reddy et al. 2016; Del Valle et al. 2020). For example, in soybean (*Glycine max*), UV-B radiation negatively affected a diversity of flower structures including flower size, pollen production, pollen germination, and even pollen tube lengths (Koti et al. 2005), and similarly decreased pollen and flower production in *Brassica rapa* (Demchik and Day 1996). However, depending on the intensity of UV and the sensitivity of the genotype, the effect of UV-B radiation on the reproductive function of plants can be either inhibitory or stimulating or have no effect at all (Day and Demchik 1996; Stephanou and Manetas 1998; Kravets et al. 2008). However, the available data look rather contradictory.

14.5.1 The Main Ways of Protecting the Reproductive Organs of Angiosperms from UV-B

The angiosperm flower performs at least a dual function: on the one hand, it is open and attractive to pollinators, and on the other hand, it is protected from the effects of biotic and abiotic environmental factors. As noted, phenolic compounds, especially phenylpropanoids and carotenoids, often accumulate in high concentrations in parts of flowers such as sepals, petals, and ovaries (Demchik and Day 1996; Becatti et al. 2009; Llorens et al. 2015). The role of UV-absorbing compounds in the plant susceptibility to UV exposure has been discussed (Fedina et al. 2006). Authors suggested that accumulation of UV-inducing compounds could be served not only as protective substances but also occur as a consequence of stress-induced damage. Among the flower structures, the female reproductive organs are best protected from UV-B radiation: firstly, with mechanical protection, and secondly, due to the accumulation of consistently higher concentrations of UV-B protective compounds in the integumentary tissues (Demchik and Day 1996; Day and Demchik 1996; Llorens et al. 2015). For example, for *Silene littorea*, UV exposure did not affect the ovules or seeds formation, but reduced pollen production and total plant seed production by 31% and 69%, respectively (Del Valle et al. 2020). The reduction of pollen production in plants exposed to UV radiation corresponds to the results for other species (Demchik and Day 1996; Feng et al. 2000; Koti et al. 2005). In spite of this, the male reproductive system is also relatively well protected from UV penetration. According to some reports, the anther wall absorbs up to 98% of ultraviolet radiation. In some entomophilous alpine plants, pollen grains are also well protected by flower structures (Zhang et al. 2014).

Synthesis of flavonoids and anthocyanins in response to solar UV-B radiation is known to be regulated by the receptor protein UVR8 (Wu et al. 2012; Morales et al.

2013). *Arabidopsis* mutants are an important tool for understanding the regulation of the phenylpropanoid pathway and the defense mechanisms against UV-B (Bieza and Lois 2001). Apart from their antioxidant function, flavonoids are also responsible for the pigmentation of flowers, fruits, and seeds, UV protection, and signaling during the times of stress. It has been demonstrated that mutant plants with chalcone synthase and chalcone isomerase deficiency that are unable to accumulate flavonoids have been shown to be more sensitive to ultraviolet light (Filkowski et al. 2004).

As shown in the recent studies, growth regulators of a new class, namely melatonin and serotonin, play an important role in chronoregulation and modulation of reproductive development in response to stress (Erland et al. 2015). Melatonin, which accumulates in some generative organs and fruits, has a high antioxidant potential, plays an important role as an endogenous scavenger of free radicals, and causes many physiological regulatory effects, thereby modulating plant resistance to abiotic stress (Pardo-Hernández et al. 2020).

According to some reports, UV-B radiation shortens the length of the inflorescence, weakens the apical dominance, and stimulates the growth of axillary buds (Jansen 2002; Hectors et al. 2007). The stimulating effects of UV-B radiation are manifested by an increase in the number and the size of flowers and inflorescences, an acceleration of flowering and differentiation of flowers and inflorescence elements, as well as the rate of sporogenesis and gametogenesis.

14.5.2 Pollen Grains as the Main Target of Ultraviolet Radiation

The main target of ultraviolet radiation is the male generative system and, above all, the pollen grain, especially in anemophilous plants (Demchik and Day 1996; Feng et al. 2000; Zhang et al. 2014; Koti et al. 2004, 2005; Benca et al. 2018). In the course of the evolution and development of the embryonic pathway, sexual dimorphism was fixed in plants, allowing mutagenesis and selection along the male line and reduction of mutagenesis and conservatism along the female one (Hastings 1991; Otto and Hastings 1998). In the male reproductive sphere of angiosperms, a balance between mutagenesis and the protective mechanisms of the gametophyte genome has been established, which ensures tissue and genetic homeostasis (Kravets et al. 2008; Kravets 2011). Thus, mutagenesis in the male reproductive sphere largely determines the formation of adaptive response in the case of stress, including UV-B radiation. Synthesis of UV-absorbing components of the cytoplasm and sporoderm is a dominating mechanism of PG genome protection against UV-B. It is the repair system that restores the DNA of the generative cell and sperms from damage, caused by oxidative stress and/or the penetration of radiation (Jackson and Linskens 1978; Ries et al. 2000a, b; Waterworth et al. 2002; Boubriak et al. 2008; Gill et al. 2015).

The sporoderm and its outer layer, the exine, play a special role in the structural physiological protective mechanisms of the PG. This is due to the sporopollenin that is located in the outer layer of the exine and absorbs most of the ultraviolet radiation (Rozema et al. 2001a, b; Bohne et al. 2003; Bell et al. 2018). Sporopollenin is a

complex biopolymer composed of para-coumaric (pCA) and ferulic acids (FA). The sculptural character of sexina (outer layer of exine) and the presence of pollen fungi, infiltrating the cavities between baculae in the PG sheath, also play a protective function in absorbing or screening UV radiation (Rozema et al. 2001a, b; Bohne et al. 2003). However, in sensitive genotypes, an increase in the activity of UV radiation, including due to the thinning of the ozone layer in the stratosphere, causes a structural change in the aperture and deformation of the baculae and pollen grains, which, in combination with other pathologies of the reproductive system, entails an increase in the sterility of coniferous forests (Benca et al. 2018).

The critical stage of pollination is the phase of pollen tube penetration into the stigma, when the generative cell or sperms are not protected (by the PG exine shell and pistil tissues) from ultraviolet radiation (Flint and Caldwell 1984; Torabinejad et al. 1998; Feng et al. 2000; Wang et al. 2010). This is especially dangerous for species with a two-celled type of pollen grain, in which generative cell division occurs in the pollen tube. In many angiosperm species, additional UV-B irradiation causes a decrease in the length of the pollen tubes, and in sensitive genotypes, even weak UV-B fluxes (50–70 mW/m^2) can suppress pollen germination (Torabinejad et al. 1998).

Indirect UV effects are mediated by mechanisms associated with photoreception, signaling, and hormonal regulation. The implications of the impact largely depend on the stage of plant development. One of the most sensitive stages of ontogenesis is timed to switch the developmental program to the reproductive pathway, which in most species is initiated by a certain photoperiod and spectral composition of light. The increased level of UV-B radiation alters the light signal of the bloom, affects the photoreceptors and the hormonal status of the plant, thereby altering the phenology of flowering (Santos et al. 1998; Conner and Neumeier 2002; Koti et al. 2004; Kravets et al. 2008; Kravets 2013).

Thus, UV-B has a complex effect on the embryonic processes and sexual reproduction of plants. Depending on the intensity, UV-B can have both a depressing and a stimulating effect on the reproductive function of plants. In general, due to the high degree of protection of the generative sphere from UV-B radiation, a positive reaction to moderate UV-B is often manifested. However, in sensitive genotypes, an increase in UV-B intensity is likely to delay the onset of flowering and decrease the yield of fruits and/or seeds. At present, the nature of these effects and the mechanisms underlying them remain unclear. There are practically no detailed data on embryonic processes, dose–response relationships, and their analysis.

Having considered the above, we have been investigated the effect of various doses of UV radiation on the formation of the male generative system (on microsporogenesis and development of pollen grain) in the sensitive genotype (*Hordeum distichum*). Most of these data have already been published (Kravets et al. 2008, 2012; Kravets 2011, 2013). However, some data on UV-induced cytomixis are presented here for the first time.

14.5.3 Impact of UV Radiation on the Development of Barley Reproductive System

Our results demonstrated that additional UV-B irradiation in all variants of the experiment (see below) accelerated the formation and differentiation of spike elements, sporogenesis, and the development of pollen grain in barley plants. Herewith, the sizes of the spike and its elements were somewhat inferior to the control ones, and in terms of the rate of generative organ differentiation, they were ahead of the control ones. No shifts in the synchronous development of male and female generative systems (heterochrony) were found (Kravets et al. 2008).

In three series of experiments, three-day seedlings of *H. distichum* (Scarlet variety of French selection) were irradiated with doses 0.5, 2.2, and 4.3 kJ/m^2 at the intensity equal to 0.5 W/m^2; 21.6 and 43.2 kJ/m^2 at an intensity of 6 W/m^2, which were approximately 3 to 5 times higher than the natural level of UV radiation per day. In another group of plants, the oversoil part was irradiated at doses of 86.4, 183.6, and 388.8 kJ/m^2, which exceeded the natural daytime radiation level by approximately 10, 20, and 45 times, respectively. Three days later following the irradiation, the seedlings were planted in open ground to study reproductive processes.

The response of the male reproductive system to UV-B-irradiation was manifested with an increase in the heterogeneity of the generative tissue of anther, the asynchrony of microsporogenesis, and the amount of cytopathology in microsporogenesis and microgametogenesis. By their nature, UV-induced cytological disorders were nonspecific.

Microsporogenesis. Induction of cytomixis. The results show that the male reproductive sphere of plants is more sensitive to the effects of UV-B than the female one. Besides, the male reproductive system of angiosperms is characterized by an increased mutability of germ cells, which is important for adaptation to stress and evolution (Otto and Hastings 1998).

Meiosis, or microsporogenesis in plants, plays an important role in the release of germ cells from the genetic loading. Performing DNA repair, recombination of alleles, sorting and filtering of mutations, as well as genome haploidization, meiosis has an essential function in plant survival (Subramanian and Hochwagen 2014; Zickler and Kleckner 2015).

Microsporogenesis in barley, as shown in classical works on cereal embryology (Romanov 1970; Batygina 1974), proceeds according to the successive type with the formation of tetrads of an isobilateral structure. Microsporogenesis usually takes place without significant deviations. A feature of the microsporangium structure of cereals is the single-layer arrangement of microsporocytes (MSC) along the tapetum cells. In some cases, according to our observations, microsporocytes are displaced into the anther cavity, lose contact with the tapetum and neighboring cells, and are delayed or stop developing (Kravets 2011, 2013).

Another way of behavior of microsporocytes in the prophase of microsporogenesis in barley is cytomixis. It is known as a type of cell-to-cell interaction through the exchange of nuclear and cytoplasmic materials (Bellucci et al. 2003, Pierre and de Sousa 2011, Lone and Lone 2013, Mandal et al. 2013, Mursalimov et al. 2013, 2019;

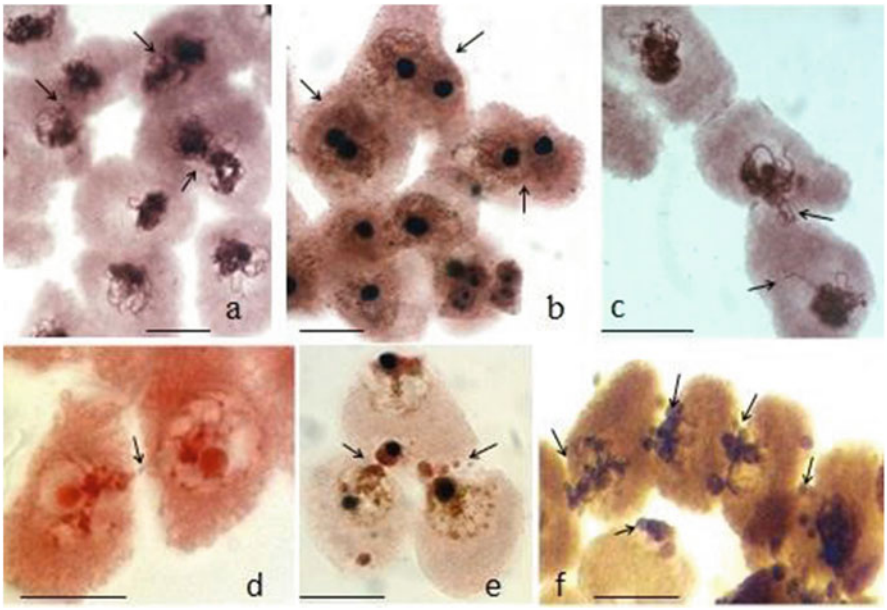

Fig. 14.1 Cytomixis in prophase of microsporogenesis of barley: (**a**–**d**) direct internuclear pairwise paired loop MSC interactions, control; (**e**, **f**) indirect micronuclear interactions, UV-B (4.3 kJ/m^2). Symbols: arrows indicate paired contacts and transient chromatin. Staining: (**a**, **e**–**g**) aceto-hematoxylin, (**c**) aceto-carmine, (**g**) silver nitrate. Scale: 10 μm (Adopted with permission from Kravets 2018; Sidorchuk et al. 2016)

Mursalimov and Deineko 2018; Kravets 2012, 2018, Kravets et al. 2021). Although the issue of cytomixis function and its effect on the course of meiosis are not completely clear, many researchers believe that such interaction is accompanied by synchronization of development and the achievement of heterozygosity. Moreover, the wide occurrence of cytomixis in terrestrial plants can testify its involvement in important genomic reorganization processes, which allow its carriers to be maintained due to natural selection process (Kravets 2012, 2013, 2018; Kravets et al. 2021).

Cytomixis is the physiological norm for some barley species. The cytological picture of cytomixis in control plants is dominated by direct paired loop interactions between neighboring microsporocytes (Fig. 14.1a–c). This type of interaction is usually accompanied by polarization of microsporocytes, partial "unraveling" ("uncoiling"), or directed "weaving" of chromosomes between adjacent nuclei followed by movement of chromatin along the channel (Fig. 14.1a–d). Paired loop MSC interactions are usually limited to the premeiotic interphase, leptotene, or zygotene, occur without the formation of micronuclei, and terminate by divergence of nuclei in the zygotene to their previous position in the cell with the continuation of

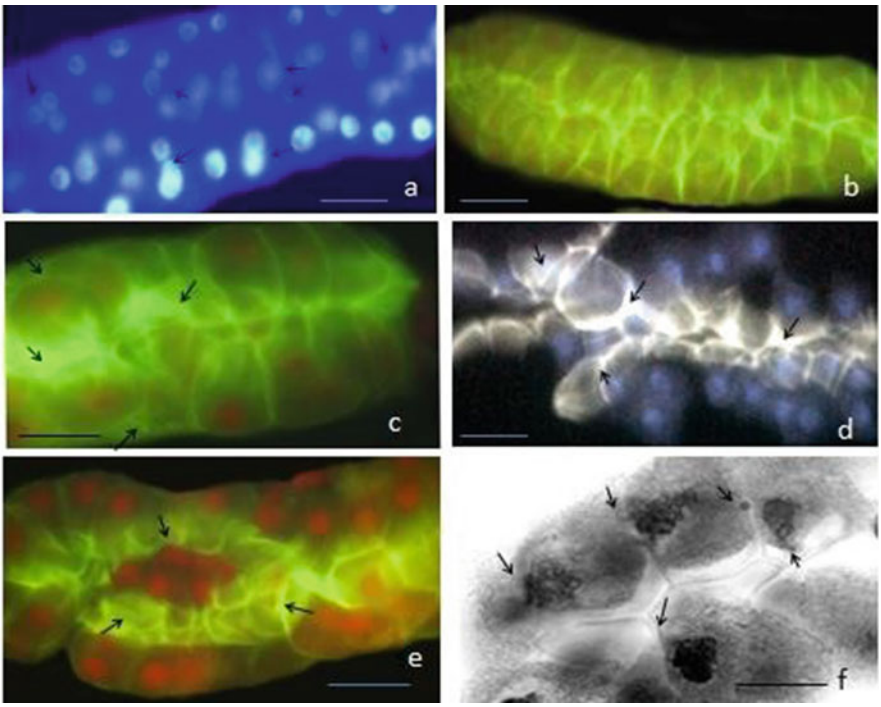

Fig. 14.2 Callose depositions in the MSC wall in microsporogenesis, the formation of callose ridges: (**a**, **b**) anther, control; (**c**) callose deposition, control; (**c**–**f**) callose secretion and hypersecretion in the anther, UV-B (86.4 and 183.6 kJ/m^2). Symbols: arrows indicate cytomictic interactions and callose depositions. Staining: DAPI (**a**), a dyes fluorescent mixture (**b**–**e**), aceto-hematoxylin (**f**) Scale: 20 μm (**a**–**c**), 10 μm (**d**–**f**) (Adopted with permission from Kravets 2013; Sidorchuk et al. 2016)

meiosis. In some cases, paired loop interactions completed by the joining of microsporocytes result in polyploidization.

It has also been established that UV-B irradiation of barley seedlings activated cytomixis in microsporogenesis. The maximum activity of cytomixis shifted toward the zygotene. Herewith, there was a transition from pair intercellular interactions to chain interactions with the formation of multicellular clusters and syncytia (Fig. 14.1e, f). Frequently, the movement of nuclei occurred simultaneously along several cytomictic channels with the formation of micronuclei of different sizes opposite the channels. It seems that the volume of chromatin entering the cell is balanced by the same volume of chromatin entering the neighboring cell (Fig. 14.1e, f).

At the beginning of the prophase of meiosis, callose begins to be deposited on the MSC shell, reaching a maximum secretion at the stage of formation of the tetrad microspore (Romanov 1970; Pacini 1994; Nishikawa et al. 2005). From the side of the tapetum, corns do not settle or are deposited in small quantities. During meiosis,

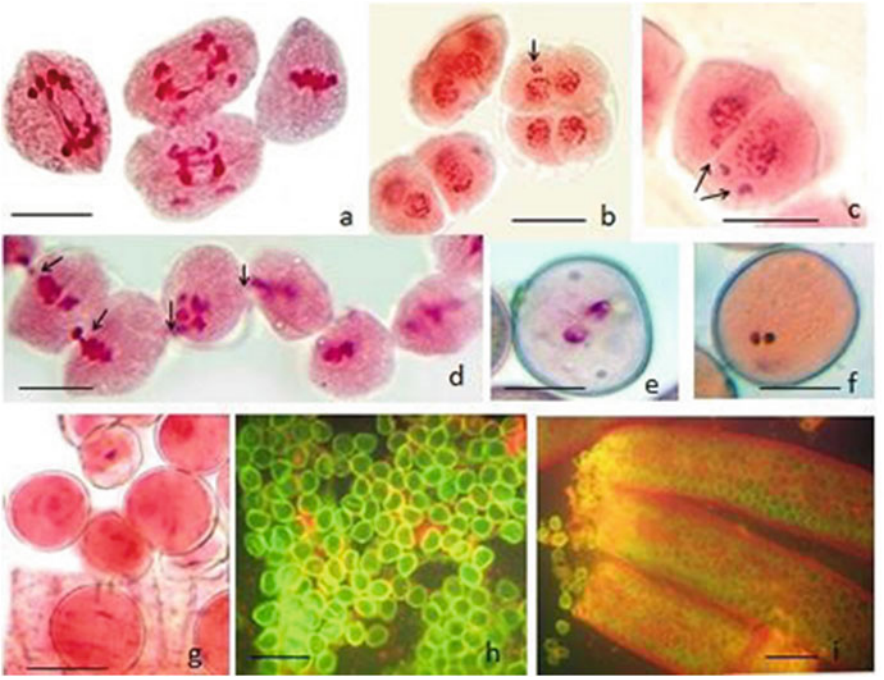

Fig. 14.3 Consequences of cytomixis, cytopathology, and pollen fertility after UV-B action (4.3 kJ/m^2): (**a**, **d**) meta-, anaphase I; (**b**, **c**) tetrads of microspores; (**e**) two-nucleus "low-plasma" PG; (**f**) degeneration of sperm in the mature PG; (**g**) PG polymorphism; (**h**, **i**) pollen fertility and anther productivity. Symbols: arrows indicate cytomictic interactions and micronucleus. Staining: (**a**–**g**) aceto-carmine, (**h**, **i**) mixture of fluorescent dyes. Scale: 10 μm (**a**–**g**), 50 μm (**h**–**i**) (Adopted with permission from Kravets 2013)

MSCs maintain close contact with tapetum cells. On the opposite side of the MSCs, facing the anther cavity, dense deposits are formed, the so-called callose ridges (Fig. 14.2b–f). At the beginning of prophase, cytomyctic channels penetrate into the callose shell of MSCs, then they are blocked by callose deposits (Mursalimov and Deineko 2011; Sidorchuk et al. 2016). Although massive callose ridges usually block intercellular interactions, single cytomictic channels can still pass through them (Fig. 14.2f). Callose secretion, growth of callose ridges, and the formation of callose partitions in anthers are amplified by UV radiation (as well as high temperatures of the summer season, which acts in addition to UV) (Fig. 14.2b, d–f). It is possible that cytomixis activation and callose hypersecretion are conjugated processes in response to UV stress.

In the subsequent course of meiosis, anomalies typical of cytomixis associated with impaired segregation and chromosome separation were identified (Fig. 14.2). These disorders can be caused by the appearance of additional chromatin and micronuclei in the cell (Kravets et al. 2021). In some cases, cytomixis extends to the following stages of meiosis (Fig. 14.3d).

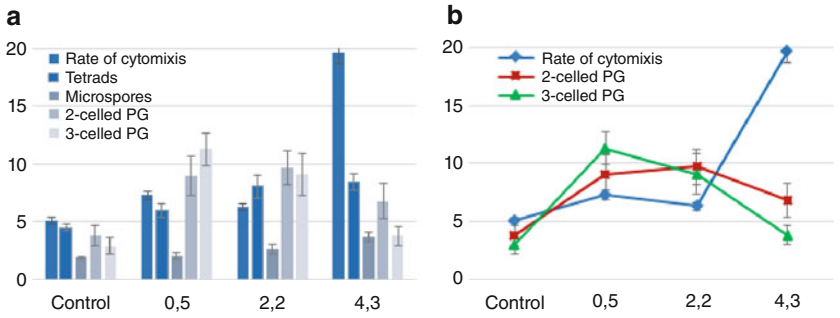

Fig. 14.4 The cytomixis rate and pollen sterility dependence on UV-B dose in male reproductive system of *H. distichum*; (**a**) diagram, (**b**) graph, horizontally—UV-B dose (kJ/m^2), vertically—anomalies on the stages, % (Adopted with permission from Kravets 2011, 2013)

Table 14.1 The indices of cytogenetic disturbances in the male generative sphere of barley plants by UV irradiation (from Kravets 2011, 2013)

UV-B dose, kJ/m^2	Microsporogenesis and the stage of the development of the pollen grain (PG)				
	Rate of cytomixis, %	Abnormal tetrads, %	Sterility of microspores, %	Sterility of two-celled PGs, %	Sterility of the three-celled PGs, %
Control	5.1	4.5 ± 0.3	1.9 ± 0.1	3.8 ± 0.9	2.9 ± 0.7
0.5	7.3	6.0 ± 0.6	2.1 ± 0.3	9.0 ± 1.7	11.3 ± 1.4
2.2	6.3	8.1 ± 1.0	2.7 ± 0.4	9.7 ± 1.5	9.1 ± 1.8
4.3	19.7	8.5 ± 0.7	3.7 ± 0.4	6.8 ± 1.5	3.8 ± 0.8

The activity of cytomixis was positively correlated with the dose (Fig. 14.4a) and the number of pathologies at the stage of tetrads and microspores (Fig. 14.4b). At the same time, most of the microsporocytes in all variants of the experiment ended in meiosis with the formation of correct tetrads of microspores, and some of them contained a micronucleus (Fig. 14.3b, c). The sterility of microspores was insignificant (Table 14.1). The negative correlation between cytomixis and PG sterility indicates the function of cytomixis as a cell selection, so that the size of the microsporocyte population can be regulated and tissue homeostasis maintained.

Interestingly, cytomictic chromatin, the appearance of which is accompanied by various cytopathologies, usually, does not induce MSC PCD. As we have shown in our recent studies, microsporocytes get rid of cytomictic chromatin during meiosis using a wide range of cellular tools, including chromosomal rearrangements, chromatin diminution, asymmetry of division, cytomixis, and finally PCD (Kravets et al. 2021).

As for callose, its functions in the generative sphere of plants are diverse. Callose can serve as a molecular filter, help to improve the carbohydrate metabolism of the anther, prevent water deficiency in the anther, etc. (Heslop-Harrison 1966a, b; Pacini 1994; Nishikawa et al. 2005). Indeed, disturbances in the synthesis and hydrolysis of callose under abiotic stress may be the result of anomalies in the carbohydrate

metabolism of the plant, as shown by analysis of gene expression in sterile and fertile rice lines (Kong et al. 2007). In our opinion, hypersecretion of callose can be considered as a marker of increased autolytic activity in the anther. Under conditions of UV-B irradiation, as well as heat stress, activation of cytomixis, accompanied by hypersecretion of callose, leads to the disruption of contacts of microsporocytes with tapetum and switching their connections, including those competing for trophic supply, with surrounding cells (Kravets et al. 2016).

Microgametogenesis. Microgametogenesis, or the development of the male gametophyte, i.e., pollen grain, in barley includes two mitotic divisions: the first (asymmetric) division of the microspore with the formation of two-cell PG, and the second division—mitosis of the generative cell with the formation of two sperm cells. Further development of PG is associated with sperm differentiation, cytoplasm synthesis, and amyloplast deposition in the vegetative cell (Batygina 1974; Mascarenhas 1989; Berger and Twell 2011). The asymmetry of the first division determines the difference in size, reduction of the cytoplasm, structure of chromatin, and transcriptional activity of vegetative and generative cells, which is necessary for the subsequent development of a pollen grain.

UV-B irradiation induced an increase in the percentage of nonspecific cytopathologies during microgametogenesis. The sterility of pollen grains when exposed to UV-B radiation is due to the following disorders in the course of their development:

1. The absence of a normally formed shell in microspores, which indicates problems in the functioning of the tapetum.
2. Cytomixis, which causes PG polymorphism (Fig. 14.3g).
3. A change in the polarity of microspores and the nature of the first (asymmetric) mitosis, which leads to the formation of two identical nuclei or two equal cells in the PG (Fig. 14.3f).
4. Abnormal differentiation and enlargement of the generative cell membrane, preventing its migration into the vegetative cell.
5. Deficiency of cytoplasm in the PG (the formation of the so-called “low-plasma” PG), indicating the problems of the trophic supply of the anther (Fig. 14.3g).
6. Incomplete differentiation of sperm due to cytoplasmic deficiency in the vegetative cell (Fig. 14.3f).

Indeed, pollen grain polymorphism is often associated with cytomixis, suggesting the participation of cytomictic chromatin in the rearrangement of their karyotype (Malallah and Attia 2003; Wu et al. 2003; Reis et al. 2015). The appearance of “low-plasma” PGs is most likely associated with the processes of autophagy in response to deficiency of trophic supply of the anther. UV-induced damages, occurring during the development of PG, were characterized by a nonlinear dependence on the dose of radiation (Fig. 14.4). UV radiation negatively impacted the sterility of mature pollen. It was established that with the radiation dose growing, the number of abnormal pollen grains initially increased up to 11.3% and then decreased down to 3.8%.

At a maximal dose of UV-B, the level of pollen sterility went down to the level of control (Table 14.1; Fig. 14.4b). Cytomixis activity positively correlated with the number of pathologies at the tetrad and microspore stages and negatively correlated with the sterility of mature pollen. Despite the increase in the sterility of PGs (maximum up to 12%) in response to UV irradiation, the pollen productivity (fullness of anther) of mature anthers in barley remained high (Table 14.1; Fig. 14.3h, i). Considering cleistogamy, we believe that additional UV doses within the range of the experiment did not inhibit the reproductive function of barley plants.

However, higher UV-B exposures (from 21.6 to 388.8 kJ/m^2) did not trigger PG sterility to grow. In the dose range up to 100 kJ/m^2, the sterility index of the PG showed a positive correlation, while a further increase in the dose resulted in the opposite (negative) effect (Table 14.2; Fig. 14.5). Our results demonstrated that sterility of two-celled PGs correlated positively with dose (0.61), while sterility of mature PGs correlated slightly negatively (−0.17). However, the productivity of anthers in plants irradiated with high UV-B doses was lower compared to the same parameter with low doses of UV-B irradiation, which indirectly indicates an intensification of cell selection, viz. the activation of PCD mechanisms. Indeed, it has been shown that high UV exposures can induce AL-PCD (McCabe and Leaver 2000; Lytvyn et al. 2010).

Our results have revealed that the type of pollination in the irradiated plants remained unchanged. Pollination took place in a tightly closed "bud," due to two floral scales, cleistogamous. Cleistogamy reliably protects the germinated PG and pollen tubes (PT) from external factors and contributes to the creation of a moist chamber, in which, after the germination of the PG and pollination, unused pollen is quickly utilized by the pistil tissues.

Plant productivity. The length of the juvenile spike negatively correlated with the radiation dose (−0.91); the length of a mature spike also revealed a low negative dose response (−0.28) (Fig. 14.5b; Table 14.2). Nevertheless, the weight of the caryopses positively correlated with the radiation dose (0.67), which could be due to other reasons, for example, a change in the size of the spike. No visual changes in the color of spike, flowering scales, and integument of caryopses were observed. As noted above, the photochemical efficiency of plants grown under conditions of intense UV radiation usually decreased (Musil 1996; Hollósy 2002; Yadav et al. 2020). It has been shown that UV halved the photosynthetic activity in *Silene littorea*, although their ability to recover from light stress was not affected (Del Valle et al. 2020). The yield reduction under the conditions of high temperature and ultraviolet radiation may be due to the negative impact of these factors on the reproduction at both organ and process levels (Teramura and Ziska 1996; Koti et al. 2005).

Thus, the productivity of a plant is largely determined by the sensitivity of the genotype, the ways of protection, adaptability of the plant to UV radiation, including the protection of generative organs, and cross-interactions with other mentioned above abiotic stresses.

The negative correlation between cytomixis and PG sterility indicates, as noted above, the function of cytomixis as a cell selection, activated with an increase of the

Table 14.2 Influence of increased doses of UV-B irradiation on the spike development and productivity of barley plants (Kravets et al. 2008)

N	Experiment variants, dose of kJ/m^2	Juvenile spike length, cm	Cc	Mature spike length, cm	Cc 1	Sterility of two-cell PGs, %	Cc 2	Sterility of mature PGs, %	Cc 3	Weight of 100 caryopses, g	Cc 4
1	Control	5.2 ± 0.8	−0.91	5.6 ± 0.7	−0.28	0.9 ± 0.1	0.61	2.8 ± 0.4	−0.17	3.67 ± 0.4	0.67
2	21.6 (1.1)	5.1 ± 0.9		5.8 ± 0.9		3.2 ± 0.1		5.9 ± 0.8		3.78 ± 0.5	
3	43.2 (1.2)	5.2 ± 1.0		6.4 ± 1.0		2.9 ± 0.1		6.5 ± 0.9		4.05 ± 0.6	
4	86.4 (2.1)	4.6 ± 1.1		5.3 ± 0.9		4.4 ± 0.2		6.9 ± 0.9		4.08 ± 0.6	
5	183.6 (2.2)	4.9 ± 1.0		5.9 ± 0.9		3.4 ± 0.1		6.5 ± 1.1		4.12 ± 0.8	
6	388.8 (2.3)	4.0 ± 1.2		5.5 ± 1.2		4.3 ± 0.2		3.9 ± 0.9		4.12 ± 0.8	

Cc the correlation coefficient between the radiation dose and the length of a juvenile spike, *Cc 1* the correlation coefficient between the radiation dose and the length of mature spike, *Cc 2* the correlation coefficient between the radiation dose and sterility of two-cell PGs, *Cc 3* the correlation coefficient between the radiation dose and sterility of mature PGs, *Cc 4* the correlation coefficient between the radiation dose and weight of 100 caryopses

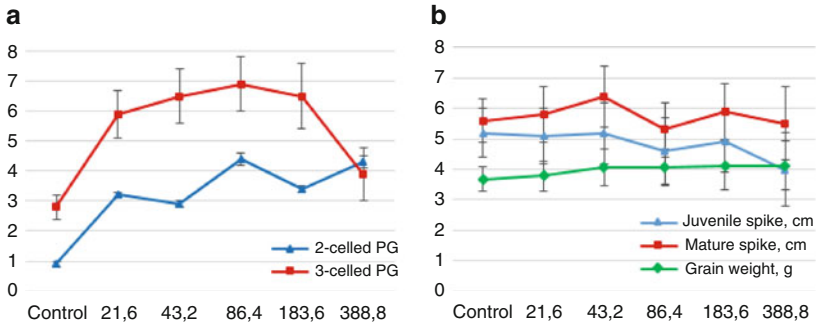

Fig. 14.5 Dose dependence of the pollen sterility (**a**), length of spike and the weight of the grain (**b**); horizontally—UV-B dose (kJ/m^2), vertically—parameters of pollen sterility (**a**), length of spike and grain weight (**b**) (Adopted with permission from Kravets et al. 2008)

UV dose. At the same time, in the range of low doses of ultraviolet radiation, the induced damage was not eliminated by the cell selection and, as a result, the number of violations during the development of the PG can increase.

However, with increasing UV irradiation dose, the number of cytopathologies decreased by the end of the haplophase. This allows us to conclude that meiosis and the concomitant cytomixis are apparently the most important part of a cellular (haplontic) selection in the male generative sphere of plants. It can also be assumed that the intensity of the selection increases proportionally to the increase in mutagenesis, weakening of homeostasis, and tissue integration (Kravets 2011, 2013). Pathology of PG development is usually accompanied by morphological signs of autophagy (Conner and Neumeier 2002; Tang and Bassham 2018) and the death of sperms and the nucleus of a vegetative cell occurs in the form of apoptotic-like PCD (AL-PCD) (Danon et al. 2000, 2004; Nawkar et al. 2013).

Results of PCR and PCR-RFLP analysis. To study the genome variability of barley, we performed PCR analysis with primers to microsatellite repeats (Kravets et al. 2012). These repetitive sequences are widespread in the plant genome, and they are considered a source of genetic polymorphism. The results obtained by PCR and PCR-RFLP analyses revealed an increasing genome variability in plants exposed to UV. It is possible that UV irradiation induced recombination processes involving repetitive sequences used in our studies as DNA markers. The increase of genome variability was detected both for vegetative and reproductive tissues. However, the polymorphic level was higher in vegetative tissues than in reproductive ones (Kravets et al. 2013). This testifies that reproductive organs of plants are better adapted to UV-B exposure than vegetative ones. An increased level of genetic polymorphism in response to solar UV-B radiation has also been found in other species (Puchta and Hohn 1996; Cuadra et al. 2010). As it has been shown (Puchta and Hohn 1996), rearrangements between homologous DNA sequences in somatic cells are strongly stimulated by DNA-damaging agents. However, prolonged exposure to high UV-B levels may affect reproductive tissues and cause DNA damage (Ries et al. 2000b). Homologous recombination, as previously reported, is one of the

main strategies to minimize DNA damage in plants (Hutchinson 1987; Ries et al. 2000a, b; Liu et al. 2000; Dubest et al. 2002; Molinier et al. 2008; Gill et al. 2015). We assume that genome rearrangement can be one of the many mechanisms of plant adaptation (Kovalchuk et al. 2004). Besides, the development of the adaptive response of plants under stress can be attributed to the high level of genome variability, which allows plants to adapt to the environment. Possibly, reproductive tissues have more robust defense mechanisms that activate DNA repair processes, homologous DNA recombination, and cell selection, including PCD, in response to mutagenic agents. The strategy of enhancing the resistance to natural UV levels may be dominated by sublethal DNA damage that activates repair systems, while high UV levels may predominate over potentially lethal DNA damage (double-strand breaks) that trigger cell selection, including PCD.

14.6 Conclusion

Having analyzed the obtained results, we would like to conclude that in the strategy of enhancing the resistance of the generative organs of flowers to UV-B, a great importance is attached to the activation of various protective mechanisms against UV radiation, in particular, changes in gene expression when UV-B causes damage or UV-specific UVR8-mediated photoinduction. Plants respond to UV-B radiation through the activation of synthesis of protective pigments and UV-absorbing compounds, and changes of gene expression that encode DNA repair proteins and enzymes responsible for scavenging reactive oxygen species. The generative organs of angiosperms are sufficiently effectively protected from UV-B by integumentary tissues, in which substances that absorb UV-B are accumulated. However, pollen and the pollination process are vulnerable to UV radiation. In cleistogamous or self-pollinating species, the reproductive organs are better protected from direct exposure to UV-B. The flower is indirectly exposed to ultraviolet radiation. According to our data, the response of the male reproductive system to UV is manifested in the asynchrony of microsporogenesis, increased nonspecific cytopathology (activation of cytomixis), and pollen sterility.

Increased UV-B radiation has a negative effect on the trophic supply of the plant. This is evidenced by the acceleration of flowering and differentiation of the reproductive elements of the spike, reducing its size, activation of cytomixis, accompanied by hypersecretion of callose, an increase in the content of “low plasma” PG with signs of autophagy and PCD.

The response to UV stress is accompanied by genome reorganization, which may be one of the mechanisms of plant adaptation.

Sublethal DNA damage, which activates repair systems, and potential lethal damage, which triggers cell selection, may be involved in the development of resistance to UV-B. The dose dependence of the induction of cytopathology in reproductive processes are nonlinear. With increasing UV radiation, cell selection plays an important role; its activation has a threshold character. As the UV dose increases, the “genetic load” in reproductive tissue can be more effectively

eliminated. Meiosis and cytomixis seem to play a crucial role in the mechanisms of cell selection, limiting mutagenesis and regulating the homeostasis of the microsporocyte population.

Future research may further clarify the current understanding of UV-B-mediated regulation of plant reproductive development.

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Crosstalk Between Melatonin and Nitric Oxide in Plant Development and UV-B Stress Response

15

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Abstract

In recent years, much attention has been paid to the study of melatonin functions, as well as melatonin-NO cross-talking in plant responses to stress. Melatonin, as a secondary messenger molecule and growth regulator, plays an important role in reducing the damaging effects of abiotic stress by neutralizing ROS, maintaining oxidative homeostasis in the cell, and regulating the activity of genes associated with stress response. NO is also a signaling molecule that is involved in many physiological functions and, therefore, plays an important role in responses to various abiotic stresses. The interactions between melatonin and nitric oxide occur through various intermediate biomolecules, namely phytohormones, phenolic compounds, antioxidant enzymes, ROS, and other metabolites. One of the mechanisms of the protective action of melatonin is the activity of trapping NO and peroxynitrite, as well as inhibiting the production of NO and the activity of NO synthase. However, the molecular mechanisms underlying melatonin-NO cross-interactions in plant UV-B responses are still poorly understood. The identification of key molecules involved in melatonin-NO signaling is important for the development of new strategies to reduce the effects of environmental stresses.

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Keywords

Melatonin-nitric oxide signaling · UV-B stress · Protective mechanism of melatonin · Plant response to stress

15.1 Introduction

Plants lead an attached-to-ground lifestyle and, therefore, must constantly withstand the effects of various environmental factors that negatively affect plant growth and development (Kaling et al. 2015). Ultraviolet radiation (UV-B, wavelength 280–315 nm) is an intrinsic component of solar radiation reaching the Earth's surface and affecting the biosphere (Yin and Ulm 2017). High doses of UV-B can seriously damage plant cells by disrupting the integrity and functioning of vital macromolecules (DNA, lipids, and proteins), causing oxidative damage of mitochondria and chloroplasts, reducing intensity of photosynthesis and plant biomass, impairing phenological processes, and damaging the generative system (Hideg et al. 2013; Jenkins 2009). Therefore, plants develop various mechanisms to mitigate the negative effects of stressors. Such molecules as ethylene, hydrogen sulfide, calcium, nitric oxide (NO), as well as phytohormones (JA, ABA, and GA) are involved in the plant's response to stress (Domingos et al. 2015; Dubois et al. 2018; Gilroy et al. 2016; Li et al. 2015).

In recent years, much attention has been paid to the study of the function of melatonin, which plays an important role in plant development and defense responses (Fan et al. 2018a, b; Sun et al. 2021). Through its interaction with NO and other free radicals, melatonin plays an important role in plant response to abiotic stress (Arnao and Hernández-Ruiz 2019). Melatonin, on the one hand, can reduce oxidative stress by suppressing NO production and NO synthase activity (Aydogan et al. 2006). On the other hand, it can initiate the activation of the arginine pathway, which promotes NO accumulation and increases NO synthase activity by regulating the expression of linked genes (Liu et al. 2019). The interaction between melatonin and NO is challenging due to the cross-talking of different signaling pathways. Interaction occurs through various intermediate biomolecules, namely phytohormones, phenolic compounds, antioxidant enzymes, ROS, and other metabolites. The mechanisms of interaction of melatonin with NO in plants are poorly understood. The identification of key target molecules involved in UV-B signaling is important for the development of new strategies to reduce the effects of this stress.

15.2 Regulatory Roles of Melatonin in Plants

Melatonin (N-acetyl-5-methoxytryptamine) is a biomolecule derived from tryptophan which was discovered in 1958 in the pineal gland of cattle (Hardeland et al. 2011). Melatonin has been shown to play a key role in the regulation of antioxidant

enzymes (Rodriguez et al. 2004) and circadian rhythms (Brainard et al. 2001). It affects motor activity, body temperature, mood, sleep, and immune responses (Carrillo-Vico et al. 2013). In plants, melatonin was discovered in 1995 (Hattori et al. 1995). As it was shown in a number of studies, melatonin is formed in plants from tryptophan through four main enzymatic reactions catalyzed by various enzymes (Back et al. 2016). It is contained in various organs of plants, such as roots, stems, leaves, fruits, and seeds. Many factors stimulate melatonin biosynthesis in plants such as light (Byeon et al. 2012), ultraviolet radiation B (UV-B) (Afreen et al. 2006), temperature changes (Byeon and Back 2014), and others. In most plants, melatonin biosynthesis begins with tryptophan catalyzed by tryptophan decarboxylase (TDC) to tryptamine. The latter is then catalyzed by tryptamine 5-hydroxylase (T5H) to serotonin and, finally, to melatonin in two steps (Posmyk and Janas 2009). In some other plants, tryptophan is catalyzed by tryptophan hydroxylase (TPH) to 5-hydroxytryptophan which is converted to serotonin by aromatic-L-amino-acid decarboxylase (TDC/AADC) (Murch et al. 2000). This alternative pathway is similar to the melatonin biosynthesis observed in animals. In the third stage, arylalkylamine N-acetyltransferase (AANAT) or N-acetyltransferase (SNAT) converts serotonin to N-acetyl-serotonin. In the final step, N-acetyl-serotonin is catalyzed by N-acetyl-serotonin methyltransferase (ASMT) or hydroxyindole-O-methyltransferase (HIOMT) to melatonin (Fig. 15.1). HIOMT can also convert serotonin to 5-methoxytryptamine which is then converted to melatonin by SNAT. Recently, a reverse metabolic pathway of melatonin has been shown in which N-acetyl-serotonin is converted to serotonin by N-acetyl-serotonin deacetylase (Lee et al. 2018). In addition, tryptophan is not only a substrate for melatonin biosynthesis but also a precursor of indole-3-acetic acid (IAA). This indicates a certain structural and functional identity of melatonin and IAA and the multifunctional role of these compounds in plants.

A number of studies have shown that melatonin plays a much larger role in plant development than in other organisms. As a new class growth regulator, melatonin can regulate plant growth and development including slowing down leaf aging (Murch and Saxena 2002), restoring of roots (Hardeland 2016), chronoregulation, and reproductive development (flowering, embryogenesis and ripening of fruits (Arnao and Hernández-Ruiz 2015; Erland et al. 2015; Golembeski et al. 2014). One of the most interesting aspects of melatonin is its role as a protector and a mediator against a number of stress factors such as UV radiation, chemical pollutants, extreme temperatures, fungal pathogens, drought, salt, and cold stresses (Arnao and Hernández-Ruiz 2015; Wei et al. 2019; Zhang et al. 2014a, b). In particular, it was shown that exogenous melatonin could increase the rate of root growth in *Phalaris*, *Triticum,* and *Arabidopsis* (Arnao and Hernández-Ruiz 2018). Leaves treated with different concentrations of cytokinin had a similar phenotype to those treated with melatonin indicating a synergistic role of these phytohormones in delaying plant aging (Wang et al. 2012). Melatonin can also interact with gibberellins (GA) or abscisic acids (ABA) during plant growth and stress response. It is believed that melatonin primarily functions as an antioxidant and scavenger of free radicals, in particular, by controlling active forms of oxygen and nitrogen, and

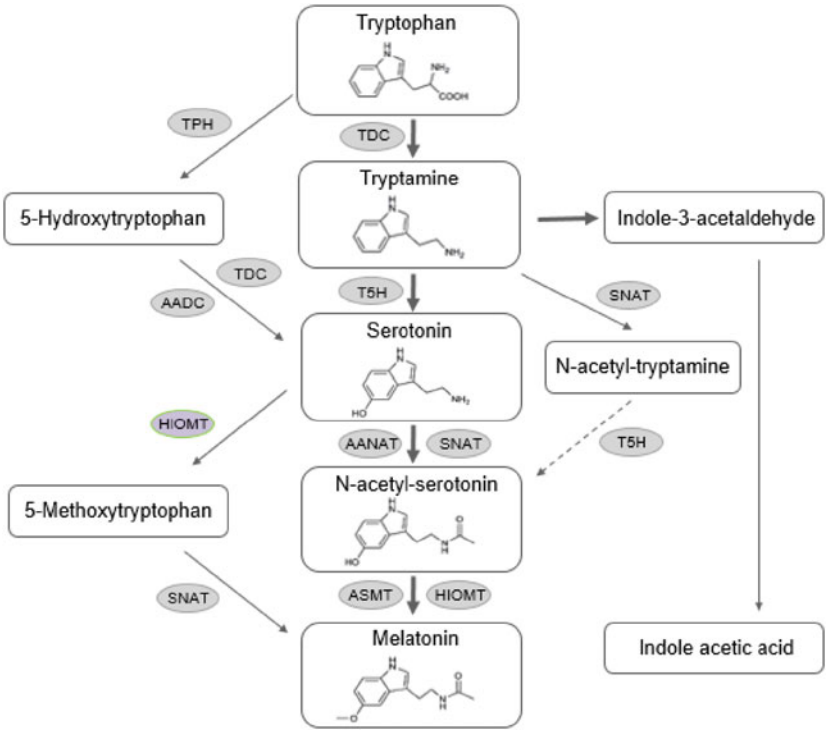

Fig. 15.1 Biosynthetic pathway for melatonin in plants. *TDC* tryptophan decarboxylase, *TPH* tryptophan hydroxylase, *T5H* tryptamine 5-hydroxylase, *AANAT* arylalkylamine N-acetyltransferase, *SNAT* serotonin-N-acetyl-transferase, *ASMT* N-acetylserotonin methyltransferase, *AADC* aromatic-L-amino-acid decarboxylase, *HIOMT* hydroxyindole-O-methyltransferase (Fan et al. 2018a, b; Khan et al. 2020)

acting as a regulator of oxidative homeostasis of plant cells (Hardeland 2016). It was also shown that low concentrations of melatonin promote roots growth while its high concentrations do the opposite. This peculiarity, in parallel with other parameters, indicates the action of melatonin being comparable to IAA (Sarropoulou et al. 2012).

15.3 Nitric Oxide Synthesis and Signaling Pathways in Plants

Nitric oxide (NO) is known to be an important signaling compound possessing both prooxidant and antioxidant properties. The dual effects of NO are mainly determined by its local concentration and spatial mode of generation. In response to stress, NO can interact with other redox molecules and regulate protein function through a variety of mechanisms (Sami et al. 2018). Apart from that, NO is involved in such biological processes as plant growth and development (Sanz et al. 2015), seed germination (Arc et al. 2013), functioning of the stomata (Gayatri et al. 2013),

response to pathogen infection (Mur et al. 2006), and response to influence of abiotic environmental factors (Krasylenko et al. 2017; Lytvyn et al. 2016; Nabi et al. 2019; Plohovska et al. 2019).

In animals, three different enzymes, NO synthases (NOS), have been identified to oxidize arginine with the formation of NO (Domingos et al. 2015). In plants, both enzymatic and non-enzymatic pathways of NO synthesis have been identified. The first identified enzyme was nitrate reductase (NR) which usually reduces nitrate (NO^{3-}) to nitrite (NO^{2-}) but which can also reduce nitrite to NO and peroxynitrite derivative ($ONOO^-$) using NADPH as a cofactor (Sakihama et al. 2002; Stöhr et al. 2001). Another key enzyme in NO biosynthesis is NO associated with *A. thaliana* (AtNOA1) which was previously described as a catalyst for the conversion of L-arginine to L-citrulline (Corpas et al. 2009). It has been confirmed that S-nitrosoglutathione reductase (GSNOR) negatively regulates accumulation of NO in some plant species (Chen et al. 2009). Non-enzymatic sources of NO include carotenoids, phenolic compounds, and ascorbic acid (Bethke et al. 2007; Santolini et al. 2017). NO can also be formed from nitrite under acidic conditions (Crawford 2006). Production of NO and ROS in plant cells can be triggered by hormones or environmental stresses. The dynamic balance of ROS and NO is a key factor in determining the redox state of cells and is important for normal functioning of plants (Lindermayr and Durner 2015).

NO molecules play an important role in posttranslational modifications (PTM) of proteins. The most common NO-mediated PTM is S-nitrosylation, which consists in adding a nitroso group to the thiol group (SH) of a specific cysteine residue (Cys). As a result of this interaction, S-nitrosothiol (SNO) is formed that can cause conformational changes in protein activity or function (Spadaro et al. 2010). The second most common NO-mediated PTM is tyrosine nitration (NO_2-Tyr) (Holzmeister et al. 2015). Tyrosine nitrification alters superoxide dismutase (SOD) activity followed by a change in ROS signaling, peroxynitrite production, and tyrosine nitration (Kolbert et al. 2017). Nitration of tyrosine residues and S-nitrosation of cysteine residues affect key amino acids involved in binding the essential FAD and molybdenum cofactors. NO-related PTMs were accompanied by ubiquitylation of lysine residues flanking the nitration and S-nitrosation sites. This self-regulating feedback can control nitrate assimilation to the production of nitrogen and nitrites, which occurs under stressful environmental conditions (Costa-Broseta et al. 2021).

The increased NO signaling enhances antioxidant protective response. Indeed, there is a positive correlation between the intensity of natural UV radiation and the accumulation of antioxidants (Lee and Back 2018). However, the functions of NO in cells remain unclear. Numerous studies indicate that NO production is a step in the signaling cascade that includes ROS, phytohormones, protein kinases and secondary messengers such as Ca^{2+} and cGMP (Astier et al. 2018). The use of exogenous melatonin can promote the production of sugar and glycerol that leads to increased levels of salicylic acid and NO. Melatonin and NO in plants can act together to promote lateral root growth, delay aging, and repair iron deficiency (Liu et al. 2019). However, further research is needed to elucidate the relationship between melatonin and NO in plant development.

15.4 Crosstalk Between Melatonin and Nitric Oxide

15.4.1 Melatonin and Nitric Oxide in Plant Growth and Development

NO interacts with melatonin as a long-range signaling molecule, and helps regulate plant growth and maintain oxidative homeostasis (Aghdam et al. 2019; He and He 2020). The primary molecule formed as a result of the interaction between melatonin and reactive nitrogen species (RNS) is N-nitrosomelatonin (NOmela) that functions as an intracellular NO reserve (Bhatla 2016). In animals, melatonin (in the nanomolar range) is known to function as a mediator of NOS-mediated NO biosynthesis in neuronal cells (Arese et al. 2012). Melatonin has been shown to induce NOS mitochondrial mRNA expression and NOS protein synthesis (Sarti et al. 2012). Recent plant studies show a pathway for NO and melatonin cross-linking associated with redox signals and induction of stress tolerance (Aydogan et al. 2006; Fan et al. 2018a, b; He and He 2020). The peroxynitrite ($ONOO^-$) anion formed by the interaction of NO and O_2^- is a toxic molecule (Beckman et al. 1994). Melatonin can neutralize peroxynitrite or peroxynitric acid anions by interacting with the indole part present in melatonin. At physiological pH, it can only react with ONOOH or its activated form (ONOOH*) (Zhang et al. 1999).

It has been shown that exogenous melatonin can increase endogenous NO levels by inhibiting GSNOR expression activity and regulating NR expression (Wei et al. 2019; Wen et al. 2016). Melatonin, which accumulates during fruit ripening in tomatoes, can act as an antioxidant to neutralize free nitrogen (Corpas et al. 2018). Also, melatonin mediates cross-links between NO and ethylene and regulates fruit ripening through NOMela (Mukherjee 2019a). The example of a pear shows that melatonin reduces the production of ethylene while regulating the synthesis of NO (Liu et al. 2019). On the other hand, using the cGMP-dependent pathway, NO induces the expression of TDC, T5H, SNAT, and COMT that leads to increased melatonin levels (He and He 2020). Therefore, the mechanism of interaction of NO and melatonin reveals a certain degree of complexity in terms of their affinity for binding (Mukherjee 2019b). The cross-links between NO and melatonin act through various intermediate biomolecules, such as plant hormones, antioxidant enzymes, ROS, and other metabolites. The mechanism of interaction between these biomolecules acts at the genomic, proteomic, and transcriptomic levels of various plant tissues.

15.4.2 Melatonin and Nitric Oxide in Stress Tolerance

During growth and development, plants are exposed to a variety of abiotic stresses that can lead to reduced yields of most agricultural crops. In response to abiotic stress, melatonin acts as a potent antioxidant that increases the levels of superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPx), glutathione reductase (GR), and glucose. Melatonin and NO show a similar mode of action in plant cells. NO reacts with ROS to improve redox homeostasis and enhance antioxidant

capacity (Correa Aragunde et al. 2015). Studies of the relationship between melatonin and NO for certain types of abiotic stress are combined by us into a summary Table 15.1.

It has been shown that melatonin can scavenge free radicals, including hydroxyl radicals, hydrogen peroxide, peroxyl radicals, singlet oxygen, nitric oxide (NO), and peroxynitrite anion (Aghdam et al. 2019; He and He 2020). An excessive amount of NO, free radicals formed by the induction of NO synthase, is known to cause cytotoxic changes in cells. Hence, NO synthase is considered a pro-oxidative enzyme, and any factor that reduces its activity would be considered an antioxidant. Recent studies have shown that melatonin inhibits the activity of NO synthase but its NO and peroxynitrite scavenging activity (Pardo-Hernández et al. 2020). Thus, inhibition of NO production may be another means whereby melatonin reduces oxidative damage under stress conditions, where NO is important in terms of the resulting damage (Aydogan et al. 2006).

15.5 Melatonin and Nitric Oxide Under UV-B Stress

15.5.1 The Role of Melatonin in Reducing the Negative Effects of UV-B on Plants

Ultraviolet-B (UV-B) is the most harmful part of UV radiation, which is an important regulator of plant growth and development (Hideg et al. 2013). However, the role of melatonin in response to UV-B stress has not been duly researched. General experience shows that alpine or Mediterranean species or varieties, which are exposed to strong sunlight and UV intensities, contain considerably higher melatonin levels than the same or related species from other habitats, as reviewed elsewhere (Hardeland 2016). However, high light intensities do not generally trigger an increase in melatonin levels, as shown recently in *Oryza* in which a heat-induced increase was antagonized by light (Byeon et al. 2012). Stress, but not necessarily the stress response, is frequently associated with an enhanced formation of oxidants due to, for example, malfunction of electron transport chains. A recent study on experimental water deficiency by polyethylene glycol in *V. vinifera* cuttings showed damage by increased superoxide and H_2O_2, and decrease in chlorophyll content and photosystem II efficiency, as well as changes in the ultrastructure of chloroplasts and leaf anatomy. All these alterations were counteracted by melatonin (Hardeland 2015; Meng et al. 2014).

Melatonin may act as a regulator of photosynthesis (Xu et al. 2016). As shown on rise and soybean plants, the protective role of melatonin in photosynthesis can be achieved due to an increased stomatal activity (Gitz et al. 2005). In particular, a higher stomatal density on the adaxial leaf surface and a larger stomatal aperture may explain why plants pretreated with melatonin were able to maintain higher photosynthetic activity under UV-B stress (Wei et al. 2019). The potential change in stomatal density is considered to be the result of UV damage to the developing

Table 15.1 The role of melatonin and NO under abiotic stresses

Stress	Plants	Effects	References
Salinity	*Solanum lycopersicum* L.	Stress-inhibited growth and photosynthetic capacity by causing serious sodium toxicity and oxidative damage in tomato plants, but this deleterious effect could be alleviated by exogenous melatonin (50 μM) or NO (100 μM)	Liu et al. (2015)
Salinity	*Helianthus annuus* L.	Melatonin (15 мМ) and NO (250 мМ SNP) differentially ameliorate salt stress effect by modulating GR activity and GSH content in seedling cotyledons	Kaur and Bhatla (2016)
Salinity	*Helianthus annuus* L.	Exogenous melatonin (15 μM) and NaCl (120 mM) inhibit seedling growth, which is also correlated with NO availability, accumulation of potential superoxide anion and peroxynitrite anion, extent of tyrosine nitration of proteins, spatial localization, and activity of superoxide dismutase isoforms	Arora and Bhatla (2017)
Salinity	*Brassica napus* L.	Application of melatonin and NO-releasing compound not only counteracted NaCl-induced seedling growth inhibition, but also reestablished redox and ion homeostasis, the latter of which are confirmed by the alleviation of ROS overproduction, the decreases in thiobarbituric acid production and Na^+/K^+ ratio	Zhao et al. (2018)
Salinity	*Oryza sativa* L.	Melatonin pretreatment (200 μM) increased the fresh and dry weight of rice seedlings under salt stress. Melatonin increased the activity of nitric oxide synthase (NOS). The polyamines content and the utilization of arginine were also increased, thereby increasing NO content in salt-stressed rice seedlings	Yan et al. (2020)
Heat	*Solanum lycopersicum* L.	Pretreatment with 100 μM melatonin (7 days) followed by exposure to heat stress (24 h) effectively reduced the oxidative stress by controlling the overaccumulation of superoxide and hydrogen peroxide lowering the lipid peroxidation content	Jahan et al. (2019)
Cold	*Lycopersicon esculentum* cv. Izmir	Chilling tolerance (4 °C) in tomato fruits in response to exogenous melatonin applying at 100 μM arise by enhancing *CBF1* gene expression giving rise to triggering endogenous NO accumulation arising from higher nitric oxide synthase (NOS) gene expression	Aghdam et al. (2019)
Cold	*Camellia sinensis* L.	Treatment with melatonin (100 μM) mitigated cold-induced reductions in photosynthetic capacity by reducing oxidative stress through	Li et al. (2018)

(continued)

Table 15.1 (continued)

Stress	Plants	Effects	References
		enhanced antioxidant potential and redox homeostasis	
Drought	*Medicago sativa* L.	Rhizospheric application of melatonin (10 μmol L^{-1}) remarkably enhanced the drought tolerance of alfalfa plants. In addition, lower levels of lipid peroxidation as well as of both H_2O_2 and NO contents resulted in the systemic mitigation of drought-induced nitrooxidative stress	Antoniou et al. (2017)
Heavy metals (Cd)	*Triticum aestivum* L.	The results showed that melatonin (50 or 100 μM) treatments increased plant growth attributes and leaf Ca^{2+} and K^+ in the leaves, but reduced MDA, H_2O_2, as well as leaf Cd content compared to those in Cd-stressed plants. Thus, melatonin enhanced tolerance of wheat seedlings to Cd toxicity by triggering the endogenous NO	Kaya et al. (2019)
Heavy metals (Cd)	*Oryza sativa*	Cd-induced melatonin synthesis was significantly impaired by treatment with either an H_2O_2 production inhibitor (10 μmol/L DPI) or an NO scavenger (100 μmol/L cPTIO). The combination of both inhibitors almost completely abolished Cd-induced melatonin synthesis, suggesting an absolute requirement for H_2O_2 and NO	Lee et al. (2017)
Heavy metals (Cd)	*Catharanthus roseus* L.	The co-application of melatonin (100 μM) and SNP (200 μM) usage augmented Cd tolerance through increasing activities of antioxidant enzymes and regulating mineral homeostasis. Furthermore, they increased Cd phytoremediation efficiency through increasing biomass and elevating uptake	Nabaei and Amooaghaie (2020)
Heavy metals (Cd)	*Brassica campestris* spp. *chinensis* L.	Metionin significantly increased the biomass and photosynthetic parameters of plants compared with the control under Cd stress. Metionin also reduced the level of Cd-induced NO, and at the same time, the enzyme activity related to NO synthesis and the expression of related genes were decreased	Wang et al. (2021)
Heavy metals (Pb)	*Zea mays* L.	Metionin (50 and 100 μM)-induced tolerance to Pb toxicity was totally eliminated by cPTIO (100 μM) by reversing endogenous NO. The present results clearly indicated that metionin mediated the endogenous NO to improve tolerance of maize plants to Pb toxicity	Okant and Kaya (2019)
Heavy metals (Al)	*Arabidopsis thaliana*	Melatonin (10 μM) alleviates Al-induced root growth inhibition by interfering with NO-mediated reduction of cell division cycle	Zhang et al. (2019)

(continued)

Table 15.1 (continued)

Stress	Plants	Effects	References
		progression and the quiescent center cellular activity in roots	

stomatal initials, rather than the result of a true photomorphogenic process (Wei et al. 2018).

Like other abiotic stresses, high doses of UV-B cause excessive ROS production in plant cells by affecting the proteins involved in light reactions as demonstrated on spinach leaves with fluorescent ROS probes (Barta et al. 2004). It has been shown that UV-B irradiation can increase the level of melatonin in the roots of *Glycyrrhiza uralensis* (Afreen et al. 2006). Melatonin induction was the highest in plants that had been exposed to high levels of UV-B radiation for 3 days followed by a reduced UV irradiation for 15 days (Afreen et al. 2006). Decreased melatonin content during longer periods of UV-B exposure suggests that melatonin synthesis may be associated with integrated magnitude (intensity/duration) of UV-B exposure.

It was found that the absorption spectrum of melatonin in water expands from 200 to 320 nm with a maximum at 278 nm and covering the region of the UV-B electromagnetic spectrum. Melatonin can relieve stress from UV-B by directly absorbing UV-B and reducing the formation of ROS. Measurement of the total number of UV-absorbing leaves indicates that melatonin-treated plants accumulate these molecules under UV-B stress more rapidly. These results show that melatonin itself, or other metabolites regulated by melatonin, may increase the ability of leaves to absorb UV-B (He et al. 2005).

15.5.2 Regulatory Role of Melatonin in UV-B Signaling Pathway

Melatonin regulates the UV-B signaling pathway and changes gene expression by affecting antioxidant systems during protective responses to UV-B exposure (Yao et al. 2021). It was shown that *Nicotiana sylvestris* plants, expressing the melatonin synthetase gene, were more resistant to ultraviolet radiation (Zhang et al. 2011). Exogenous melatonin inhibited the activity of the key chlorophyll degradation gene (PAO), induced by UV-B (Wei et al. 2019). Melatonin treatment was also associated with a higher activity and expression of genes-encoding antioxidant enzymes (ascorbate peroxidase, catalase, and peroxidase) and more substantial decline in H_2O_2 content in leaves exposed to UV-B. Moreover, exogenous melatonin treatment and UV-B stress increased the concentration of endogenous melatonin. The contents of several phenolic compounds, including chlorogenic acid, phloridzin, and quercetin-3-galactoside, also increased under UV-B stress (Wei et al. 2019).

Exposure to ultraviolet (UV–B) radiation can be deadly for plant cells since UV-B can induce production of reactive oxygen species and damage nucleic acids. In recent study, aimed to uncover the possible alleviative role of melatonin against UV-B stress, *Arabidopsis thaliana* plants were treated with melatonin (10 μM) and

were exposed to UV-B stress (46 and 92 kJ m^{-2} day^{-1}) (Haskirli et al. 2021). It was established that melatonin differentially regulated the expression of glutathione peroxidase 2 (GPX2) and GPX7 genes under UV-B stress. However, the expression of alternative oxidase 1a (AOX1a) and AOX1d was lower in plants pretreated with melatonin which indicates a lower oxidative loading in mitochondria (Haskirli et al. 2021).

Experiments using UV-B signaling component mutants of A. thaliana cop1-4 and hy5-215 revealed that melatonin not only acts as an antioxidant to strengthen UV-B stress resistance but also regulates expression of several key components of UV-B signaling pathway, including ubiquitin-degrading enzyme (COP1), transcription factors (HY5, HYH), and RUP1/2 (Yao et al. 2021). These data indicate that melatonin delays and subsequently enhances expression of COP1, HY5, HYH, and RUP1/2, which act as central effectors in UV-B signaling pathway, thus, regulating their effects on antioxidant systems to protect plant from UV-B stress (Yao et al. 2021).

Indirect effects of melatonin under ultraviolet radiation may be associated with increased levels of floridzine, as it is an excellent antioxidant (Liaudanskas et al. 2014). In addition, the increase in expression of the *CHS* gene which encodes a key enzyme in phloridzin biosynthesis, is correlated with the synthesis of phloridzin. Transcripts of most other genes related to phenolic metabolism were markedly enhanced under UV-B stress, and these genes were up-regulated by melatonin under stress conditions, suggesting a mechanism for the observed increase in phenolic compounds (Liang et al. 2018).

15.5.3 Mechanisms of NO Signaling in Plants Under UV-B Stress

A number of studies have shown that NO is involved in the response of plants to a number of abiotic factors such as extreme temperatures, drought, salinity, heavy metals, mechanical damage, and exposure to ultraviolet B (Corpas et al. 2011; Krasylenko et al. 2012; Lytvyn et al. 2016; Plohovska et al. 2019; Qiao and Fan 2008). UV-B stress causes an increase in the concentration of ABA which can activate NOX and increase H_2O_2 production. Hydrogen peroxide increases the NO content by a mechanism that is partially regulated by NR. Exposure to UV-B radiation also leads to monomerization of UVR8 (specific photoreceptor to UV-B light) which is stabilized by endogenous NO (Christie et al. 2012). Stable monomer UVR8 interacts with COP1 (constitutive photomorphogenic 1) in the nucleus and activates the transcription factor HY5 which can regulate the expression and activity of NR and induce an increase in NO (Jonassen et al. 2008). Activation of this signaling pathway leads to an increase in the content of flavonoids and anthocyanins which are able to absorb UV-B radiation and reduce the content of ROS (Fig. 15.2).

It has been established that exogenous addition of NO donors (SNP, SNAP, GSNO, etc.) reduces the accumulation of ROS resulting from exposure to UV-B radiation (An et al. 2005; Shi et al. 2005; Zhang et al. 2003). NO exhibits antioxidant activity because it contains an unpaired electron and a redox potential of 0.4 V that

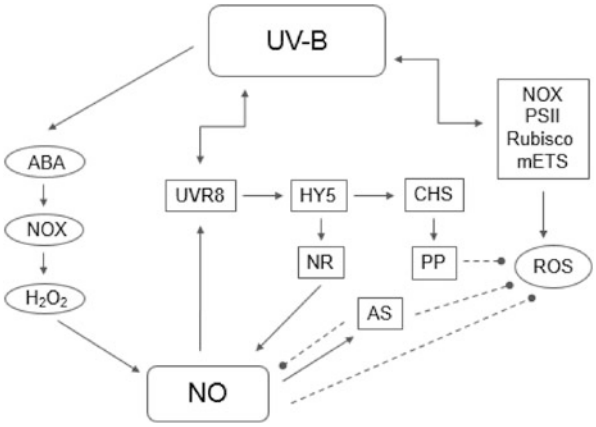

Fig. 15.2 Scheme on the role of NO in the plant UV-B response. *ABA* abscisic acid, *NOX* (NADPH)-dependent oxidases, *H_2O_2* hydrogen peroxide, *UVR8* photoreceptor, *CHS* chalcone synthase, *NR* nitrate reductase, *PP* flavonoid and anthocyanin, *AS* antioxidant system, *ROS* reactive oxygen species, *PSII* photosystem II, *Rubisco* ribulose-1,5-bisphosphate carboxylase/oxygenase, *mETC* mitochondrial electron transport chain (Zhang et al. 2014a, b)

allows it to achieve high interactions with O_2, O_2^- and redox metals. NO can reduce the formation of OH• by cleaning of iron or O_2^- (Shi et al. 2005). NO can play a signaling role by increasing the activity of antioxidant enzymes (SOD, CAT, APX and GR) or by modifying the chemical properties of cell wall polysaccharides due to changes in glucanase activity and protein content in cell walls (An et al. 2005; Qu et al. 2006; Shi et al. 2005). The example of *Glycine max* shows that NO donors alleviate oxidative stress caused by UV-B (30 kJ/m^2) by increasing the activity of SOD, CAT, and APX (Santa-Cruz et al. 2014). NO donors activate antioxidant enzymes in bean leaves by improving the oxidative stress caused by UV-B irradiation (Shi et al. 2005).

UV-B radiation can lead to increased accumulation of ABA in several plant species, including *A. thaliana*, *V. vinifera,* and *Z. mays* (Berli and Bottini 2013; Chen et al. 2013; Vishwakarma et al. 2017). In addition, the increase in ABA content induces the production of ROS which positively regulates NO synthesis and NO-induced stomatal closure (Vishwakarma et al. 2017; Zhu et al. 2014). The regulatory role of NO and H_2O_2 as signaling molecules in UV-B-induced stomatal closure has been shown (He et al. 2013). Pretreatment of SNP plants reduce the inhibitory effect of UV-B by blocking the synthesis of H_2O_2 and increasing the activity of catalase, ascorbate peroxidase, and malonic dialdehyde in *Z. mays* (Kim et al. 2010). Use of SNP (100 μM) helps to recover the growth and biomass of *Triticum aestivum* plants exposed to high-dose UV-B radiation (10.08 kJ/m^2). SNP also improves ATPase activity, chlorophyll, carotenoids, and UV-absorbing compounds in wheat leaves (Yang et al. 2013). SNP (100–300 μM) restored the

activity of numerous enzymes that had been inhibited by UV-B radiation in *Chlorella pyrenoidosa* (Chen et al. 2010).

One of the intracellular targets of UV-B radiation are the main cytoskeletal proteins associated with microtubules and active filaments. In response to UV-B radiation a reorganization of cytoskeletal structures in areas of active plant growth takes place (Chen et al. 2011; Jacques et al. 2011; Krasylenko et al. 2013). Our colleagues have shown that the most sensitive are microtubules in the zones of transition and elongation of the root because they are destroyed immediately after having been exposed to UV-B radiation in vitro (34–68 kJ/m^2) (Krasylenko et al. 2012). Changing the native transverse orientation of microtubules as well as their depolymerization may be one of the reasons for UV-B-induced inhibition of root growth as transverse orientation of microtubules is essential for root elongation (Ueda and Matsuyama 2000). Pretreatment of SNP irradiated UV-B seedlings of *A. thaliana* partially repairs root growth. It was also shown that 24 h after UV-B irradiation, a partial restoration of microtubule organization in the cells of the epidermis of the root of *A. thaliana* seedlings pretreated with SNP took place, whereas the organization of microtubules in the root of *A. thaliana* seedlings pretreated with cPTIO did not change significantly (Krasylenko et al. 2012). Thus, increased NO levels in plant cells may play a protective role in the organization of microtubules restoring the growth and development of *A. thaliana* roots under the influence of high levels of UV-B. A potential mechanism for the reorganization of microtubules induced by UV-B radiation may also be nitrotyrosilation of α-tubulin (Blume et al. 2005, 2009; Yemets et al. 2011). It has been suggested that tubulin and actin, being the targets of UV-B radiation, are located lower in the signaling cascade and are able to perceive amplification and/or transduction of the UV-B signal by NO-mediated pathways.

15.6 Conclusions and Prospects for Future

Melatonin is an important secondary messenger molecule and growth regulator. Melatonin plays an important role in reducing abiotic stress directly through the neutralization of ROS as well as through enhanced antioxidant activity and photosynthetic ability, increased osmotic metabolites, and regulation of stress-related genes in plants. In turn, NO is also a signaling molecule that is involved in many physiological functions and, therefore, plays an important role in responses to various abiotic stresses. Of great interest is the study of cross-talk between melatonin and nitric oxide in response to UV-B and other stresses. Melatonin interacts with NO to help regulate plant growth and maintain cell oxidative homeostasis. On the one hand, a positive correlation has been shown between the intensity of natural UV radiation and the accumulation of NO and melatonin. On the other hand, melatonin suppresses NO production as well as NO synthase activity in addition to its NO and peroxynitrite scavenging activity. Inhibition of NO production may be one of the mechanisms of the protective effect of melatonin under UV stress. However, the molecular mechanisms underlying melatonin-NO cross-talking in plant UV-B

responses are still poorly understood. In addition, research is needed to determine changes in endogenous melatonin and NO in response to UV-B radiation in order to understand how they interact with each other and the nature of their mechanisms of action. It is also necessary to identify target proteins for S-nitrosylation in response to UV-B radiation in order to develop new strategies to reduce the effects of this stress.

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Interaction of UV-B with Terrestrial Ecosystem

16

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Abstract

Increased solar UV-B emissions associated with ozone depletion in the stratosphere can affect terrestrial ecosystems by interacting with plants, microbes, and maybe some animals. While penetrating in cellular environment, it impacts at biological level, i.e., on the biomolecules such as photosynthetic pigments, macromolecules like DNA, proteins, enzymes, etc. and thus, can impair or alter the physiology of the organism. Some of the most important but unpredictable results are the indirect effects of increased UV-B exposure are changes in the chemical composition and morphology of plants, due to the changes in the abiotic environment. These indirect effects include changes of plant susceptibility to attack by insects and pathogens in both agroecosystems and natural ecosystems. Direction of these changes can lead to decreased or increased susceptibility. Another indirect impact of increased UV-B is a change in the balance of competitiveness in plants and nutrient cycle. Direct UV-B effects on plants that lead to changes in morphology and functions appear to be more common. Often, it is not due to damage but due to changes in gene activity. Yields of some plant varieties can be reduced by increased UV-B radiation, while others are not affected. Plant breeding and genetic engineering efforts should be able to address potential threats to plant productivity in relation with increased UV-B. This can be more difficult with forest trees if the effects of increased UV-B accumulate over the years. All effects of increased UV-B radiation are associated with other climatic changes such as elevated temperatures and carbon dioxide levels, especially in

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plants, which can alter the UV-B response. Other consequences of increased UV-B radiation at the ecosystem level are emerging and it is not easy to predict their size and orientation.

Keywords

Ultraviolet radiation · Terrestrial ecosystem · Secondary metabolites · Growth inhibition · DNA damage

16.1 Introduction

Increased UV-B radiations can alter interactions between consumers and plants due to direct effects on consumer organisms' herbivores, phytopathogens, decomposers, etc. Both direct and indirect effects were reported in different ecosystems. In many of the cases, consumers were unlikely to be directly exposed by the ultraviolet-B radiation within the field, according to the reports inhibition of spore germination, and mycelial growth was observed as a negative effect, and increased growth and induction of reproductive development was observed as a positive effect in fungi. However, fungi was found to be the less sensitive group to be effected by the consequences of ozone depletion as compared to higher plants, and the host-mediated effect of UV-B includes the alteration in the plant chemistry and the enhancement of secondary metabolites such as phenolics was observed under the increased UV-B radiations; further, the understanding of consequences related to interaction of UV-B is limited since virtually nothing is understood about the possible impacts on higher trophic levels. High doses of exposure to UV-B radiation cause accumulation of reduced biomass, damage of DNA, impairment of photosynthetic pigments, plant stress, and peroxidation of lipids. Increased UV-B also causes effects on terrestrial ecosystems through actions on plants and microbes as well as some of the animals. Different direct and indirect effects are observed on terrestrial ecosystem, but the effects are well understood on molecular and organismic levels than at ecosystem level.

Terrestrial ecosystem refers to the land-based community of organisms and the interactions of both biotic and abiotic components of the given area. This type of ecosystem includes taigas, tundra, temperate deciduous forests, grasslands, tropical rainforests, and deserts. In any of these environments, ecosystem function includes many attributes that may be potentially affected by the elevated solar UV-B radiation. The study of effects of UV-B and their interaction have been increased in the past few decades. The solar component of spectra which is most interesting for the scientific studies is the UV component of sunlight it is below 290 nm and significantly absorbed by thin stratospheric layer which is present at an altitude of 30–40 km above the earth.

On the basis of interaction of wavelengths of UV radiations with the biological materials, it is divided into three types: UV-A (400–315 nm) also known as black light; UV-B (315–280 nm) responsible for the best-known effects of radiations on

the organisms; and UV-C (280-100 nm) which does not reach on the earth surface. Many of the severe toxic gases are released into the atmosphere due to rapid industrialization, it includes carbon dioxide, methane, Sulfur dioxide, chlorofluorocarbons, etc. These gases destroy the stratospheric ozone layer, and this led to the increased UV levels in Northern mid and high latitudes (UNEP 2012).

Accordingly, surface UV-B radiations have been significantly increased by 5% and the high level of doses of UV-B radiation causes different effects such as accumulation of reduced biomass, plant stress, DNA damage, photosynthetic impairment, and lipid peroxidation (Jansen et al. 1998; Ballaré et al. 2011). Increased UV-B radiations exert effects on terrestrial ecosystem through affecting plants, animals, and microbes. The ecosystem factors which could be affected by elevated solar UV-B radiation include seed production, plant herbivore interaction, biomass production, disease incidence of plants and animals, population fluctuation, and changes in species composition as well as mineral nutrient cycling (Zepp et al. 1998). In this chapter, we describe the major breakthroughs in understanding the interaction of UV-B with terrestrial ecosystems.

16.2 UV-B Effects: Types and Levels

Effects of UV-B can be categorized into two types namely **direct and indirect,** the direct effects include the changes in form and function of the plants and can be marked by altered gene activity rather than the damage occurred. The indirect effects include most important and less predictable effects including changes in plant herbivore interaction, changes in mineral nutrient cycling and competitive balance of plants.

Yields of some crops may be decreased by increased UV-B and some are not affected. Increased UV-B is considered for high temperature and higher levels of CO_2 if we consider climate change. Effects on air quality, biogeochemical cycles, and changes in tropospheric composition are also the effects of elevated UV-B levels in the further studies that will individually discuss the effects of UV-B on different ecosystems. The indirect effects of UV-B radiation on terrestrial ecosystem are of greater importance. The effects are mediated through plants and can be expressed below as well as above the ground. The plants which are exposed to UV-B often show large reductions in herbivory by insects when they were compared to plants which were cultivated under filters that prevent the entry of UV-B component of sunlight (Mazza et al. 1999; Zavala et al. 2001).

16.3 Brief Interaction of UV-B with Plants, Animals, and Microbes

Since plants are the primary producers in any ecosystem including terrestrial ecosystem, they are the one which are directly affected by UV-B. Recent studies estimated that about 6–14% of UV-B levels have been increased over pre 1980

levels and also the current level may rise in future years (Bais et al. 2018). The sensitivity of plants to UV-B radiation is generally species specific that means it varies from species to species (Suchar and Robberecht 2018; Escobar-Bravo et al. 2017; Rai and Agrawal 2017; Vanhaelewyn et al. 2020; Teramura and Sullivan 1994). It is accepted by some scientific studies that the development of secondary metabolites and phenolic polymer metabolism is partly influenced or induced by UV-B, and it has played the major role in evolution of land plants (Ramakrishna and Ravishankar 2011; Yonekura-Sakakibara et al. 2019; Jan et al. 2021). Increased UV-B radiation causes a decrease in plant height (3–10%), total leaf area (6–13%), and the concentrations of compounds like DNA, protein, and lipids, which absorbs UV-B were increased (Searles et al. 2001). Changes in leaf and plant morphology were observed in the experiments conducted in the greenhouse by providing different doses of the two species of *Avena fatua* and *Setaria viridis* (Żuk-Gołaszewska et al. 2018). The major changes observed in plants under UV-B exposure include decrease in plant height, fresh mass of leaves, shoots and roots as well as leaf areas, and this effect also causes leaf curling and the content of the chlorophyll varied considerably (Weraduwage et al. 2015; Poorter et al. 2009; Kataria et al. 2013; Zakaria et al. 2020).

UV-B radiation does not strongly affect growth and biomass accumulation since the leaves with possible injuries shades every year. Two species of *Betula* (*B. pendula and B. resinfera*) when exposed to UV-B for upto 2.5 months, did not indicated any change which suggest that all this Betula, populations were capable of protecting themselves against UV-B radiation (de la Rosa et al. 2003). Attenuation and supplementation of UV-B radiation in experimental studies influence allocation of biomass to root systems. Large changes in roots systems were reported recently through to UV-B radiation treatment; above the ground, it suggests a systemic response to the radiation (Wan et al. 2018; Chen et al. 2019; Caldwell et al. 2007; Solomon 2008; Suchar and Robberecht 2016; Formánek et al. 2014; Ballaré et al. 2011). It was reported by Day et al. (2001) that root mass was substantially increased in the experiments conducted on potted plants in Antarctica. On the other hand, studies conducted in Finland indicated an increase in root mass with UV-B radiation supplementation (McLay et al. 2020).

UV-B not only affects the producer level but also alters consumer level. Many Phytophagous species and their ecology alter due to enhanced UV-B radiation exposure. Sensitivity of soil insects such as the *Arctic collembolan* (springtail) species was investigated in laboratory test, and they varied considerably in pigmentation which corresponds to the degree to which they were normally exposed to sunlight the range varied from heavily pigmented surface-dwelling species to soil living forms that lacked apparent pigmentation when exposed to the sun (Beresford et al. 2013; Serôdio 2012). There was an inversely correlated UV-B radiation sensitivity where well-pigmented species were considered to be tolerant to UV-B radiation corresponding to solar UV-B radiation with substantially depleted ozone (Häder et al. 2007). Many behavioral responses have been reported in different species of consumer insects like thrips (*Caliothrips phaseoli*, Thysanoptera: Thripidae), *Spodoptera litura* and *Lepidopteran species,* etc. either directly due to

physiological changes insect tissues or indirectly because metabolic changes occur in plant tissues under the influence of UV-B radiation (Mazza et al. 1999, 2002; Qi et al. 2018; Raviv and Antignus 2004; Izaguirre et al. 2007; Rousseaux et al. 2004; Stratmann 2003).

Soil microbes include that bacteria and fungi have both beneficial and harmful effects on plants with or without any mutual association. Changes in plant physiology and biochemistry may also alter the ecological patterns and behavior of affecting microbes. (Jacoby et al. 2017; Ortíz-Castro et al. 2009; Harman and Uphoff 2019; Grunseich et al. 2019; Braga et al. 2016). Colonization of *Deinococcus* species in roots of native-grown *Nicotiana attenuate* plants were observed by Santhanam (2016) and Santhanam et al. (2017) under the influence of increased UV-B exposure. Similarly, Rinnan et al. 2008 reported the alteration in peat microbial community under the influence of enhanced UV-B exposure mediated through plants. UV-B radiation has direct effect on promoting plant litter decomposition; this process is known as photodegradation, and it plays significant role in carbon cycling in arid ecosystem as discussed by (Zepp et al. 2007; Moody et al. 2004; Gallo et al. 2006; Zhou et al. 2015; Barnes et al. 2011).

16.4 Effect of UV-B on Seed Germination

Plant growth and development not only depend on the intrinsic and biotic factors, but also it is affected very much by abiotic factors too. Solar UV-B can potentially affect plant growth parameters such as seed germination, morphological characteristics of root, shoot, leaf, its area, etc. (Pandey et al. 2017; Yadav et al. 2020). Different studies were conducted to see the changes caused by the effect of UV-B irradiation on different seeds including soya bean, sunflower, and wheat (Foroughbakhch Pournavab et al. 2019; Teramura et al. 2006; Gandhi et al. 2019). Farokh et al. (2010) reported impact of UV-B on the seed germination and root morphology of Safflower plant. The soya bean seeds were manifested in the hypocotyl, presenting necrotic damage, curvature under cotyledons, interlacing of cotyledons that restricted emergence of epicotyl, as well as cracks or divisions in the radicle. Minimal sensitivity to UV-B radiation was observed in the seeds of wheat and soya bean as we increase the dose of UV-B radiation (Foroughbakhch Pournavab et al. 2019). Pine and sunflowers showed higher sensitivities than soya bean and wheat under UV-B radiation in the aging test. Harmful effects were manifested in soya bean seedlings irradiated with UV-B and UV-C including curvature and necrotic damage in the hypocotyl and cross linking of the cotyledons which restricted the emergence of epicotyl, as well as fissures in the radicle. While in sunflowers curls, fissures and curvature of the hypocotyl were reported, as well as ruptures of their tissues and malformations leading to their asymmetric growth were observed. Cracks were appeared from the base of the radicle and the curvature of hypocotyl in the pine. While in the wheat, torsions and fissures of the plumule were presented from the base of the root, it presented minimal alteration; therefore, it can be considered a species which is relatively tolerant to UV-B radiation.

16.5 Growth Inhibition Due to UV-B Radiation

Growth inhibition at the whole plant level correlates with reduced leaf expansion, and it appears to be more sensitive to UV-B radiation than photosynthesis per unit leaf areas. Net photosynthesis per unit leaf area was found to be largely unaffected by solar UV-B radiation, and detail studies have showed that the integral part of the photosynthetic system, i.e., PS-II is not affected by ambient or moderate levels of UV-B radiation enhancement under field conditions. The rate and extent of cell division and elongation changed in response to UV-B radiation in leaves which resulted in a decreased and retarded elongation leading to reduced growth (Hopkins et al. 2002).

16.6 DNA Damage

UV-B radiation generates DNA damage at the rate that overburdens its repair mechanism which leads to transient accumulation of toxic DNA photoproducts. Basic photoproducts which result from the absorption of UV-B photons by DNA are CPD (cyclobutene pyrimidine dimer), which are thought to be quantitatively to be the most important and 6–4PP (pyrimidine (6–4)pyrimidone) photoproduct. Both of this lesions have mutagenic and toxic effect and may impair DNA replication and transcription. Wild-type plants are less sensitive to UV-B radiation than mutants that are deficient in DNA repair mechanism. Studies conducted in rise added further support to the concept that DNA damage in the form of CPDs may be one of the main determinants of growth inhibition of plants induced by UV-B which are grown under physiologically meaningful conditions. There were natural variations among rise cultivars in DNA repair capacity; little variation in the enzyme involved in CPD repair has consequences for the ability of tolerance to the growth inhibitory effect of UV-B radiation in rice plants. In vascular plants of Antarctic Peninsula, growth inhibitory effects of ambient solar UV-B radiation were detected. The species of high-latitude region have the feature of low DNA repair capacity, and the repair mechanisms may also be affected by other conditions when plants are exposed to UV-B radiation, for example, by temperature and water availability (Esnault et al. 2010).

16.7 Secondary Metabolites

UV-B radiation is considered as a significant regulator of plant secondary metabolites; therefore, the lower intensity of UV-B radiation is used to produce plants with enriched secondary metabolites which have improved ability to reproduce, tolerance against fungus, early ripening, and tolerance against herbivores and bacteria. Secondary metabolites are mainly of following three types—terpenes, phenolics, and alkaloids. Out of these three metabolites, the most affected by UV-B is phenolics. The enzymes which are involved in bio synthetic pathway of

phenolics are phenyl alanine ammonia lyases and chalcone synthase; they are formed from aromatic amino acid via the phenyl propanoid pathway (Laitinen et al. 2002). These compounds are involved following processes including defense mechanism, to attract pollinators, and are used for medication purpose and to activate other pathways (Lavola et al. 1997; Schmid et al. 2001). Recent studies showed that concentration of flavonols and flavones of flavonoids were increased excessively since they absorb harmful UV-B radiations and minimize the generation of reactive oxygen species (ROS). Hence, UV-B is helpful in enhancement of secondary metabolites.

16.8 Plants Herbivore Interaction

UV-B radiations exert indirect effects on plant herbivore interactions by inducing changes in induced chemical defenses, since it modulates physiological aspects of plants. Studies in *Nymphoides humboldtiana* evaluated the action of UV-B radiations on photosynthesis and production of secondary metabolites; it also suggested the cascade effects on the relationship of this macrophyte with the general herbivore, the gastropod mollusk *Biomphalaria glabrata* (Nocchi et al. 2020). After the exposure of UV-B radiations for 13 days under laboratory conditions, the microphyte is responded by increasing its photosynthetic potential and enhancement in its antioxidant activity. In spite of the known deleterious effects of UV-B on terrestrial plants, it was found that *N. humboldtiana* does have biochemical mechanisms as a strategy to this potentially adverse agent without changing its relationship with herbivores. Plant responses to the changed abiotic conditions include modulation in their physiology and biochemistry. Plant-adaptive responses to external variations in growing conditions have a profound effect on their responses to biotic stresses (Gouinguené and Turlings 2002; Goel et al. 2008; Gutbrodt et al. 2011; Nguyen et al. 2016). In particular, light exerts a great impact on how plants are protected against herbivores or pathogens (reviewed by Ballaré 2014). To increase the plant yield, plant resistance against herbivores such as arthropods light can be used as a powerful tool. By manipulation of light conditions in green house, growers increases the plant performance in many crop species and also controls photomorphogenic processes such as flowering (Vänninen et al. 2010). Use of solar UV-B radiations for the enhancement of crop protection against pest and pathogens as well as crop production has gained interest nowadays (Wargent and Jordan 2013).

16.9 Interaction of UV-B Radiations and Its Effects on Climate Change and Humans

Some important effects include changes in the intensity of solar UV-B radiations resulting from stratospheric ozone depletion on all organisms on the planet. Some effects may be deleterious and may result to harmful effects in humans particularly in

terms of incidence of cataracts of the eye and skin cancer such as malignant melanoma. UV-B radiations also have some beneficial effects on human health in not only the terms of production of vitamin D to maintain calcium balance and bone development, but also it appears to have a protective effect in several other human diseases. Sun exposure in early life, to episodes of severe sunburn and to number of moles are related to cutaneous malignant melanomas (Bauer et al. 2005). Increased cases of melanoma have been reported in the countries, with the highest number of cases, absolute incidence continuous to rise (O'Dowd 2007;Stang et al. 2006). The importance of human behavior particularly in relation to exposure to solar UV Radiations to skin cancer has been recognized (Agredano et al. 2006; Marks 2002); however, behavioral factors have lesser risk than genetic factors (Berwick and Wiggins 2006). UV-B radiations may have adverse effects on individual organisms in the environment, an ecosystem processes or this effect may be compensated for individual species or group of species which results in little overall harm. Increases in UV-B radiations can have effects on material and nutrient cycling in terrestrial ecosystem and in fresh and salt surface water due to directs effects on humans and ecosystem. Some effect of UV-B radiations can be counteracted by protective fillers, but there may be interactions with increased environmental temperatures that affect the efficiency of this protectants. The effects of UV-B radiations or organisms, the environment, and materials are expected to decrease as the stratospheric ozone recovers; however, the potential effects of climate change on this end point is uncertain, and it is possible that increases in temperature may combine in synergistic or antagonistic ways with the effects of UV-B radiations that are currently unpredictable.

16.10 Conclusion

UV-B radiations can cause constructive as well as deleterious effects on terrestrial ecosystems depending upon the intensities of light they are exposed to. It affects growth and development with the slight decrease in plant height and total leaf area and above ground biomass as well as reduction in photosynthetic cell and increase in leaf thickening so that soluble sugars start accumulating inside it. The ultimate effects of UV-B radiations include DNA damage by breakdown or removal of nucleotide sequences which result in reduced net photosynthetic rate. By changing the number of petals and sepals, flower size, and number, it reduces rate of sexual reproduction causing ultimate reduction in seed dispersion of plants. To cope up with elevated UV-B radiations, plants synthesize more and more solar UV-B-absorbing compounds which include several flavones, phenols, and flavonoids, other photoprotective agents such as proteins and carotenoids, and some antioxidant system as well. Changes at morphological level for adaptation for UV-B include increase in the amount of nectaries and the diameter of nectar produced in glands by which insects stay longer to pollinate plants. Thus, the damaging effects of UV-B radiations affect the plants at biochemical, morphological, and genetic level.

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