



Acclimation of Photosynthetic Apparatus to UV-B Radiation

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Marian Brestic, Marek Zivcak, Dominika Mlynarikova Vysoka, Mária Barboricova, Kristina Gasparovic, Xinghong Yang, and Sunita Kataria

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

M. Brestic (✉) · M. Zivcak (✉) · D. M. Vysoka · M. Barboricova · K. Gasparovic
Institute of Plant and Environmental Sciences, Slovak University of Agriculture, Nitra, Slovak Republic
e-mail: marian.brestic@uniag.sk; marek.zivcak@uniag.sk

X. Yang
College of Life Science, State Key Laboratory of Crop Biology, Shandong Agricultural University, Taian, China

S. Kataria
School of Biochemistry, Devi Ahilya Vishwavidyalaya, Indore, Madhya Pradesh, India

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 ($\bullet OH$), 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 CO₂ 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 Rancėlienė 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 CO₂ assimilation processes (Romanatti et al. 2019).

In addition to UV-B-induced upregulation of leaf thickness (Bornman and Vogelmann 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 CO₂ assimilation were particularly severe when combining UV-B stress with other stresses, such as drought or low nutrient stress (Musil and Wand 1994; Nogueis 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 CO₂ 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 lower 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 ($\bullet OH$), 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 luminal 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 fluorescence rise during 1 s light pulse, showing visual changes due to UV-B stress (Fig. 11.1).

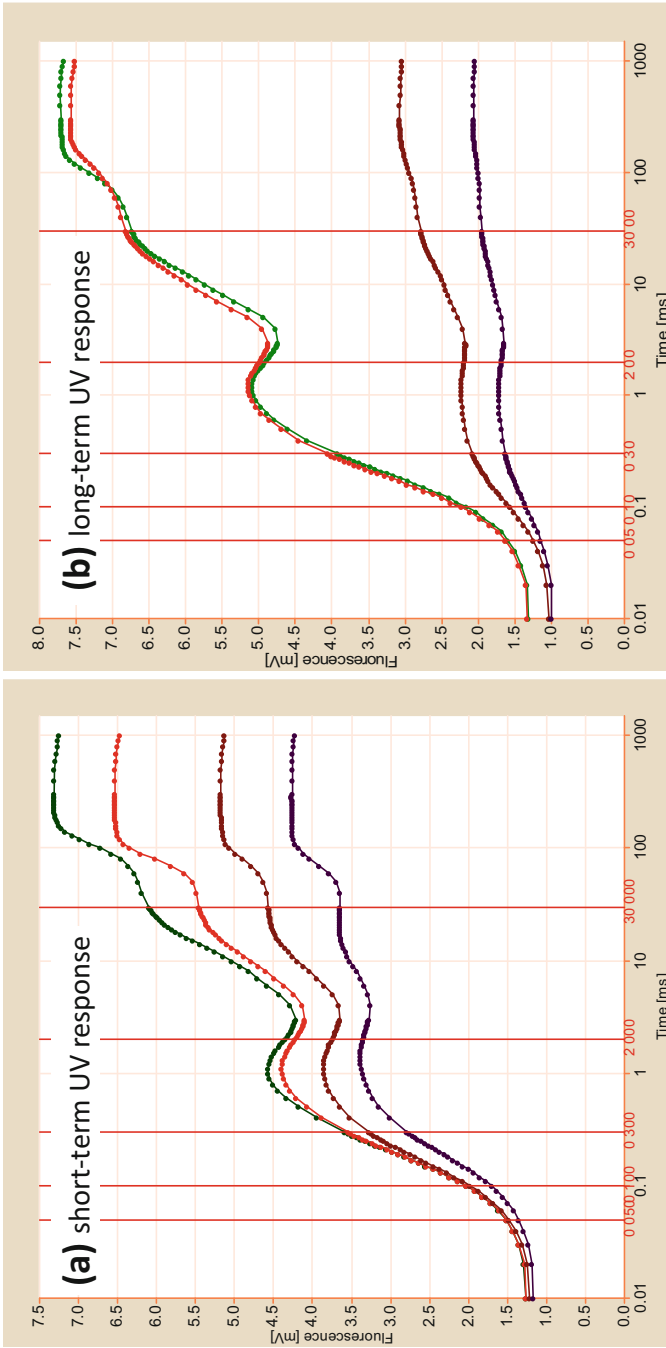


Fig. 11.1 OJIP transient measured in control variant without UV (green), moderate UV (red), high UV (brown), and very high UV (purple). The figure left shows the short-term response (day 1, after 4 h of UV exposure); the figure right shows the long-term effects (after 7 days of treatments). The fluorescence curves were processed and visualized using the BioIzyer 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 CO₂ assimilation rate and the contents of chlorophyll and carotenoids. The chlorophyll fluorescence indices, such as quantum yield of primary photochemistry (Φ_{P_0}), electron transport (Φ_{E_0}), and efficiency per trapped excitation (Ψ_0), 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 CO₂ 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

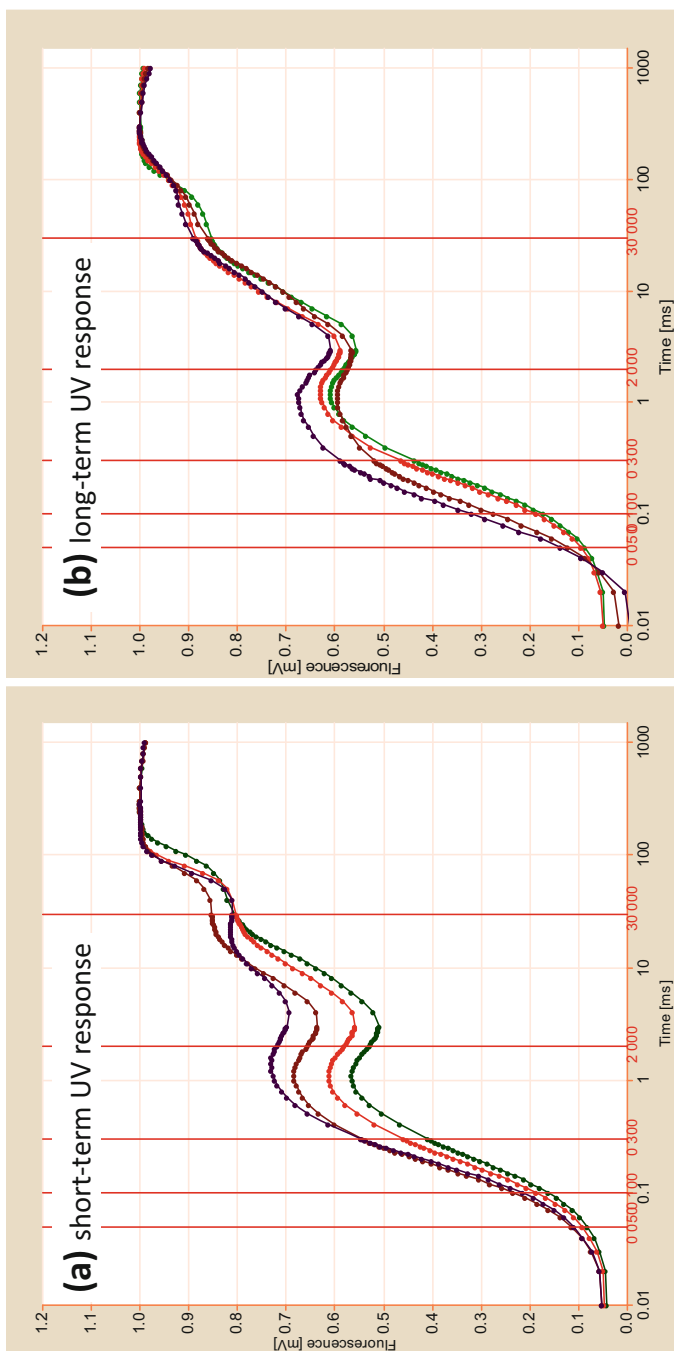


Fig. 11.2 Double normalized OJIP transient (Fo-Fm normalization) measured in control variant without UV (green), moderate UV (red), high UV (brown), and very high UV (purple). The figure left shows the short-term response (day 1, after 4 h of UV exposure); the figure right shows the long-term effects (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

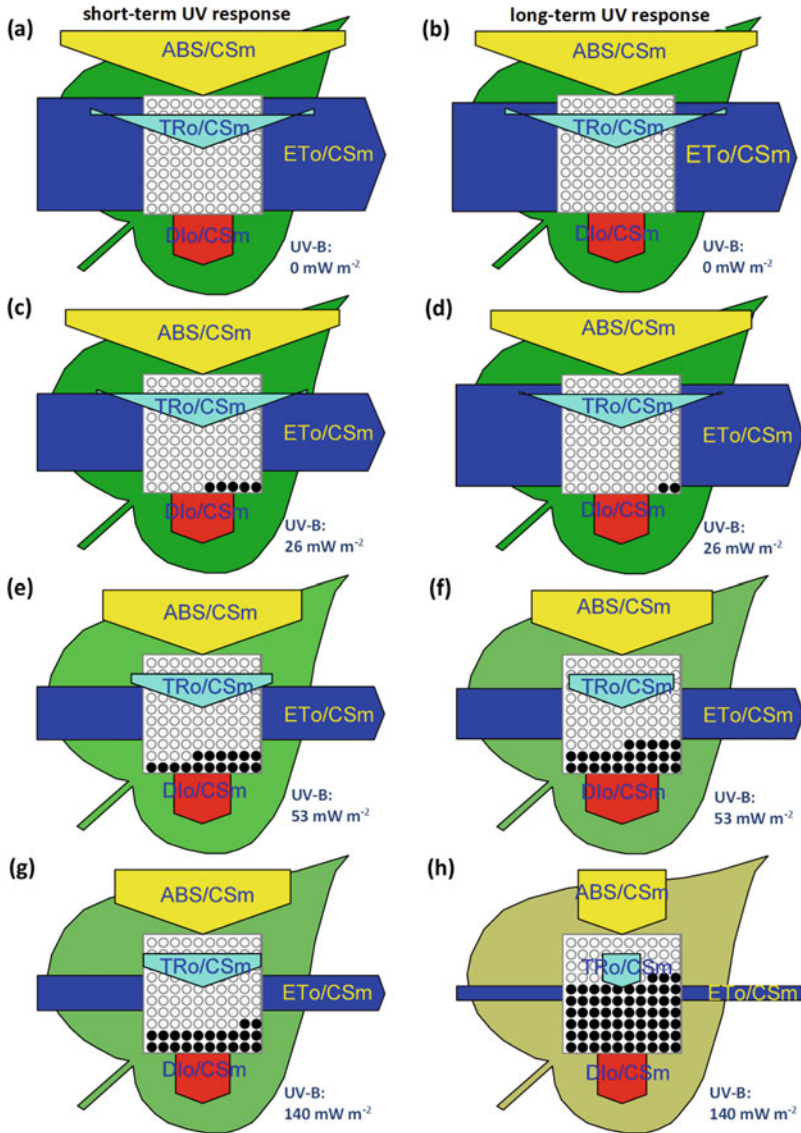


Fig. 11.3 Leaf models showing phenomenological energy fluxes per excited cross-section (CS) of lettuce leaves exposed to a different level of UV-B radiation. The models left (**a, c, e, g**) show the short-term response (day 1, after 4 hours of UV exposure), the models right (**b, d, f, h**) show the long-term effects (after 7 days of treatments). *ABS/CSm* absorption flux per excited CS approximated by F_m , *TRo/CSm* trapped energy flux per CS, *ETo/CSm* electron transport flux per CS, *DIo/CSm* dissipated energy flux per CS. Each relative value is represented by the size of proper parameters (arrow), empty circles represent reducing Q_A 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 Bolyzer software. The models were produced using the Bolyzer 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.

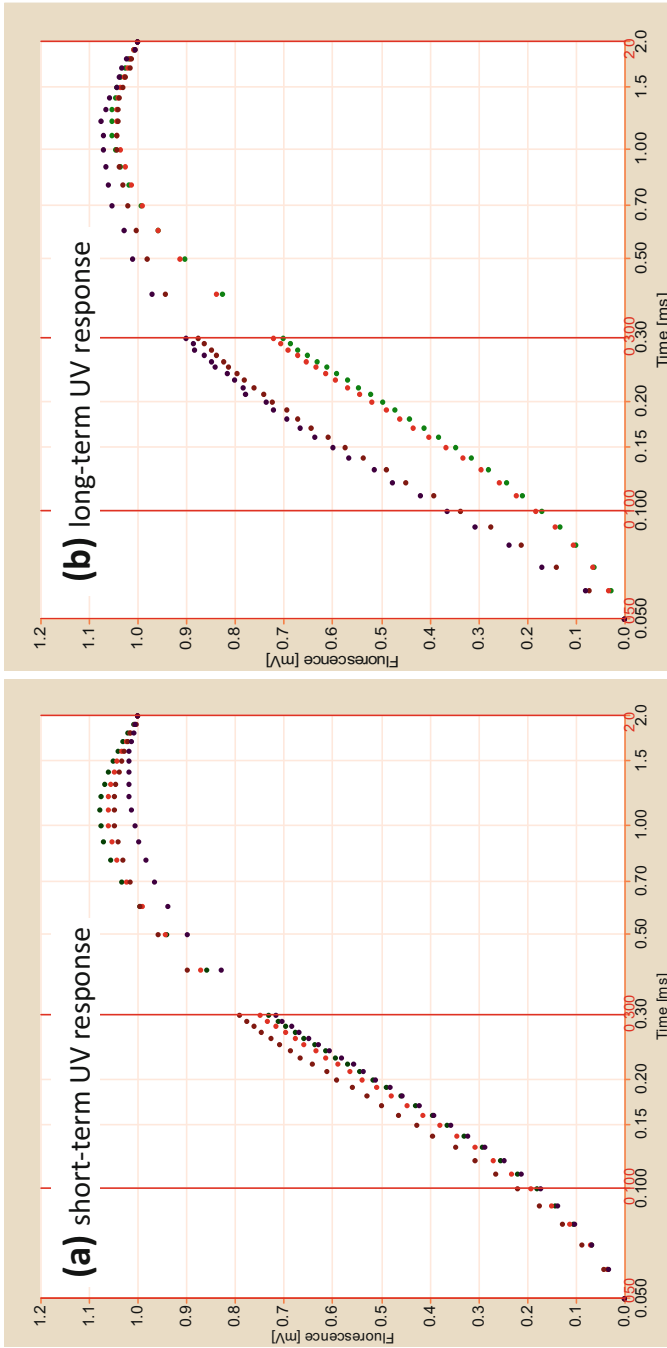


Fig. 11.4 Double normalized O-I step of OJIP transient (Fo-Fj normalization) measured in control variant without UV (green), moderate UV (red), high UV (brown), and very high UV (purple). The figure left shows the short-term response (day 1, after 4 hours of UV exposure); the figure right shows the long-term 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.

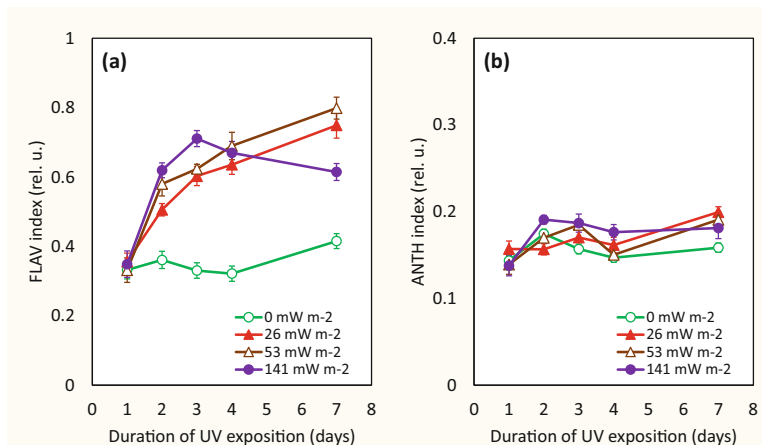


Fig. 11.5 The values of flavonoid index (a) and anthocyanin index (b) measured in the control variant without UV (green), moderate UV (red), high UV (brown), and very high UV (purple). The figure left shows the short-term response (day 1, after 4 h of UV exposure); the figure right shows the long-term 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 (Hide et al. 2002).

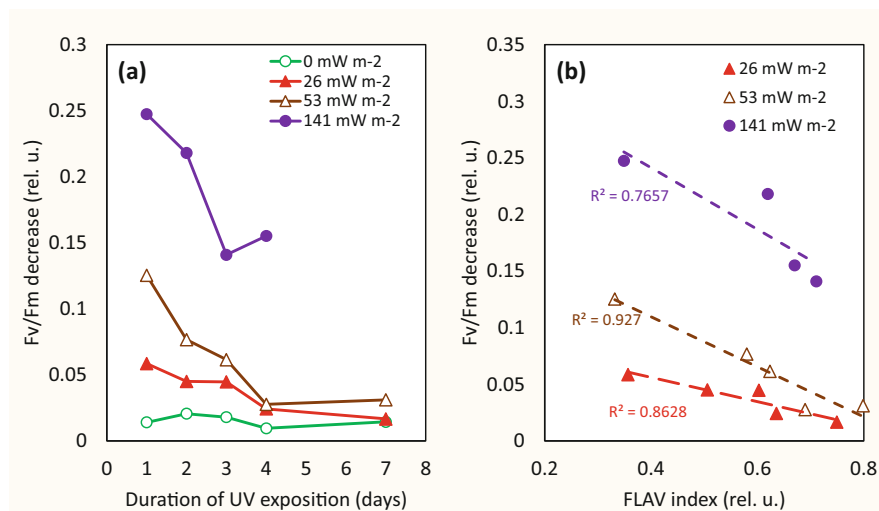


Fig. 11.6 (a) The decrease of parameter Fv/Fm parameters after 4 h of UV exposition (difference of Fv/Fm between morning and afternoon measurements) in control variant without UV (green), moderate UV (red), high UV (brown), and very high UV (purple). (b) The relationship between the values of flavonoid 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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