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Review

Light Controls in the Regulation of Carotenoid Biosynthesis in Leafy Vegetables: A Review

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Abstract: Leafy vegetables are excellent dietary sources of carotenoids, offering various nutritional benefits to human health. With the growing interest in health, the enhancement of functional compounds in crops through environmental control is emerging as an important topic in the field of agricultural research. Light serves as a major environmental signal regulating carotenoid levels. Light-activated photoreceptor proteins initiate intracellular signaling pathways that regulate carotenoid metabolism in response to environmental changes. Recent studies have shown that blue and ultraviolet (UV) light wavelengths are particularly effective in accumulation of foliar carotenoids, as they trigger photo-oxidative stress while activating defense mechanisms to mitigate it. Light intensity and exposure time, as quantitative aspects of light, are also involved in carotenoid biosynthesis in a similar manner. However, although previous studies provide valuable insights into light-mediated carotenoid accumulation, the interplay of light parameters (e.g., spectrum, intensity, exposure) with crop species and growth stages remains unclear due to the lack of well-organized data. In this review, we summarize recent advanced information about light-mediated carotenoid biosynthesis in leafy vegetables and highlight an integrated experimental approach to explore optimal light conditions for maximizing carotenoid accumulation in commercial production systems.

Keywords: leafy green; carotenoid accumulation; light signaling pathway; ROS; light condition; growth stage

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1. Introduction

Carotenoids are hydrophobic pigments that occur naturally and are synthesized in higher plants, algae, bacteria, and fungi [1,2]. Carotenoids absorb light in the range of approximately 400–550 nm [3], so they emit the remaining light and appear mainly as red, orange, and yellow. They are accumulated in plastids, where they contribute to plant coloration and help attract pollinators and seed dispersers. Additionally, carotenoids serve as precursors for the synthesis of plant hormones such as strigolactone and abscisic acid [4]. Carotenoids are recognized for their high nutritional value and are used in the food and pharmaceutical industries. Carotenoids provide precursors of vitamin A and are a central component of the macular pigment necessary for the human eye [5,6]. Carotenoids also protect against cardiovascular diseases, lung cancer, prostate cancer, colon cancer, and diabetes owing to their antioxidant and anti-inflammatory properties [7–9].

Humans are unable to produce carotenoids internally, so they must obtain them through dietary intake. The primary sources of carotenoids are greenish-yellow, yellow, orange, and red fruits and vegetables. In this context, increasing interest in personal health has led to a growing demand for carotenoid-rich crops. The growing demand for carotenoid-rich crops has driven research efforts in breeding, genetic modification, and gene editing [10]. In addition, practical approaches to optimizing environmental conditions are actively being explored. Environmental control to enhance carotenoid content holds significant potential for agricultural applications by inducing natural physiological responses. Carotenoid metabolism in plants is closely related to environmental factors such as light, water, temperature, and salinity, as demonstrated in numerous studies [11]. Among them, light is considered one of the most important environmental factors in carotenoid metabolism. Plants regulate the synthesis and accumulation of carotenoids based on light conditions throughout their growth [12]. Thus, light control is a valuable approach to producing high-value crops abundant in carotenoids. This approach is likely to achieve greater success in plant factories where the surrounding environment can be fully controlled. Plant factories can produce crops of consistent quality year-round through environmental control. Most commercial leafy vegetables are well-suited for cultivation in plant factories due to their high-density planting and rapid growth rate [13,14]. In particular, artificial light technologies installed in the facilities can be utilized not only to create crop-optimized growth environments but also to regulate secondary metabolism [15]. Despite its potential, variability in light conditions and crop-specific responses limit widespread implementation. Therefore, it is necessary to summarize existing research to deepen the understanding of light regulation for carotenoid accumulation.

Most of the light reaching plants is used for photosynthesis. The photosynthetic apparatus of plants is well-developed in chloroplasts, and contains various pigments for absorbing and transmitting light energy. Carotenoids are essential components of the apparatus, enhancing photosynthetic efficiency by expanding the light absorption range in close proximity to chlorophylls [16]. In fact, it has been reported that the total carotenoid content in leaves increases along with chlorophyll under low light intensities, which means that carotenoids function well as antennas to capture and transmit light together with chlorophyll [17]. Moreover, carotenoids could also protect the photosynthetic apparatus from photo-oxidative stress. When the electron transport chain becomes saturated due to excessive light during photosynthesis, photo-oxidative stress is induced through the accumulation of excited chlorophylls that have the potential to generate reactive oxygen species (ROS) [18]. Carotenoids have been reported to inhibit the generation of ROS by dissipating the energy of the excited state of chlorophyll through non-photochemical quenching. Some carotenoids also directly scavenge ROS, contributing to photoprotection [19]. In this way, light conditions during photosynthesis influence the levels and functions of carotenoids. Understanding the complex interactions between light and carotenoids can help modulate carotenoid metabolic pathways in crops to optimize photosynthetic efficiency and photoprotective mechanisms. In this review, we summarize studies in model plants that describe how light acts as a regulatory signal for carotenoid metabolism. This provides information on the interactions between specialized receptor proteins and transcription factors. Then, we will summarize previous studies on the regulation of carotenoid metabolism by different light conditions. Through this, we will comprehensively review how light conditions affect carotenoid metabolism and discuss the tasks that should be carried out together with future practical applications. Our aim is to provide comprehensive information on light regulation to produce high-value leafy vegetables rich in carotenoids.

2. Photoregulatory Mechanisms of Carotenoid Biosynthesis in Plants

Carotenoids are secondary metabolites with a 40-carbon backbone composed of eight isoprenes (C5). Carotenoid synthesis is mainly accomplished by isoprene produced in the methylerythritol phosphate (MEP) pathway, which occurs in plastids within plants. The plastid, which is an organelle found in plant cells, exists in several forms. Etioplasts are found in unopened cotyledons, which contain only trace amounts of carotenoids. Light triggers the unfolding of cotyledons, leading to the differentiation of etioplasts into chloroplasts, where photosynthesis occurs [20]. During this transformation, both chlorophyll and carotenoids are accumulated and used for photosynthesis. In addition, chromoplasts form in a tissue-specific manner to facilitate carotenoid accumulation, primarily in the flowers or fruits [20].

Many enzymes catalyze a series of reactions leading to carotenoid biosynthesis in the plastids [21,22]. Carotenoid biosynthesis begins with the condensation of isopentenyl diphosphate and dimethylallyl diphosphate, generated through the MEP pathway, forming geranylgeranyl diphosphate (GGPP) which contains a 20-carbon skeleton. Two GGPP molecules are condensed via the activation of phytoene synthase (PSY) to produce phytoene, which is a primary carotenoid with a 40-carbon skeleton. Subsequently, desaturation and isomerization of carotenoids lead to all-trans-lycopene synthesis, which serves as a gateway for the synthesis of downstream carotenoids like carotenes and xanthophylls. The cyclization of all-trans-lycopene by lycopene β-cyclase and lycopene ε-cyclase is an essential step in the synthesis of β-carotene and α-carotene, respectively. The hydroxylation of α-carotene and β-carotene leads to the synthesis of xanthophylls such as zeaxanthin and lutein, respectively. Antheraxanthin and violaxanthin are synthesized after zeaxanthin epoxidation. However, under high light stress conditions, a reversible enzymatic reaction is catalyzed by violaxanthin de-epoxidase to induce the retrograde synthesis of zeaxanthin from violaxanthin via antheraxanthin, a process known as the xanthophyll cycle [23].

Plants detect light using specialized receptor proteins called photoreceptors. These proteins sense light and transmit signals, allowing the plant to adjust its growth and development in response to changing light conditions. Photoreceptors contain chromophore molecules that absorb specific wavelengths of light, allowing them to detect different regions of the light spectrum [24,25]. Photoreceptors are classified into five groups: phytochromes (PHY), which perceive red and far-red light; cryptochromes (CRY), which detect blue and UV-A light; phototropins (PHOT) and the ZEITLUPE/FLAVIN-BINDING KELCH REPEAT F-BOX1/LOV KELCH PROTEIN2 group, which respond to blue light; and UV-B resistance 8 (UVR8), which senses UV-B light. To date, PHY, CRY, and UVR8 have been identified as key regulators of carotenoid biosynthesis and are known to interact with various transcription factors to regulate carotenoid gene expression. Transcription factors act as molecular switches, regulating the activity of structure genes involved in carotenoid metabolism. This series of processes, known as the light signaling pathway, has been extensively studied in model plants like Arabidopsis [26], providing critical insights into their regulatory mechanisms (Figure 1).

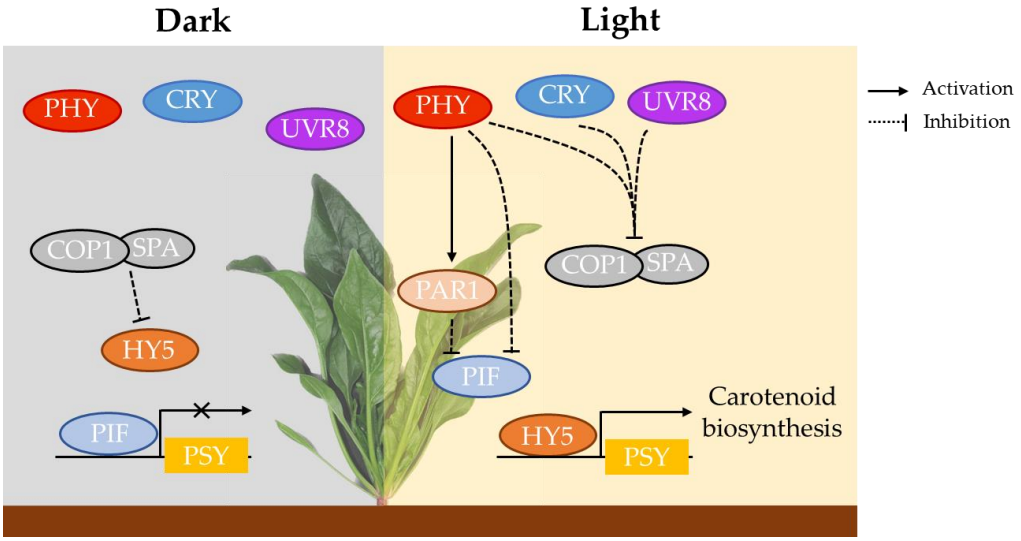


Figure 1. Light signaling pathways regulating carotenoid biosynthesis. In darkness, the CONSTITUTIVELY PHOTOMORPHOGENIC 1/SUPPRESSOR OF PHYA-105 (COP1/SPA) E3 ligase represses ELONGATED HYPOCOTYL 5 (HY5, an activator of carotenoid transcription) and stabilizes the PHYTOCHROME-INTERACTING FACTOR (PIF, a repressor of carotenoid transcription). Upon exposure to light, active photoreceptors such as PHY, CRY, and UVR8 regulate the ligase, enabling HY5 to bind the PSY (a key enzyme of carotenoid biosynthesis) gene promoter and activate carotenoid metabolism. PHYTOCHROME RAPIDLY REGULATED 1 (PAR1) inhibits the activation of PIF under shade. Concurrently, active PHY promotes the rapid ubiquitination and degradation of PIF [27]. Meanwhile, PAR1 functions as a repressor of PIF under low light intensity.

The photoreceptors have been shown to regulate the activity of COP1/SPA E3 ligase in response to light. In darkness, this ligase acts as a repressor of photomorphogenesis by ubiquitinating and degrading HY5, a key transcription factor involved in carotenoid biosynthesis [28]. However, photoreceptors activated after light absorption inhibit the ligase activity, inducing the release of HY5 from inhibition by the COP1/SPA complex [29]. This results in the induction of photomorphogenesis and the concomitant initiation of carotenoid metabolism. Meanwhile, PIF has been reported as a repressor of photomorphogenesis. PIF, which belongs to the basic–helix–loop–helix family, is involved in the inhibition of carotenoid biosynthesis in the dark by repressing PSY transcription [30]. Upon light exposure, PIF undergoes degradation, allowing PSY transcription to proceed by releasing its repression. Interestingly, HY5 and PIF compete for the same promoter site, known as the G-box, to regulate PSY transcription, indicating that they function antagonistically based on light conditions. PAR1 also positively regulates carotenoid biosynthesis as a transcriptional cofactor under shade conditions, functioning independently of HY5 [31]. The presence of surrounding plants creates shade with a lower red/far-red light ratio, which is sensed and transmitted as a signal by PHY to regulate PAR gene activity. Extensive research has been conducted using Arabidopsis as a model to understand the photoregulatory mechanisms of carotenoid biosynthesis. These studies have revealed key regulators, such as photoreceptors and TFs. Based on these findings, similar regulatory mechanisms have been identified in various crops. In rice leaves, blue light promotes carotenoid accumulation by inhibiting PIF while stimulating HY5 activity [32]. Similarly, in cabbage treated with blue light, *BrPIF1* expression was suppressed, whereas *BrHY5-2* was upregulated [33]. Consequently, the expression levels of genes involved in carotenoid biosynthesis were also increased, which was closely associated with carotenoid accumulation. Moreover, targeted genetic modulation of key regulators in the light signaling pathway, such as photoreceptor genes [34,35] and TFs [36,37] has been shown to be an effective strategy for enhancing carotenoid metabolism. These findings underscore the significant potential of genetic

engineering to optimize carotenoid content in crops, with applications in plant breeding and biotechnology research.

3. Leafy Vegetables as a Valuable Source for Carotenoid Intake

Carotenoids in leaves are essential for photosynthesis, primarily functioning in light energy harvesting and photoprotection. Carotenoids are integral components of the photosystems, assisting chlorophyll in light harvesting and enhancing photosynthetic efficiency. This characteristic significantly enhances photosynthetic efficiency. However, excessive light absorption not only reduces photosynthetic efficiency but also generates ROS in the photosynthetic electron transport chain, leading to oxidative damage in chloroplasts. Plants have developed various mechanisms to mitigate oxidative stress under high-light conditions, including leaf structural adaptations, PHOT-mediated chloroplast rearrangement, and antioxidant activity [38]. Carotenoids contribute to photoprotection by detoxifying ROS generated during photosynthesis. In chloroplasts, carotenoids primarily exist in a protein-bound form near chlorophyll molecules within light-harvesting complexes and reaction centers, while some remain as free forms in the membrane [18]. Their primary functions are recognized as preventing the formation of ROS by quenching photosensitizer molecules in their excited state, directly quenching ROS, or scavenging ROS [19]. Leaf carotenoids—β-carotene, lutein, violaxanthin, neoxanthin, and zeaxanthin—vary in composition and abundance depending on species and environmental conditions. Many studies have reported the carotenoid composition and contents of various leafy vegetables [39–43]. Based on these data, we analyzed carotenoid levels in approximately 50 leafy vegetables (Table S1) and identified 10 species particularly rich in carotenoids (Figure 2). In Figure 2, lamb's quarters are the leafy vegetable with most abundant carotenoid content (4497.9 μg g^{-1} DW), followed by jio, spinach, endive, cress, New Zealand spinach, slender amaranth, Boston lettuce, sheep sorrel, and betel leaf. The top 10 carotenoid-rich vegetables consistently exhibit high lutein and β-carotene levels. Violaxanthin is also a major carotenoid in most vegetables, except betel leaf and sheep sorrel, where it is present only in trace amounts (36.7 and 14.5 μg g^{-1} DW). However, violaxanthin is present in all 10 vegetables regardless of the quantity. On the contrary, the presence or absence of other carotenoids depends on the vegetable species. Neoxanthin is present in seven vegetables (77.0–440.0 μg g^{-1} DW), while it is not detected in cress, jio, or lamb's quarters. Zeaxanthin is present in betel leaf, slender amaranth, jio, and lamb's quarters in small amounts (below 50 μg g^{-1} DW). α-carotene is present in slender amaranth (67.5 μg g^{-1} DW) and jio (371.7 μg g^{-1} DW).

β-carotene and lutein are the predominant carotenoids in most leafy vegetables, contributing 51.8–95.9% of the total carotenoid content. These compounds are often present at higher concentrations in leaves than in other plant organs (Table 1). For example, Chinese cabbage had the highest accumulation of lutein and β-carotene in the leaves, followed by the flowers and stems, with almost no lutein present in the roots [44]. Similarly, tomato fruits are rich in lycopene, the dominant carotenoid, whereas their leaves contain higher levels of β-carotene and lutein [45]. In pepper, fruit pericarp had higher levels of lutein, zeaxanthin, and violaxanthin. However, the leaves exhibited significantly higher β-carotene levels (38.2–118.6 μg g^{-1} FW) compared to the fruit (0–11.4 μg g^{-1} FW) [46]. In addition, potato, carrot, and *Ixeris dentata* also exhibit higher total carotenoid content in leaves than in other organs [47–49], reinforcing the general trend that leaves serve as the major carotenoid reservoir in plants. These findings underscore the nutritional importance of leaves as a rich source of carotenoids, particularly β-carotene and lutein, reinforcing their value in carotenoid regulation research.

Table 1. Comparison of carotenoid content among different organs of various crops.

Plant Species	Carotenoids	Organs	Content	Unit	References
Chinese cabbage (*Brassica rapa* subsp. *pekinensis*)	β-carotene	Flower	25.0	μg g^{-1} DW	[44]
		Stem	32.0		
		Leaf	87.1–104.0		
		Root	0.2		
	Lutein	Flower	72.4		
		Stem	43.6		
		Leaf	101.9–120.3		
		Root	0.5		
	Violaxanthin	Flower	13.9		
		Stem	3.6		
		Leaf	8.2–9.6		
		Root	0.1		
Ixeris dentata var. *albiflora*	Total carotenoid	Flower	353.6	μg g^{-1} DW	[49]
		Leaf	1498.3		
Pepper (*Capsicum annuum* L.)	β-carotene	Leaf	38.2–118.6	μg g^{-1} FW	[46]
		Fruit	0–11.4		
	Lutein	Leaf	16.2–24.4		
		Fruit	0–41.3		
	Violaxanthin	Leaf	0.2–3.1		
		Fruit	0–83.2		
	Zeaxanthin	Leaf	0.6–13.5		
		Fruit	0–91.9		
Tomato (*Solanum lycopersicum*)	Lycopene	Leaf	0.0	μg g^{-1} FW	[45]
		Fruit	196.2		
	β-carotene	Leaf	14.6–23.2		
		Fruit	3.4		
	Lutein	Leaf	17.9–25.6		
		Fruit	5.0		
Potato (*Solanum tuberosum*)	Total carotenoid	Flower	78.4	μg g^{-1} DW	[47]
		Stem	17,091.1		
		Leaf	29,113.5		
		Root	14.4		
Carrot (*Daucus carota* L.)	Total carotenoid	Leaf	2880.0–8,010.0	μg g^{-1} DW	[48]
		Root	0.0–827.0		
Marigold (*Tagetes erecta*)	Lutein	Flower	22,830–63,070	μg g^{-1} DW	[50]
		Leaf	1410–1890		

DW, Dry weight; FW, Fresh weight.

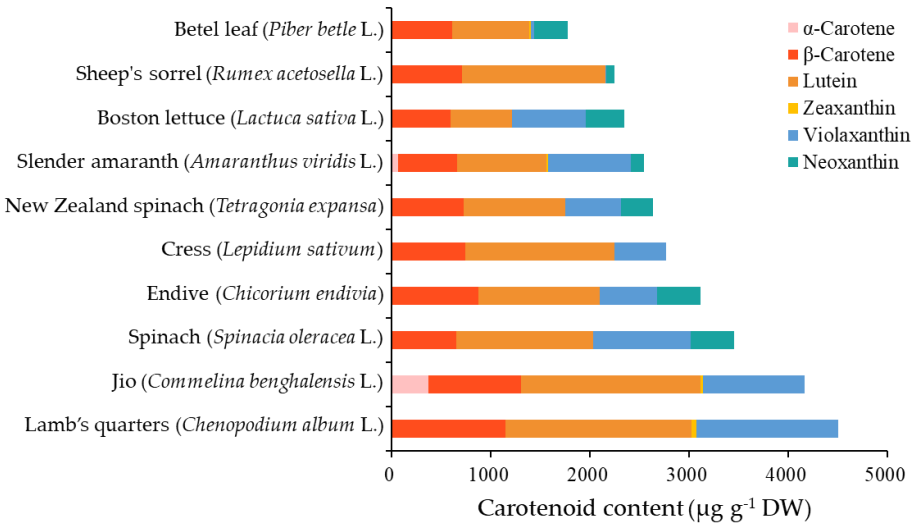


Figure 2. Carotenoid content and composition in carotenoid-abundant leafy vegetables. The content based on Supplemental Table S1 was calculated by converting fresh weight to dry weight units. This conversion was calculated based on crop-specific water content, as provided by the United States Department of Agriculture Agricultural Research Service.

4. Light-Mediated Carotenoid Accumulation in Leafy Vegetables

Recent rapid climate change has posed significant challenges to traditional agriculture by causing unpredictable weather patterns. As a result, innovative agricultural strategies beyond the conventional agricultural system are needed to ensure stable crop yields. Light is a critical factor influencing plant growth, development, and metabolic regulation. Artificial lighting technologies have proven to be essential in overcoming the limitations of sole reliance on natural light in traditional agriculture. Conventional farming is essentially dependent on natural solar radiation. However, this dependence presents significant limitations, especially in areas with frequent cloud cover, seasonal decreases in daylight hours, and other climatic constraints. To address these limitations, artificial lighting technologies have been integrated into agricultural systems to ensure optimal light conditions, independent of natural variability. Advancements in artificial lighting systems enable precise control over light spectra and intensity, allowing for highly customizable lighting strategies. Artificial lighting technologies regulate not only the visible light spectrum but also UV and near-infrared wavelengths. This spectral flexibility has facilitated the development of customized lighting environments optimized for plant growth. Moreover, the benefits of artificial lighting extend beyond fully controlled indoor agriculture to open-field agricultural systems, where supplemental lighting can not only compensate for insufficient natural light but also provide targeted spectral supplementation tailored to specific plant needs. Beyond its role in biomass accumulation, artificial light is essential for regulating plant secondary metabolism. Light quality, intensity, and exposure time significantly influence the biosynthesis of various phytochemicals, including carotenoids. Carotenoids are essential secondary metabolites that contribute to photoprotection and oxidative stress mitigation in plants while offering significant nutritional benefits to humans. Due to their functional significance, optimizing light conditions to enhance carotenoid biosynthesis is a key objective in precision agriculture. This section will discuss the accumulation of carotenoids in leafy vegetables under various light conditions, emphasizing their influence on carotenoid biosynthesis (Table 2).

Table 2. Accumulation of carotenoids in various leafy vegetables under different light conditions.

Light Wavelengths	Plant Species	Carotenoids	References
White	Komatsuna (*Brassica campestris* L.)	Total carotenoid	[51]
	Pak choi (*Brassica rapa* subsp. *chinensis*)	Total carotenoid β-carotene Lutein	[52]
	Brussels sprout (*Brassica oleracea* var. *gemmifera*)	Total carotenoid	[53]
Red	Kale (*Brassica oleracea* L.)	Lutein	[54]
	Pak choi (*Brassica rapa* subsp. *chinensis*)	Total carotenoid β-carotene Lutein	[52]
Orange	Mustard (*Brassica juncea* L.)	α-carotene β-carotene Lutein + Zeaxanthin Neoxanthin	[55]
Yellow	Mustard (*Brassica juncea* L.)	α-carotene β-carotene Neoxanthin Lutein + Zeaxanthin	[55]
	Tatsoi (*Brassica rapa* subsp. *rosularis*)	Violaxanthin	[55]
Green	Red chard (*Beta vulgaris*)	Total carotenoid	[56]
	Red pak choi (*Brassica rapa* subsp. *chinensis*)	Violaxanthin Neoxanthin	[55]
	Tatsoi (*Brassica rapa* subsp. *rosularis*)	Violaxanthin	[55]
Blue	Komatsuna (*Brassica campestris* L.)	Total carotenoid	[51]
	Lettuce (*Lactuca sativa* L)	Total carotenoid	[57–59]
	Spinach (*Spinacia oleracea* L.)	Total carotenoid β-carotene Lutein	[51,57,58]
	Kale (*Brassica oleracea* L.)	Total carotenoid β-carotene	[54,57]
	Pak choi (*Brassica rapa* subsp. *chinensis*)	Total carotenoid β-carotene Lutein	[52,60,61]
	Brussels sprout (*Brassica oleracea* var. *gemmifera*)	Total carotenoid	[53]
	Basil (*Ocimum basilicum*)	Total carotenoid	[57]
	Red chard (*Beta vulgaris*)	Total carotenoid	[56]
UV-A	Lettuce (*Lactuca sativa* L.)	Total carotenoid β-carotene Lutein	[62]
	Pak choi (*Brassica rapa* subsp. *chinensis*)	Total carotenoid	[61]
UV-B	Lettuce (*Lactuca sativa* L.)	Total carotenoid β-carotene Lutein	[62]
	Red cabbage (*Brassica oleracea* var. *capitata f. Rubra*)	Total carotenoid	[63]
	Kale (*Brassica oleracea* L.)	Total carotenoid	[64]
	Amaranth (*Amaranthus tricolor* L.)	Total carotenoid	[65]

Sunlight reaching Earth's surface is categorized into three spectral regions: UV (about 100–400 nm), visible (about 400–700 nm), and infrared (about 700–1000 nm). Infrared radiation is known to influence the photochemical activity of photosystem II during photosynthesis [66], the germination rate of seeds [67], and secondary metabolism levels [68]. In particular, far-infrared supplementation during postharvest processing has been shown to effectively preserve carotenoid levels [69]. Despite its significance, the precise mechanisms through which infrared radiation affects carotenoid accumulation and biosynthesis in leafy vegetables remain unclear. Although the effect of wavelength on carotenoid accumulation varies somewhat among species, most studies have shown that blue and UV light are particularly effective in enhancing carotenoid accumulation in various leafy vegetables. In the cases of UV application, amaranth seedlings exhibited greater carotenoid accumulation during the recovery phase after UV-B exposure than those in the untreated group [65]. Similar results were observed in experiments applying UV to red cabbage seedlings. Postharvest UV-B treatments at 10 and 15 kJ m^{-2} increased total carotenoid content by approximately 36% and 32%, respectively, compared to untreated seedlings [63]. In cases of greenhouse-grown lettuces, supplementation with UV-A and UV-AB increased carotenoid levels only of green-type lettuces [62]. In contrast, carotenoid levels in red-type lettuces decreased under supplemental UV exposure, highlighting intraspecific differences in light responses. Similarly, UV-A light significantly increased the total carotenoid content in green-type pak choi but had no effect on red-type cultivars [57]. Meanwhile, exposure to 300 μmol m^{-2} s^{-1} blue light in spinach seedlings increased total carotenoid content, including lutein, neoxanthin, violaxanthin, antheraxanthin, zeaxanthin, and β-carotene, compared to white light controls [51]. Similarly, under a red/blue (R/B) ratio of 91:9, total carotenoid content increased by approximately 1.4-fold in spinach and lettuce seedlings and by 1.6-fold in pepper seedlings compared to 100% red light treatment [57]. However, under the same conditions, kale and basil seedlings did not show significant changes in carotenoid levels. The carotenoid contents of these seedlings increased approximately 1.3- and 1.8-fold, respectively, compared to 100% red light treatment under an R/B = 83:17 wavelength composition. All seedlings used in this experiment showed a tendency for the total carotenoid content to increase when supplemented with blue light wavelengths, although there were differences depending on the species. In lettuce seedlings, treatment with a mixture of white and blue light at an intensity of 300 μmol m^{-2} s^{-1} resulted in a 6–8% increase in total carotenoid concentration compared to the white light control. This increase was associated with higher levels of xanthophylls and β-carotene [58]. Brussels sprout outer leaves subjected to postharvest mixed white and blue light treatments also exhibited significantly higher total carotenoid content than those kept in dark conditions [53]. In komatsuna seedlings, total carotenoid content was highest under white light, followed by R/B = 1:1 mixed light and blue light, with the lowest levels observed under red light alone [51]. A similar pattern was observed in red lettuce seedlings, where exposure to Light-emitting diode (LED) lighting containing blue wavelengths increased carotenoid levels compared to white light, whereas 100% red light treatment resulted in a decline in total carotenoid content [59]. These results suggest that blue light has a greater influence on carotenoid accumulation than red light. According to Mohanty et al. (2016), promoter analysis of genes responsive to blue and red light in rice leaves revealed that blue light enhances the expression of the transcription factors involved in carotenoid biosynthesis. Additionally, blue light was found to be associated with hormonal pathways related to carotenoid accumulation, including gibberellin (GA) and abscisic acid (ABA) signaling [32]. In contrast, red light influenced GA biosynthesis pathways but did not activate HY5 as effectively as blue light. Interactions between light signaling and hormonal pathways have also been observed under UV-B conditions. UV-B signaling suppresses GA biosynthesis,

leading to the accumulation of DELLA proteins, which are known regulators of HY5 and PIF activity [70]. In addition, UV-B induces ABA accumulation, which is known to play an important role in the defense mechanism against UV-B stress. These findings indicate that carotenoid biosynthesis is not simply a product of light signaling, but rather involves a complex mechanism connected to hormonal signals. Furthermore, both blue and UV light share a common ability to induce oxidative stress within plant cells, activating antioxidant mechanisms as a protective response [71,72]. Carotenoids are structurally well-suited for scavenging ROS generated by oxidative stress [73]. Stress-induced carotenoid synthesis alleviates the negative impacts of stress and enhances the plant's ability to adapt to environmental challenges. Carotenoid accumulation induced by blue light and UV goes beyond simple pigment changes, functioning as a key physiological strategy for plants to protect themselves from photo-oxidative stress and adapt to fluctuating conditions.

Besides blue and UV light, other wavelengths may also influence carotenoid accumulation. In komatsuna leaves, white light resulted in higher total carotenoid content compared to mixed light conditions [51], suggesting that certain wavelengths beyond red and blue may contribute to carotenoid biosynthesis. Similarly, red chard treated with green light during storage exhibited carotenoid levels comparable to those observed under blue light [56], suggesting that green light may play a more prominent role in carotenoid metabolism than previously thought. Further evidence supporting the influence of additional wavelengths comes from studies on Brassicaceae microgreens, where carotenoid accumulation was affected by exposure to supplemental green, yellow, and orange light, with species-specific variations observed [55]. In mustard microgreens, the addition of these wavelengths to standard lighting set increased total carotenoids as well as α-carotene, β-carotene, lutein + zeaxanthin, and neoxanthin levels. However, in red pak choi microgreens, all supplemental light treatments led to a decrease in total carotenoid content, with neoxanthin and violaxanthin being the only exceptions, showing an increase under green light supplementation. Moreover, in tatsoi microgreens, total carotenoid content increased exclusively under supplemental yellow light, while violaxanthin levels were significantly enhanced across all treatments. These findings suggest that green, yellow, and orange light may influence carotenoid metabolism; however, they also underscore the complexity of species-specific and carotenoid-specific responses. Additionally, pak choi exposed to monochromatic blue LEDs showed higher expression levels of carotenoid biosynthetic genes compared to white and monochromatic red LEDs; however, the overall carotenoid contents were lower than observed under white LEDs and similar to the levels observed under red LEDs [52]. In subsequent experiments, combining blue and white light significantly increased lutein and β-carotene levels compared to white light alone or mixed red–white light [60]. According to [60], the authors suggested that wavelengths beyond blue may influence carotenoid biosynthesis at the post-transcriptional level. While the precise mechanisms remain unclear, these findings highlight the need for further studies on the interaction among different light spectra. In summary, optimizing carotenoid accumulation demands a strategic lighting approach that accounts for species-specific responses and pigment composition. Blue and UV light are well-established as primary regulators of carotenoid biosynthesis across various plant species, with particularly pronounced effects in green-type crops. Beyond direct light signaling, carotenoid accumulation mediated by blue and UV light is closely linked to hormonal pathways. This regulation plays a crucial role in ROS scavenging and antioxidant responses, enabling plants to mitigate stress conditions. Furthermore, considering the positive effects of other wavelengths on carotenoid accumulation, an optimized light combination strategy which exploits the synergistic effects of multiple spectra is essential. In particular, as supplemental green, yellow, and orange light have been suggested to regulate carotenoid accumulation in specific crops,

further research is needed to establish an optimal lighting environment that accounts for the interactions among different light spectra.

Light intensity also influences ROS-mediated antioxidant activity, including carotenoid accumulation, similarly to light wavelength. For instance, excessive light intensity exceeding the level required for photosynthesis can cause photoinhibition, leading to ROS accumulation [74]. ROS act as signaling molecules that regulate secondary metabolite accumulation, including carotenoid biosynthesis. A well-known example of ROS-mediated carotenoid regulation is the xanthophyll cycle, which plays a key role in protecting the photosynthetic apparatus under high light conditions [23]. This cycle is activated in response to excessive light energy, dissipating it as heat through non-photochemical quenching. During this process, the interconversion of violaxanthin to zeaxanthin is promoted, while the activity of zeaxanthin epoxidase is suppressed. Additionally, the accumulation of hydrogen peroxide, a type of ROS, has been shown to contribute to this suppression [75]. Given these findings, optimizing light conditions for leafy vegetables is crucial for balancing carotenoid accumulation and photoprotection. The light conditions for leafy vegetables need to be carefully considered. While adequate light intensity is essential for promoting carotenoid accumulation, excessive light can have a negative effect on accumulation levels. For example, spinach seedlings exhibited higher carotenoid content under high light intensity (300 μmol m^{-2} s^{-1}) compared to low light intensity (100 μmol m^{-2} s^{-1}), and this trend was consistent across different light spectra [76]. Similarly, red pak choi and tatsoi seedlings exhibited significantly higher total carotenoid content at light intensities of 330–440 μmol m^{-2} s^{-1} compared to 110–220 μmol m^{-2} s^{-1} [55]. However, high intensity light has been reported to decrease endogenous carotenoid levels, suggesting photoinhibition of secondary metabolites by light conditions [77]. As reported by Brazaitytė et al. (2015) [55], light intensities above 330–440 μmol m^{-2} s^{-1} (545 μmol m^{-2} s^{-1}) negatively impacted the total carotenoid content in all *Brassicaceae* microgreens. High light intensity (463 μmol m^{-2} s^{-1}) also significantly reduced most carotenoid levels in mustard microgreens, except for zeaxanthin, relative to lower light intensity (275 μmol m^{-2} s^{-1}) [78]. Additionally, light exposure time could contribute to regulating carotenoid accumulation in a similar way as light intensity. This is because both the quantitative aspect of light (intensity) and the temporal aspect (exposure time) interact to influence plant light responses [79]. For example, a 6 h exposure to UV-B at 3 W m^{-2} significantly enhanced total carotenoid levels in kale compared to the non-treatment, whereas a 12 h exposure resulted in a decline [64]. Under identical daily light integral conditions, lettuce exhibited higher carotenoid content with 16 h of light exposure compared to 12 h, whereas 20 h of exposure resulted in intermediate carotenoid levels [80]. As these studies show, light conditions do not simply act as independent variables but rather act in a complex way to affect carotenoid metabolism. It is also important to note that the effects of these light conditions can vary greatly depending on the growth stage of the plant. Growth stages play a crucial role in determining how plants respond to light conditions, their ability to regulate ROS, and the extent to which they accumulate secondary metabolites (e.g., carotenoids) [81,82]. Plant leaves undergo significant changes in photochemical composition, hormone levels, and nutrient sink–source balance in response to internal and external factors during the aging process, including development and senescence [83]. These processes play an important role in determining how plants respond to future stress by influencing antioxidant mechanisms, stress signaling, and nutrient redistribution. Jung (2004) reported that the degree of leaf development is an important determinant of the antioxidant response to secondary photo-oxidative stress [84]. Superoxide dismutase, a key antioxidant enzyme in barley leaves, was activated under light stress caused by high intensity; however, the enzyme activity decreased with leaf aging [85]. Moreover, the accumulation of secondary metabo-

lites in pak choi sprouts were influenced by interactions between the development stage and UV-B treatment [86]. These results indicate growth stages and light conditions do not act as independent factors, but rather interact in a complex manner to affect carotenoid accumulation. Despite extensive research on carotenoid accumulation under different light conditions, few studies have systematically analyzed the interaction between light environment and developmental stage in a comprehensive manner. Current data offer insights into specific conditions but have limitations in deriving optimal light conditions or explaining differences in plant responses to light conditions across different growth stages. For example, in spinach, blue light is recognized for enhancing carotenoid accumulation, with a light intensity of 300 μmol m^{-2} s^{-1} proving more effective than 100 μmol m^{-2} s^{-1}. However, the precise optimal intensity range remains unclear. Additionally, its effects on carotenoid accumulation across various developmental stages require further investigation. Similarly, blue light has been shown to enhance carotenoid accumulation in lettuce cultivation; however, studies on the optimal wavelength composition and intensity of blue light for lettuce cultivation remain limited, even with UV treatment. For practical agricultural applications, understanding the complex interaction between light conditions and growth stage is crucial for optimizing crop quality [81]. In this context, there is a growing need for modeling studies that comprehensively analyze crop growth stages and light environmental factors. To optimize carotenoid accumulation, selecting the appropriate light wavelength, intensity, and exposure time is essential for eliciting a beneficial stress response. Given that stress sensitivity differs by maturation stage, it is essential to conduct evaluations across multiple growth stages. This enables a more comprehensive understanding of factor interactions beyond the assessment of individual variables and provides essential insights for refining crop quality management strategies.

5. Conclusions

The nutritional benefits of carotenoids have increased consumer demand for carotenoid-rich crops. Leafy vegetables, in which β-carotene and lutein are abundant, are important resources in agricultural research. The photoregulatory mechanisms of carotenoid metabolism have been extensively studied in model plants and are briefly summarized in this review. Light is a key environmental factor that is transmitted through the light signaling pathway, which consists of photoreceptors and transcription factors, to trigger a series of photomorphogenesis events, including carotenoid metabolism. Genetic regulation studies of light signaling pathways have provided important clues for carotenoid metabolic engineering studies. It has been revealed that pathway components are conserved in various crops [87,88], suggesting that the light mechanism may be widely applicable to various plant species.

Carotenoids not only play an auxiliary role in light harvesting during photosynthesis but also help mitigate photo-oxidative damage by dissipating light energy and scavenging ROS under light stress conditions. These functional characteristics suggest that specific light conditions may regulate carotenoid biosynthetic pathways. Most studies show that blue and UV light are particularly effective in promoting carotenoid accumulation in leafy vegetables during both cultivation and postharvest storage. These wavelengths not only induce photo-oxidative stress but also activate antioxidant mechanisms [89,90].

In addition to wavelength, light intensity and exposure time influence carotenoid metabolism as quantitative factors. While an adequate light level is essential for carotenoid accumulation, excessive light exposure can be detrimental, leading to reduced carotenoid levels [77]. This reduction may result from excessive ROS production [91]. These findings suggest that carotenoid accumulation may be regulated by a combination of light wavelength, intensity, and exposure time, which interact through interdependent mechanisms.

Additionally, the growth and developmental stage of leaves plays a crucial role in modulating light-mediated carotenoid biosynthesis. Different developmental stages exhibit varying sensitivities to light-induced regulatory mechanisms, which necessitates an integrative approach that considers both light conditions and leaf growth stage. Despite this complexity, most existing studies primarily focus on analyzing carotenoid accumulation under specific light conditions or growth stages in controlled environments. While such studies provide valuable insights, their limited scope restricts their practical applications in agriculture. Therefore, a comprehensive approach that integrates multiple variables will guide practical light management for producing high-value leafy vegetables with enhanced carotenoid content.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/horticulturae11020152/s1, Table S1: Carotenoid content in various leafy vegetables.

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Abbreviations

The following abbreviations are used in this manuscript:

ABA	Abscisic acid
COP1/SPA	CONSTITUTIVELY PHOTOMORPHOGENIC 1/SUPPRESSOR OF PHYA-105
CRY	Cryptochrome
GA	Gibberellin
GGPP	Geranylgeranyl diphosphate
HY5	ELONGATED HYPOCOTYL 5
LED	Light-emitting diode
MEP	Methylerythritol phosphate
PAR1	PHYTOCHROME RAPIDLY REGULATED 1
PHOT	Phototropin
PIF	PHYTOCHROME-INTERACTING FACTOR
PHY	Phytochrome
PSY	Phytoene synthase
ROS	Reactive oxygen species
UV	Ultraviolet
UVR8	UV-B resistance 8

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