

Review

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Review

# Manipulation of Light - A Futuristic Approach to Adjust Growth, Physiology, Nutrient Uptake and Yield Of Crops for Future Food Security Under Changing Climate

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**Abstract:** Globalization and technological advances have brought both challenges and opportunities to plant growth processes. The light spectrum contains various wavelengths and compositions, which play a critical role in the physiological development and yield of plants. Fluctuating light conditions trigger rapid molecular changes in plants, potentially impacting photosynthesis and crop quality. With advances in artificial plant lighting, cell imaging tools, and molecular biology, researchers can now explore the effects of light on plants at the cellular and genetic levels, providing insights into optimizing growth and addressing agricultural challenges. Modern technology empowers farmers to finely manage light in controlled environment agriculture (CEA). Artificial lighting, sunlight manipulation, and hybrid systems offer essential photons for photosynthesis, ensuring a consistent energy supply to plants regardless of natural light availability. Emerging data highlight the pivotal role of light in plant growth and morphology, but the precise mechanisms governing nutrient absorption remain elusive. This review explores the influence of light on crop development, yield, nutrient absorption, and utilization in agricultural and horticultural crops, offering insights to enhance crop production, optimize fertilizer efficiency and maintain global food security under changing climate.

**Keywords:** Light manipulation; CEA; Crop productivity; Climate change

## 1. Introduction

In recent decades, climate-induced factors have affected the crop production, causing the severe food and energy challenges in the world (Wang et al., 2021a). The increasing global demand for nutritious food has led to unsustainable agricultural practices and overuse of natural resources, worsening environmental issues. Open field farming is threatened by pest, drought, and frost stress exacerbated by climate change, prompting the exploration of alternative methods (Keutgen, 2023).

Controlled environment agriculture (CEA) has emerged as a viable solution, creating controlled plant growth environments that minimize external influences (Tan et al., 2021). CEA actively adjusts

plant growth conditions to optimize yield and quality, offering a promising approach to evolving agricultural challenges (Lefers et al., 2020). Light is a critical factor in plant development, impacting photosynthesis and growth as the primary source of energy (Leister, 2023). Beyond photosynthesis, light influences the production and quality of various plant macromolecules (Nassarawa et al., 2021).

The natural distribution of sunlight is uneven around the world, leading to seasonal fluctuations and varying energy availability (Konapala et al., 2020). Additional grow lights are used to compensate for insufficient sunlight, especially in indoor farms. The light spectrum, encompassing various wavelengths or light qualities, significantly influences plant growth, morphology, physiological process, and yield (Gawande et al., 2023). Plants rely on 16 essential elements for growth, obtaining carbon (C), hydrogen (H), and oxygen (O) from air and water, while other elements come from soil through roots (Bhatla et al., 2018). Macronutrients like nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulphur (S) are crucial for plant growth and development (Toor et al., 2021). Plants have evolved diverse strategies to optimize the absorption and utilization of these nutrients. They adapt to the changing environment by perceiving light signals and adjusting nutrient absorption accordingly (Ferrante et al., 2017).

Light, the primary energy source for plants, fluctuates with time, seasons, and circadian rhythms, influencing these processes. Many studies have shown that changes in light quality, intensity, and photoperiod impact the growth, physiology, nutrient uptake, and yield of plants (Tan et al., 2021). Photosynthetically active radiation (PAR), crucial for plant growth, spans 400-700 nm, with red/orange (610-720 nm) and blue/purple (400-510 nm) light accounting for about 85% and 12%, respectively (Han et al., 2020). In contrast, yellow and green light (510-610 nm) are minimally absorbed (Xu et al., 2019). By leveraging plant's response to light, agriculture aims to enhance crop yield and quality through tailored lighting strategies.

Horticulture employs light quality manipulation using photo-selective nets or films to enhance plant productivity, quality, and phytochemical composition (Gawande et al., 2023). These tools shield crops from adverse environmental conditions such as excess sunlight, heat, drought, wind, hail, and pests, ultimately increasing crop yield and quality. Additionally, this approach can extend the shelf life of vegetables and reduce postharvest losses (Xu et al., 2019). Greenhouses are vital for extending the growing season and mitigating the impact of fluctuating weather conditions, addressing the food demands of our growing global population (Keutgen, 2023). However, the expenses related to power grid installation and electricity consumption for climate control, particularly in remote areas, can be prohibitively high (Han et al., 2020). Traditional greenhouse lighting sources including fluorescent, metal halide, high-pressure sodium, and incandescent bulbs often emit excess low-quality wavelengths, which are unsuitable for optimal plant growth (Lefers et al., 2020).

To tackle these challenges, light emitting diode (LED) technology offers a means of modifying plant traits to enhance crop yield and quality in targeted crops. This innovation conserves resources and promotes sustainable food production, particularly in challenging environments such as deserts and interplanetary platforms (Paradiso and Proietti, 2022). LEDs are revolutionizing plant cultivation by efficiently converting electrical energy into light. They offer high luminous efficiency, energy efficiency, low heat production, compactness, long lifespan, eco-friendliness, energy conservation, and easy controllability (Lefers et al., 2020). LEDs shape the light environment for plant growth and find broad applications in tissue culture (Konapala et al., 2020). Considered cutting-edge, they enhance horticultural crop yield under controlled conditions. The function of light signalling in plant growth and development and the transcriptional regulatory network of the light signalling pathways have been summarized. However, the mechanisms of light signalling have not been further explored in terms of nutrient uptake and yield. Here, we review the key lighting technologies in indoor agriculture, focusing on the latest LED advancements. While optimizing light for plant growth is vital, the current review aims to fine-tune the light spectrum to enhance not only growth and yield but also the production of bioactive compounds and secondary metabolites, addressing the challenge of maximizing the nutritional quality of crops.

## 2. Light Signaling in Plants - A Selective History

The history of light signaling research in plants has fundamentally shaped our understanding of how plants perceive and respond to light. Early research in the 19th century established that light functions not only as an energy source for photosynthesis but also as a signal to regulate growth (Liebers and Pfannschmidt, 2024). In the early 20th century, the discovery of photoperiodism demonstrated that plants could measure day length to time flowering, linking light perception to seasonal transitions in plant life cycles (Gendron and Staiger, 2023). Further advances came with the identification of phytochromes (responsive to red and far-red light), which play pivotal roles in regulating germination, stem elongation and flowering by switching between active and inactive forms (Sharma et al., 2023a). This adaptability led to the discovery of other photoreceptors, such as cryptochromes (responsive to blue light), which regulate growth, circadian rhythms, and stress responses and phototropins. The identification of light-responsive transcription factors, including PHYTOCHROME-INTERACTING FACTORS (PIFs) and ELONGATED HYPOCOTYL 5 (HY5), marked a significant step forward in understanding light signal transduction (Cai and Huq, 2024). PIFs, which are repressed by phytochromes in light, promote compact growth by controlling genes associated with cell elongation and shade avoidance. HY5, on the other hand, integrates signals from multiple photoreceptors to coordinate light-driven growth, thereby acting as a central regulator in photomorphogenic development (Wang et al., 2022).

At the molecular level, the transcriptional regulatory network of light signalling pathways orchestrates growth, survival, and development (Liebers and Pfannschmidt, 2024). The circadian clock, governed by light signalling pathways, plays an essential role in timing the vegetative-to-reproductive transition, aligning flowering with favourable environmental conditions. This clock modulates gene expression in 24-hour cycles, allowing plants to synchronize their growth processes with day-night rhythms (Sharma et al., 2023a). For example, in long-day plants like *Arabidopsis*, the key gene *CONSTANS* (CO) activates *FLOWERING LOCUS T* (FT) in response to light. FT then moves from leaves to the shoot apical meristem, initiating flowering under ideal conditions (Yu et al., 2024). In short-day plants, CO and FT are regulated to delay flowering until shorter days signal optimal seasonal conditions (Cai et al., 2024). Understanding these pathways offers agricultural potential, as adjusting flowering times can optimize crop yields across diverse climates. As a central player in light signaling, HY5 not only integrates photoreceptor signals but also links light conditions to nutrient acquisition (Cai and Huq, 2024). HY5 enhances nitrate uptake by upregulating nitrate transporter genes, increasing nitrogen availability essential for protein synthesis and growth. It similarly affects phosphate transporter genes, promoting phosphorus acquisition for energy transfer and metabolic processes (Wang et al., 2022). These coordinated interactions enable plants to dynamically adapt to their environment, with this regulatory network offering genetic targets to improve crop yields, light efficiency, and resilience in agriculture.

Beyond light, plants must also adapt to temperature changes, and the integration of light and temperature signalling pathways is crucial for coordinating growth and survival in fluctuating environments (Liebers and Pfannschmidt, 2024). In warm conditions, certain phytochromes become less stable, allowing increased PIF activity, which promotes cell elongation and rapid growth to adapt to the season. Conversely, stable phytochromes in cooler temperatures inhibit PIFs, resulting in more compact growth that conserves energy (Wang et al., 2022). In response to abiotic stresses like drought, salinity and temperature extremes, regulatory molecules such as 14-3-3 proteins help plants adapt by modulating key processes. The 14-3-3 proteins interact with H<sup>+</sup>-ATPases, proton pumps that maintain ion homeostasis and cellular pH (Pertl-Obermeyer et al., 2022). This interaction stabilizes the phosphorylated state of H<sup>+</sup>-ATPases, facilitating proton pumping into the apoplast. For instance, in drought conditions, the 14-3-3/H<sup>+</sup>-ATPase complex helps maintain turgor pressure, which is critical when water is scarce (Cai et al., 2024). In saline environments, activated H<sup>+</sup>-ATPases enable Na<sup>+</sup> exclusion through Na<sup>+</sup>/H<sup>+</sup> antiporters, reducing salt toxicity. Furthermore, photoreceptors like phytochrome B (phyB) assist in osmotic adjustment by modulating abscisic acid (ABA) levels, while cryptochrome1 (CRY1) and phototropins mitigate oxidative stress from salt exposure (Yu et al., 2024). Insights into the integration of these pathways deepen our understanding of plant adaptability, showcasing the profound impact of light signalling research on both plant biology and agriculture.



### 3. Importance of Light in Crop Growth

Light is essential for photosynthesis, which is crucial for healthy plant development. Light quality profoundly impacts plant phenotypic traits through photomorphogenic mechanisms and metabolic regulation (Alsanius et al., 2019). Day length regulates the biological clock, influencing phenological events such as flowering, seed germination, and biomass allocation (Osnato et al., 2022). Alterations in these light factors can trigger transitions in plant development, affecting the distribution of photosynthates among leaves, roots, supporting tissues, and symbiotic partners (Gawande et al., 2023). Initially, Thomas Engelmann's research during 1882 addressed the role of blue light in leaf development and the influence of red light on flowering and fruiting, while green light was considered the least effective due to reflection (Neo et al., 2022). However, recent studies have revealed that green light, ultra violet (UV), and near-infrared radiation also contribute to plant growth (Huché-Thélier et al., 2016). Blue and red light activate photosynthesis mainly on the upper leaf surface, absorbed by chlorophyll a and b pigments, while green light penetrates deeper, aiding carbon fixation in the lower leaf layers facilitated by the accessory pigment  $\beta$ -carotene, which further enhances the photosynthetic process (Simkin et al., 2022).

Photosynthesis relies on the absorption of three primary pigments: chlorophyll a, chlorophyll b, and  $\beta$ -carotene (Neo et al., 2022). Recent researches highlight the importance of light beyond the PAR range, including UV (A and B) and far-red light, which extends the usable light spectrum from 300 to 800 nm (Fortineau et al., 2021). The photosynthetic photon flux (PPF) quantifies the available light for plants, with 1  $\mu\text{mol}$  corresponding to approximately  $6.022 \times 10^{17}$  photons per second (Gorjian et al., 2023). The photosynthetic photon flux density (PPFD) is crucial for comparing different light sources, representing the number of PAR photons landing on a specific surface per unit area ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) (Simkin et al., 2022). Higher PPFD values indicate more accessible PAR photons for photosynthesis per unit area. Comparing different light sources, photon efficacy was measured in  $\mu\text{mol J}^{-1}$ , which is the ratio of PAR photons per second ( $\mu\text{mol s}^{-1}$ ) to the energy consumed by the lighting system per second (Watts or  $\text{J s}^{-1}$ ) (Fortineau et al., 2021). Additionally, the daily light integral (DLI) measures the total PAR photons received by a plant in a day, expressed as  $\mu\text{mol m}^{-2} \text{day}^{-1}$  (Gorjian et al., 2023). This metric is crucial because different plants have varying total light requirements.

#### 3.1. Different Types of Light and Its Effect on Crops

Conflicting findings on the effects of light on plant development arise from variations in study materials, shading intensity, duration, the number of shading days, and ecological factors. Shading affects not only light intensity but also environmental parameters like light quality, air humidity,  $\text{CO}_2$  levels, and soil temperature (Ferrante et al., 2017). In addition to intensity and duration, light composition such as blue, red, and far-red light also play pivotal roles in plant photomorphogenesis (Nassarawa et al., 2021). Variations in light quality significantly impact crop biomass. Red (R) light reduces internode elongation, enhances lateral branching, and boosts tillering, improving resistance to abiotic stress (Huber et al., 2021). Different red/far-red ratios affect salt and temperature tolerance, coleoptile length, and rootlet quantity in rice (*Oryza sativa*) (Cao et al., 2018). Red light influences chloroplast, stem, petiole growth, and reproductive activity, while blue (B) light predominantly governs plant growth, leaf size, photomorphogenesis, stomatal opening, photosynthesis, and pigment development (Li et al., 2021). Due to their similarity to photosynthesis spectra, research often focuses on monochromatic or mixed red and blue LED lighting effects.

Research on the effects of white (W), far-red (FR), green (G), yellow (Y), and orange (O) LEDs on plant growth is limited. However, previous studies have shown that monochromatic light can have beneficial effects on root development and physiological metabolism in plants, although these effects vary depending on the plant species (Konapala et al., 2020). For example, red LED light inhibits root growth in *Doritaenopsis* plants, while blue LED light promotes root formation in *Chrysanthemum* plants and enhances the rate and number of roots in *Achillea millefolium* and *Vanilla planifolia* cultures (Cavallaro et al., 2022). Furthermore, red light can enhance antioxidant activity in pea (*Pisum sativum*)

seedlings, *Dendrobium officinale* seedlings, and *Eleutherococcus senticosus* somatic embryos, with enzyme responses differing based on the quality of light (Xu et al., 2019).

Li et al. (2010) demonstrated that red light enhanced root activity, sucrose, and starch levels in *Gossypium hirsutum* tissue culture seedlings, but adding more blue light to red LEDs resulted in larger, healthier plants with higher biomass. Kulus and Woźny (2020) found that the combination of red and blue light stimulated root growth and increased leaf area in *Doritaenopsis* tissue culture seedlings. Additionally, carbohydrate synthesis (starch, sucrose, glucose, and fructose) was significantly higher under this light quality compared to monochromatic red, blue, or fluorescent light treatments (Achour et al., 2021).

Green light plays a crucial role in plant growth and development, influencing seed germination, flowering, and regulating fruit and shoot development (Paradiso and Proietti, 2022). In addition, green wavelengths enhance photosynthesis and carbon uptake by penetrating deep into leaf mesophyll and lower canopy layers to benefiting chloroplasts (Gorjian et al., 2023). When combined with red and blue lights, green and orange lights enhance photosynthesis and translocation by impacting source/sink relationships among plants (Huber et al., 2021). These wavelengths also increase water efficiency and overall plant development by accumulating photosynthates in leaves (Konapala et al., 2020). Therefore, incorporating green light into CEA is beneficial alongside red and blue lighting.

Although UV-B radiation is a small part of total solar radiation, it carries high energy and can cause significant biological damage to plant cells even with slight increases (Sharma et al., 2017). Plants are sensitive to elevated UV-B levels as various biological components directly absorb this radiation (Zlatev et al., 2012). Therefore, it is crucial to understand the effects of heightened UV-B exposure on the development and physiology of agricultural crops in greenhouses or open fields. UV radiation spans 100-400 nm, including UV-A (320-400 nm), UV-B (280-320 nm), and UV-C (200-280 nm) (Bosso et al., 2023). UV light serves as both a stressor and regulator, exerting a substantial influence on plant growth and nutritional quality. UV-B radiation is a significant abiotic factor with direct and indirect effects on plants. It impacts the production of secondary metabolites such as phenolics, terpenes, and nitrogen compounds (Cao et al., 2018). Studies indicate that increased UV-B exposure can impair plant physiological processes, including photosynthetic CO<sub>2</sub> uptake and efficiency, highlighting its multifaceted impact on plant biology (Sharma et al., 2017).

#### 4. Need and Type of Light Manipulations

Light manipulation in greenhouses offers the potential to increase crop yield, improve crop quality in terms of colour, compactness, and secondary metabolite content, and enhance energy efficiency in greenhouse operations (Paradiso and Proietti, 2022). Microclimate control strategies vary by location, with the need for surplus heat dissipation in sun-drenched tropical regions and heat retention in temperate zones, especially during colder seasons with limited solar radiation (Nwokolo et al., 2023). In greenhouse applications, spectral manipulation is achieved by two main methods: (i) selective transmission of specific spectral components while blocking others via reflection, scattering, or absorption, which can be accomplished using scattering nanoparticles, 1D photonic crystals (1DPCs), or plasmonic nanoparticles; (ii) converting less favourable wavelengths into those more beneficial for photosynthesis, plant growth, development, morphogenic effects, or microclimate control within the greenhouse (Otanicar et al., 2016). This conversion is facilitated by using the phenomena of light down-conversion or up-conversion.

##### 4.1. One-Dimensional Photonic Crystals

Photonic crystals (1DPCs) are engineered materials with a regularly changing refractive index along one dimension. They typically consist of alternating layers with high and low refractive indices, like multilayers (Shen et al., 2016). This periodic variation causes incoming light to undergo successive back reflections at each interface. These structural parameters define a "photonic band gap" (PBG), a range of wavelengths where back reflections align in phase, leading to constructive

interference (Zhu et al., 2023). As a result, most incident light is reflected or rejected within the PBG, effectively controlling, and modifying the passage of light through the photonic crystal.

Polymer-based 1DPCs are now gaining attention as lighter, flexible, and cost-effective alternatives, promising efficient near infra-red (NIR) blocking and improved sustainability in greenhouse coverings (Nwokolo et al., 2023). Polymer-based photonic crystals offer advantages such as lower cost and ease of sourcing, but their drawback is limited refractive index contrast between adjacent layers. This impacts band gap width and spectral blocking efficiency, necessitating improvements to match inorganic 1DPCs (Shen et al., 2016). The PBG, which is determined by back reflections' interference in multilayers, varies with the angle of the incident light, an important consideration for adapting 1DPCs to greenhouses. Due to changing orientations, shifting sunlight angles, and diffuse illumination in greenhouses, the precise position and width of the PBG may not remain constant (Otanicar et al., 2016). The true potential of 1DPCs lies in their customizable optical properties, which can be optimized through computer-based design, making them versatile solutions for greenhouse applications (Iezzi et al., 2020). Plasmonic systems, however, harness unwanted wavelengths, offering spectrally selective transmission and absorption, making them versatile in such settings (Shen et al., 2016).

#### 4.2. Plasmonics

Plasmonics hinges on "plasmon resonances," a collective oscillation of free electrons induced by electromagnetic radiation on a plasmonic system. It focuses on localized plasmon resonances, where electron oscillations are confined to the surface of metallic nanoparticles, as opposed to propagating surface plasmons, which are electron plasma waves travelling along a metal-dielectric interface (Kuppe et al., 2020). Gold or silver nanoparticles, rich in free electrons that oscillate in response to incoming light, exemplify such localized plasmon resonances (Yildirim et al., 2021). Resonance wavelength in plasmonic nanoparticles depends on their size, shape, material, and the surrounding medium, allowing for tunable spectral selectivity. Plasmons efficiently convert light to heat due to non-radiative decay of collective oscillations, making them valuable for greenhouse technology, where both light-to-heat conversion and spectral manipulation play crucial roles (Nwokolo et al., 2023).

Computational designs have proposed plasmon-based transparent filters that effectively block UV and NIR light for photo voltaic (PV) cells. However, fabricating precise nanostructures with varying plasmon diameters can be expensive (Thrithamarassery et al., 2017). Recent studies have explored cost-effective solutions, using disordered plasmonic nanostructures made from affordable materials such as Cu and Al embedded in IR-blocking glass (Yildirim et al., 2021). This innovation holds promise for cost-effective passive cooling in buildings and potentially in greenhouses. Plasmonic light-to-heat conversion is a potential solution for low-energy heating in greenhouses in cold-climate (Otanicar et al., 2016). It utilizes wavelength selectivity to absorb less useful solar wavelengths and efficiently convert them into heat.

The primary drawback of plasmon-based technology is its high cost, particularly when utilizing noble metals like Au or Ag (Yildirim et al., 2021). Ongoing research into the plasmonic properties of aluminium, an abundant and affordable metal, and promises enhanced economic feasibility and sustainability for plasmonic systems. However, at high light intensities, significant heating effects at plasmon resonance can cause nanoparticles to melt, altering their shape and size, and thereby affecting the system's spectral characteristics and performance (Thrithamarassery et al., 2017). While plasmon-driven light-to-heat conversion helps save energy in greenhouses, it does not significantly enhance PAR intensity for plant photosynthesis. Spectral conversion through luminescent processes including photon down- and up-conversion offers a more viable approach to boost photosynthetic photon flux density (Kuppe et al., 2020).

#### 4.3. Luminescence

Luminescence denotes the emission of light, which can result from electrical energy, mechanical tension, chemical reactions, or photon absorption, the latter being termed "photoluminescence" (Bai

et al., 2015). In greenhouse innovation, we explore two photoluminescent processes: down-conversion and up-conversion. A wealth of publications spanning diverse applications, including fluorescence microscopy, PV technology, and artificial photosynthesis, offer detailed insights into the mechanism, composition, and design of suitable luminescent materials (Liu and Qiu, 2015).

#### 4.3.1. Luminescent Down-Conversion

Luminescent down-converting substances absorb photons of a specific energy and subsequently emit lower-energy photons through internal conversion processes. This process, which includes down-conversion and down-shifting, broadens the absorption and emission spectra around their respective peak wavelengths (Nwokolo et al., 2023). In greenhouses, where blue and red wavelengths are crucial for photosynthesis, UV-to-blue/red or green-to-red spectral down-conversion processes are particularly relevant to optimize light conditions for plant growth (Bai et al., 2015). Lanthanide ions such as neodymium ( $\text{Nd}^{3+}$ ), ytterbium ( $\text{Yb}^{3+}$ ), and europium ( $\text{Eu}^{3+}$ ) can be employed for luminescent down conversion, either alone or in combination with organic molecules (Nalumaga, 2022). However, their limitations include poor absorption coefficients and high cost. Since the 1990s, research on plastic films with fluorescent colours as greenhouse cover for various crops, such as tomatoes and strawberries, has yielded generally satisfactory results (Bai et al., 2015). Recent advances in the commercial production of fluorophores in greenhouse materials claim positive effects on leaf and stem size, fruit size, and yields in various crops including lettuce, strawberries, tomatoes, and cannabis (Mishra et al., 2023).

However, specific studies quantifying photon flux density with and without plastic films have reported intriguing results. Boucher et al. (2023) observed an 8.7% increase in dry weight, an 11% increase in fresh weight, and a 13% increase in lettuce leaf area, despite a 12% reduction in the DLI within the PAR range. Furthermore, they found a 19-22% increase in fresh and dry weight of lettuce, even with a 20% DLI reduction. This effect may be attributed to an elevated red/far-red ratio, known to stimulate developmental activity and regulate stem elongation rates and branching (Liu and Qiu, 2015). Understanding the mechanisms behind yield increases with fluorescent films requires considering two inherent consequences: shading, where transmitted photon flux is efficiently reduced, and diffusion, stemming from isotropic photon emission by fluorophores (Bai et al., 2015). To assess shading's impact, light intensity within and outside the films, measured as photon flux density or DLI, is crucial. These factors can significantly impact production, particularly in high-light environments and for shade-tolerant crops.

A challenge with natural sunlight is to achieve significant photon down conversion to the blue band, since higher-energy wavelength bands are a small fraction of the solar spectrum (Nalumaga, 2022). Red/far-red photons are more accessible through down conversion from the UV, blue, or green wavelengths. While the red band is critical for plant growth and biomass, even slight increases in photon density in the blue and UV regions can impact photomorphogenic characteristics (important for ornamental plants) and secondary metabolites that influence flavour and nutritional content (Mishra et al., 2023). This limitation, which mainly affects spectral down conversion, can be overcome through a phenomenon known as luminescent up-conversion.

#### 4.3.2. Luminescent Up-Conversion

Luminescent up-conversion involves the absorption of multiple low-energy photons and subsequently emitting a higher-energy photon. This process is more complex than down conversion. In a simplified explanation, up conversion occurs when a system absorbs multiple low-energy photons, causing its electrons to reach higher energy levels, and then these electrons release energy by emitting a high-energy photon (Bai et al., 2015). Rare-earth ions like erbium ( $\text{Er}^{3+}$ ), thulium ( $\text{Tm}^{3+}$ ), and holmium ( $\text{Ho}^{3+}$ ) are commonly used activators due to their ladder-like energy levels (Nalumaga, 2022). Ytterbium ( $\text{Yb}^{3+}$ ) serves as a sensitizer due to its broad absorption cross section and efficient energy transfer to activator ions (Wang et al., 2023). In greenhouses, the desired up-conversion could target NIR ( $\lambda_{\text{abs}}$ ) to red/blue/UV ( $\lambda_{\text{em}}$ ) or green ( $\lambda_{\text{abs}}$ ) to red/blue/UV ( $\lambda_{\text{em}}$ ) wavelengths (Liu and Qiu, 2015).



Up-conversion transitions have been observed under low-power artificial lighting but remain far from commercialization for solar radiation in greenhouses. Applications such as bioimaging and medical treatment often demand coherent and powerful laser sources (Otanicar et al., 2016). However, in greenhouses, even slight enhancements in PAR photon flux density through up-conversion can have significant impacts, warranting further proof-of-concept studies (Liu and Qiu, 2015). Modest up-conversion to UV photons can help improve colour, flavour, and nutrient enhancement, while NIR-to-visible photon up-conversion offers both heat control and increased photosynthetic photon flux (Wang et al., 2023). Promising preliminary studies pairing up-converting systems with photosynthetic processes have shown significant benefits. *Arabidopsis thaliana* exhibited a 12% increase in photosynthetic rate under natural light enriched with UV when utilizing films combining down-converting luminophores and NIR-PAR up-converting luminophores (Nalumaga, 2022). In addition, NIR-PAR up-converting films improved tomato plants by increasing leaf number (12.5%), leaf area (33%), and chlorophyll content under artificial light (Yanykin et al., 2022).

These studies lay the groundwork for materials that can be optimized and assessed for various crops under natural sunlight. Current efforts to enhance up-conversion efficiency under lower light intensities, like Earth's incident solar radiation, involve material parameter experiments, nano structuring, employing photonic structures like dielectric micro lenses for light concentration, and utilizing plasmonic structures to amplify local fields (Nwokolo et al., 2023). These findings represent crucial initial strides toward making up-conversion a viable technology for greenhouses operating under natural sunlight conditions. Organic-based up-conversion systems offer sustainability, safety, larger absorption cross-sections, higher efficiency, and tunability compared to rare-earth-based systems (Yanykin et al., 2022). Organic systems exhibit emission wavelengths from 380-630 nm, while rare-earth-based systems cover 290-800 nm, both promising for enhancing PAR in greenhouses (Mishra et al., 2023).

## 5. Manipulation of Light and Its Response to Crops

### 5.1. Manipulation of Light on Crop Growth Changes

Light serves as a pivotal signalling factor in plant growth, influencing plant physiology and development (Bao et al., 2024). Plant photoreceptors, mainly located in leaves, receive and process light signals. This complex system coordinates with various elements including proteins, ions, and hormones to regulate gene expression, metabolic responses, and plant morphology (Kharshiing et al., 2019). Hossain et al. (2022) highlight that the management of reactive oxygen species (ROS) and their interplay with antioxidants is a key process shaping plant development and morphogenesis. Li et al. (2021) conducted a study demonstrating the significant impact of light quality on tomato seedling development. They found that plant height was highest under red (R) light and lowest under purple (P) light. Compared to white (W) light, both monochromatic P and a combination of red and blue (R and B) lights significantly inhibited plant height ( $p < 0.05$ ). The stem diameter was significantly greater when exposed to the combination of R and B lights, particularly the 3:1 ratio of red to blue light (3R1B treatment), as compared to W, R, or B monochromatic light treatments. In general, shoot dry weight was highest under 3R1B and lowest under P light. Root dry weight patterns were similar across treatments. These results suggest that plant responses to light quality may depend on factors such as species, cultivar, growth time, or light intensity (Li et al., 2021).

Diverse light qualities significantly impacted the rooting rate, mean root number, root length, surface area, volume, and activity of *C. lanceolata* tissue culture seedlings ( $p < 0.05$ ) (Xu et al., 2019). The treatment with 8:1:1:1 red, blue, purple, and green light (8R1B1P1G) showed the highest results with a 95.5% rooting rate, 4.63 average root number, 5.95 cm length, 1.92 cm<sup>2</sup> surface area, and 145.56 ng gh<sup>-1</sup> root activity. These values were significantly higher (ranging from 4.2% to 28.9%) than those under the white LED treatment. In general, the combination of red-blue-purple-green light outperformed red-blue and red-blue-purple treatments in promoting root development and activity. This effect is attributed to the complementary interplay of red, blue, and purple light, although plants have a lower demand for this combination (Carvalho and Castillo, 2018). Purple and green photons remain essential for photosynthetic radiation. Incorporating purple and green light alongside red and

blue light can potentially enhance photosynthate transport to the roots, thereby promoting root development (Yang et al., 2022).

Blue light plays a role in glycolysis by inhibiting  $\beta$ -ketoglutarate dehydrogenase, activating nitrate reductase, and increasing pyruvate kinase protein production (Bartman et al., 2017). Moreover, the higher energy of blue light photons can provide additional energy for macromolecular synthesis, especially in protein synthesis (Carvalho and Castillo, 2018). Recognizing the influence of various light regimes on crop growth is pivotal for maximizing output in controlled environments, improving resource utilization, and adapting to dynamic environmental shifts. Table 1 illustrates how light colour affects the growth, yield, and nutritional quality of greenhouse vegetables, providing valuable insights for optimizing cultivation practices.

**Table 1.** The impact of light colour on growth, yield, and nutritional quality of greenhouse vegetables.

Light colour	Intensity	Plant	Effect on growth	Effect on yield	Effect on nutritional quality	References
Far red	700 – 850 nm	Lettuce ( <i>Lactuca sativa</i> )	The addition of far-red light increased the leaf area index by 12.3%.	Increased fresh weight by 20%.	Far red light stimulates nitrogen uptake in plants. Under additional far-red light, plants showed a 11% increase in K, 25.5% increase in Ca, and 18.6% increase in Mg uptake compared to red and blue light.	Shmarev et al. (2024)
Far red	700 – 850 nm	Lettuce ( <i>Lactuca sativa</i> )	Improved shoot and root growth by 23.5%.	Increased fresh weight by 33%.	-	Meng et al. (2024)
Red	620 – 700 nm	Lettuce ( <i>Lactuca sativa</i> )	-	Shoot fresh weight decreased by 22% compared to sole white LEDs.	Increased chlorophyll and carotenoids concentrations.	Razzak et al. (2022)
Blue	425 – 490 nm	Lettuce ( <i>Lactuca sativa</i> )	Promoted lettuce growth by 15%.	-	Increased polyphenol concentrations and total antioxidant status.	Alrajhi et al. (2023)
Blue	440 nm	Lettuce ( <i>Lactuca sativa</i> )	Compact plant morphology.	-	Increased chlorophyll concentration.	Modarelli et al. (2022)
Blue	425 – 490 nm	Cabbage ( <i>Brassica oleracea</i> var. <i>capitata</i> )	Promoted petiole elongation in cabbage by 26%.	Increased fresh weight by 10%.	Increased anthocyanin contents and leaf pigmentation in cabbage.	Liu et al. (2022)
Blue	425 – 490 nm	Cabbage ( <i>Brassica oleracea</i> var. <i>capitata</i> )	Blue LEDs promote vegetative growth, while red LEDs and blue plus red LEDs support reproductive growth.	-	Concentration of vitamin C was highest under blue LEDs.	Zhang et al. (2023)

Blue	425 – 490 nm	Cucumber ( <i>Cucumis sativus</i> L.)	Leaf area decreased with up to 75% blue light treatment, but 100% blue light increased leaf area.	Plants under 50% blue light had the lowest shoot biomass, while those under 100% blue light had the highest biomass.	Enhanced chlorophyll and carotenoids concentrations.	Wang et al. (2021b)
Green	490 – 550 nm	Cucumber ( <i>Cucumis sativus</i> L.) and tomato ( <i>Solanum lycopersicum</i> )	Increased leaf area by 15% and 20.5%, respectively.	Increased fresh and dry weight by 10% and 12.5%, respectively.	Increased photosynthetic pigment concentrations in both vegetable transplants.	Liu et al. (2023)
Green	490 – 550 nm	Mustard ( <i>Brassica nigra</i> )	-	-	Increased total carotenoids	Singh et al. (2021)
UVB	280 – 315 nm	Lettuce ( <i>Lactuca sativa</i> )	-	Increased fresh and dry weight by 24% and 15%, respectively.	Pre-harvest UV-B light stimulated anthocyanin concentration, with significantly higher levels observed at 310 nm compared to 325 and 340 nm.	Lee et al. (2021)

5.2. Manipulation of Light on Crop Physiological Changes

For more than half a century, research has shown that the conversion of incoming irradiance into chemical energy through photosynthesis is influenced by the wavelength of light. Pioneering studies by McCree (1972), Inada (1976), and Evans (1987) revealed that red light has the highest quantum yield for CO<sub>2</sub> fixation in many species within the photosynthetically active light spectrum. Given the superior photosynthetic quantum yield of red light and the exceptional electrical efficiency of red LEDs, researchers have increasingly utilized high proportions of red light to create optimal conditions for photosynthesis and plant growth (Yang et al., 2018). Hogewoning et al. (2010) quantitatively demonstrated how leaves adjust their photosystem composition in response to diverse light spectra (sun, shade, and blue light). Mixing different wavelengths of light was shown to substantially enhance the quantum yield of for CO<sub>2</sub> fixation, offering valuable insights into photosystem adaptation (Kunz et al., 2020). The intricate light signaling pathways play important role in regulating the absorption and utilization of essential nutrients in plants (Figure 1).

Plants exhibit dynamic responses and adaptations to their external light conditions. The increased presence of far-red light (FR), often characterized by a low R:FR ratio, in shaded areas beneath dense canopies is due to the wavelength-dependent interactions of leaves with natural light (Lazzarin, 2023). These spectral shifts are not restricted to plant communities but are also observed within individual plants. Li et al. (2021) conducted a 30-day study on tomato seedlings to assess how light quality impacted photosynthetic rates (Pn). The results showed that the leaf Pn of seedlings exposed to red (R) and blue (B) light combinations and monochromatic blue light significantly outperformed those under white (W) light (p < 0.05). The highest Pn was recorded in plants exposed to a 3:1 ratio of red and blue (3R1B) light, while the lowest occurred in those grown under purple (P) light.

Under dye-sensitized solar cell-covered greenhouses, tomato photosynthesis decreased (Ntinis et al., 2019), while a NIR-reducing coating enhanced cucumber photosynthesis (Alsadon et al., 2016). These responses in greenhouse vegetables reflect their adaptation to altered light conditions caused by different cover materials. This adaptation encompasses various processes like light sensing, absorption, and energy conversion (Lazzarin, 2023). The light environment created by these materials has a significant effect on photosynthesis. Pigments, such as chlorophyll and carotenoids, capture

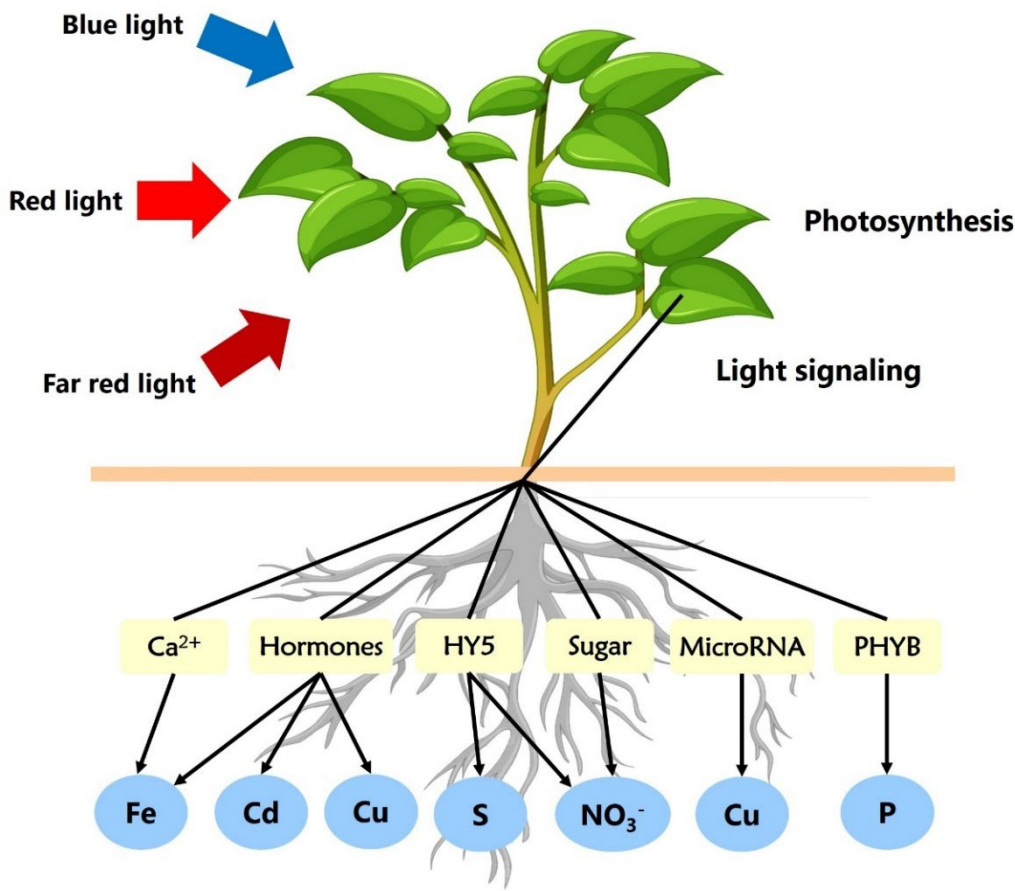
light, especially PAR, initiating electron transport and energy conversion (Ramanna et al., 2017). The mobility of chloroplasts and pigments at the cellular level and thylakoid membrane orientation adjustment in response to varying light conditions play essential roles in this complex process (Kirchhoff, 2019).

Photosynthesis relies on light sensing and the activities of photosystem I (PSI) and photosystem II (PSII) (Kunz et al., 2020). Pigments in PSII absorb light, initiating water molecule splitting to create a proton gradient. Optimal photosynthetic conditions vary with plant types and light spectrums (Kaiser et al., 2015). Young tomato plants thrive with  $300 \text{ mol m}^{-2} \text{ s}^{-1}$  PPFD and at least 8 hours of daily light, while leafy vegetables do well with  $200 \text{ mol m}^{-2} \text{ s}^{-1}$  (Wojciechowska et al. 2015). For instance, elevating the blue light ratio can enhance leaf photosynthesis, photosynthetic rate, and PSII quantum yield under monochromatic red light (Wang et al. 2018). Understanding these findings on light receptors and acclimation could predict yield under different cover materials.

Cope and Bugbee (2013) highlighted two likely factors restricting the relative quantum efficiency of blue light in photosynthesis: (1) some blue photons are absorbed by non-photosynthetic pigments including anthocyanins, leading to energy loss as heat or fluorescence. (2) Accessory pigments such as carotenoids consume some blue photons and are 10% to 65% less efficient than chlorophyll molecules at transferring light energy to the photosynthetic reaction centre. In many plant species, increased exposure to blue light inhibits cell division and growth, resulting in reduced leaf area, shorter stems, and thicker leaves.

Monochromatic LED lighting can induce physiological anomalies in specific plant species or varieties not typically observed under broad-spectrum light (Kume, 2017). For example, the condition known as intumescence, characterized by abnormal cell outgrowth on plant surfaces due to abiotic stress, was initially associated with a lack of ultraviolet (UV; 300 to 400 nm) and far-red light in the spectrum (Ullah et al., 2019). Studies have shown that UV light can suppress intumescence formation in susceptible tomato (*Solanum lycopersicum*) and ornamental sweet potato (*Ipomoea batatas*) cultivars (Williams et al., 2016). Intumescence not only disrupts plant physiology but also negatively affects the aesthetic quality of plant products, a significant concern for decorative plants grown under narrowband LED lighting (Anjum et al., 2017). Fine-tuning the spectrum, intensity, and duration of light exposure allows researchers and farmers to modulate plant physiology. This manipulation impacts photosynthesis, transpiration, hormone regulation, and stress responses, altering growth, nutrient uptake, and overall health. Understanding these processes is crucial for optimizing crop production. Table 2 illustrates the effects of red and blue light on nutrient accumulation in horticultural crops in controlled environments.





**Figure 1.** Systematic representation of multiple light signaling pathways regulating nutrient uptake in plants (HY5 – Long hypocotyl 5, PHYB – Phytochrome).

**Table 2.** Effects of red and blue light wavelengths on macro and micronutrient accumulation in horticultural crops grown in a controlled environment.

Light sources	Crops	Nutrient level	References
Red	Chinese chive ( <i>Allium tuberosum</i> )	N↑, P↑	Xu et al. (2021)
Red	Spinach ( <i>Spinacia oleracea</i> L.)	Zn↑, Fe↑	Vaštakaitė-Kairienė et al. (2022)
Red	Cucumber ( <i>Cucumis sativus</i> L.)	P↑, K↑, Zn↑	Zhong et al. (2024)
Red	Lettuce ( <i>Lactuca sativa</i> L.)	$\text{NO}_3^-$ ↓, Fe↑, Zn↑	Bi et al. (2024)
R/B (4:1)	Celery ( <i>Apium graveolens</i> L.)	Zn↑, Mg↑, P↑, S↑	Sharma et al. (2023b)
R/B (1:4)	Broccoli ( <i>Brassica oleracea</i> var. <i>italica</i> )	Ca↑, Mg↑, P↑, S↑, B↑, Cu↑, Fe↑	He et al. (2020)
R/B (3:1)	Sweet basil ( <i>Ocimum basilicum</i> L.)	N↑, P↑, K↑, Ca↑, Mg↑, Fe↑	Lin et al. (2021)
R/B (7:1)	Celery ( <i>Apium graveolens</i> L.)	Zn↑, P↑, K↑, Fe↑	Budavári et al. (2024)
R/B (1:3)	Rapeseed ( <i>Brassica napus</i> L.)	P↑, K↑, Ca↑, Mg↑, S↑, Mn↑, Fe↑, Zn↑, Cu↑, B↑	Brazaitytė et al. (2021)
R/B (1:3)	Einkorn ( <i>Triticum monococcum</i> L.)	N↑, P↑, Mg↑, Fe↑, Zn↑	Bartucca et al. (2020)

5.3. Manipulation of Light on Flowering and Fruiting Changes

The flowering responses to light quality, similar to growth and development, are specific to plant species or cultivars and are primarily influenced by the duration of the uninterrupted darkness period within a day, called the critical night length (Ahn et al., 2015). Plants are typically classified into response groups based on how this critical night length affects their flowering regulation. In the absence of other limiting environmental or cultural factors, day-neutral plants will flower regardless

of the photoperiod (Osnato et al., 2022). Short-day (SD) plants flower most rapidly when the continuous dark period surpasses a species-specific required night length (Proietti et al., 2022). Conversely, long-day (LD) plants induce flowering more quickly when the dark periods are shorter than a critical duration (Wang et al., 2021b). In LD plants, when daylight periods are short, extending the days (i.e., reducing the length of the night) by artificial lighting can induce flowering while inhibiting blooming in SD plants may promote vegetative growth (Craig and Runkle, 2016).

Similarly, night interruption (NI) can effectively disrupt the dark phase and enhance the photoperiodic responses of LD. NI is more efficient than day extension in inducing flowering in LD plants (Osnato et al., 2022). Blue light, which is minimally absorbed by phytochromes, has been demonstrated to influence flowering at higher intensities ( $30 \text{ mol m}^{-2} \text{ s}^{-1}$ ) compared to the typical  $2 \text{ mol m}^{-2} \text{ s}^{-1}$  required from red and/or far-red light (Proietti et al., 2022). Red and far-red light remain the primary photoreceptors governing flowering in photoperiodic species (Bartucca et al., 2020). To manipulate the flowering and production cycles of plants, low light intensity is typically applied at night. This approach promotes flowering in LD plants, shortening their production cycle, while inhibiting flowering in SD plants, encouraging vegetative growth (Klein et al., 2018). Artificial lighting is employed to extend day length, stimulating vegetative growth, or as a night break to prevent premature flowering. This ensures year-round availability for market demand in the case of SD plants like chrysanthemums and allows for programmed flowering on specific market dates (Craig and Runkle, 2016).

In addition to photoperiod, spectral composition has a profound effect on flowering in both SD and LD plants. Distinct light qualities trigger the transition of flower by orchestrating the transcriptional control of genes that encode flowering activators, such as photoreceptors (Proietti et al., 2022). Multiple photoreceptors play essential roles in wavelength perception and absorption, including phytochromes (absorbing red/far-red light), cryptochromes (absorbing blue/UV-A wavelengths), and phototropins (primarily absorbing UV-B light). For LD plants, blue and far-red light are often used to stimulate flowering (Xu et al., 2021). Blue light accelerates LD flowering, resulting in a higher flowering index, more visible flower buds, and open flowers. This effect is associated with reduced phytochrome activity, also known as a phytochrome photo equilibrium (Wang et al., 2021b).

The impact of green light on photoperiodic flowering has been studied in a few instances. SD plants exposed to green light exhibited delayed or inhibited flowering, akin to responses seen with blue light (Zhao et al., 2020). The effects depend on the species, exposure duration, and light intensity. Meng and Runkle (2014) found that green light fluxes can act as a signal for long-day responses. To achieve optimal flowering responses in petunias, snapdragons, and ageratum floriculture crops required a light spectrum with moderate levels of green light for several hours. In contrast, green light delayed flowering in chrysanthemum and marigold SD plants, underscoring its role in regulating flower induction in photoperiodic species (Kisvarga et al., 2023).

The use of UV light can either promote or delay flowering, with outcomes varying by species, UV spectrum region, and fluence rate (Nazir et al., 2020). Excessive UV radiation can significantly affect flower quality. *Phacelia campanularia* A. Gray and *Salvia splendens* Sellow ex Nees plants exposed to high UV doses experienced reduced flowering period and flower numbers, while flower transitions were impeded in *Limnanthes alba* Hartw. ex Benth. Plants (Trivellini et al., 2023). Conversely, UV-C radiation improved flowering and increased the flower quantity in wild pansy and freesia decorative plants (Chandel et al., 2023). Fukuda et al. (2016) investigated the response of *Petunia* to light quality in relation to the regulation of gibberellin (GA) content. Their research revealed that blue and red light had contrasting effects on shoot elongation, which appeared to be linked to GA signalling. However, they could not establish a direct connection between light quality and flowering via GA signalling. Dueck et al. (2016) proposed that phytohormones responsible for bud break and inflorescence elongation in *Phalaenopsis* could be influenced by light rather than temperature. This finding is intriguing, suggesting that light quality could offer alternative signals to substitute for other environmental factors.

The rapid adoption of LEDs replaced incandescent bulbs as photoperiodic lamps due to their longer lifespan and, more importantly, the phasing out of incandescent bulb production in many countries due to their energy inefficiency (Younas et al., 2018). Compact fluorescent lamps are more energy-efficient and longer-lasting than incandescent bulbs, but their spectra have limited influence on flowering regulation (Trivellini et al., 2023). LEDs, with their narrow bandwidths, offer precise control over light quality, enhancing our understanding of how different wavelengths affect flowering. LEDs offer several advantages, including cost savings, accelerated flowering, and prevention of abnormal stem elongation in some plants (Cuong et al., 2019).

Research indicates that not all LED lights are equally effective in regulating flowering; their success depends on their specific spectral composition (Nadeem et al., 2019). Meng and Runkle (2014) found that both cool-white and warm-white LEDs were equally effective in regulating flowering when compared to red or blue plus red LEDs. Limited research has explored the role of green light in photoperiodic flowering control. In the comparison of LED and traditional lamps for their effectiveness in regulating photoperiodic plant flowering, LEDs prove to be as effective as traditional sources with the added advantage of lower overall operational costs (Khurshid et al., 2020). Kohyama et al. (2014) found that combining far-red and red + white light in night interruption enhances flowering in ornamental plants at low DLI ( $6 \text{ mol m}^{-2} \text{ d}^{-1}$ ) but not at high DLI ( $12 \text{ mol m}^{-2} \text{ d}^{-1}$ ).

The ripening phase represents the final stage of fruit development, marked by significant physicochemical and sensory changes (Gill et al., 2017). It encompasses processes such as cuticle thinning, cell wall degradation, softening, and hormonal interactions. The ripening mechanisms differ between climacteric and non-climacteric fruits (Kisvarga et al., 2023). The light spectrum plays an important role in regulating fruit growth, impacting cell proliferation, sensory attributes including appearance and taste, and is linked to carotenoid production and chlorophyll loss (Sergejeva et al., 2018). Khan et al. (2022) conducted research using specific wavelengths of green (515-525 nm), blue (464-474 nm), and red (617-627 nm) light to study post-harvest banana properties. LED light exposure promoted ethylene production, along with increased levels of polyphenols, sugars, and ascorbic acid, resulting in accelerated ripening, noticeable changes in peel colour, flesh firmness, and sugar content (Miao et al., 2019).

LED therapy enhanced banana ripening by promoting sugar accumulation and regulating starch-to-sugar conversion through starch-degrading enzymes (Trivellini et al., 2023). Different LED lights had significant effects on banana metabolism, with blue light being the most effective in accelerating banana ripening during storage, followed by red and green lights (Gill et al., 2017). Dhakal and Baek (2014) found that subjecting green tomatoes to blue light with a wavelength of 440-450 nm before placing them in dark conditions significantly accelerated their ripening. Compared to green tomatoes kept in the dark for the same period, those exposed to blue LED treatment showed a slower colour change from green to red over 7 days. In addition, red and dark LED-treated tomatoes were less firm than blue LED-treated tomatoes, with red LED-treated tomatoes showing the lowest firmness even after 21 days. Although blue light-treated tomatoes acquired lycopene at a slower rate, pre-treatment with blue light is an effective method to reduce ripening time and enhance postharvest economic benefits.

Kisvarga et al. (2023) observed an increased ethylene production in the blue light-exposed peaches. Additionally, blue light treatment appeared to sustain higher levels of total soluble solids while reducing the total titratable acid content in peach fruit. Meanwhile, Mashabela et al. (2015) demonstrated that pearl photo-selective nets, which allow increased transmittance of blue and red light relative to far-red light (R/FR and B/FR ratios), could influence ripening processes. In green peppers, higher R/FR photon ratios during development may reduce the activation of phytochrome, subsequently affecting genes related to ripening, including those responsible for colour,  $\beta$ -carotene, and lycopene production (Loconsole et al., 2019).

The influence of cover materials on fruit ripening and shelf life remains unclear. However, light receptors responding to light changes could play a key role in regulating the interactions between fruit maturation and nutrient metabolism (Rouphael et al. 2019). The timing of harvest, cultivar performance, fruit ripening, and nutrient ion metabolism can all be influenced by the intricate

interplay between light and the penetration of cover materials into the crop canopy and onto the fruit surface (Fan et al., 2019). By carefully adjusting the spectral composition, intensity, and duration of light exposure enables researchers and growers can influence the timing, duration, and abundance of flowering and fruiting. Specific light cues can trigger or inhibit these processes, affecting plant hormone levels, floral initiation, and fruit development. This knowledge facilitates targeted interventions to enhance reproductive processes, thereby improving crop productivity and economic outcomes.

#### 5.4. Manipulation of Light on Reducing Incidence of Pest and Disease Pressure

Manipulation of light is emerging as a promising strategy for managing pest and disease pressure in plants. Light treatments can disrupt pest behaviour, impede pathogen development, or enhance plant defences, effectively reducing infestation and disease severity (Ahn et al., 2015). As LED technology advances, the integration of light quality into pest management strategies is gaining traction, reducing reliance on environmentally harmful chemicals (Gallé et al., 2021). While studies demonstrate the potential of LEDs to suppress disease and pests in economically significant crops, it is crucial to consider the indirect effects of light-quality treatments on plant growth and development (Loi et al., 2020).

Light not only governs fundamental metabolic processes and plant growth aspects like flowering, stem elongation, and morphology, but it also plays a pivotal role in regulating the intricate system that oversees the production and accumulation of secondary metabolites through the modulation of photosensory signalling pathways led by photoreceptors (Rahman et al., 2010). Secondary metabolites serve multiple functions, including defense against herbivores, communication within or between species, protection against harmful solar radiation, and as cues for pollination or seed dispersal (Murdoch et al., 2013). Manipulating the light spectrum stands as an intriguing strategy to actively and precisely intervene in biosynthetic pathways, augmenting the levels of vital phytochemicals that can be harnessed to enhance growth and the ultimate product quality, ultimately bolstering plant fitness (Gallé et al., 2021). Table 3 illustrates the effects of UV and LED light on key secondary metabolites in controlled plant cultivation, offering valuable insights into their influence on plant health and resilience.

Illuminating plants with specific LED wavelengths can mitigate insect infestation and reduce plant diseases in agricultural environments, ultimately enhancing production efficiency by limiting crop losses (Kook et al., 2013). Light-triggered signalling pathways that intersect with plant defence mechanisms highlight the importance of light quality in enhancing plant resistance to diseases (Ahn et al., 2015). Light quality affects the accumulation of secondary metabolites, such as flavonoids, which are closely linked to plant immunity, disease susceptibility, and interactions with insects. While numerous studies have highlighted how light-induced secondary metabolites can enhance the nutritional qualities of plant products, there is a paucity of research investigating the degree of plant protection resulting from metabolite-based resistance triggered by light (Kim et al., 2013).

For instance, ultraviolet LEDs, particularly those peaking in the ultraviolet-B (UV-B; 320 to 290 nm) range, have proven effective in suppressing powdery mildew caused by *Sphaerotheca aphans* in strawberries and *Podosphaera pannosa* in roses (Meyer et al., 2021). Blue LEDs have demonstrated the ability to inhibit the development of *Botrytis cinerea* in detached tomato leaves and reduce the incidence of black leaf mold (*Pseudocercospora fuligena*) in greenhouse-grown tomatoes (Hui et al., 2017). Green LEDs have been found useful in mitigating strawberry anthracnose (*Glomerella cingulata*), perilla leaf spot disease (*Corynespora cassiicola*), cucumber anthracnose (*Colletotrichum orbiculare*), and gray mold (*Botrytis cinerea*) (Peralta-Ruiz et al., 2023). Red LEDs, too, have exhibited disease resistance effects, suppressing powdery mildew in roses due to *Podosphaera pannosa*, *Sphaerotheca fuliginea* in cucumbers, and downy mildew in basil caused by *Peronospora belbahrii* (Carvalho and Castillo, 2018).

The incorporation of narrowband LEDs into traditional insect traps has proven to be an interesting method to enhance their attractiveness, specificity, and adaptability (Kim et al., 2013). Adding UV, green, and/or yellow LEDs to insect traps increases their capture efficiency for various



pests such as fungus gnats (*Bradysia difformis*), oriental fruit flies (*Bactrocera dorsalis*), sweet potato weevils (*Euscepes postfasciatus*), greenhouse whiteflies (*Trialeurodes vaporariorum*), red flour beetles (*Tribolium castaneum*), biting midges (*Culicoides brevitarsis*), cotton bollworms (*Helicoverpa armigera*), and others, outperforming traps without LED supplementation (Meyer et al., 2021).

Controlled exposure to low levels of UV-B light for 6 hours effectively reduced powdery mildew infection in densely grown roses in greenhouses, enhancing the production of secondary bioactive compounds and acting as a preventive measure against disease (Ahn et al., 2015). Red LED light has the potential to reduce powdery mildew disease in roses by reducing the amount of conidia produced (Gallé et al., 2021). Blue light and UV radiation have shown promise in reducing *B. cinerea* growth on harvested vegetables, indicating their potential use for gray mold-sensitive ornamental crops (Hui et al., 2017). The antibacterial properties of LEDs were investigated in fresh pineapple slices exposed to different intensities (254.7, 147.7, and 92  $\mu\text{W cm}^{-2}$ ) and temperatures (25°C, 16°C, and 7°C) (Ghate et al. 2017). The research found that the samples exposed to blue light (460 nm) had more antibacterial effects compared to a control group and temperature had a significant impact on antibacterial activity, while irradiation did not affect it.

Photo-selective filtering of sunlight can influence plant pests and diseases, making crops under these shade nets susceptible to infestation (Suthaparan et al., 2010). Despite openings that may permit aphids, whiteflies, and thrips to pass through, their responses differ to various photo-selective shade nets (Peralta-Ruiz et al., 2023). Whiteflies are drawn to yellow nets, while thrips show an affinity for blue ones (Carvalho and Castillo, 2018). Coloured cladding materials hold promise for enhancing agricultural productivity and insect control. They have the potential to enhance crop protection by visually deterring or obstructing pests, reducing the need for pesticides (Kook et al., 2013).

Goren et al. (2011) observed that red peppers grown under 35% pearl and yellow shade nets exhibited significantly improved fruit quality preservation over two consecutive years. This enhancement was evident after 16 days at 7°C and three days at 20°C, primarily attributed to reduced decay incidence caused by *Alternaria alternata*. No significant differences were found in weight loss, hardness, or total soluble solids among fruits grown under differently coloured shade nets. Pearl and yellow shade nets notably reduced the population of *Alternaria spp.* in the field, as confirmed by *Alternaria*-selective growth media. In contrast, the red shade net showed the highest *Alternaria* population (Loi et al., 2020). This innovative approach holds great potential for enhancing crop health, minimizing reliance on chemical interventions, and promoting environmentally friendly agricultural practices. Table 4 depicts the effects of LED light spectra on induced disease resistance in crops, providing valuable insights into harnessing light to bolster plant defences and mitigate disease impacts.

**Table 3.** Effects of UV and LED light as elicitors of key secondary metabolites in controlled plant cultivation.

Light sources	Light intensity	Exposure time	Crop species	Secondary metabolites	Yield increase	References
UV-B	40 J cm <sup>2</sup>	6 days	Sessile joyweed ( <i>Alternanthera Sessilis</i> )	Flavonoids and phenolics	51%	Hashim et al. (2021)
UV-B	313 nm	7 – 14 days	Ginkgo ( <i>Ginkgo biloba</i> )	Phenylpropanoid and flavonoid	16.7 – 42 fold	Zhang et al. (2021)
UV-B	30 $\mu\text{W cm}^{-2}$	4 days	Wheat ( <i>Triticum aestivium</i> )	Phenolics	26.3%	Wong et al. (2023)
UV-C	3 W m <sup>-2</sup>	60 min	Garden cress ( <i>Lepidium sativum</i> )	Chlorogenic acid and kaemferol	2.5 fold	Singh et al. (2024)
UV-C	3 W m <sup>-2</sup>	10-20 min	Sweet basil ( <i>Ocimum basilicum</i> )	Chichoric acid	4.1 fold	Sipos et al. (2021)
	3.6 kJ m <sup>-2</sup> + 16 h photoperiod	10 – 60 min	Flax ( <i>Linum usitatissimum</i> )	Secoisolariciresinol diglucoside (SDG)	1.86 fold	Anjum et al. (2017)

UV-C + Photoperiod and UV-C + Dark	1.8 kJ m <sup>-2</sup> + 24 h dark			Lariciresinol diglucoside (LDG)	2.25 fold	
				Total phenolic production	2.82 fold	
				Total flavonoid production	2.94 fold	
				Dehydrodiconiferyl alcohol glucoside (DCG)	1.36 fold	
				Rosmarinic acid	2.3 fold	
Blue LED	200 μmol m <sup>-2</sup> s <sup>-1</sup>	8-14 h	Lettuce ( <i>Lactuca sativa</i> )	Flavonoids	2 fold	Bucky et al. (2024)
Blue LED	50 μmol m <sup>-2</sup> s <sup>-1</sup>	8 h	Jewel orchid ( <i>Anoectochilus roxburghii</i> )	Flavonoids and polyphenols	24.2%	López et al. (2022)
Blue LED	50 μmol m <sup>-2</sup> s <sup>-1</sup>	7-14 days	Chinese foxglove ( <i>Rehmannia glutinosa</i> )	Phenolics and flavonoids	39.3 and 33.6%	Dsouza et al. (2024)
Red LED	40 μmol m <sup>-2</sup> s <sup>-1</sup>	4 weeks	Sweet basil ( <i>Ocimum basilicum</i> )	Rosmarinic acid and eugenol	2.46 and 2.25 fold	Fayezizadeh et al. (2024)
				Peonidin and cyanidin	3.5 and 4.53 fold	
Red and Blue LED (2:1 ratio)	120 μmol m <sup>-2</sup> s <sup>-1</sup>	12-24 h	Sweet basil ( <i>Ocimum basilicum</i> )	Phenolics and flavonoids	1.63 – 1.87 and 2.06 fold	d’Aquino et al. (2024)
Red LED	660 nm	24 h	False daisy ( <i>Eclipta alba</i> )	Phenolics and flavonoids	2 fold	Khurshid et al. (2020)

Table 4. Effects of LED light spectra on induced disease resistance in crops.

LED light	Light intensity	Crops	Effect on disease	References
Red	550 μW cm <sup>-2</sup>	Thale cress ( <i>Arabidopsis thaliana</i> )	Induced resistance against <i>Meloidogyne javanica</i> (root-knot nematode)	Hong et al. (2024)
	150 μW cm <sup>-2</sup>	Cucumber ( <i>Cucumis sativus</i> )	Induced resistance against <i>Colletotrichum cassiicola</i> (causal agent of anthracnose)	Zare Mehrjerdi et al. (2024)
	80-100 μmol m <sup>-2</sup> s <sup>-1</sup>	Grape ( <i>Vitis vinifera</i> )	Induced resistance against <i>Botrytis cinerea</i> (gray mold fungus)	Gallé et al. (2021)
Blue	150-200 μmol m <sup>-2</sup> s <sup>-1</sup>	Lettuce ( <i>Lactuca sativa</i> )	Induced resistance against gray mold caused by <i>Botrytis cinerea</i>	Zhu et al. (2024)
	50-150 μmol m <sup>-2</sup> s <sup>-1</sup>	Tomato ( <i>Solanum lycopersicum</i> )	Induced resistance against gray mold caused by <i>Botrytis cinerea</i>	Kukri et al. (2024)
	100 μmol m <sup>-2</sup> s <sup>-1</sup>	Rose ( <i>Rosa rubiginosa</i> )	Suppression of sporulation of <i>Alternaria cichorii</i>	Rezaei et al. (2024)
Green	50-80 μmol m <sup>-2</sup> s <sup>-1</sup>	Strawberry ( <i>Fragaria x ananassa</i> )	Induced resistance against <i>Glomerella cingulata</i>	Smith et al. (2022)

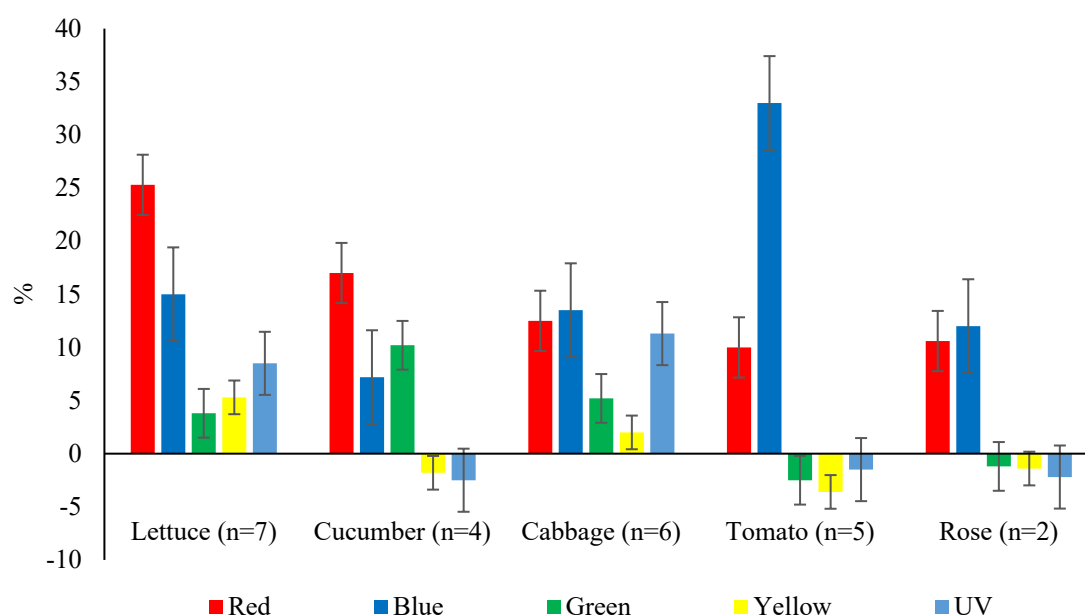
5.5. Manipulation of Light on Crop Yield

Yield is crucial in assessing production processes, and manipulating light is a potent method for boosting crop productivity. Given light's role in photosynthesis and plant growth, additional lighting is often employed to enhance yields (Paradiso and Proietti, 2022). By adjusting the spectral composition, intensity, and duration of light exposure, researchers and farmers can optimize photosynthesis, nutrient uptake, and plant growth, leading to higher yields. Growers encounter challenges in providing adequate lighting due to factors like shading, cloud cover, and seasonal changes, leading to spatial and temporal light distribution variability (Brazaitytė et al., 2021). Given the diverse light characteristics perceived by plants, it is evident that at least one source of broad-spectrum light, whether from natural lighting, metal halide (MH), High-Pressure Sodium (HPS) lamps, or white and multi-spectral LED arrays, is essential (Jones, 2018). Beyond this requirement, there are further opportunities to tailor the specific light environment for optimal plant growth and increase overall plant production.

Glasshouses have long relied on supplemental overhead lighting to enhance crop productivity during periods of reduced natural light, whether to extend shorter winter days or during inclement weather (Appolloni et al., 2021). In general, a 1% increase in illumination leads to a 1% rise in yield, although interactions with other factors such as temperature and CO<sub>2</sub> can complicate this relationship (Brazaitytė et al., 2021). Despite these evident benefits, several studies highlight the diverse responses of different crops to supplemental lighting regimes (Gao, 2015). Therefore, customized lighting regimes for specific crops, considering the local natural lighting conditions, may be more beneficial than a uniform approach.

Under extremely low light intensity, variation in light quality conditions didn't significantly impact yield and yield components. The decrease in rice yield, including low spikelet filling and a drop in 1000-grain weight, was mainly associated with reduced light intensity (Hu, 2018). In contrast, barley seedlings grown under blue light had a significantly higher photosynthetic rate compared to those under red and blue light at the same light intensity. This increase in the blue light fraction notably elevated plant protein content (Jones, 2018).

A pot experiment by Chen et al. (2021) revealed that the effects of light and water treatments on the influence on yield and 2AP (2-acetyl-1-pyrroline) production in two prominent Chinese aromatic rice varieties, Xiangyaxiangzhan and Yuxiangyouzhan. Compared to the control (natural light and adequate water), low light and well-watered conditions (LL-WW) as well as low light with water stress (LL-WS) significantly reduced grain production in Xiangyaxiangzhan by 39.2% and 34.6%, respectively. Compared to the control, grain yield in Yuxiangyouzhan was reduced by 25.4% with LL-WS and 30.8% with LL-WW. These treatments also decreased the proportion of filled grain, with LL-WW and LL-WS experiencing a significant decrease compared to control. Figure 2 illustrates the impact of diverse light spectra on crop yields in controlled environments, observed across various studies.



**Figure 2.** Impact of diverse light spectra on crop yield over control as observed across various studies.

## 6. Unexplored Area of Light Manipulation

The use of artificial lighting in horticulture, whether as the primary source or to complement natural sunlight, is a hot topic. There's a growing interest in exploring lighting strategies to increase crop yield, hasten plant growth, and optimize water and nutrient usage (Rahman et al., 2021). The choice of light source can have diverse effects on plant development, influencing factors such as stem elongation, leaf expansion, root growth, and nutrient levels. These interactions are complex and vary depending on the plant species (Paradiso and Proietti, 2022). An unexplored area of light manipulation for crop development is the optimization of dynamic light settings to mimic natural conditions.

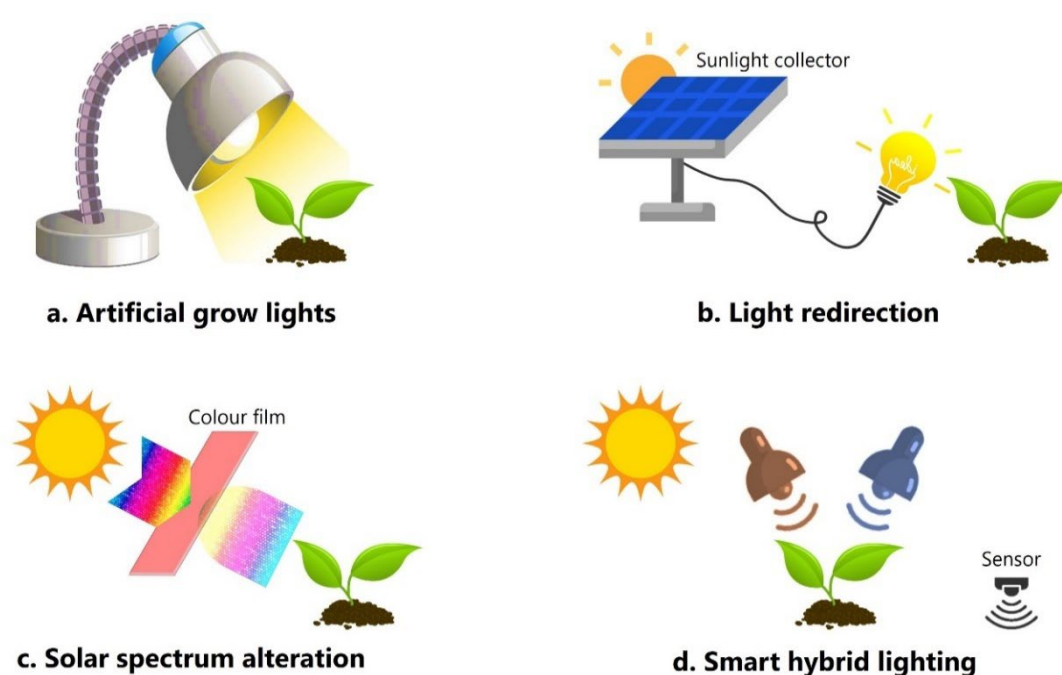
Plants in natural environments experience fluctuating light intensity and spectral composition, affecting various aspects of growth and development. Mimicking these conditions in controlled environments could improve crop production by aligning with natural responses of plants (Schumann et al., 2017). A method to create dynamic light environments is through modern lighting technology, like dynamic LED systems. These can mimic natural light patterns by adjusting intensity, spectral composition, and spatial distribution over time (Chew et al., 2017). Researchers can study plant responses to more realistic light conditions by simulating diurnal and seasonal sunlight fluctuations, potentially uncovering new strategies for increasing agricultural output and resilience (Rahman et al., 2021). Integrating dynamic light with other variables like temperature and humidity could reveal how plants optimize growth and resource use in response to environmental cues.

Recent technological advances in LEDs have revolutionized the horticulture sector, surpassing traditional light sources such as fluorescent lamps. LEDs offer superior energy efficiency, longer lifetime (up to ~50,000 hours), reduced heat generation, and significant user and environmental safety advantages due to their lack of toxic elements like mercury found in fluorescent lamps (Viana et al., 2022). LEDs allow for precise wavelength selection, minimizing energy waste on less crucial spectrum components for plant photomorphogenesis and photosynthesis (Schumann et al., 2017). Exploring the impact of dynamic light conditions on plant-microbe interactions and soil microbiome dynamics holds promise for advancing sustainable farming practices. Light-induced changes in plant physiology and exudate composition can influence rhizosphere microbial communities, impacting nutrient cycling, disease suppression, and soil health (Li et al., 2023). Understanding these interactions may lead to light-based strategies to enhance soil fertility and plant health.

The integration of IoT architectures and distributed monitoring systems provides a practical solution for incorporating sensors, actuators, and wireless connectivity into traditional greenhouses



(Rayhana et al., 2020). This integration ensures stable environmental conditions by collecting sensor data for control functions. IoT infrastructures are popular due to their effective balance of data transmission coverage, cost-effectiveness, and low power consumption, finding applications in environmental monitoring and industrial settings (Farooq et al., 2022). While WiFi is widely used, its relatively high-power consumption makes it less ideal. Bluetooth or ZigBee are viable alternatives, but their limited transmission ranges, spanning hundreds of meters, are insufficient for monitoring extensive greenhouse installations encompassing multiple greenhouses over hundreds of meters (Rayhana et al., 2020). The study of dynamic light conditions for optimizing crop development is a promising yet underexplored area. By simulating realistic light conditions and integrating them with environmental factors, researchers may revolutionize sustainable agriculture. Further exploration could lead to innovative approaches addressing global food security challenges. In the cutting-edge lighting systems for smart farming, dynamic LEDs are used to mimic natural light to enhance crop growth (Figure 3).



**Figure 3.** Advanced lighting systems for smart farming by utilizing dynamic LEDs to mimic natural light and optimize crop growth.

## 7. Prospects

Both conventional and modern lighting systems, such as LEDs, are employed to supplement natural light in greenhouse settings and have been extensively studied across various species, using different combinations to enhance photosynthesis of bioactive phytochemicals and overall production. With the ongoing climate change and environmental stimuli, LED-based lighting solutions have become more popular among horticulturists in recent years. LED illumination has been demonstrated to control various anatomical, morphological, physiological, photosynthetic, developmental, and metabolic aspects in horticultural species. This wealth of data enables breeding companies to focus on the traits and qualities relevant to each crop species, developing LED light-efficient genotypes. It's crucial that researchers fully understand this information while considering how diverse environmental conditions and practices may influence outcomes, determining the suitability of introducing light-use efficient genotypes into commercial practice.

Recent studies have shown that LEDs can impact metabolic and physiological processes in vegetables by altering gene and enzyme expression in biosynthetic pathways. Future studies should investigate the effects of supplemental green (G) LED light combined with basal red (R) and blue (B)

light on photosynthesis to directly influence secondary metabolism near the blue light spectrum. While green light is not as strongly absorbed by chlorophylls, it can penetrate deeper into leaf tissue and be absorbed by chloroplasts in lower leaves under a canopy, thereby increasing photosynthesis under the prevailing conditions. An interesting area for future research is the investigation of the phytochemical composition of various edible horticultural species, which are known for their high antioxidant content and used in pharmaceuticals. Significant breakthroughs are expected from interdisciplinary research and development efforts involving close collaboration among LED manufacturers, greenhouse growers, researchers, and government stakeholders.

## 8. Conclusions

Light is essential for regulating crucial aspects of plant growth and development, impacting flowering, structure, nutrient uptake, secondary metabolite production, and yield. Research into various combinations of light, ranging from monochromatic to polychromatic spectra (including UV to FR), has extensively explored their proportions and effects on different plant species. Key highlights include: a) the critical role of the ratio of red (R) to blue (B) light and R to far-red (FR) light in regulating high-quality plant growth; b) the essential role of blue light in enhancing the production and accumulation of phytochemical compounds, thereby boosting plant antioxidant activity; and c) the potential for exploring the effects of ultraviolet (UV) radiation on plant development and secondary metabolism, despite its limited current use in horticulture. While initial studies focused on red (R) and blue (B) light due to chlorophyll absorption peaks, recent research is expanding to include white (W), green (G), and far-red (FR) light, demonstrating their impact on physiological and metabolic processes. Further research is crucial to validate the optimal wavelength combinations for major plant species and phytochemicals, as well as to explore the effects of less studied wavelengths such as UV, yellow (Y), and green (G).

This report presents a comprehensive study of light manipulation and the effects of LED lighting on crops, covering a wide range of plant species and types. The analysis highlights that red LED lighting (45%) and blue LED illumination (40%) are the most prevalent light spectra for indoor-grown plants. However, far-red (5%) LED light is primarily suited to specific plant applications and is rarely used in greenhouses. Despite its potential benefits, such as compensation for shading, far-red LED illumination has not seen widespread adoption, possibly due to its recent introduction in commercial LED fixtures and the lack of conclusive data on its impact on maximizing plant nutritional quality. These investigations are expected to improve our understanding of the effects of spectral quality on plant development and morphology and highlight the importance of LED lighting in CEA.

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