

# Bioactive Compounds in Agricultural Plants

Subjects: **Plant Sciences**

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Plants continuously rely on light as an energy source and as the driver of many processes in their lifetimes. The ability to perceive different light radiations involves several photoreceptors, which in turn activate complex signalling cascades that ultimately lead to a rearrangement in plant metabolism as an adaptation strategy towards specific light conditions. This entry introduces the main classes of secondary metabolites and specifically focuses on the influence played by the different wavelengths on the content of these compounds in agricultural plants, because of their recognised roles as nutraceuticals.

photoreceptors

plants

bioactive compounds

ultraviolet

visible light

secondary metabolism

## 1. Introduction

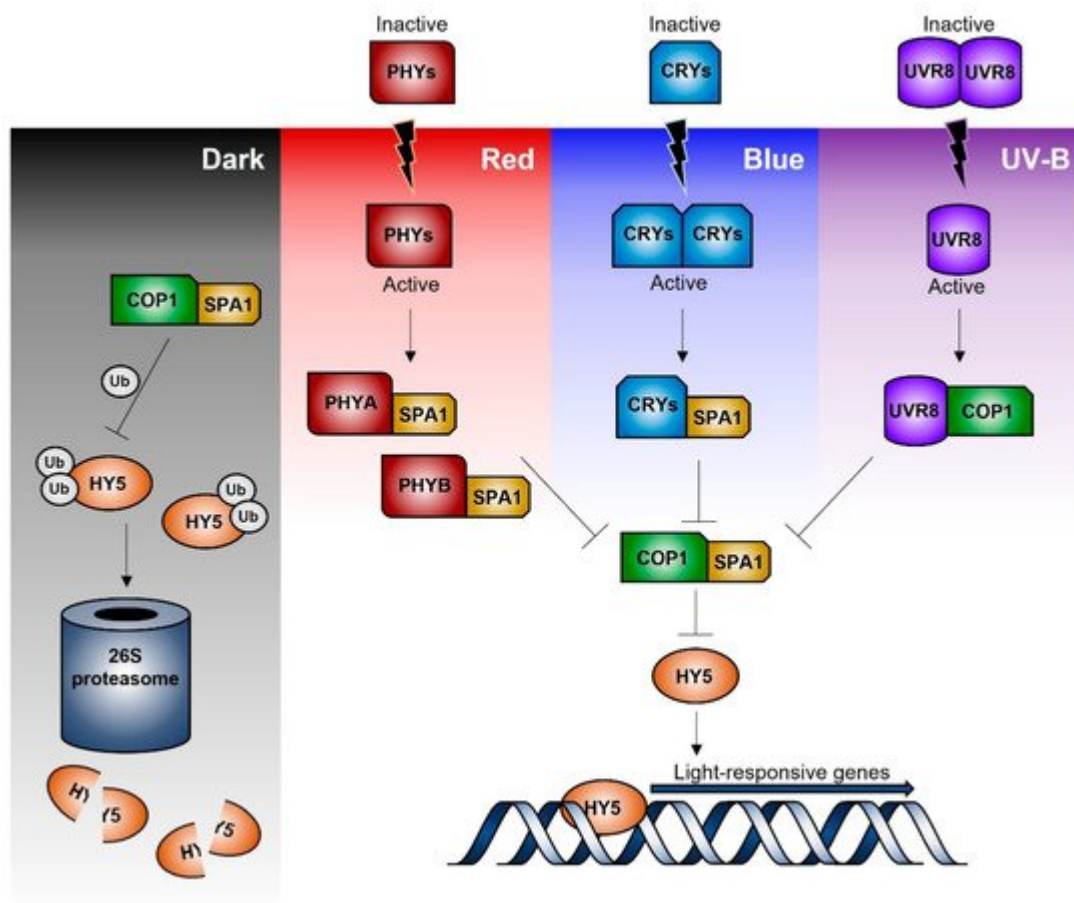
Plants rely on an uncountable number of secondary metabolites during their lifespans in order to perform several fundamental functions, such as attracting pollinators, mechanical support, protection from solar UV radiation, deterrents against pests, pathogens, and herbivores, interaction with other plants, and response to environmental stimuli/stresses <sup>[1]</sup>. Thanks to a network of photoreceptors and the following complex signalling routes, the different light wavelengths may impact the content of these metabolites by up- or downregulating specific sets of biosynthetic and regulatory genes.

## 2. Signal Transduction Pathways

Independently from the light quality and kind of photoreceptor involved in light perception, the downstream event proceeds via a complex network of early signalling factors, central integrators, and final effectors. Please refer to some recent reviews <sup>[2][3][4][5]</sup> for a detailed summary of the current knowledge of the transcriptional network and mechanisms regulating the response to the different light spectral composition. Interestingly, CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1), which promotes the proteasome-mediated degradation of key factors involved in light signalling, is involved in the response to any light radiation, from UV to far-red wavelengths <sup>[6]</sup>. Similarly, the transcription factor ELONGATED HYOCOTYL 5 (HY5) has a central role as a final effector of all the light-dependent signalling routes, being able to bind to the promoters of about 4000 genes in Arabidopsis <sup>[6]</sup>.

**Figure 1** represents a simplified scheme of the signal transduction pathways leading to gene regulation in response to blue, red/far-red, and UV-B radiation. Briefly, under dark conditions, COP1/SPA (suppressor of

Phytochrome A) ubiquitin ligase complex promotes the ubiquitination and degradation of HY5 via the 26S-proteasome pathway [4]. Upon light perception, the active blue- and red/far-red-photoreceptors (cryptochromes and phytochromes) interact with the COP1/SPA complex binding to SPA; thus, leading to COP1 disassembly and migration outside the nucleus. This prevents HY5 ubiquitination and subsequent degradation, so that HY5 may bind the promoter sequence of the light inducible target genes. Similarly, UVR8, after UVB-induced monomerization, can bind to COP1, leading to a functional disruption of the COP1/SPA complex and a consequent HY5 stabilization and functioning [7][8].



**Figure 1.** Simplified plant perception mechanisms of different types of solar radiation (dark, red, blue, and UV-B), together with the intracellular rearrangements leading to the transcription of specific light-responsive genes.

### 3. Plant Metabolism and Light

This review specifically focuses on the influence of the different light radiations, from red–far-red to UV-B, on the main classes of secondary metabolites, such as phenolic compounds, terpenoids, tocopherols, glucosinolates, and ascorbic acid in agricultural plant species, because of the recognised role that these compounds generally play as promoters of human wellness [9][10][11][12]. UV-C radiation was reported to modulate accumulation of health-promoting compounds in different plants and fruits of food interest, such as tomato fruit [13], bean seedlings [14] and peanut sprouts [15], this review exclusively discusses the effects of those wavelengths that reach the Earth's

surface, and to which plants have adapted fine-tuning perception mechanisms and consequent molecular and biochemical responses through evolution.

According to their chemical structures, terpenoids fulfil essential functions during plant life as, e.g., direct/indirect defensive compounds against biotic stressors, deterrent towards herbivores, photosynthetic pigments, signalling molecules mediating plant-plant, and plant–environment interaction [\[16\]](#)[\[17\]](#)[\[18\]](#)[\[19\]](#).

Vitamin E has been widely studied due to its high antioxidant activity, especially preventing the oxidation of mono- and poly-unsaturated lipids. In addition, vitamin E compounds were shown to have hypolipidemic, antiatherogenic, antihypertensive, neuroprotective, anti-inflammatory, and many other beneficial effects for human health [\[20\]](#)[\[21\]](#)[\[22\]](#)[\[23\]](#)[\[24\]](#). The main plant sources of tocopherols and tocotrienols are seeds (especially oilseeds) and nuts. In addition, they can be found in many plants and fruits, although their concentrations are limited due to their low lipid content [\[25\]](#).

Vitamin C, like the majority of the hydrosoluble vitamins, participates as a cofactor for many enzymes, e.g., members of the mono- and dioxygenases family [\[26\]](#), essentially contributing to the maintenance of the cell redox state, together with several other antioxidant molecules and enzymes. In plants, vitamin C is involved in many pathways and processes, e.g., the xanthophyll cycle, the flavonoids, and the glucosinolates pathways, and in the biosynthesis of plant hormones, such as ethylene, gibberellins, and abscisic acid [\[27\]](#)[\[28\]](#)[\[29\]](#)[\[30\]](#)[\[31\]](#). Studies on the role of vitamin C role and its benefits in humans started when it was first noticed that vitamin C deficiency determined a potentially lethal disease called scurvy [\[32\]](#), negatively affecting the immune system, the collagenous architecture, and the regeneration process from wounds. Moreover, pharmacological effects of ascorbic acid against cancer and cardiovascular diseases were also observed [\[33\]](#)[\[34\]](#). The main dietary sources of vitamin C are fresh fruits and vegetables; therefore, their consumption has been widely encouraged by the main food and health organisations (e.g., the Food and Nutrition Board of the National Academy of Sciences, the European Food Safety Authority (EFSA), and the Food and Drug Administration (FDA)) throughout the years, and vitamin C deficiency symptoms have progressively reduced worldwide.

## 4. Red and Far-Red Light

Similarly, when bilberries ( *Vaccinium myrtillus* L.), plants were exposed to monochromatic red light ( $7.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) during the berry ripening period, a significant increment of total anthocyanins occurred, due to the positive effect of this radiation on petunidins and delphinidins, while peonidins decreased, and cyanidins and malvidins were unaffected [\[35\]](#). This finding underlines an interesting aspect of the light–phenolic interaction, i.e., the diversity of response to the same stimulus shown by different subclasses of molecules belonging to the same metabolic class. A similar phytochemical specificity of response was also observed in wheat ( *Triticum aestivum* L.) sprouts grown under a 16-h light/8-h dark photoperiod under white, red, or blue light, for up to 12 days. Specifically, red light, at the end of the growing period, did not lead to a significant increase in the content of total phenylpropanoids in comparison to white light, but modified their composition, inducing an increase in quercetin and a decrease in 4-hydroxybenzoic acid [\[36\]](#).

A 7-day exposure of red clover (*Trifolium pratense* L.) sprouts to red-light (630 nm, 150  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , LEDs as lighting sources) induced a significant decrease in zeaxanthin concentration, while  $\beta$ -carotene and lutein were unaffected by the treatment [37]. A negative impact of this radiation on  $\beta$ -carotene concentration (−42.5%) was instead observed in Romaine green baby leaf lettuce (cv. Thumper) treated with supplemental red light (638 nm, 150  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , LEDs lighting sources) for 3 days [38]. These results differed from the ones by Li and Kubota (2009) [39], who found that 12 days of supplemental far-red light, but not red-light, irradiation determined a decrease in xanthophylls and  $\beta$ -carotene concentration in “Red Cross” baby leaf lettuce. Moreover, red light (380  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , LED lighting sources) was ineffective in modifying the carotenoid content of another lettuce cultivar (“Red Fire”) when compared to white light [40].

Tocopherols are reported to be influenced by red light. Exposure to supplemental red light (638 nm, 150  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , LEDs lighting sources, 3 days) was effective in significantly increasing  $\alpha$ - and  $\gamma$ -tocopherols of Romaine green baby leaf lettuce (cv. Thumper) [38]. The same authors [41] also detected significant accumulation of  $\alpha$ -tocopherol in basil microgreens grown under increased or sole red radiation (638 nm). However, increased red radiation lowered the  $\alpha$ -tocopherol content of parsley microgreens, which was instead incremented when cultivation occurred with sole red lightning. It is therefore evident that, as observed for phenolic compounds, tocopherols are also influenced by red radiation in a species-depending way.

The limited data available on light quality influence on glucosinolates show that the effect is highly dependent on the wavebands and the plant species. Under red irradiation (730 and 640 nm) sinigrin content of kale was higher as compared to plants grown under blue light [42]. Similarly, when three Chinese cabbage varieties were exposed for 24 h to fluorescent light supplemented with red LEDs (625 nm), the content of total glucosinolates increased in the variety characterised by a low content of these metabolites, while the variety with high glucosinolates positively reacted to supplemental blue radiation [43]. These authors also reported that different set of genes involved in glucosinolates biosynthesis were upregulated by red or blue radiations in Chinese cabbage. To confirm the genotype dependence of the light influence on glucosinolates biosynthesis, Qian et al. [44] did not observe any variation in the content of these compounds in Chinese kale sprouts exposed to red LED light.

## 5. Green Light

Green light, among the whole solar spectrum reaching the Earth’s surface, was considered of less importance in the past, since it was a common belief that it did not affect plants’ growth and development. It has been instead observed that plants reflect just 10–50% of green light [45], contributing to the green appearance of most plant organisms, while the remaining part is mainly absorbed by cryptochromes and by a putative, yet uncharacterised, green-light photoreceptor, and weakly by chlorophylls [46][47][48]. By consequence, green light plays several key roles during plant lifespan, e.g., the shade avoidance responses across the bottom layers of the canopies [47][49]. The LED technology, which is progressively replacing the conventional greenhouse lighting that mostly relies on high-pressure sodium lamps or fluorescent tubes, has allowed researchers worldwide to deepen the knowledge on individual wavelengths, which were previously less considered, e.g., the green light. However, few studies have investigated the effects of green light supplementation on the biosynthesis of bioactive compounds in crops so far

(**Table 1**); therefore, this section will include the most recent literature in the field, without splitting phenolics, terpenoids, and other secondary metabolites.

**Table 1.** Biochemical responses of crops and plants of food interest to green light wavelengths considered in this review. Tot, total phenolics; Flav, flavonoids; Ant, anthocyanins; AC, antioxidant capacity; T, terpenoids; AA, ascorbic acid; TP, tocopherols; GSL, glucosinolates. For each plant species and cultivar, and for each secondary metabolite or metabolic class considered, the symbols “↓”, “↑” and “=” mean a decrease, increase or no variations, respectively, compared to the control plants of each study.

Species	Cultivar	Phenolics			AC	T	AA	TP	GSL	Ref.
		Tot	Flav	Ant						
Lettuce ( <i>Lactuca sativa</i> . L.)	Youmaicai					↑				[50]
	Butterhead					↑				[51]
Tea leaves ( <i>Camellia sinensis</i> L.O. Kuntze)	Zhonghuang 3		↑					↑		[52]
Tomato plants ( <i>Solanum lycopersicum</i> L.)	Komeett'					=/ ↑				[53]
Basil ( <i>Ocimum basilicum</i> L.)	Improved Genovese Compact	=/ ↓	=/ ↓	=/ ↓	=/ ↓					[54]
	Red Rubin	=/ ↓	=/ ↓	=/ ↓	=/ ↓					

The tea yellow-leaf mutant plants (O. Kuntze ‘Zhonghuang 3’ (ZH3)) irradiated during the dark period with supplemental green light (520 nm, 300 μmol m<sup>-2</sup> s<sup>-1</sup>, LEDs lighting sources) for 4 h daily up to 12 days showed enhanced concentration of procyanidin B2/B3, and L-ascorbate [52]. However, when the green light was applied together with the blue light, the increase in secondary metabolites (especially anthocyanins and catechins) was more pronounced than when the green light was applied alone, mainly due to the activation of structural genes of the phenylpropanoid pathway.

When lettuce (var. youmaicai) was grown by cutting out the green light (480–560 nm), the content of photosynthetic pigments and the chlorophylls/carotenoids ratio were reduced, consequently decreasing the CO<sub>2</sub> assimilation and the growth of the plants [50]. Similar to these findings, another study on lettuce (cv. Butterhead) [51] showed that supplementation of green light (200 μmol m<sup>-2</sup> s<sup>-1</sup>, LEDs lighting sources) to a 48-h continuous blue and red lighting resulted in increasing the chlorophyll content by inducing an overexpression of photosynthetic genes *LHCb* and *PsbA*; thus, enhancing the photosynthetic rates and the maximal photosynthetic capacity. The positive role of green light in stimulating the accumulation of photosynthetic pigments was also observed in tomato plants (cv. ‘Komeett’) irradiated with 7, 20, or 39% of green light (531 ± 19 nm, 171 μmol m<sup>-2</sup> s<sup>-1</sup>, LEDs lighting sources) [53].

The authors found an increased chlorophyll *a/b* ratio and carotenoids content in the middle leaf layer of the canopy together with the increase of the percentage of green light provided.

Very few studies have investigated the effects of green light irradiation on other secondary metabolites, e.g., phenolic compounds. A comparative study on two basil cultivars, a green leaf (cv. ‘Improved Genovese Compact’), and a purple leaf (cv. ‘Red Rubin’) one, irradiated with increasing proportions of supplemental green light ( $220 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) resulted in a progressively greater decrease of several bioactive compounds, e.g., phenolics, flavonoids, and anthocyanins [54]. Considering the importance of the genetic background in driving the metabolic responses to the different light radiations, such a negative influence of green light on these metabolites needs to be confirmed in other species and cultivars.

## 6. Blue Light

While effects of red and far-red light on phytochemicals accumulation are strictly dependent on the plant species considered, blue light irradiation has been generally reported to enhance the content of most nutraceutical substances, especially in terms of phenolic compounds. However, genotype- and structure-dependent specificity of response was observed as well, as commented in this specific paragraph and depicted in **Table 2**.

**Table 2.** Biochemical responses of crops and plants of food interest to blue light wavelengths considered in this review. Tot, total phenolics; Flav, flavonoids; Ant, anthocyanins; AC, antioxidant capacity; T, terpenoids; AA, ascorbic acid; TP, tocopherols; GSL, glucosinolates. For each plant species and cultivar, and for each secondary metabolite or metabolic class considered, the symbols “↓”, “↑” and “=” mean a decrease, increase or no variations, respectively, compared to the control plants of each study.

Species	Cultivar	Phenolics			ACT	AA	TP	GSL	Ref.
		Tot	Flav	Ant.					
Green leafy lettuce ( <i>Lactuca sativa</i> . L.)	Thumper	↓		=		↓/ ↑	↑		[133]
						↑			[167]
	Grizzly					↑			[168]
Red leafy lettuce ( <i>Lactuca sativa</i> . L.)	Red Cross	=		↑					[131]
Red clover ( <i>Trifolium pratense</i> L.)					↑				[144]
Chinese cabbage ( <i>Brassica campestris</i> L.)						↑			[169]
Mustard ( <i>Brassica juncea</i> L.)	Red Lion				↑		↑		[170]

Species	Cultivar	Phenolics Tot Flav Ant.	ACT	AA	TP	GSL	Ref.
Beet ( <i>Beta vulgaris</i> L.)	Bulls Blood		↑		↑		
Parsley ( <i>Petroselinum crispum</i> Mill.)	Plain Leaved or French		↑		↑		
Buckwheat ( <i>Fagopyrum esculentum</i> )	Möench	↑	↑				[128]
Wheat ( <i>Triticum aestivum</i> L.)			↑/ ↓				[145]
Soybean ( <i>Glycine max</i> L.)	Dongnong 690	↑	↓				[166]
Bilberry fruit ( <i>Vaccinium myrtillus</i> L.)			↑				[148]
Apple fruit ( <i>Malus domestica</i> Borkh.)	Mishima Fuji		↑				[171]
	Jonathan		↑				
Strawberry ( <i>Fragaria</i> × <i>Ananassa</i> )			↑				[172,173]
	Fengguang			↑			[174]
Cowpea ( <i>Vigna unguiculata</i> L. Walp.)			↓/ ↑/=				[147]
Tartary buckwheat ( <i>Fagopyrum tataricum</i> Gaertn.)			↓				[146]
Pak choi ( <i>Brassica rapa</i> ssp. <i>chinensis</i> )			↓/=				[150]
Tomato fruit ( <i>Solanum lycopersicum</i> L.)	Micro-Tom		↑				[175]
Satsuma mandarin fruit ( <i>Citrus unshiu</i> Marc.)			↓/ ↑/=				[152]
Tea leaves ( <i>Camellia sinensis</i> )	Jinxuan		↑				[149]
Basil ( <i>Ocimum basilicum</i> L.)	Genovese		↑				[176]
Satsuma mandarin fruit ( <i>Citrus unshiu</i> Marc.)				↑			[177]
Valencia orange fruit ( <i>Citrus sinensis</i> Osbeck)				↑			



Species	Cultivar	Phenolics Tot Flav Ant.	ACT	AA	TP	GSL	Ref.
Lisbon lemon fruit ( <i>Citrus limon</i> Burm.f.)				↑			
Canola ( <i>Brassica napus</i> L.)						↑/=	[178]
Mustard ( <i>Brassica juncea</i> L.)					↓		[179]

## 7. UV-A Radiation

The physiological and biochemical effects of UV-A radiation are strictly dependent on both the plant species and the UV-A dose. Endemic plants (and crops) from high altitude areas and/or low latitude regions are well acclimated to high UV (-A and -B) condition and, therefore, care must be given when establishing the UV dose needed to stimulate their secondary metabolism further. **Table 3** lists some main biochemical responses observed in different plant species or cultivars subjected to UV-A irradiation, as detailed in the following paragraph.

**Table 3.** Biochemical responses of crops and plants of food interest to UV-A wavelengths considered in this review. Tot, total phenolics; Flav, flavonoids; Ant, anthocyanins; AC, antioxidant capacity; T, terpenoids; AA, ascorbic acid; TP, tocopherols; GSL, glucosinolates. For each plant species and cultivar, and for each secondary metabolite or metabolic class considered, the symbols “↓”, “↑” and “=” mean a decrease, increase or no variations, respectively, compared to the control plants of each study.

Species	Cultivar	Phenolics Tot Flav Ant.	AC	T	AA	TP	GSL	Ref.
Pak-choi ( <i>Brassica rapa</i> ssp. chinensis var. communis)	Red leaf cv.	↑/=	↑	↑	↑	↑/=	↑/ ↓	[55][56]
	Green leaf cv.	↑/=	↑/=	↑	↑	=	↓	
Turnip ( <i>Brassica rapa</i> subsp. <i>rapa</i> )	Tsuda			↑				[57]
Broccoli ( <i>Brassica oleracea</i> L., var. <i>italica</i> )	Waltham 29	=/↓					=/↓	[58]
	Monopoly	=/↓					=	[59]
Broccoli ( <i>Brassica oleracea</i> L., var. <i>gemmifera</i> DC)		↑/↓					↑/=	[60]
Lettuce ( <i>Lactuca sativa</i> . L.)	Yanzhi	=	↑	↑	↑	↓	↑	[61]
	Red butter	↑	↑	↑	=	↓	↑	
	Klee	↑/=	↑/=	↑			↑	[62]



Species	Cultivar	Phenolics			AC	T	AA	TP	GSL	Ref.
		Tot	Flav	Ant						
Tomato plant ( <i>Solanum lycopersicum</i> L.)	Red leaf cvs.					=				[63]
	Green leaf cvs.					=				
	Hongyeom	↑/=		↑/=		↑/=				[64]
	Oxheart	↓		=	=	=				
	Cherry	=		↓	↓	↓/=				[65]
Tomato fruit ( <i>Solanum lycopersicum</i> L.)	Roma	=		=	↓	↑/=				
	MicroTom			↑						[66]
	Budenovka	↑	↑			↑/=				
	Bull Heart	↑	↑			↑/=				[67]
Sowthistle ( <i>Ixeris dentata</i> Nakai)	Gina	↑	↑			↑/=				
	Micro-Tom			↑						[66]
		↑/=	↑/=		↑/=					[68]
Grape berry ( <i>Vitis vinifera</i> L.)	Cabernet Sauvignon		↑							[69]
Blueberry ( <i>Vaccinium corymbosum</i> L.)	Duke	↓		=						[70]
Peach fruit ( <i>Prunus persica</i> L. Batsch)	Hujingmilu			↑						[71]
	Yulu			=						
Basil ( <i>Ocimum basilicum</i> L.)	Genovese	↑/=				↑	↓	↑/↓		[56][72][73][74][75]
Beet ( <i>Beta vulgaris</i> L.)	Bulls Blood						↑/↓	↑		[56]
	Kanchana	↑				↑				
Rice ( <i>Oryza sativa</i> L.)	Mattatriveni					↓/=				[76]
	Harsha					↑/=				

Species	Cultivar	Phenolics			AC	T	AA	TP	GSL	Ref.
		Tot	Flav	Ant						
Broccoli ( <i>Brassica oleracea</i> L. var. <i>italica</i> )	Waltham 29	=							↑	[77]
Wheat ( <i>Triticum aestivum</i> L.)	Sumai188	↑								[78]
Mung bean ( <i>Vigna radiata</i> )		↑/↓	↑				↑			[79]
Peppermint ( <i>Mentha piperita</i> L.)	Rubescens	↑				↑/↓				[80]

## 8. UV-B Radiation

Similar to the findings reported for the other wavelengths, the influence of UV-B radiation on the content of bioactive compounds in different species and cultivars is variable and often dependent on the dose and metabolite considered. Examples of these specific responses are reported in the following paragraphs and listed in **Table 4**.

**Table 4.** Biochemical responses of crops and plants of food interest to UV-B wavelengths considered in this review. Tot, total phenolics; Flav, flavonoids; Ant, anthocyanins; AC, antioxidant capacity; T, terpenoids; AA, ascorbic acid; TP, tocopherols; GSL, glucosinolates. For each plant species and cultivar, and for each secondary metabolite or metabolic class considered, the symbols “↓”, “↑” and “=” mean a decrease, increase or no variations, respectively, compared to the control plants of each study.

Species	Cultivar	Phenolics			ACT	AA	TP	GSL	Ref.
		Tot	Flav	Ant					
Basil ( <i>Ocimum basilicum</i> L.)	Genovese	↑/=				↑/=			[72][73] [74][75]
	Cinnamon				↑/↓	↑/=/ ↓			[81]
Rice ( <i>Oryza sativa</i> L.)	Kanchana	↑				↑			
	Mattatriveni					↓/=			[76]
	Harsha					↑/=			
Broccoli ( <i>Brassica oleracea</i> L. var. <i>italica</i> )	Waltham 29	=				↑/=		↑	[58][77] [82]
Broccoli ( <i>Brassica oleracea</i> var. <i>gemmifera</i> DC)								=	[60]
Wheat ( <i>Triticum aestivum</i> L.)	Sumai188	↑							[78]

Species	Cultivar	Phenolics		ACT	AA	TP	GSL	Ref.
		Tot	Flav Ant					
Mung bean ( <i>Vigna radiata</i> )		↑/↓	↑		↑			[79]
Peppermint ( <i>Mentha piperita</i> L.)	Rubescens	↑			↑/↓			[80]
Lettuce ( <i>Lactuca sativa</i> . L.)	Red leaf cvs.	↑	↑	↑	↓			[63][83]
	Green leaf cvs.	↑	↑		↑			
Peach fruit ( <i>Prunus persica</i> L.)	Suncrest	↑/=/ ↓	=	↓/ ↑		=/↓		[84][85]
	Big Top	↑/=/ ↓	↓/ ↑	↑				
	Babygold 7	↓	↓/ ↑	=				[86][87]
	Fairtime	↓/↑	↓/ ↑	↓/ ↑	↓			
	Yulu			↑				
	Hujingmilu			↑				
Tomato fruit ( <i>Solanum lycopersicum</i> L.)	Money Maker				↑	↑		[88][89]
	Zhenfen 202					↓		[90]
Bell pepper fruit ( <i>Capsicum annum</i> L.)	Angus				↑			[91]
Green lime fruit ( <i>Citrus latifolia</i> Tan.)					↑			[92]
Spinach ( <i>Spinacia oleracea</i> L.)	Meridian						↑	[93]
Maize ( <i>Zea mays</i> L.)							↓	[94]
Cucumber ( <i>Cucumis sativus</i> L.)	Long green						↓	[95]
Apple fruit ( <i>Malus domestica</i> Borkh.)	Aroma				↑			[96]

## 9. Conclusions

The light-induced modulation of plant secondary metabolism has gained great attention within the last decades, particularly in regard to enhancing the nutraceutical value of fruits and vegetables. In light of ever-increasing consumer demands (i.e., of health-promoting plant-based foods), application of light treatments is considered a sustainable and eco-friendly way to achieve this goal, both pre- and post-harvest. Biosynthesis of any molecular class addressed in this review was found regulated by light. Though some responses of a certain class of bioactive compounds to a specific wavelength were recorded more frequently than others (i.e., accumulation vs. depletion), one common feature of the light influence on secondary metabolites, irrespective of the spectral radiations considered, is the species- or cultivar-dependent specificity of response. The genetic background witnesses the evolutionary pressure experienced by a plant. Specifically, the predominant light environment during evolution had led to the selection of different degrees of sensitivity to light intensity and quality, and resulted in different abilities to adapt to specific habitats. Geographical origin of the plant is therefore important in this context, though, in the case of domesticated species/cultivars, the breeding history (use of landraces or modern breeding programs) is of pivotal importance as well. Moreover, the radiation intensity and duration of exposure, as well as the chemical structure of compounds belonging to the same molecular class, were often important determinants of the output. In greenhouses, light has long been controlled and designed on specific crops to improve and standardize production, but the need to adopt a light environment that also improves the nutraceutical quality of products is now becoming even more important. This aspect is also critical in post-harvest when the products undergo an inevitable qualitative impoverishment during storage. The development of high-performing LEDs and the setup of specifically designed experiments will make it possible to furnish lighting recipes and irradiation protocols to optimize the production of plant foods with high added value.

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