Chapter

Ultraviolet Radiation and Its Effects on Plants

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Abstract

Ultraviolet radiation is a portion of the electromagnetic spectrum ranging from 10 to 400 nm, classified into three main categories: UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (100–280 nm). The UV radiation from the sun that crosses the atmosphere and reaches the earth's surface is composed largely of UV-A radiation (95%) and, to a lesser extent, UV-B (5%), which is normally filtered by stratospheric ozone. With the thinning of the ozone layer, UV-B radiation penetrates deeper into the earth's surface, where it becomes dangerous due to its high energy content that acts at the molecular level, affecting the cycles of carbon, nitrogen, and other elements, thus, having a direct impact on global warming. On the other hand, UV radiation alters numerous essential organic compounds for living organisms. Since its discovery, it has been established that e UV-B causes alterations in plant development and metabolism, both primary and secondary. In this chapter, we summarize the current knowledge about the effects of UV radiation on the morphological, biochemical, and genetic processes in plants.

Keywords: UV radiation, secondary metabolites, oxidative stress, photomorphogenesis, photosynthesis, UV transcription factors

1. Introduction

As sessile organisms, plants are constantly exposed to a wide variety of stress factors, such as desiccation, environmental pollution, temperature changes, and UV radiation. Ultraviolet radiation is a part of the nonionizing radiation region of the electromagnetic spectrum and comprises about 9% of the emitted solar

radiation; according to the ISO 21348 standard, it is divided into three types: UV-C (200–280 nm), UV-B (280–315 nm), and UV-A (315–400 nm) [1, 2].

The ozone layer (O^3) efficiently filters much of the shortwave UV radiation (UV-C). However, this absorption decreases rapidly for radiation with wavelengths greater than 280 nm, reaching a rate of 0% absorption for wavelengths greater than 330 nm. Factors, such as elevation above sea level, cloud cover ground reflectance, geographic latitude, and ozone gradient and can affect the amount of UV-B and UV-A radiation that reaches the Earth's surface [3].

In normal conditions, the ozone layer filters around 80% of UV-B radiation, but human activities have caused a decrease in the stratospheric ozone concentration through the emission of compounds such as chlorofluorocarbons (CFCs), carbon tetrachloride (CCl_4) and hydrochlorofluorocarbons (HCFCs). Therefore, UV-C radiation and an increased percentage of UV-B radiation can pass through [3, 4].

Although UV radiation is a minor fraction of solar energy that reaches the earth's surface, it significantly affects plants. UV-B radiation affects important biomolecules directly, including nucleic acids and proteins; these molecules absorb UV radiation easily when presenting π electrons, and this absorption can lead to metabolic, biochemical, and morphological alterations, as well as alterations in the genetic material [5, 6]. UV-A radiation produces similar effects, although they are part of the constitutive regulation of plant metabolic and morphological processes, such as photosynthesis, biomass production, and synthesis of pigments and antioxidant compounds [7].

Since the discovery of the thinning of the ozone layer, the consequent penetration of UV-B radiation into the atmosphere and its undisputable contribution to global warming of the planet, the effects of UV radiation on plants have been closely studied. Plants can use sunlight not only as a source of energy to produce carbon compounds but also as a source of environmental information; that is, they can detect it as a signal and trigger different systemic responses related to photosynthesis, phototropism, photoperiodicity, and photomorphogenesis. These same processes can be affected by the abnormal incidence of UV radiation in the atmosphere; therefore, the impact of its damage has been studied in recent decades [8]. This assessment has led to the creation of initiatives such as the Montreal Protocol, which aims at mitigating the negative effects of climate change-derived increased UV exposure through international policies [9].

In addition, the analysis of the causes of the morphological alterations shown by plants under UV light stress is difficult because they can be affected simultaneously by other environmental factors such as temperature, salinity, or drought, which together can modify development at the cellular level. The objective of this chapter is to describe the effects of UV radiation on different biochemical, morphological, and genetic processes in plants.

2. Morphological alterations

Photomorphogenesis (light-regulated plant development) in the presence of UV light has been extensively studied [10]. Plants of several species modify the development of their organs in the presence of UV light; for example, the length of the stems tends to shorten, although they form a greater number of axillary buds, while the roots tend to be longer and more abundant, akin to the development of plants that grow in conditions of low light radiation [11].

One of the stages of plant development most susceptible to the incidence of light is germination, which is also greatly affected by UV-B radiation. In *Arabidopsis thaliana* seedlings irradiated with UV light, the growth of the hypocotyl was slower [12] compared to seedlings germinating under normal conditions; even the growth of the hypocotyl is lower in etiolated plants developed in the shade but irradiated with UV light [13]. On the contrary, in this same species, it has been observed that, under these conditions, the cotyledons tend to expand, even with short periods of UV light exposure [14].

Leaves also modify their structure, tending to decrease their surface area and increase their thickness in many broadleaf plant species that have been tested for their response to UV light. Apparently, this change in morphology depends on the imbalance between cell proliferation and elongation among the different leaf tissues, which can cause a decrease in leaf area, abnormal thickening, or rolling, resulting in slow plant development [15]. While searching for modifications at the cellular level that explain the alterations in the morphology of plants under UV stress, Krasilenko et al. demonstrated in 2013 [16] that UV radiation can cause depolymerization or fragmentation of microtubules in *A. thaliana* cells, causing the reorganization of the cytoskeleton and the cell in general, so that elongation and cell division are reduced, resulting in the formation of shorter leaves, which affects the development and the complete morphology of the plant.

It is currently accepted that some plant species avoid excess light radiation by forming a waxy cuticle on the epidermis. Exposure to UV radiation-induced deposition of wax in plants of species, such as *Coffea arabica*, *Coffea canephora*, *Hordeum vulgare*, *Cucumis sativus,* and *Phaseolus vulgaris*, which results in an increase in the thickness of the cuticle. Additionally, molecules such as phenolic acids and flavonoids can accumulate in the cuticle, functioning as photoprotectors against UV light or as UV light attenuators, respectively [17].

Stomata, the structures where gas exchange occurs, are also affected by the presence of UV light. High UV irradiation causes loss of stomatal opening and closing control in response to environmental stimuli, apparently due to an altered guard cell conductance. Since the stomatic function is vital for CO_2 fixation in the light-independent reactions of photosynthesis, its deregulation can deeply affect plant development and physiology [18].

UV light plays an important role in plant development, but extreme exposure can be detrimental. Unable to relocate, plants must balance the positive and negative effects of UV radiation mostly through intracellular mechanisms, as described in the following sections.

3. Photosynthetic alterations

Photosynthesis is a light-dependent process, so it is almost inevitable that it be affected by the presence of UV radiation. There are several reports about the damage caused by UV radiation in specific sites of the photosynthetic apparatus of green plants (**Figure 1A**) [17]. Much of the damage is caused by the enhanced production of reactive oxygen species (ROS) that are involved in UV-induced responses, both as signaling agents within normal cellular processes and as damaging agents. ROS can cause damage to the proteins that make up the light-harvesting complexes of the photosystems or to those found in the protein complexes where the electron carriers of photosynthesis are concentrated, their accumulation is even known to cause the
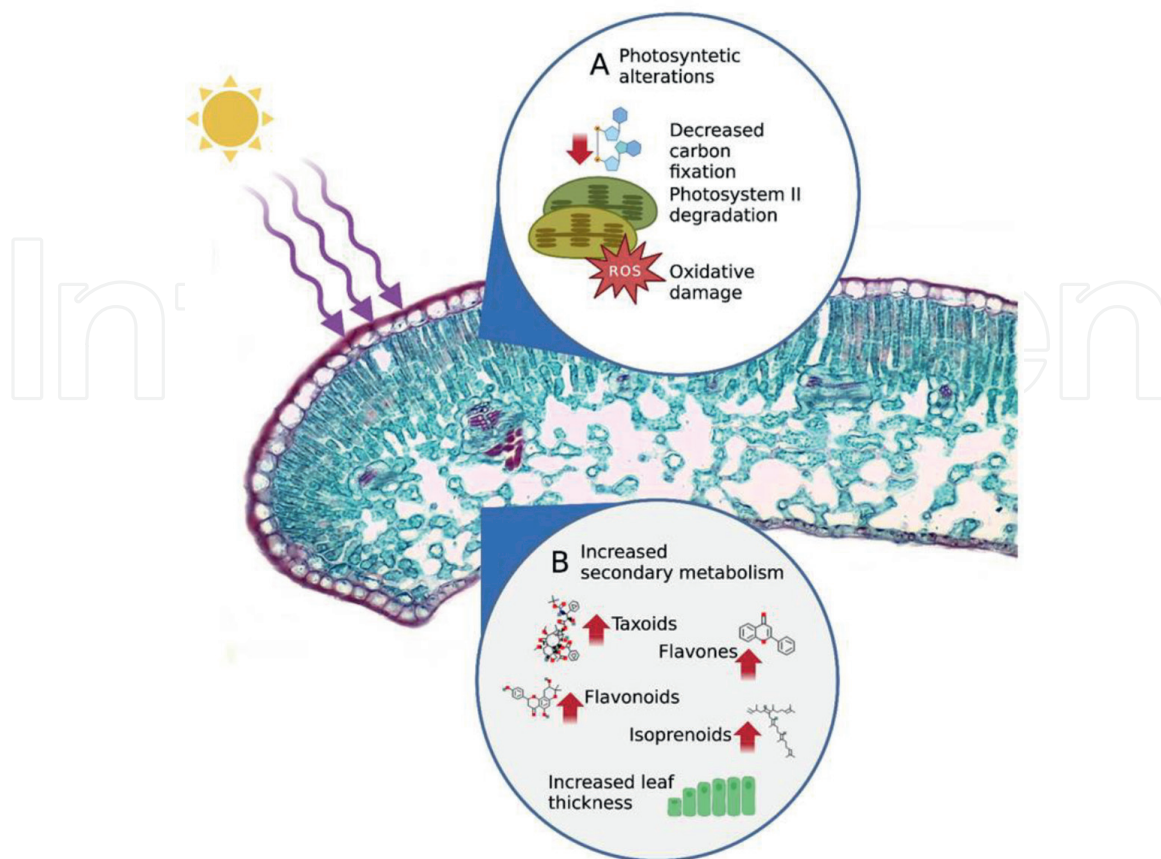
Figure 1.
Effects of UV-B light on plants and alterations caused by UV-B radiation in photosynthetic metabolism (A) and secondary metabolism (B).

destruction of ribulose bisphosphate carboxylase/oxygenase [19], and, therefore, a decrease in atmospheric carbon fixation and plant biomass occurs. Another important damage caused by ROS is the oxidation of fatty acids in the membranes, which, in combination with peroxidation and photooxidation because of UV light, breaks the essential integrity of the thylakoid membranes in the chloroplast, generating alterations in the organization of the membrane-embedded photosynthetic complexes, decreasing their photosynthetic capacity [20].

Ultraviolet light also causes damage to plant proteins; in fact, one of the effects on photosynthesis is the damage, it exerts on the enzymes that synthesize pigments such as chlorophylls [21]. In addition, pigments are also degraded by UV light, especially chlorophyll b and carotenoids, so exposure to this type of radiation can cause an imbalance in the proportion of pigments, with the consequent alteration of the photosynthetic apparatus, as has been observed recently in maize. After being exposed to UV radiation for 19 days, fluorescence and chlorophyll concentration decreased in several maize lines, although in different proportions in a line-dependent manner [22].

Several elements at Photosystem II, the site where photosynthesis begins, are sensitive to UV radiation. This complex is formed by the association of pigments and proteins, and many of these proteins are part of electron transport centers; therefore, their alteration or degradation affects the electron transport chain of photosynthesis, reducing their levels under UV light stress. In an elegant work, Ihle [23] reported that proteins D1 and D2, which are found in the reaction center of photosystem II, are

especially susceptible even to low intensities of UV radiation (1 μmol m^{-2} s^{-1}) [24]. The degradation of proteins D1 and D2 adds to the alteration of the manganese (Mn) oxidizing group of water, which together cause the loss of function of the reaction center and, therefore, the inhibition of electron transport [25]. Damage at the beginning of the electron transport chain of photosynthesis makes it difficult to investigate downstream transporters; however, some reports indicate the change in the ratio of photosystems II and I due to the decrease in absorption at 700 nm—absorbed by Photosystem I—observed after prolonged exposure to UV light [26].

Plants are highly susceptible to the presence of ultraviolet light. Through research over the past four decades, it has been possible to discover the mechanisms related to damage in plant morphology, development, and metabolism. However, many questions remain to be investigated until the problem of the penetration of UV radiation into the atmosphere is resolved.

4. Oxidative stress by UV light induction

Ultraviolet radiation is an important stress in plants that elicits protective mechanisms such as the accumulation of secondary metabolites in the cell (**Figure 1B**) [27–29] and an increase in leaf thickness [30]. Interestingly, UV radiation is a hormetic stimulus, that is severe exposure is harmful, but exposure to lower sub-acute levels can stimulate protective mechanisms [31]. Consequently, plants can become resilient to UV after repeated exposure [32].

The changes in the secondary metabolism of plants from all taxa under exposure to UV radiation have been widely documented. For instance, in the moss *Pohlia nutans*, UV-B radiation enhanced flavone biosynthesis through increasing type I flavone synthase activity [33]. In *Taxus cuspidate*, UV-B radiation (3 W/m^2) provoked the accumulation of toxoids and flavonoids [34]. Also, the flavonoid contents in *Scutellaria baicalensis* reached the maximum concentration (41.86 mg/g^{-1}) after seven days under UV-A radiation [35]. In *Pisum sativum* leaves, exposure to UV-B radiation increased the nicotinamide and trigonelline content; the nicotinamide induction is an oxidative stress reaction [36]. In an analysis performed on two different ecotypes of the *Paubrasilia echinata* tree, it was shown that UV-B radiation inhibited stem growth, biomass accumulation, CO_2 assimilation, and photochemical efficiency in a shade-tolerant ecotype inhibition; in contrast, a sun-tolerant ecotype showed a positive response: UV-B increased flavonoids, lignin, and antioxidant properties, but reduced cell respiration [37]. In *Pinus radiata,* UV radiation provoked an early response reducing photosystem activity and accumulation of photoprotectors; even the primary metabolism was rearranged to minimize ROS production, also the isoprenoids compounds like carotenoids, tocopherols, phytol, and gibberellins were decreased [38]. Under exposure to UV-B radiation followed by dark treatment, the number of flavonoids and coumarins in *Clematis terniflora* increased significantly; while proteins related to photorespiration, the tricarboxylic acid cycle, and mitochondrial permeability showed differential expression profiles, indicating that UV-B radiation induces a reduction in energy consumption and maintains energy balance [39]. *Nymphoides humboldtiana* increased antioxidant activity and production of flavonoids like phloroglucinol, chlorogenic acid, epicatechin, quercetin, and ferulic acid after 13 days of exposition of UV-B radiation [40]. *Colobanthus quitensis* under UV-B radiation increased the biosynthesis of flavonoids, particularly flavone C-glycosides,

metabolites located within the most metabolically active cells [41]. *Melisa officinalis* showed changes in the glycolysis and phenylpropanoid pathway under UV radiation stress with differential recovery times [28].

Studies on algae have shown similar mechanisms, as expected by their phylogenetical relation to plants. For example, UV-B radiation-induced ROS production in peroxisomes and chloroplasts in *Ulva prolifera* provokes irreversible damage under 5 W m^{-2} [42]. In *Chlamydomonas reinhardtii,* UV-C radiation stress increased ROS levels and production of antioxidant polyphenols, a phenolic including caffeic acid, cinnamic acid, coumaric acid, salicylic acid, and protocatechuic acid, among others [43].

A notable example among plant-derived compounds is the alkaloid mimosine, present in the seedlings of *Leucaena leucocephala* spp. Glabrata is particularly interesting due to its therapeutic uses as anti-cancer, antifungal, and antimicrobial, which increase its economic interest. Acute UV-C exposure of *L. leucocephala* seedlings induced a strong accumulation of mimosine, which could be implicated in general oxidative stress modulation [44].

The effect of UV-radiation stress has also been extensively studied in plants used in traditional medicine. For example, *Morus alba*, used in traditional Chinese medicine, reduces its growth and secondary metabolism after exposure to UV-B [45]. *Gingko biloba* leaves, after long-term exposure to UV-B radiation, increase flavonoids biosynthesis, and these are beneficial as therapeutic active ingredients [29]. Two different species of the Chinese herb Astragalus modified their secondary metabolite production under UV-B radiation; *A. mebranaceus* produced increased hydroxycinnamic acid derivates, while *Astragalus mongholicus* accumulated myricitrin and isoflavones, showing different tolerance to UV-B stress [30]. The flowers of *Lonicera japonica* are used as a medicinal herb in Asian countries. Under UV radiation, *L. japonica* increases the levels of oxidative pentose phosphate and secondary metabolites such as secologanic acid, secoxyloganin, and isochlorogenic acid [46]. In *Adhatoda vasica*, also used in Asiatic traditional medicine, UV-B radiation (7.2 kj m^{-2} day^{-1}) induces a reduction of superoxide radical production while increasing hydrogen peroxide production [47]. Finally, *Centella asiatica*, used in Asian and African traditional medicine, accumulated saponins and epidermal flavonols under UV-B radiation in younger leaves with high levels of saponins; in contrast, in older leaves, sapogenins were the most abundant metabolites [48].

As shown in these studies, UV light has forced algae, bryophytes, and plants to modify their metabolism—particularly the secondary metabolism—to increase their ecological success rate. However, this also has important consequences for plants of commercial interest, as seen below.

5. UV radiation as functional quality of plant foods of commercial interest

Historically, economically important plants have been exhaustively studied; recent studies have focused particularly on UV light stress, searching for alterations in organoleptic properties and secondary metabolism. In modern horticulture, plants of economic interest have been irradiated with UV light during the flowering/fruiting period, with the purpose of stimulating oxidative stress pathways as well as antioxidant production [49]. In tomato juice production, the stress caused by UV radiation in plants decreased pectolytic enzymes, improving and preserving tomato characteristics for a longer period of time [50]. Also, in a tomato cultivar, UV-A and B radiation produced higher ripening synchronization and smaller fruits.

Exposure to UV-A radiation-induced accumulation of phenolics and flavonoids, making these fruits more appealing to consumers [51]. Furthermore, in tomato seedlings under UV-B radiation, carotenoid content increased as well as antioxidant enzyme activities [52].

Another plant of great economic importance is soybean (*Glycinine max*), which increases the isoflavone content of the sprouts under UV radiation [53]. In soybean seedlings, nitric oxide is induced as a protection against UV-B stress [54]. Meanwhile, on germinated soybean, UV-B radiation increased the contents of linoleic acid and erucic acid content, as well as isoflavones, phenolic acids, vitamin C, folate, and chlorophyll, improving nutritional and functional qualities [55]. Conversely, excessive UV-B exposure damaged cells and decreased the amount of isoflavones within them [56]. In cultured soybean, UV-C radiation increased the amount of genistein-O-glucoside and genistein-O-glucosyl-malonate, suggesting *in vitro* culture to obtain a high level of metabolites [57]. Moreover, in germinated soybean under UV-B radiation, total protein content and endogenous H_2O_2 were increased [58].

Cereals and ornate flowers also have responses to UV radiation. Wheat seedlings under UV stress showed an increase of phenylalanine ammonia-lyase only in the roots, indicating that UV-B radiation has a positive or negative impact, depending on the type of secondary abiotic stress factor observable in the production of phenolic compounds [59]. Also, germinated wheat under UV-B radiation increased phenols, ferulic acid, and coumaric acid. Exogenous Ca^2+ positively affected free and bound phenolic accumulations [60]. In amaranth (*Amaranthus cruentus* L.), UV-C radiation improved postharvest quality by increasing levels of quercetin, kaempferol, copene, lutein, β-carotene, and caffeic acid derivates [27]. In lily bulbs, UV-C radiation increased total phenolic content and antioxidant activity, indicating that UV-C radiation is a safe alternative for processing lily bulbs in storage [61].

Likewise, the effects of UV radiation have been studied in economically important herbs. In spinach cultivars, UV-C induced a hormetic effect that increased total phenolic compounds and reduced the presence of the parasite fungi *Alternaria* ssp. in the crops [62]. In barley seedlings, UV-B radiation up-regulated enzymatic activity, resulting in the accumulation of phenolic acids [63]. *Mentha aquatic* responded to UV-B radiation on a morphological level, increasing glandular trichomes, and on a biochemical level, increasing oxidative metabolism and overexpressing genes implicated in terpene biosynthesis, particularly volatile oils as camphene, β-pinene, and germacrene [64]. In wounded carrots under UV-A and C radiation, ROS increased, acting as a signal for ethylene synthesis, which activated the synthesis of jasmonic acid leading to the accumulation of phenolic compounds [65]. In fresh-cut carrots, UV-C doses inhibited ascorbic acid, total carotenoid, respiration, total phenols, lignin, malondialdehyde, and ethylene production; all data collected indicated extended shelf-life and overall quality maintenance [66]. In parsley, UV-C doses resulted in an increase of antioxidants such as phenylpropanoid and phenolic compounds, as well as enzymes involved in the synthesis of phenylpropanoid [49]. The effect of UV radiation induces the production of 6″-0-malonylapiin, which is a flavone glycoside, as well as the 12-oxo-phytodienoic acid [67]. UV-B radiation (1.5 kJ m^{-2}) maintained the color of broccoli florets during storage, and induced glucosinolates and hydroxylcinnamates, raising their antioxidant properties. These findings suggested that UV-B radiation is likely to induce the indole glucosinolate pathway [31], maintaining the quality of broccoli florets in low-temperature storage [68].

Fruits are also of economic interest and respond differentially to UV. Grape berries (Jumeigui variety) decreased sugar content under UV-C, promoting the

accumulation of stilbenes and some flavonoids [69]. In contrast, berry clusters (red table emperor) under UV-A and B radiation decreased the amount of quercetin 3-O-glucoside and quercetin 3-O-glucuronide, suggesting that UV radiation induces postharvest changes in phenolic metabolites [70]. In fresh-cut strawberries, UV-C increased phenolic compounds, anthocyanin, cyanidin 3-glucoside, pelargonidin 3-glucoside, and cyanidin 3-glucoside-succinate, activating the phenylpropanoid pathway, thus improving antioxidant capacity without losing fruit quality [71]. In two blueberry cultivars (*Vaccinium corymbosum*), exposure to UV radiation showed that the amount of phenylpropanoid compounds was higher in the Legacy cultivar than in the Bluegold cultivar, which indicates that UV-B acclimation is different between cultivars [72]. Moreover, in highbush blueberry leaves (*V. corymbosum* L. cv. Brigitta and Bluegold), photosynthesis decreased in the Bluegold variety under UV-B radiation; in contrast, the Brigitta variety increased the photosynthesis rate as well as antioxidant activity [73]. In fragrant pear, postharvest UV-C radiation controlled blackhead disease through chitinase, β-1,3-glucanase, peroxidase, superoxide dismutase, catalase, ascorbate peroxidase, and phenylalanine ammonia-lyase [74]. In nectarine, UV-C radiation induced an increase in anthocyanin biosynthesis and promoted the antioxidant system, stimulating the phenyl propane pathway. Together, these compounds exerted antifungal action against *R. stolonifera* [75]. In young leaves of *Vitis vinifera*, low UV-B radiation increase sitosterol, stigmasterol, and lupeol, probably as an acclimation response. In contrast, diterpenes, tocopherol, phytol, E-nerolidol, monoterpenes as careen, α-pinene, and terpinolene were present in high amounts in mature leaves; these results showed that the synthesis of terpenes is an adaptive response to UV-B radiation stress [76]. In postharvest lemon fruits after UV-B radiation, phenolic compounds increased in flavedo, indicating that lemon peel modifies enzymatic activities involved in sucrose metabolism [77].

Furthermore, in *Olea europaea*, UV-B radiation increases secoiridoids and 2″-methoxyoleuropein metabolites, while decreasing oleuropein as an antioxidant defense against UV [78]. The peach (*Prunus persica*) diminishes the synthesis of anthocyanins and phenolic compounds under UV-B exposure, but after 36 h, it increases anthocyanins, cyanidin, and delphinidin compounds [79]. In Luffa seedlings, the oxylipins such as methyl jasmonate and 12-Oxo-phytodienoic acid mitigated the UV-B stress via improved photosynthetic and nitrogen metabolism, respectively [80].

Even economically important algae respond to UV radiation. In several Spirulina species, mild stress by UV-B radiation has been useful in increasing physiological and nutritional competencies in growth, rendering UV radiation useful in producing this functional food [81].

Although most of the above-mentioned economically important species appeared to benefit from UV exposure, it has been detrimental to some species. Rice (*O. sativa*) plants treated with UV-C had less palatability and were easily infested by the weevil *Sitophilus oryzae*, which provoked lower consumer acceptance and purchase intention [82]. Also, sweet cherry fruits under UV-C radiation diminished respiration, but increased rhamnose, mannose, galactarate, threonate, and aspartate contents [83].

This evidence highlights the importance of studying UV stress in plants of economic interest, as it can lead to higher yields and thus higher profits. However, care must be taken before implementing UV irradiation as a production-boosting resource because some species might be impacted negatively, as evidenced by the effects of the increased exposure to UV derived from climate change. Plant litter decomposition,

especially in regions with low annual rainfall and reduction of photosynthetically active radiation (PAR), further strain crop production [84].

6. Genetic response

Several studies have focused on changes in gene expression in plants exposed to long- and short-wave UV-B radiation to identify the cellular components that regulate response to UV [85]. The results showed that UV-B radiation triggers cell growth and morphogenesis pathways [86]. UV-B response signals are also transmitted from cell to cell and are usually organ-specific [87].

Genetic approaches for phenotypic responses to UV-B are based on models of increased tolerance or aberrant responses (e.g., changes in hypocotyl growth) to UV-B irradiation [86]. Transcriptomic analysis from *Arabidopsis* seedlings exposed to different UV-B radiation intensities showed that more than 20% of the genes that modified their expression are transcription factors [85]. These approaches allowed the identification of mutants that lacked or overexpressed photoprotective compounds or inhibited hypocotyl growth in response to UV-B [14, 88].

UV-B radiation induces changes in the expression of genes that affect growth and development, as seen in *UV-B light insensitive* (*uli*) mutant plants, which present reduced hypocotyl growth relative to wild-type after UV-B exposure. Also, UV-B affects *chalcon synthase (CHS)* expression [14]; low levels of irradiation activate this gene, which is key in the biosynthesis of phenylpropanoids [89]. *CHS,* along with transcription factors, allows plants to protect themselves against UV-B.

LONG HYPOCOTYL5 (HY5) is a bZIP transcription factor that regulates morphogenesis in response to UV-B. *HY5* gene expression is a component of the UV-B-induced signaling network. Transcriptomic analysis in *Arabidopsis thaliana* showed the importance of HY5-dependent regulation in response to low-level UV-B irradiation [85]. If HY5 is lost, transcriptional induction of the UV-B response genes is impaired [86] and cells undergo programmed death [90].

HY5 is a light-induced transcription factor required for many light-responsive genes; in the dark, it is degraded by the proteasome [91]. This transcription factor is key for phytochrome and cryptochrome regulation networks [85, 92, 93]. So, it seems that HY5 does not respond to UV-B radiation exclusively, which opens the door for research on other components that specifically drive plants' response to UV-B.

Several genes are induced by UV-B independently from traditional photorecep-tors, such as phytochromes and cryptochromes, through the activity of the LONG HYPOCOTYL5 (HY5) transcription factor [85]. This independence suggests that there must be a specific UV-B photoreceptor that activates HY5; however, the identity of this putative element is still unclear [94].

CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1) is an E3 ubiquitin ligase that participates in the UV-B response [95]. COP1 has three functional domains, a RING finger (ligase activity), a coiled-coil for dimerization, and a WD40 repeat domain with binding activity [93]. COP1 targets bZIP transcription factors and is required to activate *HY5* gene expression. Both proteins are localized in the nucleus and regulate photomorphogenesis under UV-B conditions in a specialized pathway [95]. COP1 was identified as a photomorphogenesis repressor in darkness and light [93, 96]. Visible light inactivated COP1 and separated it from HY5 [93], allowing HY5 stabilization and, therefore, activation of light-responsive genes [91, 97] through the

interaction of phytochromes and cryptochromes [98, 99]. Phytochromes and cryptochromes interact with the SUPPRESOR OF PHYTOCHROME A (SPA) proteins, causing light-dependent COP1 inactivation. COP1 response to UV-B radiation is independent of the SPA proteins [95, 100]; rather, COP1 responds to UV-B through the interaction with the UV RESPONSE LOCUS 8 (UVR8) protein [96].

UVR8 is a seven-bladed b-propeller protein that forms a homodimer in its inactive state [101, 102] and is capable of UVR-B perception [103, 104]. In contrast to other photoreceptors (phytochrome and cryptochrome), UVR8 does not employ a bound chromophore; instead, it uses a tryptophan residue localized in the b-propeller blade [101, 102, 105]. Upon UV-B absorption, the UVR8 dimer destabilizes and the monomeric form interacts with COP1 [104]. The UVR8-COP1 heterodimer activates the transcription factor HY5, consequently activating downstream genes that are implied in metabolic and morphological alterations [104, 106]; this mechanism activates UV-B acclimation and tolerance [96]. UVR8 is usually located in the cytoplasm, while COP1 is in the nuclear bodies of hypocotyl cells. When plants are irradiated with UV-B, UVR8 translocates to the nucleus [107] and colocalizes to the COP1-rich nuclear bodies [96]. After UV-B exposition, the UVR8 dimer COP1 prevents HY5 degradation, so that HY5 can exert its transcriptional activation function [108].

In Arabidopsis plants, *uvr8* mutants do not respond when grown under UV-B radiation; they lack a photomorphogenic signal and therefore do not display the damage usually found in wild-type plants [96]. UV-B-induced gene expression is important for UV acclimation and survival. When *urv8* and *cop1* mutants are initially grown in weak UV-B exposure and later moved to high UV-B irradiance, the mutants do not show an acclimation effect. When exposed to a natural spectral balance, the *uvr8* mutant shows leaf damage. Also, *HY5* or *CHS* gene expression is undetectable
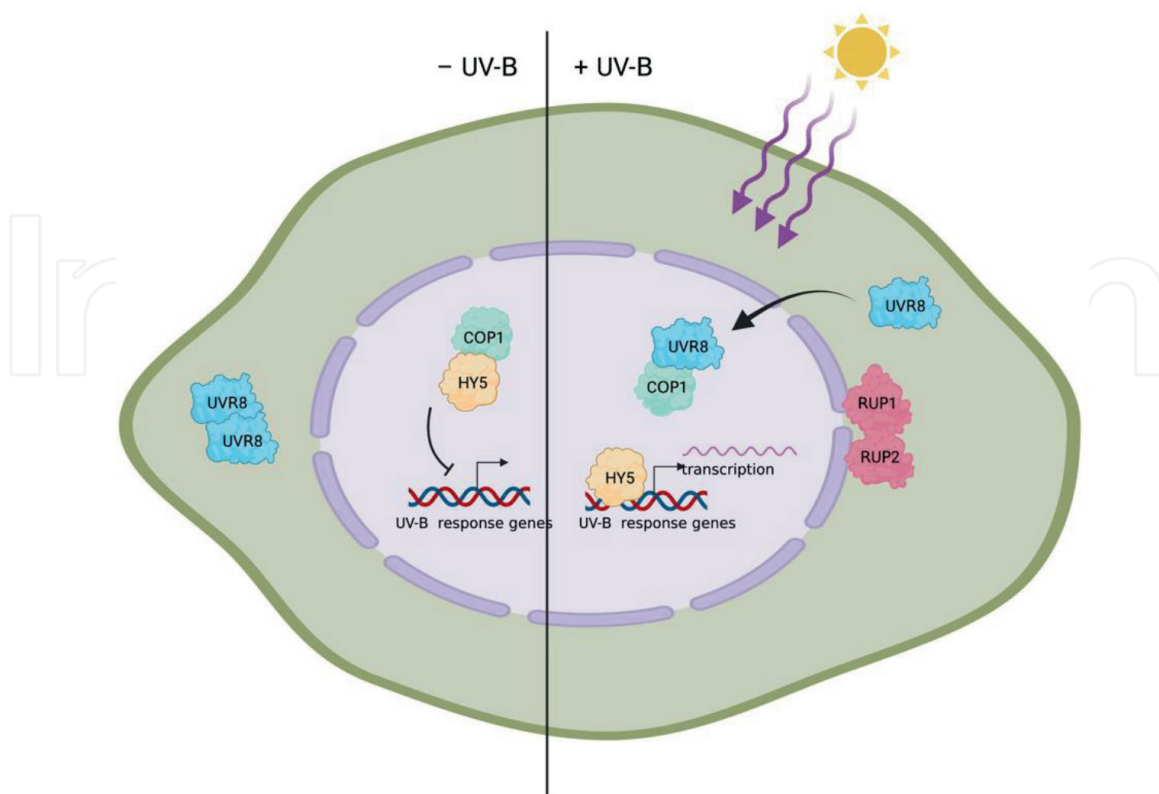
Figure 2.
ELONGATED HYPOCOTYL5 (HY5) transcription factor activation.

in both mutants. Consequently, the interaction between COP1 and UVR8 proteins is required for the regulation of UV-B response and confers UV-B protection. On the other hand, overexpression of *UVR8* leads to UV-B photomorphogenic hypersensitivity, presenting inhibition of hypocotyl growth, activation of *HY5* and *CHS* gene, and accumulation of anthocyanin [96].

COP1 is related to the repression of photomorphogenesis but it seems that UVR8 provides UV-B-specific signaling and that the interaction COP1-UVR8 occurs within minutes [96]. UVR8 is reverted to homodimer (inactive form) through the REPRESSOR OF UV-B PHOTOMORPHOGENESIS proteins (RUP1 and 2). RUP1 and RUP2 are two highly related WD40-repeat proteins that interact directly with UVR8 promoting its homodimerization, thus acting act as negative regulators [104, 108, 109]. *RUP 1* and *RUP 2* are induced by UV-B but act downstream of UVR8-COP1 forming a negative feedback loop that balances UV-B defense [109] (**Figure 2**).

Inhibition of the transcription factor HY5 by binding with COP1 in the absence of UV-B light, the expression of the response genes remains inactive (left). In the presence of UV-B light, the monomeric form of UVR8 enters the nucleus, binds to COP1, and activates HY5 (right).

7. Conclusions

The effects that UV radiation causes on plants have been extensively investigated from different perspectives. Studies on alterations in photomorphogenesis, primary metabolism, particularly photosynthesis, secondary metabolism, or gene expression have been carried out with model plants such as *Arabidopsis thaliana*; however, several other aspects still need to be addressed. Current technologies, such as omics tools, allow for the study of plants in their natural environments, considering all their complexity, and will, undoubtedly, lead to a better understanding of the impact of UV radiation in plants, an important constituent of climate change. Looking into the future, an integral view of plant responses to UV radiation has broad applications in agriculture and conservation, while providing scientific foundations for upcoming international regulations.

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