



Effect of LED spectra on growth, physiology, and biochemical profiles of African marigold (*Tagetes erecta* L.)

N.H. NGUYEN* , Q. PHAN* , H.T.T. CHU* , Q.C. TONG** , T.T.H. HOANG* ,
T.Q. TRAN** , B.N. BUI** , T.V. NGUYEN* , Q.T. HO* , H.H. CHU*,*** , and P.T. DO*,***,†

*Institute of Biology, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Nghia Do, 100000 Hanoi, Vietnam**

*Institute of Material Science, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Nghia Do, 100000 Hanoi, Vietnam***

*Graduated University of Science and Technology, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Nghia Do, 100000 Hanoi, Vietnam****

Abstract

The effects of the light-emitting diode (LED) spectra on plant growth, flowering, and phytochemical accumulation of African marigold were assessed under controlled conditions. The combination of white, blue, and red LEDs prolonged the time to flower by up to 20 d compared to full white LEDs and other light treatments. The white LEDs are an insufficient lighting condition for marigold growth, indicated by the lower plant and flower biomass. The dichromatic blue-red light and the white-blue-red (WBR) light were most suitable for marigold growth, biomass production, as well as flower quantity and quality. In addition, the highest contents of flavonoids and phenolics were observed in leaves and petals of marigold plants under the WBR treatment. Importantly, the extended spectrum of LEDs, achieved by supplementing white LEDs with the blue-red LEDs, could provide a friendly visual environment for researchers and workers under closed environments and plant factories.

Keywords: African marigold; biomass production; light-emitting diodes; light spectrum; plant factory.

Introduction

African or American marigold (*Tagetes erecta* L.), which belongs to the Asteraceae family, is an important medicinal and ornamental plant. Marigold flowers are rich in carotenoids, especially lutein, which could account for over 80% of carotenoids and is the primary commercial source for dietary supplements (Sams *et al.* 2016, Singh *et al.* 2016, Mir *et al.* 2019, Peralta-Sánchez *et al.* 2023, Kim *et al.* 2024). The other secondary compounds, such

as alkaloids, flavonoids, and volatile compounds, are also present in high content in the flowers (Laosinwattana *et al.* 2018, Manimegalai and Selvam 2023). In addition, essential oils were found to accumulate in different parts of the marigold plant depending on growth and development stages (Ogunwande and Olawore 2006). The accumulation of these valuable secondary compounds in marigold, as well as other medicinal plants, is firmly associated with environmental conditions, especially light and temperature. For example, the hypericin and

Highlights

- The blue-red LEDs and white-blue-red LEDs promote marigold growth
- The phytochemical content of marigolds was improved under white-blue-red LED lighting
- White-blue-red LEDs provide a visually pleasing environment for workers' inspection

Received 9 February 2026
Accepted 22 June 2026
Published online 2 July 2026

*Corresponding author
e-mail: dtphat@ib.ac.vn

Abbreviations: ANOVA – analysis of variance; AP-3 – APETALA3; Chl – chlorophyll; F3H – flavonoid 3'-hydroxylase; HIDL – high-intensity discharge lamp; LEDs – light-emitting diodes; LFY – LEAFY; PSY – phytoene synthase; qPCR – quantitative polymerase chain reaction.

Acknowledgements: This work was funded by the Vietnam Academy of Science and Technology (Project code: CN4000.01/23-25).

Conflict of interest: The authors declare that they have no conflict of interest.

pseudohypericin concentration of *Hypericum perforatum* increased from 100 ppm in the winter to > 4,000 ppm in the summer (Southwell and Bourke 2001). Thus, environmental control during cultivation is necessary to ensure the yield and quality of bioactive compounds in medicinal plants.

In the last decade, controlled cultivation has become a potential strategy for modern agricultural production (Kozai 2018). Different plant species have been successfully planted under artificial controlled environments, e.g., pepper, lettuce, and chrysanthemum (Lee *et al.* 2016, Nissim-Levi *et al.* 2019, Kim and Son 2022, Paradiso and Proietti 2022, Abhijita *et al.* 2023). For medicinal plants, the success of plant factories with artificial lighting has been limited. Many commercially used medicinal plants are still selected and harvested from their natural habitat. This could lead to the depletion of the genetic resources of many important local plants. In addition, the natural harvest could not meet the demands of the high-quality medicinal plant market every year. Therefore, the indoor cultivation of medicinal plants has gained more attention from researchers and industries.

Light is one of the most important factors for plant growth (Kozai 2018). Plant development and biochemical composition in different plant tissues and organs can be modulated by manipulating light spectrum, intensity, and photoperiod. Different light sources, such as high-intensity discharge lamps (HIDL), fluorescent lamps, incandescent lamps, and light-emitting diodes (LEDs), have been utilised for plant cultivation in closed environments. Blue and red LED lights have been used alone or in combination to generate optimal spectra for the cultivation of various plant species (Kozai 2018, Al Murad *et al.* 2021). Such light sources not only influence the concentration of chlorophyll but also raise phenolic and alkaloid content in various plants (Johkan *et al.* 2010, Kopsell *et al.* 2015, Nam *et al.* 2018). For instance, the artemisinin content in *Artemisia annua* or vinblastine and vincristine in *Catharanthus roseus* significantly increased under monochromatic blue and red LEDs compared to white light (Zhang *et al.* 2018a, Nagy *et al.* 2023). Recently, the combination of blue and red LEDs has been selected as a sufficient light treatment for growing various plants, including marigolds. Plant growth, morphology, and flower quality improved under the use of LEDs alone or in combination with other light sources (Heo *et al.* 2002, Kopsell *et al.* 2016, Sams *et al.* 2016, Kong *et al.* 2020). However, pink or purple hues generated by blue and red LEDs reveal visual limitations for crop inspection, such as evaluating plant growth, searching for pests, investigating fungal infections, *etc.* (Meng and Runkle 2023). Therefore, mixing red and blue with white light is important, especially for working in indoor conditions.

In this study, we examined the effect of several new composite spectra on the marigold plant grown indoors. Our results showed broad impacts of different composite spectra on plant morphology, growth, flowering, yield performance and other quality parameters of the marigold. This research also showed the positive effects of extended spectra, produced by adding white LEDs to dichromatic

blue-red LED combinations, for marigold growth and development. This light spectrum could be utilised for other crops to create a friendly visual environment under plant factories.

Materials and methods

Growth conditions, light treatments, and plant morphological evaluation: African marigold seeds (*Tagetes erecta* L.) were purchased from *Phuong Hoang Ltd.* company (HCMC, Vietnam) and sown in 50 seed-holding trays. One-month-old seedlings were transferred to the walk-in growth chamber under a 16-h light/8-h dark photoperiod. The temperature was controlled at $24 \pm 2^\circ\text{C}$ during the daytime and $21 \pm 2^\circ\text{C}$ at night. Twelve marigold seedlings were transplanted into a plastic tray ($38 \times 45 \times 12$ cm) filled with a mixture of peat moss, vermiculite, and perlite at 3:1:1 (v/v). The seedlings were irrigated every two days with water and once a week with $\frac{1}{2}$ MS solution.

Six LED treatments, including WR1 (7 white:1 red), BR (1 blue:5 red), WBR (1 white:2 blue:3 red), WRp (white LEDs coated with red-emitting phosphor), WR2 (3 white:2 red), and WL (full white light) (Table 1S, *Supplement*; Fig. 1S, *Supplement*), were tested. These light treatments were provided using LED bars at a light intensity of approximately $2,500 \text{ lm m}^{-2}$, measured with a *T-10A Illuminance Meter* (Konica Minolta, Japan).

Morphological parameters of marigold plants, including stem height, number of branches, width of canopy, fresh mass, and dry mass, were measured at 60 d under LED-light treatments. In addition, characteristics of marigold flowers, such as the initial flowering time, the number of buds, the number of fully-opened flowers, the diameter of fully-opened flowers, and the flower mass, were recorded and analysed at different time points under the LED treatments.

Chlorophyll measurement: The chlorophyll was extracted according to the method of Senthilkumar *et al.* (2021). Briefly, 1 gram of fresh leaves was finely ground in the dark, and then 10 mL of 80% acetone (fresh) was added to form a homogeneous suspension. The mixture was centrifuged at 5,000 rpm for 5 min at room temperature. Total chlorophyll in the supernatant phase was measured at 643, 645, and 663 nm wavelengths using a UV-Vis spectrophotometer (*Spectronic CamSpec Ltd.*, UK) (in the dark). Chlorophyll contents were calculated by the following formulas:

$$\text{Chl } a = (12.7 \times A_{663} - 2.69 \times A_{645}) \times V / (1,000 \times w)$$

$$\text{Chl } b = (22.9 \times A_{643} - 4.68 \times A_{645}) \times V / (1,000 \times w)$$

$$\text{Total Chl} = 20.2 \times A_{645} + 8.02 \times A_{663} \times V / (1,000 \times w)$$

where V is the volume of the extracted solution; w is the mass of the sample.

Flavonoids and phenolic compounds: The total flavonoid and phenolic contents were measured in leaves and fully opened petals, using the method described by Peralta-Sánchez *et al.* (2023) with some modifications. Briefly,

mature leaves or full-opened flower petals were dried and finely ground. Proceeded materials were added with 1.5 mL of 80% methanol, incubated at 4°C overnight and then centrifuged at 12,000 rpm to collect the supernatant. For the total flavonoids, 200 µL of the supernatant was transferred into a new 1.5-mL tube, followed by adding 600 µL of 80% methanol, 40 µL of 10% aluminum chloride, 40 µL of 1 M potassium acetate, and 1,120 µL of deionised water, sequentially and mixing well. The reaction was kept in the dark for 1 h at room temperature. The flavonoid absorbance was measured at 355 nm by the *Multiskan SkyHigh Microplate Spectrophotometer* (ThermoFisher Scientific, USA), and the total flavonoid content was calculated as the equivalent of rutin ($C_{27}H_{30}O_{16}$) concentration. For the total phenolic component, 50 µL of the extracted supernatant was diluted by an equal volume of deionised water, then added with 100 µL of Folin & Ciocalteu's phenol reagent (Sigma-Aldrich, Germany). The mixture was kept at room temperature for 1 min before adding 200 µL of 20% Na_2CO_3 and left in the dark for at least two hours. The total phenolic content was calculated using the gallic acid standard curve at 760 nm in a microplate spectrophotometer.

Carotenoids: Carotenoid contents were extracted from dry petals of fully-opened flowers and qualified by the procedure of Zhang and colleagues, with some modifications (Zhang *et al.* 2018b). Briefly, 50 mg of dry petals were homogenised in 1 mL of 90% ethanol, and the solution was then sonicated for 45 min in the Branson ultrasonic bath at 47 kHz (Emerson Electric, USA). Next, the supernatant was collected by centrifugation at 12,000 rpm for 5 min. The absorbance was measured at 445 nm in a microplate spectrophotometer, and the total carotenoid content was calculated by the following formula: Carotenoid content = (the absorbance × the volume of the extraction reagent × dilution factor)/(0.16 × dry mass).

Gene expression: Total RNA was extracted from young leaves of marigold plants at the bud formation stage using *TRIzol*® reagent according to the manufacturer's instructions (Invitrogen, USA) and followed by cDNA synthesis using *RevertAid First Strand cDNA Synthesis Kit* (ThermoFisher Scientific, USA). The real-time qPCR was performed to analyse transcription abundance of related genes, including *TeF'3H* encoding flavonoid 3'-hydroxylase (F'3H) involved in flavonoid biosynthesis pathway (NCBI ID: FJ216430.1), *TePSY* encoding phytoene synthase (PSY) responsible for the biosynthesis of carotenoid (NCBI ID: AY099482.1), and *TeLFY* encoding LEAFY as a transcription factor in flower induction (NCBI ID: JF825877.2) (Table 2S, Supplement). The β -actin was used as a reference gene, and the relative expression patterns of the tested genes were calculated utilising the $2^{-\Delta\Delta Ct}$ method (Livak and Schmittgen 2001).

Data analysis: All experiments were conducted with at least three replicates. Data was collected and analysed with one-way analysis of variance (ANOVA) followed by post-hoc Tukey's test using R software (R Core Team 2025).

Results

Marigold growth and morphological changes under LED treatments: After 60 d of LED lighting, marigold growth and morphological traits, including plant height, branch number, leaf size, and plant canopy width, varied significantly depending on light sources (Figs. 1, 2). Plant height ranged from 17.63 to 20.51 cm (Fig. 2A). The tallest plants (20.51 cm and 20.36 cm) were observed from two LED treatments (WR2 and WBR), while the shortest plants (17.63 cm) were found in the full white LED (WL) treatment. WR1 and BR treatments produced higher plants as compared to the WL; however, no significant difference was noted between the WRp and WL treatments. These results indicate that blue and red LED lights promote stem elongation in marigold plants under close growth chamber conditions.

The number of branches was the highest under the combination of blue and red lights (BR); however, there was no significant difference between other light treatments (Fig. 2B). The canopy width also varied under different lighting conditions (Fig. 2D). Specifically, the smallest canopy (18.57 cm in width) was observed in WRp. It increased significantly to 21.25, 20.58, and 21.59 cm in WBR, WL, and WR2, respectively. The largest canopies (25.32 and 24.71 cm) were observed under WR1 and BR treatments. In contrast, the leaf size was significantly larger in WRp than in other treatments (Fig. 2A–C; Fig. 2S, Supplement). In particular, the leaf length and width under the WRp reached 14.94 and 10.94 cm, respectively. However, there was no significant change in the leaf size among other tested light conditions. Thus, the single white light (WL) and the white LEDs

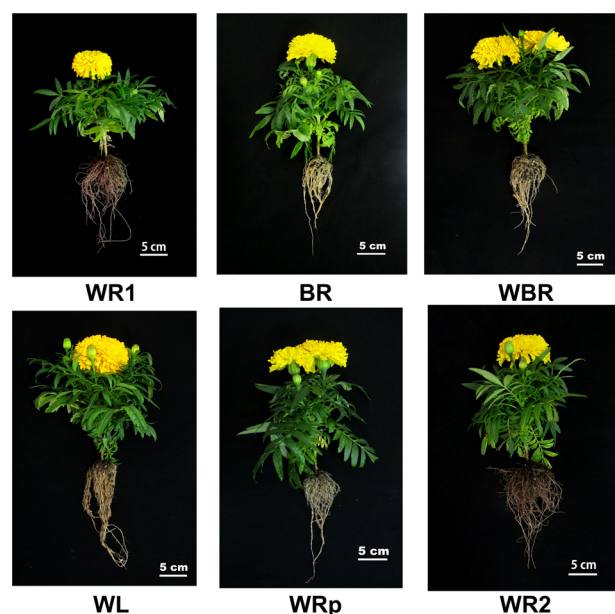


Fig. 1. Marigold plants under different light conditions. WR1 (7 white:1 red); BR (1 blue:5 red); WBR (1 white:1 blue:3 red); WL (white only); WRp (1 white:1 red phosphor); WR2 (3 white:2 red); pictures were taken on the 60th day after transplanting in the controlled chamber.

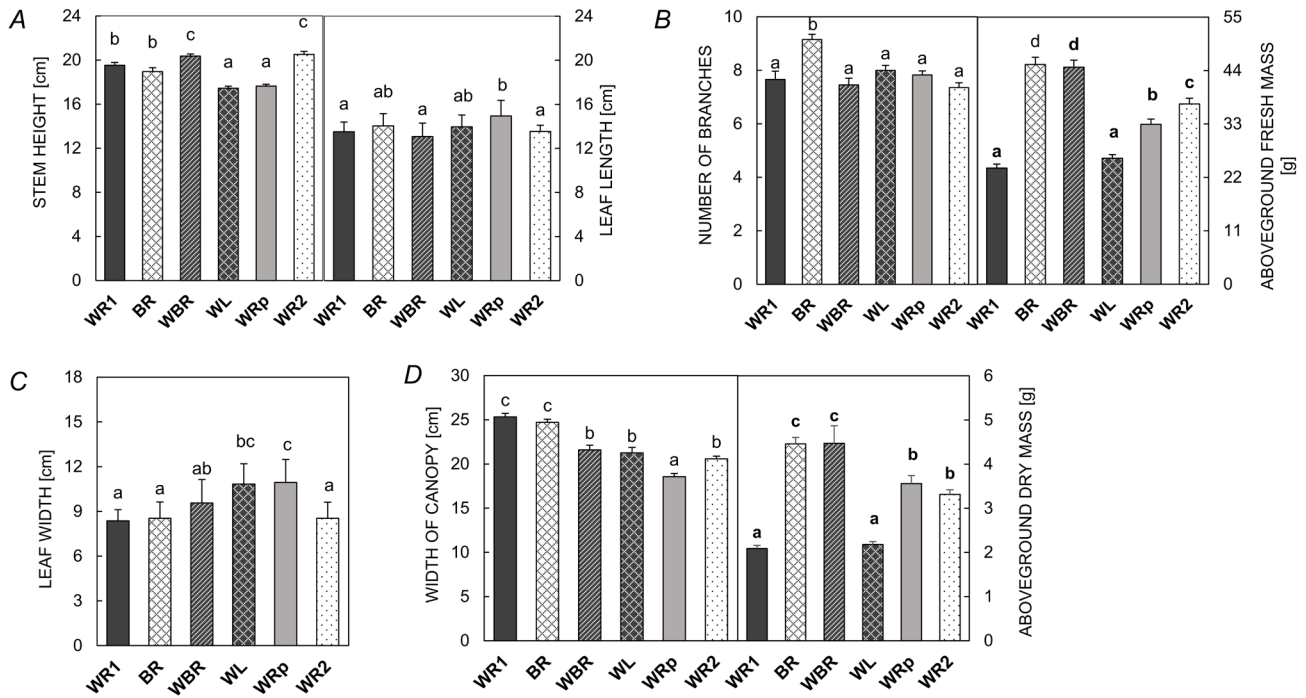


Fig. 2. Marigold plant parameters under different light treatments. WR1 (7 white:1 red); BR (1 blue:5 red); WBR (1 white:1 blue:3 red); WL (white only); WRp (1 white:1 red phosphor); WR2 (3 white:2 red). Data was collected at 60 d in the controlled growth chamber and analysed by one-way ANOVA method followed by Tukey's post-hoc test ($n = 36$); letters indicate significant differences at $p < 0.05$.

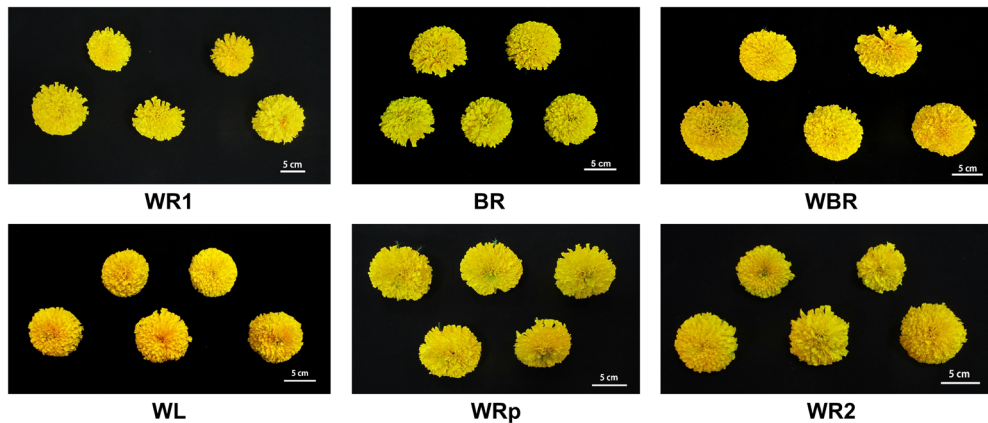


Fig. 3. Marigold full-opened flowers from the LED light treatments. WR1 (7 white:1 red); BR (1 blue:5 red); WBR (1 white:1 blue:3 red); WL (full-white LEDs); WRp (1 white:1 red-emitting phosphor); WR2 (3 white:2 red).

coated with the red-emitting phosphor (WRp) treatments are not recommended for lighting marigold plants under indoor conditions.

Biomass production of marigolds varies under different LED treatments: In line with changes in plant morphology, different LED spectra also impacted the biomass production of marigold plants (Figs. 2B–D, 3). The single white LED light (WL) and the least red LED addition (WR1: 7 white and 1 red) showed the lowest fresh biomass productions (25.94 and 23.92 g, respectively). The fresh plant biomass increased to over 30 g in WRp and WR2 treatments. The highest fresh biomass (> 40 g) was recorded in the presence of both blue and red LED lights (BR and

WBR), indicating the benefits of these monochromatic LED lights on marigold growth. Consequently, the lowest dry biomass (≈ 2 g) was observed in the WL and WR1 treatments (Fig. 2D). The total dry biomass also increased to over 3 g under WRp and WR2 conditions. Especially, the plant dry masses in BR and WBR treatments increased more than twofold (4.5 g) compared to those under the single WL and WR1 lighting conditions. These results indicated that LED white light itself is unfavourable for the growth and biomass production of marigold plants under completely artificial lighting. Both a mixture of white, red, and blue LEDs and a combination of red and blue lights provided the optimal lighting for enhancing the biomass production of marigolds.

LED components affect the reproductive phase transition, flower quantity, and quality of marigold plants: Different LED components directly affected the reproductive phase transition of marigolds (Fig. 4A). The first bud was observed in the BR, WL, and WRp light conditions around 40 d (39–44 d after transplanting). All plants under the WRp treatment showed the first buds on the same day (the 39th after transplanting), indicating that this lighting condition could strictly control early flowering of marigolds. However, in the other treatments, including WR1, WBR, and WR2, the first buds were visually observed between 59 and 64 d after transplanting. These results suggest that red LED light prolongs vegetative growth and delays flowering in marigold plants grown under completely artificial lighting conditions.

The total bud number per plant varied among the tested LED treatments (Fig. 4B). The highest number of visible buds (5 per plant) was observed in the WRp light, and the lowest number of 3.24 and 2.64 buds per plant was in WR1 and WBR treatments. In other treatments, this number ranged from 3.42 to 3.54. Similarly, the highest number of fully opened flowers was obtained from marigold plants grown under the WRp treatment, while the lowest number of fully opened flowers was under the WR1 treatment (Fig. 4B). Other lighting treatments produced the number of fully opened flowers ranging from 1.37 to 1.42, and there was no significant difference between them. Thus, the WRp can be used as the light source to promote the number of buds and flowers of marigold plants.

The components of light not only affected the reproductive phase transition, the bud and flower numbers, but also resulted in the differentiation of flower sizes in marigold plants. The diameter of the marigold flower in the BR and WBR treatments was the biggest,

respectively, at 8.81 and 8.64 cm. Following, the medium flowers were recorded in three light treatments – WL, WRp, and WR2, in which the diameter varied around 7.52 cm (Figs. 3, 4C). WR1 condition produced the smallest flowers (6.11 cm in diameter). Similarly, the fresh mass of the flowers was the highest in the BR and WBR treatments (18.54 g and 17.75 g) and the lowest in the WR1 treatment (6.53 g). Under other light treatments, the flower fresh mass ranged from 9.73 to 16.28 g. This data indicated that red and blue LED lights promoted marigold plant growth and consequently enhanced the flower size of marigolds under closed environmental conditions.

LED treatments alter biochemical characteristics of marigold plants: At the 60th d of transplanting, biochemical profiles in leaves under the LED treatments were assessed. Our data showed no significant difference in the total chlorophyll content and the chlorophyll *a/b* ratio among all tested LED treatments (Fig. 5A). The contents of secondary compounds varied among the LED-light conditions. The flavonoid content ranged from the highest of 17.6 mg in WBR treatment to an average of 5.65 mg in the rest of the treatments (Fig. 5B). In addition, the phenolic contents were high in three light treatments, BR, WBR, and WRp (from 354 mg to 384 mg), but dramatically decreased to 184.4 mg in the WR1 light condition (Fig. 5C).

In the petals, the colour changes were visually observed among the tested light conditions (Fig. 3). Particularly, BR and WRp treatments produced flowers of lighter yellow, while dark yellow or orange petals were observed in the WL, WBR, and WR2 conditions. Biochemical analysis also exhibited the highest carotenoid content in the WBR treatment and lower levels in the treatments of BR and WRp (Fig. 5D). WR1, BR, and WL produced

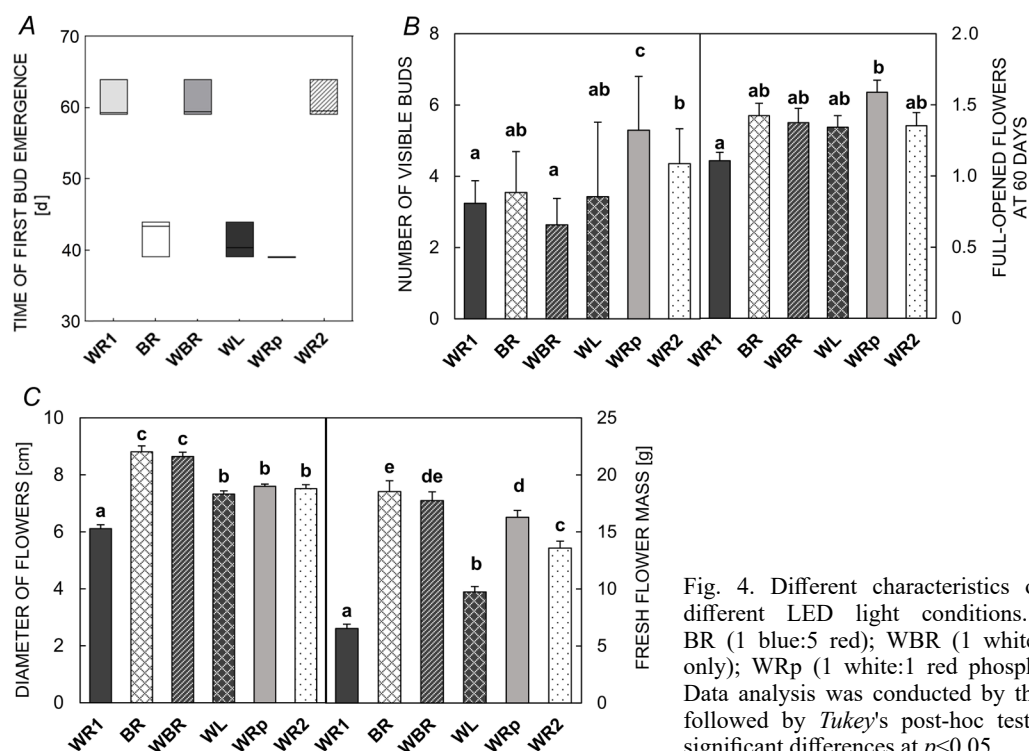


Fig. 4. Different characteristics of marigold flowers under different LED light conditions. WR1 (7 white:1 red); BR (1 blue:5 red); WBR (1 white:1 blue:3 red); WL (white only); WRp (1 white:1 red phosphor); WR2 (3 white:2 red). Data analysis was conducted by the one-way ANOVA method followed by Tukey's post-hoc test ($n = 36$); letters indicate significant differences at $p < 0.05$.

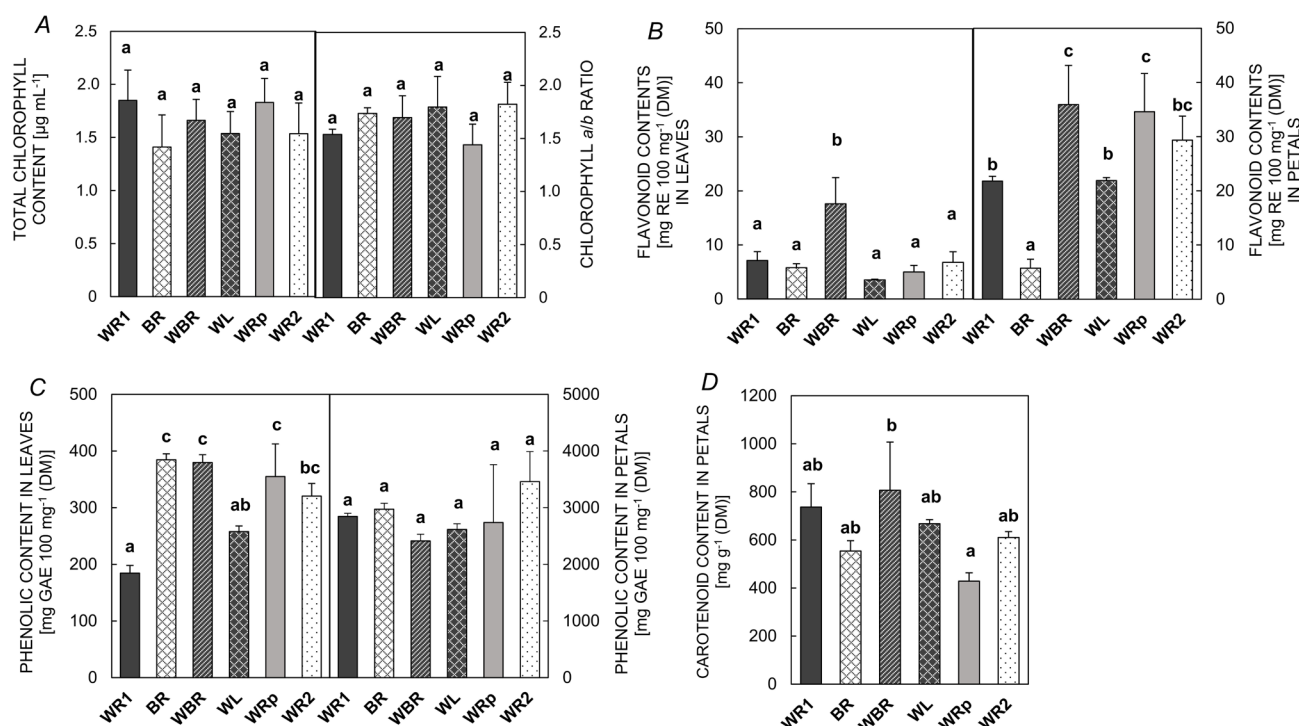


Fig. 5. Biochemical profiles of marigold plants under different LED light conditions. WR1 (7 white:1 red); BR (1 blue:5 red); WBR (1 white:1 blue:3 red); WL (white only); WRp (1 white:1 red phosphor); WR2 (3 white:2 red). (A) The total chlorophyll content and the chlorophyll *a/b* ratio in marigold leaves. (B) The flavonoid content in marigold leaves and petals. (C) The phenolic content in marigold leaves and petals. (D) The carotenoid content in the marigold petals. Data analysis was conducted in the one-way ANOVA method followed by Tukey's post-hoc test ($n = 36$); letters indicate significant differences at $p < 0.05$.

the lower flower flavonoid contents as compared to the three other light conditions (Fig. 5B). However, there was no difference in the phenolic content in the petals among all tested light treatments (Fig. 5C).

Therefore, the combination of full-white LEDs and dichromatic blue-red LEDs (red, blue, and white – WBR) was an optimal light condition for marigold plant growth, development, and secondary metabolite accumulation under the completely artificial light.

Related gene expression under the LED components:

LED components demonstrated their effects on the expression of genes related to metabolism pathways of different secondary compounds, such as carotenoids, flavonoids, polyphenols, *etc.*, in various plant species (Dutta Gupta and Pradhan 2017). In this study, the transcription abundance of representative genes related to flavonoid biosynthesis (*TeF3'H*), carotenoid metabolism (*TePSY*), and flowering transition mechanism (*TeLFY*) was assessed under different LED light conditions (Fig. 6). There was no significant change in expression levels of the *TePSY* gene under different LED treatments, even though small variations were observed. Higher expression of the *TeLFY* gene was found in the WR1 treatment; however, other light conditions showed the same transcript abundance. Similarly, there was no critical change in the transcription level of the *TeF3'H* gene under different light conditions except for a small increase in the WR1 treatment. More candidate genes need

to be tested in further research in combination with added biochemical analysis to investigate the effects of LED components on different secondary metabolism pathways in marigolds.

Discussion

The reproductive phase transition of short-day plants is strongly regulated by both spectral composition and photoperiodic signalling (Cerdán and Chory 2003, Trivellini *et al.* 2023). In Asteraceae species, different monochromatic LEDs or spectral combinations can either promote or suppress floral induction depending on wavelength composition and duration of exposure (Sams *et al.* 2016, Frąszczak *et al.* 2021, Munyanont *et al.* 2024). In chrysanthemum, red light (630–660 nm) has consistently been reported to inhibit flower initiation (Jeong *et al.* 2012, Craig and Runkle 2013, Nissim-Levi *et al.* 2019), suggesting that phytochrome activation under red wavelengths interferes with the floral transition in short-day species. Similarly, the delayed flowering observed in our WR1, WR2, and WBR treatments indicates that supplemental red light prolonged the vegetative phase of marigold even when provided against a white-light background. This response is likely associated with phytochrome-mediated regulation of flowering pathways. Red light promotes conversion of phytochrome to its biologically active Pfr form, which can alter the transcription of floral integrator genes and downstream

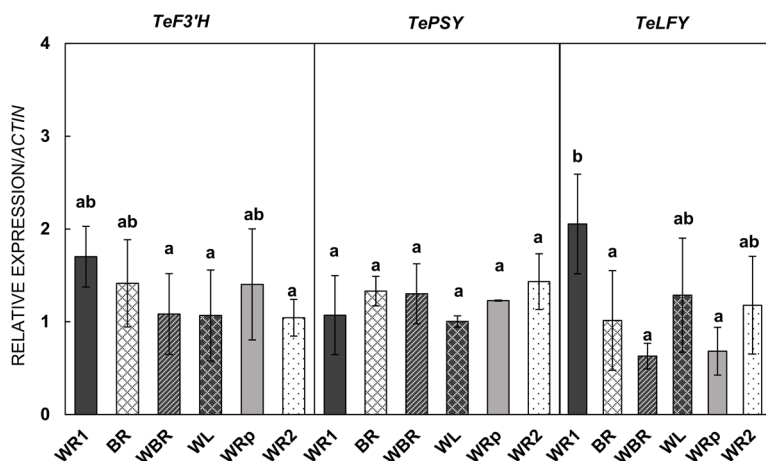


Fig. 6. Transcription abundance of candidate genes in marigold under different LED light conditions. WR1 (7 white:1 red); BR (1 blue:5 red); WBR (1 white:1 blue:3 red); WL (white only); WRp (1 white:1 red phosphor); WR2 (3 white:2 red). *TeF3'H* – flavonoid 3'-hydroxylase (genebank ID: FJ216430.1); *TePSY* – phytoene synthase (genebank ID: AY099482.1); *TeLFY* – LEAFY (genebank ID: JF825877.2). Data analysis was conducted in the one-way ANOVA method followed by Tukey's post-hoc test ($n = 36$); letters indicate significant differences at $p < 0.05$.

meristem identity genes. Previous studies demonstrated that genes such as *APETALA3* (*AP-3*), *AGAMOUS*, and *LEAFY* (*LFY*) are closely involved in floral meristem development (William *et al.* 2004), while loss-of-function *LFY* mutants in *Arabidopsis* exhibit delayed floral bud formation (Weigel *et al.* 1992). Therefore, the flowering inhibition observed under red-enriched spectra may reflect a shift in resource allocation toward vegetative growth before reproductive commitment. This interpretation is supported by the enhanced vegetative performance detected under WBR and WR treatments in our study. Such spectral control of the vegetative-to-reproductive transition is particularly important in ornamental crop production because delayed flowering can be commercially advantageous when growers aim to increase biomass accumulation, synchronise flowering time, or improve plant architecture before market distribution.

Interestingly, supplementation of white LEDs with dichromatic blue-red light (WBR) produced growth and developmental responses comparable to those observed under pure blue-red LEDs (BR). This finding suggests that the physiological effects of blue-red spectra can be maintained even when incorporated into a broader white-light environment. Previous studies have demonstrated that monochromatic or dichromatic blue-red LEDs enhance photosynthetic performance, biomass accumulation, and flowering traits in ornamental crops grown indoors (Jeong *et al.* 2012, Sams *et al.* 2016, Dou *et al.* 2017, Kozai 2018, Nam *et al.* 2018, Trivellini *et al.* 2023). However, although BR lighting is efficient for plant growth, its strong purple-pink colouration limits accurate visual assessment of leaf colouration, nutrient deficiency symptoms, and overall plant quality during commercial production (Kim *et al.* 2004, Meng and Runkle 2023). Our results, therefore, have practical significance because they indicate that adding blue-red wavelengths to a white-light background can preserve the physiological advantages of BR lighting while improving visual working conditions in indoor cultivation systems. This outcome further suggests that white LEDs may provide sufficient broad-spectrum support for normal morphogenesis, whereas supplemental red and blue wavelengths specifically optimise photosynthetic and photomorphogenic responses. Such interactions

between broad-spectrum white light and targeted spectral supplementation may represent an effective strategy for balancing plant productivity, morphology, and operational practicality in controlled-environment agriculture.

Light quality also substantially influenced the accumulation of secondary metabolites in marigold leaves and petals. In our study, red-enriched composite spectra (BR, WBR, WRp, and WR2) increased both flavonoid and phenolic contents relative to white LEDs alone, indicating that spectral composition modifies not only growth but also metabolic allocation. Secondary metabolites such as flavonoids and phenolics are closely associated with antioxidant activity, photoprotection, and stress adaptation. Their increased accumulation under red-enriched treatments may therefore reflect enhanced activation of defence-related metabolic pathways under specific spectral cues. Previous work in mulberry and *Camellia nitidissima* showed that LED spectra can regulate flavonoid biosynthesis through altered expression of genes such as flavonoid 3'-hydroxylase (*F3'H*), thereby increasing total phenolic and flavonoid concentrations (Jiang *et al.* 2021, Dai *et al.* 2022). The observed increase in secondary metabolites under our treatments may similarly result from spectral regulation of phenylpropanoid pathway activity (Abhijita *et al.* 2023). Although blue light is often associated with flavonoid induction through cryptochrome signalling, our findings suggest that red-light enrichment also contributes substantially to metabolite accumulation when combined with a white-light background. This indicates that flavonoid biosynthesis in marigold may depend on coordinated interactions between multiple photoreceptors rather than responses to a single wavelength alone. Such spectral interactions could explain why WBR treatment produced stronger responses than white light alone.

In addition to leaf metabolites, WBR treatment resulted in the greatest carotenoid accumulation in petals, together with improved vegetative growth. This finding is particularly important because carotenoids are major ornamental quality determinants in marigold flowers and also possess commercial value as natural pigments and antioxidant compounds. Previous studies in Signet marigold demonstrated that red-enriched spectra increase

carotenoid accumulation in petals (Kopsell *et al.* 2016), while blue-red combinations have been associated with enhanced biosynthesis of secondary metabolites and improved photosynthetic efficiency in several horticultural species (Lee *et al.* 2016, Sams *et al.* 2016, Frąszczak *et al.* 2021, Trivellini *et al.* 2023). Our results expand these findings by demonstrating that a combination of white LEDs and blue-red LEDs can simultaneously support biomass production and metabolite enrichment under indoor conditions. *TePSY*, which encodes phytoene synthase, is a key regulatory gene in carotenoid biosynthesis because it catalyses the first committed step of phytoene formation. Previous studies demonstrated that *PSY* expression is strongly influenced by light quality through phytochrome-mediated signalling pathways (Moehs *et al.* 2001, Toledo-Ortiz *et al.* 2010, Frede *et al.* 2023). Red light can enhance *PSY* transcription *via* phytochrome activation, whereas blue LEDs have also been reported to strongly stimulate *PSY* expression in several plant species. In marigold, *TePSY* expression was shown to vary according to developmental stage and light conditions, indicating that light quality may regulate carotenoid accumulation through transcriptional modulation of carotenoid biosynthetic genes (Zhang *et al.* 2025). Importantly, in our study, enhanced carotenoid accumulation under WBR may indicate that the combined action of red and blue wavelengths optimises both carbon assimilation and pigment biosynthesis pathways. Red light efficiently drives photosynthetic electron transport, whereas blue light regulates chloroplast development, stomatal opening, and photomorphogenic signalling (Yoshi *et al.* 2026). The synergistic interaction between these wavelengths may therefore increase precursor availability for carotenoid biosynthesis while also stimulating expression of carotenoid-related genes. This dual effect could explain why WBR treatment achieved superior ornamental quality without compromising growth performance.

Overall, our findings demonstrate that spectral extension of white LEDs through supplemental blue-red lighting is an effective strategy for regulating flowering time, enhancing vegetative growth, and increasing secondary metabolite accumulation in marigolds cultivated under controlled environments. Beyond confirming the importance of red and blue wavelengths for plant development, this study highlights the value of integrating targeted spectral supplementation into broad-spectrum lighting systems to improve both crop productivity and visual management in indoor ornamental production systems.

Conclusions: Our study found that LED spectra affected plant growth, development, reproductive phase transition, and flower quality of marigolds under the controlled-light environment. The use of full white LEDs mixed with the dichromatic blue-red LEDs not only enhances plant growth and phytochemical accumulation in marigolds but also provides a visually pleasing environment for plant inspection under indoor conditions. This potential spectrum could be extended for the cultivation of other crops in the controlled environment. Further studies

should be conducted to investigate the effects of these LED spectra on the biochemical metabolisms of different secondary metabolites in marigold plants.

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