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Original Article

Flowering time response of Nasturtium (*Tropaeolum majus L.)* cultivar '*Empress of India*' to photoperiod, light integral and temperature using photo-thermal model

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Abstract

Experiments were carried out to study flowering response of Nasturtium under four distinct controlled photoperiods (8, 11, 14, and 17 $h.d^{-1}$), shading materials (0, 20, 30 and 40%) and five temperature regimes (10, 15, 20, 25, and 30°C). A curvilinear facultative response was observed in all experiments. Cultivar 'Empress of India' took minimum time to flower when grown under a 17 hr-photoperiod (57 days) however, it was significantly ($P<0.05$) increased when photoperiod decreased to 8h (83 days). Similarly, days taken to flowering were increased significantly ($P<0.05$) when plants were grown under low light integrals (40%, 30%, and 20% shade). Flowering was delayed up to 17 days when plants were grown under intense shade (40%). Temperature also had a significant effect on the developmental phases of flower as low temperature (10°C) decreased flowering up to 46 days as compared to plants grown at 25°C. However, the quality of flowering plant (including plant height, spread and leaf number, data not shown) was decreased at higher temperatures (25 and 30°C). Best quality plants were obtained when grown between 15 to 20°C. These findings revealed a prospect of plant scheduling of the flowering time of Nasturtium grown under short day photoperiod to extend their marketing period. A steady supply of this flowering annual can be maintained in the market by grown them under different shades (low light integrals). Similarly, an optimum growing temperature between 15-20°C would also be a beneficial effect on the quality of plant in the market.

Keywords: nasturtium, *Tropaeolum majus L.*, photoperiod, light integral, temperature, shade, flowering time

1. Introduction

Nasturtium (*Tropaeolum majus L.*) is also known as Indian Cress or Monks Cress and is native to the South American Andes from Bolivia to Columbia. It is widely cultivated, both as an ornamental and as a medicinal plant. This herbaceous annual adds up rainbows of cheerful colour in annual beds and borders. Its trailing cultivars are used on low fences or trellises, on a gravelly or sandy slope, or in a hanging container. Nasturtiums are not only grown for their flowers but also because both their leaves and flowers are edible and used in salads, revealing a delicately peppery taste (Huxley *et al.,* 1992). As medicinal plant, it contains glucosinolates, a mustard-oil glycoside called glycotropeoline, which have antibiotic, antifungal, antiviral and antibacterial properties to treat infections, colds, flu and digestive upsets. Some small amounts of usable iodine are also present, helping to regulate metabolism (Kunkel, 1984; Duke *et al.,* 2002; Niizu and Rodriguez-Amaya, 2005). Major anthocyanins,

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ascorbic acid content, total phenolic content and the radical scavenging activity were also reported by Garzóna and Wrolstadb (2009).

Nasturtiums are grown in summer and do well in full sun or light shade (Brickell, 2008). It is well documented that flowering is the end result of physiological processes, biochemical sequences, and gene action, with the whole system responding to the influence of environmental stimuli and their duration (Zheng *et al.,* 2006) which is not comprehensively studied in Nasturtium. Evans (1969) referred flowering as the inductive processes occurring in the leaf, mediated by the photoreceptor, phytochrome that leads to the initiation of flowering at the meristem (evocation). Inductive processes occur in the leaf (O'Neil, 1992) and result in floral initiation in which the apical meristem changes towards floral development (McDaniel *et al.,* 1992). When the apical meristem of the plant is committed to flowering, its fate becomes irreversible (Bernier, 1988), although flower or inflorescence reversion to vegetative growth can also occur spontaneously in some species. This condition can be caused if plants are transferred to certain specific photoperiod or temperature regimes, which favor vegetative development (Tooke *et al.,* 2005).

The timing of the transition from juvenile to reproductive development of a plant is of fundamental and applied interest. The genetic variation present within the plant with an early or late flowering phenotype greatly affected by both environmental (photoperiod and temperature) and endogenous factors (gibberellins) that influence the transition to flowering. The genetic, molecular and physiological studies have led to identify different components involved, such as elements of photoperception and the circadian rhythm (Koornneef *et al.,* 1998). Many flowering plants use a photoreceptor protein (light absorbing pigments), such as phytochrome (red and far red), cryptochrome and phtototropins (blue and UV), to sense seasonal changes in day-length (photoperiod), which they take as signals to flower (Weller and Kendrick, 2008). Thomas and Vince-Prue (1997) categorized the photoperiodic response of flowering into three main groups: short-day plants (SDPs) in which flowering is hastened by longer nights; long-day plants (LDPs) where shorter nights promote flowering; and day-neutral plants (DNPs) which flower irrespective to day-length. SDPs and LDPs can be further classified as obligate (species that require a specific minimum or maximum photoperiod for flowering) and facultative (flowering process is hastened by a specific minimum or maximum photoperiod).

Findings of a study conducted in ambient environment showed that late sowing of LDPs (1st to 15th July) significantly delayed flowering time because they received SD and less light integrals during flower induction phase (Baloch *et al.,* 2009a). Similar response was observed when LDPs were grown under control photoperiod conditions (Baloch *et al.,* 2009a; Baloch *et al.,* 2011). Seasonal variation in light integrals also affect flowering process such as optimum rate of flowering was observed in cyclamen when they were grown under 12 mol $d^{-1} m^{-2}$ (Karlsson, 2001). In another study inbreeds of *Antirrhinum majus* did not flower under low light intensity (4000 lux) while at higher light intensity (30000 lux) all plants flowered after 110 days (Cremer *et al.,* 1998). *Antirrhinum* cultivar Chimes White flowered earlier when grown under ambient day-length however the flowering time increased with the decrease in light integrals under shades (Munir *et al.,* 2004b). Similarly, Baloch *et al.* (2009c) reported that flowering time was significantly delayed when LDPs were grown under shades.

Temperature has a direct effect on the rate of many chemical reactions, including respiration which is the process responsible for growth and development of plants including photosynthesis (Adams *et al.,* 1997). The different temperature requirements of a cultivar, not only determine the climate in which they are best produced, but also the season most suited to them. Optimum temperature for horticultural crops refers to best productivity or quality plants and not necessarily the fastest growing plants. By understanding the relationship between plant growth rate and temperature, a grower can often increase or slow down crop growth, in order to get ready the specific crop at the desired time. Temperature has been shown to have different effects on the flowering and bedding time of genotypically different inbred lines of *Antirrhinum*. For most cultivars, a temperature of 25°C almost halved the flowering time compared to a 12°C temperature (Edwards and Goldenberg, 1976; Munir *et al.,* 2004a). In another study, it has been revealed that flowering time cannot be enhanced by temperature but it was more likely the concentration of CO_2 (330 ppm) to hasten phenology in long-day species (Johnston and Reekie, 2008). No proper research has been done on Nasturtium to observe its response towards the environmental stimuli. Therefore, present study has been designed to determine the flowering response of Nasturtium to photoperiod, light integral and temperature under temperate (Reading, UK, 51°27' N, 0°58' W) ecological conditions.

2. Materials and Methods

2.1 Experiment 1: Effect of different photoperiods on flowering time

The objective of this experiment was to determine the flowering response of Nasturtium cv. 'Empress of India' grown under four photoperiods. Seeds were obtained from Thompson and Morgan, UK. and were sown into module trays (P135, volume per cell 20 ml; Plantpak Ltd., Maldon, UK.) containing SHL (William Sinclair Horticulture Ltd., Lincoln, UK.) peat-based seed modular compost at the University of Reading (51°26´ N). Seed trays were placed in an environment-controlled growth room at 20±2°C temperature providing lighting using a mixture of warm white fluorescent and tungsten bulbs (6.3% tungsten calculated by nominal wattage) 72 mmmol m^{-2} s^{-1} (Photosynthetic Photon Flux Density, PPFD) at plant height with a 16 $h.d^{-1}$ photoperiod. After 70% seed germination, ten randomly selected plants were potted into 9 cm pots (370 ml volume) containing SHL

peat based potting compost and perlite (3:1 v/v) and were placed in four photoperiod chambers (1.3 m × 2.9 m) sealed from external light source which provided 8, 11, 14, and 17 h.d^{-1} photoperiods and 20±2°C night temperatures. Plants remained for 8h (from 08:00 to 16:00 hrs) in a glasshouse adjacent to the eight chambers where they were exposed to natural daylight at a set-point temperature of 20±2°C. Ventilation occurred automatically at 2°C above set point temperature. At 16:00 hrs each day, all plants on three shade trolleys were moved into the photoperiod chambers where they remained until 08:00 hrs the following morning. Photoperiod within each of the chambers was extended by three 60 W tungsten light bulbs and two 36 W white fluorescent tube lights (60% tungsten calculated by nominal wattage) providing a light intensity (PPFD) of 5 mmmol m^{-2} s^{-1} (60:40) (Adams *et al.,* 1997; Munir, 2003). Light intensity inside the photoperiod chambers were measured using a quantum sensor (Li-Cor) attached to a Comarck 122 DC microvoltmeter. In the glasshouse compartments K type thermocouples were connected to a Campbell CR10 (Campbell Scientific Inc, Logan, UK.) data logger to record temperature after every 15s and stored the hourly average. Tube solarimeters (in house manufacture, Szeicz *et al.,* 1964) were positioned about three meters above the ground to measure the ambient light transmission into the glasshouse.

2.2 Experiment 2: Effect of different light integrals (shades) on flowering time

The aim of experiment was to find out the effect of different light integrals (shading material) on flowering time of Nasturtium cv. 'Empress of India'. Seeds were raised in modular trays and the germination chamber was similar as mentioned in Experiment 1. After 70% germination, ten randomly selected plants were potted (9 cm pots) and placed on moveable trolleys covered from all sides with three shading nets (20, 30, and 40% shade). Ten plants were also grown as control (without shade) for cross comparison with the plants grown under shade. Plants remained for 8 hrs (from 08:00 to 16:00 hrs) in a glasshouse adjacent to photoperiod chamber where they were exposed to natural daylight (8.26 MJ m^{-2} d^{-1}) at a set-point temperature of 20±2°C. Ventilation occurred automatically at 2°C above set point temperature. At 16:00 hrs each day, all plants in Experiment 2 on three shade trolleys were moved into the 17 h.d^{-1} photoperiod chamber for photosynthesis purpose where they remained until 08:00 hrs the following morning (Adams *et al.,* 1997; Munir, 2003). Photoperiod chamber detail is already given in Experiment 1. Shade percentage within the shading nets were measured using a quantum sensor (Li-Cor) attached to a Comarck 122 DC microvoltmeter. Same glasshouse was used as mentioned is Experiment 1 where K type thermocouples were connected to a Campbell CR10 data logger to record temperature and tube solarimeters were used to measure the ambient light transmission into the glasshouse.

2.3 Experiment 3: Effect of different temperatures on flowering time

This experiment was carried out to establish the flowering response of Nasturtium to a wide range of temperatures. Seeds of cv. 'Empress of India' were sown in seed trays (P135) containing SHL peat-based compost and were placed in the same environment-controlled growth room as described in the previous experiment. After 70% seed germination, plants were potted into 9 cm pots containing SHL peat based potting compost and perlite (3:1 v/v). Ten randomly selected plant pots were transferred to the five temperature-controlled glasshouse compartments (3.7 m × 7 m) set to provide minimum temperatures of 10, 15, 20, 25, and 30°C and automatically vent 2°C higher. These plants were grown under ambient daylight (8.57 MJ m^{-2} d^{-1}) and day-length (Dawn to Sunset, 18.5 hrs). Temperatures were recorded inside the glasshouse compartments using a sensor situated in an aspirated screen attached to a data-logger, 1.85 m above ground level. In five temperature controlled compartments PT100 4 wire platinum resistance sensors were connected to a data-logger (Datataker 500, Data Electronics, Letchworth Garden City, UK.). The data-logger recorded the temperature every 15s and stored the hourly averages. Tube solarimeters were positioned about three meters above the ground in each temperature compartment to measure the light transmission into the glasshouse. In the 10 and 15°C compartments, temperature control was carried out by the use of air conditioning units.

Seedlings in seed trays were irrigated with tap water (without any added nutrients). After potting, the plants were watered when necessary and nutrients (182 ppm N; 78 ppm P; 150 ppm K) were given in the form of a soluble fertilizer, Sangral 111 (William Sinclair Horticulture Ltd., Lincoln, U.K.) at pH 5.7 and conductivity of 1500 µS cm^{-2}. Pots were gradually re-spaced to avoid mutual shading effect. Present study was focused on the floral time (the perception of plant to the external signal and commitment to flower) and not on the further emergence of flowers on same plant which otherwise restricted the application of photo-thermal model. Therefore, the numbers of days taken to first flower opening from emergence (corolla fully opened) were recorded at harvest and the data were analyzed using GenStat-11 (Lawes Agricultural Trust, Rothamsted Experimental Station, U.K. and VSN International Ltd. UK.). The rate of progress to flowering ($1/f$) per day is represented as the reciprocal of the time to flowering, which was analyzed using the following linear photo-thermal model:

$$1/f = a + bx$$

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 $1/f = a + bx$ using environmental factor x as P, T and LI. For each data set, the

model was solved using a frequentative computational procedure against running means of average daily temperature, photoperiod and light integral, 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.

3. Results

3.1 Experiment 1: Effect of different photoperiods on flowering time

Findings of the first experiment confirmed a statistically significant ($P<0.05$) difference among four photoperiods regarding flowering time (Figure 1A) which was enhanced when plants of Nasturtium cv. 'Empress of India' were grown under short day environment (8 h.d^{-1}) whereas it was decreased significantly under long day environment (17 h.d^{-1}). Plants grown under 8 h.d^{-1} photoperiod flowered after 83 days as compared to 17 h.d^{-1} photoperiod plants (57 days). Similarly, plants grown under 14 and 11 h.d^{-1} photoperiod flowered after 63 and 72 days from emergence respectively. Rate of progress to flowering (Figure 1B) was inversely proportional to the days of flowering that was higher under inductive environment (17 h.d^{-1}) and linearly decreased with the decline of photoperiod. Data of rate of progress to flowering were analyzed using the following model:

$$1/f = a + bP$$

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

$$1/f = 106.49\ (\pm 3.66) + [-2.997\ (\pm 0.28)]\,P \qquad \text{Eq. 1}$$
$$(r^2 = 0.99,\ \text{d.f. } 39)$$

3.2 Experiment 2: Effect of different light integrals (shades) on flowering time

Time taken to flowering was significantly ($P<0.05$) affected by different shading materials (Figure 2A). Nasturtium as LD plant obviously took minimum time (45 days) to flower when grown under control (no shade) which was linearly increased in 20 (50 days), 30 (57 days) and 40% (62 days) shades. Similarly, rate of progress to flowering was increased when light integrals were increased from higher shade level to the lower ones i.e. the rate of progress to flowering was higher in control treatment which gradually decreased at 20, 30 and 40% shade (Figure 2B).

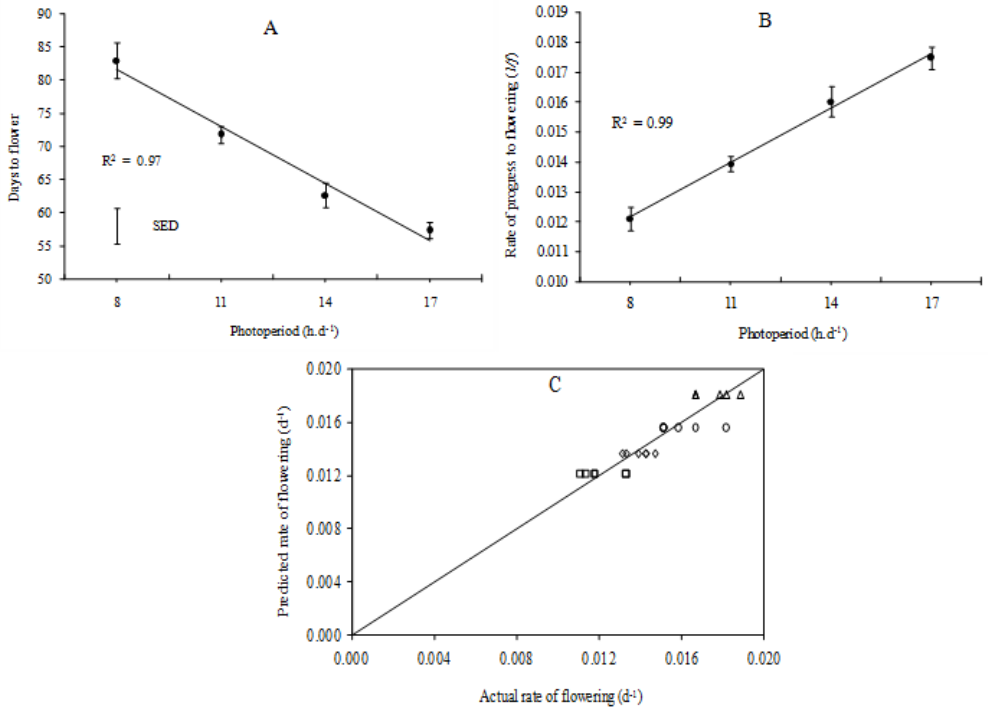

Figure 1. Effects of different photoperiods (8, 11, 14, and 17 h.d^{-1}) on (A) flowering time and (B) rate of progress to flowering ($1/f$) of Nasturtium cv. 'Empress of India'. Each point represents the mean of 10 replicates. Vertical bars on data points (where larger than the points) represent the standard error within replicates whereas vertical bar showing standard error of difference (SED) among means. (C) The relationship between the actual rate of progress to flowering against those fitted by the flowering model ($1/f = a + bP$) for Nasturtium grown under 8 (□), 11 (◊), 14 (○), and 17 (Δ) h.d^{-1} photoperiod. The solid line is the line of identity.

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

$$1/f = a + bLI$$

The best fitted model describing the effects of mean light integrals (*LI*) on the rate of progress to flowering (1/*f*) can be written as:

$$1/f = 43.81\ (\pm 1.45) + 0.4289\ (\pm 0.55)\ LI \qquad \text{Eq. 2}$$
$$(r^2 = 0.99, \text{d.f. } 39)$$

3.3 Experiment 3: Effect of different temperatures on flowering time

A curvilinear response of flowering time to temperatures was observed which was significantly ($P<0.05$) varied in 10, 15, 20, 25, and 30°C temperature regimes (Figure 3A). Nasturtium took minimum time to flower (41 days) when grown in 25°C temperature which was increased to 45 days when grown at 30°C. Plants received lowest temperature took maximum time to flower (91 days) followed by 15°C (65 days) and 20°C (50 days) temperature regimes. Similarly, rate of progress to flowering was increased when temperature was increased i.e. higher rate of progress to flowering was observed at 25 and 30°C temperatures which was decreased with the decrease in temperature and the lowest rate of progress to flowering was recorded at 10°C (Figure 3B).

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

$$1/f = a + bT$$

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

$$1/f = 101.11\ (\pm 5.16) + [-2.085\ (\pm 0.24)]\ T \qquad \text{Eq. 3}$$
$$(r^2 = 0.96, \text{d.f. } 39)$$

Above equations (1-3) 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 this model indicated that photoperiod and light integrals 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 photoperiod (Figure 1C) and light integrals (Figure 2C) had a significant effect on the rate of progress to flowering. However, the values of temperature were somehow away from the line of identity which indicated that the rate of progress to flowering is not temperature dependent (Figure 3C).

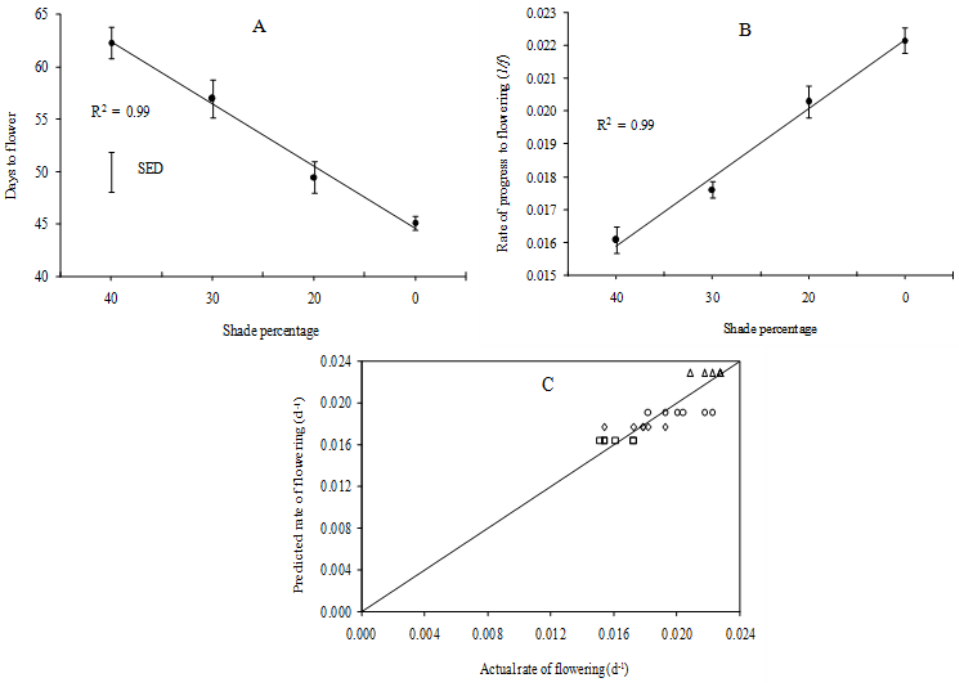

Figure 2. Effects of different shading materials (0, 20, 30, and 40%) on (A) flowering time and (B) rate of progress to flowering (*1/f*) of Nasturtium cv. 'Empress of India'. Each point represents the mean of 10 replicates. Vertical bars on data points (where larger than the points) represent the standard error within replicates whereas vertical bar showing standard error of difference (SED) among means. (C) The relationship between the actual rate of progress to flowering against those fitted by the flowering model ($1/f = a + bLI$) for Nasturtium grown under 40 (□), 30 (◊), 20 (○), and 0% (Δ) of shade levels. The solid line is the line of identity.

4. Discussion

Previously it has been believed that Nasturtium is a LDP at high temperature and DNP at low temperature (Hanan, 1998). However, no appropriate research has been conducted on this important garden and medicinal plant to quantify light duration, light intensity and suitable temperature for a good quality crop. Present study conducted under controlled environment has shown that Nasturtium cv. 'Empress of India' is a facultative LDP and its phenology is also affected by temperature. The LDP response of Nasturtium observed in present study supporting the fact that this plant is from Mediterranean origin where the day-length is much longer and plant originating from this region prefers an open environment with ample sunshine (Summerfield *et al.,* 1997). Moreover, this study also enlightened the promising effect of light integrals which has not been previously reported in this ornamental annual. Nasturtium flowered in all photoperiods however its timing enhanced at minimum photoperiods particularly when received 8 and 11h day-length that delayed flowering up to 26 and 15 days, respectively as compared to 17h day-length. However, plants of same cultivar grown under a 14 hr-photoperiod produced five days late flowers as compared to the 17 hr-ones. Similar results were obtained in Pansy cv. 'Universal Violet' (LDP) where 21 days earlier flowering was observed under controlled environment when grown in 17 hr-photoperiod (Adams *et al.,* 1997). Similarly, flowering time was delayed up to 17 days in a dwarf and early flowering cultivar 'Chimes White' of *Antirrhinum* (LDP) at 8h photoperiod (Munir, 2003). However, this difference was increased to 58 days in late flowering cultivar 'Jackpot' of *Antirrhinum* when grown under 6h day-length (Flint, 1960). It is therefore envisaged that the difference in flowering time could be varied within cultivars of same species even when raised in a similar day-length. Nasturtium grown under inductive environment (LD) induced flowering earlier than those grown below this. The reason of early flowering under inductive environment is due to the stimulation of floral genes which are implicated in the transition of flowering (phase change) are those that encode photoreceptors are triggered by photoperiod for example phytochromes A and B along with the cryptochromes 1 and 2 are involved in the photoperiodic response in *Arabidopsis* (Mouradov *et al.,* 2002). Therefore, any downward alteration in photoperiod from the optimum one affects plants' perception of light and can delay phase change from juvenile to reproductive (flower). Even the quality of light can affect the floral transition such as in *Arabidopsis*, far-red and blue light promote flowering whereas red light inhibits it (Lin, 2000). However, due to limited facilities this sort of further investigation was not carried out in present research.

Flowering time of Nasturtium was also delayed up to 17 days under low light integrals (40% shade). Similar results were obtained in *Eustoma grandiflorum* (Islam *et al.,* 2005),

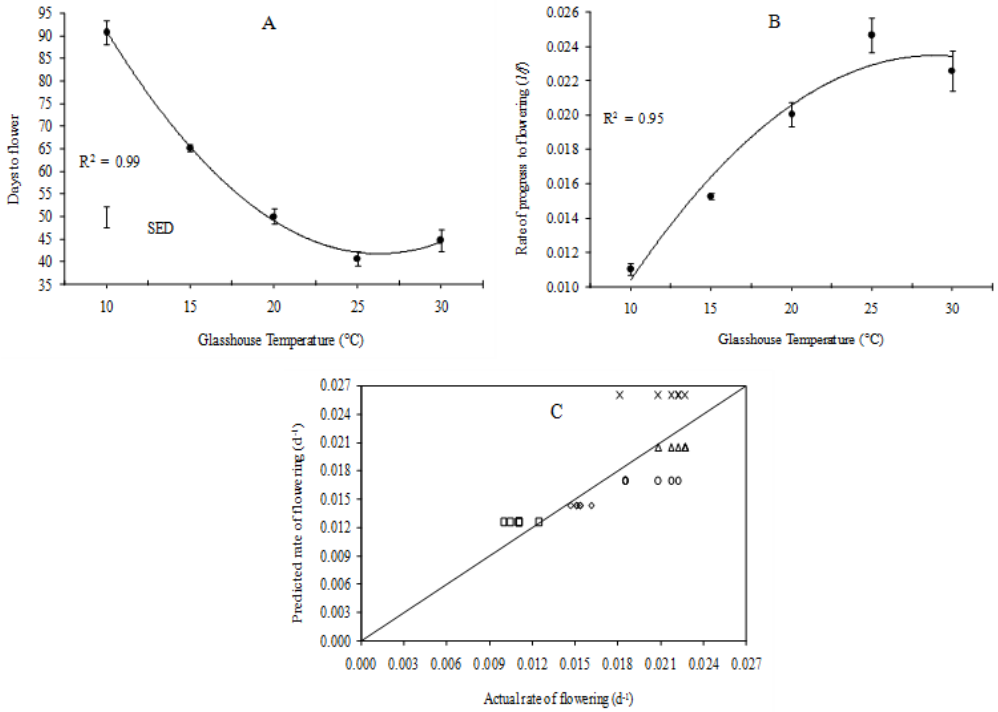

Figure 3. Effects of different temperatures (10, 15, 20, 25, and 30 °C) on (A) flowering time and (B) rate of progress to flowering (*1/f*) of Nasturtium cv. 'Empress of India'. Each point represents the mean of 10 replicates. Vertical bars on data points (where larger than the points) represent the standard error within replicates whereas vertical bar showing standard error of difference (SED) among means. (C) The relationship between the actual rate of progress to flowering against those fitted by the flowering model ($1/f = a + bT$) for Nasturtium grown under 10 (□), 15 (◊), 20 (○), 25 (Δ), and 30°C (×) temperatures. The solid line is the line of identity.

Antirrhinum (Munir, 2003; Munir *et al.,* 2004b), Petunia (Adams *et al.,* 1999) and Pansy (Adams *et al.,* 1997). Floral induction was significantly delayed in all these LDPs when raised under low light integrals. The reason could be the extended vegetative plant growth due to increased assimilate availability under low light. Present piece of information on the effects of light integral on flowering time is of significant value, since growers could control flowering time under controlled environment, and therefore can plan year-round plants scheduling by manipulating the light environment.

A curvilinear temperature response indicated that the flowering time in Nasturtium significantly affected as reported for many other species (Selander and Welander, 1984; Adams *et al.,* 1997; Munir *et al.,* 2004a). Increase in temperature after 25°C showed a four days increase in flowering time which presented 30°C as a supra-optimal temperature for Nasturtium cv. 'Empress of India'. Though plants took minimum time to flower at 25°C but the quality of crop (plant height, spread, flower size, etc.) was severely affected (data not shown). Although, plants grown at 15 and 20°C temperatures delayed flowering time up to 24 and 9 days respectively compared to plants at 25°C, however, we suggest that to obtained better quality plants a temperature between 15 and 20°C will be the optimum. Otherwise, plants can be reciprocally transferred between 15 and 20°C compartments to obtain desirable plant characteristics. Some studies have shown that optimum temperature varies with plant growth and development such as in *Osteospermum jucundum* the optimum temperature for flower induction was lower than for flower development (Pearson *et al.,* 1995). However, in present study it might be the plant developmental phases (leaf number, stem height, size of apical meristem) which were hastened by the temperature (Munir *et al.,* 2004a) and eventually plant become competent in a minimum time to perceive the signal and induce flower (McDaniel *et al.,* 1992).

Besides comparing significant difference among means of each experiment, data were also plotted against predicted values generated through photo-thermal model which indicated a best fit and can be used to predict flowering time for the other Nasturtium cultivars, as it has been used for other plant species (Munir, 2003; Adams *et al.,* 1997). Therefore, cultivars with lower b value (Equation 3, the constant for temperature response) would flower earlier. Similarly, cultivars with low values of b in Equation 1 (the photoperiod response constant) and 2 (the constant for the light integral response) have great possibility to flower in winter conditions. Hence, the general photo-thermal model can be used to improve plant scheduling for year-round production otherwise the glut production of flowering plants in a particular season would be mere wasted. Usually, crop schedules are developed by sowing crops on various dates and estimating their flowering time, but such schedules are often incorrect due to varying ambient environmental factors (Baloch *et al.,* 2009a). Present findings are highly dependent not only on the environmental conditions during the development of a crop, but also the latitude, since photoperiod and light integrals change with latitude. However, by using the photo-thermal model, plant scheduling can be developed for year-round production, since the model considers environmental factors (photoperiod, light integrals and temperature) which vary between different locations.

5. Conclusions

It can be concluded from the present research findings that flowering time in Nasturtium cv. 'Empress of India' can be prolonged under controlled SD non-inductive environment in order to develop plant schedules. However, this LDP can be subjected to LD inductive environment if an early flowering is required. However, flowering time could be delayed under low light integrals and low temperatures. The general photo-thermal model successfully quantified the rate of progress to flower affected by photoperiod, light integrals and temperature, which indicated a possibility of year-round production of Nasturtium if these three environmental factors are sensibly manipulated.

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