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Photomorphogenic and thermomorphogenic responses influencing growth and flowering in *Chrysanthemum morifolium* cv. Zembla

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ABSTRACT

Light and temperature act as key environmental signals that synergistically influence plant growth and development. Strategically manipulating photothermal regimes offers remarkable potential to optimize plant architecture and flowering. The study was carried out during 2023–24 and 2024–25 at ICAR-Indian Agricultural Research Institute, New Delhi to evaluate the photomorphogenic and thermomorphogenic responses in *Chrysanthemum morifolium* cv. Zembla. Plants were subjected to different monochromatic light treatments (W, R, B, RB, and FL) under 15 h of long-day photoperiod across five temperature regimes (24/20°C, 22/2°C, 20/20°C, 18/20°C, and 16/20°C). The research revealed significantly distinctive responses across different morphophysiological and flowering parameters. Morphological results revealed that red light (R, LD15) at 24/20°C significantly increased plant height (92.97 cm) and internodal length (2.73 cm), while, blue light (B, LD15) at 24/20°C enhanced vegetative growth, attributed by maximum leaf number (35.82), leaf area (379.87 cm^2), total plant dry weight (10.80 g), and enhanced physiological mechanisms including relative growth rate (0.046 g/g/day) and crop growth rate (2.030 $g/m^2/day$). For flowering responses, blue light accelerated bud induction across all temperatures, with plants under B, LD15 achieving anthesis earlier than alternative spectral treatments. Sub-optimal temperature (16/20°C) under blue light accelerated the induction of visible bud formation and flowering, whereas optimal temperature conditions (24/20°C) under blue light resulted in superior capitulum development characterized by maximum floral diameter (9.97 cm). The synergistic interaction between light and temperature proved to effective for modulating chrysanthemum growth and development, providing valuable insights for optimizing environmentally controlled cultivation practices.

Keywords: Chrysanthemum, Flowering, Monochromatic light, Temperature regimes

Plants exhibit remarkable adaptability to diverse environmental stimuli, encompassing variations in light quality, temperature gradients, and distinct varietal groups. For many species, the intricate synergy between thermal regimes and photoperiodic rhythms is the primary regulatory mechanism for synchronizing flowering with seasonal transitions. The nexus between vegetative growth and reproductive transition is critical, with factors such as leaf proliferation and ecological conditions governs the phenological progression (Peer *et al.* 2021).

Chrysanthemum morifolium (Ramat), a prominent ornamental species in the Asteraceae family, represents one of the globe's four preeminent cut flower crops, accounting 9.77% of global floriculture commerce (Pan *et al.* 2025). Esteemed for their morphological diversity and vibrant hues, they hold a pivotal position in global floricultural industry (Datta and Janakiram 2015). As an obligate short-day plants, they require a critical photoperiod of ≤14.5 h for floral induction, with cultivar-specific variations (Nissim-Levi *et al.* 2019).

Light modulation enhances photosynthesis efficiency and regulates photomorphogenic responses through photoreceptors (Weller and Kendrick 2008). Temperature represents another pivotal regulatory factor, influencing both floral initiation and subsequent development, with variables such as average temperatures (ATs), diurnal temperatures (DTs), and nocturnal temperatures (NTs) can be experimentally manipulated (Van Der Ploeg and Heuvelink 2006). Cultivars exhibit genotype-dependent thermal responses, classified as thermo-zero, thermo-positive, or thermo-negative, with each group displaying unique flowering responses (Cathey 1954). Light and thermal factors interact across multiple temporal dimensions. As a result, the preponderance of plant species necessitates precise photoperiodic and thermal synergies to coordinate optimal flowering events (Franklin 2009).

To address the global demand for quality flowers throughout the year, flowering can be programmed through regulating photoperiods by limiting natural

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light with blackout screening during long-day season or introducing artificial lighting for night interruption and day-length extension (Yang *et al.* 2022). Additionally, precise temperature regulation can be achieved through advanced thermal control systems, effective ventilation, and humidification (Proietti *et al.* 2022). While traditional lighting systems present limitations, Light-Emitting Diodes offer superior alternatives due to their spectral versatility and energy efficiency (Ma *et al.* 2021). Despite extensive research on spectral manipulation in chrysanthemum, thermal intervention methods and their implications on flowering phenology relatively underexplored (Carvalho *et al.* 2005, Sangma *et al.* 2016, SharathKumar *et al.* 2024). The advent of LED-based greenhouse systems enables year-round cultivation through precise management of environmental factors. Nevertheless, the effect of sole-source monochromatic illumination under long-day conditions with varied diurnal temperature regimes remain inadequately elucidated. Considering Chrysanthemum's commercial significance and responsiveness to spectral quality and temperature gradients, this investigation aimed to evaluate light and temperature-mediated responses influencing growth, flowering, and physiological characteristics in *Chrysanthemum morifolium* cv. Zembla.

MATERIALS AND METHODS

Plant material and growth conditions: The study was carried out during 2023–24 and 2024–25 at ICAR-Indian Agricultural Research Institute (28.08°N and 77.12°E), New Delhi. Terminal cuttings of standard-type Chrysanthemum cv. Zembla were sourced from Centre for Protected Cultivation Technology, Indian Agricultural Research Institute, New Delhi, and propagated as self-rooted plants in plug trays containing soil-less substrate (coco-peat, vermiculite, and perlite, 3:1:1). Upon rooting, 30-days old plants were transplanted to UV-stabilized containers (9 cm × 9 cm × 10 cm) filled with growing medium composed of soil, vermicompost, sand, and leaf manure (3:1:1:1). They were acclimatized for 15 days in a greenhouse under a 15 h photoperiod, 26/18 ± 2°C temperatures, with 65% relative humidity, and ambient CO_2 levels. Irrigation through an overhead irrigation system on alternate days, supplemented with a fertigation schedule comprising weekly applications of 19:19:19 (2 g/L) and bi-weekly applications of Calcium Nitrate (1 g/L), throughout the experiment.

Photoperiodic light and thermoperiodic temperature treatments: Following acclimatization, uniform plants were transferred to growth-chambers equipped with custom-built illumination systems (Fig. 1A). Five distinct light regimes were employed for 15 h photoperiods, viz. W, LD (100% White LED); R, LD (100% Red LED); B, LD (100% Blue LED); RB, LD (80% Red LED + 20% Blue LED); and FL, LD (fluorescent light) (Fig. 1B). Using quantum light sensor (3415^{FX}Fieldscout^{TM}) spectral output was standardized at a consistent PPFD of 110 µmol/m^2/s. Parallelly, five differential temperature regimes were maintained in independent growth chambers, equipped with advanced thermal control systems. The day/night thermal set points were, 24/20°C ± 0.2°C; 22/20°C ± 0.2°C; 20/20°C ± 0.2°C; 18/20°C ± 0.2°C; and 16/20°C ± 0.2°C, with 65 ± 2% relative humidity and ambient CO_2 levels.

Measurements of different parameters: Morphological traits were evaluated 45 days following the commencement of photothermal treatments. Growth parameters, including plant height, internodal length, number of leaves per stem (leaves exceeding 2 cm in length were counted), and leaf area (measured using LI-COR 3100 Area Meter). Biomass estimation involved drying segregated leaf and stem samples in a hot air oven at 70°C for 72 h and the cumulative dry weight was determined using a Mettler Toledo MA204 Precision Balance, providing the total plant dry weight. Physiological parameters were assessed with the computation of Relative growth rate (RGR) (g/g/day) (Radford 1967) and partitioning coefficient, calculated at full bloom stage. Additionally, time taken to bud induction, time taken to flowering and flower diameter were recorded during flowering phase.

$$\text{RGR} = (\ln W_2 - \ln W_1)/T_2 - T_1;$$

$$\text{Crop growth rate (CGR) (g/m}^2\text{/day) (Watson 1952)} = (W_2 - W_1)/T_2 - T_1;$$

Where W_1 and W_2, Plant dry weights (g) at times T_1 (Start of photothermal treatments) and T_2 (45 days after exposure to photothermal treatments).

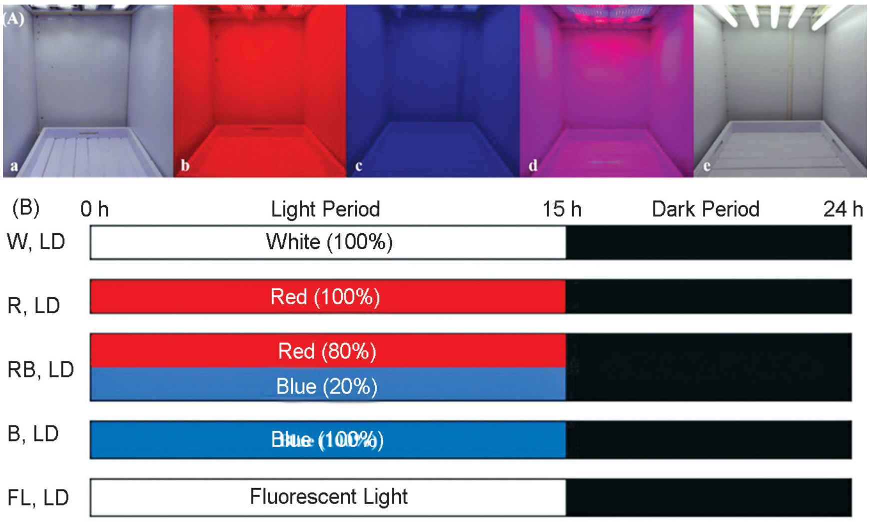

Fig. 1 (A) The illumination systems of the different light spectra (a) White LED, (b) Red LED, (c) Blue LED, (d) Red-Blue LED, and (e) Fluorescent light. (B) Schematic representation of light treatments.
White, red, blue and grey colours indicate respective light period; black colour indicate dark period.

Partitioning coefficient = (Flower dry weight/Plant dry weight) × 100

Statistical analysis: The experiment was conducted in homogeneous conditions employing a three-replication complete randomized block design (CRBD). Pooled mean data exhibiting statistically significant variations among the treatments were analysed through two-way analysis of variance (ANOVA) utilizing the ‘car’ package in R version 4.3.2 (R Core Team 2023). Statistical significance was ascertained through LSD test at $p \leq 0.001$, executed via ‘Agricolae’ package (R Core Team 2023). Multidimensional rose diagram was generated using the ChiPlot (https://www.chiplot.online/).

RESULTS AND DISCUSSION

Plant species manifest complex adaptive physiological responses through photomorphogenic and thermomorphogenic pathways. The empirical investigation demonstrates that discrete light spectra and temperature regimes has found to impact morphophysiological and flowering attributes in *Chrysanthemum morifolium* cv. Zembla.

Effect of photothermal treatments on morphophysiological parameters: Morphological traits exhibited significant variation in response to photothermal treatments (Fig. 2). Red light, LD15 spectrum induced a 35.16% increment in vertical growth compared to W, LD15 treatment, regardless of temperature regimes. Concurrently, plants under 24/20°C temperature conditions displayed a substantial 142.85% increase in height compared to those grown under 16/20°C conditions. Among all interactions, tallest plant height (92.97 cm) was recorded under the R, LD15 condition at 24/20°C regime with highest internodal length (2.73 cm). This phenomenon may be attributed to light-mediated growth regulation, particularly red and blue spectra upregulating photoreceptors specifically cryptochromes and phytochromes promoting gibberellic acid biosynthesis and stem elongation, corroborating the present findings of red light-induced elongation in chrysanthemum (Zhao *et al.* 2007, Nissim-Levi *et al.* 2019). These photomorphogenic responses operate in tandem with temperature-driven growth dynamics, specifically through differential day-night temperature (DIF). Positive DIF conditions, characterized by higher daytime temperatures than night-time, facilitate pronounced stem elongation due to shade-avoidance mechanisms, whereas negative DIF conditions, with cooler days and warmer nights, promote a more compact plant architecture. This is attributed to disruptions in the endogenous circadian cycle, which elevate dark-phase respiratory fluxes, exacerbate carbon depletion, and impair energy homeostasis, ultimately limiting biomass allocation for vertical growth (Cockshull *et al.* 1993, Carvalho *et al.* 2002, Gil and Park 2019, Venkat and Muneer 2022).

Furthermore, B-LD15 light spectrum augmented foliar growth, manifesting as a 34.55% rise in number of leaves per cut stem, 50.94% increase in leaf area, and 55.92% increase in plant dry weight compared to W, LD15 spectrum across all temperature regimes. Prolonged photoperiods substantially enhance the accumulation of dry matter, with blue light spectrum boosting photosynthetic carbon assimilation and biomass production (Hao and Papadopoulos 1999, Menard *et al.* 2005). Under different temperature regimes, 24/20°C conditions exhibited enhanced morphogenesis and biomass accumulation relative to other thermal regimes. This was evidenced by a 114.03% rise in number of leaves per cut stem, 196.45% increase in leaf area, and a 123.39%

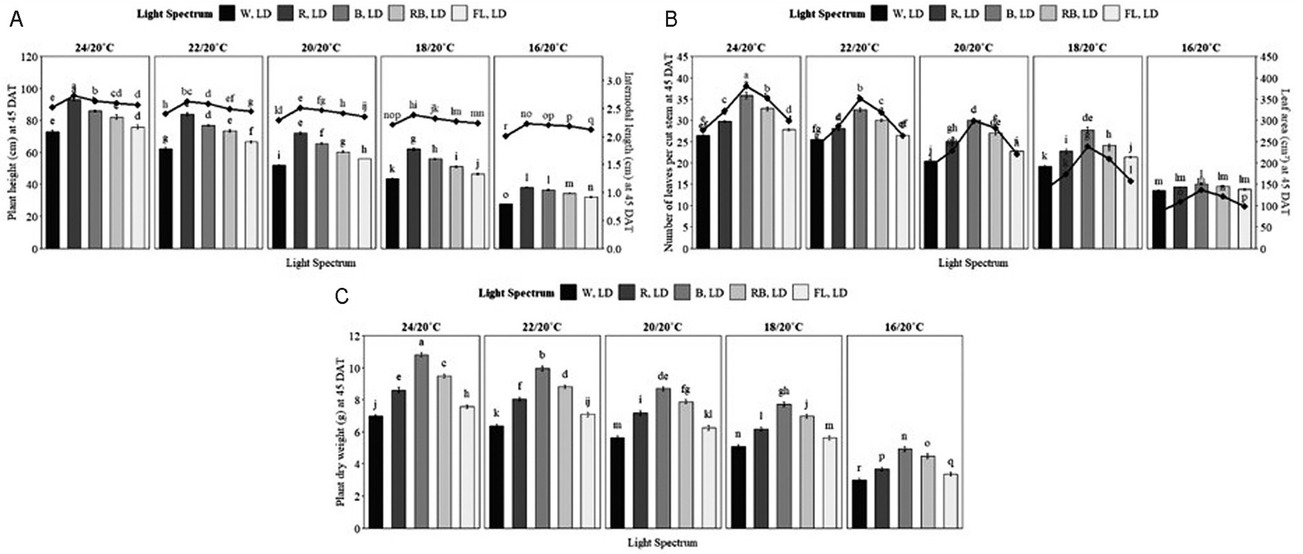

Fig. 2 Effect of light spectrum on (A), Plant height and internodal length; (B), Number of leaves per cut stem and leaf area; and (C), plant dry weight of Chrysanthemum cv. Zembla under different monochromatic light spectra and temperature regimes, after 45 days of exposure to photothermal treatments.

Vertical bars indicate the values representing the pooled mean of 2023–24 and 2024–25 (mean ± standard error) (n=3). Different letters indicate significant differences according to LSD test ($p \leq 0.001$).

enhancement in dry matter content. This could be attributed to accelerated leaf growth (Nishar *et al.* 2017). Among all treatments, B, LD15 at 24/20°C conditions induced maximum leaf number (35.82), leaf area (379.87 cm^2), and total plant dry weight (10.80 g). These outcomes are governed by intricate signal transduction cascades regulating plant metabolism (Li *et al.* 2022).

Physiological parameters, such as RGR and CGR exhibited significant variation across different photothermal treatments (Table 1). The results demonstrate that, RGR and CGR were increased when exposed to Blue LEDs and registered a maximum growth rate (0.040 g/g/day and 1.520 g/m^2/day) at 45 days post-treatment, with a significant increase of 29.03% and 73.12% over White LED conditions. The increased biomass accumulation is likely attributed to reduced respiratory activity during short-night period (Parups and Butler 1982). Under differential temperature regimes, an increase in diurnal temperature from 16–24°C led to a 75% rise in RGR and a remarkable 191.48% increase in CGR. Likewise, De Jong and Smeets (1982) observed that elevating daytime temperatures from sub-optimal to optimal levels during long-day photoperiods significantly enhanced biomass production. This effect is likely driven by increased photosynthetic efficiency per unit of leaf dry matter as temperatures near their optimal range (Van Der Ploeg and Heuvelink 2006). The synergistic interaction between blue light and optimum temperature (24/20°C) elevated RGR and CGR by 155.55% and 463.88%, respectively, compared to White LED.

Photothermal treatments significantly impacted the partitioning coefficient (Fig. 3). Blue light at 24/20°C generated the most favourable resource distribution, achieving a partitioning coefficient of 32.02. This could be attributed to enhanced photosynthate assimilation and efficient translocation to flowers. Temperature influences assimilate partitioning through regulation of plant developmental processes (Van Der Ploeg and Heuvelink 2006). Conversely, white LED and fluorescent light under 16/20°C temperature resulted in the minimal partitioning coefficients, likely due to suboptimal conditions that suppressed flower evocation which redirected assimilates towards vegetative growth for plants survival suggesting these treatments are not conducive to flowering. This demonstrates that optimizing the day/night temperature alongside light spectral treatments could enhance floral induction and elevate resource partitioning towards reproductive structures.

Effect of photothermal treatments on flowering: Flowering traits shown significant variability across treatments (Fig. 4), with floral bud initiation occurring under all treatment conditions. Blue LD15 treatment accelerated bud formation compared to other long-day photoperiodic light spectra, also promoting early capitulum development and anthesis. Eventually, all plants grown under B, LD15

Table 1 Physiological traits of Chrysanthemum cv. Zembla under different monochromatic light spectra and temperature regimes, after 45 days of exposure to photothermal treatments

Light spectra (L)	Temperature regimes (T)					
	24/20°C	22/20°C	20/20°C	18/20°C	16/20°C	Mean
Relative growth rate (g/g/day) at 45 DAT						
W, LD	0.037^{h} ± 0.002*	0.035^{i} ± 0.002	0.032^{k} ± 0.002	0.030^{l} ± 0.002	0.018^{q} ± 0.004	0.031^{E} ± 0.003
R, LD	0.042^{d} ± 0.004	0.040^{e} ± 0.003	0.038^{g} ± 0.001	0.034^{j} ± 0.002	0.023^{o} ± 0.002	0.035^{C} ± 0.003
B, LD	0.046^{a} ± 0.002	0.045^{b} ± 0.002	0.042^{d} ± 0.002	0.039^{f} ± 0.001	0.029^{m} ± 0.002	0.040^{A} ± 0.003
RB, LD	0.044^{c} ± 0.003	0.042^{d} ± 0.001	0.040^{e} ± 0.004	0.037^{h} ± 0.002	0.027^{n} ± 0.003	0.038^{B} ± 0.003
FL, LD	0.039^{f} ± 0.002	0.037^{h} ± 0.002	0.035^{i} ± 0.002	0.032^{k} ± 0.003	0.021^{p} ± 0.001	0.033^{D} ± 0.003
Mean	0.042^{A} ± 0.002	0.040^{B} ± 0.002	0.037^{C} ± 0.002	0.035^{D} ± 0.001	0.024^{E} ± 0.002	
LSD (*p*≤0.001)			L=0.0004; T=0.0004; L × T=0.0008			
Crop growth rate (g/m^2/day) at 45 DAT						
W, LD	1.215^{j} ± 0.022*	1.082^{k} ± 0.014	0.925^{m} ± 0.010	0.805^{n} ± 0.011	0.360^{r} ± 0.018	0.878^{E} ± 0.147
R, LD	1.562^{e} ± 0.016	1.440^{f} ± 0.013	1.255^{i} ± 0.013	1.040^{l} ± 0.018	0.510^{p} ± 0.015	1.161^{C} ± 0.185
B, LD	2.030^{a} ± 0.017	1.849^{b} ± 0.020	1.578^{de} ± 0.018	1.372^{gh} ± 0.012	0.771^{n} ± 0.016	1.520^{A} ± 0.218
RB, LD	1.745^{c} ± 0.014	1.602^{d} ± 0.010	1.402^{g} ± 0.015	1.214^{j} ± 0.015	0.679^{o} ± 0.013	1.329^{B} ± 0.186
FL, LD	1.341^{h} ± 0.015	1.237^{ij} ± 0.018	1.060^{kl} ± 0.013	0.922^{m} ± 0.016	0.439^{q} ± 0.011	1.000^{D} ± 0.158
Mean	1.579^{A} ± 0.132	1.442^{B} ± 0.123	1.244^{C} ± 0.106	1.071^{D} ± 0.092	0.552^{E} ± 0.069	
LSD (*p*≤0.001)			L=0.016; T=0.016; L × T=0.035			

W, LD, White LED; R, LD, Red LED; B, LD, Blue LED; RB, LD, Red-Blue LED; FL, LD, Fluorescent light. *Values represent the pooled mean of two consecutive seasons, 2023–24 and 2024–25 (mean ± standard error) (n=3). Data followed by different upper-case in vertical column represents significant differences between light spectra and in horizontal row represent significant differences between temperature regimes. Different lower-case letters represent significant differences in the interactions between light spectra and temperature regimes.

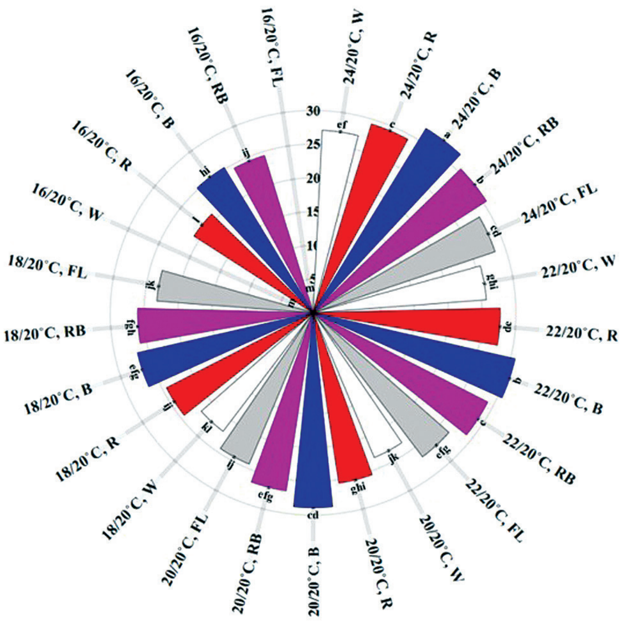

Fig. 3 Multidimensional rose chart illustrates the effect of different monochromatic light spectra and temperature regimes on partitioning coefficient in Chrysanthemum cv. Zembla, after 45 days of exposure to photothermal treatments. Vertical bars indicate the values representing the pooled mean of 2023–24 and 2024–25 (mean ± standard error) (n=3). Different letters indicate significant differences according to LSD test ($p \leq 0.001$).

reached flowering in 78 days from the start of the light treatment, while the plants exposed to red and red-blue light under long-day conditions reached full bloom in 82 and 86 days respectively, merely 4–8 days later than blue light (mean effect data for photothermal regimes not presented). Although, W, LD15 and FL, LD15 induced flowering but showed most pronounced delays. This demonstrates normal flower induction in chrysanthemum even under long days through smart LED illumination providing photosynthetically active radiation without disrupting short-day requirements (Singh *et al.* 2013). Higuchi *et al.* (2012) determined blue light's crucial role in flower induction under long-day photoperiods, potentially due to perception of blue light being as a 'dark' signal, or weaker long-day signal than red or combined red-blue light (SharathKumar *et al.* 2024). Polychromatic White LED illumination and fluorescent lighting under longer photoperiod similarly triggered flower induction, apparently attributed to their comprehensive broad-spectrum distribution mimicking solar irradiance and augmented red:far-red ratios, which regulate phytochrome photoequilibrium and mitigate long-day suppressive mechanisms (Park and Runkle 2018).

Temperature critically regulates chrysanthemum flowering, with optimal bloom occurring between 17–22°C (Langton and Horridge 2006). In this study, plants under 16/20°C conditions exhibited earlier bud visibility (49 days) and flowering (71 days), while those at 24/20°C experienced a delayed flowering (97 days) but exhibited superior floral quality. Among all experimental conditions, B, LD15 consistently enhanced floral attributes across all temperature regimes, with plants under 24/20°C achieving maximum floral diameter (9.97 cm). In contrast, plants exposed to W, LD15 and FL, LD15 under 16/20°C developed visible buds but failed to complete flower development. This inhibition of capitulum development may be linked to high far-red ratios disrupting phytochrome-mediated signalling, thereby impairing floral differentiation and development (SharathKumar *et al.* 2024).

Based on the results of the present study, this investigation demonstrates that photothermal interactions significantly influenced morphophysiological and flowering attributes in *Chrysanthemum morifolium* cv. Zembla. Blue light (B, LD15) at 24/20ºC temperature regime optimized plant morphogenesis through biomass accumulation, while also facilitating efficient assimilate partitioning to flowers. Although lower temperature regime (16/20ºC) accelerated flowering, optimal thermal conditions (24/20°C) under long-day blue light illumination produced superior floral quality. These findings underscore the critical role of photoperiod and temperature in regulating chrysanthemum growth and flowering, emphasizing the need for specific spectral compositions alongside optimal temperature conditions to precisely modulate plant architecture and flowering traits in accordance with commercial requirements.

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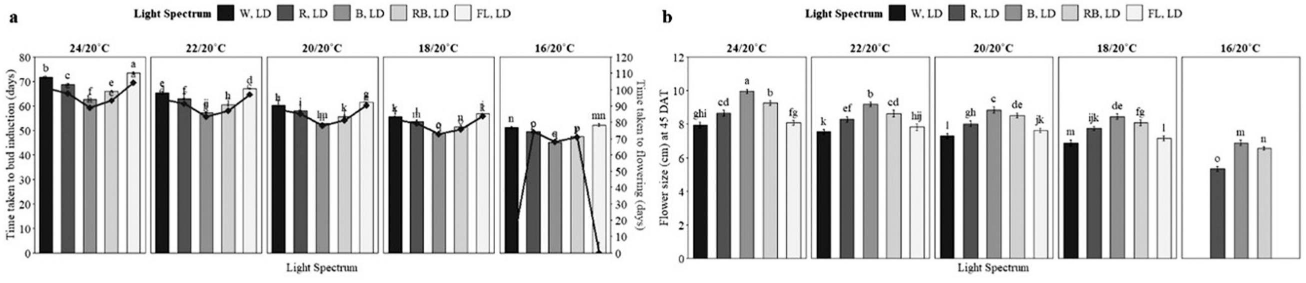

Fig. 4 Effect of different monochromatic light spectra and temperature regimes on (A), Time taken to bud induction and time taken to flowering; and (B), Flower size of Chrysanthemum cv. Zembla under, after 45 days of exposure to photothermal treatments. Vertical bars indicate the values representing the pooled mean, 2023–24 and 2024–25 (mean ± standard error) (n=3). Different letters indicate significant differences according to LSD test ($p \leq 0.001$).

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