Theor. Exp. Plant Physiol. (2026) 38:2
https://doi.org/10.1007/s40626-026-00394-7

Blue-enriched LED light stimulates flowering in aeroponic *Matricaria chamomilla*

Luisa Fernanda Lozano-Castellanos ·
Aurora Arroyo · **Adriana Correa-Guimaraes** ·
Luis Manuel Navas-Gracia

Received: 28 May 2025 / Accepted: 12 January 2026

Abstract The indoor cultivation of *Matricaria chamomilla* represents a promising strategy for optimizing medicinal plant production. This research evaluated the effects of LED spectral composition on the morphological and biochemical development of chamomile in an aeroponic system. Three light treatments were applied: Red predominant + Far-red + Blue (Rh + FR + B), Blue predominant + Red + Far-red (Bh + R + FR), and Red + Blue (R + B), with a photosynthetic photon flux density (PPFD) of 255.96 ± 5.8 μmol m^{-2} s^{-1}. Seedlings were germinated under controlled conditions and later transferred to an aeroponic system with mist irrigation. The treatment Bh + R + FR significantly enhanced flowering, increasing flower and bud production, floral head diameter, and petal length. In contrast, R + B promoted higher chlorophyll accumulation and nitrogen balance index, favoring greater leaf expansion, particularly in pinna length. Although anthocyanin and flavonoid concentrations increased over time in all treatments, their accumulation was not significantly affected by spectral composition. These findings highlight that optimizing chamomile flower production requires a higher proportion of blue light, while a balanced red-to-blue ratio is more effective for maximizing leaf development. This study provides new insights into spectral optimization for controlled *M. chamomilla* cultivation, supporting its application in the medicinal and aromatic plant industry.

Keywords Chamomile · Indoor agriculture · LED lighting · Light spectra · Soilless

1 Introduction

Agriculture faces increasing challenges in meeting global demand for food and agricultural products while enhancing sustainability and production quality. In response, technological innovations have been developed to optimize traditional systems, particularly through indoor agriculture. This approach enables plant cultivation in controlled environments where key variables such as light, temperature,

L. F. Lozano-Castellanos (✉) · A. Arroyo ·
A. Correa-Guimaraes · L. M. Navas-Gracia
Recognized Research Group in Advanced Technologies Applied to Sustainable Rural Development - TADRUS, Department of Agricultural and Forestry Engineering, University of Valladolid, 34004 Palencia, Spain
e-mail: luisafernanda.lozano@uva.es

A. Arroyo
e-mail: aurora.arroyo@uva.es

A. Correa-Guimaraes
e-mail: adriana.correa@uva.es

L. M. Navas-Gracia
e-mail: luismanuel.navas@uva.es

L. F. Lozano-Castellanos
Research Group on Biodiversity and Dynamics of Tropical Ecosystems - GIBDET, Faculty of Engineering Forestry, University of Tolima, 730006 Ibague, Colombia

humidity, and nutrient availability can be precisely regulated (Engler and Krarti 2021). Indoor cultivation offers several advantages, including enhanced resource-use efficiency, stable year-round production, and improved chemical profiles of harvested species. Prominent strategies include vertical farming, artificial LED lighting, and soilless systems such as hydroponics, aeroponics, and aquaponics (Lozano-Castellanos et al. 2025). In parallel, automation with robotics and environmental sensors have significantly increased the precision and feasibility of these systems by optimizing critical growth parameters, including temperature, humidity, CO_2 concentration, and nutrient availability (Ojo and Zahid 2022).

Light is one of the most important factors in these systems, as its spectral composition, intensity, and photoperiod directly influence photosynthesis and morphogenesis. In this context, LED lighting has gained widespread attention due to its energy efficiency and tunability, allowing spectral configurations to be adapted to the physiological requirements of different species (Promratrak 2017). Research has shown that LEDs can improve total biomass and the accumulation of secondary metabolites relevant for medicinal and cosmetic applications (Samuolienė et al. 2017; Paradiso and Proietti 2022).

Among the most influential wavebands, blue (400–500 nm) and red (600–700 nm) light play central roles in plant development. Blue light regulates stomatal conductance, chlorophyll biosynthesis, and inhibits excessive stem elongation, promoting compact architecture. Red light, the most efficiently absorbed for photosynthesis, is associated with increased biomass accumulation, flowering induction, and overall productivity (Orsini et al. 2020; Liu et al. 2022). Far-red light (700–800 nm), although not photosynthetically active, modulates photomorphogenic responses by shifting phytochrome photoequilibrium, thereby influencing stem elongation, shade avoidance, and biomass partitioning (Kump 2020). Recent studies suggest that combining far-red with red and blue can enhance leaf expansion, improve light capture, and alter resource allocation, potentially increasing total biomass in certain crops (Zhang et al. 2021; Appolloni et al. 2022). However, species-specific responses to light spectra remain highly variable, underscoring the need to determine optimal combinations tailored to specific production goals, such as leaf, flower, root, or fruit yield.

Water-use efficiency is another critical consideration in indoor agriculture, given that traditional agriculture remains the largest consumer of freshwater globally. Aeroponics represents an advanced soilless technique that enables plants to grow with roots suspended in air and intermittently misted with nutrient-rich solutions (Lakhiar et al. 2020). This system minimizes water waste and enhances nutrient uptake, resulting in accelerated growth and increased biomass. Moreover, aeroponic systems offer pathogen-free conditions that reduce the prevalence of soilborne diseases and decrease agrochemical inputs (Min et al. 2023). Their efficiency and sustainability make them a promising solution for high-value crop production in water-scarce regions, ensuring consistent output while mitigating the impact of climate variability.

Although indoor systems have primarily focused on leafy vegetables and commercial crops, interest in the controlled cultivation of medicinal and aromatic plants (MAPs) has grown due to the increasing demand for bioactive compounds in pharmaceutical, cosmetic, and nutraceutical sectors (Bafort and Jijakli 2024). However, only a limited number of studies have evaluated the effect of light spectra on growth, flowering, and metabolite biosynthesis in MAPs. In particular, little is known about *Matricaria chamomilla*, a species of high pharmacological value due to its anti-inflammatory, antimicrobial, sedative, and antispasmodic properties (El Joumaa and Borjac 2022; El Mihyaoui et al. 2022). Among the few available studies, one examined the impact of LED lighting and soilless conditions on antioxidant enzyme activity and secondary metabolite concentrations in chamomile seedlings (Hassanpour 2023), while another assessed biomass and apigenin accumulation under hydroponics and LED exposure (Maynard et al. 2025). However, further studies are needed to optimize environmental conditions and elucidate how spectral composition affects the physiology and biochemical profiles of this species.

Matricaria chamomilla is native to southeastern Europe, North Africa, Macaronesia, central and southwest Asia, and the Himalayas, and has been introduced to North America (Chauhan et al. 2022). Its wide geographical distribution reflects its adaptability to varied environments. The species thrives in temperate climates, with optimal growth at daytime temperatures of 15–20 °C and can tolerate overnight lows of −10 °C. Full sun and long photoperiods enhance its growth and flowering (Chauhan et al. 2022; El Mihyaoui et al. 2022). In Spain, although climate conditions are generally suitable, high summer temperatures (> 24 °C) and low winter temperatures (< 15 °C) limit open-field cultivation. Chamomile's low water requirement (300–500 mm annually) makes it ideal for controlled systems in arid regions (Chauhan et al. 2022).

To date, no published research has evaluated the effects of specific LED spectral combinations—including far-red wavelengths—on the full developmental cycle of *M. chamomilla* cultivated in aeroponic systems. Existing studies have either focused on early growth stages, single spectra, or hydroponic systems, without exploring broader physiological responses under precisely defined light conditions. Thus, the present study is the first to assess how distinct spectral compositions affect growth, flowering, and physiological traits in *M. chamomilla* grown under fully controlled aeroponic conditions. We hypothesize that the spectral composition of LED light differentially affects reproductive and vegetative development in *Matricaria chamomilla*, with a blue-enriched spectrum expected to promote a stronger flowering response than red-enriched or red–blue spectra under identical photoperiod and photosynthetic photon flux density (PPFD) in aeroponic conditions. This research provides new insights for the controlled production of *M. chamomilla*, contributing to the development of sustainable, high-efficiency cultivation protocols for the MAP industry.

2 Material and methods

2.1 Plant material

Seeds of *M. chamomilla* provided by the Aragón Agri-Food Research and Technology Center (CITA), Spain, were germinated under controlled conditions in an IBERCEX growth chamber (model IGCS 900 HR LED, Madrid, Spain) at a PPFD of 195.87 µmol m^{-2} s^{-1}, 23 °C, and 80% relative humidity for 15 days in a peat-perlite mixture (90:10 v:v). Once the seedlings reached the appropriate developmental stage, they were transplanted into the aeroponic system, where the substrate was carefully removed from the roots before securing them in 4.0 × 2.5 × 2.5 cm rock-wool blocks (Groho Hidroponía, Madrid, Spain).

2.2 Cultivation conditions

The experiment was conducted using an aeroponic system designed at the University of Valladolid, Campus of Palencia, Spain, under controlled conditions with an average temperature of 18.3 °C and a relative humidity of 54.3% (Climate data logger, Parkside, Germany). The system consisted of three cultivation trays with a total capacity of 48 M. *chamomilla* plants, distributed as 16 plants per tray, with three replicates per treatment (Fig. 1).

The irrigation system operated through water nebulization using a CoolNET PRO nebulizer (Regaber, Barcelona, Spain) with dual nozzles, generating 65-µm droplets at 3.0–5.0 bar pressure. A biomineral fertilizer, Aero Supermix (GroHo Hidroponía, Madrid, Spain), was applied at 1 min intervals every 4 min during the 16 h photoperiod. The nutrient solution was prepared at 27 mL per 10 L of water and recirculated in a closed-loop system to minimize waste. pH was measured weekly using a soil pH meter PCE–PH20S (PCE Instruments, Meschede, Germany). When increases were detected, a pH-reducing solution was applied according to the manufacturer's specifications (GroHo Hidroponía, Madrid, Spain).

Light treatments followed a 16 h light / 8 h dark cycle across the three cultivation trays, using a lighting system supplied by Boos Technical Lighting SL (Valladolid, Spain). Spectral measurements were conducted with an AvaSpec-ULS2048CL EVO series spectrometer equipped with a CMOS detector (Avantes, Apeldoorn, Netherlands) within a spectral range of 360–1100 nm. Three distinct lighting treatments were established (Fig. 2): Rh + FR + B (Red predominant + Far-red + Blue), with a PPFD of 264.26 µmol m^{-2} s^{-1}; Bh + R + FR (Blue predominant + Red + Far-red), with a PPFD of 252.11 µmol m^{-2} s^{-1}; and R + B (Red + Blue), with a PPFD of 251.52 µmol m^{-2} s^{-1}.

Morphological and biochemical data were collected weekly over a 10-week period for each replicate. Morphological parameters included the number of flowers and buds, flower head diameter, petal length, and pinna length and width. Biochemical parameters—nitrogen balance index (NBI), chlorophyll (Chl), flavonoids (Flav), and anthocyanins

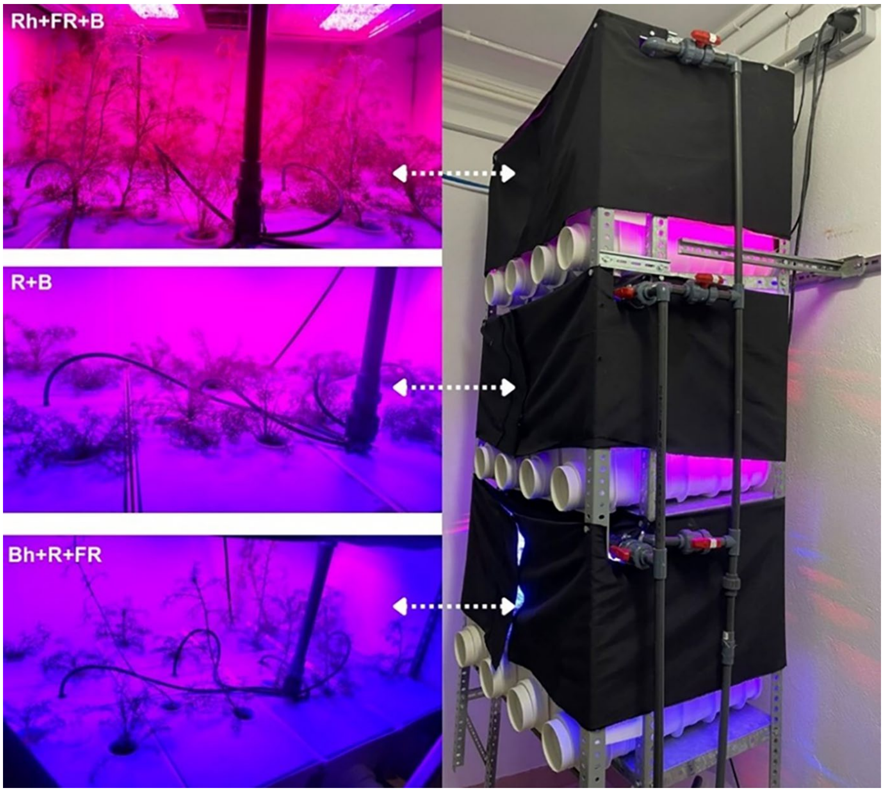

Fig. 1 Aeroponic system with three cultivation trays under different artificial lighting treatments for *Matricaria chamomilla:* Rh + FR + B (Red predominant + Far-red + Blue), Bh + R + FR (Blue predominant + Red + Far-red), and R + B (Red + Blue)

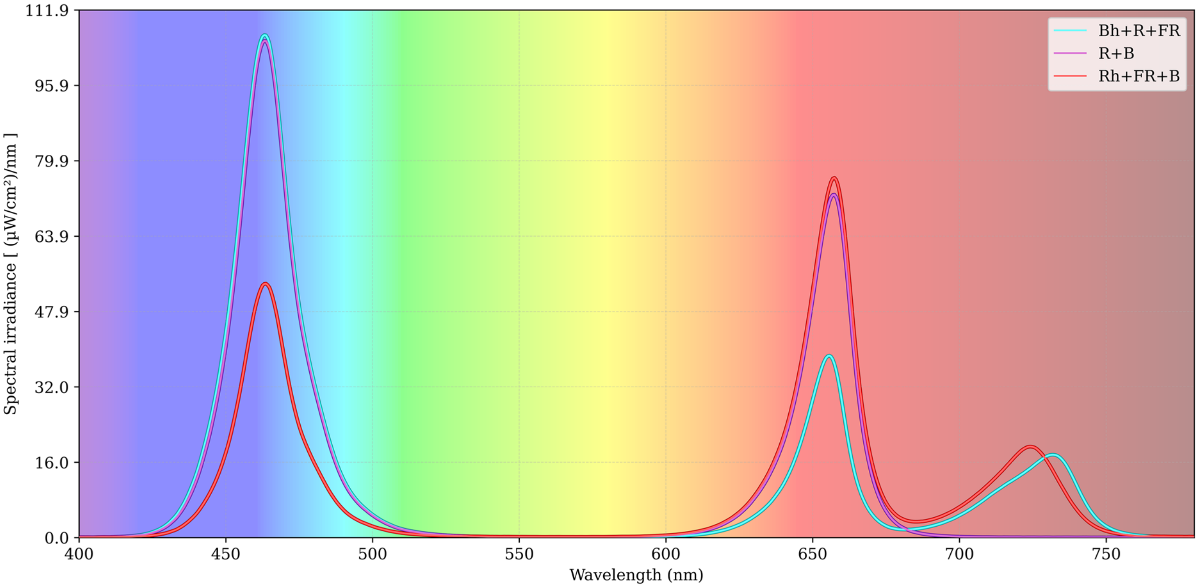

Fig. 2 Spectral distribution of light treatments: Rh + FR + B (Red predominant + Far-red + Blue), Bh + R + FR (Blue predominant + Red + Far-red), and R + B (Red + Blue)

(Anth)—were assessed using the Dualex METOS® leaf sensor (Pessl Instruments, Werksweg, Austria), which quantifies these compounds through transmittance and foliar fluorescence analysis using a non-destructive method.

2.3 Data analysis

Statistical analyses were conducted using Python version 3.11, an open-source programming language. Morphological and floral traits of *M. chamomilla* were evaluated using two-way analysis of variance (ANOVA) to test for the effects of light treatment, time (sampling week), and their interaction. Statistical significance was set at $\alpha = 0.05$. When the treatment effect was significant, post hoc comparisons among treatment means were performed using Tukey's Honest Significant Difference (HSD) test. In the figures where letters are shown, different letters indicate statistically distinct groups according to Tukey's HSD test. All graphical outputs, including plots of means with associated standard errors (mean ± SEM), were generated in Python.

3 Results

3.1 Morphological and floral development

No flower production was observed during the first three sampling weeks across all treatments (Table 1, Fig. 3a). At sampling week 4, flower development initiated under Bh + R + FR (mean: 1.63 flowers, "a") and Rh + FR + B (mean: 0.63, "a"), while no flowers were recorded in R + B (mean: 0.00, "a"). Flower production progressed steadily, peaking at sampling week 9 under Bh + R + FR (mean: 20.00, "a"), which was significantly higher than in Rh + FR + B (mean: 11.29, "a") and R + B (mean: 3.88, "b"). This pattern persisted in sampling week 10, where Bh + R + FR maintained the highest number of flowers (mean: 21.00, "a"), while Rh + FR + B (mean: 7.33, "a") showed a slight decline and R + B (mean: 7.00, "a") an increase. From sampling week 6 onward, R + B consistently exhibited significantly lower flower numbers, often belonging to a different statistical group ("b") according to Tukey's HSD test, indicating reduced floral development under this spectral combination.

Significant differences in bud number were observed from sampling week 5 onward (Table 1, Fig. 3b). At sampling week 5, plants under R + B showed significantly lower bud production (mean: 0.25, "b") compared with Bh + R + FR (mean: 1.50, "a") and Rh + FR + B (mean: 2.88, "a"). A similar pattern was observed at sampling week 7, where R + B again exhibited the lowest mean (0.63, "b") relative to Bh + R + FR (4.88, "a") and Rh + FR + B (3.86, "a"). This pattern continued at sampling week 9, with R + B producing only 0.25 buds ("b"), whereas Bh + R + FR and Rh + FR + B reached higher values of 4.75 and 3.14, respectively ("a"). Overall, bud formation increased progressively in all treatments, with Bh + R + FR consistently displaying the highest means. Although no significant differences were detected at early stages (sampling weeks 1 to 4) due to the absence or minimal bud development, R + B consistently showed the lowest bud production from

Table 1 Results of two-way analysis of variance (ANOVA) for morphological and biochemical variables of *M. chamomilla* evaluated weekly under different light treatments

Variable	*p*-value (treatment)	*p*-value (time)	*p*-value (treatment × time)
Flower number	< 0.0001	< 0.0001	0.0034
Bud number	< 0.0001	< 0.0001	0.1458
Flower head diameter	< 0.0001	< 0.0001	0.0002
White petal length	< 0.0001	< 0.0001	0.0049
Pinna length	< 0.0001	< 0.0001	< 0.0001
Pinna width	0.0554	< 0.0001	< 0.0001
Nitrogen balance index (NBI)	< 0.0001	< 0.0001	0.0022
Chlorophyll (Chl)	< 0.0001	< 0.0001	0.2338
Flavonoids (Flav)	< 0.0001	< 0.0001	0.0056
Anthocyanins (Anth)	< 0.0001	< 0.0001	0.0205

p-values ≤ 0.05 indicate statistically significant effects

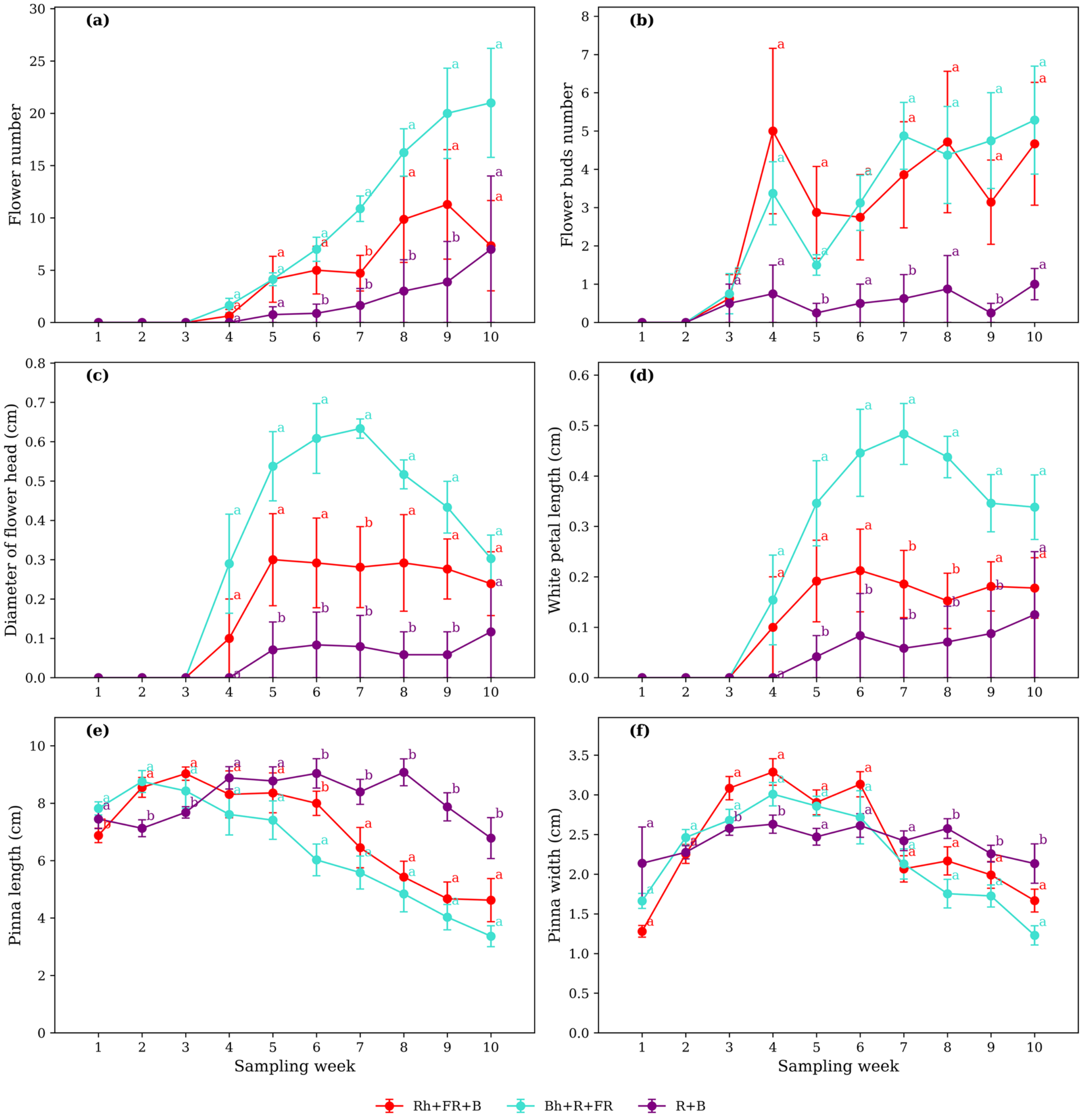

Fig. 3 Flower number, **a** Flower bud number, **b** Diameter of flower head, **c** White petal length, **d** Pinna length, **e** and Pinna width **f** of *M. chamomilla* under three LED light treatments: Rh + FR + B (Red predominant + Far-red + Blue), Bh + R + FR (Blue predominant + Red + Far-red), and R + B (Red + Blue) across ten sampling week periods. Data represent means ± standard error of the mean (SEM). Treatments sharing the same letter within each sampling week are not significantly different according to Tukey's HSD test ($\alpha = 0.05$)

mid to late stages and was frequently assigned to lower statistical groups according to Tukey's HSD test.

Flower head diameter exhibited significant differences among treatments from sampling week 4 onward (Table 1, Fig. 3c). At sampling week 4, although all treatments presented low values (Bh + R + FR: 0.29 cm, Rh + FR + B: 0.10 cm, R + B: 0.00 cm), no statistical differences were detected. However, from sampling weeks 5 to 9, plants under

R + B consistently showed significantly smaller diameters and were assigned to a distinct statistical group according to Tukey's HSD test. For instance, at sampling week 5, R + B reached a mean of only 0.07 cm ("b") compared to 0.54 cm in Bh + R + FR and 0.30 cm in Rh + FR + B (both "a"). At sampling week 7, this pattern was accentuated, with R + B maintaining the lowest mean (0.08 cm, "b"), while Bh + R + FR reached 0.63 cm ("a") and Rh + FR + B 0.28 cm ("b"). R + B was also consistently placed in group "b" across sampling weeks 6, 8, and 9, suggesting a delay or restriction in capitulum expansion under this light regime. By sampling week 10, although no significant differences were observed (Bh + R + FR: 0.30 cm, Rh + FR + B: 0.24 cm, R + B: 0.12 cm), overall diameters decreased slightly in all treatments. These results indicate that R + B limited flower head growth.

White petal length showed significant differences among treatments beginning at sampling week 5 (Table 1, Fig. 3d). At this point, plants under Bh + R + FR and Rh + FR + B reached similar mean values (0.35 cm and 0.19 cm, respectively), both statistically higher than those under R + B (0.04 cm, "b"). This pattern continued through sampling week 6, where R + B maintained a lower mean (0.08 cm, "b") compared to Bh + R + FR (0.45 cm) and Rh + FR + B (0.21 cm), both grouped as "a". At sampling week 7, petals in Bh + R + FR extended to 0.48 cm, while both Rh + FR + B and R + B remained significantly shorter (0.19 cm and 0.06 cm, respectively), confirming the separation into group "a" for Bh + R + FR and group "b" for the others. This same grouping pattern was retained in sampling weeks 8 and 9, with R + B persistently showing the shortest petals (0.07 cm and 0.09 cm, respectively), always classified as "b". By sampling week 10, the differences diminished (Bh + R + FR: 0.34 cm, Rh + FR + B: 0.18 cm, R + B: 0.13 cm), and no statistical separation was observed. These results suggest that the R + B light regime constrained petal elongation during the floral development peak, whereas Bh + R + FR supported the highest petal growth throughout the flowering period.

During the first sampling week for pinna length, Bh + R + FR and R + B reached similar average values (7.82 cm and 7.45 cm, respectively), both classified in group "a", while Rh + FR + B recorded a lower mean (6.88 cm), assigned to group "b" (Table 1, Fig. 3e). This pattern shifted by sampling week 2, where R + B declined slightly (7.13 cm, "b"), and both Bh + R + FR and Rh + FR + B increased (8.75 cm and 8.55 cm, respectively), remaining in group "a". In sampling week 3, Rh + FR + B peaked at 9.03 cm, surpassing Bh + R + FR (8.43 cm), whereas R + B remained lower (7.68 cm, "b"). From this point forward, R + B maintained a consistently higher pinna length than the other treatments. Between sampling weeks 4 and 6, R + B showed a continuous increase, reaching its highest value at sampling week 6 (9.04 cm). In contrast, Bh + R + FR and Rh + FR + B presented a gradual decline. The divergence between treatments became more pronounced from sampling week 7, where R + B maintained the highest values (8.40 cm to 6.78 cm from sampling weeks 7 to 10, respectively), consistently assigned to group "b", while Bh + R + FR and Rh + FR + B exhibited a steady decrease, reaching 3.37 cm and 4.62 cm, respectively, by the final sampling week. These results indicate that R + B sustained longer pinna throughout the experiment, while Bh + R + FR and Rh + FR + B supported earlier development, followed by progressive reduction in pinna length.

During the first sampling week, all treatments showed relatively low values (Bh + R + FR: 1.66 cm, Rh + FR + B: 1.28 cm, R + B: 2.14 cm), and no statistical differences were observed among them in pinna width (Table 1, Fig. 3f). From sampling week 2 onwards, pinna width progressively increased across treatments, reaching the highest values between sampling weeks 3 and 6. At sampling week 3, Rh + FR + B reached a peak value of 3.08 cm, while Bh + R + FR and R + B showed lower and statistically different means (2.68 cm and 2.58 cm, respectively, with R + B assigned to group "b"). At sampling week 4, Rh + FR + B maintained the highest width (3.29 cm), followed by Bh + R + FR (3.01 cm), whereas R + B was again significantly lower (2.63 cm, "b"). A similar progression was observed at sampling week 5, with all treatments showing a slight decline. Although no statistical differences were observed at this point, from sampling week 6 onward, R + B consistently remained in group "a", except at sampling weeks 8 to 10, where it shifted to group "b" as its values surpassed those of the other treatments. Notably, from sampling weeks 7 to 10, Bh + R + FR and Rh + FR + B showed a marked decrease in pinna width, dropping to 1.23 cm and 1.67 cm, respectively, by the final sampling week. Conversely, R + B maintained higher values (2.13 cm at sampling week 10), consistently separated from the others by statistical grouping ("b"). These results indicate that while Bh + R + FR and Rh + FR + B supported earlier expansion of pinna width, R + B preserved a wider pinna in the later stages of development.

3.2 Physiological traits across development

NBI, during the initial sampling week, showed values ranged from 12.68 in Bh + R + FR to 19.87 in Rh + FR + B and 19.51 in R + B, with no statistical differences among treatments (Table 1, Fig. 4a). From sampling week 2, NBI increased in all treatments, with R + B reaching the highest mean at this stage (25.38), although not statistically different from Bh + R + FR and Rh + FR + B. From sampling weeks 4 to 7, a clear separation became evident, with R + B consistently displaying higher values and being assigned to group "b", while Bh + R + FR and Rh + FR + B remained lower and grouped as "a". The most pronounced difference occurred at sampling week 5, where R + B reached its peak (37.06), contrasting with Bh + R + FR and Rh + FR + B (22.49 and 18.86, respectively). After sampling week 7, NBI values decreased in all treatments, especially in Bh + R + FR (from 15.03 to 8.83) and Rh + FR + B (from 16.65 to 9.03), while R + B also declined (from 34.49 to 15.94), yet consistently maintained the highest means. Notably, in sampling weeks 8 to 10, R + B remained statistically distinct in group "b", whereas Bh + R + FR and Rh + FR + B remained in group "a", except at sampling week 8, where Rh + FR + B joined R + B in group "b". These results suggest that

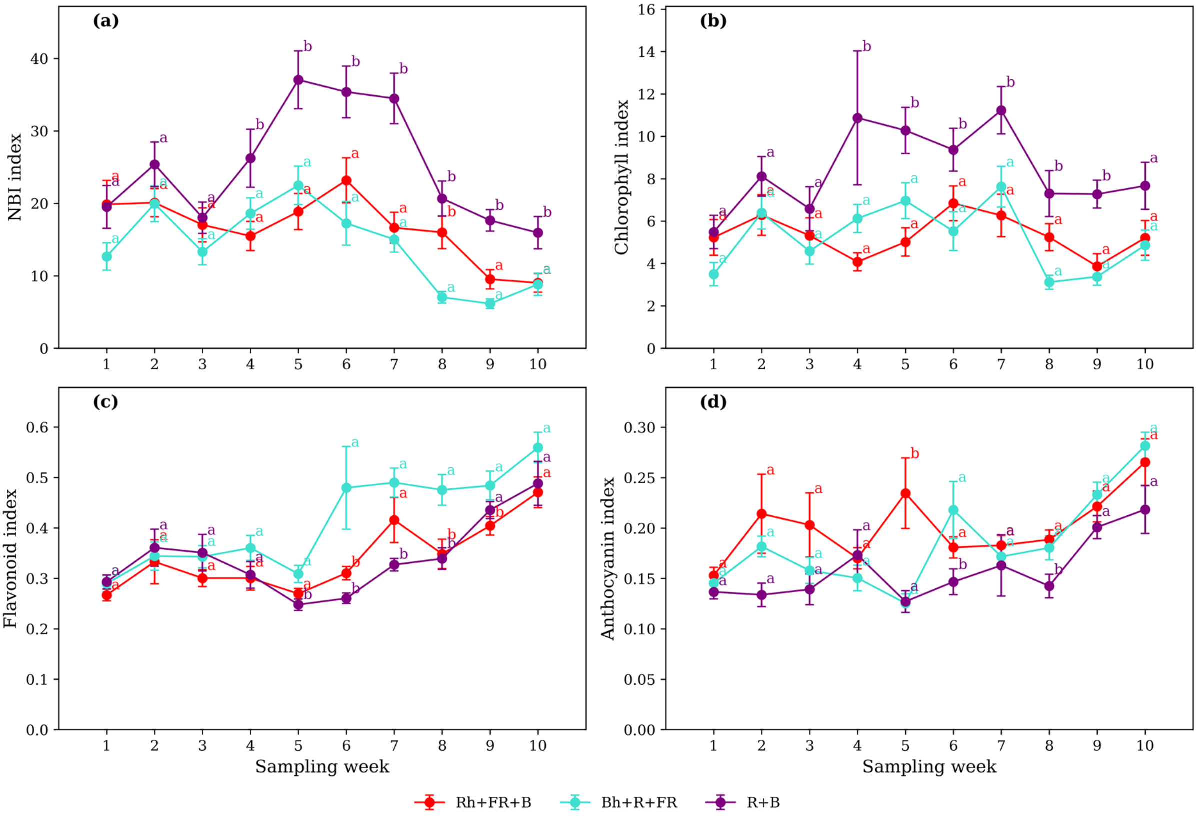

Fig. 4 Nitrogen balance index (NBI), **a** Chlorophyll (Chl), **b** Flavonoid (Flav), **c** and Anthocyanin (Anth), **d** of *M. chamomilla* under three LED light treatments: Rh + FR + B (Red predominant + Far-red + Blue), Bh + R + FR (Blue predominant + Red + Far-red), and R + B (Red + Blue) across ten sampling week periods. Data represent means ± standard error of the mean (SEM). Treatments sharing the same letter within each sampling week are not significantly different according to Tukey's HSD test ($\alpha = 0.05$)

the R + B treatment enhanced NBI values during the peak vegetative and reproductive stages, maintaining a higher nitrogen status than the other treatments.

In Chl concentration, during the first three sampling weeks, no statistical differences were detected among treatments, although R + B consistently showed the highest means (5.49, 8.11, and 6.58, respectively), followed by Rh + FR + B and Bh + R + FR (Table 1, Fig. 4b). From sampling week 4 onward, R + B consistently displayed significantly higher Chl concentrations compared to the other treatments, entering group "b" in every sampling week except the first three and the final one. At sampling week 4, in R + B sharply increased to 10.87, while Bh + R + FR and Rh + FR + B remained lower (6.13 and 4.08, respectively), both grouped as "a". A consistent separation was maintained in sampling weeks 5, 6, and 7, with R + B exhibiting the highest means (10.28, 9.37, and 11.23, respectively). The most marked contrast occurred at sampling week 7, when Chl in R + B peaked at 11.23, whereas Bh + R + FR and Rh + FR + B reached only 7.63 and 6.27, respectively. In sampling weeks 8 and 9, values declined in all treatments. By sampling week 10, the statistical separation disappeared, with values converging to 7.67 in R + B, 5.21 in Rh + FR + B, and 4.86 in Bh + R + FR. These results indicate that the R + B light regime stimulated and sustained the highest Chl accumulation during the central phase of development, while Bh + R + FR and Rh + FR + B supported lower Chl across time.

During the initial four sampling weeks of Flav concentration, no statistical differences were observed among treatments, and mean values remained low and similar across groups (0.29–0.36) (Table 1, Fig. 4c). However, beginning at sampling week 5, differences began to emerge. At this point, Bh + R + FR (0.31) and Rh + FR + B (0.27) remained within the same statistical group ("a"), and R + B recorded the lowest mean (0.25). Statistical separation became evident at sampling week 6, where Bh + R + FR significantly surpassed both Rh + FR + B and R + B (0.48 vs. 0.31 and 0.26, respectively), with the latter two grouped as "b". This pattern was reinforced at sampling week 7, with Bh + R + FR maintaining the highest flavonoid concentration (0.49), while Rh + FR + B and R + B remained significantly lower (0.42 and 0.33, respectively). At sampling week 8, Bh + R + FR continued to dominate (0.48), significantly higher than both Rh + FR + B (0.35) and R + B (0.34), which again fell into group "b". At sampling week 9, Bh + R + FR (0.48) and R + B (0.44) shared group "a", while Rh + FR + B (0.40) remained in group "b", indicating a transient increase in R + B. By sampling week 10, differences among treatments were no longer statistically significant, with values converging to 0.56 (Bh + R + FR), 0.47 (Rh + FR + B), and 0.49 (R + B). These results suggest that the Bh + R + FR light regime promoted the highest and most consistent accumulation of Flav throughout the experiment, especially from sampling weeks 6 to 8, whereas Rh + FR + B and R + B induced lower concentrations, with R + B showing partial compensation toward the end of the evaluation period.

Anth showed no statistical differences among treatments during the first four sampling weeks, and all values remained stable, ranging from 0.13 to 0.21 (Table 1, Fig. 4d). However, beginning at sampling week 5, Rh + FR + B exhibited a significant increase (0.23), surpassing both Bh + R + FR (0.13) and R + B (0.13), which remained grouped as "a". At sampling week 6, Bh + R + FR showed a further increase to 0.22, while Rh + FR + B and R + B reached 0.18 and 0.15, respectively. In this case, R + B was statistically separated as group "b", indicating a delayed Anth concentration under this treatment. A comparable separation was observed in sampling week 8, where Bh + R + FR and Rh + FR + B remained statistically similar (0.18 and 0.19), whereas R + B dropped to 0.14, remaining in group "b". This separation was also evident in sampling week 9, where Bh + R + FR (0.23) and Rh + FR + B (0.22) continued to show higher values than R + B (0.20), although all treatments were grouped as "a". By sampling week 10, Anth increased across all treatments, with Bh + R + FR reaching the highest value (0.28), followed by Rh + FR + B (0.27) and R + B (0.22), but statistical differences were no longer detected. These results indicate that the Bh + R + FR and Rh + FR + B light regimes favored a higher accumulation of Anth, while R + B consistently showed the lowest values during the period of most active pigment synthesis.

4 Discussion

The application of distinct LED spectra induced differentiated morpho-physiological responses in *M.*

chamomilla, demonstrating the critical role of light quality in modulating developmental processes. Blue-enriched light, particularly in the Bh + R + FR treatment, was consistently associated with enhanced reproductive development, including earlier flower initiation, higher bud and flower numbers, and larger floral structures. These effects are consistent with the regulatory role of blue light in photomorphogenesis and flowering, mediated by cryptochrome activation and downstream signaling involving gibberellin biosynthesis and floral integrators (Runkle and Heins 2001; Ghareeb et al. 2022). The concurrent inclusion of far-red light likely contributed to these outcomes through phytochrome-related signaling processes, which in other species have been associated with transitions toward low Pfr/Ptotal states that promote flowering in long-day plants (Wollenberg et al. 2008).

However, the flowering response observed cannot be attributed solely to individual wavebands; rather, it reflects a dynamic interplay between spectral components and their physiological thresholds. As highlighted by Kong and Zheng (2024), the balance between red and far-red light often exerts a stronger regulatory influence on flowering than the absolute intensity of blue light. Moreover, light quantity and quality are inherently interdependent, and previous studies have shown that blue light may act either as a promoter or suppressor of flowering depending on its irradiance and spectral context (Meng and Runkle 2015; He et al. 2024). Therefore, the flowering enhancement observed under Bh + R + FR likely emerged from the combined effect of spectral synergy and optimal PPFD, jointly modulating photoreceptor networks and hormonal pathways that govern the reproductive transition in *M. chamomilla*.

The differences observed between Bh + R + FR and Rh + FR + B underscore the regulatory impact of spectral ratios on organogenesis, extending beyond floral induction alone. Although both treatments included far-red wavelengths that, according to previous studies, can favor reproductive transition through reduced phytochrome B activation, the more pronounced response under Bh + R + FR suggests a more favorable spectral balance for engaging photoreceptor-related signaling pathways previously associated with floral morphogenesis. In this context, a blue-dominant spectrum likely enhanced cryptochrome activity, which has been associated with increased expression of genes involved in cell expansion and floral morphogenesis, such as EXPANSINs and HY5 (Kong and Zheng 2024; X. Wang and Lin 2025). Concurrent far-red exposure has also been reported to facilitate DELLA protein turnover and activate gibberellin-responsive pathways in other species (Courbier et al. 2021; Gautam et al. 2015), which may help explain the enhanced floral organ development observed under Bh + R + FR. Moreover, the suppressed floral development under R + B further highlights the functional relevance of far-red light for maintaining phytochrome-mediated regulatory networks described in the literature, including pathways involving CONSTANS and SOC1 (King et al. 2008). Together, these findings support the view that reproductive and morphogenetic outcomes in *M. chamomilla* result from the integration of multiple light-sensing pathways and their downstream interactions with hormonal and transcriptional regulators.

In this context, the pronounced divergence between the number of buds and the number of fully developed flowers in the Rh + FR + B treatment indicates a decoupling between floral initiation and the completion of reproductive development. While this spectral combination promoted the formation of floral primordia, its lower conversion into mature flowers points to an interruption in late-stage floral development. In several species, the progression from visible bud to anthesis depends on regulatory modules involving SOC1, LFY, AP1, and GA-responsive pathways, all of which show sensitivity to red:far-red balance and phytochrome-mediated signaling (López et al. 2021; Lee et al. 2023). Reports also indicate that far-red exposure can accelerate early meristem differentiation while limiting organ expansion or increasing reproductive abortion under red-dominant contexts (Chen et al. 2024; Xia & Mattson 2024). The pattern observed in Rh + FR + B is consistent with these findings and reflects wavelength-dependent regulation of the final phases of floral development in *M. chamomilla*.

Vegetative traits were strongly influenced by light quality. The R + B treatment, which excluded far-red light, resulted in the greatest leaf elongation and broader pinnae during the later stages of development. This response reflects the effect of red and blue light in balanced proportions, which promotes cell expansion, optimal chloroplast development, and efficient stomatal conductance, thereby enhancing leaf growth (R. Li et al. 2019; Flores-Pérez et al. 2021). In contrast, the inclusion of far-red light in Rh + FR + B and Bh + R + FR is consistent with shade-avoidance responses reported in the literature for far-red–associated phytochrome signaling, which can limit lateral organ expansion and favor reproductive allocation (Demotes-Mainard et al. 2016; Kong and Nemali 2021). Due to this spectral modulation, the reduction in pinna width observed under these treatments corresponds to a developmental trade-off, where resource allocation shifts toward floral structures at the expense of leaf development (Kami et al. 2010; Craine and Dybzinski 2013).

In addition to promoting vegetative growth, the R + B treatment consistently enhanced physiological performance, as evidenced by increased values of both NBI and Chl concentration. These parameters reflect key aspects of plant metabolic activity, particularly nitrogen assimilation and photosynthetic efficiency (Viršilė et al. 2020). The combined action of red and blue wavelengths is known to support chlorophyll biosynthesis, maintain Rubisco activity, and optimize chloroplast development, thereby sustaining higher carbon fixation rates (Y. Li et al. 2020). Furthermore, a high NBI is indicative of an elevated chlorophyll-to-flavonoid ratio, which is associated with efficient nitrogen use and reduced oxidative imbalance, both critical for sustained leaf development (Fan et al. 2013; Gao et al. 2022). These coordinated biochemical responses under R + B conditions are consistent with the observed dominance of vegetative traits, reinforcing the role of spectral balance in supporting biomass accumulation and delayed resource diversion toward reproductive sinks.

In contrast, the inclusion of far-red light in Bh + R + FR and Rh + FR + B treatments altered this physiological profile, resulting in reduced pigment accumulation. In previous studies, far-red exposure has been associated with phytochrome-mediated modulation of developmental and photosynthetic gene networks, contributing to shade-avoidance responses and reduced chlorophyll accumulation. This shift includes the downregulation of chlorophyll biosynthesis and impaired chloroplast maturation, particularly when far-red is combined with high red light irradiance (Oh and Montgomery 2017; Q. Wang et al. 2024). As a result, assimilates are preferentially allocated to floral structures rather than to expanding vegetative organs, limiting the development of photosynthetically active tissues. These findings underscore the critical role of far-red light in redirecting metabolic investment and shaping the developmental trajectory of the plant through light-quality-dependent regulation of hormonal and genetic pathways.

Flavonoid concentration exhibited greater temporal variation than treatment-dependent differences, but a transient increase was observed in Bh + R + FR during peak flowering. This may reflect blue light–induced activation of chalcone synthase (CHS) and other enzymes in the flavonoid biosynthetic pathway, which are sensitive to blue/UV-A regions (Zoratti et al. 2014; H. Li et al. 2018). Similar induction of CHS and other phenylpropanoid-related genes under UV-B has been demonstrated in red rubin basil, suggesting a shared regulatory mechanism linking high-energy light exposure with secondary metabolite biosynthesis (Ali et al. 2025). While overall differences among treatments were not significant, the progressive accumulation observed in all groups supports the idea that these metabolites also respond to internal developmental programs and mild oxidative signals associated with maturation (Paschko et al. 2023; Su et al. 2024). Similarly, anthocyanins increased gradually throughout the experiment, with a visual indication of higher accumulation under far-red–enriched treatments. Although statistical differences were minimal, the overall behavior aligns with the role of far-red light in promoting anthocyanin biosynthesis under high red:far-red ratios, potentially as a compensatory mechanism to optimize light harvesting in spectral environments with limited blue photons (Collado and Hernández 2022; Trivellini et al. 2023). A similar compensatory pattern was observed in variegated *Solenostemon scutellarioides* grown under sun and shade, where anthocyanins accumulated in the palisade parenchyma acted as optical filters, reducing chlorophyll excitation under low light but contributing to photoprotection under high irradiance (Gaion et al. 2025). The anthocyanin accumulation observed in far-red–enriched conditions may serve dual functions depending on ambient photon availability: shielding the photosystems from excess light or compensating for spectral imbalances.

5 Applicability and future research

This study provides a basis for developing more refined experimental approaches to explore the complex interactions between light spectra and metabolic regulation in *M. chamomilla*. Its methodological framework can be readily applied to assess other medicinal species or cultivar-specific responses in indoor systems aimed at pharmaceutical-grade production. However, several limitations open new avenues for investigation.

The present work focused primarily on morphological and physiological traits; further studies are needed to elucidate the biochemical and molecular responses to spectral variation. Specifically, the analysis of essential oils, polyphenols, and other secondary metabolites using chemical profiling techniques such as gas chromatography–mass spectrometry (GC–MS), liquid chromatography–mass spectrometry (LC–MS), or nuclear magnetic resonance (NMR) would help determine whether different light spectra induce qualitative or quantitative changes in metabolic pathways. Additionally, while three representative spectral compositions were tested, all treatments maintained comparable PPFD. Future studies should evaluate the effect of varying light intensity under constant spectral composition to distinguish responses attributable to light quantity versus quality. This would clarify potential dose-dependent effects and enable more precise light regime designs.

Together, these extensions would provide a deeper mechanistic understanding of spectral effects and support the development of targeted lighting protocols for high-value medicinal plant cultivation.

6 Conclusions

This study demonstrates that the spectral composition of LED lighting drives key physiological processes in *M. chamomilla* grown aeroponically. Blue-enriched spectra promoted floral differentiation and reproductive development, whereas red–blue combinations favored vegetative growth and leaf expansion. Secondary metabolite accumulation increased progressively across treatments, suggesting a stronger influence of developmental cues than of specific light wavelengths. Overall, these results confirm that targeted spectral manipulation can optimize physiological performance under controlled environment agriculture.

Acknowledgements The authors would like to acknowledge the collaboration and invaluable support of Francisco Tomatis, Ouiam Fatiha Boukharta and Diana Alexandra Murcia. The main author of this article thanks her tutors who motivated the writing of this article. Luisa Fernanda Lozano-Castellanos has been financed under the call predoctoral recruitment of research staff, co-financed by the Ministry of Education (Junta de Castilla y León, Spain) and the European Social Fund.

Author contributions Conceptualization, L.M.N.-G., A.C.-G. and L.F.L.-C.; methodology, L.M.N. G., A.C.-G., A.-A. and L.F.L.-C.; software, L.F.L.-C. and A.-A.; validation, L.M.N.-G. and A.C.-G.; formal analysis, L.F.L.-C. and A.-A.; investigation, L.F.L.-C.; resources, L.M.N.-G. and A.C.-G.; data curation, L.F.L.-C.; writing—original draft preparation, L.F.L.-C. and A.-A.; writing—review and editing, L.M.N.-G. and A.C.-G.; visualization, L.M.N.-G., A.C.-G. and L.F.L.-C.; supervision, L.M.N.-G. and A.C.-G.; project administration, L.M.N.-G. and A.C.-G. All authors have read and agreed to the published version of the manuscript.

Funding Open access funding provided by FEDER European Funds and the Junta de Castilla y León under the Research and Innovation Strategy for Smart Specialization (RIS3) of Castilla y León 2021-2027.

Data availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no competing interests. No funding was received to assist with the preparation of this manuscript. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

References

Ali A, Santoro P, Mori J, Ferrante A, Cocetta G (2025) Intermittent UV-B irradiation optimizes secondary metabolite production and growth in red rubin basil. Theor Exp Plant Physiol 37(1):23

Appolloni E, Pennisi G, Zauli I, Carotti L, Paucek I, Quaini S, Orsini F, Gianquinto G (2022) Beyond vegetables: effects of indoor LED light on specialized metabolite biosynthesis in medicinal and aromatic plants, edible flowers, and microgreens. J Sci Food Agric 102(2):472–487. https://doi.org/10.1002/jsfa.11513

Bafort F, Jijakli MH (2024) Vertical farming of medicinal plants. In: Priyadarshan PM, Jain SM, Penna S, Al-Khayri JM (eds) Digital agriculture a solution for sustainable food and nutritional security. Springer, Berlin, pp 129–177

Chauhan R, Singh S, Kumar V, Kumar A, Kumari A, Rathore S, Kumar R, Singh S (2022) A comprehensive review on biology, genetic improvement, agro and process technology of German chamomile (*Matricaria chamomilla* L.). Plants 11(1):1. https://doi.org/10.3390/plants11010029

Chen S, Marcelis LFM, Offringa R, Kohlen W, Heuvelink E (2024) Far-red light-enhanced apical dominance stimulates flower and fruit abortion in sweet pepper. Plant Physiol 195(2):924–939

Collado CE, Hernández R (2022) Effects of light intensity, spectral composition, and paclobutrazol on the morphology, physiology, and growth of Petunia, Geranium, Pansy, and Dianthus ornamental transplants. J Plant Growth Regul 41(2):461–478. https://doi.org/10.1007/s00344-021-10306-5

Courbier S, Snoek BL, Kajala K, Li L, van Wees SCM, Pierik R (2021) Mechanisms of far-red light-mediated dampening of defense against *Botrytis cinerea* in tomato leaves. Plant Physiol 187(3):1250–1266. https://doi.org/10.1093/plphys/kiab354

Craine JM, Dybzinski R (2013) Mechanisms of plant competition for nutrients, water and light. Funct Ecol 27(4):833–840. https://doi.org/10.1111/1365-2435.12081

Demotes-Mainard S, Péron T, Corot A, Bertheloot J, Le Gourrierec J, Pelleschi-Travier S, Crespel L, Morel P, Huché-Thélier L, Boumaza R, Vian A, Guérin V, Leduc N, Sakr S (2016) Plant responses to red and far-red lights, applications in horticulture. Environ Exp Bot 121:4–21. https://doi.org/10.1016/j.envexpbot.2015.05.010

El Joumaa MM, Borjac JM (2022) *Matricaria chamomilla*: a valuable insight into recent advances in medicinal uses and pharmacological activities. Phytochem Rev 21(6):1913–1940. https://doi.org/10.1007/s11101-022-09817-0

El Mihyaoui A, da Esteves Silva JCG, Charfi S, Candela Castillo ME, Lamarti A, Arnao MB (2022) Chamomile (*Matricaria chamomilla* L.): a review of ethnomedicinal use, phytochemistry and pharmacological uses. Life 12(4):4. https://doi.org/10.3390/life12040479

Engler N, Krarti M (2021) Review of energy efficiency in controlled environment agriculture. Renew Sustain Energy Rev 141:110786. https://doi.org/10.1016/j.rser.2021.110786

Fan X, Zang J, Xu Z, Guo S, Jiao X, Liu X, Gao Y (2013) Effects of different light quality on growth, chlorophyll concentration and chlorophyll biosynthesis precursors of non-heading Chinese cabbage (*Brassica campestris* L.). Acta Physiol Plant 35(9):2721–2726

Flores-Pérez S, Castillo-González AM, Valdez-Aguilar LA, Avítia-García E (2021) Use of different proportions of red and blue leds to improve the growth of *Lilium* spp. Rev Mex Cienc Agric 12(5):835–847. https://doi.org/10.29312/remexca.v12i5.2607

Gaion LA, Galati VC, Cardoso ACR, Rossatto DR, Carvalho RF (2025) Shifting the anthocyanins from light to shade: what roles do these pigments play? Theor Exp Plant Physiol 37(1):16. https://doi.org/10.1007/s40626-024-00353-0

Gao Q, Liao Q, Li Q, Yang Q, Wang F, Li J (2022) Effects of LED red and blue light component on growth and photosynthetic characteristics of coriander in plant factory. Horticulturae 8(12):12. https://doi.org/10.3390/horticulturae8121165

Gautam P, Terfa MT, Olsen JE, Torre S (2015) Red and blue light effects on morphology and flowering of Petunia × hybrida. Sci Hortic 184:171–178. https://doi.org/10.1016/j.scienta.2015.01.004

Ghareeb YE, Soliman SS, Ismail TA, Hassan MA, Abdelkader MA, Abdel Latef AAH, Al-Khayri JM, ALshamrani SM, Safhi FA, Awad MF, El-Moneim DA, Hassanin AA (2022) Improvement of German chamomile (*Matricaria recutita* L.) for mechanical harvesting, high flower yield and essential oil content using physical and chemical mutagenesis. Plants 11(21):21. https://doi.org/10.3390/plants11212940

Hassanpour H (2023) Growth mechanism of *Matricaria chamomilla* plant under space lighting system: induction of pigment synthesis, enzyme defense system, and antioxidant metabolites. J Space Sci Technol. https://doi.org/10.30699/jsst.2023.1412

He W, Chai Q, Zhao C, Yin W, Fan H, Yu A, Fan Z, Hu F, Sun Y, Wang F (2024) Response of blue light in different proportions on the growth & flowering in sunflower. Sci Hortic 338:113689. https://doi.org/10.1016/j.scienta.2024.113689

Kami C, Lorrain S, Hornitschek P, Fankhauser C (2010) Chapter Two—light-regulated plant growth and development. In: Timmermans MCP (ed) Current topics in developmental biology, vol 91. Academic Press, Cambridge, pp 29–66

King R, Hisamatsu T, Goldschmidt E, Blundell C (2008) The nature of floral signals in Arabidopsis. I. Photosynthesis and a far-red photoresponse independently regulate flowering by increasing expression of flowering locus T (FT). J Exp Bot 59:3811–3820

Kong Y, Nemali K (2021) Blue and far-red light affect area and number of individual leaves to influence vegetative growth and pigment synthesis in lettuce. Front Plant Sci. https://doi.org/10.3389/fpls.2021.667407

Kong Y, Zheng Y (2024) Diverse flowering response to blue light manipulation: application of electric lighting in controlled-environment plant production. Horticulturae 10(6):6

Kump B (2020) The role of far-red light FR in photomorphogenesis and its use in greenhouse plant production. Acta Agric Slovenica 116(1):93–105

Lakhiar IA, Gao J, Syed TN, Chandio FA, Tunio MH, Ahmad F, Solangi KA (2020) Overview of the aeroponic agriculture–an emerging technology for global food security. Int J. Agric Biol Eng 13(1):1–10

Lee Z, Kim S, Choi SJ, Joung E, Kwon M, Park HJ, Shim JS (2023) Regulation of flowering time by environmental factors in plants. Plants 12(21):3680. https://doi.org/10.3390/plants12213680

Li H, Lin Y, Chen X, Bai Y, Wang C, Xu X, Wang Y, Lai Z (2018) Effects of blue light on flavonoid accumulation linked to the expression of miR393, miR394 and miR395 in longan embryogenic calli. PLoS ONE 13(1):e0191444. https://doi.org/10.1371/journal.pone.0191444

Li Y, Xin G, Liu C, Shi Q, Yang F, Wei M (2020) Effects of red and blue light on leaf anatomy, CO2 assimilation and the photosynthetic electron transport capacity of sweet pepper (*Capsicum annuum* L.) seedlings. BMC Plant Biol 20(1):318. https://doi.org/10.1186/s12870-020-02523-z

Li, R., Mu, Y., Wei, H., Zhu, L., Tang, W., & MA, Z. (2019). Effects of Different Ratios of Red and Blue Light on the Morphology and Photosynthetic Characteristics of Anoectochilus roxburghii. *2019 16th China International Forum on Solid State Lighting & 2019 International Forum on Wide Bandgap Semiconductors China (SSLChina: IFWS)*, 116–120. https://doi.org/10.1109/SSLChinaIFWS49075.2019.9019755

Liu X, Xu Y, Wang Y, Yang Q, Li Q (2022) Rerouting artificial light for efficient crops production: a review of lighting strategy in PFALs. Agronomy. https://doi.org/10.3390/agronomy12051021

López ME, Santos IS, Oliveira RRde, Lima AA, Cardon CH, Chalfun-Junior A, López ME, Santos IS, Oliveira RRde, Lima AA, Cardon CH, Chalfun-Junior A (2021) An overview of the endogenous and environmental factors related to the *Coffea arabica* flowering process. Beverage Plant Res 1(1):1–16. https://doi.org/10.48130/BPR-2021-0013

Lozano-Castellanos L, Sánchez-Hernández E, Navas-Gracia L, Martín-Ramos P, Correa-Guimaraes A (2025) Effects of different types of artificial light on the phytochemicals of *Lactuca sativa* L. variety Great Lakes 118 cultivated under aeroponic system. Food Biosci 64:105950. https://doi.org/10.1016/j.fbio.2025.105950

Maynard RCI, Ogundipe SO, Ferrarezi RS, Suh JH, Lombardini L (2025) Apigenin accumulation in *Matricaria chamomilla* and *Petroselinum crispum* produced in a vertical hydroponic system. HortScience 60(1):17–22. https://doi.org/10.21273/HORTSCI18240-24

Meng Q, Runkle ES (2015) Low-intensity blue light in night-interruption lighting does not influence flowering of herbaceous ornamentals. Sci Hortic 186:230–238. https://doi.org/10.1016/j.scienta.2015.01.038

Min A, Nguyen N, Howatt L, Tavares M, Seo J (2023) Aeroponic systems design: considerations and challenges. J. Agric Eng 54(1):1. https://doi.org/10.4081/jae.2022.1387

Oh S, Montgomery BL (2017) Phytochromes: where to start? Cell 171(6):1254–1256. https://doi.org/10.1016/j.cell.2017.11.020

Ojo MO, Zahid A (2022) Deep learning in controlled environment agriculture: a review of recent advancements, challenges and prospects. Sensors 22(20):7965. https://doi.org/10.3390/s22207965

Orsini, F., Pennisi, G., Zulfiqar, F., & Gianquinto, G. (2020). *Sustainable use of resources in plant factories with artificial lighting (PFALs)*. https://doi.org/10.17660/eJHS.2020/85.5.1

Paradiso R, Proietti S (2022) Light-quality manipulation to control plant growth and photomorphogenesis in greenhouse horticulture: the state of the art and the opportunities of modern LED systems. J Plant Growth Regul 41(2):742–780. https://doi.org/10.1007/s00344-021-10337-y

Paschko K, Grabovac N, Böhme MH (2023) Nutritional value of Asian herbaceous plants under different light conditions suitable for indoor farming. Acta Horticulturae 1369:191–200

Promratrak L (2017) The effect of using LED lighting in the growth of crops hydroponics. Int J Smart Grid Clean Energy. https://doi.org/10.12720/sgce.6.2.133-140

Runkle E, Heins R (2001) Specific functions of red, far red, and blue light in flowering and stem extension of long-day plants. J Am Soc Hortic Sci. https://doi.org/10.21273/JASHS.126.3.275

Samuolienė, G., Brazaitytė, A., & Vaštakaitė, V. (2017). Light-Emitting Diodes LEDs for improved nutritional quality. In S. Dutta Gupta (Eds), *Light emitting diodes for agriculture: smart lighting*. pp 149–190 Springer, Berlin

Su P, Ding S, Wang D, Kan W, Yuan M, Chen X, Tang C, Hou J, Wu L (2024) Plant morphology, secondary metabolites and chlorophyll fluorescence of *Artemisia argyi* under different LED environments. Photosynth Res 159(2):153–164. https://doi.org/10.1007/s11120-023-01026-w

Trivellini A, Toscano S, Romano D, Ferrante A (2023) The role of blue and red light in the orchestration of secondary metabolites, nutrient transport and plant quality. Plants (Basel) 12(10):2026. https://doi.org/10.3390/plants12102026

Viršilė A, Miliauskienė J, Haimi PJ, Laužikė K, Samuolienė G (2020) The comparison of constant and dynamic red and blue light irradiation effects on red and green leaf lettuce. Agron 10(11):11. https://doi.org/10.3390/agronomy10111802

Wang X, Lin C (2025) The two action mechanisms of plant cryptochromes. Trends Plant Sci. https://doi.org/10.1016/j.tplants.2024.12.001

Wang Q, Bian Z, Wang S, Zhao Y, Zhan X, Yang Q (2024) Far-red light inhibits soybean biomass and yield by modulating plant photosynthesis. Agron 14(11):11. https://doi.org/10.3390/agronomy14112684

Wollenberg AC, Strasser B, Cerdán PD, Amasino RM (2008) Acceleration of flowering during shade avoidance in *Arabidopsis* alters the balance between flowering locus C-mediated repression and photoperiodic induction of flowering. Plant Physiol 148(3):1681–1694. https://doi.org/10.1104/pp.108.125468

Xia J, Mattson N (2024) Daily light integral and far-red radiation influence morphology and quality of liners and subsequent flowering and development of petunia in controlled greenhouses. Horticulturae 10(10):1106. https://doi.org/10.3390/horticulturae10101106

Zhang S, Zhang L, Zou H, Qiu L, Zheng Y, Yang D, Wang Y (2021) Effects of light on secondary metabolite biosynthesis in medicinal plants. Front Plant Sci. https://doi.org/10.3389/fpls.2021.781236

Zoratti L, Karppinen K, Luengo Escobar A, Häggman H, Jaakola L (2014) Light-controlled flavonoid biosynthesis in fruits. Front Plant Sci. https://doi.org/10.3389/fpls.2014.00534