




## Interval-Based LED Lighting Enhances Phytochemical Production in Cannabis under Greenhouse Conditions

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### ABSTRACT

Cannabis has gained increasing economic importance in Thailand following recent regulatory changes. Cannabis sativa L. cultivar Charlotte's Angel, a cannabidiol (CBD)-rich variety, is valued for its anti-inflammatory, analgesic, and anxiolytic properties without psychoactive effects. This study evaluated the effects of supplemental LED light spectra on plant growth, production efficiency, and CBD content of Charlotte's Angel under greenhouse conditions. Six light treatments were examined: natural sunlight (control), blue:red LED ratios of 50:50 (B:R 5:5), 20:80 (B:R 2:8), and 80:20 (B:R 8:2), as well as two full-spectrum LED treatments (Full1 and Full2). Full1 produced the highest plant height, canopy width, and total biomass, indicating strong potential to maximize structural growth and yield. The red-dominant B:R 2:8 treatment significantly enhanced lateral branching, leaf production, and overall yield by 5-, 5-, and 1.8-fold, respectively, highlighting its suitability for biomass-oriented commercial production. Physiological analyses showed that B:R 2:8 and B:R 8:2 treatments most strongly enhanced photosynthetic efficiency, while the balanced B:R 5:5 treatment exhibited the highest antioxidant activity and significantly increased CBD concentration and floral quality by 85%. Collectively, these results demonstrate that strategic LED spectral supplementation for day-extension in greenhouse systems can optimize biomass production, CBD accumulation, and production efficiency, offering a cost-effective approach for commercial cannabis cultivation.

**Keywords:** Spectral quality, Greenhouse cultivation, Cannabidiol, Antioxidant, Photosynthesis.

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### INTRODUCTION

Light serves as the primary source of energy for photosynthesis, the fundamental process driving plant growth and cannabinoid biosynthesis in cannabis. Among the environmental factors influencing cannabis physiology, light is particularly pivotal in regulating morphological traits such as branching, leaf size, and bud density, as well as in modulating biochemical pathways that affect cannabinoid and terpene profiles (Danziger and Bernstein, 2021; Rodriguez-Morrison et al., 2021).

Previous studies have demonstrated that both light intensity and spectral composition strongly influence cannabis productivity and metabolite accumulation.

Danziger and Bernstein (2021) reported that after a brief vegetative phase, cannabis flowered under a 12/12 photoperiod achieved peak yields, chlorophyll A, carotenoid, water use efficiency and CBGA accumulation using a 1:1 Blue: Red (B: R) Light Emitting Diode (LED) ratio. In contrast, low-blue HPS light produced cultivar-specific effects on CBDA. Similarly, Rodriguez-Morrison et al. (2021) showed that after a two-week vegetative phase, flower yield and apical inflorescence density increased linearly with light intensity up to  $1,800\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  during a 12-week flowering period. Although higher light intensities substantially enhanced biomass accumulation and harvest index, cannabinoid potency remained largely unaffected.

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Beyond intensity, light quality exerts distinct morphological and biochemical effects. Under a constant photosynthetic photon flux density of  $600\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (16 h vegetative/12 h flowering), 1:1 and 1:4 B:R LED ratios maximized flower yield and CBD concentration in CBD-rich cultivars, while higher blue light proportions resulted in more compact plant architecture. In contrast, red-dominant or full-spectrum lighting promoted stem elongation (Umnajkitikorn et al., 2025). These findings highlight the critical role of spectral optimization in cannabis cultivation, particularly in controlled-environment systems where LED lighting allows precise manipulation of wavelength composition. Plants grown under white LED light accumulated higher CBD concentrations (11.9–13.4%) than those under red-enriched spectra. Although red-rich LED treatments reduced plant height, leaf area, and shoot biomass by 4–26.7%, 21–55%, and 1.9–30.3%, respectively, they promoted greater biomass allocation to inflorescences (40.1–51.6%) at the expense of vegetative tissues (Carranza-Ramírez et al., 2025).

At the physiological level, spectral composition influences photosynthetic efficiency, morphogenesis, and secondary metabolism. Red wavelengths (600–700 nm) are generally associated with stem elongation and flowering induction, whereas blue wavelengths (400–500 nm) enhance leaf development, plant compactness, and cannabinoid accumulation (Park & Runkle, 2018; Paradiso & Proietti, 2022). Consequently, a balanced blue:red spectrum optimizes both photosynthetic performance and secondary metabolite accumulation (Magagnini et al., 2018). Although less extensively studied, green light (500–600 nm) can penetrate deeper into the canopy, potentially improving photosynthesis in lower leaves (Terashima et al., 2009). Photoperiod further functions as a metabolic switch by regulating bHLH and MYB transcription factors, thereby controlling the expression of key biosynthetic genes such as *1-deoxy-D-xylulose-5-phosphate reductoisomerase (DXR)* and *olivetolic acid cyclase (OAC)*, which catalyzes olivetolic acid synthesis. Together, these regulatory mechanisms govern cannabinoid and terpene biosynthesis (Livingston et al., 2020).

Although research on the spectral regulation of cannabinoid biosynthesis remains less extensive than studies on light intensity and photoperiod, emerging evidence highlights the importance of balanced spectra. A 1:1 B:R ratio has been shown to upregulate cannabinoid biosynthetic genes, including *Farnesyl pyrophosphate synthase (FPS)*, *Geranylgeranyl pyrophosphate synthase (GPPS)* and, *cannabidiolic-acid synthase (CBDAS)*, thereby enhancing precursor flux through both the MEP and hexanoate pathways and promoting CBGA and CBDA synthesis (Umnajkitikorn et al., 2025). However, most of this research has been conducted in fully indoor cultivation systems, with comparatively limited attention to greenhouse-based production. Indoor cannabis cultivation offers high environmental stability but is associated with substantial energy consumption and environmental impact. Indoor systems are among the most energy-intensive agricultural production methods, exhibiting carbon footprints up to 25 times greater than

those of greenhouse or outdoor systems (Bilodeau et al., 2019). While indoor cultivation can achieve high standardized THC concentrations, it has also been linked to increased cannabinoid degradation and oxidation, potentially reducing chemical complexity (Zandkarimi et al., 2023). In contrast, sun-grown cannabis often exhibits richer and more diverse phytochemical profiles, including higher levels of minor cannabinoids such as C4- and C6-THCA, greater sesquiterpene abundance (e.g.,  $\beta$ -caryophyllene and  $\alpha$ -humulene) and enhanced aromatic intensity driven by exposure to full-spectrum solar radiation, including ultraviolet wavelengths (Zandkarimi et al., 2023; Ullah et al., 2025).

Greenhouse cultivation represents a potential middle ground between indoor and outdoor systems, combining access to natural sunlight with the ability to supplement and fine-tune spectral quality using LEDs (Campiglia et al., 2020; Yano & Fu, 2023). In solar-rich regions such as Thailand, greenhouse systems offer a particularly promising and sustainable alternative, enabling reduced energy consumption while maintaining high-quality secondary metabolite profiles. Nevertheless, greenhouse environments are inherently more variable, with fluctuations in temperature, humidity, and light quality that can significantly influence plant morphology, yield, and cannabinoid composition (Weissman et al., 2020). While supplemental lighting has been explored to extend photoperiods and improve flower quality under greenhouse conditions (Massa et al., 2008; Nelson & Bugbee, 2014; Bilodeau et al., 2019), research examining how specific LED spectra interact with natural sunlight to regulate cannabinoid biosynthesis remains limited.

Charlotte's Angel, a short-day hemp cultivar that initiates flowering under photoperiods of less than 16 hours per day, is particularly susceptible to premature flowering in regions where natural daylight spans approximately 10-12 hours daily, such as Thailand. This premature flowering can adversely affect yield and cannabinoid quality. Therefore, this study aimed to evaluate the effects of various LED light spectra supplemented to natural sunlight on the growth, antioxidant capacity, and CBD content of Charlotte's Angel. The findings might provide valuable insights for optimizing greenhouse cannabis cultivation in emerging markets characterized by high natural light availability.

## MATERIALS & METHODS

### Plant Materials

*Cannabis sativa* L. subsp. *sativa* cultivar Charlotte's was cultivated at the SUT Cannabis Farm, Suranaree University of Technology, Nakhon Ratchasima, Thailand (The location map was shown in Supplementary Fig. 1). Cannabis plants were propagated by cutting, following by rooting in moist vermiculite for 2 weeks in greenhouse, before transferring to 3.5-inch black nursery plant bags filled with SUT potting material (coconut coir dust: chopped coconut shell: filter cake = 3:1:1; the chemical properties were analyzed and shown in Supplementary Table 1) to let them adjusted to the environment.



**Supplementary Fig. 1:** Location map of Cannabis farm, Suranaree University of Technology, Thailand. The GPS location is N 14.871345, E 102.025902 in the northeastern part of Thailand.

**Supplementary Table 1:** Chemical properties of the SUT potting material

Sample	EC (ds/m)	1:5	pH 1:5	% OM	% N	% P	% K	% Ca	% Mg
Potting material	1.60		6.51	36.98	1.02	0.75	0.06	1.24	0.5

Greenhouse condition were controlled at the average temperature  $30 \pm 2^\circ\text{C}$  and 16-hour light (8-hour supplemented light from 3 am – 8 am and 6 pm to 9 pm). One-week after adjusting in the greenhouse, plants were transplanted into the 17-inch-plastic baskets filled with SUT potting material, based with the plastic bowls in the evaporative greenhouse. Plants were fertilized 1.5 L every day with the SUT AB fertilizer (Greetatorn et al., 2025), which was developed based on the nutrient requirement of cannabis plants (Supplementary Table 2). The pests and diseases were controlled under the common organic practice.

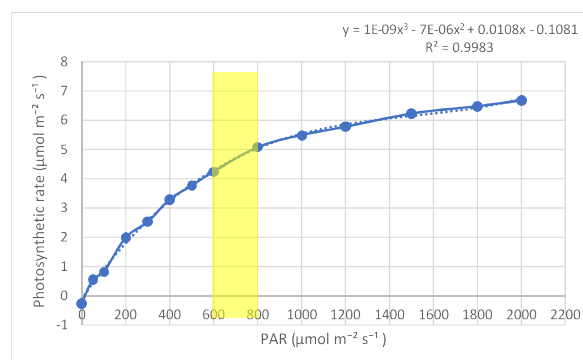
### Experimental Design and Treatment

The experimental cannabis cultivar Charlotte's angel in 17-inch-plastic baskets 2 plants per pots were placed under 6 light treatments, including no supplement light (control), the ratio of red and blue LED lights 50:50 (B: R 5:5), Full spectrum 1 LED (Full1), Full spectrum 2 LED (Full2), Blue LED to Red Ratio 20: 80 (B: R 2: 8) and Blue LED to Red Ratio 80:20 (B: R 8:2) using light intensity at  $600 \mu\text{mol m}^{-2} \text{s}^{-1}$  for 8 hours (3.00-8.00 and 18.00-21.00). Light intensity was determined based on the maximum photosynthetic return per unit of incident light, as derived from the light response curve of this cultivar (Supplementary Fig. 2). The spectra of all 6 light treatments were shown in Fig. 1. The primary differences between the Full1 and Full2 treatments were the presence of far-red radiation and the distribution of spectral energy. Full1 provided a broader spectral distribution with greater relative intensity in the 450–500 nm range and included far-red wavelengths, providing a better sunlight spectral mimic, whereas Full2 was characterized by higher proportions of blue (420–450 nm) and green (500–560 nm) light and lacked far-red radiation. Six pots per light condition were set. The lights were supplemented for 8 hours for 5 weeks, then

changing to supplement 8 hours during daytime (8.00-16.00) until harvested (another 8 weeks).

### Growth Parameters

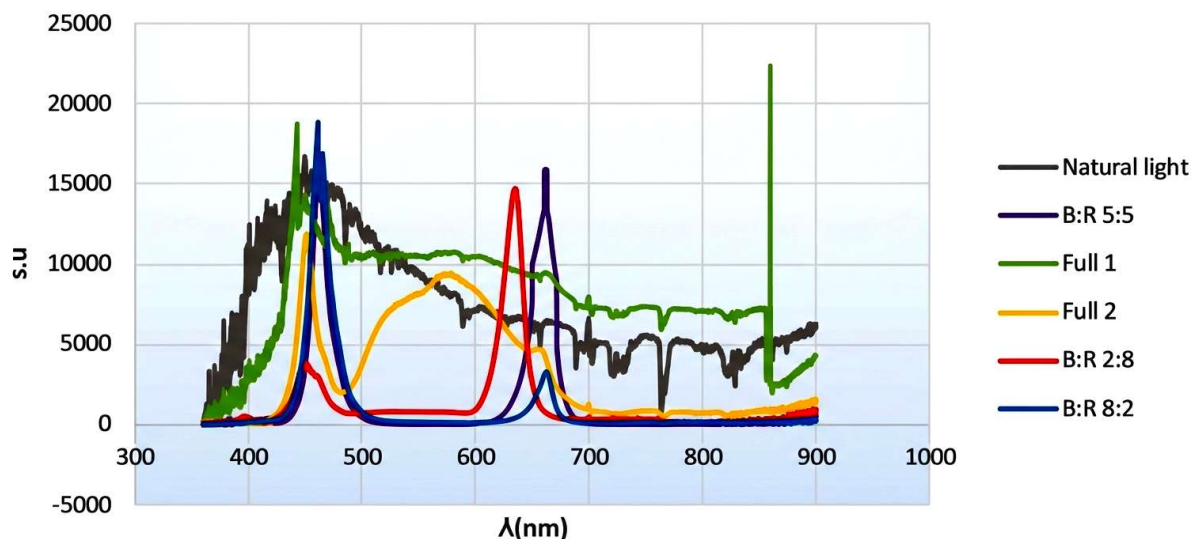
Prior to initiating the light treatments, baseline measurements of plant height and canopy width were recorded from 5 plants per treatment. Plant height and canopy width were measured every 7 days for a duration of 4 weeks. At the end of the treatment period, 5 plants per treatment were randomly selected for destructive sampling. Plant tissues, including leaves, stems, and roots, were harvested and separated. Fresh weights were immediately recorded, and samples were subsequently dried in a hot air oven at  $72^\circ\text{C}$  for 72 hours to obtain dry weight measurements.



**Supplementary Fig. 2:** Light response curve of Charlotte's Angel cannabis at the age of 30 days after transplant under the 16h/8h light/dark regime. The curve was generated from the average data from 3 plants at different light intensity. The yellow highlight was representing the last light intensity before the slope entering the literally plateau response (maximum photosynthetic return per unit light). The curve was generated by using the LICOR6800 gas exchange system from 9.00 am – 12.00 pm.

**Supplementary Table 2** Nutrient requirement of cannabis plants

Plant parts	N	P	K	Ca	Mg
Stem	0.84	0.16	0.75	0.60	0.28
Root	1.96	0.22	1.24	0.57	0.39
Leaf	3.54	0.49	1.92	3.15	0.59
Total	6.34	0.87	3.91	4.32	1.26



**Fig. 1:** Spectral properties of the experimental treatments. Natural light (control), the ratio of red and blue lights 50:50 (B:R 5:5), Full spectrum 1 (Full1), Full spectrum 2 (Full2), Blue LED to Red Ratio 20: 80 (B:R 2:8) and Blue to Red Ratio 80:20. (B:R 8:2).

## Physiological Parameters

### Gas Exchange Parameters

The analysis of gas exchange parameters was carried out by using a portable Infrared Gas Analyzer - IRGA, LCiSD ADC system®. Measurements were made on expanded leaves at the primary branch, being measured on the third leaf (youngest fully expanded leaves), between 9.00 and 12.00 when the plants were exposed for 65 days under each treatment. All 6 treatments from 5 repetitions were used for randomized measurements of photosynthesis rate, transpiration rate (E), the light interception on the leaf ( $Q_{leaf}$ ), and intercellular  $CO_2$  ( $C_i$ ).

### Leaf Area

The leaf area was quantified by area meter (Li-cor, Li-3100C, USA). Five plants from each treatment were randomly selected. All leaves from each plant were removed and inserted into the area meter. The leaf area was recorded in  $cm^2$ .

### Chlorophyll Quantification

Leaf samples were collected from the youngest fully expanded leaves of each treatment group to assess chlorophyll content. Sampling was conducted between 9:00 and 12:00, following the method described by Sade et al. (2017). Fresh leaf samples (approximately 300 mg) in 4 biological replications were collected from 4-week-old plants and immediately placed in liquid nitrogen. The samples were ground to a fine powder using a mortar and pestle.

For chlorophyll extraction, 5 mL of 80% acetone was added to the ground leaf tissue, and the mixture was transferred to a 15 mL centrifuge tube. The samples were centrifuged at 9,500 rpm for 10 minutes to extract chlorophyll pigments. Subsequently, 200  $\mu$ L of the supernatant was transferred to a microplate, and absorbance was measured using a microplate reader at specific wavelengths (A645 and A663) to determine chlorophyll a and chlorophyll b concentrations.

Chlorophyll concentration was calculated using the

following equations:

$$\text{Chlorophyll a } (\mu\text{g/mL}) = (12.7 \times A_{663}) - (2.69 \times A_{645})$$

$$\text{Chlorophyll b } (\mu\text{g/mL}) = (22.9 \times A_{645}) - (4.68 \times A_{663})$$

$$\text{Total Chlorophyll } (\mu\text{g/mL}) = (8.02 \times A_{663}) + (20.20 \times A_{645})$$

The absorbance readings were normalized using 80% acetone as a blank control.

### Antioxidant Capacity

Collect cannabis leaves treatments with different light treatments 4 replicates each and then grind the samples in liquid nitrogen. Keep in  $-80^\circ\text{C}$  until use.

Antioxidant capacity measurement was modified from Umnajkitikorn et al. (2013) as follows: 50 mg of the ground cannabis samples were placed in 1 mL tubes, 1 mL of 80% ethanol, placed in tubes and shaken for 10 min, then centrifuged at 16000 rpm at  $4^\circ\text{C}$  for 20 min, the separation was achieved to obtain a clear solution and collect this clear solution. For analyzing DPPH for antioxidant determination. For antioxidant analysis using DPPH, 50  $\mu$ L of the clear supernatant from the sample was aspirated and mixed with 400  $\mu$ L of 0.3M acetate buffer (pH5.5) and 0.06 mM DPPH in 1 ml of 95% methanol. Mix the solution and incubated in the absence of light for 30 min. A spectrophotometer measured the solution for absorbance at a wavelength of 517 nm. Antioxidant capacity of solution samples. It can be predicted from the decrease in the intensity of the violet in the sample solution. Trolox was used as the standard. The results were reported as Trolox equivalent antioxidant capacity (TEAC;  $\mu$ mol Trolox/g fresh weight).

### Cannabinoid Quantification

Evaluation the effects of light spectra to the cannabinoids. Samples was collected from the tips of inflorescences in 3 biological replications from each treatment to analyze Delta-9-Tetrahydrocannabinol (THC) and cannabidiol (CBD) and Cannabigerol (CBG) from the flower and stem. The tissues were sampled. For the analysis 8-week after the switch to the short photoperiod.

When observed with stereo microscope, approximately 40% of the trichomes are amber, the inflorescence is trimmed by hand (i.e. the leaf tip protruding from the peduncle is removed), as is routine practice in the cannabis industry (Saloner & Bernstein, 2021). The samples were then sent for Gas Chromatography-Mass Spectrometry (GC-MS) at the Cassava Research Center, Suranaree University of Technology. The cannabinoid mixed (CE combination, Thailand) was used as the standard.

### Statistical Analysis

All data are presented as mean  $\pm$  SE. A one-way analysis of variance (ANOVA) was conducted using SPSS software under a completely randomized design (CRD) to evaluate the effects of light treatments. Prior to analysis, the assumptions of ANOVA were verified by testing the normality of residuals using the Shapiro-Wilk test and homogeneity of variances using Levene's test; all datasets met these assumptions ( $P > 0.05$ ). When significant treatment effects were detected ( $P < 0.05$ ), mean comparisons were performed using the least significant difference (LSD) test at  $P < 0.05$ . The LSD test was selected due to the limited number of treatments and predefined comparisons among LED spectral treatments, providing sufficient statistical power to detect biologically meaningful differences.

## RESULTS

### Morphological Parameters and Biomass

The Full1 treatment exhibited the greatest increase in plant height between weeks 2 and 4, followed by Full2, B:R

2:8, B:R 5:5, and B:R 8:2; all of these treatments resulted in significantly taller plants than the control (no supplemental lighting) (Fig. 2A). Canopy expansion was most pronounced under the B:R 2:8 treatment, followed by Full1, B:R 5:5, B:R 8:2, and Full2, all of which showed significantly greater canopy width than the control (Fig. 2B and C). Overall, all supplemental lighting treatments enhanced vegetative growth compared with the control (Fig. 2C).

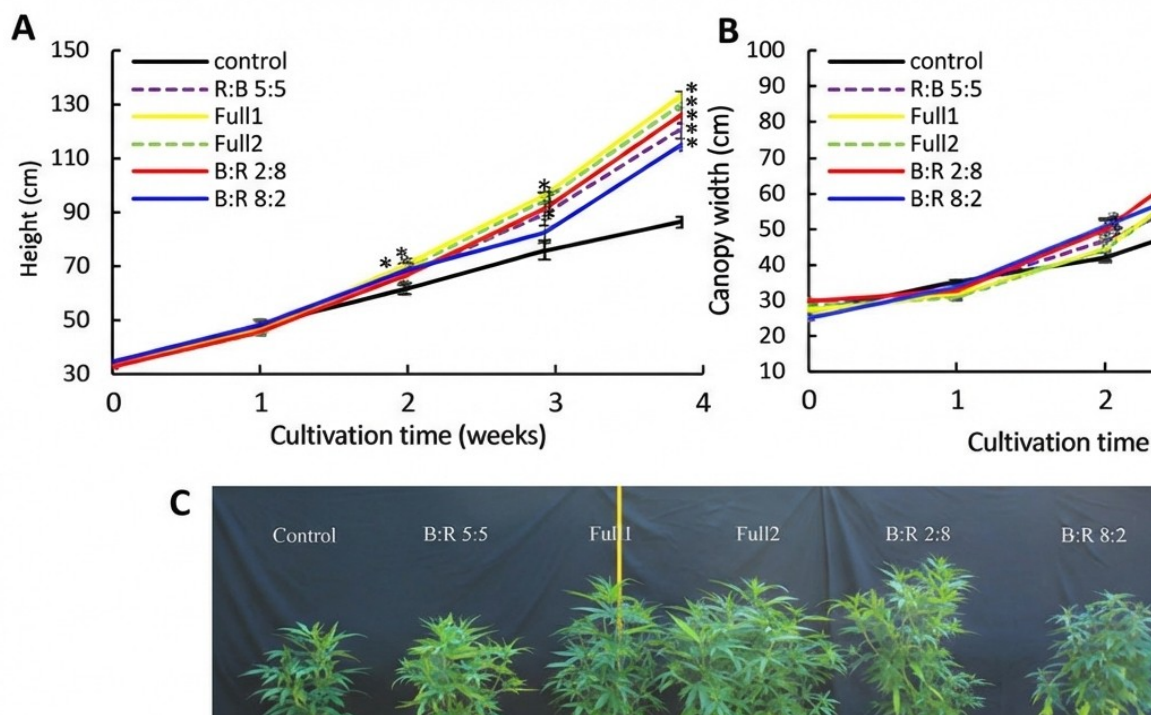
Biomass accumulation was greatest under the B:R 2:8 treatment, which produced the highest fresh and dry weights across all plant organs (Fig. 3A–H). However, maximum flower dry weight was observed under both the Full2 and B:R 2:8 treatments (Fig. 3H).

### Gas Exchange Parameters

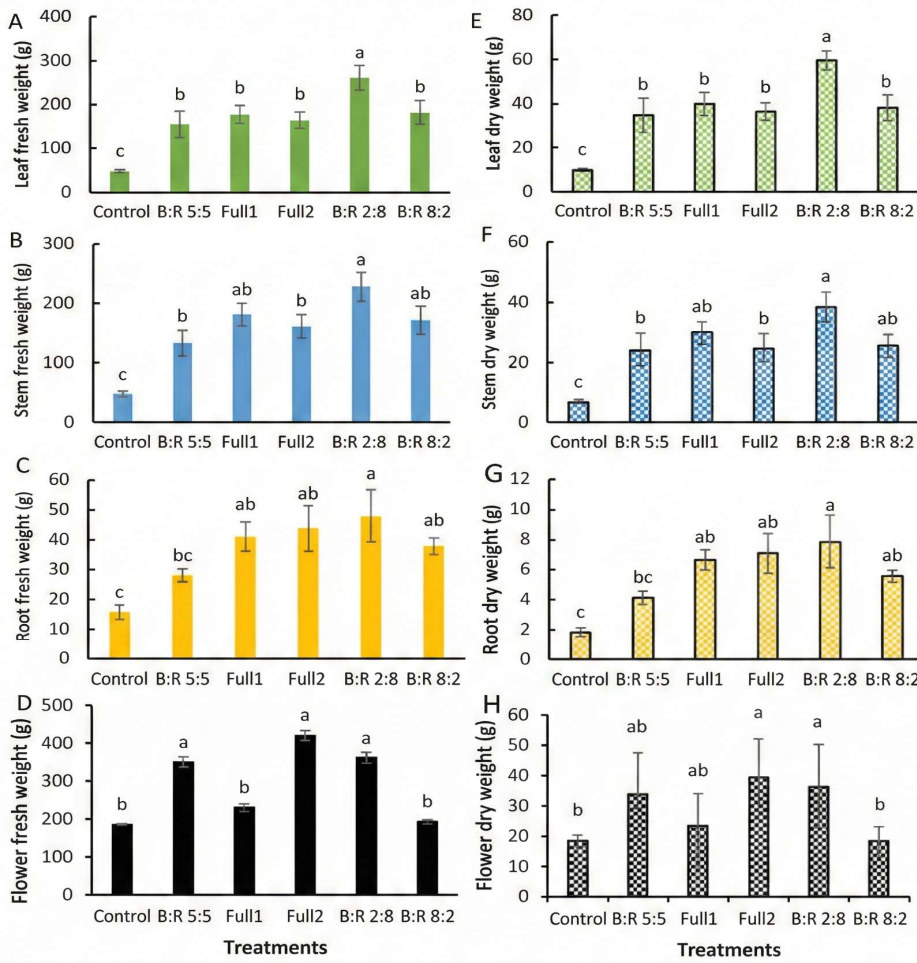
Light quality of the supplemental greenhouse lighting did not significantly affect photosynthetic rate or intercellular  $\text{CO}_2$  concentration ( $C_i$ ) (Fig. 4A and B). However, the balanced B:R 5:5 treatment exhibited a significantly higher transpiration rate ( $E$ ) compared with the other treatments (Fig. 4C). Although all light-supplemented treatments showed reduced leaf light interception ( $Q_{\text{leaf}}$ ) (Fig. 4D), they exhibited significantly greater leaf area than the control (Fig. 4E). Among these, the Full1 treatment induced the greatest leaf area across all treatments (Fig. 4E).

### Antioxidant Capacity and Chlorophyll Contents

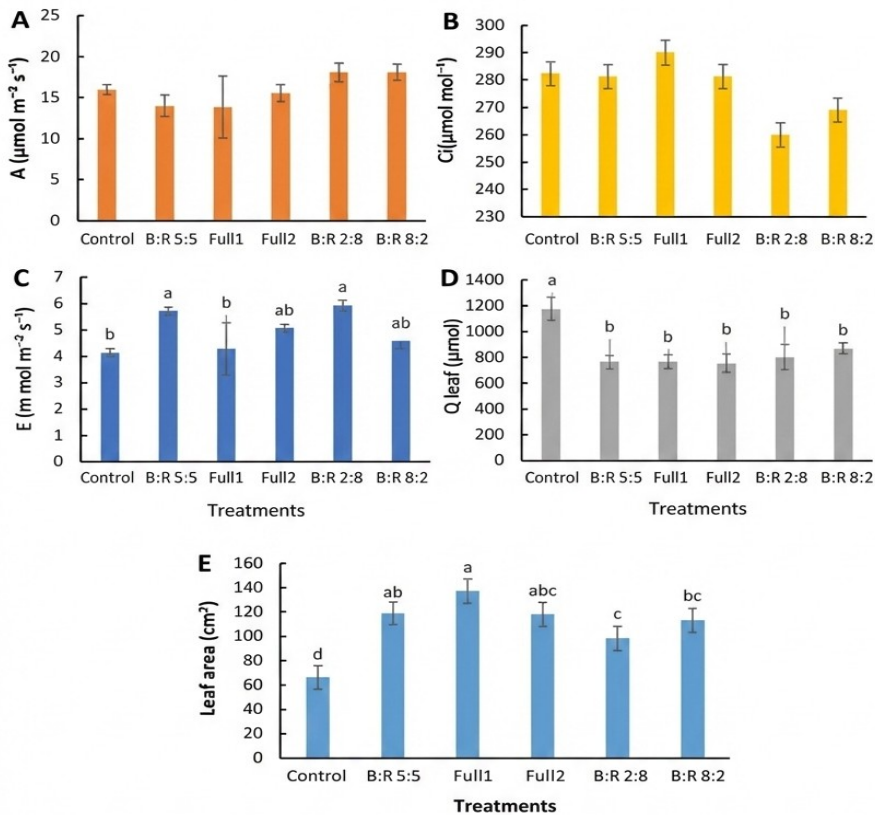
Antioxidant capacity, assessed using the DPPH assay, was significantly enhanced only under the B:R 5:5 treatment in cannabis leaves (Fig. 5A). In contrast, total chlorophyll content did not differ significantly among treatments (Fig. 5B).



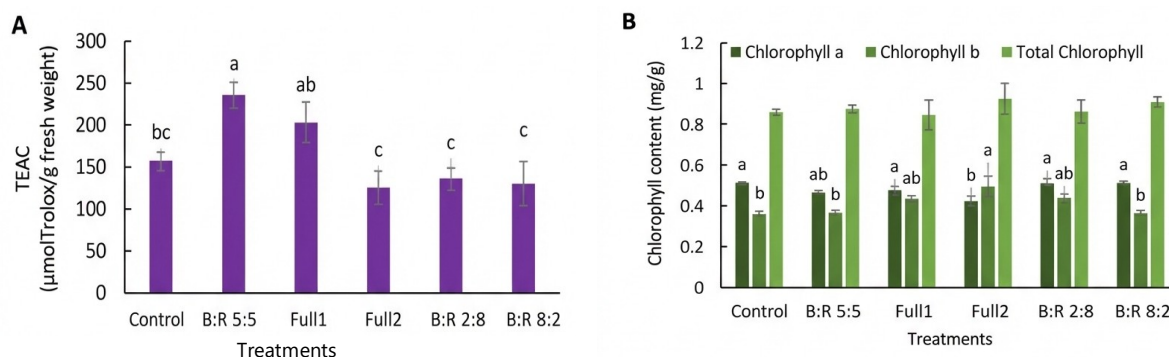
**Fig. 2:** Effects of four weeks of exposure to different LED spectral treatments on plant height (A), canopy width (B), and overall growth (C) of cannabis plants. Values represent means ( $n = 5$ ), and error bars indicate the standard error (SE). Asterisks denote statistically significant differences among treatments as determined by one-way analysis of variance (ANOVA) followed by the least significant difference (LSD) test at  $P \leq 0.05$ .



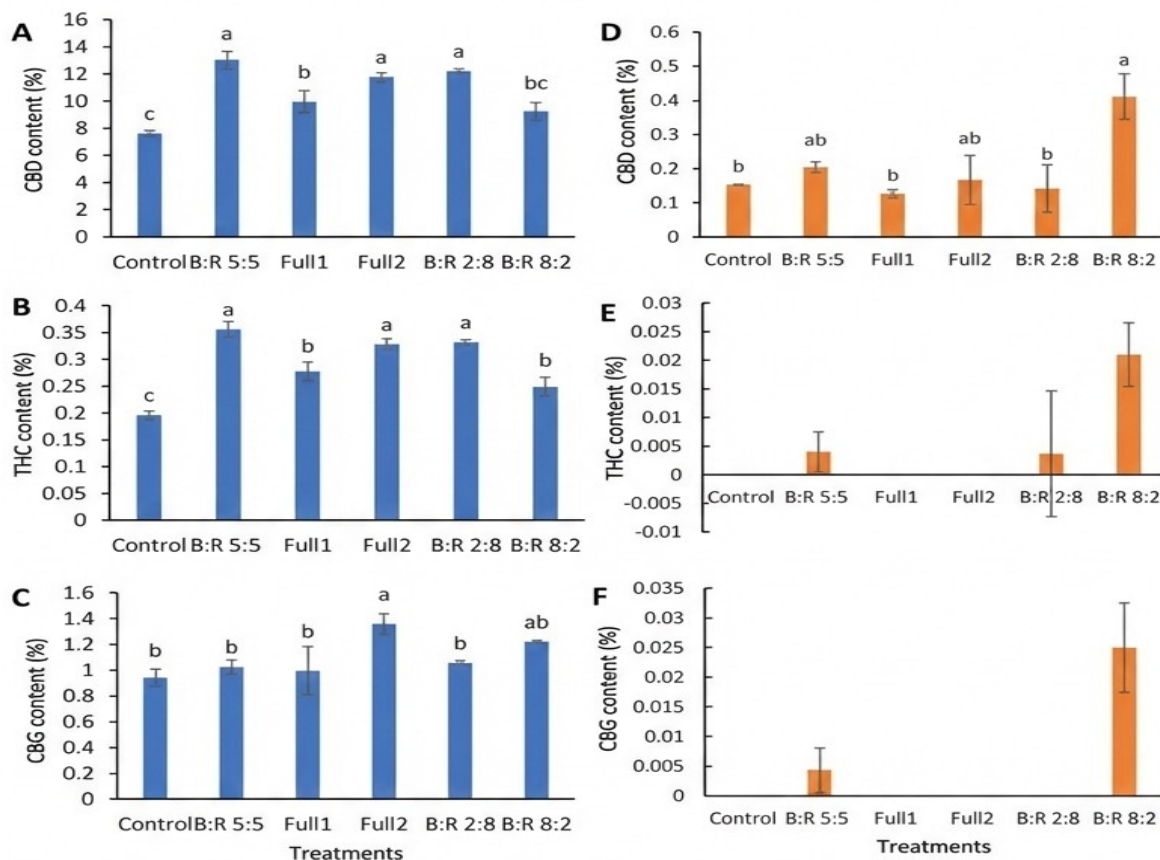
**Fig. 3:** Effects of 65 days of exposure to different supplemental LED spectral treatments on biomass accumulation in cannabis plants. Fresh weight of leaves (A), stems (B), roots (C), and flowers (D), and dry weight of leaves (E), stems (F), roots (G), and flowers (H) are shown. Values represent mean  $\pm$  SE ( $n = 5$ ). Different letters above bars indicate statistically significant differences among treatments as determined by one-way ANOVA followed by the least significant difference (LSD) test at  $P \leq 0.05$ .



**Fig. 4:** Effects of different supplemental LED spectral treatments on photosynthetic parameters of cannabis plants. Photosynthetic rate (A), intercellular  $\text{CO}_2$  concentration (B), transpiration rate (C), photosynthetically active radiation incident on the leaf surface ( $Q_{\text{leaf}}$ ) (D), and leaf area (E) are shown. Values represent means  $\pm$  standard error (SE) ( $n = 5$ ). Different letters above bars indicate statistically significant differences among treatments as determined by one-way analysis of variance (ANOVA) followed by the least significant difference (LSD) test at  $P \leq 0.05$ .



**Fig. 5:** Effects of different supplemental LED spectral treatments on antioxidant capacity and chlorophyll content of cannabis plants. DPPH antioxidant capacity (A) and total chlorophyll content (B) are shown. Values represent means  $\pm$  standard error (SE) ( $n = 5$ ). Different letters above bars indicate statistically significant differences among treatments as determined by one-way ANOVA followed by the least significant difference (LSD) test at  $P \leq 0.05$ .



**Fig. 6:** Effects of different supplemental LED spectral treatments on cannabinoid content in cannabis plants. Cannabidiol (CBD) concentration in flowers (A) and stems (D),  $\Delta^9$ -tetrahydrocannabinol (THC) concentration in flowers (B) and stems (E), and cannabigerol (CBG) concentration in flowers (C) and stems (F) are shown. Values represent mean  $\pm$  SE ( $n = 5$ ). Different letters above bars indicate statistically significant differences among treatments as determined by one-way ANOVA followed by the least significant difference (LSD) test at  $P \leq 0.05$ .

### Cannabinoid Contents

The cannabinoid profiles of Charlotte's Angel responded differentially to the various LED spectral treatments. Among these, the B:R 5:5, Full2, and B:R 2:8 treatments produced the highest CBD concentrations in floral tissues (Fig. 6A). These same treatments also resulted in significantly elevated THC levels in the flowers (Fig. 6B). Notably, Full2 was the only treatment to significantly increase CBG concentration in floral tissues (Fig. 6C). In contrast, the blue-dominant B:R 8:2 treatment uniquely enhanced CBD accumulation in stem tissues (Fig. 6D), but

did not increase floral CBD content, unlike the other supplemental lighting treatments. No significant differences were observed in THC or CBG concentrations in stem tissues across treatments (Fig. 6E and F).

### DISCUSSION

This study evaluated the effects of six LED spectral treatments on growth, physiological performance, antioxidant capacity, and cannabinoid biosynthesis of *Cannabis sativa* cv. Charlotte's Angel under greenhouse

conditions. Collectively, the results demonstrate that light spectral composition acts as a central regulator linking plant morphology, physiological function, redox balance, and secondary metabolite production.

### **Morphological Development as a Foundation for Physiological Performance**

Light spectrum markedly influenced plant architecture and biomass allocation. Among treatments, Full1—characterized by a broad spectral distribution including violet, blue, green, red, and far-red wavelengths—produced the tallest plants, suggesting that spectral diversity supports shoot elongation and canopy expansion (Fig. 2). Previous studies indicate that low red:far-red (R:FR) ratios induce elongation responses through phytochrome-mediated shade-avoidance signaling (Magagnini et al., 2018), while RGB and RBFR spectra promote shoot multiplication and elongation more effectively than red–blue combinations alone (Li et al., 2025). Consistently, our indoor experiments showed a strong positive correlation between red light proportion and branch dry weight, with B:R 2:8 and full-spectrum treatments producing the greatest stem biomass (Umnajkitikorn et al., 2025).

The enhanced growth under Full1 may also reflect improved light penetration within the canopy. While red and blue wavelengths are predominantly absorbed by upper leaf layers, green light penetrates deeper into leaf tissues and can enhance photosynthesis in lower canopy layers (Terashima et al., 2009; Rehman et al., 2024). The synergistic interaction among green, red, and blue wavelengths in Full1 likely improved whole-canopy light utilization, contributing to increased shoot elongation. However, the presence of far-red radiation may also promote excessive cell elongation and expansion, which could be disadvantageous at later developmental stages (Pashkovskiy et al., 2024; Li et al., 2025).

In contrast, the red-dominant B:R 2:8 treatment produced the highest biomass accumulation across all plant organs, including roots, stems, leaves, and flowers. This response aligns with established roles of red light in stimulating stem elongation, leaf expansion, and root growth (Umnajkitikorn et al., 2025). Conversely, treatments with higher blue light proportions (B:R 8:2 and B:R 5:5) exhibited smaller canopy sizes, consistent with the known inhibitory effects of blue light on cell elongation and leaf expansion. Increasing the blue light fraction from 4% to 20% has previously been shown to reduce yield by approximately 12% (Mitchell Westmoreland et al., 2021), supporting the observed reduction in vegetative expansion under blue-enriched spectra. Moreover, far-red light (>700 nm) can substantially modify plant morphology by promoting internode elongation and leaf expansion, thereby enhancing canopy light interception and yield (McKay et al., 2025). This aligned with our results that Full1, the only light supplement that contain far-red spectrum induced the highest leaf area. Together, these findings indicate that supplemental LED spectra in greenhouses can reproduce growth patterns observed in indoor systems when spectral composition is carefully managed.

### **Physiological Responses: Linking Structure to Gas Exchange and Water Use**

Morphological differences induced by light spectra were closely associated with physiological responses. Although photosynthetic rate did not differ significantly among treatments, the B:R 8:2 and B:R 2:8 treatments consistently exhibited higher photosynthetic performance (Fig. 4A). Similar enhancements under red–blue LED combinations have been reported in lettuce and strawberry, where these spectra increased CO<sub>2</sub> assimilation, stomatal conductance, and water-use efficiency (Esmailizadeh et al., 2021; Ahmed et al., 2022).

Notably, transpiration rate was significantly higher under the B:R 2:8 and B:R 5:5 treatments (Fig. 4C), suggesting distinct but complementary mechanisms. Red-dominant spectra likely increased transpiration indirectly through enhanced leaf area and vascular development, increasing evaporative surface area and water transport capacity (Taiz et al., 2015; Pashkovskiy et al., 2023). In contrast, blue light directly stimulates stomatal opening via phototropin-mediated signaling in guard cells (Shimazaki et al., 2007). The balanced B:R 5:5 treatment likely integrated these anatomical and physiological mechanisms, resulting in optimized stomatal regulation and water vapor exchange. This interpretation is supported by indoor studies showing that balanced red–blue spectra enhance photosynthetic efficiency, reduce biochemical limitations, and upregulate photosynthesis-related genes (Umnajkitikorn et al., 2025). Importantly, although blue light alone can reduce water-use efficiency, its combination with red light mitigates this effect, highlighting interactive spectral regulation of plant water dynamics (Tarakanov et al., 2022).

### **Antioxidant Responses as a Metabolic Link to Secondary Metabolite Production**

The enhanced physiological activity under balanced spectra was accompanied by changes in redox regulation. The B:R 5:5 treatment exhibited the highest antioxidant capacity, consistent with previous studies showing that red–blue LED combinations stimulate antioxidant compound accumulation (Stutte et al., 2009; Zhiponova et al., 2025). Blue light is known to regulate antioxidant enzyme systems, while red light supplies the photosynthetic energy required for secondary metabolism. Accordingly, balanced spectra have been shown to increase the activities of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT) in cannabis and other medicinal plants (Wang et al., 2017; Islam et al., 2021).

Cannabis antioxidants include cannabinoids, flavonoids, and polyphenols (André et al., 2020; Eaves et al., 2020). In this study, the increase in antioxidant capacity observed in leaves under B:R 5:5 was not associated with changes in chlorophyll content (Fig. 5B), suggesting that antioxidant enhancement was driven primarily by secondary metabolites rather than photosynthetic pigments (Wu et al., 2025). This supports a mechanistic link between spectral regulation, oxidative stress management, and metabolic allocation toward specialized compounds.

### Cannabinoid Biosynthesis

Cannabinoid accumulation reflected the integrated effects of morphology, physiology, and antioxidant regulation. The B:R 5:5, Full2, and B:R 2:8 treatments significantly increased CBD content in floral tissues (Fig. 6A), likely due to increased leaf area and sustained photosynthetic capacity supplying carbon precursors for secondary metabolism (Fig. 4E). These findings are consistent with our indoor experiments, which also reported maximal CBD accumulation under B:R 5:5 and B:R 2:8 treatments (Umnajkitikorn et al., 2025).

Interestingly, only Full2 significantly enhanced CBG content in flowers, suggesting that full-spectrum LEDs may preferentially promote the synthesis of minor cannabinoids. Previous studies have reported that blue light has limited effects on CBD accumulation but strongly influences CBG and terpenoid biosynthesis (Danziger & Bernstein, 2021; Morello et al., 2022). Namdar et al. (2019) also reported that supplementing high-pressure sodium lighting with blue-dominant LEDs—similar to the Full2 spectrum used in this study—resulted in the highest CBGA accumulation 14 days after light exposure. This indicates that specific spectral components may selectively regulate branch points within the cannabinoid biosynthetic pathway (Reichel et al., 2022).

The mechanisms underlying cannabinoid accumulation in stem tissues remain unclear. However, the observed spectral effects suggest that light quality can influence cannabinoid partitioning among plant organs, potentially through localized metabolic regulation or transport processes. Overall, this study demonstrates that targeted manipulation of LED spectra under greenhouse conditions can modulate cannabinoid composition by coordinating plant structure, physiological performance, antioxidant capacity, and secondary metabolism.

### Conclusion

This study highlights the critical role of LED light spectra in regulating growth, physiological performance, and cannabinoid biosynthesis in *Cannabis sativa* cv. Charlotte's Angel under greenhouse conditions. The red-dominant B:R 2:8 treatment produced the highest fresh and dry biomass across plant organs, indicating strong potential for maximizing vegetative growth and yield. In addition, red and balanced red–blue spectra (B:R 2:8 and B:R 8:2) enhanced photosynthetic and transpiration rates, reflecting improved physiological efficiency. Notably, the B:R 5:5, Full2, and B:R 2:8 treatments significantly increased CBD and THC concentrations in floral tissues, with Full2 uniquely promoting CBG accumulation.

From a commercial perspective, these results demonstrate that strategic spectral supplementation in greenhouses can be used to tailor production goals, allowing growers to prioritize either biomass accumulation or cannabinoid enrichment while reducing reliance on energy-intensive indoor systems. Such targeted lighting strategies offer a practical pathway for improving yield consistency, phytochemical quality, and production efficiency in large-scale greenhouse cannabis operations. Future research should focus on stage-specific spectral

optimization and its long-term effects on cannabinoid and terpene profiles.

### DECLARATIONS

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**Data Availability:** The data used for this research is available from the corresponding author upon request.

**Ethics Statement:** Cannabis cultivation and production for this research were formally authorized under license 13/2563. All processing of plant materials was conducted under the direct oversight of the Thailand Food and Drug Administration (TFDA), ensuring strict adherence to established Standard Operating Procedures (SOPs) for legal compliance.

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