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Influence of Light Management on Fruit Quality and Sugar Accumulation in Strawberry

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Abstract Light is a critical environmental factor regulating strawberry growth, fruit development, and quality formation. With the expansion of protected cultivation systems, optimizing light management has become an effective strategy for improving fruit yield and enhancing nutritional and sensory attributes. This review summarizes recent advances in the effects of light intensity, photoperiod, light quality, and canopy light distribution on strawberry fruit quality and sugar accumulation. Light regulation influences photosynthetic carbon assimilation, carbohydrate transport, and source-sink relationships, thereby affecting the accumulation of soluble sugars, organic acids, anthocyanins, and flavor compounds. Artificial lighting technologies, particularly LED supplemental lighting, provide precise control of spectral composition and light dosage, promoting photosynthetic efficiency and improving fruit sweetness under low-light conditions. In addition, canopy management practices, including leaf removal, planting density optimization, and reflective mulching, enhance light interception and improve fruit uniformity. At the physiological and molecular levels, light signals regulate sugar metabolism-related enzymes, photosynthetic pathways, and hormone interactions through photoreceptors and transcriptional networks. Case studies demonstrate that optimized light environments can significantly enhance strawberry fruit quality in greenhouse production. Future research should focus on integrating intelligent sensing technologies, environmental modeling, and multi-factor regulation to establish precise and sustainable light management systems for high-quality strawberry production.

Keywords Strawberry; Light management; Fruit quality; Sugar accumulation; LED supplemental lighting

1 Introduction

Strawberry (*Fragaria* × *ananassa* Duch.) is one of the world's most important and widely consumed fruit crops, valued not only for its economic significance but also for its sensory and nutritional attributes, including sweetness, color, aroma, vitamins, fiber, and antioxidant compounds. Current production systems are under increasing pressure to deliver fruit that satisfies consumer expectations for appearance, flavor, firmness, and health-promoting value while remaining profitable under climate instability, pest pressure, and protected-cropping constraints. For this reason, improvement of fruit quality has become a central goal in strawberry research and industry, alongside yield stability and postharvest performance. Sweetness is especially important because it strongly influences consumer acceptance and marketability, yet it is a complex trait shaped by both genotype and environment. Recent advances in breeding and molecular research have improved understanding of quality-related traits, but practical crop-management tools are still needed to consistently enhance sweetness and overall fruit quality under commercial conditions (Hernández-Martínez et al., 2023).

Among environmental factors, light is one of the most decisive regulators of strawberry growth, flowering, ripening, and metabolite accumulation. Light does not act only as an energy source for photosynthesis; its intensity, duration, and spectral composition also function as developmental signals that influence plant architecture, floral induction, fruit coloration, sugar accumulation, and the synthesis of phenolics and other secondary metabolites. In strawberry, inadequate or suboptimal light conditions can reduce fruit quality, causing poor coloration and weaker accumulation of desirable compounds, whereas suitable light exposure promotes soluble sugars and anthocyanins in ripening fruit. Mechanistically, light-mediated quality formation is linked to regulation of photoreceptors and downstream transcriptional networks that control biosynthetic genes associated

with sugar and pigment metabolism. Thus, the strawberry light environment is directly relevant to both source activity in leaves and sink metabolism in fruits, making it a key target for quality-oriented crop management (Warner et al., 2021).

Research over the last decade has shown that light management can be used strategically to improve strawberry production in greenhouses and controlled environments, particularly where winter radiation is limited or canopy structure creates local shading. Supplemental LED lighting has received the greatest attention because it allows precise control of wavelength, intensity, and photoperiod, and different spectra can produce distinct outcomes. Red light often promotes productivity and anthocyanin accumulation, while blue light can enhance certain quality traits and, in some systems, increase soluble sugar content. Combined red-blue lighting has also been reported to improve soluble solids, anthocyanin concentration, and vegetative performance, although cultivar dependence remains an important limitation. In addition, newer work suggests that far-red or other spectrum adjustments can further alter flowering, biomass partitioning, fruit yield, and sweetness. Collectively, these findings indicate that light management is no longer a purely supplemental practice for maintaining growth, but an active production tool for steering fruit quality formation in strawberry (Lauria et al., 2023; Ries and Park, 2024).

Despite this progress, important gaps remain in understanding how light management specifically influences sugar accumulation while simultaneously affecting other fruit-quality components. Available studies show that supplemental lighting can increase total sugar, glucose, and fructose concentrations, and can also modify soluble solids, acidity, polyphenols, and anthocyanins, but responses vary with season, cultivar, irrigation status, and the precise light regime applied. Moreover, the physiological and molecular coordination between carbon assimilation, carbohydrate transport, ripening metabolism, and light signaling has not yet been fully resolved for strawberry production systems. Therefore, a focused synthesis of current knowledge is needed to clarify how light intensity, spectral composition, and light-management strategies shape fruit quality, with particular emphasis on sugar accumulation. The objective of this paper is to examine the influence of light management on strawberry fruit quality and sweetness-related traits, summarize current research progress, and provide a basis for optimizing lighting strategies in modern strawberry cultivation (Qiu et al., 2023; Xu et al., 2023).

2.Light Characteristics and Their Effects on Strawberry Photosynthetic Performance

2.1 Effects of light intensity on photosynthesis and carbon assimilation

Light intensity is a primary determinant of strawberry photosynthetic performance because it directly affects carbon fixation, stomatal behavior, and assimilate supply. Under greenhouse shading, reduced irradiance decreased photosynthetic rate, stomatal conductance, sugar accumulation, and marketable fruit yield, showing that inadequate light restricts both source activity and carbon allocation to developing sinks (Choi, 2021). Similar responses were observed during transplant production in LED systems, where increasing intensity within an effective range enhanced stomatal conductance, net photosynthetic rate, and dry matter accumulation, confirming that carbon assimilation improves as photon supply approaches the cultivar's physiological requirement.

However, the effect of intensity is not simply linear, because optimal ranges differ with developmental stage and production environment. During runner propagation, unrooted plants performed best at $90 \mu\text{mol m}^{-2} \text{s}^{-1}$ during rooting, whereas rooted seedlings responded positively up to $270 \mu\text{mol m}^{-2} \text{s}^{-1}$, with no further growth improvement at $360 \mu\text{mol m}^{-2} \text{s}^{-1}$, indicating saturation of biomass gain at higher irradiance. Recent controlled-environment work also showed that moderate supplemental illumination directed to the abaxial leaf surface increased CO_2 assimilation, fruit yield, and fruit quality with greater energy efficiency than equivalent adaxial lighting, emphasizing that both light dose and light distribution influence whole-canopy carbon gain (Wang et al., 2026).

2.2 Influence of photoperiod on vegetative growth and reproductive development

Photoperiod modifies strawberry growth by changing the daily duration of carbon acquisition and by regulating the timing of developmental transitions. In indoor sole-source systems, extending the photoperiod from 12 to 16 h accelerated flowering by 17-21 days, advanced first harvest, and increased fruit production by 372%–989%, while increases in PPFD mainly enhanced vegetative biomass, indicating that day length can dominate reproductive

output even when light intensity is adequate (Park et al., 2023). This interaction between light duration and growth is reinforced by recent synthesis work showing that PPFD and photoperiod act synergistically in controlled production, although cultivar-specific sensitivity remains an important constraint on universal lighting prescriptions (Wang et al., 2025).

Photoperiodic regulation also acts through flowering and vegetative signaling pathways that differ among strawberry types and developmental stages. In seasonal flowering cultivars, long days induce FaCO responses yet can delay flowering through repression pathways involving FaTFL1, while FaSOC1 functions as a strong repressor of flowering and promoter of vegetative growth (Muñoz-Avila et al., 2022). After floral initiation, photoperiod continues to shape reproductive progression: in ‘Akihime’, long-day treatment delayed the first inflorescence but increased flower number in the secondary inflorescence and accelerated later fruit maturation, showing that post-flowering photoperiod can redistribute reproductive timing rather than simply promote or inhibit it (Ren et al., 2024).

2.3 Regulation of light quality on plant morphology and physiological responses

Light quality regulates strawberry morphology and physiology by altering chlorophyll formation, stomatal behavior, photochemistry, and downstream metabolic programming. Under different LED spectra, strawberry leaves showed significant changes in chlorophyll content, minimal fluorescence, and net photosynthetic rate, and transcriptomic analysis linked these responses to pathways related to photosynthesis, carbon fixation, chlorophyll metabolism, and hormone biosynthesis (Li et al., 2024). Spectral composition also affected propagation-stage morphology: adding green or far-red light to red-blue backgrounds increased shoot multiplication and plant height, while green light enhanced chlorophyll biosynthesis and far-red stimulated photomorphogenesis-related gene expression (Li et al., 2025).

Different wavebands, however, do not contribute equally to photosynthetic efficiency, and narrow spectra can produce contrasting physiological outcomes. White supplemental light supported higher photosynthesis after prolonged exposure, whereas monochromatic red and blue reduced maximal photosynthetic rate and increased superoxide formation, suggesting that broader spectra better sustain leaf function over time (Lauria et al., 2023). At the leaf level, blue and green light increased intercellular CO₂ concentration and transpiration through stronger stomatal opening, while red light more strongly promoted photochemical reactions and CO₂ fixation, indicating that balanced spectral combinations are more effective than single wavelengths for coordinating morphology with carbon assimilation.

3 Mechanisms of Light Regulation on Strawberry Fruit Quality Formation

3.1 Regulation of light environment on fruit growth and development

Light regulates strawberry fruit growth and development by controlling both whole-plant carbon supply and ripening-related signaling. When light intensity is reduced, strawberry plants show lower photosynthetic rate, stomatal conductance, sugar accumulation, and fruit yield, indicating that insufficient irradiance restricts assimilate production needed for fruit expansion and maturation (Choi, 2021). In contrast, supplemental LED lighting in commercial systems generally increases yield and can accelerate maturation-related changes in fruit quality, showing that managed light environments can shift fruit development toward earlier and more productive harvests (Figure 1) (Tang et al., 2023; Pérez-Romero et al., 2024).

Beyond total irradiance, spectral composition shapes developmental timing and fruit formation through photoreceptor-mediated pathways. Additional far-red light accelerates flower and fruit formation and increases soluble sugar, whereas low red:blue ratios alter metabolite composition without strongly changing fruit set, suggesting that developmental and quality responses can be partially uncoupled (Li et al., 2025). At the molecular level, light signaling also acts as a brake-or-release system during ripening, because COP1 suppresses fruit quality formation by destabilizing HY5-, RIF-, and MYB10-dependent downstream regulators, while light relieves this repression and promotes visible changes in fruit color and shape (Bi et al., 2025).

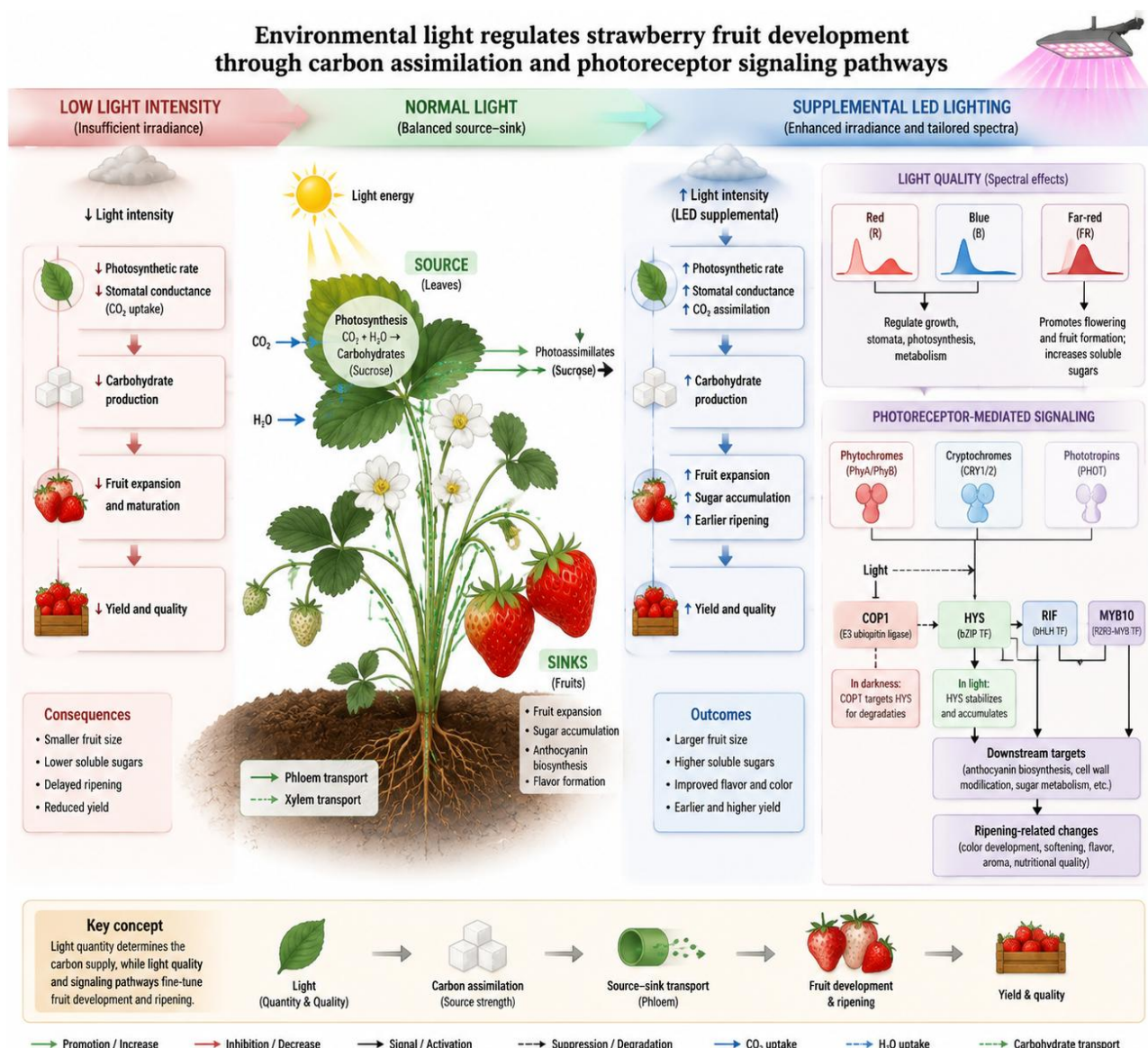


Figure 1 Mechanistic framework illustrating how light quantity and quality regulate strawberry fruit growth, carbon allocation, and ripening processes

Light management also modifies fruit growth indirectly by changing source-sink balance under greenhouse stress or resource limitation. Supplemental light combined with elevated CO₂ increases yield across the production season and improves sweetness, supporting the view that fruit development responds strongly when carbon acquisition is simultaneously enhanced by atmospheric and radiative inputs (Qiu et al., 2023). Similarly, under full or deficit irrigation, supplemental light improves fruit size and elevates quality-related metabolites, indicating that light can partially buffer suboptimal water conditions during fruit development (Xu et al., 2023).

Recent synthesis work indicates that light effects on fruit growth are stage-specific rather than uniform across the crop cycle. Phase-specific strategies that adjust spectral composition from vegetative growth to flowering and maturation appear to improve quality formation more effectively than static lighting, because the developmental roles of light differ across fruit set, enlargement, and ripening (Warner et al., 2021; Wang et al., 2025). This helps explain why responses vary across cultivars and experiments: light acts through interacting effects of wavelength, developmental stage, and preharvest versus postharvest exposure rather than through a single universal mechanism (Warner et al., 2021).

3.2 Effects of light on sugar accumulation and carbohydrate metabolism

Light promotes sugar accumulation in strawberry fruit at both physiological and molecular levels. Dark-treated fruit fail to accumulate sugars normally, whereas light-treated fruit show increased soluble sugar levels together with stabilization of FvMYB10, indicating that ripening-associated sugar accumulation depends on active light signaling. In greenhouse production, supplemental light increases total sugar, glucose, and fructose concentrations, especially late in the season, confirming that improved carbohydrate status under better light translates into sweeter fruit (Xu et al., 2023).

This regulation is mediated by specific photoreceptors and downstream metabolic genes. Blue-light receptors FvCRY1 and FvCRY2 directly promote anthocyanin and sugar accumulation, and their overexpression increases soluble solids, glucose, and fructose together with higher expression of FvINV and FvSFP9, linking light perception directly to carbohydrate metabolism and transport (Zhang et al., 2025). A parallel negative pathway is mediated by COP1, which represses sugar accumulation by inhibiting HY5-, RIF-, and MYB10-regulated transcriptional activation of downstream biosynthetic genes (Bi et al., 2025).

Spectral quality also changes the balance among carbohydrate-related metabolites. Red-light supplementation alters inositol metabolism and affects compounds such as D-mannose-6-phosphate, sorbitol, and inositol, while transcriptomic enrichment in galactose metabolism suggests that red light reshapes broader carbohydrate networks beyond simple soluble sugar accumulation. Consistent with this, recent review evidence indicates that spectral optimization can balance sucrose-to-hexose partitioning through FaSPS1-related regulation, providing a mechanistic explanation for why different light recipes produce different sweetness outcomes (Wang et al., 2025).

Not all light treatments increase sugars in the same way, and responses can depend on treatment context. In detached fruit, most red-, blue-, and white-light treatments decreased the TSS/TA ratio and the soluble sugar/acid ratio, especially when sucrose was added exogenously, indicating that postharvest or detached-ripening responses can differ from whole-plant preharvest lighting effects (Jiang et al., 2023). Likewise, some commercial greenhouse experiments found that supplemental spectra changed individual sugars by sampling date without altering Brix overall, so sugar regulation by light appears to be dynamic and environment-dependent rather than uniform across all systems (Pérez-Romero et al., 2024; Roosta et al., 2024).

3.3 Light-induced regulation of organic acids, anthocyanins and flavor compounds

Light has especially strong effects on anthocyanin accumulation, which is one of the clearest mechanisms by which it improves strawberry fruit quality. Light is essential for anthocyanin accumulation in ripening fruit, and dual red and blue irradiation appears to optimally activate the flavonoid pathway by co-upregulating structural genes such as CHS, F3H, DFR, and ANS together with regulatory factors including FaMYB10 and FaHY5 (Wang et al., 2025). Blue light tends to induce upstream phenylpropanoid enzymes, whereas red light enhances proanthocyanidin production, showing that different wavebands regulate distinct branches of secondary metabolism rather than producing identical quality responses (Lauria et al., 2023; Wang et al., 2025).

Experimental studies broadly support the quality benefits of preharvest supplemental lighting, although the specific metabolite profile depends on the spectrum. Red light improves productivity and promotes anthocyanin accumulation in fruit, while blue, red, and red/blue combinations also increase anthocyanin concentration across cultivars, indicating that multiple spectra can stimulate pigmentation but with different strengths and accompanying effects on other metabolites (Lauria et al., 2023; Roosta et al., 2024). Under stress conditions, red and blue-red light also raise fruit anthocyanin levels, suggesting that light quality can preserve or enhance color development even when salinity or alkalinity constrains normal metabolism.

Light also regulates acidity and volatile flavor formation, which are critical for perceived eating quality. Supplemental light can increase titratable acids in some greenhouse systems, whereas LED supplementation combined with elevated CO₂ decreases titratable acidity, showing that acid responses are not uniform and depend on the broader production environment (Qiu et al., 2023; Tang et al., 2023). For aroma, red light promotes synthesis of furanones and esters, and blue or red postharvest LED exposure increases key aroma-related volatile esters, supporting a persistent light-triggered effect on flavor chemistry (Farneti et al., 2025; Wang et al., 2025).

Postharvest evidence further shows that light can continue regulating quality after harvest. Continuous red LED during storage increases anthocyanin and TSS while preserving firmness and reducing weight loss, whereas brief early LED exposure enhances anthocyanins and aroma-related VOCs during subsequent storage without major color changes, indicating that strawberries retain light responsiveness after picking (Farneti et al., 2025). Overall, light-induced fruit quality formation in strawberry reflects an integrated response in which photoreceptors, transcription factors, carbohydrate metabolism, pigment biosynthesis, acid balance, and volatile production are coordinately modulated by the intensity, duration, and spectrum of the light environment.

4. Artificial Light Supplementation Strategies in Strawberry Cultivation

4.1 Application of LED supplemental lighting in strawberry production

LED supplemental lighting has become a central strategy in strawberry production because it can compensate for low winter radiation and improve both productivity and fruit quality in protected systems. Across greenhouse studies, supplemental LEDs increased vegetative growth, marketable yield, soluble solids, and overall berry quality, especially during off-season production when natural light is limiting (Stuemky and Uchanski, 2020). Similar benefits were observed across multiple cultivars grown under different spectra, where artificial LED light enhanced early yield, increased total soluble solids, and raised anthocyanin concentrations, indicating that supplemental lighting can improve both commercial output and quality traits relevant to consumer acceptance (Roosta et al., 2024).

The effectiveness of LED supplementation depends on spectral design and production context rather than simply adding photons. In plastic greenhouse cultivation, ambient light supplemented with blue or blue-plus-red LEDs produced higher fruit output, whereas red or blue-plus-red supplementation promoted greater accumulation of organic acids and phenolic compounds, showing that different spectra can target yield and quality differently. In commercial and research greenhouses, blue and red LED combinations also increased flowering substantially and reduced second-quality fruit without compromising overall quality, supporting their practical use for improving production uniformity and marketable fruit proportion.

4.2 Effects of light duration and intensity regulation on yield and quality

Regulation of light duration and intensity is a major determinant of how effectively supplemental lighting translates into yield and fruit quality. In indoor strawberry production, extending the photoperiod from 12 to 16 h accelerated flowering and first harvest and increased fruit production by 372%–989%, while increasing PPFD mainly promoted vegetative growth and had comparatively little effect on fruit production, indicating that photoperiod can dominate reproductive performance in some systems (Park et al., 2023). Evidence from multi-tier vertical systems also showed that both light intensity and duration increased yield, and that longer lighting duration increased sugar content, although the economic return remained constrained by electricity cost (Swann et al., 2021).

Optimal duration and intensity are not universal, because cultivar and cultivation system alter the response. In forcing culture, a 12-h LED photoperiod increased leaf photosynthesis, accelerated flower bud differentiation, improved fruit quality, and produced the highest marketable yield, whereas longer than 12 h inhibited later floral development and reduced total yield. By contrast, under time-differential supplemental lighting in soilless greenhouse culture, the combination of lower supplemental intensity at $132 \mu\text{mol m}^{-2} \text{s}^{-1}$ with a 16-h photoperiod produced the highest fruit yield and improved water and fertilizer use efficiency, showing that longer duration with moderate intensity can outperform higher-intensity strategies in other environments.

4.3 Integration of supplemental lighting with greenhouse environmental control

Supplemental lighting is most effective when integrated with broader greenhouse environmental control rather than used as an isolated input. Combining LED supplemental light with elevated CO₂ increased light-saturated photosynthetic rate, leaf area index, biomass, and yield, and also improved soluble sugar content while reducing titratable acidity, demonstrating a clear synergy between radiative and atmospheric management (Qiu et al., 2023). At the seasonal scale, this combined treatment raised yield by 51.3%, exceeding the effects of either elevated CO₂ or LED lighting alone, and therefore represents a strong strategy for improving winter-to-spring greenhouse productivity and sweetness (Qiu et al., 2023).

Integration with temperature and greenhouse control systems is equally important. In a subtropical forcing system, controlled-environment greenhouses increased yield relative to conventional houses, and adding daytime LED supplemental lighting produced a further increase, especially during winter periods of persistent cloudiness and low solar radiation, although benefits became limited in spring under high external radiation (Nakayama and Nakazawa, 2023). More intensive combinational control that included supplemental lighting, elevated CO₂, and regulated air temperature accelerated flowering, increased fruit number, and, when paired with movable beds and higher planting density, achieved more than a twofold increase in yield per unit land area, underscoring that lighting delivers its greatest value when embedded in whole-system greenhouse optimization.

5 Canopy Light Management and Cultivation Practices

5.1 Effects of leaf removal and canopy structure optimization

Canopy structure strongly determines how much radiation reaches strawberry leaves and fruits, and fruit quality changes measurably with fruit light exposure. Under field conditions, light incidence altered flavor and antioxidant content, and the response was genotype-dependent, indicating that canopy-opening practices such as leaf removal are most likely to be effective when they improve fruit exposure without overexposing sensitive cultivars. The same study found that cultivars with larger canopies compensated by producing longer peduncles, which helped maintain a similar proportion of exposed fruits despite canopy-size differences, showing that canopy architecture itself is a plastic determinant of fruit light interception.

Broader photobiology evidence supports canopy optimization as a quality-management tool because strawberry responses depend on how light is distributed through the plant rather than on total irradiance alone. Controlled-environment studies summarized in recent review work show that tailored light strategies can optimize fruit production and consumer-desired quality traits, while wavelength-specific effects on flavonoids vary enough that better canopy light penetration should be paired with spectral management rather than treated as a stand-alone intervention (Warner et al., 2021). This logic is reinforced by shading experiments showing that low light reduces photosynthetic rate, sugar synthesis, and commercial fruit yield, implying that canopy-thinning practices that relieve self-shading can improve assimilate supply to fruit as long as total leaf area is not excessively reduced (Choi, 2021).

5.2 Influence of plant density and training systems on light distribution

Plant density is one of the clearest cultivation variables affecting canopy light distribution in strawberry, and its effects extend to photosynthesis, fruit quality, and profitability. In southern Brazil, plant spacing altered photosynthetic efficiency, production, fruit quality, and economic return, with 5-15 cm spacing providing a practical compromise for the high-quality cultivar ‘Pircinque’. In alpine mountain production, lower density increased aboveground biomass, leaf photosynthetic rate, and the number of crowns and flower trusses per plant, while fruits from low density also showed a higher color index, consistent with improved within-canopy light penetration (Soppelsa et al., 2023).

Higher density, however, often increases yield per unit land area even when individual plants receive less light and produce smaller fruit. A recent review found positive linear relationships between density and hectare-scale yield across annual hill culture, protected systems, and matted rows, with no clear upper limit imposed by light competition in most experiments, likely because inter-row spacing still allowed acceptable interception (Menzel, 2024). In hydroponic and vertical systems, higher planting density similarly reduced yield per plant but increased yield per square meter, while light limitation inside vertical structures remained a key reason why optimum density depends on greenhouse irradiance and system configuration.

5.3 Application of reflective mulching and light redistribution materials

Reflective mulches and light-redistribution materials improve the light environment around the lower canopy and fruiting zone, where direct interception is often limited. In one of the clearest demonstrations, strawberries ripened over red mulch were about 20% larger and had higher sugar-to-organic-acid ratios and higher concentrations of favorable aroma compounds than fruit over black mulch, indicating that reflected red and far-red light can directly improve flavor-related chemistry. Highly reflective polythene mulches also increased growth and yield through

greater fruit size and number, while raising total ellagic acid and ascorbic acid concentrations, showing that reflected PAR can enhance both productivity and bioactive quality traits.

More recent work shows that the effect of mulch-based light management depends on the optical properties of the material used. In greenhouse winter production, white reflective mulch reflected far more PAR than red, olive, or black mulch and supported consistent saleable berry production, suggesting that highly reflective surfaces are useful where ambient light is seasonally limiting. Other light-redistribution materials have also shown strong promise: red light-selective plastic film improved photosynthetic performance, fruit weight, total sugar, and anthocyanin content, while rare-earth photoconversion films increased net CO₂ assimilation, soluble solids, soluble sugar, vitamin C, flavonoids, and yield by modifying spectrum, temperature, and greenhouse light transmission (Peng et al., 2020; Zhao et al., 2025).

6 Molecular and Physiological Mechanisms Underlying Light-Induced Sugar Accumulation

6.1 Regulation of photosynthetic carbon fixation pathways

Light-induced sugar accumulation in strawberry begins with enhanced source activity and more efficient allocation of newly fixed carbon from leaves to fruit. When light intensity declines, strawberry plants show lower photosynthetic rate, stomatal conductance, and sugar accumulation, indicating that reduced carbon fixation at the source directly limits the carbohydrate supply available for developing fruit (Choi, 2021). At the same time, greater daylight integrals increase the rate and amount of photosynthate translocation into individual fruits, showing that stronger leaf assimilation under longer light exposure improves sink loading as well as source production.

The fate of this additional carbon depends on how strawberry leaves partition assimilates between transportable sugars and temporary storage pools. Under high photosynthetic activity, carbon is first allocated to sucrose, but once leaf sucrose concentration exceeds storage capacity, excess carbon is diverted into starch, indicating that starch functions as an overflow product rather than the primary export form (Nakai et al., 2023). More broadly, fruit sugar accumulation depends on coordinated regulation of sugar transporters and metabolic enzymes that govern long-distance translocation, sink unloading, and post-translational control of carbohydrate metabolism, so light-driven increases in fixation must ultimately be coupled to these downstream allocation processes to raise fruit sweetness (Ren et al., 2023).

6.2 Light signaling pathways involved in fruit development

Beyond its role in carbon supply, light also acts as a developmental signal that directly regulates strawberry fruit maturation and sugar-related gene expression. Light-treated fruits accumulate more soluble sugar than dark-treated fruits, and this response is accompanied by stabilization of the ripening regulator FvMYB10, indicating that light promotes sugar accumulation partly through transcriptional and post-translational control during ripening. Blue-light receptors FvCRY1 and FvCRY2 provide a more direct mechanism, because their overexpression increases soluble sugar content and they bind promoters of sugar metabolism genes such as FvSFP9 and FvINV, with blue light enhancing their transcriptional activation capacity (Zhang et al., 2025).

Light signaling in fruit development also includes repressive modules that prevent sugar accumulation when photomorphogenic signaling is attenuated. FvCOP1 acts as a molecular brake by suppressing sugars, anthocyanins, and flavonoids through inhibition of downstream transcriptional activation mediated by FvHY5, FvRIF, and FvMYB10, and by ubiquitinating these regulators to reduce their stability (Bi et al., 2025). Far-red signaling likely contributes as well, because FxAPHY15 is strongly responsive to far-red light and peaks transcriptionally during the fruit turning stage while interacting with PIF3-related regulatory networks, supporting a role for phytochrome-mediated signaling in the transition from vegetative growth to fruit maturation.

6.3 Interaction between light signals and hormonal regulation

Light-induced sugar accumulation is closely integrated with hormone signaling, especially the balance between abscisic acid and auxin during ripening. Fruit grown under light accumulates more ABA than bagged fruit, whereas dark treatment delays sugar accumulation and softening, indicating that light promotes ripening in part by

sustaining ABA-associated developmental progression (Sun et al., 2024). Mechanistically, blue or red light combined with sucrose promotes detached ripening by increasing ABI4 expression, decreasing SnRK2.6 expression, and suppressing AUX/IAA11 and ARF6, consistent with activation of ABA signaling alongside inhibition of auxin signaling (Jiang et al., 2023).

This hormonal crosstalk extends to direct control of sugar transport and signaling outputs. ABA regulates sugar accumulation through the FaRIPK1-FaTCP7-FaSTP13/FaSPT module, in which ABA-enhanced FaRIPK1 interaction with FaTCP7 relieves repression of sugar transporter genes and thereby promotes soluble sugar accumulation during ripening. Light and ABA also converge, but not identically, on downstream ripening regulators: both induce FaMYB10 and enhance anthocyanin accumulation, yet their effects are additive rather than strictly linear, indicating partly independent pathways that intersect at common transcriptional targets controlling fruit maturation and quality formation.

7 Case Studies: Application of Light Management Technologies in Strawberry Production

7.1 LED spectrum optimization for improving strawberry sugar content and fruit quality

Case studies of LED spectrum optimization show that spectral composition can be used to target both sugar accumulation and visual fruit quality in greenhouse strawberries. In a four-cultivar greenhouse experiment, blue, red, and red/blue supplemental lighting all increased early fruit yield in most cultivars, while supplemental light also raised total soluble solids and anthocyanin concentration, indicating that spectrum selection can simultaneously improve sweetness-related and pigmentation traits (Roosta et al., 2024). A complementary preharvest study found that red LED supplementation produced the highest productivity and selectively enhanced anthocyanin accumulation, whereas blue and green light preferentially increased other primary and secondary metabolites, showing that different spectra shift fruit quality in different biochemical directions (Lauria et al., 2023).

Recent synthesis studies suggest that the most effective strategy is not a fixed wavelength but a phase-specific spectral program matched to crop development. Red-blue combinations are reported to improve photosynthetic efficiency and accelerate fruit maturation when applied at moderate photon flux and long daily duration, while dynamic spectral adjustment across vegetative growth, flowering, and maturation is proposed to better coordinate yield formation with sugar and anthocyanin accumulation (Wang et al., 2025). More broadly, controlled-environment evidence indicates that manipulating light intensity and spectral composition can substantially modify strawberry secondary metabolism and fruit antioxidant properties, although blue-light effects remain less consistent across studies than responses to mixed or red-dominant spectra (Figure 2) (Warner et al., 2021).

7.2 Supplemental lighting in greenhouse strawberry production under low-light conditions

Under winter and spring greenhouse conditions, supplemental lighting consistently improves strawberry growth and fruit quality when natural radiation is inadequate. A commercial greenhouse study using an hourly light integral strategy showed that supplemental LEDs increased daily light integral to about 10 mol m⁻² d⁻¹, raised canopy temperature by 1 °C-2 °C, and improved net photosynthetic rate, fruit yield per plant, soluble solids, and sugar-acid ratio, demonstrating that real-time light compensation can directly enhance both productivity and eating quality (Yang et al., 2024). Similar benefits were observed in a subtropical forcing system, where daytime LED lighting further improved dry matter accumulation and yield during cloudy winter periods, although the yield advantage became limited in spring when solar radiation was already high (Nakayama and Nakazawa, 2023).

Case studies also show that supplemental lighting is most effective when integrated with other greenhouse controls. In autumn-to-spring production, the combination of elevated CO₂ and LED supplemental light increased photosynthetic capacity, biomass, and yield, while also improving fruit soluble sugar content and reducing titratable acidity across the growth cycle (Qiu et al., 2023). Under full and deficit irrigation, supplemental lighting likewise increased fruit polyphenols early in the season and total sugar, glucose, and fructose later in the season, indicating that added light can stabilize or improve fruit quality even when water management differs (Xu et al., 2023).

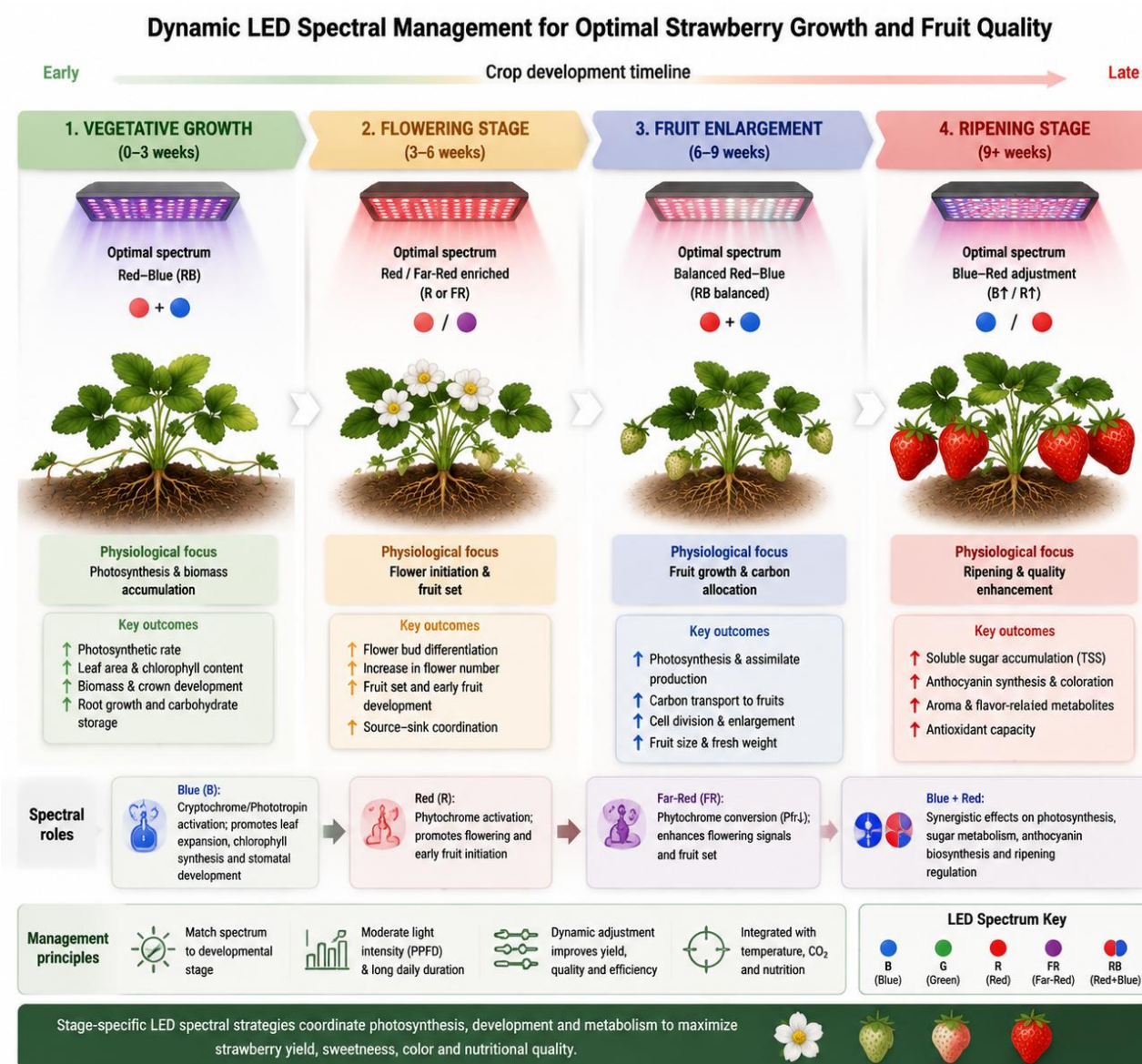


Figure 2 Developmental stage-specific LED spectral management strategy for optimizing strawberry yield and fruit quality

7.3 Canopy light optimization through leaf management and reflective mulching

Canopy light optimization depends both on plant architecture and on practices that increase fruit-zone light exposure. Field evidence shows that fruit light exposure changes strawberry flavor and antioxidant content, and that the magnitude of this response is cultivar-dependent, suggesting that leaf removal or canopy opening should be calibrated to genotype rather than applied uniformly. The same work found that cultivars maintained similar proportions of exposed fruit despite canopy-size differences by adjusting peduncle length, which highlights that canopy architecture itself influences how effectively management can redistribute light to the fruiting zone.

Reflective mulches provide a more direct case study of canopy light redistribution by increasing upward-reflected radiation into shaded fruit and lower canopy positions. In strawberry, highly reflective mulches increased growth and yield through larger fruit size and fruit number, and also increased ellagic acid and ascorbic acid concentrations, showing that improved reflected PAR can enhance both production and nutraceutical quality. More recent evidence indicates that mulch choice also affects fruit biochemical quality during ripening, with silver-black mulch outperforming paddy straw, black, and red mulches for fruit color and compositional traits, supporting reflective mulch as a practical tool for improving canopy light distribution and final fruit quality (Supreetha et al., 2024).

8 Future Perspectives and Conclusions

Future strawberry production will likely move from fixed supplemental lighting schedules to precision systems that regulate spectrum, intensity, and timing in response to plant demand and greenhouse conditions. Recent work on controlled environments identifies optimized spectral quality and spatial distribution as a promising route to improve yield, fruit quality, and resource-use efficiency, while emphasizing that dynamic and spatially adaptive lighting solutions will be essential for modern sustainable horticulture. This direction is reinforced by broader photobiology reviews showing that LEDs allow growers to tailor spectrum and intensity to crop needs and developmental stages, creating a practical basis for more precise regulation of strawberry growth and quality.

A second priority is the development of sensor-based and model-driven lighting control. Hourly light integral control has already shown that real-time monitoring of PPFD and temperature can determine when supplemental lighting should be applied or withheld, improving yield, soluble solids, and sugar-acid ratio under commercial greenhouse conditions. More advanced frameworks are now pointing toward remote monitoring, weather-linked forecasting, and centralized smart control, suggesting that future strawberry systems will combine sensor networks with predictive algorithms to regulate light proactively rather than reactively.

Stage-specific lighting is another major future direction because strawberry responses differ across vegetative growth, flowering, fruit development, and postharvest storage. Recent synthesis work argues that current reviews have often treated only part of the crop cycle and that a full developmental framework is needed to design stage-specific lighting strategies that improve both yield and quality. Consistent with this view, earlier review evidence identified unresolved questions on cultivar-dependent wavelength effects, blue:red ratios during vegetative and flowering phases, and flavonoid retention during storage and transport, all of which remain highly relevant for precision recipe design.

An additional frontier is dynamic lighting aligned with biological rhythms rather than static daily light delivery. Recent review evidence on circadian regulation shows that spectrum-tunable LEDs can now enable real-time control of light quality, intensity, and timing, and that dynamically combining these factors can coordinate biological rhythms with light-energy use more effectively than simple adjustments of intensity or spectrum alone. This suggests that future strawberry lighting systems should not only meet daily photon targets, but also test whether circadian-aligned light programs can improve sugar accumulation, metabolite balance, and energy efficiency in ways that fixed schedules cannot.

Future light management strategies will also need to fit within broader sustainability goals, because greenhouse production is energy-intensive and lighting is one of its most consequential inputs. Energy reviews show that greenhouses have substantial energy consumption and greenhouse gas emissions, and that energy-saving strategies in design and operation are therefore essential for sustainable crop production. Within that context, light regulation should be evaluated not only by its effect on yield and quality, but also by its contribution to whole-system energy conservation, carbon footprint, and environmental performance.

Low-carbon optimization provides a concrete framework for this integration. Multi-objective modeling work shows that supplemental lighting can be regulated against both photosynthetic performance and carbon-emission targets, reducing carbon emissions by as much as 14.85% while maintaining 95.49% of the net photosynthetic rate relative to light-saturation objectives. For strawberry systems, this implies that future lighting recipes should be selected by balancing fruit quality gains against electricity demand and carbon cost, rather than simply maximizing photon delivery.

Sustainable integration also includes combining light regulation with other resource-management practices. In greenhouse strawberry, supplemental light increased fruit polyphenols and sugars under both full and deficit irrigation, and the combination of silicate spray with LED lighting was recommended as a route to produce high-quality fruit while allowing deficit irrigation for water conservation. More broadly, informed management of sunlight through materials, structures, and monitoring can improve food quality and yield while potentially reducing water, energy, and pesticide use, indicating that artificial and natural light management should be treated as part of the same sustainability framework.

Another important sustainability perspective is that targeted light regulation may reduce dependence on chemical inputs and labor-intensive corrective practices. Preharvest red LED light has been shown to increase fruit yield and quality while improving tolerance to *Botrytis cinerea*, supporting the possibility that optimized light environments could contribute to future reductions in agrochemical use. At the industry level, broader strawberry production reviews also emphasize that future commercial systems will rely on new technologies, protected-environment systems, and management innovations to maintain high-quality production under mounting climatic and biological pressures.

The accumulated evidence indicates that light management is already a powerful tool for improving strawberry yield, sugar accumulation, pigmentation, and overall fruit quality, but the next advance will depend on moving from empirical recipes to mechanism-guided control. Existing reviews agree that artificial lighting can optimize fruit production and sensory quality, yet also stress that information remains limited on how specific light properties shape productivity and secondary metabolite accumulation in strawberry. Recent biotechnology-focused synthesis reaches a similar conclusion by emphasizing that strawberry quality formation is shaped by interactions among developmental stage, stress, and external regulation, and that modern tools such as omics, LED regulation, and gene-based approaches now offer a stronger basis for targeted intervention.

Several research gaps stand out clearly. One is the need for more work on underexplored spectral regions and treatment windows, especially preharvest UV-A, preharvest UV-C, and cultivar-by-temperature interactions under visible spectra. Another is the need for longer-term validation, because recent controlled-environment engineering work explicitly calls for studies on scalability across environments and long-term effects on plant health, yield stability, nutritional quality, and flavor characteristics.

Postharvest performance should also become a more central research target, because fruit quality benefits produced before harvest are only valuable if they persist through storage and transport. Current synthesis highlights rapid postharvest deterioration as a major constraint in strawberry and calls for more development of green prevention and control measures to support disease-free, high-quality fruit. This complements earlier calls to monitor flavonoid degradation after harvest and determine how long light-induced benefits are retained during storage and distribution.

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