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Review

Modification of Light Characteristics Affect the Phytochemical Profile of Peppers

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Abstract: *Capsicum* is one of the most economically important genera in the Solanaceae family. *Capsicum* fruits (peppers) are rich in phytochemicals with high nutritional value and significant health-promoting characteristics. The phytochemical profile of peppers consists of capsaicinoids, carotenoids, and phenolics, primarily. Currently, most of the pepper production is carried out under protected horticulture conditions. The objective of this article was to provide a comprehensive review on how light characteristics and manipulation by different horticultural technologies can affect the biosynthesis and accumulation of phytochemicals in *Capsicum* fruits. The use of shade nets or plastic covers to reduce light intensity does not seem to yield consistent responses on the phytochemical profile, as the final profile results from the interaction of several factors. Other factors involved in the accumulation of phytochemicals include temperature, water availability and plant nutrition. Exposure of plants to supplemental light with specific wavelengths (using LEDs) seems to result in a more precise stimulation of specific metabolites. In this article, we examine the effects of light irradiance and spectrum on the specific phytochemicals of *Capsicum* fruits.

Keywords: capsaicinoids; carotenoids; irradiance; phenolic compounds; plant secondary metabolites; spectrum light; solar radiation

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1. Introduction

Capsicum is one of the most economically important genera in the *Solanaceae* family. This genus encompasses five domesticated species with more than 50,000 cultivars [1]. The fruits of *Capsicum* (peppers) are associated with significant health-promoting properties attributable to their nutritional composition and metabolite contents. These properties include analgesic, anti-obesity, cardioprotective, pharmacological, neurological, and dietetic, among others [2]. The specific phytochemicals associated with these properties include carotenoids (provitamin A), phenolic compounds, and capsaicinoids, primarily [3].

The phytochemical and secondary metabolite profiles of peppers are also a good source of nutrients and bioactive compounds [4,5]. Secondary metabolites are a large group of organic compounds with low molecular weight and specific physiological functions. These metabolites serve as chemical adaptations to stress conditions, or as defensive, protective, or offensive chemical agents against micro-organisms, insects, and herbivores [6].

The chemical composition of peppers is closely related to genotype, the process of fruit ripening [3,7], and environmental conditions [8,9]. The environmental factors that affect the biosynthesis, metabolism, and accumulation of phytochemicals in peppers include light, temperature, soil-water availability, and plant nutrition [10]. Thus, changes in environmental conditions can affect the biosynthesis of bioactive compounds in peppers [8].

Peppers vary in color, shape, and chemical composition [7]. Color properties vary by genotype and cultivar. Color changes occur during fruit maturation when the plastids transition from chloroplast to chromoplast in the fruits' pericarp [3].

Currently, the production of peppers is carried out predominantly under protected horticulture conditions [11]. In particular, the manipulation of natural light by photo-selective netting or plastics, and supplemental lighting (artificial light) can be used to reduce heat and light stress and improve the yield and quality of horticultural crops [12]. These horticultural practices modify the light intensity and spectrum intercepted by the plants and may also affect the production levels of total phenols, ascorbic acid, and antioxidants due to the influence of modified light conditions on the metabolic pathways that lead to the formation of the phytochemicals [13]. Controlled growing conditions in glasshouses impacted the carotenoid contents in sweet peppers [14]. Thus, light intensity (irradiance) and spectrum are environmental factors that affect the phytochemical contents of peppers [15].

Even though the pathways for the biosynthesis of the secondary metabolites of peppers have been described, limited information is currently available on the interaction between the effects of light on the synthesis and accumulation of bioactive compounds in *Capsicum* species. The objective of this review article is to examine how changes in light characteristics affect the biosynthesis and accumulation of metabolites of *Capsicum* fruits, and, in turn, alter the phytochemical profile of peppers.

2. Light Interactions with *Capsicum* Plants

The growth and productivity of pepper crops are affected by environmental factors [16]. Among these factors, light is the principal source of energy that drives physiological processes, which include: photosynthesis, photomorphogenesis, fruit development, and maturation [17,18]. Plants interact with light through specific pigments that acquire light energy, and photoreceptors which are proteins that elicit different responses based on light conditions [19]. The most important plant photoreceptors reported for pepper plants include phytochromes, cryptochromes, phototropins, and UV-B-Resistance 8 (UVR8) photoreceptors (Figure 1) [20]. These photoreceptors have peak absorbance wavelengths for the induction of the responses.

Currently, most of the horticultural production of peppers is carried out under protected agriculture conditions [21] primarily by the implementation of photo-selective shading nets [22], plastics [23], and, in some cases, artificial lighting [9,24] which includes ultraviolet radiation (UV), fluorescent lamps, and light-emitting diodes (LEDs) [25]. The active manipulation of light can improve plant productivity and the quality of peppers [26,27].

The biosynthesis of phytochemicals changes depending on light intensity and spectral quality. Plants accumulate phenolic compounds and other antioxidants such as carotenoids, flavonoids, and anthocyanins to protect against damaging high irradiance and UV radiation. Thus, spectral and irradiance manipulation could promote morphological and physiological responses and influence the biosynthesis, accumulation, and retention of phytochemicals [28,29]. UV radiation and excessive irradiance produced by different light sources may cause stress conditions and activate the defense response, changing a variety of bioactive compounds [25].

Shade nets and plastic covers reduce the light intensity (irradiance) and alter the light spectra that reach the crops. Reduced light intensity affects the physiological responses by decreasing photosynthetic rate and promoting an increase in leaf area [12], while scattering improves the penetration of spectrally modified light into the inner canopy of the crop [28,30]. Currently, the use of black shade nets is the predominant practice in the horticultural production of peppers. Black nets reduce light intensity and have a limited effect on light quality [31,32]. By contrast, colored shading nets selectively filter the solar radiation and promote specific wavelengths [33]. Colored shading nets could promote plants' physiological and morphological responses [34]. Colored shading nets can selectively change the red to far-red ratios that are detected by the phytochromes, enhance the radiation available to activate the blue/ultraviolet-A photoreceptors, alter the blue light involved in phototropic responses mediated by phototropins, or enhance radiation at other wavelengths that influence plant response [35].

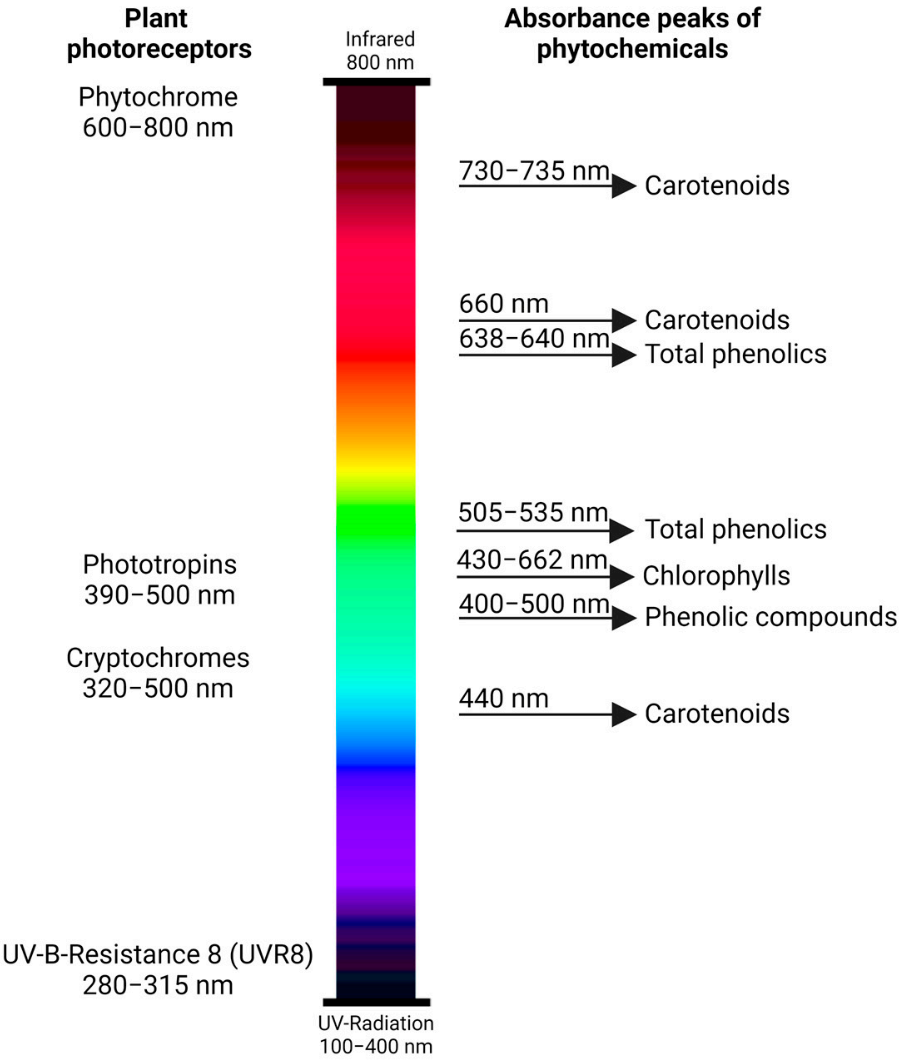

Figure 1. Plant photoreceptors (phytochrome, phototropins, cryptochromes, and UV-B-Resistance 8 (UVR8)) with the corresponding absorbance peaks (wavelengths of the electromagnetic spectrum) for each light-sensing photoreceptor protein. The light-responding groups of phytochemicals in plants in the specific wavelength ranges are provided on the right.

The traditional supplemental light sources used for greenhouse and in vitro applications include fluorescent, metal halide, high-pressure sodium, and incandescent lamps. These light sources have certain limitations as they produce an impractical mixture of wavelengths for plant growth [36], and their electricity consumption is high [37]. LEDs are considered improved light sources for greenhouse production as they can emit specific wavelengths aimed at increasing crop yield, higher quality yield, manipulation of harvest dates, and enhanced nutritional value in cultured plants [38]. Currently, these technologies are preferred for in vitro propagation and indoor plant growth, which are effective for the stimulation of plant phytochemicals during fruit development and postharvest [39].

3. Effects of Light Characteristics on the Phytochemicals of *Capsicum* Fruits

The most abundant secondary metabolites in *Capsicum* fruits include capsaicinoids, carotenoids, phenolic compounds, flavonoids, and a wide range of volatile compounds.

The accumulation of phytochemicals in peppers is light-dependent, and the high variability of these compounds determines the diversity of aroma and flavor of peppers [40].

3.1. Capsaicinoids

Capsaicinoids are secondary metabolites biosynthesized exclusively by the fruits of *Capsicum* plants [41]. These metabolites are the bioactive compounds responsible for the pungent taste of peppers [42]. Capsaicinoids may occur in peppers in a wide range of contents from 'Bell peppers', where they are practically non-existent, to other high-pungency cultivars such as 'Naga peppers' [43]. Capsaicinoids are considered natural defense mechanisms against herbivores ranging from insects to rodents [1]. Capsaicinoids also mediate interactions with birds, who act as seed dispersers for wild peppers [44].

In recent years, capsaicinoid research has been influential in the development of innovative applications in the food and pharmaceutical industries [41] due to their value as antioxidants (free radical scavengers) [45], anti-arthritic [46], gastroprotective [47,48], anti-cancer [49], and analgesic agents [50], among others.

The most abundant capsaicinoids in peppers are capsaicin and dihydrocapsaicin [51,52]. Together, these compounds encompass more than 90% of the total capsaicinoid content of peppers [53]. Nonetheless, at least nine other capsaicinoids including nordihydrocapsaicin, homodihydrocapsaicin, and homocapsaicin have also been identified [43]. Capsaicinoid levels are influenced by the ontogenetic development of the peppers. The accumulation of capsaicinoids starts at the early stages of fruit development, followed by a high peak and a rapid decline [54].

3.1.1. Biosynthesis of Capsaicinoids

Capsaicinoid biosynthesis is derived from the phenylpropanoid pathway (Figure 2) [54–56] and occurs after the enzymatic condensation of a molecule of vanillylamine derived from phenylalanine, valine, or leucine to a branched-chain amino acid. The enzymes whose alleles determine pungency levels in peppers are CaMYB31, *pAMT*, *CS/AT3/Pun1*, and *CaKR1* [57]. Capsaicin synthase (*CS*) is the last enzyme (encoded by the *Pun1* gen) responsible for the condensation between vanillylamine and a fatty acid-CoA while the aromatic vanillylamine moiety is paired with many acyl groups, mostly medium-length (from 9 to 11 carbon atoms), giving the immediate reaction of capsaicin biosynthesis [58,59]. Capsaicinoids differ in their chemical structures, specifically in the side chain with a variable number of double bonds placed in different positions; the type of capsaicinoid depends on the products obtained from the different fatty acids in the dehydration synthesis reaction [55].

Differences in capsaicinoid contents can be attributed to changes in the gene expression of the phenylpropanoid pathway. This biosynthetic pathway depends on the genotype and is affected by environmental conditions that include light, temperature, soil-water availability, and mineral nutrition [36,41]. Light intensity directly affects the biosynthesis and accumulation of capsaicinoids in peppers. Light exposure has a positive influence on the expression of the capsaicin synthase gene (*CS*) that has light-responsive motifs in its promoter region *KAS* (keto-acyl ACP synthase) and *AMT* (aminotransferase), with a negative effect through the induction of peroxidases that can degrade capsaicin. Currently, it is not well understood how this balance is controlled and adjusted [54]. The expression of the CaMYB31, *KAS*, and *pAMT* is affected in peppers of the *C. annuum* genus mainly by light but also by temperature, mechanical stress, and plant hormones [60]. The promoter of the *Pun1* gene has light-responsive motifs and consensus elements that promote capsaicinoid biosynthesis [61].

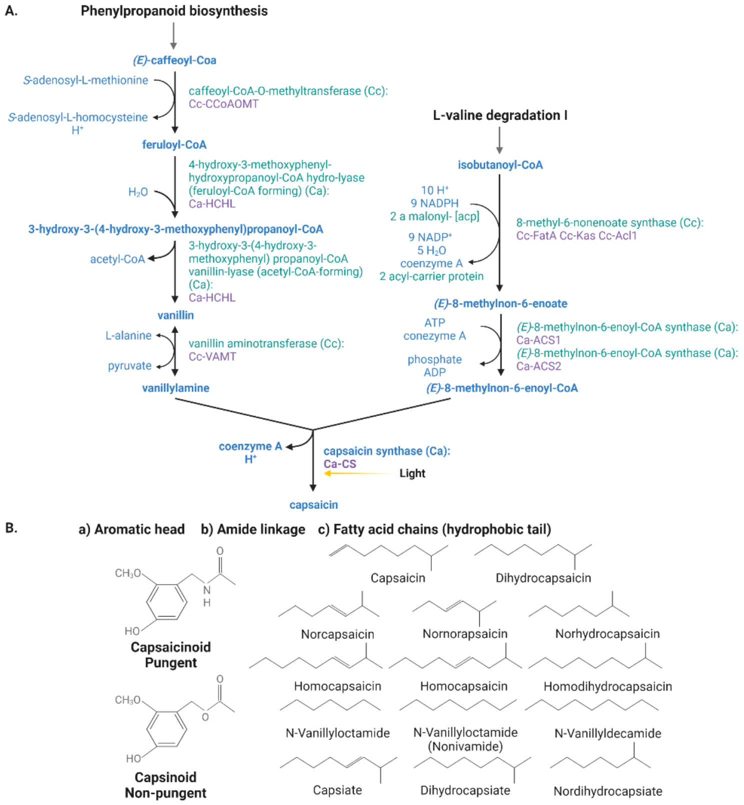

Figure 2. (**A**) Capsaicinoid biosynthetic pathway in peppers (*Capsicum* spp.) via phenylpropanoid and L-valine Degradation I. The yellow arrow indicates the light signal that regulates transcription factors at the molecular level. (**B**) Chemical structure of the most abundant capsaicinoids (pungent) and capsinoids (non-pungent) molecules of *Capsicum* fruits. Capsaicinoids and capsinoids differ in the R group (fatty acids) present.

3.1.2. Effects of Light on Capsaicinoids

In a study on bell pepper production, the optimum light intensity reported to obtain maximum fruit yield was estimated in the range of 1365 to 1470 μmol$\cdot$m$^{-2}\cdot$s^{-1} [62]. Horticultural practices that modify irradiance may result in the enhancement or reduction of capsaicinoid contents (Table 1), depending on the species and the light modification mechanisms (e.g., color and degree of shading, or quality of light emitted by artificial illumination) [63].

Capsaicinoid accumulation is affected by the interaction of light intensity with temperature and relative humidity. In high-pungency peppers (*C. chinense* Jacq.), reduced light intensity and temperature caused lower capsaicinoid production of 4.82 and 3.49 mg plant^{-1} when plants were grown under 50% and 70% shade, respectively [63]. Reduced capsaicinoid accumulation also occurred at high irradiance levels and high temperatures. In addition, environments with reduced light intensity (713–783 μmol$\cdot$m$^{-2}\cdot$s^{-1}) and higher relative humidity increased capsaicinoid production [64]. Thus, the authors suggest an optimum light intensity of 700 to 950 μmol$\cdot$m$^{-2}\cdot$s^{-1} for capsaicinoid production in these cultivars [63].

Total capsaicinoid contents were significantly affected by the interaction of reduced light intensity using different color shades and harvest time in *C. annuum* 'Star flame' and 'Fire flame' [65]. The capsaicinoid contents of peppers grown under colored shading net treatments (white, red, and green) were higher than the unshaded treatment. Of those, the green shade treatment had a considerably higher capsaicinoid content at the first harvest time. This effect could be related to a higher average temperature (22–28 °C) during the cycle. However, other studies showed that higher average temperature and increased solar radiation were associated with lower capsaicinoid contents [41].

Exposure of pepper plants (*C. chinense* Jacq.) to reduced light intensities using shade nets increased the contents of secondary metabolites, including capsaicinoids and other phenolic compounds [63]. Reduced light intensities increased the contents of the phenylalanine ammonia-lyase (PAL) enzyme, which plays a vital role in capsaicinoid biosynthesis. Thus, an increase in the contents of PAL may also cause an increase in capsaicinoids in peppers [66]. Currently, there is not a full understanding of how capsaicinoid accumulation relates to the relevant biochemical reactions with precursors and environmental factors [58].

As for supplemental light, pepper fruits accumulated more capsaicinoids in plants grown in a closed environment under continuous fluorescent illumination (150–350 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and constant temperature (28 °C) than pepper fruits grown under greenhouse conditions during the summer season [67].

Table 1. Effect of light condition treatments on the capsaicinoid content in *Capsicum* species.

***Capsicum* spp.**	**Light Treatment**	**Effects on Capsaicinoids Compared to Control**	**Biosynthetic Effect**
C. chinense Jacq. Seven hot hybrid peppers	Light intensities (1200, 1313, 713, 1112, 774, and 783 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in different locations with shading net with 50% shade	Reduced light intensity (713–783 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and higher relative humidity increased capsaicinoid production in cultivars	Not reported [64]
C. chinense Jacq. 'Bhut Jolokia' 'Akanee Pirote' 'Habanero'	Shading nets with 50%, and 70% shade, and unshaded as control	'Bhut Jolokia' showed the highest capsaicinoid yield under 70% shading, 'Akanee Pirote' under 50% shading, and habanero peppers showed the lowest capsaicinoid content under shading treatments	Levels of phenylalanine ammonia-lyase (PAL) increased under low light intensities [63]
C. annuum 'Star flame' 'Fire flame'	Colored shading nets: white, red, and green with 40% shade, and unshaded as control	Capsaicinoid content increased in color-shading treatments, specifically in green treatment in both cultivars	A high average temperature of 22–28 °C may have promoted capsaicinoid biosynthesis [65]
C. annuum 'Super hot'	Greenhouse conditions with LED lighting treatments: blue, red, and a mixture of blue and red light, and 12 h of sunlight as control	Blue LEDs significantly increased nordihydrocapsaicin, capsaicin, dihydrocapsaicin, homocapsaicin, and homodihydrocapsaicin contents by 57, 43, 56, 28, and 54%, respectively	Capsaicin and dihydrocapsaicin accumulation helped in oxidative stress defense. Valine and phenylalanine increased in blue LED lights contributing to a higher content of capsaicinoids [68]
C. annuum 'Cheonyang'	LED lighting treatments: red, blue, and red plus blue, and fluorescent lamps as control	Blue LEDs increased capsaicinoid contents, red LEDs reduce two times the capsaicinoid content compared to fluorescent light	Not reported [36]
C. annuum 'Shishito pepper'	Continuous fluorescent illumination (150–350 $\mu mol \cdot m^{-2} \cdot s^{-1}$) at constant temperature (28 °C), and greenhouse conditions as control	Fewer seeds and higher concentration of capsaicin in fruits under continuous fluorescent illumination	There is a negative correlation between seed formation and capsaicin biosynthesis [67]

Table 1. *Cont.*

Capsicum spp.	Light Treatment	Effects on Capsaicinoids Compared to Control	Biosynthetic Effect
C. annuum Serrano 'Tampiqueño 74′ Sweet pepper 'California wonder′	Artificial light in postharvest (50 µmol·m^{-2}·s^{-2}) and dark conditions as control	Light factors increased capsaicin content in 'Tampiqueño 74′	CaMYB31-expression analysis from placental tissue of pungent and non-pungent fruits showed a positive correlation with the structural genes *Ca4H*, *Comt*, *KAS*, *pAMT*, and *AT3* expression, and with the content of capsaicin and dihydrocapsaicin during fruit development [60]

Differences in light spectral quality can also affect the accumulation of capsaicinoids in peppers. Peppers produced under blue spectrum light-emitting diodes (LEDs) increased capsaicinoid contents in comparison to plants exposed to fluorescent lights [36]. In a similar study under greenhouse conditions, supplemental blue light LEDs placed at the top and between plant rows also increased capsaicinoid levels in peppers. This was attributed to the blue wavelength, which is near the UV spectra, and causes the same oxidative stress response during the biosynthesis of capsaicin. Blue light also plays a role in chloroplast development, chlorophyll formation, and stomatal opening [68]. In postharvest, Serrano pepper fruits ('Tampiqueño 74′) treated with light or dark conditions with varying exposure times, the expression of the structural genes *KAS*, *pAMT*, and the transcription factor gene CaMYB31 was higher under the light stimulus than fruits stored in the dark [60].

3.2. Carotenoids

Carotenoids are a numerous family of more than 850 naturally occurring lipophilic isoprenoid compounds widely distributed in nature [69]. All photosynthetic organisms, including plants, algae, and cyanobacteria, and some non-photosynthetic micro-organisms, including fungi and bacteria, synthesize carotenoids [70]. In plants, the principal function of carotenoids is the protection of cells and organelles against oxidative damage. Carotenoids prevent the accumulation of harmful oxygen species by interacting with singlet oxygen molecules and scavenging peroxy radicals [71]. Carotenoids are also involved in the photosynthetic process and play a role in photo-protection, photo-morphogenesis, and plant development. Carotenoids also promote the biosynthesis of other essential compounds and play a role in the attraction of insects for pollination and seed dispersal [4,71,72].

Carotenoids have several important essential functions in human nutrition and health. This group of compounds can prevent and protect from cardiovascular diseases, inhibit carcinogenic cells, macular degeneration, and cataracts [73]. Carotenoids are considered the most effective antioxidant compounds found in peppers, besides phenolic and flavonoid compounds, which act synergistically as efficient free radical scavengers [74,75]. Carotenoids deactivate free radicals and quench reactive oxygen species due to the presence of conjugated double bonds [42,76]. In addition, plant carotenoids are endogenous isoprenoid precursors of vitamin A, β-carotene, α-carotene, γ-carotene, and β-cryptoxanthin which can be converted into retinol, the assimilable form of vitamin A in the human body [77].

Capsicum fruits are rich sources of carotenoids. The wide range of colors in peppers is related to the stage of maturation and the differential accumulation of carotenoids [78,79]. Specifically, oxygenated carotenoids are responsible for the yellow, orange, and red colors of pepper fruits [80].

3.2.1. Biosynthesis of Carotenoids

Carotenoids are derived from the universal five-carbon precursor isopentenyl pyrophosphate (IPP, C5) [7]. In *Capsicum*, the plastidial isoprenoid biosynthesis pathway starts with the mevalonic acid which is entered into several reactions to produce the C5 building block precursors—isopentenyl diphosphate and dimethylallyl pyrophosphate. In plants, carotenoids are synthesized in the plastid using IPP generated from the methylerythritol-4-phosphate (MEP) pathway (Figure 3) [4,81]. The MEP pathway receives substrates, G3P and pyruvate, from primary metabolism and delivers IPP to the prenyl lipid pathway. Phytoene, the first carotenoid in the pathway, is synthesized from eight IPP units in the prenyl lipid pathway [72]. The carotenoid biosynthesis pathway is split into the α and β branches. The addition of a hydroxyl group to the end rings characterizes the transition from carotene to xanthophyll. The end-products found in red *Capsicum* fruits are the red pigments capsorubin and capsanthin with κ end groups, the latter being the most abundant [7].

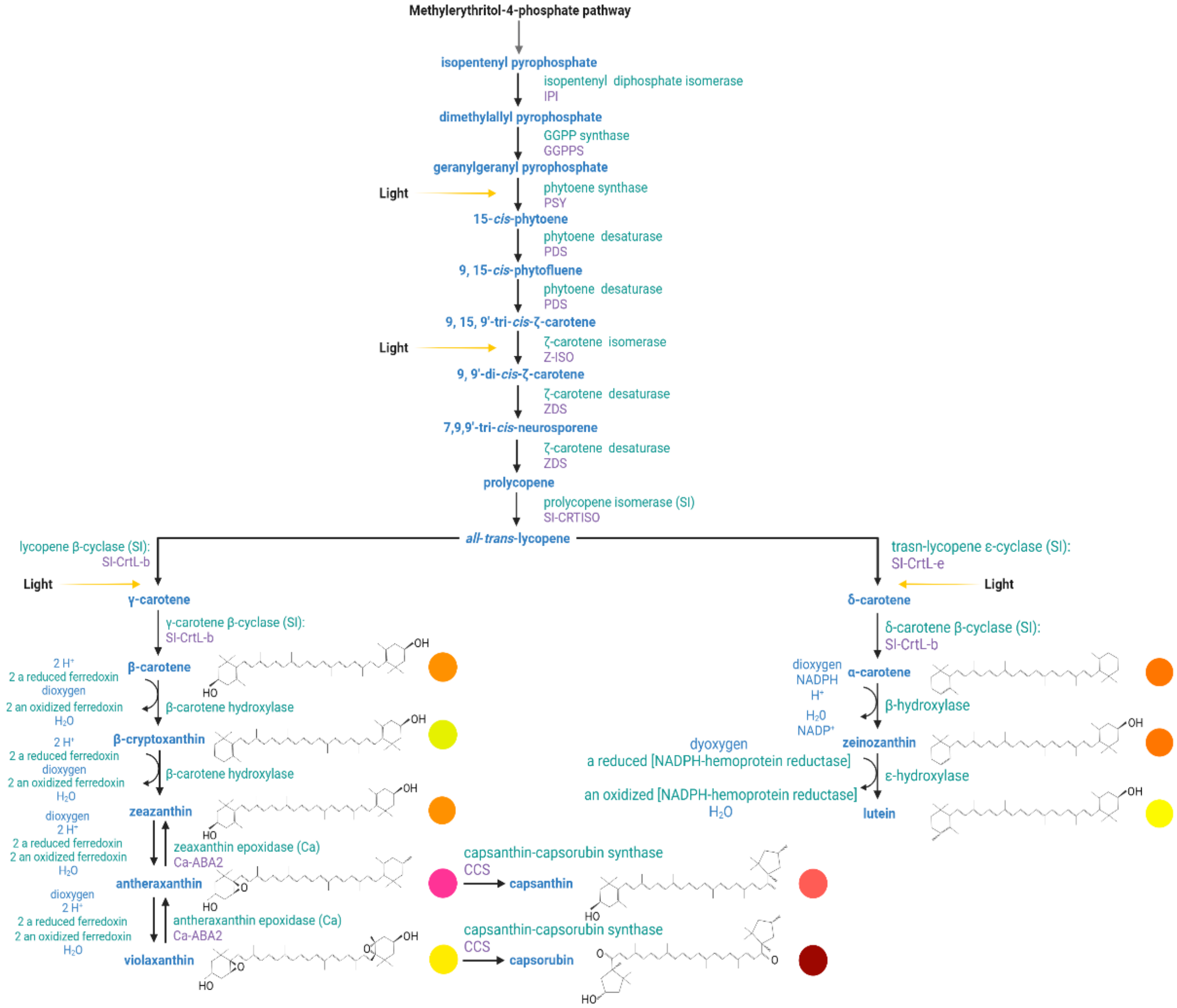

Figure 3. Carotenoid biosynthetic pathway in peppers (*Capsicum* spp.). Yellow arrows indicate the specific reaction steps at which light signal regulates the transcription factors at the molecular level. Chemical structures of the most abundant carotenoids present in *Capsicum* fruits. The circles indicate the color to which each carotenoid is associated in plant tissue.

In *Capsicum* fruits, carotenoid accumulation has been associated with the esterification of xanthophylls to allow for more efficient storage and increased stability, with the expression of a putative carotenoid acyl transferase, and an increased fibril content within the plastid [7].

3.2.2. Effects of Light on Carotenoids

Light signaling regulates the biosynthesis and accumulation of carotenoids through molecular mechanisms by which photoreceptors detect light signals in different plant organs [82]. Light regulates *Psy* (Figure 2) to modulate carotenoid biosynthesis during photomorphogenesis or de-etiolation, which is the process that occurs by the transition from the etioplast to the chloroplast [69]. Phytoene (15-cis-phytoene) has two sequential desaturations by *PDS* to produce 9,15-cis-phytofluene and 9,15,9′-cis-ζ-carotene, which can isomerize to ζ-carotene by light [71]. In peppers under protected cultivation, carotenoid content and *Psy* expression decreased compared to fruits grown under direct white light [83]. The expression of the *Psy* gene has also been reported in other plants including tomato exposed to blue LEDs [84]. The similarities between these two crops include the transition of tissues from chloroplast to chromoplasts during ripening and the high content of carotenoids in these chromoplast-containing fruits, resulting in the characteristic red color [84].

The biosynthesis and final contents of carotenoids are related to the fruit maturation process. Carotenoid accumulation is associated with a reduction in chlorophyll content. In immature fruits, chlorophylls are abundant and contribute to the characteristic green color. As the pepper fruits mature and the chloroplasts differentiate into chromoplasts, the chlorophyll contents of the epicarp lower significantly, and the biosynthesis of carotenoids occurs. During this process, carotenoids start to accumulate and contribute to fruit color [42,76]. The final carotenoid concentration is diverse, and the carotenoid profile is related to fruit color at harvest [74]. Color changes in response to more than thirty types of carotenoids [42]. In mature peppers, the most diverse carotenoid profile consisted of β-carotene, violaxanthin, antheraxanthin, zeaxanthin, and the intense red ketocarotenoids (capsanthin, capsorubin, and capsanthin-5,6-epoxide) [74].

In addition to the maturation process, other factors that affect carotenoid contents in peppers include genotype differences [85,86], environmental conditions during agricultural production [87,88], postharvest handling [9], processing [89], and storage (Table 2) [76].

Light is an important environmental factor involved in carotenoid biosynthesis. The quality and intensity of the light intercepted by the crop have a direct effect on the production and accumulation of carotenoids in peppers [15].

In sweet pepper cultivars, enhanced accumulation of carotenoids was obtained by a reduction in light intensity on the crop using shade nets. The five identified carotenoids were capsanthin, lutein, β-cryptoxanthin, β-carotene, and phytoene. Of these, capsanthin was the major carotenoid compound [8]. Similarly, reduced light stress in a shaded greenhouse also promoted carotenoid accumulation in three orange-fruited pepper cultivars. For these cultivars, the primary carotenoids present at the highest concentrations were lutein, zeaxanthin, and violaxanthin [90]. The increase in carotenoid contents caused by shaded conditions was also observable in postharvest studies. The use of black nets increased the carotenoid contents of β-carotene and lycopene in two different red and yellow sweet pepper cultivars [27].

The use of shading nets (black or colored) affects the accumulation of carotenoids in peppers. Plants cultivated in unshaded conditions (open field) produced peppers with the lowest levels of carotenoids in comparison to plants covered by black or colored shading nets [91]. Unshaded plants yielded fruits with less than 50% of the carotenoid contents in comparison to those grown under white nets. As for colored nets, peppers grown under yellow and red nets contained the lowest amounts of carotenoids (except for the unshaded control plants). However, 'Kapia'-type red sweet peppers grown under white shading nets resulted in significantly higher carotenoid contents in comparison to the green and yellow shades [92].

In postharvest studies of peppers, the exposure of green 'Takanotsume' peppers to different light wavelengths affected the carotenoid profile (including β-carotene, free-capsanthin, and total carotenoids). Peppers treated with red LEDs (660 nm) presented the highest increase in carotenoid contents, followed by those exposed to blue LEDs (470 nm). This response was associated with a reduction of chlorophyll in the fruits [9].

Accumulation of carotenoids can be induced by UV radiation (wavelengths from 100 to 400 nm). Of these, UV-A ranges from 315 to 400 nm, UV-B from 280 to 315 nm, and UV-C from 100 to 280 nm [93]. UV-C wavelengths do not reach the Earth's surface but can be applied in horticulture by artificial illumination to enhance the biosynthesis of metabolites. UV-C radiation has shown increased carotenoid levels when applied at low intensities. Nonetheless, high intensities can negatively affect photosynthesis and damage plant tissues [92].

The application of UV radiation to red sweet peppers during postharvest increased the levels of carotenoids after 14 days at 7 °C. Carotenoids increased exponentially by exposure to UV-C and UV-B in comparison to the non-UV treatment [94]. The UVR8 protein may be the principal UV-B receptor, and its action spectrum also includes the UV-C region. Thus, the application of low levels of single UV-C can also stimulate carotenoids and other phytochemicals. Exposure to red and blue (RB) LEDs light and RB with far-red wavelengths in red and yellow sweet pepper fruits increased the carotenoid content when compared to natural light exposure. The major carotenoids found in red fruits were capsanthin and capsorubin, whereas in yellow fruits, they were violaxanthin and lutenin [95]. In peppers that accumulate plastids after the breaker, the far-red wavelengths can act as a signal for the initiation of plastid accumulation [84]. Storage of habanero fruits in closed packages at low temperatures under blue and UV-C treatments affected carotenoid biosynthesis. During the first five days, the contents of chlorophylls and total carotenoids were reduced in comparison to the untreated peppers. This response could be attributed to the synthesis of photosynthetic pigments in chloroplasts to protect the photosystems [96].

Table 2. Effect of light-condition treatments on the carotenoid content in *Capsicum* species.

***Capsicum* spp.**	**Light Treatment**	**Effects on Carotenoids Compared to Control**	**Biosynthetic Effect**
C. annuum Sweet pepper	Colored shading net: white with 40% shade and controlled-temperature plastic tunnel environment	Controlled temperature plastic tunnel enhanced the accumulation of carotenoid components	Capsanthin biosynthesis was not affected by treatments in most of the cultivars; peppers showed a homogeneous behavior in β-cryptoxanthin biosynthesis, which was not significantly affected in most cultivars in any of the treatments. Shading effect influences a change in the active form of phytochrome, facilitating the degradation of phytochrome interacting factor (PIF1a) and activating *PSY1* expression and carotenoid biosynthesis [8]
C. annuum Sweet pepper 'Cameleon'	Plastic tunnel plus colored shading nets: red, black, pearl, and blue shading nets with 40% shade, and open field as control	Black nets increased the carotenoid contents of β-carotene and lycopene	Not reported [11]

Table 2. *Cont.*

Capsicum spp.	Light Treatment	Effects on Carotenoids Compared to Control	Biosynthetic Effect
C. annuum Sweet pepper 'Karpex'	Colored shading nets: red, yellow, red, green, and white with 40% shade and unshaded as control	The unshaded control produced more than 50% less carotenoid than that under the white net. Peppers under the yellow and red nets produced the lowest content of carotenoids	Exposure to high temperature and radiation can lead to inhibition of carotenoid biosynthesis [91]
C. annuum Sweet pepper 'Kapia'	Colored shading nets: white, green, yellow, red, and unshaded as control	White shade net resulted in significantly higher carotenoid content compared to the green and the yellow nets	Not reported [92]
C. annuum 'Fogo' 'NuMex' 'Sunset' 'Orange Grande'	Shaded greenhouse with 40–50% shade, greenhouse conditions, and open field as control	Carotenoid concentrations decreased in fruits grown under increased light levels and increased in treatments with lower light intensity level	Not reported [90]
C. annuum Red and yellow sweet pepper	LED lighting treatments: natural light with red and blue LED, red and blue LED with far-red light, and natural light as control	In both colored fruits, carotenoid content was higher in LED treatments	Far-red light can act as a signal for starting plastid accumulation. Carotenoids changed by adding far-red light to the red and blue lighting [95]
C. annuum Red sweet pepper 'Angus'	UV lighting: UV-C, UV-B, UV-B+C, and no UV treatment as control	UV treatments induced carotenoid accumulation; after 14 days at 7 °C, UV-B and UV-C increased by 59% the total carotenoid content, and UVB + C by 94%	The active form of UVR8, a UV photoreceptor specific for UV-C and UV-B wavelengths, directly interacts with COP1 and regulates the expression of the *HY5* gene, which promotes the production of carotenoids [94]
C. chinense Habanero pepper	Irradiation treatments: blue lamps (0, 1.5, and 3 min), and UV-C light (0, 0.5, and 1 min) at 4–5 °C	Both lights stimulated bioactive compounds. Carotenoid content increased only in the first days of storage	Blue and UV-C light may stimulate the synthesis of chlorophylls and total carotenoids [96]
C. annuum Sweet peppers	LED lighting treatments in postharvest: yellow light at a wavelength of 590 nm and dark conditions as control	LED light slightly accelerated the ripening of fruits and increased the content of β-carotene, α-tocopherol, γ-tocopherol, chlorophyll, and lutein. Fruits showed higher antioxidant potential	Not reported [97]

3.3. Phenolic Compounds

Phenolic compounds constitute another essential group of secondary metabolites in *Capsicum* fruits. This group of compounds is usually reported as total phenolic compounds (TPC) and include phenols, phenolic acids, flavonoids, anthocyanins, lignans and lignins, stilbenes, and tannins. In peppers, the highest levels of TPC are found in the pericarp of fruits [95,96]. Peppers are rich in polyphenols, such as p-coumaric, ferulic, p-hydroxybenzoic, caffeic acid, sinapic acid, and quercetin-3-glucoside (Figure 4) [8].

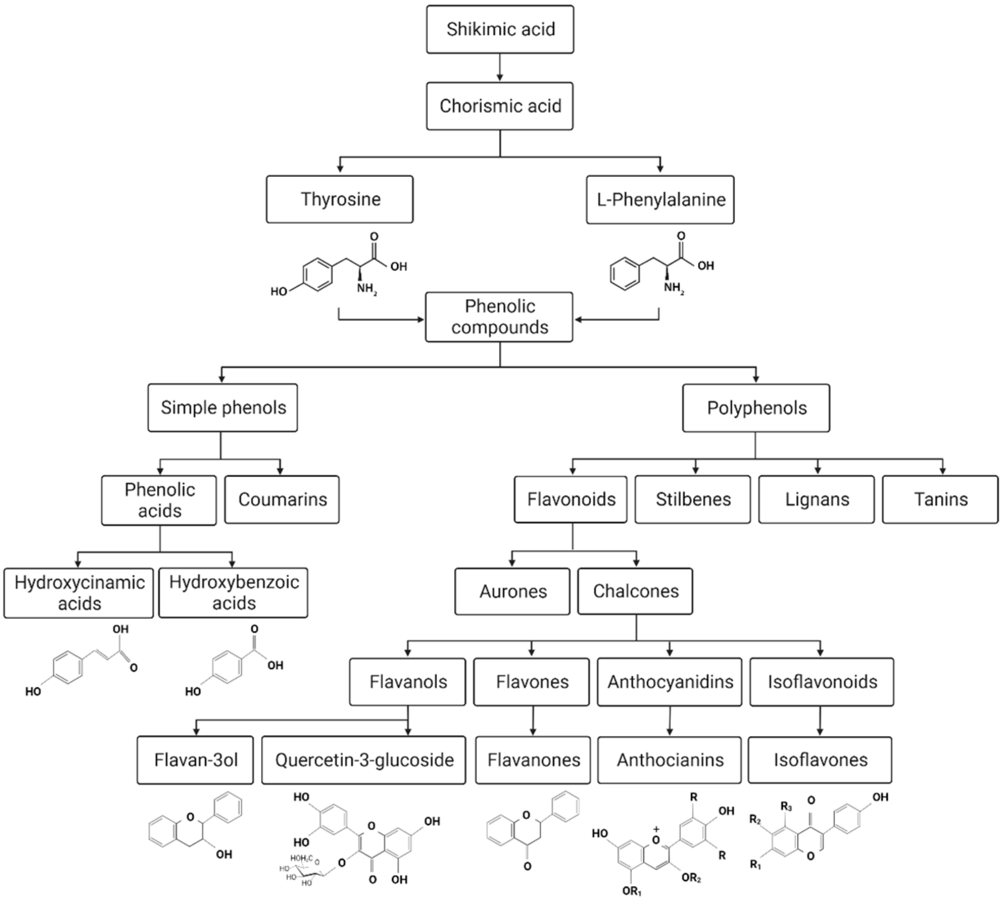

Figure 4. Phenolic compounds pathway in peppers (*Capsicum* spp.). Chemical structure of the most abundant phenolic compounds in *Capsicum* fruits (from their precursors).

Phenolic compounds result from the adaptation of plants to biotic and abiotic conditions that include infection, wounds, water, cold, and light intensity stress, among others [80,98,99]. Phenolics assist and interact as defense mechanisms with biotic and abiotic factors [52,100]. Phenolics quench the reactive oxygen species (ROS) produced during stress and protect the photosynthetic cells, and are related to the capacity of plants to absorb UV-B radiation [80,101].

Phenolic compounds are considered health-promoting metabolites [102]. Flavonoids are associated with the prevention of cancer, cardiovascular and autoimmune diseases, and are involved in the delay of the aging process [2]. These effects can be attributed to their direct role as free radical scavengers; modulators of detoxification enzymes, oxidation, and reduction processes; and strengtheners of the immune system, regulating gene expression, cell signaling, and hormone metabolism [103,104].

Phenolic compounds are phytochemicals with one aromatic ring attached to a hydroxyl group at a minimum. Phenolic compounds are divided into different classes by their chemical structure and the number of carbon atoms in their molecule [105]. The classification of phenolic compounds depends on the number of phenol units as simple phenols or polyphenols. Phenols contain one phenol unit, and polyphenols consist of two or more phenolic groups, up to polymeric structures [98]. Polyphenols rarely appear as free compounds and can be found in plants in the form of esters or glycosides with other natural compounds such as flavonoids, alcohols, and sterols [2,106].

3.3.1. Biosynthesis of Phenolic Compounds

Phenolic compounds are products of the secondary metabolism, in particular the shikimate pathway. Even though the precursors, phenylalanine or tyrosine, are the same, this pathway has different branches that lead to different compounds, which makes the biosynthetic pathway very complex [107,108]. Multiple genes are involved in the regulation of the different transcription factors involved in this pathway. Nonetheless, in *Capsicum*, only a few of the genes are known. The synthesis of flavonoids and other phenolic compounds can be regulated through a series of internal and external factors, including light [103]. The biosynthesis of phenolics is closely related to PAR irradiation and spectral quality; therefore, the manipulation of light conditions can cause changes in the content of metabolites and, consequently, alter photoprotection mechanisms [109].

The biosynthesis of flavonoids follows the phenylpropanoid pathway, which is impacted by environmental conditions. Nutrient deficiency, UV radiation, or an increase in stress levels caused by pathogens can influence the biosynthesis of flavonoids in many types of peppers [101].

In sweet pepper cultivars, the interaction between cultivar and growing conditions under protected cultivation affected the accumulation of phenolic compounds and antioxidant activity. Light intensity modified by white shade nets increased the accumulation of phenolic compounds and antioxidant activity in most of the studied cultivars. Similarly, the cultivation of peppers in plastic tunnels also favored the production of phenolics in other cultivars [8]. Similar results under white and red nets were reported, where higher R/FR ratios in spectral quality and reduced PAR increased the accumulation of phenols, quercetin, and other flavonoids in peppers [22].

3.3.2. Effects of Light on Phenolic Compounds

Light intensity and spectral quality during cultivation enhance the content of TPC in peppers [22,88] during cultivation, postharvest, and storage (Table 3) [96].

In postharvest studies, the spectral characteristics of light affect the accumulation and retention of bioactive compounds and physicochemical parameters in green peppers at harvest and during postharvest storage [22]. The antioxidant activity in peppers also increases during postharvest storage; this activity is associated with the metabolic pathways involved during the ripening and the production of lipophilic antioxidants [110]. Peppers produced under black or yellow nets showed a reduction of TPC. A further reduction was observed in fruits under black nets after postharvest storage. By contrast, peppers produced under pearl and red nets had a higher concentration of total phenols at harvest and remained high after postharvest storage. Total phenols, flavonoids, and even the antioxidant capacity in bell peppers were among the highest in unshaded conditions [89].

Exposure of pepper fruits during postharvest to red and blue LED also changed the TPC. Blue LED resulted in a significant increase in phenolic compounds in fruits when compared to the red LED and the control (fruits incubated in darkness). This effect was spectrum-specific as the red LED did not cause a significantly different response of the TPC [78]. Similar studies revealed an increase in total phenolic compounds in yellow and green sweet peppers exposed to red LED light and red peppers exposed to blue LED light during postharvest by increasing phenylalanine ammonia-lyase activity [24]. As described before, a wide variety of enzyme-catalyzed reactions are involved in the biosynthesis of phenols and flavonoids. However, only some of the genes involved in the *Capsicum* genus are known [98]. Therefore, detailed studies at the genomic and transcriptional levels are needed to elucidate the mechanism of light effects on phenolic compound production in peppers.

Table 3. Effect of light-condition treatments on the phenolic compounds content in *Capsicum* species.

***Capsicum* spp.**	**Light Treatment**	**Effects on Phenolic Compounds Compared to Control**	**Biosynthetic Effect**
C. annuum Sweet peppers c.v. 'California Wonder'	Polytrench greenhouse, shaded greenhouse (Polytrench + red shade net), and open field as control	The total contents of phenols and flavonoids were reduced by 35.2 and 14.6%, respectively, in the greenhouse treatment.	Not reported [106]
C. annuum Green sweet peppers	Colored shading nets: pearl, red, and yellow with 40% shade, and black net with 25% shade as control	Fruits produced under the pearl nets showed higher ascorbic acid content, and antioxidant scavenging activity after postharvest storage	Red–far-red photon ratio under the pearl net could have improved the ascorbic acid content and the antioxidant scavenging activity in green peppers [22]
C. annuum Sweet peppers	Colored shading nets: black, red, silver, white with 30% to 46% shade, and unshaded as control	Total phenols and flavonoids were among the highest in the unshaded treatment and under the white net, and the lowest content under the black net	Not reported [87]
C. annuum Sweet peppers, eleven cultivars	Colored shading net: white with 40% shade and controlled temperature plastic tunnel	White shade nets increased the accumulation of phenolic compounds and antioxidant activity in most of the studied cultivars	Not reported [8]
C. annuum c.v. 'Takanotsume'	LED lighting treatments: red (660 nm) and blue (470 nm) light at an intensity of 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$	The total phenolic, vitamin C content, and antioxidant capacity were higher in the blue LED-treated fruits	The blue LED was more effective in increasing the expression of the phytoene synthase (*Psy*) gene [78]
C. annuum Red sweet peppers	HPS and LED lighting in a glass greenhouse	LEDs at 622 nm enhanced phenolic compounds. HPS lighting supplemented with different LEDs was not efficient.	Not reported [111]
C. annuum Purple bell pepper	LED lighting treatments: white-red, and blue light	High blue-light fractions increased anthocyanin levels; white-red light is not efficient in the accumulation of anthocyanins	Increasing anthocyanin levels, via enhancing anthocyanin biosynthesis, was supported by kinetic modeling and higher expression levels of the anthocyanin biosynthetic genes *CaMYB*, *CaCHS*, *CaDFR*, *CaANS* and *CaUFGT* [85]
C. annuum Yellow, green, and red sweet peppers	LED lighting treatments: red, blue, and white light, and darkness as control	Red LED light for 8 h per day during storage at 7 °C was beneficial to retain bioactive compounds such as phenols and flavonoids	PAL activity in the yellow and green peppers exposed to red LED light increased and was correlated with the number of bioactive compounds [24]

Exposure of bell peppers to UV-C radiation in postharvest studies reduced the incidence and severity of the chilling injury and reduced the accumulation of phenolic compounds [112]. The response to UV-C radiation is highly dose-dependent as exposure to UV-C may significantly affect the enzymes involved in the biosynthesis of phytochemicals [113]. Moderate doses induce physiological responses, whereas high doses may reduce the enzymatic role, which causes a reduction in the production of bioactive phenolic compounds and other antioxidants [114].

4. Summary

Light is an elicitor of bioactive compounds in peppers and affects the biosynthesis and accumulation of phytochemicals. Current horticultural technologies that modify light intensity and spectrum aimed at improving pepper yields can also cause changes in the accumulation of bioactive compounds. The use of shade nets or plastic covers to reduce light intensity does not seem to yield consistent responses on the phytochemical profile, as the final profile results from the interaction of several factors. Exposure of plants to supplemental light with specific wavelengths seems to result in a more precise stimulation of specific metabolites. The molecular mechanisms underlying the specific effects of light on the phytochemical profile of peppers are still unclear. Further research is needed for a better understanding of the biochemical and molecular mechanisms of phytochemicals to reveal the complete effects of light on the phytochemical profile of peppers.

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