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Application of photo-thermal models to quantify flowering time and development response of Chrysanthemum (*Chrysanthemum* × *morifolium* Ramat.)

Muhammad Munir[1,2*]

*[1]Date Palm Research Center of Excellence, King Faisal University, Al-Ahsa, P.O. Box 31982, Saudi Arabia. [2]Frontier Agriculture, SOYL Precision Crop Production Division, Newbury, United Kingdom. *E-mail: mmunir@kfu.edu.sa*

Abstract

Chrysanthemum is a short-day plant, which flowers when the night length is longer. Photoperiod and temperature are two key environmental factors that affect time of flowering. In the current research, experiments were carried out to study the flowering response of two cultivars of chrysanthemum, *i.e.*, Crimson Glory and Snowscape under four distinct photoperiods (8, 11, 14 and 17 h d^{-1}), shading levels (20, 30, 40, and 60%), and temperatures (10, 15, 20 and 25 °C). A qualitative short-day response was observed in all experiments. Both cultivars took minimum time to flower when grown under 8 h d^{-1}, however, it was significantly delayed when photoperiod decreased. Similarly, days taken to flowering were decreased significantly when plants were grown in 30% shade, which was delayed by increasing shade level (40 and 60%). Temperature also had a significant effect on the developmental phases of flower as above (25 °C) and below (10–15 °C) 20 °C temperature delayed flowering time. The present study also confirms that per day rate of progress to flowering was higher at 8 h d^{-1} photoperiod, in 30% shade level, and at 20 °C temperature. These findings revealed a prospect of plant scheduling of the flowering time of chrysanthemum cultivars grown in long-day photoperiod to extend their marketing period, as the plants remains vegetative. A steady supply of this flowering annual can also be maintained in the market by growing them under different shades. The quality of plants would also benefit from an ideal growing temperature of between 15-20 °C.

Key words: Chrysanthemum, *Chrysanthemum* × *morifolium*, flowering time, photoperiod, shade, temperature, photo-thermal models

Introduction

The chrysanthemum genus belongs to the family Asteraceae and is a widely recognized ornamental plant. It is currently the second most popular flower traded internationally after roses. Its origin is in East Asia, and has great ornamental, medicinal, environmental, and industrial values. It is amongst the most valuable floricultural crops in the world and is extremely popular for its wide range of flower colors. It is grown for the cut flower industry and flowering pots nursery business. It is widely cultivated for indoor and outdoor beautification, fragrance, clean air, and serenity (Bircumshaw and Damp, 1992; Spaargaren and van Geest, 2018; Hadizadeh *et al.*, 2022).

In an ambient environment, flowering plants bloom at the same time each year. One of the most important phases in a plant's life cycle is the transition from vegetative to reproductive growth. This switch is activated by a range of endogenous signals (hormone and carbohydrate) and also environmental stimuli (photoperiod and temperature) that are recognized by the shoot apical meristem (Simpson and Dean, 2002; Thomas, 2006; Fornara *et al.*, 2010; Srikanth and Schmid, 2011). Plant flowering responds to the changing environment, particularly photoperiod and temperature as the season progresses. Based on the light requirement, plants were categorized as long-day, short-day, and day-neutral (Thomas and Vince-Prue, 1997). The floral time response of long-day and short-day plants to photoperiod (Baloch *et al.*, 2009b, 2010, 2011, 2012, 2013b, 2014; Munir *et al.*, 2015a), light intensity (Baloch *et al.*, 2009a; Munir *et al.*, 2017), and temperature (Munir *et al.*, 2004a, 2015b) is reported in many ornamental plants. Duration of light (photoperiod) is measured by the biological clock (circadian rhythm) within the leaves (O'Neil, 1992), and in response, a stimulus is released towards the apex to induce flowering (McDaniel, 1996; Corbesier and Coupland, 2005). Light is also a critical resource for plants, and competition for light under shade affects their growth and development (Munir *et al.*, 2004b; Alhajhoj and Munir, 2016). Plants are not sensitive to light throughout their juvenile and reproductive developmental phases (Adams *et al.*, 2003; Munir *et al.*, 2010; Baloch *et al.*, 2013a). Plant height is also manipulated in an inductive and non-inductive light environment (Baloch *et al.*, 2013c; Munir and Alhajhoj, 2017).

The growth of chrysanthemum is significantly influenced by environmental factors, and year-round production can be achieved in greenhouses by manipulating these conditions (SharathKumar *et al.*, 2021). Depending on the cultivar, chrysanthemum is an obligate short-day plant induced to flower when the photoperiod is 12–13.5 hours or less (McMahon and Kelly, 1999; Higuchi *et al.*, 2013). Flower opening of chrysanthemum *cv.* Zembla was delayed with an increase in photoperiod (Kumar and Singh, 2017). The exposure of *cv.* Indian Summer to 8 h d^{-1} photoperiod and low temperature hastened inflorescence bud initiation (Schwabe, 1950). The high temperature (27–34 °C), however, impacts on flowering and the quality of chrysanthemum and other cut flowers (Whealy *et al.*, 1987; Karlsson *et al.*, 1989; Pearson *et al.*, 1993). Flower initiation was enhanced by 8 h d^{-1} photoperiod and delayed by extending it by an incandescent light (Kahar, 2008). Sajid *et al.* (2016) reported that chrysanthemum took minimum days to

flower at 9 h d^{-1} photoperiod. Long-day and high temperatures significantly affect flowering in chrysanthemums (Nakano *et al.*, 2015). However, the summer–autumn flowering cultivars such as *cv.* Floral Yuuka bloom on both long-days and short-days, though it flowers earlier in the short-day environment (Sun *et al.*, 2017).

It is possible to determine whether the given cultivars are suitable for particular photo-thermal conditions by comprehending the variation in flowering time of chrysanthemum cultivars and their responses to light and temperature. The purpose of this study was to use photo-thermal models to assess how two chrysanthemum cultivars respond to various photoperiod, shade, and temperature regimes in terms of flowering time and flower development.

Materials and methods

Experiment 1. Effect of different photoperiods on flowering: Terminal rooted cuttings of chrysanthemum cvs. Crimson Glory and Snowscape were taken from the well-established mother plants and planted in 9 cm (370 mL) plastic pots. These plants remained in the glasshouse for two weeks at 20±2 °C to get established. After two weeks, plants of both cultivars were placed in four photoperiod-controlled chambers (1.3 × 2.9 m) sealed from external light source, which provided 8, 11, 14, and 17 h d^{-1} photoperiods. Ten plants of each cultivar were placed in each photoperiod compartment. Plants remained for 8 h (from 08:00 to 16:00 h) in a glasshouse adjacent to the four photoperiod chambers where they were exposed to 8 h natural daylight at a set-point temperature of 20±2 °C. Ventilation occurred automatically at 2 °C above set-point temperature. At 16:00 h each day, all plants on trolleys were moved into the photoperiod chambers where they remained until 08:00 h the following morning. Photoperiod within each of the chambers was extended by three 60W tungsten light bulbs and two 36W white fluorescent tube lights (60% tungsten calculated by nominal wattage) providing a light intensity of 7 µmol m^{-2} s^{-1} (60:40) (Munir *et al.*, 2015a). Light intensity inside the photoperiod chambers were measured using a quantum sensor (LiCor Inc., Lincoln, NE, USA) attached to a Comark 122 DC microvoltmeter (Comark Instruments, Norwich, Norfolk, UK). HOBO MX1104 Temp/RH/Light data logger (Onset Computer Corporation, Bourne, MA, USA) was installed inside glasshouse chambers to record microclimate after every 15s.

Experiment 2. Effect of different shades on flowering: Terminal rooted cuttings of the two chrysanthemum cultivars were established as described in Experiment 1. Ten randomly selected established plants were placed on moveable trolleys covered from all sides with four shading nets (20, 30, 40, and 60% shade). All shading nets were green in colour (WireFence, Manchester, M19 3DH, UK). Plants remained in the glasshouse where they were exposed to natural daylight at a set-point temperature of 20±2 °C. Shade percentage within the shading nets were measured using a quantum sensor attached to a Comark 122 DC microvoltmeter. The detail of the glasshouse setup is already given in Experiment 1.

Experiment 3. Effect of different temperatures on flowering: The crop husbandry was same as mentioned in Experiment 1. The established potted cuttings were transferred to the four temperature-controlled glasshouse compartments (3.7 × 7 m) set to provide minimum temperatures of 10, 15, 20, and 25 °C and automatically vent opened when the temperature reached 2 °C above the set-point. These plants were grown under ambient daylight. Temperatures were recorded inside the glasshouse compartments using HOBO data loggers, 1.85 m above ground level, and recorded after every 15s. The air conditioning units were used to maintain 10 and 15 °C temperatures.

After potting, the plants were watered when necessary and compound fertilizer (5-8-11+2 NPK+Mg) was applied @ 70 g m^{-2}. Pots were gradually re-spaced to avoid mutual shading effect. The present study was focused on the flowering time, therefore, the numbers of days taken to first flower opening from emergence were recorded at harvest and the data were analysed using GenStat-11 (General Statistics Software, VSNi International Ltd., Hemel Hempstead, UK). The rate of progress to flowering ($1/f$) per day is represented as the reciprocal of the time to flowering, which was analysed using the following photo-thermal model:

$1/f = a + b$x (where a and b are constants and x is the environmental factor)

Independent data of each experiment were used to test the validity of the flowering model $1/f = a + b$x using environmental factor x as P, S, and T. For each data set, the model was solved using a frequentative computational procedure against running means of photoperiod (P), shade levels (S), and temperature (T), up to the day on which the product of the average daily contributions to flowering equaled one (determined as the days from sowing multiplied by the average daily progress to flowering). The accuracy of the predicted data was fitted against the actual data to validate the model (Munir *et al.*, 2015a).

Results

Experiment 1. Effect of different photoperiods on flowering: The outcomes confirmed a statistically significant ($P<0.05$) difference among four photoperiods regarding flowering time (Fig. 1A), which was reduced when plants of chrysanthemum cvs. Crimson Glory and Snowscape were grown in short-day environment (8 h d^{-1}) whereas it was enhanced significantly in long-day environment (17 h d^{-1}). Plants grown in 8 h d^{-1} photoperiod flowered after 73 (cv. Crimson Glory) and 63 (cv. Snowscape) days as compared to 17 h d^{-1} photoperiod plants, 155 days for *cv.* Crimson Glory and 147 days for *cv.* Snowscape. Similarly, plants grown in 14 and 11 h d^{-1} photoperiod chambers took more time compared to the plants in 8 h d^{-1} photoperiod chamber. Rate of progress to flowering (Figure 1B) attribute was inversely proportional to the days to flowering that was higher under inductive environment (8 h d^{-1}) and gradually decreased with the increase in photoperiod from 11 to 17 h d^{-1}.

Data of rate of progress to flowering were analysed using the following polynomial model:

$1/f = a + bP + cP^2$

The best fitted model describing the effects of mean photoperiod (P) on the rate of progress to flowering ($1/f$) can be written as:

For *cv.* Crimson Glory:

$1/f = 0.030260\ (\pm 0.003059) + [-0.002673\ (\pm 0.000516)\ P + 0.000076\ (\pm 0.000021)\ P^2$ Eq. 1

($r^2 = 0.96$, d.f. 39)

For *cv.* Snowscape:

$1/f = 0.042050\ (\pm 0.0039966) + [-0.004316\ (\pm 0.000674)\ P + 0.000132\ (\pm 0.000027)\ P^2$ Eq. 2

($r^2 = 0.96$, d.f. 39)

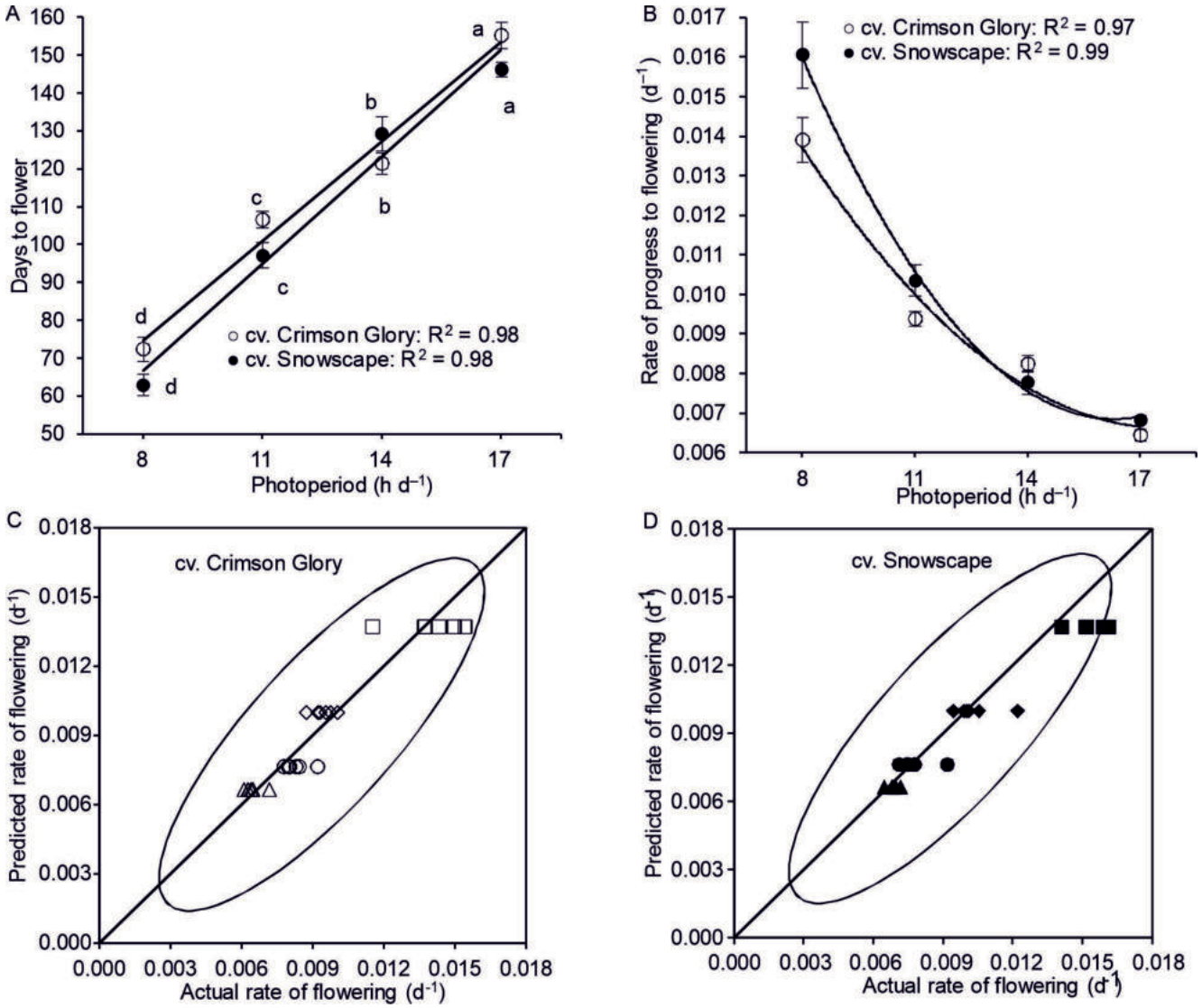

Fig. 1. Effects of different photoperiods (8, 11, 14 and 17 h d^{-1}) on (A) flowering time and (B) rate of progress to flowering ($1/f$) of Chrysanthemum cvs. Crimson Glory and Snowscape. Each point represents the mean of 10 replicates. Vertical bars on data points (where larger than the points) represent the standard error within replicates. The relationship between the actual rate of progress to flowering against those fitted by the photo-thermal model ($1/f = a + bP + cP^2$) for cvs. (C) Crimson Glory and (D) Snowscape grown under 8 (□, ■), 11 (◊, ♦), 14 (○, ●), and 17 h d^{-1} (Δ, ▲) photoperiods. The solid line in (C) and (D) is the line of identity.

Experiment 2. Effect of different shades on flowering: Time taken to flowering was significantly ($P<0.05$) affected by different shading levels (Fig. 2A). Chrysanthemum cvs. Crimson Glory and Snowscape as short-day plant took minimum time 65 and 52 days to flower, respectively when grown under 30% shade, which was increased in 40 and 60% shades. Similarly, rate of progress to flowering was increased when shade levels were increased from lower shade level to the higher shades, *i.e.*, the rate of progress to flowering was higher in 30% shade level, which decreased at 40 and 60% shade levels (Fig. 2B).

Data of rate of progress to flowering were analysed using the following polynomial model:

$$1/f = a + bS + cS^2$$

The best fitted model describing the effects of mean shade levels (S) on the rate of progress to flowering ($1/f$) can be written as:

For *cv.* Crimson Glory:

$1/f$ = 0.014465 (±0.002047) + 0.000041 (±0.000112) S + [–0.000002 (±0.000001) S^2 Eq. 3

(r^2 = 0.73, d.f. 39)

For *cv.* Snowscape:

$1/f$ = 0.017817 (±0.003014) + 0.000067 (±0.000165) S + [–0.000002 (±0.000001) S^2 Eq. 4

(r^2 = 0.74, d.f. 39)

Experiment 3. Effect of different temperatures on flowering: A curvilinear response of flowering time to temperatures was observed, which was significantly ($P<0.05$) varied in 10, 15, 20, and 25 °C temperature regimes (Fig. 3A). Chrysanthemum cvs. Crimson Glory and Snowscape took minimum time to flower (65 and 57 days, respectively) when grown in 20 °C temperature, which was increased to 98 and 89 days, respectively when grown at 10 °C and 88 and 79 days, respectively when grown at 25 °C. Both high (25 °C) and low (10-15 °C) temperatures increased flowering time. Similarly, rate of progress to flowering was increased when temperature was increased linearly from 10 to 20 °C, which was higher at 20 °C. It was decreased afterwards

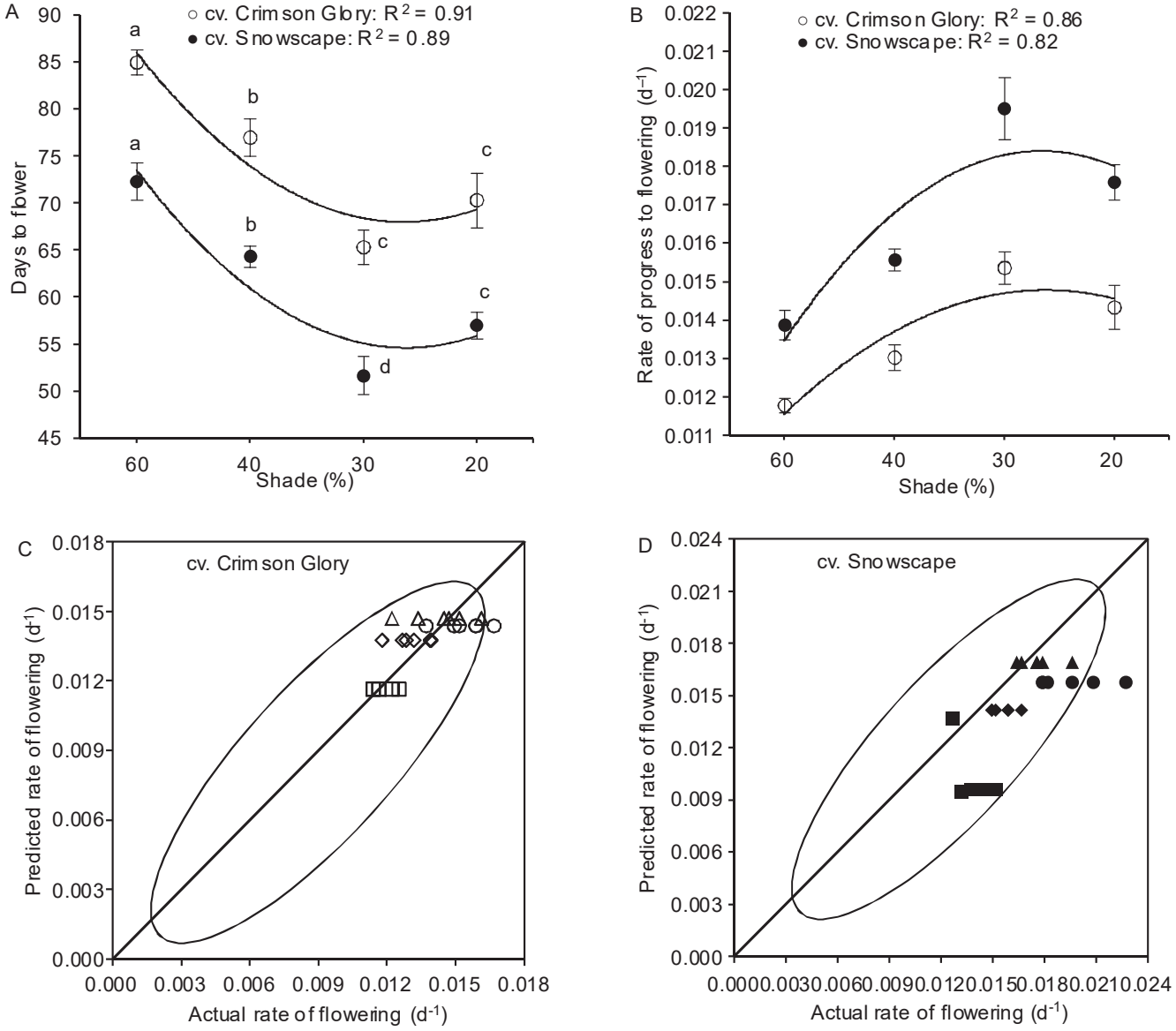

Fig. 2. Effects of different shade levels (20, 30, 40 and 60%) on (A) flowering time and (B) rate of progress to flowering ($1/f$) of Chrysanthemum cvs. Crimson Glory and Snowscape. Each point represents the mean of 10 replicates. Vertical bars on data points (where larger than the points) represent the standard error within replicates. The relationship between the actual rate of progress to flowering against those fitted by the photo-thermal model ($1/f = a + bS + cS^2$) for cvs. (C) Crimson Glory and (D) Snowscape grown under 20 (Δ, ▲), 30 (○, ●), 40 (◊, ♦), and 60% (□, ■) shade levels. The sold line in (C) and (D) is the line of identity.

at 25 °C. The lowest rate of progress to flowering was recorded at 10 and 25 °C (Fig. 3B).

Data of rate of progress to flowering were analysed using the following polynomial model:

$$1/f = a + bT + cT^2$$

The best fitted model describing the effects of mean temperature (T) on the rate of progress to flowering ($1/f$) can be written as:

For *cv.* Crimson Glory:

$$1/f = -0.006819\ (\pm 0.003299) + 0.002281\ (\pm 0.000406)]\ T + [-0.000061\ (\pm 0.000011)\ T^2 \quad \text{Eq. 5}$$

($r^2 = 0.79$, d.f. 39)

For *cv.* Snowscape:

$$1/f = -0.010266\ (\pm 0.003836) + 0.002888\ (\pm 0.000472)]\ T + [-0.000078\ (\pm 0.000013)\ T^2 \quad \text{Eq. 6}$$

($r^2 = 0.81$, d.f. 39)

Above equations (1–6) are based on individual arithmetic means of respective factors, although all data were originally tested. The values in parenthesis show the standard errors of the regression coefficients. The outcome of the photo-thermal model indicated that photoperiods, shade levels, and temperature regimes had significant effects on the rate of progress to flowering. For validation of the model actual data of rate of progress to flowering were plotted against the predicted ones to develop a fitted relationship and almost all values were successfully plotted near the line of identity, which also showed that the photoperiods (Fig. 1C,D), shade levels (Fig. 2C,D), and temperatures (Fig. 3C,D) had a significant effect on the rate of progress to flowering.

Discussion

A variety of endogenous and external stimuli influence flowering, which is critical for crops (Thomas and Vince-Prue, 1997; Amasino and Michaels, 2010). At the molecular level,

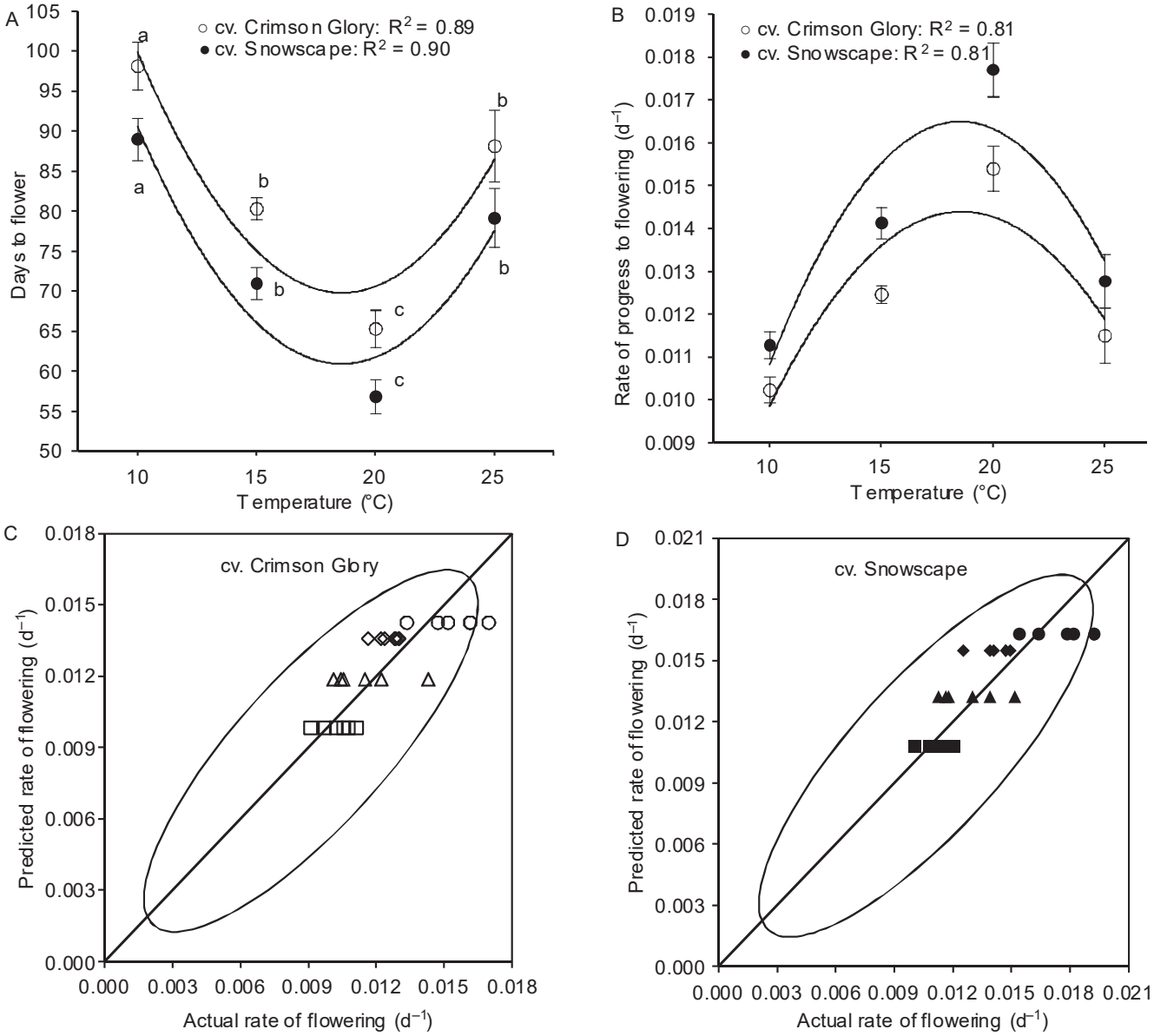

Fig. 3. Effects of different temperatures (10, 15, 20 and 25 °C) on (A) flowering time and (B) rate of progress to flowering ($1/f$) of Chrysanthemum cvs. Crimson Glory and Snowscape. Each point represents the mean of 10 replicates. Vertical bars on data points (where larger than the points) represent the standard error within replicates. The relationship between the actual rate of progress to flowering against those fitted by the photo-thermal model ($1/f = a + bT + cT^2$) for cvs. (C) Crimson Glory and (D) Snowscape grown under 10 (□, ■), 15 (◊, ♦), 20 (○, ●), and 25 °C (Δ, ▲) temperatures. The sold line in (C) and (D) is the line of identity.

the timing of flowering is controlled by interactions between gene networks that are responsive to various endogenous and/or exogenous signals (Wang *et al.*, 2011). Plants sense photoperiodic information to regulate developmental processes and anticipate environmental change (Shim and Imaizumi, 2015), ensuring that the transition occurs at the appropriate time. The appropriate time for ornamental plants to flower is a major issue (Jung and Müller, 2009). A technique for plant adaptation called photomorphogenesis enables plants to adjust to their environment. Light directly influences this relationship, which is controlled by light receptors such as phytochromes, which are sensitive to red light (600-700 nm), cryptocryptochromes, and phototropins, which are sensitive to blue light (415-455 nm). The signals sent by light receptors cause physiological and metabolic changes in many developmental pathways (Kami *et al.*, 2010; Yu *et al.*, 2010; Xu *et al.*, 2015).

The findings from the experiments mentioned above can be summed up as follows: It is evident that the flowering time and rate of chrysanthemum (cvs. Crimson Glory and Snowscape) was accelerated significantly at 8 h d^{-1} short-day photoperiod, 30% shade level, and 20 °C temperature. In *cv.* Zembla, a short-day photoperiod shortened flower opening time, whereas a long-day photoperiod delayed flowering time from 6 to 15 days (Kumar and Singh, 2017). When compared to short-day environments, long-day conditions caused the Yellow Reagan and White Reagan cultivars to flower 42 days later (Kazaz *et al.*, 2010). Higuchi *et al.* (2012) suggested that at least two different phytochrome responses were involved in the chrysanthemum's flowering. According to Abrol *et al.* (2018), the production of chrysanthemum cultivated under short-day photoperiodic conditions does not require the application of growth regulator to enhance flowering time.

One of the most crucial environmental factors for crop physiology and biochemistry is light intensity (Yang *et al.*, 2018). A certain light intensity is required by plants for growth; light levels that are too high or too low may inhibit photosynthesis (Shafiq *et al.*, 2021). The light intensity can be reduced by using shading nets. In response to shade, plants typically lengthen stem-like structures like hypocotyls and leaf petioles and orienting their leaves higher upward (Ruberti *et al.*, 2012). Furthermore, plants that were grown in shade also reduced branching (Yang *et al.*, 2018). In long-day plants flowering time is increased by reducing light intensity under shade conditions (Munir *et al.*, 2004b; Munir *et al.*, 2015a; Alhajhoj and Munir, 2016). The present findings indicated that flowing time and rate was higher when both chrysanthemum cultivars were placed under 30% shade, which were significantly affected under 40 and 60% shade levels. Strawberry flowering was delayed when plants were either kept in 30% red or blue photoselective shade nets (Takeda *et al.*, 2010). These results are in contradiction with the current study, which may be due to the different species or by the colour and composition of the net, as a conventional green colour net was used in the current study. Light irradiance between 16-45 W m^{-2} decreased flowering time of various cultivars of chrysanthemum, whereas plants grown below 6 W m^{-2} irradiance remained vegetative (De Jong, 1986).

The leaf unfolding rate and time to flowering are two developmental processes that are significantly influenced by temperature. The results of present study indicated that flowering time significantly varied at different temperatures and 20 °C was found ideal temperature for both cultivars. Ploeg and Heuvelink (2006) reported that the optimum temperature for chrysanthemum flowering is between 17 and 22 °C depending on the cultivar (De Jong, 1984). Pearson *et al.* (1993) stated that the rate of progress to flowering of different chrysanthemum cultivars increased linearly with increasing light integral and effective temperature. Temperatures above 20 °C had minimal impact on the time of floral initiation, however temperatures below this resulted in a significant delay in floral initiation (20.5 days at 9.6 °C). The inflorescences developed most rapidly at 20.2 °C once they were initiated, but unlike the process of flower initiation, subsequent flower development was delayed by both warmer and cooler temperature regimes (Adams *et al.*, 1998). Results reported by Nozaki and Fukai (2008) showed that under short-day conditions, two distinct high-temperature (20 and 30 °C) events take place in the shoot apex of spray chrysanthemums. High temperatures delayed flowering by slowing two processes: first, the rate of inflorescence development after the budding stage reduced, and second, the time taken to reach the bud break stage was prolonged.

In conclusion, the application of photo-thermal models offers a promising approach for optimizing chrysanthemum cultivation and enhancing the resilience of this economically significant ornamental crop in response to changing environmental conditions. By elucidating the multifaceted relationships between environmental factors and flowering dynamics, this study paves the way for informed decision-making in chrysanthemum production, contributing to the sustainability and profitability of the floricultural industry.

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