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Review

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EFFECTS OF ULTRAVIOLET-B RADIATION IN PLANT PHYSIOLOGY

RANA NASSOUR*, ABDULKARIM AYASH

Al-Andalus University for Medical Sciences, Tartous, Syria

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Over the past few decades, anthropogenic activities contributed to the depletion of the ozone layer, which increased the levels of solar ultraviolet-B (UV-B) radiation reaching the Earth`s surface. Generally, UV-B is harmful to all living organisms. It damages the cell`s Deoxyribonucleic acid (DNA), proteins, and lipids, and as a consequence, it affects the bio-membranes negatively. In this review, we summarize the major effects of UV-B in the plant`s main molecules and physiological reactions, in addition to the possible defence mechanisms against UV-B including accumulating UV-B absorbing pigments to alleviate the harmful impact of UV-B.

Key words: ultraviolet-B radiation, reactive oxygen species, respiration, photosynthesis, phenolic compounds

Solar radiation is a part of the electromagnetic field and is considered an essential condition for life on Earth. The electromagnetic spectrum includes different types of waves; gamma radiation (<0.1 nm), X-rays (0.1 – 100 nm), ultraviolet radiation (100 – 390 nm), visible waves (390 – 780 nm), infrared radiation (780 nm – 1 mm), microwaves (1 mm – 1 cm) and radio waves (1 cm – 100 km) (Sliney & Chaney 2006; Mandi 2016; Zwinkels 2016).

Although visible light forms only a very small part of the entire sun`s electromagnetic spectrum, it provides the energy needed for plants to perform photosynthesis, the most important process for the production of reduced carbon (e.g. carbohydrates, amino acids, fatty acids, etc.) and oxygen. That makes photosynthesis the main source of building blocks and energy-supplying molecules in living organisms.

Ultraviolet (UV) radiation comprises three types of waves varying by their wavelengths and energy: UV-C (100 – 280 nm), UV-B (280 – 320 nm), and UV-A (320 – 390 nm). UV-C has the highest energy level and it is the most hazardous part of the ultraviolet radiation. Luckily, it is completely absorbed by the atmospheric oxygen (O_2) and stratospheric ozone (O_3), while most of the UV-B radiation is absorbed efficiently by O_3, and UV-A is fully transmitted to the Earth's surface to a large extend (Madronich *et al.* 1998; Mandi 2016). In this context, the ozone acts as a natural barrier to the Earth from sunlight and its effects. It blocks and isolates harmful UV radiation before it reaches the surface of our planet, damaging the cells of humans and other organisms.

The stratospheric ozone is continuously produced and broken down according to a natural pro-

Rana Nassour (*Corresponding author), Department of Basic Science, Faculty of Pharmacy, Al-Andalus University for Medical Sciences, Tartous, Syria. E-mail: ranahn1985@gmail.com
Abdulkarim Ayash, Department of Basic Science, Faculty of Pharmacy, Al-Andalus University for Medical Sciences, Tartous, Syria. E-mail: abdulkarimayash@gmail.com

cess with dynamic equilibrium, via oxygen photolysis by short ultraviolet radiation (UV-C shorter than 250 nm). The released atomic oxygen (O) then bonds with molecular oxygen (O_2), resulting in ozone (O_3). The O_3 is then broken down by long ultraviolet radiation (UV-B) to produce O_2 and O, according to the following equations (Häder 1991; Mandi 2016):

$$O_2 \xrightarrow{\text{short UV radiation (>250 mm)}} 2O$$

$$2O + 2O_2 \longrightarrow 2O_3$$

$$2O_3 \xrightarrow{\text{long UV radiation (UV-B)}} 2O + 2O_2$$

Unfortunately, the ozone layer has been undergoing a gradual decline in its quantity for nearly four decades due to gaseous pollutants, such as chlorinated fluorocarbons (CFCs), chloroform, hydrochlorofluorocarbons (HCFCs), carbon tetrachloride, methyl bromide, and reactive nitrogen species (nitric oxide, nitrous oxide, etc.) (Rastogi *et al.* 2014; Sreelakshmi & Raza 2014; Mandi 2016). These stable compounds can remain in the upper atmosphere for millions of years (20 – 100 million years), where chlorine and bromine atoms are released from them via UV. Each atom, which acts as a free radical, is capable of initiating a series of reactions that can destroy more than 100,000 ozone molecules. This significant destruction of O_3 reduces the UV absorption efficiency, so more of this radiation reaches the surface of the Earth (1% reduction of O_3 causes 1.3 – 1.8% increase of UV-B on the Earth's surface) (Caldwell & Flint 1994; Sivasakthivel & Reddy 2011; Lidon *et al.* 2012).

It`s worth noting that due to the ban of hydrochlorofluorocarbons according to the 1987 Montreal Protocol, the ozone layer is about to recover, although there is still a long way to go (Chipperfield *et al*. 2017). Still, latitudes between 60° S and 60° N did not show recovery for unclear reasons (Ball *et al*. 2018).

UV-B INDUCES REACTIVE OXYGEN SPECIES PRODUCTION

Reactive oxygen species (ROS) are toxic by-products generated during metabolism, even under natural conditions. They are produced in plants in various subcellular sites, including mitochondrial respiration, photosynthesis, and photo-respiratory reactions (Mhamdi & Breusegem 2018).

Plants possess an antioxidant system to protect their cells from ROS. The major antioxidants are enzymes, including superoxide dismutase (SOD), catalase (CAT), various peroxidases like ascorbate peroxidase (APX), and glutathione peroxidase (GPX). Besides, there are some low molecular weight antioxidants (LMWAs) in plant cells, such as ascorbate (vitamin C), tocopherols (vitamin E), *β*-carotene, and phenolic compounds such as the flavonoids (Ren *et al.* 2006; Hatier & Gould 2009; Reboredo & Lidon 2012; Zlatev *et al.* 2012; Fu & Shen 2017; Zhang *et al.* 2017; Bhattacharjee 2019).

ROS formation increases in the plant cell under stress conditions, such as ultraviolet radiation due to their high-energy photons that damage the cell structure (oxidize proteins, lipids, and other biomolecules), disrupt the functionality and integrity of enzymes and cell membranes, and cause an imbalance in the redox reactions. So, a considerable part of the electrons leaks from electron transport systems to oxygen (O_2), reducing it to superoxide free radical ($O_2^{\bullet-}$) (Hideg *et al*. 2013; Bhattacharjee 2019; Dmitrieva *et al.* 2020).

In general, it is agreed that chloroplasts are the major sources of ROS in the plant cell, particularly under illumination, while the mitochondria are the main source of ROS in the darkness and non-green parts of the plant. The excitation of oxygen (O_2) produces singlet oxygen ($^1O_2$), while reduction produces superoxide radicals ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($OH^{\bullet}$), (Figure 1) (Mhamdi & Breusegem 2018). Chloroplasts produce $^1O_2$, $O_2^{\bullet-}$ and H_2O_2 during photosynthetic electron transport, whereas mitochondria produce $O_2^{\bullet-}$ mainly at complex I and III of electron transport chain (Bhattacharjee 2019; Huang *et al.* 2019). The latter can be explained by the direct reduction of oxygen to $O_2^{\bullet-}$ in complex I (the flavoprotein region of NADH (reduced nicotinamide adenine dinucleotide) dehydrogenase segment). Regarding complex III (the ubiquinone-cytochrome region), it is believed that fully reduced ubiquinone donates an electron to cytochrome C1 and leaves an unstable highly reducing ubisemiquinone radical that is favourable for the electron leakage to O_2 and, hence, to $O_2^{\bullet-}$ formation

(Bhattacharjee 2019). The increased production of ROS in living organisms under stress conditions is very toxic because it can react with vital biomolecules, altering and reducing their biochemical activities, causing oxidative damage and eventually resulting in cell death (Jithesh *et al*. 2006; Piri *et al*. 2011; Pessoa 2012; Zlatev *et al*. 2012; Kataria *et al*. 2014; Yokawa *et al*. 2016)

UV-B EFFECTS IN PLANTS

Although UV-B is just a small fraction of the electromagnetic field, it adversely affects the lives of all living organisms, including plants. Plants exposed to UV exhibit a decline in photosynthesis, protein synthesis, and other biochemical processes. These impairments lead to the reductions in plant height, dry weight, leaf area, relative growth rate, and total biomass (Caldwell *et al.* 2007; Kumari *et al*. 2009; Piri *et al*. 2011; Reddy *et al*. 2013; Bacelar *et al*. 2015; Reyes-Díaz *et al*. 2016; Fina *et al*. 2017; Fu & Shen 2017; Rai & Agrawal 2017; Neugart & Schreiner 2018; Parani & Vidhya 2018; Alves & Deschamps 2019; Alemu & Gebre 2020), an increase in the leaf thickness and downward leaf curling (Golaszewska *et al*. 2003; Bacelar *et al*. 2015; Rai & Agrawal 2017), and a decline in transpiration rate,

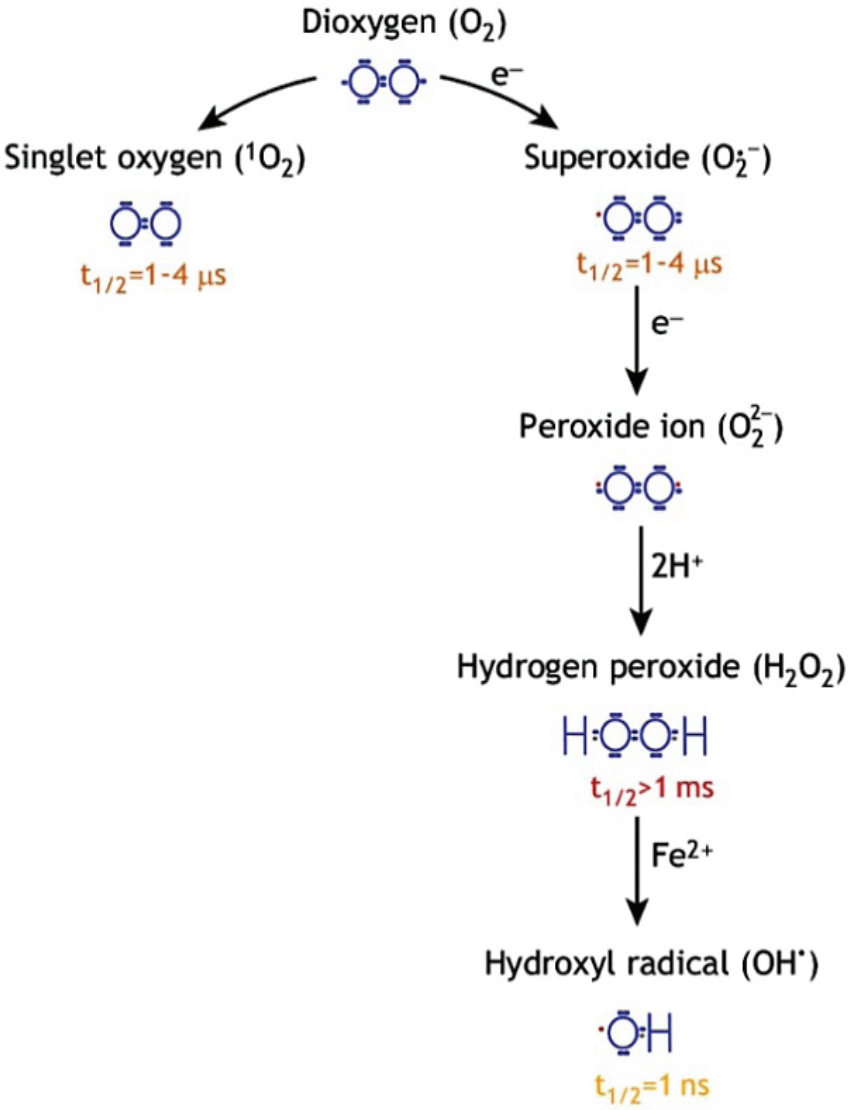

Figure 1. Oxygen-derived reactive oxygen species (Mhamdi & Breusegem 2018)

Note: e^- – electron; $2H^+$ – 2 protons; Fe^{2+} – iron divalent ion; $t_{1/2}$ – the half-life time; µs – microsecond; ns – nanosecond; ms – millisecond

beside a delay in flowering and fruiting (Bassman *et al*. 2003; Reddy *et al*. 2013; Rai & Agrawal 2017). In addition, many studies referred to the negative impact of UV-B on stomatal conductance, which reduces the amount of CO_2 available for photosynthesis (Cechin *et al*. 2007; Lidon *et al*. 2012; Bacelar *et al*. 2015; Cechin *et al*. 2018; Reyes *et al*. 2018; Reyes *et al*. 2019).

UV-B effects in cellular compounds

UV-B forms a small part of the electromagnetic field, yet it is very energetic affecting and modifying a wide range of important biochemicals and breaking them into smaller molecules. That makes it destructive for the organism's life in general.

Proteins: UV-B has negative effects on structural and functional proteins. It destroys the peptide bonds in the protein and breaks them into polypeptides. Proteins highly absorbance to UV-B (around 280 nm) is due to the absorbance of their aromatic amino acids (such as tyrosine, phenylalanine, tryptophan, histidine, and cysteine), so they are considered as one of the main targets for UV-B (Nawkar *et al*. 2013; Parihar *et al*. 2017).

Proteins may undergo photomodification directly through photooxidation reactions or indirectly by the photosensitized production of reactive oxygen species (ROS) and free radicals. Ultraviolet radiation modifies the structure of amino acids, which leads to protein denaturation and enzyme deactivation. This can be due to UV-B destruction of aromatic amino acids (free and within proteins), or to its effect on the disulphide bonds (S-S) in amino acids, which contain a sulfhydryl group in their reaction centre (Hollosy 2002; Vass *et al*. 2005; Xue *et al*. 2005; Castenholz and Garcia-Pichel 2012; Nawkar *et al*. 2013; Wang *et al*. 2017).

Lipids: When exposed to UV-B, lipids undergo lipid peroxidation whether they are glycolipids, phospholipids, or unsaturated fatty acids. UV-B exposed phospholipids are sensitive to ROS in two sites: the unsaturated double bond between the carbon atoms and the ester bond between glycerol and fatty acids (Kramer *et al*. 1991; Moorthy & Kathiresan 1998; Hollosy 2002; Bhandari & Sharma 2006; Noaman 2007; Pérez *et al*. 2012; Ganapathy *et al*. 2017; Wang *et al*. 2017). Polyunsaturated fatty acids (PUFAs) in the membrane`s phospholipids are also sensitive to ROS; since hydroxyl radical and singlet oxygen can react with methylene groups of PUFA and form lipid peroxy radicals and hydroperoxide. In their turn, the peroxy radicals can abstract hydrogen from other unsaturated fatty acids, leading to a chain reaction of peroxidation (Nasibi & M-Kalantari 2005; Vass *et al*. 2005; Rastogi *et al*. 2014; Sharma *et al*. 2014; Kumar *et al*. 2018).

Based on the above, the negative impact of UV-B causes destruction of biomembranes (cellular membranes, mitochondrial membranes (cristae), thylakoids, tonoplast, etc.), because each one of these membranes consists of a bilayer of phospholipids with proteins interspersed throughout. Therefore, any damage to the components of these membranes will lead to rupture them and disrupt the biochemical reactions in them (Bidlack & Jansky 2018).

Carbohydrates: they are the main product of photosynthesis. Carbon is fixed in C3-plants within Calvin cycle in the form of phosphorylated triose and then convert to glucose, which binds to each other to be stored as polysaccharides. UV-B causes a steep drop in total carbohydrate content either directly by inhibition of enzymes involved in the Calvin cycle, or indirectly by inhibition of the photochemical reactions required to produce NADPH + H^+ and ATP needed for the Calvin cycle (Prasad *et al*. 1998; Bhandari & Sharma 2006; Ganapathy *et al*. 2017; Kurinjimalar *et al*. 2019; Reyes *et al*. 2019).

Deoxyribonucleic acid (DNA): UV-B damages nuclear, mitochondrial, and chloroplast DNA by indirect oxidative stress or direct absorption of purines and pyrimidines to these wavelengths (between 220 – 300 nm), although pyrimidines are more affected. DNA lesions induced by UV-B include dimers between two adjacent pyrimidine bases, cis-syn cyclobutane pyrimidine dimers (CPDs), especially thymine dimers (TTs) and pyrimidine (6 – 4) pyrimidone photoproducts [(6 – 4)PPs] (Draper & Hays 2000; Sinha *et al*. 2001; Frohnmeyer & Staiger 2003; Roleda *et al*. 2006; Babele *et al*. 2012; Pfeifer & Besaratinia 2012; Nawkar *et al*. 2013; Rastogi *et al*. 2014; Gill *et al*. 2015; Li *et al*. 2015; Robson *et al*. 2019). These DNA lesions together can act as the principal cause of UV-B induced growth inhibition in plants. Additionally, these photoproducts block

the activity of DNA and RNA polymerases along the DNA strand, which inhibit replication and transcription, respectively, and can lead to genetic code misreading and causing mutations and death (Sinha *et al*. 2001; Takahashi *et al*. 2015; Jansen 2017).

UV radiation causes a decline in the cell division rates as well as in cell number. This can be due to the genetic material destruction and disrupting transcription processes (as mentioned above) beside inhibition of protein synthesis in G1 – S phases of the cell cycle (Buma *et al*. 1996; Nogués *et al*. 1998; Hopkins *et al*. 2002; Juan *et al*. 2005; Gill *et al*. 2015). Jiang *et al*. (2011) implied that UV-B-induced G1 to S arrest may be a protective mechanism that prevents cells with damaged DNA from dividing and may explain the plant growth inhibition under increased solar UV-B. Besides, UV-B-treated cells age more quickly than those of the controls (Hopkins *et al*. 2002).

Effect of UV-B in respiration

A very few studies investigated the impact of UV-B on respiration. Under UV-B stress, respiration increase significantly in the plant cell. This increment can be explained by the rise of energy demands, which is used in protection and repair mechanisms, including the increase of the leaf thickness and phenolic compounds biosynthesis (Gwynn-Jones 2001; Bassman & Robberecht 2006; Suchar & Robberecht 2016).

Effect of UV-B in photosynthesis

Photosynthesis is the most important process in the plant, because it is the main source of organic matter on our planet, besides being responsible for producing and releasing oxygen to the Earth's atmosphere, which is essential for the respiration of aerial organisms. UV-B affects photosynthetic apparatus in many sites as the following:

Effects of UV-B in pigmentation

Photosynthetic pigments are bound to structural proteins in the thylakoid membranes in higher plants and algae to form Light-harvesting complexes (LHCs) within photosystem II (PSII) and photosystem I (PSI). Researches indicate that high intensity of UV-B leads to a functional disconnection between LHC and photosystems (particularly within PSII), which impairs the absorbed energy transfer to the reaction centres (Bornman 1989; Takeuchi *et al*. 2002; Kataria *et al*. 2014).

UV-B reduces the content of photosynthetic pigments in the chloroplast, especially chlorophyll *a,* which is considered the principal pigment in photosynthesis (Qi *et al*. 2003; Gupta *et al*. 2008; Juozaityte *et al*. 2008; Lidon & Ramalho 2011; Singh & Singh 2014; Sztatelman *et al*. 2015; Ayash *et al*. 2017; Fu & Shen 2017; Sebastian *et al*. 2018). This loss in chlorophyll can be attributed to protochlorophyllide photoreduction to chlorophyllide by protochlorophyllide oxidoreductase during the early stages of chlorophyll biosynthesis, as well as chlorophyllase induction, which is responsible for chlorophyll breakdown (Agrawal 1996; Marwood & Greenberg 1996; Pradhan *et al*. 2006; Sakalauskaite *et al*. 2013; Ganapathy *et al*. 2017; Rai & Agrawal 2017).

Concerning carotenoids, they are photosynthetic accessory pigment. They invariably increase in response to UV-B (Kurinjimalar *et al.* 2019).

Effects of UV-B in the thylakoid membranes

The thylakoid membranes consist of a bilayer of phospholipids with proteins interspersed throughout. UV-B destroys the basic components of these membranes (proteins and phospholipids), leading to rupture them partially or completely, thus preventing the binding of electron acceptors, and disrupting photoelectron transport (Sinha *et al*. 2001; Lidon & Ramalho 2011; Kataria *et al*. 2014; Allorent *et al*. 2016; Bidlack & Jansky 2018).

Based on the mentioned above, many studies revealed that UV-B increases the permeability of thylakoids membranes, which causes protons leakage to stroma and lowers ATP synthesis rates (Salama *et al*. 2011; Zlatev *et al*. 2012; Rai & Agrawal 2017). Also, swelled, disintegrated, and scattered thylakoids and the absence of grana can be noticed under UV-B stress (Yu *et al*. 2013).

Effects of UV-B in light reactions

PSII: PSII is a multifunctional pigment-protein complex embedded in the thylakoid membranes, especially in the grana regions of the chloroplasts. This complex contains more than 20 protein subunits and redox components that mediate light-induced electron transport (Vass *et al*. 2005). Many negative effects of UV-B have been reported in dif-

ferent sites of PSII, including the following:

- Oxygen evolving complex (OEC): It is located in the lumenal side of the thylakoids, and includes four manganese atoms and one calcium atom forming a Mn_4Ca cluster (Najafpour & Govindjee 2011). According to Kok scheme, Mn shifts between five states during water oxidation (S0, S1, S2, S3, S4), releasing one proton and one electron in each state. The outcome of this process is the evolving of four electrons, four protons, and an oxygen molecule (Figure 2). Various studies indicated that UV-B might inhibit the OEC complex directly by absorbing this radiation via the Mn cluster, which breaks the bonds between the manganese atoms, or by damaging the intermediates of the water evolving process. There is a gradual increase of UV-B sensitivity from S0 to S3 due to increased susceptibility to absorption of these rays, which may result in the separation of the Mn-OH bond and the formation of the hydroxyl radical and thus obstruct the release of oxygen (Sicora *et al*. 2006; Szilárd *et al*. 2007; Vass 1996; Vass 2012; Kataria *et al*. 2014; Allorent *et al*. 2016; Ayash *et al*. 2018; Mosadegh *et al*. 2019).
- D1 protein: It is one of the most important structural protein (38.021 kDa) of PSII, binding essential electron transporters such as tyrosine (Tyr-Z) (Barber 2014). Under UV-B, D1 is degraded to a 20 kDa fragment which is subsequently completely degraded by proteases enzymes in a light-dependent manner (Bergo *et al*. 2003). Besides the stability decrement of D1 and imbalance between its synthesis and breaking down

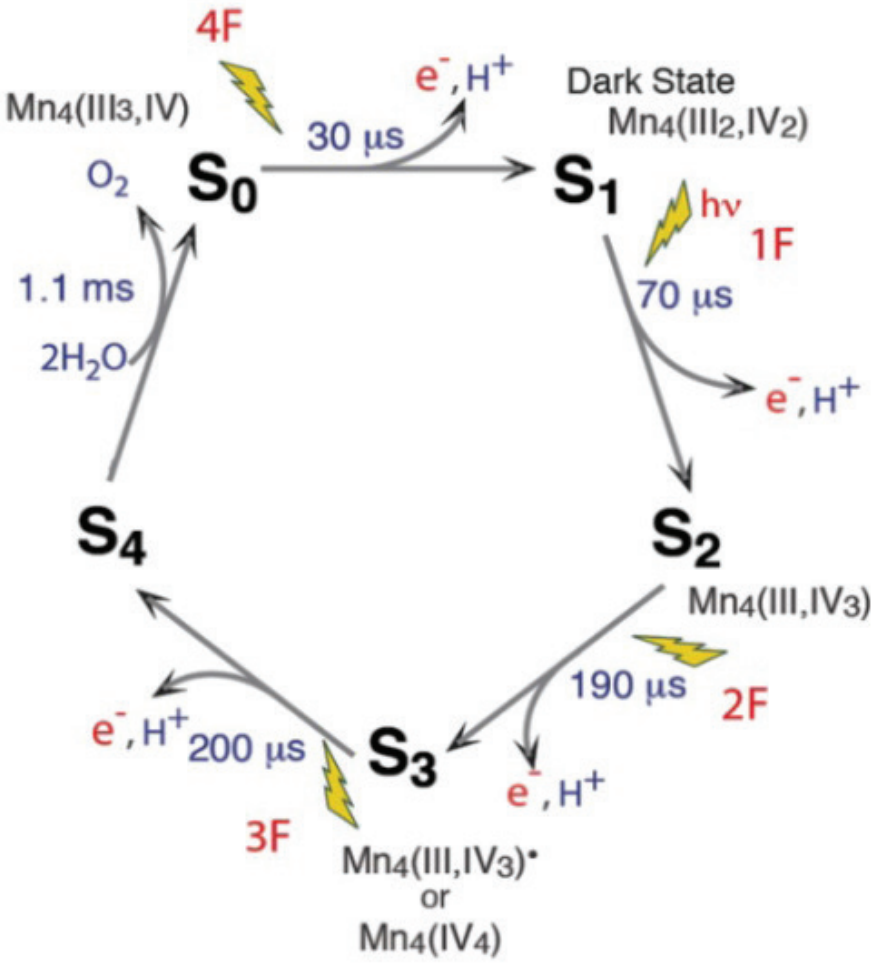

Figure 2. S-state Kok scheme (Yano & Yachandra 2014)
Note: hν – light; µs – microsecond; ms – millisecond; e^- – electron; H^+ – proton; F – flash

rates, as the amount of ROS increases (in particular the active atomic oxygen) (Booij-James *et al*. 2000; Beardall & Raven 2004; Holzinger & Lütz 2006; Cai *et al*. 2016; Tilbrook *et al*. 2016; Parihar *et al*. 2017).

- Tyrosine: Released electrons from OEC are transferred to the reaction centre (RC) of PSII (P680) via a redox-active tyrosine residue (Tyr-Z) of the D1 protein. PSII contains another redox-active tyrosine, called Tyr-D (on the D2 subunit) which can donate electrons to P680, but is not involved in electron transfer from OEC (Sicora *et al*. 2003). Under UV-B, tyrosine may be inactivated and/or photo-oxidized to 3,4-dihydroxyphenylalanine (DOPA) and form di-tyrosine as a result (Vass 1996; Vass *et al*. 2005; Parihar *et al*. 2017).
- D2 protein: It is considered an essential structural protein (39.418 kDa) of PSII, binding crucial electron transporters, such as plastoquinone (PQ) (Barber 2014). A significant decrease in D2 content is reported in the exposed to UV-B thylakoids (Booij-James *et al*. 2000; Tilbrook *et al*. 2016; Parihar *et al*. 2017).
- Plastoquinone: It is the mobile charge carrier responsible for the electron transport from PSII to cytochrome b_6f (Cyt b_6f). PQ is double reduced and takes up two protons from the stroma to become quinol (PQH2). Then, the lipophilic PQH2 is separated from protein D1 and moves within the lipid bilayer of the thylakoid membrane, transferring the electrons to Cyt b_6f, releasing protons into the lumen, and returning to the oxidized form (PQ) (Eerden *et al.* 2017). Since main absorption of quinones in the UV region (oxidized PQ: 250 nm, redox PQ; quinol (PQH2): 280 nm and semiquinone (PQH): 320 nm), they can be destroyed, modified, or lost in the thylakoids exposed to UV, preventing protons from binding to them (Melis *et al*. 1992; Vass *et al*. 2005; Rensen *et al*. 2007).

Cytochrome b_6f: The Cyt b_6f complex (217 kDa) consists of four large subunits (18 to 32 kDa), including cytochrome f, cytochrome b_6, the Rieske iron-sulfur protein (ISP), and subunit IV, together with four small hydrophobic subunits (PetG, PetL, PetM and PetN) (Kurisu *et al*. 2003). This complex mediates the electron transport chain between photosystems II and I; it oxidizes PQH2 produced by PSII and reduces plastocyanin (PC – the electron donor for PSI) (Vass *et al*. 2005). The previous studies suggest that the Cyt b_6f complex is the least affected thylakoid component by UV-B, which can be explained by the fact that Cyt b_6f complex contains two quinine binding sites (one of them for quinol oxidation and the other for quinone reduction). Besides the UV-B minor sensitivity for genes encoded in the chloroplast, such as subunit IV of this complex (Kataria *et al*. 2014; Parihar *et al*. 2017).

PSI: PSI of higher plants contains approximately 15 protein subunits. PsaA and PsaB (each ≈80 kDa) form the central heterodimer of the reaction centre and most of the electron carriers and pigments of LHCI are bound to them (Niyogi *et al*. 2015). Uneven distribution of the effect of UV-B has been demonstrated by various studies to display minor or no effects on PSI compared to PSII (Hollosy 2002; Kataria *et al*. 2014; Parihar *et al*. 2017). This can be attributed to the significant down-regulation of many genes encoding PS I protein subunits in UV-B-exposed cells (Kataria *et al*. 2014).

ATPase complex: The ATPase is a large (400 kDa) enzyme complex responsible for adenosine triphosphate (ATP) synthesis. It consists of two parts: a hydrophobic membrane-bound portion called coupling factor O (CFo) and another portion that sticks out into the stroma called coupling factor 1 (CF1). CFo forms a channel across the membrane for protons to pass through. CF1 is responsible for binding inorganic phosphate (P) to adenosine diphosphate (ADP) to produce ATP. It is made up of several peptides; including three copies of each of α and ß peptides arranged alternately (Taiz & Zeiger 2010). ATPase is significantly affected by UV-B, as the amount of coupling factor (CF1) decreases, as well as the activity of the whole complex (photophosphorylation). The later can be due to minimizing the difference of the proton concentrations between the two sides of the thylakoid membrane (stroma and lumen), caused by the changes in the thylakoid permeability (Zhang *et al*. 1994; Yu *et al*. 2013; Parihar *et al*. 2017).

Effect of UV-B in Calvin cycle enzymes:

The Calvin cycle is the primary cyclic pathway of carbon fixation and in higher plants is located in the stroma. The light reactions provide reducing

power represented by the reduced form of nicotinamide adenine dinucleotide phosphate NADPH+H^+ and energy as ATP (Heineke & Scheibe 2007).

The Calvin cycle can be subdivided into three phases: (i) the carboxylation of ribulose 1,5-bisphosphate (RuBP), leading to the formation of two molecules of 3-phosphoglycerate (3PGA), (ii) the reduction of 3PGA, and (iii) the regeneration RuBP. The products of these reactions are triose phosphates, which are exported into the cytosol by a specific transporter to be converted to sucrose (Heineke & Scheibe 2007).

UV-B adversely affects all Calvin cycle enzymes including ribulose-1,5-biphosphate carboxylase/oxygenase (RubisCO). RubisCO is the key enzyme in photosynthesis in algae and C3-plants, as it is responsible for the initial carbon dioxide (CO_2) fixation. Each RubisCO holoenzyme consists of eight large subunits (LSU, 53 kDa) and eight small subunits (SSU, 14 kDa). Both subunit types contain tryptophans (Trp) that are the potential sites for UV-B induced photochemistry. Hence, UV-B causes a decline in RubisCO activity as well as the amounts of both subunits (Xiong & Day 2001; Lidon *et al*. 2012; Reboredo & Lidon 2012; Kataria *et al*. 2014; Parihar *et al*. 2017). A previous study attributed the reduction of RubisCO to the lack of nitrogen supply for protein biosynthesis; thus suppression of protein biosynthesis and/or enhancement of protein degradation (Takeuchi *et al*. 2002).

In conclusion, the decrease in CO_2 fixation rates under UV-B can be attributed to several reasons, including thylakoid membranes rupture and photoelectron transport disruption, in addition to the negative impact of the enzymes involved in Calvin cycle. Accordingly, UV-B causes a steep drop in total carbohydrate content either directly by inhibition of enzymes involved in the Calvin cycle, or indirectly by inhibition of the photochemical reactions required to produce NADPH + H^+ and ATP needed for the Calvin cycle (Prasad *et al*. 1998; Gwynn-Jones 2001; Bhandari & Sharma 2006; Ganapathy *et al*. 2017; Ayash *et al*. 2018; Kurinjimalar *et al*. 2019).

DEFENCE MECHANISMS AGAINST UV-B

Photosynthetic organisms have developed various protective mechanisms against UV-B such as:

Increasing the dermal tissue thickness, which blocks and prevents the harmful UV-B from reaching the photosynthetically active mesophyll (Rozema *et al.* 1997; Kakani *et al.* 2003; Qi *et al.* 2003; Rai & Agrawal 2017; Neugart & Schreiner 2018). In addition to increasing wax production and/or the number of trichomes on the surface of some plants (Skaltsa *et al.* 1994; Barnes *et al.* 1996; Liakoura *et al.* 1997; Long *et al.* 2003; Chen *et al.* 2020).

Enhancing the concentrations of secondary metabolites

Phenolic compounds

The phenylpropanoid pathway is ubiquitous in plants for secondary metabolites biosynthesis. It leads to the biosynthesis of various phenolic compounds, which play an important role in plant adaptation to abiotic stresses and survival, not to mention its essential role in plant health and nutrition (Takshak & Agrawal 2016). These compounds often accumulate within the vacuoles of the upper epidermis leaves and effectively absorb UV radiation thus preventing it from penetrating the leaf mesophyll cells (Xu *et al*. 2008; Piri *et al.* 2011; Germ *et al.* 2015; Surjadinata *et al*. 2017).

Flavonoids are important natural products with polyphenolic structure. They belong to a group of low-molecular-weight phenolic compounds that are sub-divided into flavones, flavonols, flavanones, flavanonols, flavanols (catechins), anthocyanins, and chalcones (Panche *et al.* 2016).

It`s worth noting that flavonoids are sensitive to light quality, thus their concentrations are higher in plant cells exposed UV radiation (Olsson *et al*. 1998; Izaguirre *et al.* 2007; Katerova *et al*. 2012; Inostroza-Blancheteau *et al*. 2014; Li *et al*. 2014; Singh & Singh, 2014; Suleman *et al*. 2014; Köhler *et al*. 2017; Bilodeau *et al*. 2019; Liu *et al*. 2020).

Increased flavonoid content under lower exposure correlates well with higher activity of phenylalanine ammonia-lyase (PAL), a key enzyme of flavonoid biosynthesis (Kolb *et al*. 2001; Kumari *et al*. 2009; Singh & Singh, 2014; Suleman *et al*. 2014; Azarafshan *et al*. 2020).

Concerning anthocyanins, they are phytopigments responsible for attractive colours in many plant tissues, principally flowers, leaves, and fruits (Vermerris & Nicholson 2006; Panche *et al*. 2016).

Several studies implied the rise in anthocyanins under UV-B stress (Tsormpatsidis *et al*. 2008; Inostroza-Blancheteau *et al*. 2014; Singh & Singh 2014; Reyes-Díaz *et al*. 2016; Sebastian *et al*. 2018; Del Valle *et al*. 2020).

UV-B induces the down-regulation of photosynthesis and other essential processes as mentioned above, thereby increasing the plant's susceptibility to photo-inhibition. It is conceivable that anthocyanins protect the plant cells against photo-damage by reducing the penetration of UV-B to the photosynthetic mesophyll tissue since these pigments concentrate in the epidermal tissues (Steyn *et al*. 2002; Mahdavian *et al*. 2008; Goto *et al*. 2016).

These compounds are potent antioxidants, even though that they are located away from oxidant generation sites in the chloroplast and mitochondria. Many ROS (especially H_2O_2) may leak to the vacuole during severe stress and then it could be quenched by anthocyanin and other phenolics (Yamasaki 1997; Steyn *et al*. 2002; Takshak & Agrawal 2014; Panche *et al*. 2016; Zhou *et al*. 2016).

Certain flavonoids, including the more common anthocyanin pigments, have ROS-scavenging capacities up to four times greater than those of vitamin E and C analogues (Rice-Evans *et al*. 1997; Wang *et al*. 1997; Hatier & Gould 2009; Agati *et al*. 2007), helping to reduce photooxidative damage (Cechin *et al*. 2012; Tsurunaga *et al*. 2013).

Carotenoids

Carotenoids are photosynthetic accessory pigments that absorb visible light between 400 – 550 nm (Frank & Cogdell 1996). They are hydrocarbons containing 40 carbon atoms and are resulting from the polymerization of eight units of isoprene. In general, they are subdivided into two basic classes 1) carotenes (linear lacking oxygen hydrocarbons) such as α-carotene, β-carotene, and lycopene and 2) xanthophylls (oxygenated derivatives of carotenes) such as lutein, violaxanthin, neoxanthin, and zeaxanthin (Mezzomo & Ferreira 2016; Bhatt & Patel 2020).

Carotenoids act as protective compounds against photo-oxidative damage of the photosynthetic apparatus and other cell components by quenching the single excited chlorophyll (1Chl*) and possibly a triplet excited chlorophyll (3Chl*) within reaction centres of the photosystems and thermal dissipating of the excess energy, thus preventing the formation of reactive oxygen species. They may also scavenge any evolved singlet-oxygen ($^1O_2$) directly (Müller *et al*. 2001; Mozzo *et al*. 2008; Latowski *et al*. 2011; Bilodeau *et al*. 2019; Bhatt & Patel 2020). That is accomplished by carotenes and xanthophylls, but the latter to a greater extent via xanthophyll cycle (the violaxanthin cycle in plants and higher algae and diadinoxanthin cycle in lower algae) (Müller *et al*. 2001). It is worth noting that some carotenoids, such as astaxanthin, have antioxidant power 500 times higher than vitamin E, which is found in aquatic animals and algae (Mezzomo & Ferreira 2016).

CONCLUSIONS

Intensive researches during the last four decades have yielded significant improvement in the understanding of the molecular and physiological background of ultraviolet radiation and its effects on plant physiology. The most sensitive sites for ultraviolet-B (UV-B) radiation in the plant cell are the biomolecules; deoxyribonucleic acid (DNA), proteins, and lipids. On the other hand, UV-B`s adverse effects on photosynthesis gained a lot of attention in the last few years, considering the importance of this process for life on Earth. The main targets of UV-B in the photosynthetic apparatus are the thylakoid membranes, which affect both photosystems and the electron carriers attached to them. Plants developed different mechanisms to cope with UV-B stress, including the leaf dermal tissue increment and enhancing the concentrations of secondary metabolites like carotenoids and anthocyanins. Although information about the different effects of UV-B on plant physiology and defence systems have accumulated in the last few decades, further studies are necessary to fully understand the mechanism of these effects.

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