



## UV-B Radiations and Secondary Metabolites

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<p><i>Review Article</i></p> <p>Received : 11/08/2019 Accepted : 17/12/2019</p> <p><b>Keywords:</b> Carotenoids Glucosinolates Phenolic compounds Secondary metabolites Ultraviolet-B</p>	<p>Ultraviolet-B (UV-B: 280 to 320 nm) radiations have appeared to be detrimental to plants, due to their damaging effects on proteins, lipids, membranes and DNA. UV-B radiations are a significant regulator of plants' secondary metabolites. High intensity of ultraviolet radiations may interfere with growth and productivity of crops. But low levels of UV-B radiations give rise to changes in the plants' secondary metabolites such as phenolic compounds, carotenoids and glucosinolates. Therefore, low intensity of UV-B radiations may be used to generate plants, enriched with secondary metabolites, having improved reproductive ability, early ripening and tolerance against fungi, bacteria and herbivores.</p>

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### Introduction

Ultraviolet-B (UV-B: 280 to 320 nm) radiations are absorbed by stratospheric ozone (O<sub>3</sub>) and a very small percentage is transmitted to the Earth's surface which is harmful to plants (Ravindran et al., 2010; Kumari and Prasad, 2013; Frohnmeyer and Staiger, 2003; Gupta, 2017; Klein et al., 2018). Secondary metabolites, like flavonoids, alkaloids, and lignin are UV-B absorbing compounds, which can preserve the genetic material of plants (Gu et al., 2010; Katerova et al., 2012). Exposure of plants to UV-B radiations may cause changes in the production of secondary metabolites (Klein et al., 2018) and pigment composition (Delgado-Vargas et al., 2000). Kakani et al. (2003 b) stated that although the amount of UV-B radiations changed from 2 to 12 kJ m<sup>-2</sup> per day, most of the UV-B studies were conducted under fairly high UV-B radiation levels (>15 kJ m<sup>-2</sup> per day), that are likely to be unusual in the future climates.

Ultraviolet wavelength (400–200 nm) refers to electromagnetic radiations between visible light and X-rays, with significant influence on the living organisms, including plants (Katerova et al., 2012; Mao et al., 2017). Climate change refers to seasonal variations, defined as increased atmospheric temperatures, carbon dioxide concentrations and intensity of Ultraviolet-B radiations, having significant influences on plants (Teramura et al., 1990; Torres et al., 2016). UV-B (280–315 nm) radiations reach the Earth as a result of stratospheric ozone depletion due to pollutants.

The aim of this review is to evaluate the effects of elevated UV-B radiations on the secondary metabolites of plants. Moreover, yield and yield components, leaf morphology and anatomy, flowering and pollination of some important crops under elevated UV-B condition were also reviewed.

## Crop Yield and Morphological Characters

It is emphasized in the important crops such as pea, soybean and cotton that the most commonly observed morphological changes, due to UV-B radiations, include decreased leaf area or increased leaf thickness (Figure 1). Decrease in leaf area is attributed to reduction in size, number, division and expansion of cells. Together with the reduced leaf area, heliotropism reduced the amount of UV-B radiations absorbed by the soybean leaves. (Gao et al., 2003; Gupta et al., 2017). Epicuticular wax content of cotton leaves was increased by elevated UV-B radiations but leaf thickness was reduced due to decrease in thickness of palisade and mesophyll tissue (Kakani et al., 2003 a). Shorter internodes are observed in UV-B treated pea plants as a consequence of reduction in number rather than cell length (Gonzalez et al. 1998). The tolerance to UV-B radiations has been considered as an important selection criterion by pea and rice breeders (Brosché and Strid, 2000; Hidema and Kumagai, 2006; Sharma, 2001). Besides Mao et al. (2017) have reported that elevated UV radiations significantly decreased soybean yield.

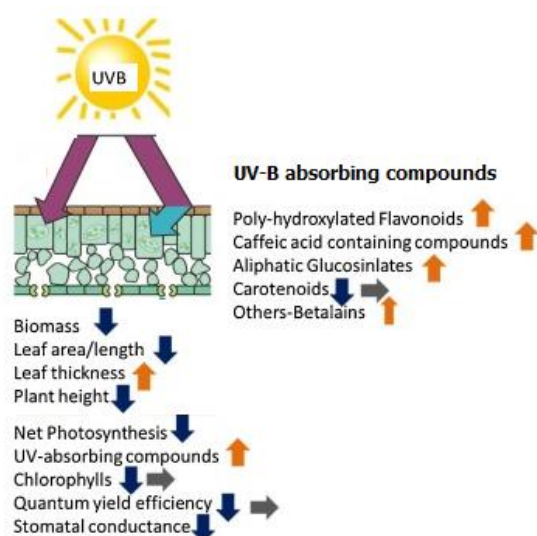


Figure 1 Changed from Verdaguer et al., 2017 and Neugart and Schreiner, 2018

Some researchers have emphasized that the reduction in root elongation, caused by UV-B radiations, was due to changes in photo hormones such as IAA (Mark and Tevini, 1996). Ultraviolet-B radiations can affect pollination directly or indirectly. Higher intensity of UV-B radiations delays the onset of flowering in annual plants with consequent reduction in fruit and/or seed production. Flower morphology, pollen production, pollen germination, pollen tube length and pollen morphology are adversely affected by elevated UV-B radiations. In addition, UV-B radiations in soybeans are associated with the effect of temperature, CO<sub>2</sub> and other stressors (Koti et al., 2005). Plants on higher latitudes and longitudes, where UV levels are higher, show greater tolerance to UV radiation than those grown on plains.

UV-B radiation penetration is affected by photochromes / cryptochromes, aromatic amino acids, DNA and phospholipids because they absorb UV-B to some degree.

The content of chlorophyll a, b and total chlorophyll decreases with increasing UV radiation level (Figure 1). As a result of decrease in photosynthetic pigments in plants, due to structural damage, a decrease in the rate of photosynthesis is observed. Besides, prolonged exposure of plants to UV-B radiations results in reduced yields. Quan et al. (2018) stated that the UV-B induced a decline in photosynthesis with consequent loss in leaf and stem biomass in *Scutellaria baicalensis*. High doses of UV-B radiations impede plant growth and development by limiting photosynthesis, overproduction of reactive oxygen species (ROS) and development of oxidative stress, which may decrease cell viability and ultimately can death of plants (Katerova et al., 2012; Mao et al., 2017). On the other hand, low UV-B doses may trigger acclimation responses in plants. Frohnmeyer and Staiger (2003) pointed out that low doses of UV-B induce photo morphogenesis in etiolated seedlings. Similarly, Katerova et al. (2012) observed enhanced production of secondary compounds in plants, exposed to low UV-B doses.

## Signalling and Perception of Uv-B Radiation

Plants have the extensive ability to respond to the UV-B exposure. Such kind of plant responses can be measured by (1) specific physiological and morphological changes (2) alternations in gene expression and (3) accumulation of definite secondary metabolites (Lake et al., 2009; Mewis et al., 2012). Plants possess five different kinds of sensory photoreceptors which help the plants precisely perceive the ambient light and generate the responses that prevent the damage and improve photosynthesis. These photoreceptors include UVB (UVR8) photoreceptor, phototropism, blue light-sensing cryptochromes, red/far-red light-sensing phytochromes and Zeitelupe (Heijde and Ulm, 2012). UVR8 is the most widely reported UV-B photoreceptor as stated by different researchers (Yin and Ulm, 2017; Yang et al., 2018).

UVR8 signalling considerably promotes the UV-B acclimation and establishment of UV-B tolerance (Gonzalez et al., 2012). UV-B acclimation is significantly linked with expression of UVR8-activated gene associated with the biosynthesis of flavonoids, protection against oxidative stress, photo inhibition and DNA repair (Favory et al., 2009; Stracke et al., 2010). Different physiological responses have been associated with the activity of UVR8 photoreceptor, including phototropism (Vandenbussche et al., 2014), stomatal opening (Tossi et al., 2014), leaf development (Wargent et al., 2009) downward leaf curling (Fierro et al., 2015), salt stress tolerance (Fasano et al., 2014), shade avoidance responses (Hayes et al., 2014; Mazza and Ballare, 2015), thermos morphogenesis (Hayes et al., 2017), auxin signalling (Hayes et al., 2014) and UV-B signalling influencing defence responses (Demkura et al., 2012). UVR8 photoreceptor exists as active homodimer in cytosol which is quickly monomerized during UV-B absorption, where tryptophan residue act as chromophores UV-B. Monomer of the UVR8 receptor, induced by UV-B, then straightaway react with E3 ubiquitin ligase CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1), thereby starting signal pathways that transduce changes in gene expression (Favory et al., 2009; Christie et al., 2012; Wu et al., 2012). Downstream of COP 1 and UVR8, the

bZIP transcription factors HY5 HOMOLOG (HYH) and ELONGATED HYPOCOTYL 5 (HY5) are needed for the obvious regulation of UV-B regulated genes (Stracke et al., 2013; Binkert et al., 2014). WD40 repeat gene protein REPRESSOR OF UV-B PHOTOMORPHOGENESIS 1 (RUP1) and REPRESSOR OF UV-B PHOTOMORPHOGENESIS 2 (RUP2) are quickly and briefly encourage by UV-B irradiation in COP1, UVR8 and HY5-Dependent Way (Gruber et al., 2010). Both RUP1 and RUP2 perfectly interact with UVR8 to enable the reversion of UVR8 monomers to homodimers in order to stabilize the signal pathways (Gruber et al., 2010; Heijde et al., 2013).

### Uv-B Radiation Stress and Plant Response

Upon continuous UV-B exposure, plants usually display weakened metabolic stress response due to governing feedback loops. This exposure subsequently increases the accumulation of stress-induced metabolites (Höll et al., 2019). Response of plants to stresses creates considerable metabolic cost. Subsequently, adaption in metabolic processes are usually accompanied by deceptive growth penalties (Herms & Mattson, 1992). Exposure to UV-B radiations is one of the most destructive factors due to their subsequent interaction with biological molecules such as proteins, nucleic acid, photo hormones and lipids, with subsequent decline in overall performance of plants (Kataria et al., 2014). Exposure to UV-B radiations affects the growth of plants, yield, physiological processes, morphology, DNA and denaturation of proteins. Dose and proportion of UV-B radiations are critical factors regarding the plant responses. Spectral balance between UV-B and photo synthetically active radiations (PAR) is also an important factor in determining plants' sensitivity (Sharma et al., 2017). Particularly, PAR can alleviate negative effects of enhanced exposure of plants to UV-B radiation (Nithia et al. 2005).

Plants have developed protective mechanisms to combat the heightened UV-B irradiance by safeguarding the sensitive targets (Rizzini et al., 2011). UV-B radiations provoke the generation of reactive oxygen species (ROS) through nicotinamide adenine dinucleotide phosphate (NADPH) oxidase in different cellular components like mitochondria (Huang et al., 2016) and chloroplasts (Dietz et al., 2016). Over-generation of ROS in plants, as a consequence of excessive exposure to UV-B radiations, results in oxidative damage and cell death (Sharma et al., 2012). Plants counterbalance the oxidative stress via accumulation and synthesis of various antioxidant enzymes and secondary metabolites like ascorbic acid,  $\beta$ -carotene, flavonoids and some alkaloids which assist in neutralizing the impact of oxidative stress (Kasote et al., 2015). Secondary metabolites like flavonoids, free phenolic acids, tannins and anthocyanin's have shown tremendous potential in ROS scavenging and oxidative stress amelioration in plants (Dyduch-Siemińska et al., 2015; Pandeya et al., 2018). Flavonoids act as sunscreen to protect the inner cells of epidermis from harmful radiations, thus forming a common protective mechanism in plants (Morales et al., 2010; Petersen et al., 2010). Biosynthesis of these secondary metabolites is noticeably controlled by phenylalanine ammonia lyase (PAL), and it is extensively studied enzymes in plants' responses to

abiotic stress (Kim and Hwang, 2014). Increase in UV-B irradiance significantly enhances the activity of PAL which, in turn, promotes the accumulation of secondary metabolites which either directly or indirectly protect the plants from UV-B radiation (Hideg et al., 2013).

### Metabolic Changes Induced by Uv-B Radiations

Plants specifically sense and precisely react to the UV-B radiations which can be observed as a modification in different morpho-physiological attributes including gene expression and secondary metabolites (Schreiner et al., 2009; Schmidt et al., 2011; Robson et al., 2015). High levels of UV-B radiations have been widely established to harm macromolecules, such as proteins, lipids and DNA, initiating with the impairment of DNA replication, photosynthesis and gene transcription (Gill et al. 2015; Liu et al. 2015; Khudyakova et al. 2019). UV-B radiations of 80–320 nm wavelength are potentially much more damaging to proteins, RNA, DNA, with increased generation of free radicals and reactive oxygen species (ROS) (Kusano et al. 2011). These harmful effects are partially aggravated by the reactive oxygen species (ROS). Plants over the years has developed different strategies to improve their growth under UV-B Stress. Secondary metabolites act as growth regulators, enzyme inhibitor, chemical signals, antioxidants and UV-B screens (Takshak and Agrawal, 2015). UV-B irradiance significantly controls the biosynthesis of secondary metabolites such as flavonoid, glucosinolate and carotenoids (Schreiner et al. 2012).

Generally, the effects of UV-B radiations on secondary metabolites are greatly dose dependent. Detrimental level of irradiance depends upon the morphological structure of the plant organs. Spherical shaped vegetables and fruits, with comparatively small surface area, require higher UV-B irradiance to induce metabolic alterations. This effect has been demonstrated in apple (Hilal et al., 2008), lemon (Interdonato et al., 2010) and tomato (Liu et al., 2011). Physiologically young plants respond differently in contrast to the fully developed plant organs. Similarly, receptivity of plant organs against UV-B application appears to be enhanced with the increase in the surface area (Huyskens-Keil et al., 2010) along with radical physiological development (Ma et al. 2018). Dose of UV-B application further regulates the dynamics of metabolite accumulation in plants. Secondary metabolites such as glucosinolates and carotenoids are induced at lower dose of UV-B radiations, as compared with flavonols, which are triggered by higher UV-B levels (Hagen et al., 2007; Schmidt et al. 2011). Some metabolites are rapidly unregulated, subsequent to the UV-B radiations, and other display a late response. Polyamines seem to increase quickly, while accumulation of flavonoids is comparatively slow (Jansen et al., 2008).

### Uv-B Radiations Induce Changes in Secondary Metabolites

Ultraviolet radiations cause accumulation of secondary metabolites such as flavonoids, glucosinolat, terpen, alkaloid and phenolic acids which impact several physiological processes in plants. Tolerance to UV-B is associated with the induction of different signal

transduction pathways, secondary metabolite production and DNA repair mechanisms. Besides, Mao et al. (2017) stated that the rutin, quercetin and total flavonoids contents were significantly increased under the enhanced UV radiation at flowering and podding stages of soybean. Some research reports indicate that UV radiations are used to prepare plant products enriched with phytochemicals (Schreiner et al. 2009). Menghini et al. (1993) summarized that after exposure to UV-B radiations, the amount of quercetin glycosides in *Brassica napus* was increased.

One of the mechanisms of adaptation to UV-B radiation is the accumulation of secondary metabolites in leaf tissues. Some studies have shown that UV-B radiations induced 10 to 300% increase in some secondary metabolites of plants. One of the most effective defence mechanisms against UV-B radiations in plants is the accumulation of phenolic compounds. The epidermal layer accumulates many of the secondary metabolites such as phenolic compounds and flavonoids which protect the tissues against harmful effects of UV-B radiations. Isoprenoids are a large group of C<sub>5</sub> - isoprene units containing compounds accumulated in plants, including carotene, xanthophylls, terpenes and others. Terpene provides protection against the deleterious effects of UV-B radiations through absorbent compounds in plants. The accumulation of tannin, salicylate and flavonoids in the leaf, induced by UV-B radiations, was more pronounced in male, as compared with female plants. Exposure to UV-B radiation changed the composition of sterols and fatty acids and increased the abundance of antioxidants in *Stereum hirsutum* (Torres et al. 2016). In a study on aquatic plants such as *Alternanthera sessilis* (Klein et al., 2018) the highest estimated flavonoid levels were noted UV-B exposure for 8 h, followed by a 24 h recovery period.

Hao et al. (2009) exhibited that UV-B in *Ginkgo biloba* callus enhanced nitric oxide production, activities of nitric oxide synthase and phenylalanine ammonia lyase and flavonoid content. Glycyrrhizin, a biologically active glycosidic triterpenoid of *Glycyrrhiza uralensis*, is accumulated in response to UV-B exposure. Glucosinolates are a sulphur-rich amino acid-derived metabolite group found only in plants against biotic and abiotic stresses. Some researchers have emphasized that the effects of UV-B on glucosinolate metabolism and the biosynthesis of genes are regulated in a different way by UV-B. An increase in the concentration of glucotropolin of *Tropaolum majus* with UV - B was observed (Gupta et al., 2017). It was found that UV-B exposure significantly increased flavonoids in *Betula pendula* (de la Rosa et al. 2001) and *Pinus sylvestris* (Lavola et al. 2003). UV-B exposure increased the flavonoid, quercitrin, the minor flavonoid, myricetin-3-galactoside chlorogenic acid contents in birch seedlings (Lavola et al. 1998). Similarly, Wulff et al. (1999) also observed an increased amount of quercetin 3-glycoside in European silver birch seedlings, exposed to high UV-B radiation. UV-B influences carotenoid contents in plants.

The flavones, flavonols, isoflavonoids, anthocyanins and phenolic acids play a protective role against prolonged exposure to high intensity solar radiations (Schreiner et al., 2012.). UV-B radiations improve the quality of medicinal plants by increasing the content of secondary metabolites (Kumari and Prasad, 2013; Pandey and Pandey-Rai, 2014).

Similarly, Ramani and Chelliah (2007) observed that mild dose of UV-B radiation is effective to increase the biosynthesis of catharanthine from *Catharanthus roseus*. UV-B exposure induces negative effects on tea plant growth but significantly increases the soluble phenolics and flavans (Zagoskina et al. 2003). The amount of carnosic acid, a ROS-retaining terpene, in rosemary (*Rosmarinus officinalis*) leaves, was doubled on exposure to UV-B radiations. UV-B exposure caused a significant increase in phenylpropanoids and terpenoids levels of *Ocimum basilicum* plants (Johnson et al. 1999).

UV-B radiation changed the content of amino acids, proteins and total sugars of wheat grain. These changes are indirect effects of alterations in plant vigour or reproductive capacity. No significant difference was observed in terms of coarse starch values between varieties. It has been observed that UV-B radiations decreased RNA activity and changed the expression of defence genes, leading to a change in leaf chemistry including protein, starch and soluble sugars in wheat, barley, corn, beans, tomatoes and radish leaves. Ultraviolet-B radiations can influence amino acids metabolism protein synthesis in both chloroplasts and cytoplasm. UV-B radiations are affected by the microclimate and environmental factors including temperature, precipitation, photosynthetic photon fluence, UV-A, CO<sub>2</sub>, soil fertility (Zu et al., 2004). Janetta Nithia and Shanthi (2017) investigated the effect of enhanced UV-B radiations under field conditions and suggested that the synthesis of secondary pigments like flavonoids and anthocyanin varied among species. The accumulation of UV-B absorbent pigments is one of the effective methods of reducing the harmful effects of UV-B radiations in plants. Flavonoids can accumulate in the leaf epidermis either in the cuticle, cell wall or in the vacuole. These absorbent compounds may not be effective against UV-B radiations if contained within the mesophyll (Ravindran et al., 2010; Katerova et al., 2012). The largest UV-B absorbing compounds were observed in barley plants (Liu et al. 1995). Flavonoid content of wheat plants, exposed to UV-B and irrigation deficiency, increased with synergistically effects of both stress factors (Feng et al., 2007). Under UV-B exposure, saponarin (a flavonoid found in young green barley leaves possessing potent antioxidant activities) content was significantly increased (Kaspar et al. 2010). In a study on soybean by Mao et al. (2017), it was found that enhanced UV-B with elevated O<sub>3</sub> damaged soybean growth mediated by changes in secondary metabolites and endogenous hormones. The duration and intensity of UV-B radiations disturb glucosinolate biosynthesis. It also influences the phenylpropanoid and flavonoid pathways, leading to changes in glucosinolate and phenolic compound concentrations (Schreiner et al., 2009).

Ultraviolet radiation has the capacity to affect a very wide array of plant metabolites including a range of antioxidants like xanthophyll's, ascorbate, tocopherol and glutathione (Topcu et al., 2015). Various polyamines such as supermini, spermidine and putrescine are known to be up regulated by the Ultraviolet radiations (Radyukina et al 2017). Soluble phenolic compounds in plants act as UV screening pigments and antioxidants as well (Nascimento et al. 2105; Wang et al.2017). Various phenolic compounds



are favourable antioxidants and anticancer agents (Roleira et al. 2015). Similarly, synthesis of carotenoids is encouraged by the UV-B radiations via rise in phytoene synthase expression (Shen et al. 2017). Carotenogenesis is mainly managed by quality of light and controlled by UV-B receptors and phytochrome (Becatti et al. 2009).

### UV-B Radiation Induces Change in Phenolic Compounds

Phenolic compounds, predominantly flavonoids are commonly known as secondary metabolites in plants that holds aromatic ring having no less than one hydroxyl groups. Approximately 800 phenolic compounds have been reported from the plants as naturally occurring substances (Tungmunnithum et al. 2018). Half of phenolic compounds are flavonoids such as glycosides, aglycone and methylated derivatives (Kumar and Pandey, 2013; Ahmed et al., 2016). Bio-synthesis and accumulation of flavonoids in chloroplasts, vacuoles and cell wall of the plants are extensively controlled by the intensity and exposure of UV-B radiations ((Tilbrook et al., 2013). Flavonoids have gain considerable attention due to its prospective health promoting advantage for humans, as they are reported as effective cardio protective (Mozaffarian et al., 2018), antioxidants (Tatullo et al., 2016), anticancer (Madunić et al., 2018), anti-inflammatory (Nile et al., 2018) and anti-bacterial agent (Xie et al., 2015).

Increase in Ultraviolet-B light extensively affects the flavonoids pathways and transforms the flavonoids profile of various plants (Nascimento et al., 2015; Heinze et al., 2018; Henry-Kirk et al., 2018). Effect of Ultraviolet-B light is modified by the dose of UV-B (Xie et al., 2015), flavonoids structure along with other environmental aspects such as temperature (Virjamo et al., 2014), light quality and intensity (Fu et al., 2016) and photosynthetic photon flux density (Bilodeau et al., 2018). Idris et al. (2018) also reported that intensity, duration and wavelength of UV-B affects the accumulation of flavonoids. Generally, higher UV-B radiations tend to enhance the flavonoids accumulation in plants. UV-B improved leaf quercetin (plant flavonol) content and boosted up the total antioxidant capacity in *Coriandrum sativum* (Fraser et al., 2017). Noticeable accumulation of anthocyanin was observed at high light (HL) as compared to Low light (LL) in leaves tissues of *P. coleoides* after 4<sup>th</sup> day of UV-B exposure (Vidovic et al., 2015). Climate change is a driving force behind the change in land and air temperature (Hannah et al., 2013). Slight change from mild to moderate temperature showed phenological modification in grapevine (Jones et al., 2005). It was reported that low temperature (LT) administration delayed the ripening phase of the grape and showed a remarkable impact on the activities of some enzymes which were involved in the bio-synthesis of flavonoids, resulting in enhanced accumulation of flavonols and anthocyanins. Contrarily, berries grown-up under high temperature (HT) displayed a great boost up in activity of peroxide, which could ultimately restrict the accumulation of flavonoids originated under these conditions (Pastore et al., 2017).

Photo synthetically active radiations (PAR) and UV-B application significantly regulates the accumulation of

flavonoids and net photosynthesis of plants as given in Figure 2. Much higher generation of flavonoids was detected under PAR and UV-B application in old and young leaves (Klem et al., 2012; Morales et al., 2013). Similarly, synthesis of flavonoids, induced by the UV-B, can further be regulated by other abiotic factors such as temperature and water stress as well (Escobar-Bravo et al., 2017). Biosynthesis of flavonoid in plants is closely linked with the light intensity, histone deacetylase-6 and photoreceptor phytochrome-B. Red/far-red (R/FR) ration and intensity of ultraviolet light are most studied aspects with respect to the effect of light quality on flavonoids concentration (Tessadori et al., 2009). Flavonoid methyltransferases and flavonoid glycoside transferases were significantly regulated through light quality via series of regulation mechanisms. flavonoid methyl derivatives showed positive correlation with far-red (FR) and near infrared (NIR) while negatively correlated with fraction of R/FR ratio and UV-A radiations. However, flavonoids and glycoside contents exhibited opposite correlation (Fu et al., 2016).

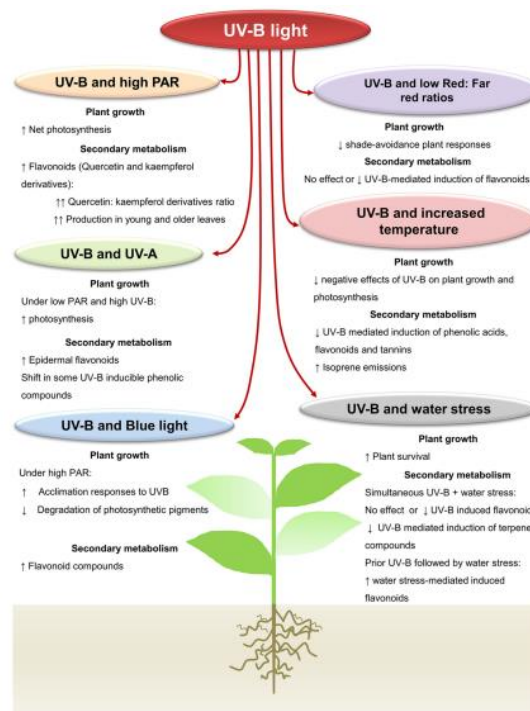


Figure 2. Interactive effects of UV-B light with other abiotic factors on plant growth and production of plant secondary metabolites (Source: Escobar-Bravo et al., 2017).

Different studies have demonstrated that repetitive application of UV-B also regulates the plants' phenolic contents. Repeated doses of UV-B considerably increases the phenolic contents in *Lactuca sativa* (Lee et al., 2014). Bio synthesis of important flavonoids and phenolic compounds depends upon the threshold dose of UV-B irradiation. Strawberries (*Fragaria × ananassa*) under high dose of UV-B level demonstrated the much higher concentrations of anthocyanins, phenolic acids and total phenols (Ordidge et al., 2010). It is extensively studied that quercetin, along with ortho-dihydroxylated flavonoids, was significantly enhanced, whereas, kaempferol and Vitol ortho-monohydroxylated flavonoids usually remained

unaffected by the higher doses of solar radiation especially UV-B (Winter and Rostas, 2008; Jansen and Bornman, 2012). Modest temperature and moderate dose of UV-B irradiation were also found helpful in improving phenolic contents in plants. Moderate UV-B radiations ( $0.25 \text{ kJ m}^{-2} \text{ d}^{-1} - 0.75 \text{ kJ m}^{-2} \text{ d}^{-1}$ ) successfully enhanced the level of structurally different hydroxycinnamic acid derivatives and flavonol glycosides in kale (*Brassica oleracea* var. *sabellica*) under successive doses of UV-B radiation (Neugart et al., 2014).

### UV-B Radiation Induces Change in Carotenoids

Carotenoids, as tetraterpenoid pigments, are a bunch of natural compounds widely found in photosynthesizing organisms like green plants, fungi, algae and bacteria as well (Sun et al., 2018). There are around 750 naturally existing carotenoids. Among them, main carotenoids such as  $\alpha$ -carotene,  $\beta$ -carotene, lutein,  $\beta$ -cryptoxanthin, astaxanthin, lycopene, fucoxanthin and zeaxanthin are well documented. Carotenoids play an exceptional role in photo protection and photosynthesis of plants (Hashimoto et al., 2016). Carotenoids work as necessary pigment in the process of light harvesting. Carotenoid plays a vital role in scavenging of reactive oxygen species (ROS) produced under UV-B radiation stress and also safeguards the chlorophyll contents from photo oxidation (Shen et al., 2018). Excessive production of ROS may otherwise irreversibly damage the DNA, proteins and lipids eventually leading to cell death. White and Jahnke (2002) reported that  $\beta$ -carotene successfully protected the cells of *Dunaliella* sp by scavenging the free radicals and ROS produced as a result of oxidative stress induced by UV-A and UV-B radiations. Polyene backbone is the core structural component in carotenoids as it contains a sequence of conjugated bonds (C=C bonds). This special feature is predominantly accountable for pigmentation properties and the potential of these compounds to effectively interact with ROS and other free radicals, thus acting as active antioxidants (Andrew and Lowe, 2018). Increased UV-B irradiance ( $+9.75 \text{ mW cm}^{-2}$  to  $+20.76 \text{ mW cm}^{-2}$ ) encourages the enhanced accumulation of lutein (carotenoid), which further improves the total antioxidant capacity (TAC) of the antioxidant system to prevent photo oxidative damage in tobacco plant (Shen et al., 2017).

Temperature and light intensity are the main environmental aspects affecting the growth and development of plants. Slight change in intensity, duration and range of light can cause cellular damage and eventually leads to the death of the plant. Different plants have adapted numerous protective mechanisms that help them survive under unfavourable conditions of light and temperature stress (Szymańska et al., 2017). A crucial part of the antioxidant system usually operates in the chloroplast where carotenoids exist (Sun et al., 2018). Carotenoid pathways at the transcript level appear to be associated with stress response e.g. light stress. High intensity of light increases the steady state of carcinogenic enzymes such as phytylene desaturase (PDS) and phytylene synthase (PSY). Maximum steady-state of  $\beta$ -LCY at mRNA levels was observed when exposed to maximum light intensity of  $500 \text{ Imol m}^{-2} \text{ s}^{-1}$ . Similarly,  $\beta$ -carotene content accumulation at the cellular level was twice at maximum light intensity of ( $500 \text{ Imol m}^{-2} \text{ s}^{-1}$ ) as compared

to the value attained at low light ( $45 \text{ Imol m}^{-2} \text{ s}^{-1}$ ) conditions in *Dunaliella salina* (Ramos et al., 2008). Improved accumulation of antheraxanthin and zeaxanthin was observed under high intensity light in *Chlamydomonas reinhardtii* (Couso et al., 2012). Zeaxanthin fractions were also enhanced in cells of *Dunaliella salina* with the increase in light irradiance (Fu et al., 2013). Light intensity significantly affects the biomass and lutein productivity in *Chlamydomonas* sp. The highest lutein productivity of  $5.08 \text{ mg/L/d}$  was attained at high light irradiance of  $625 \text{ } \mu\text{mol/m}^2/\text{s}$  (Ma., 2019).

Temperature affects the quality and yield of the crops by altering their important biochemical and physiological processes (Wang et al., 2016; Sunoj et al., 2016; Yang et al., 2016; Xu et al., 2016). Environmental temperature significantly affects the carotenogenesis as well. Accumulation of carotenoids increases with the increase in temperature. A threefold increase in astaxanthin was observed in *Haematococcus pluvialis* with an increase in temperature from  $20$  to  $30^\circ\text{C}$ . High temperature induces higher accumulation of carotenoid contents (Juneja et al., 2013). Significant reduction in carotenoid contents was observed in *Pisum sativum* L. (Juozaitytė et al., 2008), *Phyllanthus amarus* L. (Indrajith and Ravindran, 2009) and *Dolichos lablab* (Singh et al., 2011) as a result of UV-B stress. Oxidative stress destroys the carotenoid contents at a much higher pace than their capability of scavenging the ROS, which results in reduced ability to mitigate the UV-B stress. Therefore, a complex relationship exists between carotenoids and ROS under UV-B stress.

### UV-B Radiation Induces Change in Glucosinolates

Glucosinolates (GSL) are well known secondary metabolites having sulfur- and nitrogen-compounds. They are well known for keeping auxin homeostasis in plants, and preventing cancer in humans. Glucosinolates are classified into three categories; (1) aliphatic glucosinolate derived from leucine, alanine and valine, (2) indolic glucosinolate derived from tryptophan and (3) benzoic glucosinolate derived from tyrosine and phenylalanine (Kliebenstein et al., 2005). Around 130 glucosinolates are identified so far, and they belong to the family Brassicaceae (Baskar et al., 2012). Production and accumulation of phenolic compounds and flavonoids against exposure to UV-B radiation is well documented. Whereas, effects of UV-B irradiance on production and accumulation of glucosinolates has gained little and no consideration in the past. Reports on the outcomes of UV-B radiations on preharvest and postharvest glucosinolate contents are scarce in the previous literature. UV-B irradiance ( $5.5 \text{ kJ m}^{-2}$ ) significantly affected the expression of genes responsible for the synthesis of indolyl GLS in *A. thaliana* (Demkura and Ballaré, 2012). UV-B irradiation ( $20 \text{ kJ m}^{-2} \text{ d}^{-1}$ ) also influenced the indolyl GLS, total aliphatic and total GLS in *Brassica oleracea* L. var. *italica* (Rybarczyk-Plonska et al., 2016). An increase in total GLS was observed in mustard, nasturtium (Reifenrath and Mueller, 2007) and canola (Moghadam et al., 2012) under UV-B treatment. Even low level exposure of UV-B ( $0.3$  to  $0.6 \text{ kJ m}^{-2} \text{ d}^{-1}$ ) considerably enhanced the total glucosinolate contents in broccoli sprouts (Pérez-Balibrea et al., 2010). Recently, Moreira-Rodríguez et al. (2017) also reported an extensive increase in total glucosinolate content ( $\sim 148\%$ ) of

young broccoli sprouts under UV-B (7.16 W/m<sup>2</sup>) treatment. While in contrast, Wang et al. (2012) reported a significant decline in total glucosinolate in *A. thaliana* on continuous exposure to UV-B for 12 hours.

### Future outlook

This review revealed that UV-B radiations affected the morphologic and anatomic characteristics of leaf. It is a fact that the most important mechanisms of adaptation to UV-B radiation are the accumulation of secondary metabolites in leaf tissues. Especially, flavonoids protected DNA from UV-induced DNA damage can accumulate in the leaf epidermis, either in the cuticle, cell wall or in the vacuole as a clear example of this mechanism. External moderate dose of UV-B irradiation together with modest temperature were also found helpful in improving phenolic contents in plants. Moreover, carotenoid plays a vital role in scavenging of reactive oxygen species (ROS) produced under UV-B radiations stress and also safeguard the chlorophyll contents from photooxidation. Similarly, increased UV-B irradiance stimulated the accumulation of carotenoid such as lutein, which further improves the total antioxidant capacity (TAC) of antioxidant system to prevent the photooxidative damage in plant. As a result, review explained that UV radiations altered many aspects of plant growth and metabolism, including the development of defence compounds and structures.

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