Pak. J. Bot., 49(1): 181-186, 2017.

MODIFICATION OF PHOTO-THERMAL MODEL BY ACCOMMODATING LIGHT INTEGRALS USING *ANTIRRHINUM* FLOWERING AND LEAF NUMBER DATA FROM RESTRICTED RANGE OF ENVIRONMENTAL CONDITIONS

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Abstract

The objective of study was to quantify the flowering and leaf number response of *Antirrhinum majus* L. cv. Chimes White to different photoperiods, night temperatures and light integrals using photo-thermal model. Two experiments were conducted i.e. first one in February (under low ambient light integrals) and the second one in June (under high ambient light integrals). In each experiment plants of an early flowering cv. Chimes White were transferred (after 80% germination) to two night temperature suits (set-point temperatures 10 and 20°C), each having four photoperiod chambers (8, 11, 14 and 17 h.d^{-1}). Results revealed that plants flowered earlier at long photoperiod (17 h.d^{-1}), higher mean diurnal temperature (19.2°C in February and 23.4°C in June) and high ambient light integrals (8.26 MJ.m^{-2}.d^{-1}) and *vice versa*. These findings were successfully incorporated in to photo-thermal model, which was not reported before in *Antirrhinum*. The simple linear model hence updated, which would be helpful for growers to predict and quantify flowering time and leaf number (plant quality) of *Antirrhinum* well before their plantation to maintain its continual supply to the market.

Key words: Snapdragon, *Antirrhinum majus* L., Photoperiods, Night temperatures, Light integrals, Photo-thermal model, Flowering time, Leaf numbers.

Introduction

Photoperiod and temperature are important environmental signals to determine the rate of growth and development in plants (El-Keblawy *et al*., 2015; Munir *et al*., 2015). These factors not only signify the seasonal changes but also trigger various physiological processes to assist plants to fix carbon into organic matter that is essential for their survival (Toledo-Ortiz *et al.,* 2014; Khalekuzzaman *et al*., 2015). In addition to their direct effects on plant growth, they provide important immediate and predictive cues for plants to ensure optimal development both spatially and temporally (Franklin *et al.,* 2014).These factors are also involved in floral induction process. For the best possible manipulation of these factors, a number of mathematical models have been introduced in the ornamental industry, which improve crop management and allow their steady supply to the market (Adams *et al.*, 1996).

As a facultative long day plant (LDP), the rate of progress to flowering in *Antirrhinum* is advanced incrementally when subjected to increasing photoperiods and temperatures (Munir *et al.,* 2004; Baloch *et al.,* 2011; Munir *et al*., 2015). Previous study suggested that different temperatures have curvilinear effect on rate of development of flowering in *Antirrhinum* (Munir *et al*., 2015). The rate of development to flower can be represented as the reciprocal of the time to flowering (Roberts & Summerfield, 1987). According to the following linear function the rate of flowering ($1/f$) can be related to the mean photoperiod (Hadley *et al.,* 1984):

$$1/f = a + bTe + cP \qquad \text{Eq. 1}$$

where a, b, c are constants, P is photoperiod (h.d^{-1}) and Te is effective temperature (°C)

In LDP as photoperiod increases the rate of progress to flowering also increases, and so c in Eq. 1 is positive. The opposite would be the case for SDP (Adams *et al.,* 1997a and 1998). In most cases there is no interaction between temperature and photoperiod as shown in Eq. 1. However, interaction between temperature and photoperiod (TeP) was determined by Adams *et al.* (1997b) in trailing petunia and so in this case Eq. 1 became

$$1/f = a + bTe + cP + dTe\,P \qquad \text{Eq. 2}$$

The photo-thermal model in Eq. 1 and 2 assumes that plants are equally sensitive to photoperiod throughout their development. Moreover, only two environmental factors (photoperiod and temperature) are included in the above photo-thermal model. However, Munir *et al*. (2015) observed 3-6 days difference in flowering time of *Antirrhinum* due to 0.9 MJ.m^{-2}.d^{-1} difference in light integrals when experiments were conducted in two consecutive years in the same month (June). Keeping in view the importance of photoperiod, temperature and light integrals in the above linear models for the prediction of flower and leaf development, two experiments were conducted in two consecutive but different time of the years (February and June) to investigate the response of *Antirrhinum* cv. Chimes White to varied photoperiods, night temperatures and natural light integrals, which was not previously studied.

Materials and Methods

The study was conducted at the University of Reading, U.K. with an objective to determine the flowering and leaf number response of *Antirrhinum majus*

L. cv. Chimes White grown at two different light integral conditions (in February and June), to four distinct photoperiods (8, 11, 14 and 17h.d^{-1}) and two night temperatures (10 and 20°C). Seeds were sown in February and June into module trays (P135, volume per cell 20ml; Plantpak Ltd., Maldon, U.K.) containing SHL peat-based modular compost (William Sinclair Horticulture Ltd., Lincoln, U.K.). Seed trays for each experiment were placed in an environment-controlled growth room at 20±2°C temperature providing lighting (72μmol m^{-2} s^{-1} photosynthetic photon flux density, PPFD) using a mixture of warm white fluorescent and tungsten bulbs (6.3% tungsten calculated by nominal wattage) at plant height with a 16h.d^{-1} photoperiod. After 80% seed germination, plants were transplanted into 9cm pots containing a mixture of SHL peat-based compost and perlite (3:1 v/v). Equal numbers of plants, randomly selected, were placed in four chambers (1.3m × 2.9m) sealed from external light source, which provided 8, 11, 14 and 17h.d^{-1} photoperiods in 10°C (actual average temperature 12°C for February experiment and 15.8°C for June experiment) and 20°C (actual average temperature 19°C for February experiment and 23.8°C for June experiment) set point night temperature (Table 1). There were total 8 photoperiod chambers in two night temperature suits. Plants remained for 8h (from 08:00 to 16:00h) in a glasshouse adjacent to the 8 chambers where they were exposed to natural daylight (5.87 and 8.26 MJ.m^{-2}.d^{-1} light integral in February and June respectively) at a set-point glasshouse temperature of 20°C (actual average temperatures were 19.6°C in the February experiment and 23°C in the June experiment). Ventilation occurred automatically at 3°C above set point temperature. At 16:00h each day, all plants were moved into the photoperiod chambers where they remained until 08:00h 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 (PPFD) of 5μmol m^{-2} s^{-1}.

Experiments were laid out on Randomized Complete Design and six replicates were used for each treatment. Plant nutrients were given in the form of a soluble fertilizer, Sangral 111 (William Sinclair Horticulture Ltd., Lincoln, U.K.) at a conductivity of 1500 to 1600μS.cm^{-2} (182ppm N; 78ppm P; 150ppm K), at pH 5.7 to 5.8. To avoid *Pythium*, water was applied manually every two or three days as required. Plants in each treatment were observed daily until flower opening (corolla fully opened). Numbers of days to flowering from date of transfer to the glasshouse and the leaf numbers (below the inflorescence) were recorded at harvest. Data of these parameters were analyzed using Genstat-11 software, (Lawes Agricultural Trust, Rothamsted Experimental Station, U.K.).

Results

Time to flowering of plants from both sowing dates (February and June) declined linearly ($p<0.05$) with increasing photoperiod (Fig. 1a). Plants sown in February received 8h.d^{-1} photoperiod and kept at15.8°C mean diurnal temperature took 86 days to flower, whereas plants under 17h.d^{-1} photoperiod at the same temperature took 21 days less to flower. Similarly, plants grown at higher mean diurnal temperature (19.2°C) took 76 days to flower under 8h.d^{-1} photoperiod and 23 days less under 17h.d^{-1} photoperiod at same temperature. The flowering times of plants grown at 11h.d^{-1} and 14h.d^{-1} photoperiods were intermediate between these extremes. Similarly, plants sown in June showed significant differences between photoperiods (Fig. 1a), for example, plants grown at 19.4°C mean diurnal temperature under 8h.d^{-1} photoperiod flowered after 61 days and time to flowering was shortened by 16 days when the photoperiod was extended to 17h.d^{-1} at same temperature. A similar effect of photoperiod was observed at higher mean diurnal temperature (23.4°C), however, flowering was hastened by 5 days.

Similarly, plants received different light integrals (5.87 MJ.m^{-2}d^{-1} for February experiment and 8.26 MJ.m^{-2}d^{-1} for June experiment) showed significant differences in flowering time. A close observation of the data revealed that plants in February experiment grown at approximately the same mean diurnal temperature (19.2°C) as in the June experiment (19.4°C) took 8 more days to flower at 17h.d^{-1} photoperiod and 15 more days at 8h.d^{-1} photoperiod. This indicated that light integral significantly affect flowering time (Fig. 1b).

Data from both experiments (February and June) were analyzed using the general photo-thermal model as follows:

$$1/f = a + bT + cP \qquad \text{Eq. 3}$$

The best fitted model depicting the effects of mean diurnal temperature (T) and photoperiod (P) on the rate of development to flowering ($1/f$) can be described as:

$$1/f = -0.0117\ (\pm 0.00308) + 0.00109\ (\pm 0.000140)\ T + 0.000679\ (\pm 0.00012)\ P \qquad \text{Eq. 4}$$

($R^2 = 0.88$, d.f. 13)*****

Table 1. Details of glasshouse environment throughout growing season.

Growing season	Actual temperature (°C)			Mean diurnal temperature (°C)	Photoperiod (h.d^{-1})	Light integral 08:00-16:00 (MJ.m^{-2}.d^{-1})
	Day 08:00-16:00	Night 16:00-08:00				
	Set-point 20°C	Set-point 20°C	Set-point 10°C			
February	19.6	19.0	12.0	19.2 and 15.8	8, 11, 14, and 17	5.87
June	23.0	23.8	15.8	23.4 and 19.4	8, 11, 14, and 17	8.26

***Eq. 4 is built-up on individual arithmetic means of corresponding factors, although all data was initially tested. In LDP, T_b(base temperature) is assumed as zero and different photoperiods were studied in these experiments, therefore T_b was not included in the general photo-thermal model. The values in brackets showed the standard errors of the R^2. Therefore, both factors, i.e. photoperiod and mean diurnal temperature, had significant effects on the rate of development to flowering (Fig. 2).

The general photo-thermal model presented in Eq. 3 does not take into account the effect of light integral. Therefore, mean light integral from transfer dates to harvest (5.87 and 8.26 $MJ.m^{-2} d^{-1}$) were also incorporated into the flowering model (Eq. 5) as a linear term and the model was re-fitted using all the data as follow:

$1/f = a + bT + cP + dM$ Eq. 5

The fitted relationship describing the combined effects of temperature (T), photoperiod (P) and light integral (M) on the rate of progress to flowering can be written as:

$1/f = -0.0140\ (\pm0.00190) + 0.000771\ (\pm0.000109)\ T + 0.000741\ (\pm6.865E.05)\ P + 0.00109\ (\pm0.000243)\ M$ Eq. 6 ($R^2 = 0.96$, d.f. 12)

The values in brackets are the standard errors of the regression coefficients. Therefore, temperature, photoperiod, and light integral each had significant effects on the rate of progress to flowering. Fig. 3 compares the actual rate of flowering versus the fitted relationship (Eq. 4).

Leaf number declined linearly as photoperiod increased from 8 to $17h.d^{-1}$ for both sowing dates (Fig. 4a), for example, plants of February experiment produced 12 leaves at $17h.d^{-1}$photoperiod and 16 at $8h.d^{-1}$ photoperiod. However, temperature had no significant ($p<0.05$) effect on leaf number. A similar trend was observed in June experiment, where plants under $17h.d^{-1}$ photoperiod produced 9 leaves and 16 leaves at $8h.d^{-1}$. Photoperiod at 11 and $14h.d^{-1}$ had intermediate effect between these extremes. The difference in leaf number between the two experiments might be due to the difference in light integrals as Fig. 4b indicated non-significant effect of gradient of four photoperiods on leaf numbers in February experiment at both diurnal mean temperature (15.8 and 19.2°C), whereas this effect was significant in June experiment at lower (19.4°C) temperature rather than at higher (23.4°C) one.

The combined model of photoperiod, temperature and light integral on flowering time and leaf number: The previous photo-thermal models were only concerned with data from each individual experiment, resulting in a number of models describing the effects of photoperiod, temperature and light integral on flowering and leaf number. Clearly, a more sensible approach would be to combine data from all experiments including temperature data from our previous study where $1/f = a + bT$ (Munir *et al.,* 2015)and the data mentioned in present study in a single model. Separate models describing effects on rate of progress to flowering and leaf number have been calculated and these can be written as follows:

$1/f = -0.0247\ (\pm0.00439) + 0.0019\ (\pm0.000327)\ T - 2.305E\text{-}05\ (\pm8.0357E\text{-}06)\ T^2 + 0.000735\ (\pm0.000211)\ M + 0.000737\ (\pm6.764E\text{-}05)\ P$ Eq. 7 ($R^2 = 0.94$, 45 d.f.)

Leaf number $= 60.176\ (\pm7.217) - 6.528\ (\pm1.779)\ M + 0.426\ (\pm0.118)\ M^2 - 2.925\ (\pm0.488)\ P + 0.080\ (\pm0.0192)\ P^2$ Eq. 8 ($R^2 = 0.90$, 45 d.f.)

The reason for including individual experiment models was to show the obscured effects of each factor in each experiment, which may not be exposed by the combined model (Eq. 7 and 8) as the data for the combined model were from a restricted range of environmental conditions.

Discussion

Although photoperiod and temperature significantly affected the floral time and leaf numbers, however, light integral was also influenced flowering time, which could be due to the Mediterranean origin of *Antirrhinum,* as plants originating from that area prefer an open environment with plenty of sunshine (Summerfield *et al*., 1997). Studies have been carried out previously reported that longer photoperiods and warmer temperatures hasten flowering (Sanderson & Link, 1967; Edwards & Goldenberg, 1976), however, no attempt has been made to combine all these environmental factors into a single model until now. Commercial cultivar Chimes White also confirms the facultative long day plant behaviour of *Antirrhinum* (Cockshull, 1985). However, the influence of different factors on flowering depends on cultivars as they can respond differently to a single changing factor (Hedley & Harvey, 1975). Most researchers have focused on the effect of temperature and photoperiod on flowering, and few have worked on the effect of artificial light intensity such as Cremer *et al.* (1998) conducted research under controlled artificial environments on two inbred lines of *Antirrhinum* and studied separately the effect of photoperiod, temperature and light intensity and reported that flowering time was enhanced and plants produced more leaves under minimum photoperiod, temperature and light intensity regimes. However, in present study, plants were grown under four fixed photoperiods chambers, subjected to two different night temperatures, grown under two different natural light conditions (February and June) and an early flowering commercial cultivar was used, which showed more or less similar trend as reported by Cremer *et al.* (1998). However, a significant difference in flowering time and leaf number data between the two studies is probably due to the difference in cultural conditions and plant material.

The shortest mean flowering time of 39 days was obtained with plants that received a $17h.d^{-1}$ photoperiod at 23.4°C diurnal mean temperature. At the same temperature when plants were exposed to $8h.d^{-1}$ photoperiod they flowered 17 days later. Similarly, leaf number also greatly decreased with increased photoperiod. This effect of photoperiod has already been described for different cultivars such as Jackpot (Flint, 1960), Rosita, Potomac Rose and Summer Pink #1 (Langhans & Maginners, 1962). Flint (1960) also reported that the cv. Jackpot flowered 58 days earlier at $12h.d^{-1}$ photoperiod than at $6h.d^{-1}$ photoperiod. Similar results were obtained by Maginnes and Langhans (1961) for the same cultivar and flowering time was found to increase as photoperiod decreased from 18 to 9h. Similar facultative long day responses have also been observed in species such as *Gypsophila elegans* (Takeda, 1996), pansy (Adams *et al.,* 1997a) and petunia (Adams *et al*., 1998).

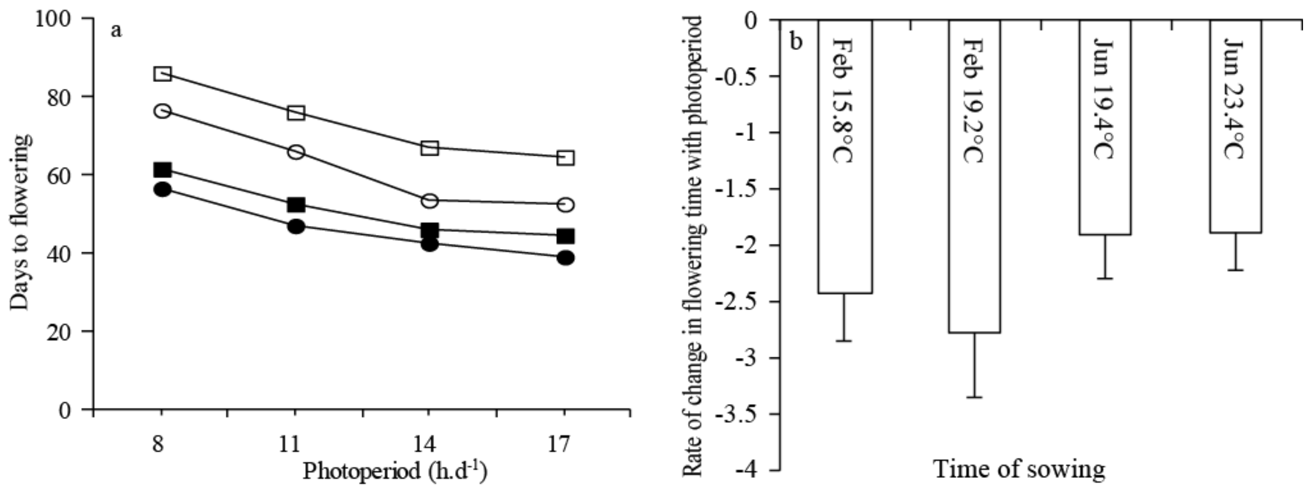

Fig. 1. (a) The effect of photoperiods on time to flowering for *Antirrhinum majus* cv. Chimes White sown in February at 19.2°C (○) or 15.8°C (□) and in June at 23.4°C (●) or 19.4°C (■). Each point represents the mean of the 6 replicate plants, vertical bars (where larger than the points) represents the standard error within replicates. (b) The gradients effect of flowering at different sowing times.

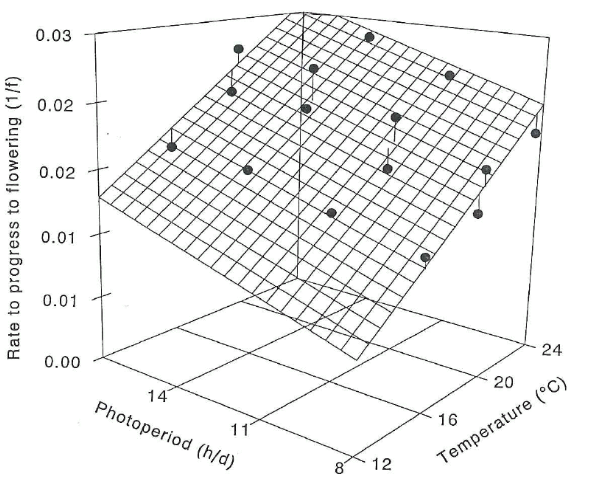

Fig. 2. The relationship between mean diurnal temperature, photoperiod and rate of progress to flowering ($1/f$) of *Antirrhinum majus* cv. Chimes White sown in February at 19.2°C or 15.8°C and in June at 23.4°C or 19.4°C, where each point represents the mean of six plants. $1/f = -0.0117\ (\pm 0.00308) + 0.00109\ (\pm 0.000140)\ T + 0.000679\ (\pm 0.00012)\ P$, where P is the mean photoperiod and T is the mean diurnal temperature. R^2 was 0.88 at 13 d.f.

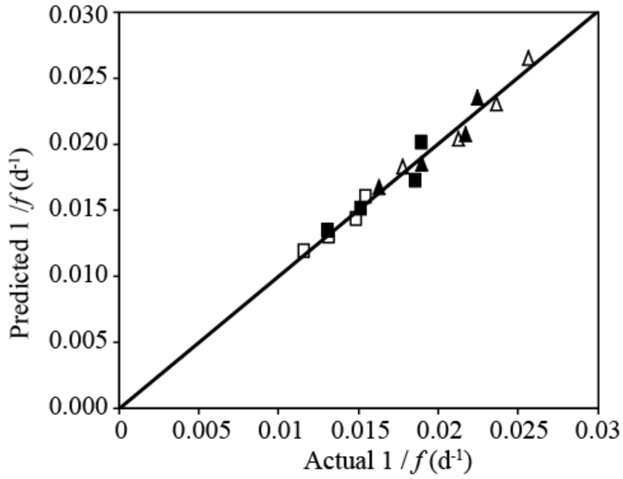

Fig. 3. The relationship between the actual rate of progress to flowering against those fitted by the flowering model ($1/f = a+bT+cP$) for *Antirrhinum majus* cv. Chimes White sown in February at 19.2 (■) and 15.8°C (□) and in June at 23.4 (▲) and 19.4°C (Δ) and grown under 8, 11, 14, and 17h.d^{-1} photoperiod. The solid line is the line of identity.

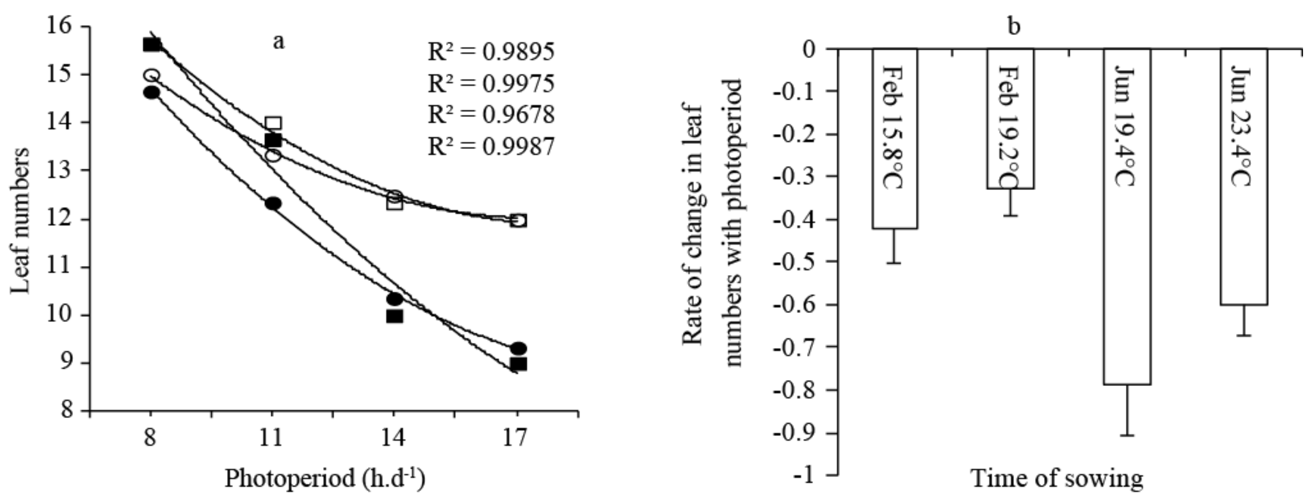

Fig. 4. (a) The effect of photoperiods on leaf number for *Antirrhinum majus* cv. Chimes White sown in February at 19.2°C (○) or 15.8°C (□) and in June at 23.4°C (●) or 19.4°C (■). Each point represents the mean of the 6 replicate plants, vertical bars (where larger than the points) represent the standard error within replicates. (b) The gradients effect of leaf numbers at different sowing times.

Similarly, it has been previously observed that *Antirrhinum* flowers earlier at higher temperatures (Maginnes & Langhans, 1961; Edwards & Goldenberg, 1976; Munir *et al*., 2015). However, difference in day and night temperatures was not studied previously in *Antirrhinum*. The response of cv. Chimes White clearly showed that the time of flowering decreased as the night temperature increased. Similar trend was noted with the mean diurnal temperatures. Cremer *et al.* (1998) reported that increasing the temperature from 20 to 25°C hastened flowering and reduced leaf numbers.

Similarly, plants grown under different natural light integrals (February and June conditions) showed remarkable difference regarding flowering time and leaf numbers in *Antirrhinum*. Both variables were reduced when light integral was increased (in June condition, 8.26 $MJ.m^{-2}.d^{-1}$), presumably as a result of increased assimilate availability having a direct effect on increased rate of development. Plants grown in February received the same photoperiod and mean diurnal temperature but a lower light integral (5.87 $MJ.m^{-2}.d^{-1}$) than the plants sown in the June (8.26 $MJ.m^{-2}.d^{-1}$), particularly during the juvenile phase of development. Plants at 19.2°C in the February experiment flowered 8 and 15 days later at 17 and $8h.d^{-1}$ photoperiod respectively than at 19.4°C in the June experiment. The flowering time difference is most likely due to the 2.39 $MJ.m^{-2}.d^{-1}$ difference of light integral between the two growing seasons (February and June). *Antirrhinum* is a plant of Mediterranean origin and prefers an open climate and high light levels. It is therefore not surprising that low light integrals significantly delayed flowering. Similar results have also been described for the cultivar Orchid Rocket while cultivar Pink Ice showed no response to increasing light intensity from 6,000 to 26,000 lux (Hedley, 1974). However, Cremer *et al.* (1998) observed an extreme effect of light intensity where decreasing light intensity from 30,000 to 4,000 lux in $8h.d^{-1}$ photoperiod led to a delay of flowering of over two years.

The general photo-thermal model (Eq. 1) has been successfully applied to the flowering response of many crops species (Pearson *et al.,* 1993; Adams *et al.,* 1997a and 1998). This model was also successfully applied to *Antirrhinum*. Moreover, significant effect of light integral on the rate of progress to first flowering and leaf number is also accommodated in the general photo-thermal model, which was not previously reported (Eq. 6, 7 and 8). Such information would be useful for successful crop scheduling by manipulation of photoperiod, temperature and light integral in regulating the supply of flowering crop to the market.

Conclusion

It is concluded from present study that flowering time and rate of progress to flower of *Antirrhinum* cv. Chimes White can be accelerated by subjecting them to high photoperiod, mean diurnal temperatures, and light integral. However, if late flowering and good quality of plants are required then these factors can be restricted, which prolong vegetative growth. These findings are useful for ornamental industry for the steady supply of ornamental plants to the market and would also save the wastage to resources, which are spend to provide photoperiod and temperature during their growth and development.

Acknowledgment

The authors are highly indebted to the Association of Commonwealth Universities, UK for providing financial assistance.

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(Received for publication 11December 2015)