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Review

UVA and UVB Radiation as Innovative Tools to Biofortify Horticultural Crops with Nutraceuticals

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Abstract: The consumption of fruits and vegetables is related to the prevention and treatment of chronic–degenerative diseases due to the presence of secondary metabolites with pharmaceutical activity. Most of these secondary metabolites, also known as nutraceuticals, are present in low concentrations in the plant tissue. Therefore, to improve the health benefits of horticultural crops, it is necessary to increase their nutraceutical content before reaching consumers. Applying ultraviolet radiation (UVR) to fruits and vegetables has been a simple and effective technology to biofortify plant tissue with secondary metabolites. This review article describes the physiological and molecular basis of stress response in plants. Likewise, current literature on the mechanisms and effects of UVA and UVB radiation on the accumulation of different bioactive phytochemicals are reviewed. The literature shows that UVR is an effective tool to biofortify horticultural crops to enhance their nutraceutical content.

Keywords: ultraviolet radiation (UVR); UVA; UVB; nutraceuticals; functional foods; biofortification

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1. Introduction

Being sessile, plants are constantly exposed to biotic and abiotic stresses. Their response to such stresses is complex, involving changes at the transcriptome, cellular, and physiological levels [1]. Secondary metabolites are well known to be related to the plant's defense response mechanisms, being induced in response to abiotic stresses and acting as natural phytoalexins to protect plants against these stresses [2]. Moreover, many of these secondary metabolites possess pharmacological activity that results in the prevention and/or treatment of chronic and degenerative diseases [3].

In this context, the application of abiotic stresses (i.e., wounding, modified atmospheres, exogenous phytohormones and ultraviolet radiation (UVR)) may be used as an approach to biofortify crops with specific health-promoting compounds with applications in the pharmaceutical, cosmeceutical, and nutraceutical industries [4,5]. For instance, mature crops such as broccoli [6–8], carrot [9], potato [10,11], and lettuce [12] have been used to study the effect of abiotic stresses on antioxidant biosynthesis and accumulation.

UVR comprises 7–9% of the total energy of solar radiation reaching the Earth surface and is sub-divided in three wavelength ranges: UVA (320–400 nm), which represents about 6.3% of the incoming solar radiation and is the least harmful range; UVB (280–320 nm), representing about 1.5% of the total spectrum, but causing several detrimental effects in plants; and UVC (100–280 nm), which is extremely harmful to organisms, but is completely absorbed by stratospheric ozone [13–15].

Plants are unavoidably exposed to UVR as they are sessile organisms and as they need to capture sunlight for photosynthesis. It is well known that UVR causes different responses in plants; some of them are detrimental, including damage to DNA and proteins, generation of ROS and initiation of cellular stress responses, changes on cell physiology,

as well as changes in plant growth, morphology and development [16–18]. Thus, plants need to evolve different mechanisms for UV-protection and repair [13]. These mechanisms include the biosynthesis of nutraceuticals such as phenolic compounds, glucosinolates, carotenoids, chlorophylls, ascorbic acid, and betalains.

In this review paper, the physiological and molecular basis of stress response in plants is described. Likewise, current literature on the mechanisms and effects of UVA and UVB radiation on the accumulation of bioactive phytochemicals is reviewed.

2. Physiology of Stress Response in Plants

It has been reported that, upon being subjected to an abiotic stress, the general cellular process and regulation for activating plant secondary metabolite starts with an extracellular or intracellular signal, which is then recognized by a receptor on the surface of the plasma membrane. In turn, this initiates a signal transduction cascade that leads to activation or de novo synthesis of transcription factors to regulate gene expression involved in the plant secondary metabolism [1].

Different signaling molecules, such as ethylene (ET), jasmonic acid (JA), reactive oxygen species (ROS), salicylic acid, and abscisic acid have been reported to be produced by abiotic stresses as well as to activate plant defense genes, including those from the phenylpropanoid metabolism, triggering the accumulation of phenolic compounds [19,20]. Models recently proposed to explain the physiological and molecular basis of these compounds state that phenolic biosynthesis under several stress conditions including wounding alone, and in combination with UV light (types A, B, and C) stresses or in combination with ET and JA treatments, is an event mainly mediated by ROS as a signal molecule to activate the plant primary and secondary metabolism, while ET and JA modulate ROS levels, although they may also play a mild role in triggering the expression of certain genes related to the synthesis of secondary metabolites [7,20]. Moreover, it has been reported that extracellular adenosine triphosphate is the primary signal that triggers the wound-response in plants [21].

Additionally, ET and methyl jasmonate (MeJA) treatments have shown to upregulate the expression of *CYP79* genes related to glucosinolate biosynthesis in *Arabidopsis*. It was concluded that MeJA was a potent inducer of both *CYP79F* and *CYP79B* genes, placing it as the most potent elicitor of glucosinolate biosynthesis [22].

On the other hand, when stress occurs, Ca^{2+} influx, alkalinization of the apoplast, and protein phosphorylation, among other intracellular events, lead to the synthesis of NADPH oxidase and trigger an oxidative burst in the plant. NADPH oxidase is the key source of the early and sustained accumulation of ROS; it is responsible for the reduction of O_2 to O_2^- and with the presence of SOD enzyme, O_2^- is converted to H_2O_2. It has been shown that ROS molecules, both O_2^- and H_2O_2, are involved in plant stress-induced defense responses [1]. Expression of genes related to plant defense pathway has been demonstrated as consequences of pathogen attack, chilling injury, wounding, and excess light [23,24].

Nitric oxide (NO) is another signaling molecule involved in adaptive plant responses to some specific abiotic stress conditions, particularly low mineral nutrient supply, drought, salinity, and high UVB radiation. NO is also an important component of the mechanisms responsible of coordinating and regulating Ca^{2+} and ROS signaling in plant defense [25]. Reaction with metal centers, thiols, oxygen molecule, and free radicals constitutes the way through which NO modulates plant responses that trigger the biosynthesis and accumulation of phytochemicals such as glucosinolates and phenolic compounds [25].

3. UV Radiation as an Abiotic Stressor

Plants need to evolve different mechanisms for UV-protection and repair. These mechanisms include deposition of UV-absorbing phenolic compounds in the outer epidermal layers and the production of antioxidant systems, action of reparative enzymes such as DNA photolyases, and expression of genes involved in both UV-protection and repair [17].

UVR regulates different aspects of metabolism, modulates biochemical composition and thus, promotes the synthesis and accumulation of secondary metabolites, such as phenolic compounds and glucosinolates [26–28]. Phenolics and carotenoids provide UV-absorbing sunscreen that limits penetration of UVB into leaf tissues. Although glucosinolates are not directly involved in UV protection, UV-mediated effects on glucosinolates are conceivable as they are involved in the common plant defense response, regulated by the signaling pathways involved in the perception of UVB [29,30]. In the following sections, the reported effects of UVB and UVA radiation on phytochemical accumulation are reviewed separately.

3.1. Mechanisms and Effects of UVB Radiation on Phytochemical Biosynthesis

Plant responses to UVR are likely to involve specific UV photoreceptors and signal transduction processes, which lead to the regulation of gene transcription [31,32]. Between the two solar UVR ranges (UVA and UVB) that reach the Earth, UVB radiation is the most harmful. Hence, numerous efforts have been focused on assessing the effects of UVB on plants. In this context, there is currently an extensive body of data concerning UVB-mediated cellular damage, as well as regulatory responses mediated by the UVB photoreceptor UV resistant locus8 (UVR8) [33].

Two main types of signaling pathways have been proposed regarding how plants perceive UVB radiation and how they regulate secondary plant metabolism. One pathway is not specific to UVB and implies that UVB-induced oxidative stress responses (rather than photomorphogenic responses to UVR) may result from damage to molecules and/or the accumulation of signaling molecules such as ROS and wound or defense-related molecules including jasmonic acid, salicylic acid, nitric oxide, and ethylene. In turn, this leads to over-expression of stress-related genes, normally induced by wound and defense signaling pathways (e.g., *PR-1*, *PR-2*, *PR-5* and the defense gene *PDF1.2*) [31,34,35]. In contrast, the signaling pathways that mediate responses to UVB as a signal appear to be UVB-specific and to result in UV-protection or morphological changes [24]. In this type of signaling, the cytosolic UVR8 photoreceptor seems to play a major role. In the presence of UVB, UVR8 monomerizes and interacts with the multifunctional E3 ubiquitin ligase constitutively photomorphogenic 1 (COP1) and translocate into the nucleus where they prevent the degradation of the photomorphogenic transcription factor elongated hypocotyl 5 (HY5). Successively, HY5 and its homolog (HYH) control expression of a range of key elements involved in UV acclimation response and UV protection, such as genes encoding enzymes of the phenylpropanoid pathway, including phenylalanine ammonia lyase (PAL), chalcone synthase (CHS) and flavonol synthase (FLS) [23,32,34,36–41]. Thus, the UVR8 photoreceptor is required for the induction of genes with important functions in UV protection. In addition, there is also the possibility that the aforementioned mechanisms are not solitary and that UVR regulates gene expression by combination of these mechanisms [9].

Moreover, it has been reported that UVB-induced signaling molecules, such as NO, exert a protective role against oxidative stress, alleviating UVB-induced photodamage [19]. For instance, UVB radiation increases both ROS and NO in plants. Then, NO reduces ROS levels and upregulates the expression of several genes involved in phenolic biosynthesis (i.e., the maize transcription factor ZmP and MYB12, its *Arabidopsis* functional homolog and their target genes *CHS* and *CHI–chalcone isomerase*). Thus, biosynthesis and accumulation of some flavonoids and anthocyanins are induced to absorb UVB and scavenge ROS [42]. UVB radiation has also been reported to stimulate ET production in plants. NO and ROS have also been implicated in UVB-induced ethylene production in maize seedlings [43].

The effect of UVB radiation on phenolic accumulation has been studied in several fruits and vegetables and, although not all phenolic compounds are similarly induced, flavonoids and flavonoid glycosides are generally more responsive to UVB than phenolic acids [41]. The accumulation of specific flavonoid glycosides appears to be an intrinsic part of the UVB response, with expression of several UDP- glucosyltransferases being directly controlled by UVB [37].

Table 1 summarizes the main finding of studies performed in several plant models suggesting the use of UVB as an abiotic stress to elicit the biosynthesis and accumulation of phytochemicals such as phenolic compounds, glucosinolates, ascorbic acid and betalains [9,27,29,44–63]. For instance, it has been shown that supplementation with UVB radiation in carrots, apples, grapes and flowering plants induces the accumulation of phenolic compounds due to an UVB-induced upregulation of key genes encoding enzymes of the phenylpropanoid pathway [9,44,46,47].

Table 1. Effect of UVB radiation on the biosynthesis of bioactive phytochemicals and on stress responses in different horticultural crops.

Plant Species	UVB Treatment Parameters and Storage Conditions	Phytochemical Evaluated	Main Findings	Reference
Red grapes (*Vitis vinifera*)	30–510 W, ID: 20–60 cm, 5 s–30 min post-harvest exposure. Storage at 20 °C.	Resveratrol and other PCs	Maximum resveratrol content per standard serving (200 g) was 3 mg (11-fold higher than untreated grapes) and was achieved 3 d after irradiation of grapes placed 40 cm below UVB lamps (510 W), for 30 s. Content of other PCs remained unaltered.	[44]
Apples (skin) (*Malus domestica*)	0.16–0.2 W m^{-2} + 15–20 µmol m^{-2} s^{-1}(visible light), ID: 50 cm, 10 or 20 °C, for 72 h.	PCs	Apples inner facing (when on the tree) accumulated more anthocyanins and Q gly than outer facing ones. Fruit maturity and lower temperature (10 °C vs. 20 °C) prevented UVB-induced phenolic accumulation. Chlorogenic acid increased (~75–500%) using UVB at both temperatures in four of five cultivars evaluated.	[45,46]
Shredded Carrot (*Daucus carota*)	1.5 kJ m^{-2}, 162 s, ID: 17.5 cm. Storage at 15 °C for 72 h.	PCs	PAL activity of UV-B and non-irradiated samples was increased by approximately 760% after 72 h. An accumulation of up to 30% in PC content after 72 h was observed versus control samples,	[47]
Wounded Carrot (*Daucus carota*)	10.44 W m^{-2}, for 0, 1, and 6 h, ID: 50 cm. Post-storage at 15 °C for 4 d.	PCs	After 6 h of UVB radiation, total phenolic content of carrot pies increased 3-fold, AOX capacity increased 7-folds, and PAL activity increased by 90-fold. Chlorogenic acid and a derivative, ferulic acid and isocoumarin were significantly accumulated after 6 h.	[9]
Rapeseed leaves (*Brassica napus* subsp. *napus*)	13 kJ m^{-2} d^{-1}, 3 h/d (at noon) for 16 d, pre-harvest.	Flavonoids	Total K and Q gly increased by ~150% and 70% in cvs. Paroll and Stallion, respectively. UV-B induced a specific increase in Q gly relative to K gly with a 36- and 23-fold increase in cvs Paroll and Stallion. Q and K 3-sophoroside-7-gly and 3-(2-E-sinapoylsophoroside)-7-gly appeared after UVB exposure.	[48]
Kale (*Brassica oleracea* var. *sabellica* L.)	0.22–0.88 kJ m^{-2} d^{-1} + 72 µmol m^{-2} s^{-1} for 1 d, ID: 30 cm, 15 °C, 24 h period of acclimatization before harvest.	Flavonol gly and HA derivatives	Q gly decreased under UVB. For K gly in the investigated UV-B range, monoacylated K tetragly decreased (46–63%), monoacylated K trigly increased depending on the acylation pattern (up to 96%), and monoacylated K digly increased strongly (197–441%) at the highest dose. The HA gly, diSg and S-Fg were enhanced by 49% and 88% in a dose-dependent manner.	[27]
Kale (*Brassica oleracea* var. *sabellica* L.)	1–5 daily doses of 0.25 kJ m^{-2} d^{-1}, for 1 h with 23 h acclimatization intervals, during 5 d (total dose: 1.25 kJ m^{-2} d^{-1}), ID: 60 cm, 5 or 15 °C.	PCs	All Q gly increased with increased UVB radiation, while K gly responded dependent on the HA residue. PCs containing a catechol structure favored in the response to UVB. 11 (of 20) PCs (e.g., monoacylated Q gly) were influenced by the interaction UV-B-temperature. Enhanced mRNA expression of *flavonol 3′-hydroxylase* showed an interaction of UV-B and temperature (highest at 0.75 kJ m^{-2}, 15 °C).	[49]
Silver birch seedlings (*Betula pendula*)	7.3–8.5 kJ m^{-2} d^{-1}, ID: 40 cm, 9 h/d for 10 d.	PCs	UVB induced production of K gly, chlorogenic acids, HA derivatives and Q gly, such as Q-3-galactoside and Q-3-rhamnoside. Leaf area was reduced by UV-B radiation.	[50]
Pak choi (*Brassica napus* subsp. *chinensis*)	0.35 W m^{-2}, 16 h/d for 7 d, pre-harvest, 9 or 22 °C.	PCs	UVB induced a 4-fold higher content in total flavonoids at 22 °C, but not at 9 °C. K-gly acylated with caffeic or coumaric acid (and not ferulic, hydroxyferulic, or sinapic acid) responded to UVB exposure. HA derivatives increased by 2-fold at lower temperatures (9 °C) and did not change at 22 °C.	[51]
Nasturtium (*Nasturtium officinale)*	0.075 and 0.15 W h m^{-2}, for 1 or 2 h, post-harvest, acclimatization period of 2 and 22 h, 20 °C.	Total PCs and GLSs	Plant response to UVB exposure is organ-, plant tissue age-, and phytochemical-specific. At lowest dose and adaptation time, GP increased by 6-, 3- and 2-fold in seeds, leaves and inflorescences, respectively. At highest dose and adaptation time, GP increased by 3- and 6-fold in inflorescences and leaves, but decreased in seeds. At both doses, total PC concentration in leaves and seeds decreased after 2 h, but increased to reach control levels after 22 h.	[52]
Brocoli sprouts (*Brassica oleracea* var. *italica*)	1 kJ m^{-2} d^{-1}, 5 h/d for 5 d, pre-harvest, ID: 40 cm.	GLSs	UV-B induced higher (<2-fold) aliphatic (but not indole) GLS levels when compared with untreated sprouts. This had a negative effect on the growth of aphid *Myzus persicae* and attack by caterpillar *Pieris brassicae*. L.	[29]
Broccoli sprouts (*Brassica oleracea* var. *italica*)	0.6 kJ m^{-2} d^{-1}, 4 h, 24 h period of acclimatization before harvest, ID: 40 cm.	Flavonoids, GLSs, carotenoids, Chls	Increases in K, Q, GRA and 4-MGBS were observed, each of them by up to roughly 2-fold. B-carotene and Chls levels remained unaffected. Increased expression of genes associated with salicylate (4- to 5-fold) and jasmonic acid (3- to 4- fold) signaling defense pathways were observed.	[29]

Table 1. *Cont.*

Plant Species	UVB Treatment Parameters and Storage Conditions	Phytochemical Evaluated	Main Findings	Reference
Broccoli (*Brassica oleracea* var. *italica*)	20 kJ m^{-2} d^{-1} + 19 µmol m^{-2} s^{-1}, 12 h/d for 3 d, post-harvest, during storage at 10 or 18 °C.	GLSs	UVB treatments applied during storage did not influence total and individual GLS levels in broccoli flower buds. Only exposure for 3 d to visible light (25 µmol m^{-2} s^{-1}) increased aliphatic GLSs stored at 10 °C, or indolic GLSs (4-HGBS and 4-MGBS) at 18 °C.	[53]
Broccoli (*Brassica oleracea* var. *italica*)	2.2, 8.8 or 16.4 kJ m^{-2} d^{-1} for 76 d (from planting until maturity stage), ID: 15 cm, post-harvest storage for 60 d at 0 °C.	PCs, GLSs, carotenoids, Chls	Total carotenoid and Chl contents decreased (up to 40 and 70%, respectively) with the increased dose of UV and storage time. The highest UVB dose increased ascorbic acid (~115%) and total PC content (~74%) prior storage. Sinigrin (~2-fold) and GP (~3-fold) contents increased by increased UVB dose and storage time.	[54]
Lettuce (*Lactuca sativa*)	4.2 W, 4 h/d for 6 d; or gradually increased irradiation from 1–7 h/d over 6 d, ID: 20 cm, 20 °C.	Total PCs	Repeated or gradual UVB exposure yielded ~3.6–3.2 times more total PCs, respectively, than the controls did 2 d after UVB exposure. These treatments boosted the antioxidant capacity by 80 and 45%, respectively, 2 d after UVB treatments. Both treatments inhibited lettuce growth.	[55]
Prickly pear (*Opuntia ficus-indica*)	6.4 W m^{-2} for 0, 15, 90, and 180 min and stored for 24 h at 16 °C. ID: 45 cm. Whole and wounded fruit samples were subjected to UVB radiation.	Betalains, total PCs, ascorbic acid	UVB radiation for 15 min was the best treatment to induce the accumulation of bioactive compounds. UVB radiation (15 min) of the wounded tissue induced an immediate accumulation of ascorbic acid (54–58%) and betalains (33–40%) in the peel and pulp of the fruit. After 24 h, the pulp of irradiated whole fruits showed the highest accumulation of betalains (49.8%) and phenolics (125.8%) as compared with the control, whereas the stored wounded tissue treated with UVB presented accumulation of ascorbic acid in the peel (84.6%) and pulp (67.2%).	[56]
Prickly pear (*Opuntia ficus-indica*)	6.4 W m^{-2} for 15 min and stored for 24 h at 16 °C. ID: 45 cm. Whole and wounded fruit samples were subjected to UVB radiation.	Betalains (indicaxantin and betanin)	UVB radiation applied in the whole tissue induced an immediate accumulation of indicaxanthin after treatment, obtaining increases of 106.5% and 325.8% in the peel and pulp, respectively. After storage, the tissue treated with UVB radiation and wounding before storage showed a synergistic effect on the accumulation of betanin in the peel (315.0%) and indicaxanthin in the pulp (447.0%).	[57]
Broccoli sprouts (*Brassica oleracea* var. *italica*)	Seven-day-old broccoli sprouts were exposed to UVB (9.47 W m^{-2}) alone and combined with methyl jasmonate	GSLs	UVB increased the content of aliphatic and indole glucosinolates, such as glucoraphanin (78%) and 4-methoxy-glucobrassicin (177%).	[58]
Broccoli sprouts (*Brassica oleracea* var. *italica*)	Seven-day-old broccoli sprouts were exposed to UVB (3.34 W m^{-2})	GSLs and PCs	After 24 h of UVB treatment, sprouts showed increases in 4-methoxy-glucobrassicin, glucobrassicin, and glucoraphanin by 170%, 78%, and 73%, respectively. Moreover, increases in gallotannic acid (~48%), 5-sinapoyl-quinic acid (~121%), and sinapoyl malate (~12%) were UVB-induced.	[59]
Peaches (*Prunus persica* L., cv. Fairtime)	Fruits were exposed to 10- or 60-min UVB treatment (1.39 and 8.33 kJ m^{-2}, respectively), and sampled at different time points from the exposure	PCs	After 24 h of 60-min UVB exposures, flavanols, flavones, flavonols, and dihydroflavonols increased by 123%, 70%, 55%, and 50% compared to the control group. Specifically, after 24 h of UVB treatment, the 60-min UVB exposure increased spinacetins, isorhamnetins, and kaempferols by 61%, 448%, and 95%, respectively.	[60]
Peaches (*Prunus persica* L., cv. Batsch)	The fruit were placed in a chamber at 20 °C followed by UVB (58 µw/cm^2) irradiation for 2 days	PCs	Cyanidin 3-glucoside reached (0.31 mg/100 g FW) after UVB treatment, value that was 3-fold higher than the fruits stored under dark conditions.	[61]
Apples (skin) (*Malus domestica*)	UVB lamp provided 1.69 W m^{-2} at fruit height. The treatment lasted 36 h (219 kJ m^{-2}).		Hydroxycinnamic acids (feruloyl glucoside, cryptochlorogenic and chlorogenic acids) showed an increase of 38% following 36 h of treatment and maintained higher values in the treated samples during storage as well as anthocyanins. At the end of the storage time (21 d) flavonols were 64% higher in the UVB-treated apples than the control, indicating that UVB treatment decreased flavonoid loss during storage.	[62]
Table grapes (*Vitis vinifera* × *Vitis labrusca* cv. Summer Black)	Grapes were exposed to 3.6 kJ m^{-2} UVB irradiation	PCs	Samples showed increses in the content of gallic acid (19.05%), protocatechuic acid (64.6%), naringenin (67.7%), quercetin 3-glucoside (13.86%), catechin (54.15%), epicatechin (23.89%), *trans*-resveratrol (23.53%), and *trans*-piceid (31.56%) after UVB treatment as compared with the control.	[63]

Abbreviations: ID: irradiation distance; PC, phenolic compound; GLS, glucosinolate, Chl, chlorophyll, K, kaempferol; Q, quercetin; gly, glycosides; HA, hydroxycinnamic acid; GP, glucotropaeolin; GRA, glucoraphanin; 4-HGBS, 4-hydroxy-glucobrassicin; 4-MGBS, 4-methoxy-glucobrassicin; diSg, disinapoylgentiobiose; S-Fg, sinapoyl-feruloylgentiobiose.

Quercetin and its glycosides, as well as kaempferol and most kaempferol glycosides, were shown to be enhanced after additional UVB radiation in broccoli, canola (*Brassica napus*), and table grapes [48,60,63]. In kale (*Brassica oleracea* var. *sabellica*), monoa-

cylated kaempferol tetraglucosides decreased following exposure to a single, low dose of UVB, whereas the monoacylated kaempferol diglucosides increased strongly under the same dose. Additionally, the hydroxycinnamic acid glycosides disinapoyl-gentiobiose and sinapoyl-feruloyl-gentiobiose were enhanced in a dose-dependent manner under UVB [27].

Tegelberg et al. [50] observed an increase in caffeoylquinic acid in silver birch exposed to slightly above-ambient UVB radiation, while Lancaster et al. [45] showed similar results in apples (*Malus domestica*).

The response of flavonoid glycosides is dependent on the type of phenolic acid that is acylated to the flavonol glycoside (mainly hydroxycinnamic acids). In pak choi (*Brassica campestris* ssp. *chinensis*), total flavonoid levels increased with exposure to additional UVB but kaempferol glycosides acylated with ferulic, hydroxyferulic, or sinapic acid did not respond to UVB light [51]. Likewise, in peaches, cyanidin 3-glucoside reached (0.31 mg/100 g FW) after UVB treatment, a value that was 3-fold higher than in the fruits stored under dark conditions [61]. In kale, the structural characteristics of the hydroxycinnamic acids themselves have an impact on the response to UVB [49]. While the levels of caffeic acid and hydroxyferulic acid monoacylated kaempferol triglycosides (containing a catechol structure) were increased with exposure to higher UVB radiation, the ferulic and sinapic acid monoacylated kaempferol triglycosides (no catechol structure) were not affected. In canola, the nonacylated kaempferol-3-*O*-sophoroside-7-*O*-D-glucoside increased with the additional UVB, while the sinapic acid monoacylated kaempferol glycoside did not respond [48]. Moreover, in peaches after 24 h of 60-min UVB exposures, flavanols, flavones, flavonols, and dihydroflavonols increased by 123%, 70%, 55% and 50% compared to the control group. Specifically, after 24 h of UVB treatment, the 60-min UVB exposure increased spinacetins, isorhamnetins, and kaempferols by 61%, 448% and 95%, respectively [60].

Hydroxycinnamic acids are known scavengers to ROS induced by UVB radiation. In kale, the hydroxycinnamic acid derivatives (caffeoylquinic acid disinapoyl-gentiobiose and sinapoyl-feruloyl-gentiobiose) were hardly affected by subsequent doses of UVB radiation [49]. However, a single moderate UVB dose led to a slight decrease in caffeoylquinic acid but an increase in disinapoyl-gentiobiose and sinapoyl-feruloyl-gentiobiose [27]. Likewise, in apples, hydroxycinnamic acids (feruloyl glucoside, cryptochlorogenic and chlorogenic acids) showed an increase of 38% following 36 h of treatment and maintained higher values in the treated samples during storage as well as anthocyanins. At the end of the storage time (21 d) flavonols were 64% higher in the UVB-treated apples than in the control, indicating that UVB treatment decreased flavonoid loss during storage. [62].

Regarding glucosinolates, reports on supplemental UVB effects on accumulation on individual glucosinolate in *Brassicaceae* plants are rare. However, it has been proposed that at higher doses, UVB induces JA defense and wound signaling, while lower UVB levels induces SA pathway signaling response and expression of genes encoding for pathogenesis-related proteins (e.g., PR-1, PR-2, PR-4, PR-5, PDF1.2), triggering alterations in the plant defense metabolism [28]. Application of low doses of UVB for 5 days increased aliphatic glucosinolate levels in broccoli sprouts, leading to a decreased plant susceptibility to insect attacks [29]. Likewise, low doses of UVB have been shown to increase levels of aliphatic glucosinolates (GRA and 4-MGBS) in *Arabidopsis thaliana* and broccoli sprouts and an aromatic glucosinolate (glucotropaeolin) in nasturtium (*Tropaeolum majus)* [29,52].

Less is known about the effect of UVB on carotenoids and chlorophylls, however, studies in soybean (*Glycine max*) plants and bean (*Phaseolus vulgaris*) leaves suggest that UVB radiation damages the chloroplast's photosystem II (PSII), enhances lipid peroxidation, ion leakage and H_2O_2 content. Nevertheless, the plant may be able to counteract these effects by producing NO, which has been shown to prevent ion leakage, lipid oxidation and chlorophyll loss; and to induce transcript levels of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and hemeoxygenase (HO) [19].

Although the application of UVB stress as an approach to enhance the phytochemical content has been reported in *Brassica* plants, including a report in broccoli sprouts [29,53,54,59],

research mainly focuses on the mature vegetables, on either glucosinolate or phenolic enhancement, on postharvest treatments [48,52], and on the accumulation of defensive metabolites to provide plant resistance against insects and pathogens, acting as natural pesticides [29,64], rather than nutraceutical-related applications.

3.2. Mechanisms and Effects of UVA Radiation on Phytochemical Biosynthesis

The UVA component of sunlight has traditionally been considered to be damaging for photosynthesis, with the PSII complex being its main target. Since solar radiation contains much more UVA than UVB, it has been recently suggested that UVA radiation could be the most detrimental component of sunlight for photosynthetic reactions, despite the lower quantum efficiency of UVA-mediated photoinhibitory damage compared to that caused by UVB exposure [33].

Despite the evident relevance of UVA radiation on plant morphology, physiology, biochemistry, and photosynthesis, there is a lack of scientific studies to elucidate the signaling mechanisms governing such responses. Available reports (Table 2) in species such as peppermint (*Mentha piperita*) and lettuce (*Lactuca sativa*) have revealed that UVA radiation, similarly to UVB, can trigger the accumulation of leaf total phenolics [9,58–70]. Changes in individual phenolic compounds, rather than total phenolic content, have been described in *Betula pendula* [69] and *Arbutus unedo* [70], where quercetin (and its derivatives) and gallic acid derivatives were induced, respectively.

Table 2. Effect of UVA (alone or in combination with UVB) radiation on the biosynthesis of bioactive phytochemicals and on stress responses in different horticultural crops.

Plant Species	UVA Treatment Parameters and Storage Conditions	Phytochemical Evaluated	Main Findings	Reference
Peppermint (*Mentha* × *piperita*)	3 h of 126 µmol m^{-2} s^{-1}(WL), 9 h of 46 µmol m^{-2} s^{-1}(UVA) + WL, 3 h WL, 9 h dark. Or 15 h WL, 9 h UVA. For 18 d.	Total PCs, Chls, essential oils (e.g., menthol)	Treatment with UVA + WL during the day increased leaf area (by 64%), total PC (2-fold) and total essential oil (by 24%) content, while UVA during the night decreased these parameters (by 14, 23 and 38%), when compared to controls. UVA did not affect total Chl content. An interference of UVA with phytochrome is suggested.	[65]
Lettuce (*Lactuca sativa*)	3.7 W, continuous radiation for 7 d, ID: 20 cm, 20 °C.	Total PCs, total ACNs	UVA treatment induced shoot growth (1–2 fold) at days 5–7. UVA caused accumulation of PCs (30% at day 3) and ACNs (4-fold at day 3) until 4 d of treatment, consistent with an increase in *PAL* gene expression (2.4-fold) and PAL activity.	[66]
Rosa hybrida, *Fuchsia hybrida*	15.9 µmol m^{-2} s^{-1}(of UVA) + 227 µmol m^{-2} s^{-1}(of WL), 12 h/d, for 6–7 weeks, 20 °C.	Flavonoids, carotenoids, Chls	Supplemental UVA did not affect plant morphology of either species. In rosa and fuchsia leaves, it induced increases in levels of Chls a (28 and 7%) and b (25 and 10%), the carotenoids antheraxanthin (65 and 23%), lutein (25 and 3%) and β-carotene (18 and 5%), K (93 and 313%) and Q (77 and 119%) aglycones, and up to 2-fold increases in individual Q derivatives in both species and K derivatives in rose leaves. Some K derivatives in fuchsia increased >2-fold or were newly induced.	[67]
Tomato seedlings (*Solanum lycopersicum*)	7 W m^{-2}, for 24 h total during cultivation, with harvest at different time points (0, 1, 3, 6, 12 and 24 h), 24 °C.	ACNs	UVA induced ACN production by up to 4-fold in tomato seedlings (at 24 h) and by ~2-fold in the fruit epidermis (at 6 h). ACN increased gradually in the hypocotyls, with maximum levels (3-fold) at 12 h. In the cotyledons, ACN content increased (4-fold) at 1 h after UVA exposure, was reduced afterward, and increased again beginning at 3 h. UVA increased PAL expression in a time-dependent manner.	[68]
Wounded Carrot (*Daucus carota*)	12.73 W m^{-2}, for 0, 1, and 6 h at room temperature, ID: 50 cm. Post- storage at 15 °C for 4 d.	PCs	After 6 h of UVA radiation, total phenolic content of carrot pies increased 1-fold, AOX capacity increased 2-folds, and PAL activity increased by 34-fold. Maximum accumulation of the individual PCs chlorogenic acid (3-fold), ferulic acid (~1-fold), 3,5-dicafeoylquinic acid (<1-fold) were observed after 6 h of treatment.	[9]
Broccoli (*Brassica oleracea* var. *italica*)	Field experiment. 14 and 985 kJ m^{-2} d^{-1} of ambient UVB and UVA. From germination until plant age of 27 or 41 d.	PCs and GLSs	Increased concentrations of total flavonoids + HAs (54.4% compared to control plants) after UV exposure was observed. 4-HGBS was the only GLS increased by UV exposure.	[64]

Table 2. *Cont.*

Plant Species	UVA Treatment Parameters and Storage Conditions	Phytochemical Evaluated	Main Findings	Reference
Silver birch seedlings (*Betula pendula*)	Field experiment (30 d). Treatments: Ambient (no filter); UVA 100%, UVB 100%; UVA 100%, UVB 50%; UVA 50%, UVB 50%; UVA 100%, UVB 0%; UVA 50%, UVB 0%; and UVA 0%, UVB 0%. UV doses: 4.48, 3.74, 2.20, 1.98, 0.38, 0.26 and 0 kJ m^{-2} d^{-1}, respectively, FD: 15 cm.	PCs	Epidermal flavonoids decreased when UVB was excluded, and transcripts of *PAL* and *HYH* were expressed at lower levels. UVA linearly accumulated Q-3-galactoside and Q-3-arabinopyranoside and had a quadratic effect on *HYH* expression. There were strong positive correlations between *PAL* expression and accumulation of 4 flavonols under the UV treatments. Chlorogenic acids were not affected by UV treatments.	[69]
Arbutus unedo	Field experiment (1 year). Treatments: 97% UVB reduction (UVA: 0.33–1.29 MJ m^{-2} d^{-1}), 95% UVA + UVB reduction (UV0) or near-ambient UV levels (UVB/A, UVB: 4.2–34.4 kJ m^{-2} d^{-1}).	PCs	Leaves exposed to near-ambient UV radiation had less total flavanol content (1.32-fold) than those developed with almost no UV exposure.UVA radiation increased (1.4-fold) the leaf content of theogallin, a gallic acid derivative. Quercitrin, the major Q derivative, increased by 1.32- and 1.26-fold with UVB/A and UVA exposure, respectively.	[70]
Broccoli sprouts (*Brassica oleracea* var. *italica*)	Seven-day-old broccoli sprouts were exposed to UVA (9.47 W m^{-2}) alone and combined with methyl jasmonate. ID: 45 cm.	GSLs, PCs, carotenoids, and chlorophyll	UVA + methyl jasmonate increased the total glucosinolate content by 154%. MJ induced the biosynthesis of indole glucosinolates, especially neoglucobrassicin (538%), showing a synergistic effect with UVA stress. UVA increased the content of phenolics such as kaempferol glucoside (25.4%) and gallic acid (57%). UVA increased lutein (~23%), chlorophyll b (31%), neoxanthin (34%), and chlorophyll a (67%).	[58]
Broccoli sprouts (*Brassica oleracea* var. *italica*)	Seven-day-old broccoli sprouts were exposed for 120 min UVA (3.15 W m^2). Harvest 2 h post-treatment. ID: 45 cm.	GSLs and PCs	UVA radiation and harvest 2 h afterwards induced the accumulation of 4-O-caffeoylquinic acid (42%), 1-sinapoyl-2,2-diferulolyl-gentiobiose (61%), gallic acid hexoside I (14%), and gallic acid derivative (48%).	[59]
Peaches (*Prunus persica* L., cv. Batsch)	The fruit were placed in a chamber at 20 °C followed by UVA (1000 µw/cm^2) irradiation for 2 days	PCs	Cyanidin 3-glucoside reached (0.61 mg/100 g FW) after UVB treatment, value that was 4-fold higher than the fruits stored under dark conditions.	[61]

Abbreviations: WL, white (visible) light; ID: irradiation distance; FD: filter distance; PC, phenolic compound; Chl, chlorophyll; PAL, phenylalanine ammonia lyase, ACN, anthocyanin; K, kaempferol; Q, quercetin.

On the other hand, scientific data is needed regarding the effects of UVA radiation on the accumulation of total and individual glucosinolates, carotenoids, and other phytochemicals. One study, evaluating the effect of supplemental UVA radiation in leaves of *Rosa hybrida* and *Fuchsia hybrida* on levels of various antioxidants, indicates that UVA induced small increments in levels of chlorophylls *a* and *b*, and the carotenoids antheraxanthin, lutein and β-carotene, and high increments in the flavonols quercetin, kaempferol and their derivatives [67]. The authors conclude that the major protection towards UVA radiation in *R. hybrida* and *F. hybrida* leaves originates from absorption of radiation, and not from ROS scavenging [67], although the mechanisms involved are not fully understood.

It has been stated that the UVA-mediated changes in phenolic composition are likely to be controlled at multiple levels of gene regulation. At the transcription level, UVA radiation induces transcript accumulation of genes involved in the phenylpropanoid pathway including *PAL*, *CHS*, and *dihydroflavonol 4-reductase* (*DFR*) [33]. Post-transcriptionally, the activity of PAL has been increased by UVA in lettuce [66] and tomato (*Solanum lycopersicum*) [67]. Unlike UVB radiation, there is limited information on the specific genetic components associated with UVA signaling in plants. Regarding the latter, early studies in leaves of *A. thaliana* suggest the likelihood that they involve the action of a photoreception system that contains three known classes of photoreceptors: (i) phytochromes (PHY) for far-red and red lights, (ii) crytochromes (CRY) for UVA/blue light, and (iii) phototropins (PHOT) for UVA light [33,71]. For instance, the UVA-induced transcription and expression of key flavonoid biosynthesis genes (e.g., *CHS*) in leaves of *A. thaliana* could be initiated via UVA absorption through CRY1, given that functional CRY1 is required for the expression of *CHS* [72]. In addition, the authors stated that the UVA photo-transduction pathway may interact synergistically with UVB-induced pathways to produce transient signals and may function additively to stimulate *CHS* promoter function [72]. Thus, once UVA light has

been perceived, these UVA specific photoreceptors may interact with COP1 and HY5 in a similar manner to UVR8 to further regulate the plant's secondary metabolism [71]. Furthermore, studies with an *A. thaliana* UVB photoreceptor mutant generated the unexpected finding that UVB-specific photoreceptor UVR8 has an impact on UVA-mediated changes in plant metabolites, as UVR8 is likely to interact with UVA/blue light signaling pathways to moderate UVB-driven transcripts [73].

4. Conclusions and Further Research

The reviewed literature shows that UVR is an effective tool to biofortify horticultural crops with nutraceuticals. Further research in this topic should be focused on increasing our understanding of the molecular and physiological mechanisms governing the UVA stress response, since most reports in the literature have assessed the effect of UVB radiation. UVR could be an easy technology to treat fruits and vegetables before eating them even at home, thus UV chambers for residential use could be an interesting piece of equipment to improve the nutraceutical content of crops in the kitchen.

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