



Artificial Light Spectra and Its Impact on Plant Physiological Processes and Secondary Metabolism

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Understanding the effects of artificial light spectra on plant physiological processes and secondary metabolism is critical for optimizing plant growth and productivity, particularly in controlled environment agriculture. This review synthesizes the current knowledge on this topic, exploring the fundamental principles of light spectra, their impacts on plant physiology, including photosynthesis and growth, as well as on secondary metabolism. Artificial light sources, such as light-emitting diodes (LEDs), have been shown to significantly influence these plant processes, owing to their controllable spectra and intensities. These artificial light spectra can enhance photosynthetic efficiency, manipulate growth and development, and stimulate the production of valuable secondary metabolites. The review further discusses the potential applications of this understanding in sectors like agriculture, pharmaceuticals, nutraceuticals, and even space agriculture. However, the interactions of artificial light spectra with other environmental factors, the development of custom light recipes for specific plant species or cultivars, and the need for long-term studies are identified as areas needing further research. This review contributes to the growing body of literature exploring the opportunities and challenges of utilizing artificial light spectra for improving plant performance and secondary metabolite production.

Keywords: Photosynthesis; econdary metabolism; light-emitting diodes; light spectra; agriculture.

1. INTRODUCTION

The interplay between light and life has always been a fundamental aspect of Earth's biological systems. Light, especially its spectra, plays a critical role in various physiological processes and secondary metabolic activities in plants, affecting their growth, development, and chemical makeup [1]. The advent of artificial lighting systems and their widespread application in controlled agricultural systems have further expanded the complexity of the light-plant interaction. As we delve into the intricate relationship between artificial light spectra and plant processes, this review aims to elucidate how variations in light spectra influence plant physiological processes and secondary metabolism. Light is a crucial environmental factor influencing plant biology. It not only serves as the primary energy source for photosynthesis but also acts as an information signal, modulating a plethora of physiological responses in plants [2]. Understanding the impact of light, particularly its spectral composition, on plant growth and development has significant implications for optimizing plant production and creating sustainable and efficient agricultural systems [3]. With the increasing global demand for food, the exploration of innovative cultivation techniques, such as using artificial light spectra, has never been more urgent. The primary objective of this review is to critically analyze and synthesize current research regarding the impact of artificial light spectra on plant physiological processes and secondary metabolism. Specifically, the review will focus on how different

light spectra influence photosynthesis, plant growth, and development, as well as secondary metabolite production. Through a comprehensive understanding of these interactions, this review aims to provide insights into optimizing artificial lighting conditions for improving crop production and quality in controlled environments like greenhouses and indoor farms. This review is structured in a manner that progressively builds an understanding of the subject matter. Initially, it introduces the basic principles of light spectra and highlights its role in plant physiological processes and secondary metabolism. Following this, the influence of artificial light spectra on these aspects is discussed in detail. Furthermore, the review delves into the potential applications and future directions of this research area, concluding with a succinct summary of the findings and implications. Light and plant interaction is a complex and multi-faceted subject. Decades of research have shown that plants do not simply use light for photosynthesis, but also perceive and respond to its intensity, duration, direction, and especially its spectral quality, thereby influencing their morphogenesis, physiology, and secondary metabolism [4]. Consequently, the investigation of the effects of artificial light spectra on plants is not merely an academic endeavor but has substantial practical implications, particularly for the controlled environment agriculture (CEA) industry. With the application of artificial light in agriculture, the possibility to manipulate the light environment and, thus, control plant growth, development, and chemical composition has dramatically increased. However, optimizing these lighting

conditions requires an in-depth understanding of how different light spectra influence plant responses. Therefore, this review aims to shed light on these aspects, providing valuable information for growers, researchers, and industry stakeholders. As we embark on this exploration of the interaction between artificial light spectra and plant physiological processes and secondary metabolism, it's essential to acknowledge the complexity of the topic and the continuing evolution of research in this area. Despite the considerable strides in our understanding, many facets remain to be fully elucidated. It is hoped that this review will not only provide a comprehensive synthesis of the current state of knowledge but also highlight the gaps that need to be addressed in future research.

2. BASIC PRINCIPLES OF LIGHT SPECTRA

Light plays an integral role in virtually all aspects of plant life, affecting their development, physiology, and survival. Central to this process is the light spectrum, which represents different wavelengths of light that plants absorb and utilize in distinct ways [5]. The present section will delve into the basic principles of light spectra, discussing its definition, importance in photosynthesis, and the characteristics of different light spectra. The light spectrum is defined as the distribution of light, or electromagnetic radiation, according to its wavelength. This spectrum is often visualized as a band of colors, known as the visible light

spectrum, which ranges from violet (400 nm) to red (700 nm). Beyond this range, the light spectrum extends to include ultraviolet (UV) light (< 400 nm) and infrared (IR) light (> 700 nm) [6].

3. IMPORTANCE OF LIGHT SPECTRA IN PHOTOSYNTHESIS

The ability of plants to convert light energy into chemical energy through photosynthesis is fundamental to life on Earth. This process primarily relies on visible light, specifically red and blue light, which are absorbed by chlorophyll pigments. The absorbed light energy is then used to power the conversion of carbon dioxide and water into glucose and oxygen, a process critical for plant growth and survival [7]. Different light spectra also influence various aspects of plant growth and development beyond photosynthesis, primarily through photoreceptors. These light-sensitive proteins detect specific light spectra, triggering physiological responses such as phototropism (growth towards light), photomorphogenesis (growth form modification in response to light), and photoperiodism (seasonal response to day length) [8].

4. DIFFERENT LIGHT SPECTRA AND THEIR CHARACTERISTICS

Understanding the interaction of plants with different light spectra requires a grasp of the distinct characteristics associated with each spectrum.

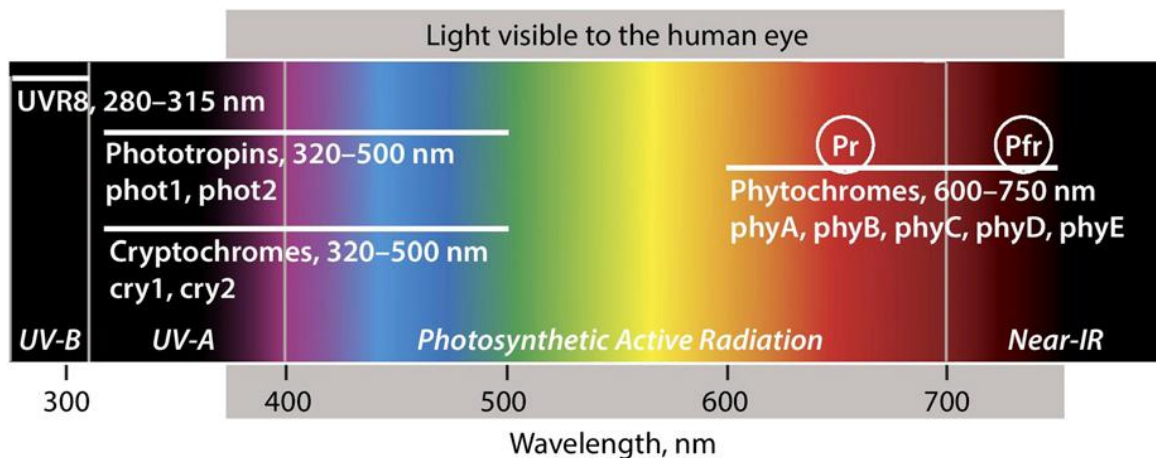


Fig. 1. The range of wavelengths that are sensed by the main plant photoreceptors (phytochromes, cryptochromes, phototropins, and UVR8) allowing light-driven developmental adaptations

(data from <http://www.biologie.ens.fr/smdgs/spip.php?article57>)

1. **Ultraviolet (UV) Light:** This spectrum, particularly UV-B (280-315 nm) and UV-A (315-400 nm), plays an influential role in plant growth and development. While high doses can cause damage, moderate UV-B radiation can induce protective responses in plants, influencing plant form and inducing the synthesis of protective secondary metabolites [9].
2. **Blue Light (400-500 nm):** This spectrum is crucial for regulating a variety of plant physiological processes. Blue light is absorbed by cryptochromes and phototropins, influencing processes such as stomatal opening, phototropism, and the suppression of elongation growth [10].
3. **Green Light (500-600 nm):** Historically overlooked, recent research highlights that green light, absorbed primarily by phytochromes, can penetrate deeper into plant tissues and canopies, thereby influencing plant growth and development [11].
4. **Red Light (600-700 nm):** Red light is predominantly absorbed by chlorophyll pigments for photosynthesis and by phytochromes to regulate numerous physiological processes, including seed germination, stem elongation, and flowering time [12].
5. **Far-red Light (700-800 nm):** Absorbed by phytochromes, far-red light plays a key role in the shade avoidance response, leading to elongated growth and early flowering when plants detect they are under a canopy [13].
6. **Infrared (IR) Light:** While IR light does not directly participate in photosynthesis, it contributes to leaf and canopy temperature, influencing plant physiology indirectly [14].

5. LIGHT SPECTRA AND PLANT PHYSIOLOGICAL PROCESSES

Light is a key environmental factor that drives many plant physiological processes. The type and intensity of light spectra significantly impact the way plants grow and develop. This section will explore the role of different light spectra in photosynthesis, plant growth, and development, and draw from specific case studies to exemplify these effects. Plant physiological processes encompass a wide range of activities, from photosynthesis, the process by which plants convert light energy into chemical energy, to photomorphogenesis, the effect of light on plant

growth and development. Other critical physiological responses to light include phototropism (growth direction towards light), photoperiodism (physiological response to day length), and circadian rhythms (internal biological clock) [15]. Photosynthesis is the primary process by which plants, algae, and some bacteria convert light energy, usually from the sun, into chemical energy in the form of glucose. During this process, light energy is absorbed mainly by chlorophylls a and b, which are particularly responsive to blue (around 430-450 nm) and red (around 640-680 nm) light. Accessory pigments like carotenoids also contribute by broadening the light absorption spectrum, particularly in the blue and green regions [16]. The efficiency of photosynthesis varies with the light spectrum. While both red and blue light can drive photosynthesis, studies have shown that red light is more efficient, especially at high light intensities, owing to its greater penetration capability into plant tissues [17]. Conversely, blue light is critical at low light intensities, promoting stomatal opening, hence increasing CO₂ absorption, and eventually, photosynthetic rates [18].

6. IMPACT OF DIFFERENT LIGHT SPECTRA ON PLANT GROWTH AND DEVELOPMENT

Apart from photosynthesis, light spectra influence a variety of other plant growth and developmental processes. Different photoreceptors in plants are responsible for detecting specific light spectra, triggering downstream physiological responses [19].

1. **Blue Light:** Blue light influences a plethora of plant responses, including stomatal opening, phototropism, chloroplast movement, and suppression of hypocotyl elongation. The photoreceptors cryptochromes and phototropins primarily mediate these responses [20].
2. **Red and Far-red Light:** Red and far-red light are primarily perceived by phytochromes, leading to germination, stem elongation, leaf expansion, and the transition to flowering. Red light promotes these processes, while far-red light typically suppresses them [21].
3. **Green Light:** Green light can also regulate plant growth and development, although the mechanisms are less understood. Some research indicates that green light

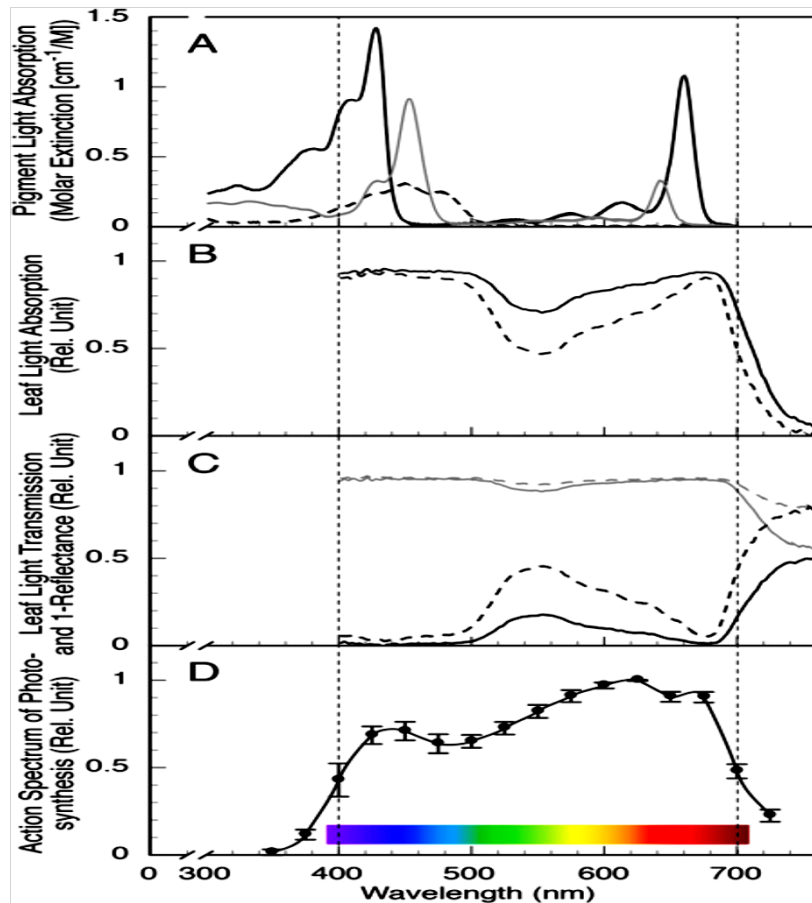


Fig. 2. Spectrum for pigments and leaves. (A) Absorption spectrum of chlorophyll a (black line) and chlorophyll b (gray line) in diethyl ether, and b-carotene (dashed line) in hexane based on data from <http://omlc.org.edu/spectra/PhotochemCAD/index.html>. Other carotenoids like lutein and zeaxanthin have a similar absorption limit as b-carotene (cf. Koning, 1994) in the green range above 492 nm. (B) Light absorption in *Chrysanthemum morifolium*; fresh leaf (black line) and vacuum infiltrated by water (dashed line) to eliminate light scattering measured by a light integrating sphere (ASD Inc., Boulder, CO) and Avaspec- 2048 spectrometer (Avantes, Apeldoorn, The Netherlands). (C) 1-Reflectance (gray lines) and transmission (black lines) of the same fresh (solid lines) and vacuum infiltrated (dashed lines) leaves. (D) The relative quantum yield of photosynthesis of eight crop species (mean values \pm SD) based on data from McCree (1972)

Table 1. Impact of varied light treatment on plant performance

Light Treatments	Species	Response	Reference
Elevated red:far red ratio from fluorescent lamps, and 20% Blue and 80% Red LED lighting in growth chambers	Rose	Enhancement in flowering compared to mixed fluorescent and incandescent lamps. Boost in leaf biomass, reduction in leaf area and shoot biomass, flowering remained unaffected	[23,24,25]
Blue light with increased red:far red ratio in external growth chambers (light selectively screened from natural light)	Chrysanthemum, Tomato, Lettuce	Decline in dry weight, plant height, and leaf area compared to plants under natural light	[26]
Blue light with far red LED lighting in growth chambers	Chrysanthemum	Photosynthetic rate decreased, number of stomata increased and stomata size	[27]

Light Treatments	Species	Response	Reference
		decreased compared to fluorescent lamps	
Daylight filtered with blue polyethylene films in a greenhouse	Chrysanthemum	Inhibited stem elongation, decreased leaf area, lowered dry weight, and increased pigment content	[28]
Blue LED lighting in controlled-environment rooms	Lettuce	Hypocotyl and cotyledon elongation suppressed compared with cool-white fluorescent lamps	[29]
Blue (10% to 30%) and red LEDs in growth chambers	Oncidium	Increased dry weight and protein accumulation compared with fluorescent lamps	[30]
Blue, red and far red LEDs in growth chambers	Oncidium	Promoted leaf expansion, leaf number, chlorophyll content, and fresh and dry weight compared with fluorescent lamps	[31]
Supplementary incandescent lighting	Campanula	Flowering percentage enhanced	[32]
Blue (10%) and red LEDs in controlled-environment chambers	Spinach, Radish, Lettuce	No significant impact on photosynthesis and stomatal conductance, but total dry weight accumulation was suppressed compared with cool-white fluorescent lamps	[33]
Supplemental blue and red LED lighting in a greenhouse	Lettuce	Small increase in phytochemicals compared with greenhouse treatments with supplementary HPS lamps. No significant effect in carotenoid concentration compared with greenhouse treatments with supplementary HPS lamps	[34,35]
Short duration of blue LED light in growth chambers	Broccoli	Increased shoot tissue beta-carotene, viola-xanthin, total xanthophyll cycle pigments, aliphatic glucosinolates, and the content of micronutrients and macronutrients, compared with blue (12%) and red (88%) LEDs	[36]
Blue fluorescent lamps in climate chambers	Cattleya	Improved the efficiency of micropropagation and benefited initiation of rhizogenesis and aerial root elongation compared to fluorescent white lamps	[37]

Note: HPS = high-pressure sodium; LED = light-emitting diode

can modulate photosynthetic efficiency and photomorphogenic responses, particularly under canopy shade conditions where green light is prevalent [22].

7. LIGHT SPECTRA AND SECONDARY METABOLISM IN PLANTS

Secondary metabolism in plants is responsible for the synthesis of a multitude of compounds that are not directly involved in growth, development, or reproduction, but that provide plants with an adaptive advantage in their environment. These secondary metabolites have diverse functions, including defense against pests and diseases, attraction of pollinators, and

protection from UV radiation. The production of these metabolites is significantly influenced by environmental factors, including light quality and intensity. This section will discuss the role of different light spectra in regulating secondary metabolism in plants. Secondary metabolism encompasses a wide array of biosynthetic pathways leading to the production of a diverse range of metabolites, including alkaloids, phenolics, and terpenoids. These metabolites often have significant ecological and medicinal properties, contributing to plant defense, plant-microbe interactions, and the potential therapeutic applications of plant-derived compounds [38]. Light spectra are known to have a considerable influence on the biosynthesis of

secondary metabolites. For example, ultraviolet-B (UV-B) radiation is a potent elicitor of phenolic compounds, including flavonoids, which absorb UV-B and mitigate its harmful effects [39]. Similarly, blue light has been shown to increase the synthesis of anthocyanins, pigments that confer colors to fruits and flowers and exhibit antioxidant properties [40]. Several studies have demonstrated that the exposure of plants to specific light spectra can enhance the production of specific secondary metabolites. For instance, high-intensity blue light was found to enhance the production of phenolic compounds in lettuce, while a combination of red and blue light increased the total phenolic and flavonoid content in sweet basil (*Ocimum basilicum*) [41].

8. ARTIFICIAL LIGHT SPECTRA AND ITS IMPACT ON PLANT PHYSIOLOGY

Artificial light sources, such as light-emitting diodes (LEDs), have gained popularity in modern horticultural practices, particularly in controlled environments like vertical farms and greenhouses. The controllability of the light spectra, intensity, and duration allows for the manipulation of plant physiology to improve growth, development, and the production of desirable compounds. This section will discuss the impacts of artificial light spectra on plant physiology, including photosynthesis, plant growth and development, and secondary metabolism. Lighting technologies for plant growth have evolved significantly over the years, from traditional sources such as fluorescent lamps and high-pressure sodium lamps to the currently popular LEDs. LEDs, with their high energy efficiency, longevity, and controllable light output, have become increasingly used in controlled environment agriculture. These lights can be tuned to specific spectral qualities, allowing researchers and growers to manipulate the light environment for optimal plant performance [42]. Artificial light sources can significantly impact photosynthesis, the process by which plants convert light energy into chemical energy. The wavelengths absorbed by the photosynthetic pigments primarily fall within the blue (around 430-450 nm) and red (around 640-680 nm) regions of the light spectrum, the regions in which most LEDs operate. LED lighting, tailored to the photosynthetically active regions, can enhance the efficiency of photosynthesis. A study conducted by Kim *et al.* [43] demonstrated that lettuce plants grown under red LEDs supplemented with blue light had similar photosynthetic rates as those grown

under white light, suggesting that artificial light sources could effectively drive photosynthesis.

9. ARTIFICIAL LIGHT SPECTRA ON PLANT GROWTH AND DEVELOPMENT

Artificial light spectra can also regulate plant growth and development. For instance, blue light is known to control plant processes such as stomatal opening, phototropism, and chloroplast movement, while red light impacts germination, stem elongation, leaf expansion, and flowering. Using LEDs, researchers have successfully manipulated light spectra to influence plant development. For example, in a study by Bian, *et al.* [44], low levels of green light were shown to significantly reduce lettuce leaf area, indicating the potential of green light in modulating plant growth. Artificial light sources can significantly influence secondary metabolism, leading to altered production of plant-derived compounds. For instance, high-intensity blue light can enhance the production of phenolic compounds in lettuce, while a combination of red and blue light can increase the total phenolic and flavonoid content in sweet basil [45]. Different light qualities can also be used to boost the synthesis of specific metabolites. For example, exposing ginseng to blue light led to an increase in the concentration of medicinal compounds, ginsenosides, compared to plants grown under white light [46].

10. ARTIFICIAL LIGHT SPECTRA AND ITS IMPACT ON SECONDARY METABOLISM

Artificial lighting systems, particularly light-emitting diodes (LEDs), can significantly influence secondary metabolism in plants. The controllable spectrum of LEDs enables researchers and growers to manipulate the biosynthesis of various secondary metabolites, such as phenolic compounds, flavonoids, and carotenoids. This section will discuss the impacts of artificial light spectra on secondary metabolism in plants. Secondary metabolites in plants, such as alkaloids, flavonoids, terpenoids, and phenolic compounds, are bioactive substances that are not essential for growth and development but contribute significantly to plant survival, protection, and interaction with the environment. These metabolites also have significant implications for human health, given their potential medicinal properties [47]. Artificial light spectra can significantly influence the production

of secondary metabolites. Certain wavelengths, including ultraviolet (UV), blue, and red light, have been found to enhance the biosynthesis of various secondary metabolites. For instance, UV-B radiation stimulates the production of flavonoids, which can absorb UV-B and protect plants from its damaging effects [48]. Blue light has been shown to increase the synthesis of anthocyanins, pigments that provide color to fruits and flowers and have antioxidant properties [49].

11. POTENTIAL APPLICATIONS AND FUTURE DIRECTIONS

The influence of artificial light spectra on plant physiological processes and secondary metabolism has wide-ranging applications in areas such as agriculture, horticulture, pharmaceuticals, and even space exploration. This section will examine the potential applications of this understanding, as well as the future directions and areas of research that are needed to fully realize these applications. Controlled Environment Agriculture (CEA), which includes practices such as vertical farming and greenhouse cultivation, can significantly benefit from the manipulation of artificial light spectra. As shown in various studies, artificial light spectra can influence plant growth, development, photosynthesis, and secondary metabolite production [50]. The ability to control these aspects can lead to enhanced crop productivity and quality, ultimately improving the efficiency and profitability of CEA systems. The pharmaceutical and nutraceutical industries can significantly benefit from the manipulation of artificial light spectra, given the impact on secondary metabolite production. By using specific light spectra, the production of medicinal compounds in plants, such as flavonoids, phenolic compounds, and terpenoids, can be enhanced [51]. This could facilitate the production of plant-based drugs and supplements, meeting the increasing demand for natural and plant-derived products. The use of artificial light spectra has significant implications for space agriculture, where it can support the growth of plants in extraterrestrial environments, such as on space stations or future Mars colonies. LEDs, with their energy efficiency, compactness, and longevity, are particularly suited for this purpose. NASA has already conducted research on the use of LEDs for growing plants in space, with promising results [52].

12. FUTURE DIRECTIONS AND AREAS FOR FURTHER RESEARCH

While the influence of artificial light spectra on plant physiology and secondary metabolism is a well-established area of research, there are still several aspects that require further exploration.

1. **Understanding of Interactions with Other Environmental Factors:** The impact of light spectra is often studied in isolation. However, in real-world scenarios, plants are exposed to multiple environmental factors simultaneously. Therefore, understanding the interactions between light spectra and other environmental factors such as temperature, humidity, and carbon dioxide levels is crucial [53].
2. **Development of Custom Light Recipes:** Further research is needed to develop 'light recipes', combinations of different light qualities, intensities, and durations that are optimal for specific plant species or even cultivars.
3. **Long-Term Studies:** Most studies on the impact of artificial light spectra on plants are short-term. Long-term studies are needed to determine if the observed effects are sustained over the entire lifecycle of the plant and across multiple generations.

13. CONCLUSION

The understanding of artificial light spectra's effects on plant physiological processes and secondary metabolism holds immense potential. Its application ranges from enhancing productivity in controlled environment agriculture to increasing the synthesis of health-promoting secondary metabolites, and even supporting space agriculture. Despite the progress, further research is crucial to unravel the interactions between light spectra and other environmental factors, develop tailored light recipes, and conduct long-term studies. With such insights, we can fully harness the power of artificial light spectra to revolutionize plant cultivation and production.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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