



**REVIEW**

# Light Regulation across Strawberry Growth Stages: A Comprehensive Review

Geng Zhang<sup>1</sup>, Xiangyu Ding<sup>2</sup>, Zidan Wen<sup>2</sup>, Chao Liu<sup>2</sup>, Duyen T. P. Nguyen<sup>3</sup>, Jinxiu Song<sup>4</sup>,  
Zejin Zhang<sup>5</sup>, Zhiming Yan<sup>1,6</sup>, Yuanhua Wang<sup>1,\*</sup> and Zhengnan Yan<sup>2,\*</sup>

<sup>1</sup>Department of Agronomy and Horticulture, Jiangsu Vocational College of Agriculture and Forestry, Jurong, China

<sup>2</sup>College of Horticulture, Qingdao Agricultural University, Qingdao, China

<sup>3</sup>Center for Environment, Health and Field Sciences, Chiba University, Kashiwa, Japan

<sup>4</sup>College of Agricultural Engineering, Jiangsu University, Zhenjiang, China

<sup>5</sup>Horticulture Research Institute, Sichuan Academy of Agricultural Science, Chengdu, China

<sup>6</sup>Jiangsu Engineering and Technology Center for Modern Horticulture, Zhenjiang, China

\*Corresponding Authors: Yuanhua Wang. Email: wangyuanhua@jsafc.edu.cn; Zhengnan Yan. Email: yanzn@qau.edu.cn

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**ABSTRACT:** As a pivotal environmental factor, light, comprising intensity, photoperiod, and spectrum, governs the entire life cycle of strawberries by mediating alterations in the plant's morphological, physiological, and biochemical traits. Although extensive research has been conducted on light-mediated growth regulation in horticultural crops, most reviews focus primarily on leafy and fruiting vegetables, with limited attention given to berry crops such as strawberries. Additionally, most existing reviews concentrate on one or several growth stages, failing to systematically characterize light's effects throughout the entire growth cycle and postharvest stage. This review briefly summarizes the regulatory roles of light across key stages of strawberry growth, including seedling propagation, vegetative growth, reproductive growth, and postharvest stages. It seeks to address the knowledge gap by systematically organizing research findings across these developmental phases. The integrated analysis provides a theoretical foundation for designing stage-specific lighting strategies to improve strawberry yield and quality.

**KEYWORDS:** Light intensity; light spectrum; strawberry; seedling propagation; vegetative growth; reproductive growth; postharvest

## 1 Introduction

Light, through its spectral composition, light intensity, and photoperiod, governs fundamental processes in plant growth and development, from seed germination to morphogenesis photosynthetic characteristics, physiological metabolism, reproductive activity, and ultimately yield and quality [1]. With the rapid development of modern agriculture, there is increasing emphasis on regulating the photic environment to optimize plant growth. Considering the challenges in precisely controlling natural daylight, the application of artificial light sources to tailor the light environment has become a common practice [2].

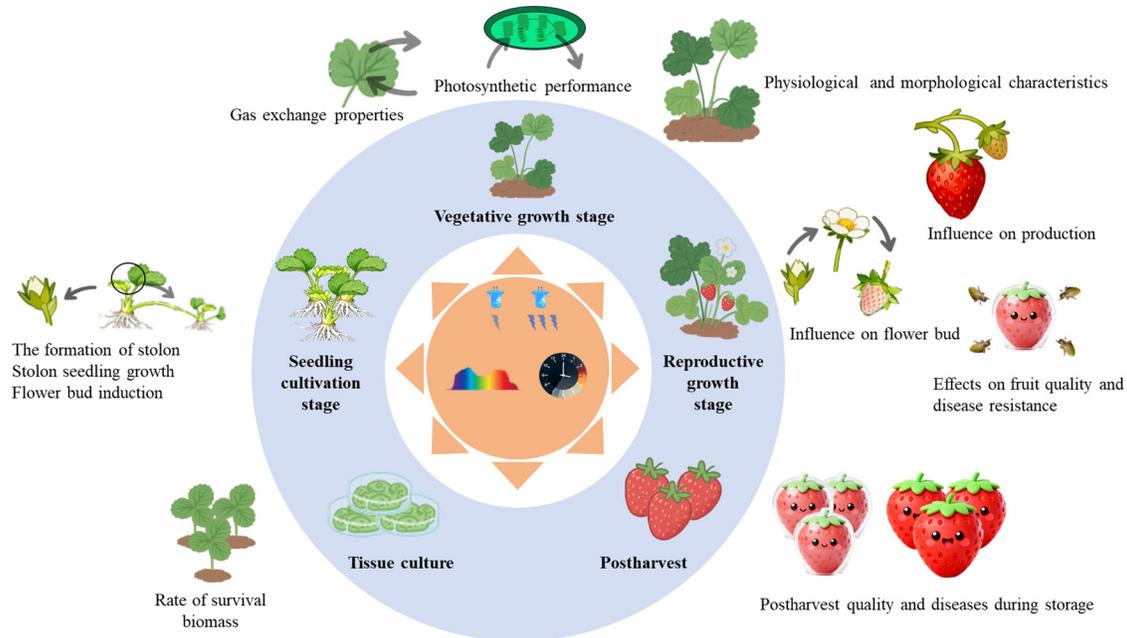
Conventional light sources, including have several drawbacks, such as non-tunable spectral characteristics, high thermal radiation, and inconsistent light intensity [3,4] In contrast, light-emitting diodes (LEDs) offer advantages such as narrow bandwidth, low energy consumption, high photoelectric efficiency, minimal thermal output, compact size, enabling precise manipulation of spectral characteristics, luminous intensity, and photoperiod [5]. This has facilitated the widespread application of LEDs across various agricultural fields [6–8]. Statistical data indicate that the LED lighting industry is geographically

concentrated in Europe and North America [9]. The United States, China, and Canada collectively supply nearly half of all LED grow lights globally, while production in Europe is more evenly distributed among countries [9].

In higher plants, chlorophylls, carotenoids, and anthocyanins serve as the three primary light-absorbing pigments [10]. Red and blue light are most effective in driving photosynthesis, as chlorophylls exhibit maximal absorption within these spectral ranges [11]. Nevertheless, other wavelengths, including green, far-red, and moderate-intensity ultraviolet (UV) light, also significantly influence plant growth [3]. For instance, green light can penetrate leaves more deeply [12], and increase anthocyanin [13] and chlorophyll [14] concentrations while reducing nitrate content in plants [15]. Far-red light can enhance the photosynthetic rate [16], but may decrease anthocyanins [17] and carotenoids [18] levels in some plant species. UV light can benefit postharvest quality [19] and enhance antioxidant levels [20]. A novel study has demonstrated for the first time that manipulating light quality with LED lights can increase the inhibitory activity of strawberry fruit extracts against digestive enzymes, thereby enhancing the functional properties of the fruit [21]. Beyond light quality, light intensity and photoperiod also critically affect plant growth. The suitable light environment for plant growth varies among species and cultivars, necessitating tailored strategies for maximum yield and optimal quality.

Strawberry (*Fragaria × ananassa* Duch.) is a common and valuable crop cultivated worldwide. Strawberry fruits are abundant in fiber, vitamins, micronutrients, and flavonoids [22], offering significant health benefits. Over the past decade, global strawberry cultivation area and yield have grown substantially, reaching approximately 0.435 million hectares and 10.49 million tonnes in 2023, respectively (FAOSTAT). The compact plant architecture, short fruit development cycle, and high genetic transformation efficiency also make strawberries a model species for fruit crop research [23,24]. However, strawberry production and nutritional quality are highly sensitive to environmental conditions [25] and vulnerable to multiple fungal pathogens, including *Botrytis cinerea*, *Podosphaera aphanis*, and *Colletotrichum* spp. [26–28].

Several reviews have summarized progress in areas like flower initiation and secondary metabolite accumulation [25,29,30], while few have focused on the effects of light across the entire strawberry lifecycle, from seedling propagation to postharvest storage. This review therefore aims to fill this gap by providing a holistic synthesis of the effects of light spectrum (Table 1), photoperiod (Table 2), and light intensity (Table 3) on strawberries across four key developmental stages: (1) seedling propagation, (2) vegetative growth, (3) reproductive growth, and (4) postharvest period (Fig. 1). By providing systematic information on the stage-specific light regulations on the growth and development of strawberries, our work offers valuable theoretical guidance for optimizing strawberry production.



**Figure 1:** Overview of the effects of light on morphological traits, photosynthetic performance, and quality preservation of strawberry at different growth stages.

## 2 The Role of Light during the Seedling Propagation

### 2.1 Impact of Light on Strawberry Plantlets in Tissue Culture

Light is a critical environmental factor influencing the growth of strawberry plantlets *in vitro*. Studies show that light quality regulates the growth of strawberry tissue-cultured seedlings. For instance, red and green plastic films (the films were used specifically to create defined spectra) promoted the highest shoot regeneration, accompanied by elevated chlorophyll b levels and antioxidant enzyme activities [31]. During the *in vitro* multiplication of ‘Sabrosa’ strawberries, red and green LEDs enhanced shoot multiplication [32]. Experiments on multiple cultivars using colored cellophane filters observed that red and green light promote adventitious bud regeneration and shoot proliferation, while blue and yellow light enhanced total chlorophyll content [33]. For various cultivars like ‘Akihime’ and ‘Camarosa’, mixtures of red and blue LEDs have been found optimal for plantlet growth [34,35]. Current research on light in strawberry tissue culture focuses on quality, showing red light consistently promoting optimal growth and development across monochromatic and mixed light regimes.

### 2.2 Role of Light in Cultivating Vigorous Strawberry Transplants

#### 2.2.1 Photosynthesis and Biomass

Light directly regulates photosynthesis, the energy source for plants [36]. During the nursery phase of strawberry plants, red light (660 nm) induced higher net photosynthetic rates compared to blue light (450 nm) [37]. Combinations of blue and red LEDs (ratio of 1:6) plus 100 mg L<sup>-1</sup> of nitrogen enhanced photosynthesis and transpiration in ‘Praratchatan 80’, leading to high fruit yield [38]. In ‘Albion’, increases in photosynthetic photon flux density (PPFD) resulted in significant enhancements in plant growth parameters like crown diameter and biomass [39]. Supplementing red and blue light with far-red light also increased leaf area and shoot dry mass of ‘Monterey’ [40].

### 2.2.2 Runner Formation and Runner Plant Growth

Indoor cultivation with artificial lighting enables high-quality, year-round strawberry production with enhanced yield and consistency [41,42]. Artificial lighting during transplant production enhances runner formation and subsequent plantlet growth [43]. For example, in 'Maehyang', elevated light intensity significantly enhanced runner formation and runner plant growth under fluorescent lighting [44]. In 'Albion', the number, dry mass, and fresh mass of daughter plants were found to increase with light intensity rising from  $250 \mu\text{mol m}^{-2} \text{s}^{-1}$  to  $450 \mu\text{mol m}^{-2} \text{s}^{-1}$  [45]. For 'Benihoppe', elevating light intensity from 90 to  $270 \mu\text{mol m}^{-2} \text{s}^{-1}$  increased crown diameter, shoot dry weight, root dry weight, and root to shoot ratio [43]. Applying high light to stock plants, rather than runners, more effectively enhanced runner growth, providing a new strategy for strawberry propagation [41]. Photoperiod is another critical factor regulating runner formation and elongation in strawberries. In several strawberry cultivars, including 'Natsuakari', 'Camarosa', and 'Camaroga', extended photoperiods have been shown to enhance runner production, elongation, and plantlet formation [46,47]. These effects may be attributed to photoperiodic effects on epidermal cell length and number [48]. However, no significant differences were detected in the number of primary runners, secondary runners, and total runners of strawberry plants subjected to a photoperiod extended from 12 to  $16 \text{ h d}^{-1}$ ; in contrast, runner length was significantly shorter under the  $16 \text{ h d}^{-1}$  photoperiod [43]. Spectral composition also modulates strawberry seedling growth. Full-spectrum LEDs (e.g., white LEDs) are increasingly used in controlled environments. Advances in LED chip technology have made diverse white LEDs (e.g., warm, neutral, cool, and mint-white) with distinct spectra commercially available [49]. Mint-white LEDs, with high efficacy in photosynthesis, enhanced runner formation and vegetative growth of 'Maehyang' strawberry in controlled environments [50]. Supplementing mint-white LEDs with optimal blue wavelengths improved growth in both stock plants and runner offspring [51]. White LEDs promoted dry mass accumulation in 'Akihime' strawberry runners, whereas adding green light to red-blue LED combinations boosted runner plant formation and proliferation [52].

Interactions among light parameters further illustrate the critical impact of light regimes on strawberry seedling development. Daily light integral (DLI), determined by light intensity and photoperiod was shown in 'Benihoppe' strawberries to suppress runner elongation and reduce photosynthetic capacity under high DLI conditions [43]. For 'Sulhyang',  $20 \mu\text{mol m}^{-2} \text{s}^{-1}$  blue light maximized runner formation irrespective of photoperiod (long-day/short-day) or supplemental lighting strategy [53]. Blue light under non-runnering short-day conditions upregulated key gibberellin pathway genes, potentially triggering runner formation. Furthermore, photoperiod beyond 16 h or night interruption lighting with various wavelengths enhanced runner induction in 'Sulhyang' and 'Maehyang' [54]. A novel side lighting strategy also improved morphophysiological traits and runner formation by stimulating photosynthesis in cuttings, offering a cost-effective approach for strawberry propagation in closed cultivation systems [42].

### 2.2.3 Flower Bud Induction

Flower bud induction is a critical step during the seedling stage. Low-intensity red light irradiation during cold storage could maintain chlorophyll and carbohydrate levels in 'Nyoho' strawberry seedlings [55]. Similarly, the accumulation of carbohydrates and the ratio of photosynthetic pigments were enhanced under mixed red and blue LEDs in cold-stored 'Elkat' [56]. A high far-red/red light ratio promoted floral bud induction [57,58], likely by inactivating phytochrome B and activating the photoperiodic flowering pathway [59]. Both far-red and blue light accelerate floral induction in multiple strawberry cultivars [60,61]. Extended photoperiods supplemented with far-red light also promoted flower bud development [62]. However, a study conducted by Sidhu et al. [63] demonstrated that photoperiod conditioning exerted no

significant effects on the flower stalk development and bud induction of strawberry plants. Crucially, there is a strong interaction between temperature and photoperiod during floral induction. High temperatures inhibit strawberry flowering and bud development [64], and seedling age affects induction [65].

### 3 The Effects of Light during the Vegetative Growth Period

#### 3.1 *Photosynthetic Characteristics*

##### 3.1.1 *Photosynthetic Pigment Content*

Studies on cultivars such as ‘Elsanta’, ‘Akihime’, and ‘Daewang’ generally report higher chlorophyll levels under red light than blue light, potentially due to blue light-induced suppression of chlorophyll b synthesis [66–68]. Compared to monochromatic light, broad-spectrum or mixed red-blue light often enhances chlorophyll content, while the influence is cultivar-specific [28,69]. Monochromatic blue light or a higher proportion of blue light generally promotes an increase in the chlorophyll a/b ratio [67,68]. Carotenoid content has been reported to decline under blue light relative to red light in some strawberry cultivars [67,68], red and blue light combinations can elevate it [70]. Studies have indicated that blue and red light can enhance the expression of genes encoding enzymes related to carotenoid pigments [71].

##### 3.1.2 *Gas Exchange Characteristics*

Blue light or cool white lamps (with higher blue light proportion) have been reported to enhance photosynthetic rates and stomatal conductance in strawberry plants [72–74], likely due to modifications in leaf biochemistry and enhanced stomatal conductance [74,75]. An optimal blue to red light ratio (e.g., 1:6) can exhibit the highest photosynthetic and transpiration rates due to synergistic interactions [38,76]. Green light also benefits plant growth and physiology [77]. A combination of 20% green, 20% blue, and 60% red light enhanced net photosynthesis, transpiration rate, and stomatal conductance in strawberry plants, but exceeding 20% green light reduced these parameters [78]. Plant gas exchange characteristics of strawberry plants are also influenced by leaf age and the orientation of light exposure [79].

##### 3.1.3 *Chlorophyll Fluorescence Parameters*

Blue LED morning supplementation enhanced the maximum quantum efficiency of PSII in ‘Maehyang’ and ‘Seolhyang’ [73]. In ‘Daeselect’, the effective quantum yield of PSII photochemistry  $Y(II)$ , photochemical quenching coefficient, and electron transport rate were optimized under 250  $\mu\text{mol m}^{-2} \text{s}^{-1}$  supplemental LED light (50% red, 20% green, and 30% blue) with a 12 h photoperiod [70]. In ‘Benihoppe’, shading reduced leaf minimal fluorescence, while red/blue LED light elevated it [80]. Red film enhanced photosynthesis in ‘Akihime’ by elevating photosynthetic pigment content, quantum yield, electron transfer efficiency, reaction center density [68].

#### 3.2 *Physiological Traits*

Essential nutrients regulate plant growth, influenced by species, stage, and environment. Blue and red light promote mineral accumulation, but responses are differential and cultivar-specific [69,81]. For example, in ‘Toyonoka’, leaf iron and magnesium levels were higher under a high red:blue ratio [82], while potassium decreased under a low red:blue ratio. In ‘Praratchatan 80’, leaf nitrogen peaked under 3:1 red:blue LED, while potassium content increased with higher red-light ratios [38]. Green light can also impact leaf nutrient status in strawberries. For instance, a high proportion (27%) resulted in elevated calcium, potassium, and phosphorus [78], possibly attributed to increased root biomass. Moreover, blue

morning light best boosted strawberry carbohydrates [73]. Supplemental lighting with distinct spectral compositions also modulates antioxidant enzyme activities and oxidative stress markers. In ‘Elsanta’, red light has been shown to enhance antioxidant enzyme activity but also increase levels of hydrogen peroxide and malondialdehyde [83].

### **3.3 Biomass and Morphological Indices**

Crop yield generally responds positively to increased PPFD, photoperiod, and DLI. Total plant dry weight in ‘Toyonok’ and ‘Fukuoka S6’ increased with PPFD elevation [82,84]. ‘Albion’ strawberry exhibited linear biomass gains as PPFD rose, and root biomass increased with photoperiod extension [39]. For ‘HS138’, dry matter accumulation was greater under high DLI [85]. Far-red light addition to red and blue light combinations increased shoot fresh and dry weights in ‘Monterey’, whereas no significant effects on ‘Albion’ [40]. Appropriate combinations of red and blue light enhanced biomass in various cultivars such as ‘Toyonoka’, ‘Darselect’, and ‘Albion’ [70,78,82,86].

Morphological characteristics of strawberry plants are also influenced by light. Supplemental lighting enhanced leaf area in ‘Clery’, ‘San Andreas’, ‘Albion’ and ‘Sabrina’ [87,88]. In ‘Monterey’, the addition of far-red light to red-blue light combinations resulted in an increase in leaf area [40]. Studies conducted on ‘Akihime’ revealed increased petiole length and leaf area when plants were grown under red plastic film [68]. Supplemental LED lighting also increased the specific leaf weight [89], which reflects leaf thickening and is likely driven by the accumulation of photosynthetic assimilation products.

### **3.4 Light-Mediated Enhancement of Strawberry Resilience to Stress**

#### **3.4.1 Biotic Stress Resistance**

Plant diseases markedly curtail agricultural productivity, especially for high-value edible fruit crops such as strawberries. Light is a key regulator of plant-pathogen interactions [67,90]. A low red: far-red ratio can suppress immunity, while red light enhances biotic stress tolerance [91–93]. In strawberries, specific red light regimens significantly boost leaf resistance to *B. cinerea* [94,95], correlating with the induction of antioxidant systems and defense pathways [67,83]. In contrast, blue light appears to exert a more direct inhibitory effect on *B. cinerea* infection [94]. Strawberry responsiveness to *B. cinerea* is under circadian control [95], and correlates with leaf developmental stage [67]. This age-dependent resistance pattern may associate with differential levels of hydrogen peroxide, chlorophyll, and carotenoids across leaf ages. UV light, particularly UV-C, has been shown to modulate susceptibility to *B. cinerea* and *Colletotrichum* in a cultivar-dependent manner [96–99]. UV-C-induced pathogen resistance may involve enhanced biosynthesis of secondary metabolites, increased defense-related enzyme activity, and accumulation of phenolic compounds [98–100]. Beyond UV-C, UV-B irradiation has also been documented to enhance plant disease resistance against pathogens (e.g., *Colletotrichum* spp.) [28,101]. These findings position light as an eco-friendly alternative to pesticides for controlling strawberry diseases. However, further optimization for specific pathogens and cultivars is needed.

#### **3.4.2 Abiotic Stress Resistance**

Strawberry is highly sensitive to salinity and alkalinity [102]. Recent research indicates that light radiation can effectively mitigate abiotic stresses like salinity and alkalinity [103,104]. In ‘Sabrina’, under salinity and alkalinity stress, combined blue and red LED treatments enhanced leaf chlorophyll content and improved the efficiency of the photosynthetic apparatus [102], which is likely due to the upregulation of key genes encoding enzymes involved in chlorophyll biosynthesis [105]. Studies on ‘Camarosa’ strawberry

demonstrated that combined blue and red light significantly increased leaf area under salinity and alkalinity stress [106]. In ‘Sabrina’, blue, red, and combined light spectra enhanced mineral content, phenolics, antioxidants, and crown starch, thereby likely improving stress tolerance to salinity and alkalinity [107]. Regulating light regimes enhances stress resistance, yet the effects of light intensity and photoperiod warrant further investigation.

## 4 The Influence of Light during the Reproductive Growth Period

### 4.1 Effect of Light on Strawberry Flowering

Strawberry flowering is regulated by genotype and environmental factors [108,109]. Strawberries are primarily categorized into seasonal (short-day) and perpetual (long-day or day-neutral) flowering types based on their photoperiodic responses and cropping season [110]. In seasonal flowering cultivars, flower bud initiation, which marks the transition from vegetative to reproductive growth, is typically induced under low temperatures (15–25°C) and short-day conditions (10–12 h of daylight) [111]. In contrast, perpetual flowering types initiate flower buds under long-day conditions (>12 h of daylight) or independently of day length (day-neutral), enabling continuous fruit production under suitable temperatures [111]. A previous study reported by Muñoz-Avila et al. [112] demonstrated conserved function of the MADS-box transcription factor FaSOC1 as a potent flowering repressor in woodland and cultivated strawberries, and its key role in photoperiodic repression of FLOWERING LOCUS T (FT) genes *FaFT2/FaFT3*—with *FaTFL1* upregulation less prominent than in the woodland strawberry. Limitations of outdoor cultivation are prompting a shift to controlled environments, which improve stability and efficiency, including through supplemental or sole-source LED lighting [40]. For example, supplementing with 13 h of combined red and blue LEDs commencing 1 h before sunset in greenhouses increased flowering up to a 300% [113]. Under monochromatic supplementary light, blue LEDs produced the highest number of flower clusters, while red LEDs produced the fewest [113], potentially due to differential effects on hormone levels [114]. Within mixed red-blue spectra, higher red light proportions can promote inflorescence initiation in some cultivars such as ‘Albion’ and ‘Praratchatan 80’ [38,86]. This effect may be attributed to red light enhancing sugar synthesis and nutrient allocation while blue light accelerates flowering through photoperiodic signaling and increased carbohydrate availability [115,116], achieving an optimal balance between vegetative and reproductive growth. Furthermore, supplementing a red-blue background lighting with far-red light reduced the time to first harvest in some long-day strawberry cultivars like ‘Albion’ [40]. Light intensity and photoperiod are also crucial. Reduced light intensity during flowering can induce stamen abortion [117], while elevated light intensity accelerates flowering and promotes uniformity [109,118]. In ‘Albion’, extending the photoperiod from 12 to 16 h under relatively high light intensity (PPFD  $\geq 300 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) accelerated flowering [39], likely attributable to increased carbohydrate accumulation in the crown and roots, a process that supports floral initiation [119,120]. To maximize profits, achieving early, uniform, and stable flowering through light environment regulation is essential in strawberry production, as it ensures timely harvests and efficient management.

### 4.2 Effect of Light on Strawberry Yield

Studies on ‘Elsanta’ strawberries demonstrated that blue LED light enhanced fruit set and final yield compared to red LEDs or fluorescent lamps [121]. For ‘Albion’, a light spectrum comprising 20% green, 20% blue, and 60% red light achieved high fruit yield, but increasing green light beyond 20% reduced productivity [78]. This phenomenon may be attributable to the higher crown biomass observed under the 20% green light regime, consistent with previous findings correlating larger crown size with increased

yield [122]. Similarly, another study reported that optimal yields under a spectrum of 20% green, 30% blue, and 50% red light were achieved at a PPFD of  $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ , whereas lower intensities reduced yield despite the inclusion of green light [70]. For 'Akihime', red-transmitting film achieved superior fruit weight, suggesting excellent cultivation suitability [68]. Furthermore, light directly regulates photosynthetic processes in plants. LED supplemental lighting boosts strawberry fruit weight, number, and marketable yield across cultivars through enhanced photosynthesis and carbohydrate accumulation that drives fruit development [21,69,123,124]. Notably, supplemental lighting generally exhibits more pronounced effects during the winter season under cloudy weather and low solar radiation conditions [125]. However, once solar radiation exceeds a critical threshold, supplemental lighting shows reduced effectiveness and diminished economic viability.

#### 4.3 Effect of Light on Strawberry Fruit Quality

Anthocyanins are ubiquitous, vital secondary metabolites that contribute to fruit coloration in a wide range of higher plants [126,127]. Blue, red, and far-red light have been shown to enhance anthocyanin accumulation in fruits [21,128]. Similarly, wavelength-selective plastic films (e.g., red or yellow filters) and light-conversion films (which convert ultraviolet to blue light) also demonstrate that light quality regulates anthocyanin content in strawberry fruits [68,74,126]. Research has indicated that light quality affects anthocyanin accumulation in strawberries by regulating genes (e.g., *PHOT2*, *LAR*, *ANR*, *MYBs*, *bHLHs*) associated with anthocyanin biosynthesis and/or modifying enzyme activities [68,129]. UV light exposure during the nighttime cultivation period also increases anthocyanin content [128,130].

Hardness is a critical parameter for evaluating fruit quality, as it serves as an indicator of the maturation stage [131]. Supplemental lighting like red, blue, and white light combination can reduce strawberry firmness, thereby accelerating ripening [131]. However, some studies indicate that preharvest UV irradiation enhances strawberry firmness and extends shelf life [132,133], possibly by downregulating the transcription of genes associated with cell-wall degradation [134].

The rich nutritional value is one of the reasons why strawberries are preferred by consumers. Exposure to UV light during the cultivation of strawberries has been demonstrated to enhance the content of ascorbic acid and ellagic acid in the fruits [130]. Similarly, another study reported that illumination using LED lights comprising red, blue, and green wavelengths led to an increase in ascorbic acid levels, with direct irradiation of the fruits being more effective than irradiation of the leaves [135]. Light quality also influences the content of phenolic compounds in strawberry fruits. For example, significant increases in phenolic content have been observed under UV-B, red light, far-red light, and blue light [21,128,136]. Exposure to red and far-red supplemental light promoted the synthesis of certain individual polyphenols in strawberry fruits [137]. Supplemental lighting (e.g., UV-B) can elevate the total soluble solids content in strawberry fruits [131], while the red light-quality selective plastic film enhances soluble protein levels [68].

Taste-driven consumer choices highlight the importance of flavor in strawberries, which is primarily determined by sugars, organic acids, and aroma [135,138,139]. Supplementary lighting enhances strawberry sugar content by increasing photosynthate accumulation [89,140]. Besides, UV light and red-light selective films alter the sugar-acid ratio [68,130]. Furthermore, red mulch enhances strawberry aroma [68,138], as its reflected red/far-red light acts through the natural phytochrome system to modify gene expression, increasing aroma compounds. This finding provides novel insights for enhancing strawberry aroma, which can improve the quality of both fresh fruits and derived products, thereby benefiting consumer health.

#### **4.4 Effect of Light on Preharvest Disease Resistance of Strawberry**

Strawberries are highly susceptible to numerous pathogens, which can cause significant yield losses both in the field and during postharvest storage [141]. UV light is the main light source applied for preharvest disease control. UV-B radiation suppresses powdery mildew by upregulating defense-related genes and stimulating biosynthesis of antifungal compounds [141]. Nighttime UV-C irradiation enhances efficacy against powdery mildew [26,142]. Visible light, such as red light, can also enhance pathogen tolerance in strawberry fruit by upregulating cell wall development-related genes (e.g., *FaPE41*) and inhibiting fungal enzymes [83]. The use of light to suppress preharvest diseases aligns with the principles of sustainable agriculture and addresses growing consumer preferences for safer, high-quality produce grown with minimal chemical inputs.

### **5 The Role of Light on Strawberries during the Postharvest Stage**

#### **5.1 Role of Light in Fruit Preservation and Quality Maintenance**

Strawberry postharvest quality is regulated by both physiological and environmental factors. Light exposure significantly influences this process, with different wavelengths inducing distinct effects. Red light (e.g., 525 nm) promotes coloration by increasing anthocyanins, maintains ascorbic acid, and enhances soluble solids [130,143,144]. In contrast, blue light (e.g., 470 nm) elevates total phenols and ascorbic acid by boosting antioxidant enzyme activity and free radical scavenging capacity, but it also accelerates ripening by increasing respiration and ethylene production [130]. Similarly, violet-blue light at 405 nm increases anthocyanin and phenol content, though without affecting firmness [145]. However, not all lighting is beneficial; white LED light, for instance, can accelerate quality deterioration by doubling transpiration and promoting ascorbic acid degradation [146]. Thus, light quality must be carefully selected to improve postharvest strawberry quality.

Light has been employed both alone and synergistically to extend strawberry shelf life. The combination of low temperature (8°C) and blue light was more effective than either alone, enhancing antioxidant defense and delaying cell wall degradation [147]. Similarly, integrating blue light with salicylic acid soaking better preserved weight, firmness, and soluble protein content [148]. Intense pulsed light (2.0 Hz, 60 s) under storage conditions of 25°C, 80% relative humidity, and 7 days, significantly reduced strawberry decay rate, stabilized color, and regulated flavor compounds via the lipoxygenase pathway [149].

Strawberry aroma, a key quality trait, is regulated by the interaction of light and temperature, influencing the biosynthesis of esters and phenylpropanoids [150]. Research has characterized the comprehensive features and genetic mechanisms of this light- and temperature-mediated aroma regulation, though its effects are cultivar-dependent [150]. For instance, postharvest blue light improved the sensory quality and key volatiles in 'Festival' strawberries but had no significant effect on 'Florida Radiance', highlighting the role of genetic variation [8].

#### **5.2 Inhibitory Effects of Light on Postharvest Diseases of Fruits**

Strawberry shelf life is challenged by postharvest diseases, which UV irradiation can address [151]. Far-UV-C shows superior bactericidal activity to UV-C (254 nm) but can impair plant physiology [26]. Combining UV with other methods, such as peracetic acid or heat treatment, more effectively reduces pathogens (e.g., *Salmonella*), delays ripening, and preserves flavor without negative sensory impact [132,152].

High-power pulsed light mitigates microbial contamination on produce. It is more effective on smooth surfaces (e.g., blueberries) than rough ones (e.g., strawberries), but excessive doses cause damage [153]. A study using specific parameters (0–3.9 J/cm<sup>2</sup> UV dose, 0–200 s) reduced strawberry surface microbial contamination, extended shelf life by 2 days without affecting nutrients [154]. Light and temperature interact to inhibit pathogens. Blue light at 4°C reduced powdery mildew incidence by 70%, whereas it was ineffective at 21°C [155].

**Table 1:** Effects of light spectrum on growth and secondary metabolites accumulation of strawberry at different growth stages.

Growth Stages	Light Spectrum	Photoperiod	Cultivars	Effects	Reference
Seedling propagation stage	Red, green, and yellow plastic films	16 h	<i>Toyonoka</i>	Achieved the highest regeneration rate under red and green plastic films and increased chlorophyll b content; the activities of SOD/CAT: red film > green film > yellow film.	[31]
		16 h	<i>Sabrosa</i>	Increased concentrations of photosynthetic pigments.	[32]
	Red light	16 h	<i>Festival, Sweet Charlie, Tudla</i>	Demonstrated the highest adventitious shoot regeneration frequency; elevated levels of N <sup>+</sup> in plant tissues.	[33]
		24 h	<i>HS138</i>	Increased the dry matter during the nursery period.	[37]
	Green light	16 h	<i>Sabrosa</i>	Decreased concentrations of photosynthetic pigments.	[32]
		16 h	<i>Festival, Sweet Charlie, Tudla</i>	Increased adventitious shoot regeneration frequency. Increased levels of K <sup>+</sup> in plant tissues.	[33]
	Blue light	16 h	<i>Festival, Sweet Charlie, Tudla</i>	Increased chlorophyll content and elevated levels of phosphorus in plant tissues.	[33]
		10 h/14 h	<i>Sulhyang</i>	In non-running short-day conditions, blue light stimulated the expression of <i>FaGRAS32</i> and <i>FaGA20ox</i> .	[53]
	Yellow cellophane films	16 h	<i>Festival, Sweet Charlie, Tudla</i>	Exhibited the higher total chlorophyll content.	[33]
		/	<i>Akihime</i>	Red:blue (7:3), 60 μmol m <sup>-2</sup> s <sup>-1</sup> : demonstrated optimal growth.	[34]
	Red light + blue light	16 h	<i>Camarosa</i>	Red:blue (9:1): the most effective <i>in vitro</i> shoot tip development.	[35]
		16 h	<i>Elkat</i>	In cryopreserved stock plants, carbohydrate accumulation and the ratio of photosynthetic pigments were enhanced.	[56]
	Red light + blue light + far-red light	18 h	<i>Monterey</i>	Increased the leaf area and shoot dry mass.	[40]
	White light	16 h	<i>Maehyang</i>	Enhanced runner formation.	[49]
		16 h	<i>Akihime</i>	Promoted dry matter accumulation.	[52]
Blue light+ white light	16 h	<i>Maehyang</i>	Enhanced the growth performance of both mother and daughter plants.	[51]	

**Table 1: Cont.**

Growth Stages	Light Spectrum	Photoperiod	Cultivars	Effects	Reference
Vegetative growth stage	Blue light	16 h	<i>Elsanta, Akihime</i>	Increased the leaf carotenoid content.	[67]
		12 h/16 h	<i>Darselect</i>	Inhibited elongation growth.	[70]
	Red light	16 h	<i>Elsanta, Akihime</i>	Enhanced plant resistance to pathogens.	[67]
		5 h	<i>Elsanta</i>	Enhanced antioxidant enzyme activities.	[83]
	Red colored light-quality selective plastic films	/	<i>Akihime</i>	Increased petiole length and leaf area in the plants.	[68]
	Red light + blue light	18 h	<i>Albion, Monterey</i>	Enhanced biomass.	[40]
		16 h	<i>Darselect</i>	Red:blue (3:7): increased chlorophyll a and chlorophyll b content.	[66]
		11 h	<i>Camarosa</i>	Enhancing CO <sub>2</sub> uptake under salinity stress conditions while under alkaline stress.	[103]
	UV light	49 s, 73 s, 104 s, 159 s, 208 s	<i>Candiss, Charlotte, Cirafine</i>	UV-C: modulated their susceptibility to <i>B. cinerea</i> .	[99]
		3 h	<i>multiple varieties</i>	UV-B: low plant injury.	[101]
Reproductive growth stage	Red light + blue light	9 h	<i>Praratchatan 80</i>	Red:blue (6:1), nitrogen application of 100 mg L <sup>-1</sup> : advanced the flowering time.	[38]
	Red light + blue light + far-red light	18 h	<i>Albion</i>	Reduced the time to first harvest in certain long-day.	[40]
		18 h	<i>Monterey</i>	Increased leaf area.	[40]
	Red light	/	<i>Akihime</i>	Increased the weight of individual fruits; enhanced strawberry production.	[68]
		16 h	<i>Toyonaka</i>	Increased phenolic content.	[129]
		/	<i>Seolhyang</i>	Red light-selective plastic mulch increased soluble protein levels.	[130]
	Red light + blue light + green light	/	<i>Albion</i>	Green:blue:red (2:2:6): achieved high fruit yield.	[78]
	Blue light	13 h	<i>Fortuna</i>	Increased the number of flower clusters.	[113]
		14 h	<i>Elsanta</i>	Improved production.	[121]
		14 h	<i>Albion</i>	Enhanced strawberry firmness.	[128]
UV light	/	<i>Seolhyang</i>	Increased anthocyanin content in strawberry fruits.	[130]	
Postharvest stage	Blue light	24 h	<i>Florida Radiance</i>	Enhanced the sensory quality.	[8]
		24 h	<i>Fengguang</i>	Increased antioxidant enzyme activity; increased antioxidant content; improved fruit color; promoted fruit ripening.	[143]
	UV light	/	<i>Camarosa</i>	UV-C: inhibited microbial growth on strawberries.	[151]

Note: The films and mulch were used specifically to create defined spectra.

**Table 2:** Effects of photoperiod on growth and secondary metabolites accumulation of strawberry at different growth stages.

Growth Stages	Photoperiod	Cultivars	Effects	Reference
Seedling propagation stage	12 h/d and 16 h/d	<i>Benihoppe</i>	Runner length decreased linearly with increasing DLI.	[43]
	12, 14, 16, 18, 20, and 22 h/d	<i>Sulhyang, Maehyang</i>	Photoperiod exceeding 16 h induced strawberry runner formation.	[54]
Vegetative growth stage	12 and 16 h/d	<i>Albion</i>	16 h/d: Increased in root biomass.	[39]
	12, 14, and 16 h/d	<i>Darselect</i>	12 h/d: Optimal performance in photosystem II parameters.	[70]
Reproductive growth stage	12 and 16 h/d	<i>Albion</i>	16 h/d: Earlier flowering period, increased strawberry fruit production.	[39]
	16 and 24 h/d	<i>Elan</i>	Extended photoperiod promoted flower bud development.	[64]
	Supplemental 13-h LED lighting	<i>Fortuna</i>	Increased Fruit quality.	[113]

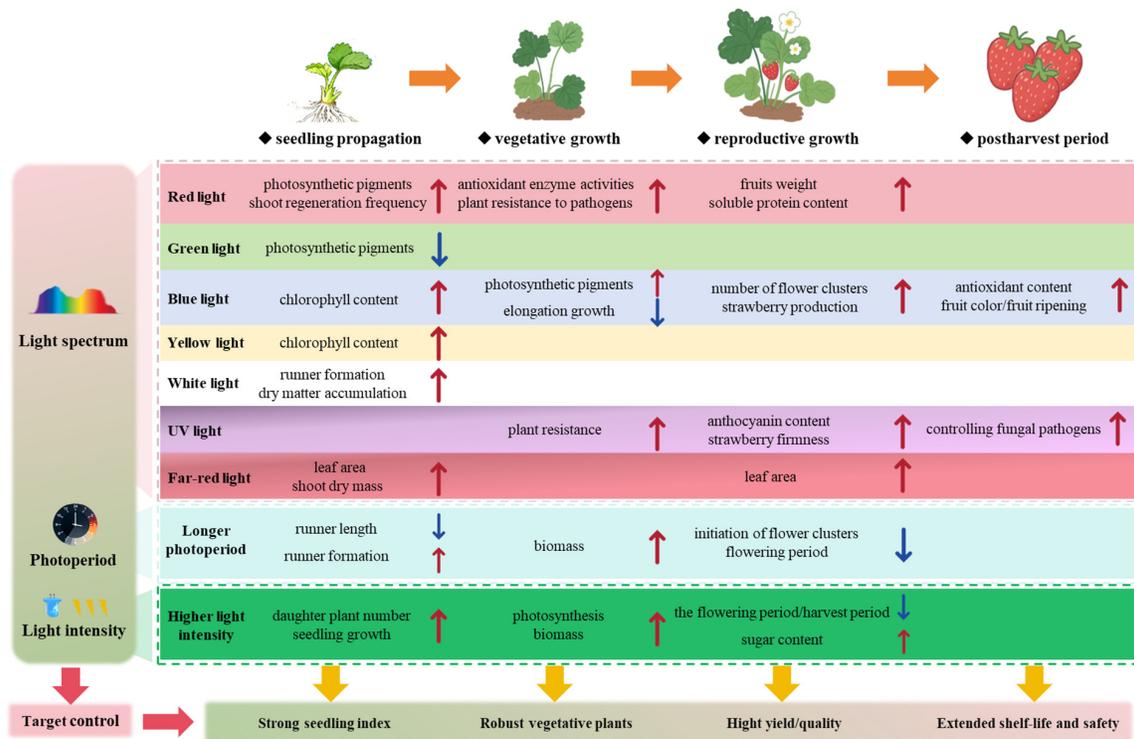
**Table 3:** Effects of light intensity on growth and secondary metabolites accumulation of strawberry at different growth stages.

Growth Stages	Light Intensity	Cultivars	Effects	Reference
Seedling propagation stage	45, 60, and 75 $\mu\text{mol m}^{-2} \text{s}^{-1}$	<i>Akihime</i>	The optimal light intensity was 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and higher light intensity improved the growth of seedlings.	[34]
	200, 250, 300, and 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$	<i>Benihoppe</i>	Length of runners decreased under photoperiod of 16 h/d.	[45]
	137.4, 217.0, and 274.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$	<i>Maehyang</i>	About 280 $\mu\text{mol m}^{-2} \text{s}^{-1}$ improved the number of strawberry seedlings and the total yield of stolons.	[44]
Vegetative growth stage	250, 350, and 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$	<i>Albion</i>	The number, total dry mass, and total fresh mass of daughter plants increased with the increase in light intensity.	[43]
	200, 300, and 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$	<i>Albion</i>	Increased strawberry plant growth with increased light intensity.	[39]
	150, 200, and 250 $\mu\text{mol m}^{-2} \text{s}^{-1}$	<i>Darselect</i>	The light intensity of 250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ showed a better performance in terms of key photosynthetic indicators.	[70]
	149, 269, and 567 $\mu\text{mol m}^{-2} \text{s}^{-1}$	<i>Toyonoka</i>	Improvement of PPFD increased the total dry weight of plants.	[82]
Reproductive growth stage	200, 300, and 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$	<i>Albion</i>	Improve PPFD advanced the flowering period and the harvest period.	[39]
	Supplementary light	<i>Red Face</i>	High light intensity improved the sugar content and strawberry production.	[140]

## 6 Conclusion

This review outlines how regulating light intensity, photoperiod, and spectrum influences the entire strawberry growth cycle (Fig. 2). Studies show these parameters affect propagation, growth, flowering, fruit quality, and postharvest preservation primarily by modulating photosynthesis, morphology, physiology, and defense responses. Notably, the effects of light regulation are developmental stage-specific and cultivar-dependent. While current research predominantly focuses on single growth stages or spectral

factors, we propose that establishing precise, stage-specific light regulation strategies represents a promising approach to simultaneously enhance yield, quality, and stress resistance in strawberry production. Future research and commercial applications should prioritize: (1) developing integrated, cost-effective “light recipes” that dynamically adapt to different cultivars and growth stages to maximize resource-use efficiency; (2) investigating the synergistic optimization of the light environment across the entire growth cycle and explore the interaction mechanisms between light signaling and other environmental factors (e.g., temperature, CO<sub>2</sub>, humidity); and (3) establishing sensor-based, automated lighting control systems that respond in real-time to plant phenotypic and physiological feedback.



**Figure 2:** Schematic diagram of the effects of light spectrum, intensity, and photoperiod on key growth and developmental parameters of strawberry at different stages. Please increase the smallest letter size inside the figure to make it readable.

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