The Effects of Temperature, Photoperiod, and Photosynthetic Photon Flux on the Time to Flowering of *Petunia* 'Express Blush Pink'

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ABSTRACT. The effects of temperature and sowing date on the time to first flowering were investigated in *Petunia* × *hybrida* Vilm 'Express Blush Pink' sown on three separate dates (8 Feb., 1 Mar. and 22 Mar. 1993) and grown in glasshouse compartments set to provide six air temperature regimes (minimum temperatures of 4, 10, 14, 18, 22, and 26 °C). Flowering was hastened under high temperatures and sowing later in the season (22 Mar.). To determine the extent to which this seasonal effect was due to photoperiod, a second experiment was conducted where plants were grown under controlled daylengths (8, 11, 14, and 17 h·d⁻¹) within six temperature-controlled glasshouse compartments (set to provide minimum temperatures of 6, 10, 14, 18, 22, and 26 °C). The rate of progress to first flowering increased linearly with lengthening photoperiod up to a critical photoperiod of 14.4 h·d⁻¹, while further increases in daylength had no further affect in hastening flowering. The rate of progress to flowering increased linearly with increasing temperature, however, the optimum temperature, at which the rate of progress to flowering was maximal, was lower under short days compared to long days. Furthermore, the rate of progress to flowering increased linearly with increasing photosynthetic photon flux (PPF). Data from both experiments were analyzed to construct a model to predict the effects of temperature, photoperiod, and PPF on time of flowering in petunia. This model accurately ($r^2 = 0.88$) predicted the flowering times of a different set of plants sown on three dates and grown under six temperature regimes (6, 10, 14, 18, 22, and 26 °C).

Petunia × *hybrida* is an important bedding plant crop. However, a considerable proportion of the crop is wasted each year through poor plant scheduling. A number of studies have investigated the factors affecting flowering in petunia, notably Piringer and Cathey (1960) showed that they were quantitative long day plants and that high temperatures hastened flowering. Kaczperski et al. (1991) showed that time to flowering was a curvilinear function of average temperature, with 25 °C being the optimum temperature at 13 mol·m⁻²·d⁻¹ photosynthetic photon flux (PPF). Thus, plants of cv. Snow Cloud grown in growth chambers flowered after 74 d at 15 °C compared to 46 d at 25 °C. Furthermore, they showed that time to flowering was significantly delayed when PPF decreased from 13 to 6.5 mol·m⁻²·d⁻¹, except when plants were grown under high average diurnal temperatures in the order of 30 °C. For example, plants grown at 20 °C flowered after 67 d at a PPF of 6.5 mol·m⁻²·d⁻¹ compared to 56 d at a PPF of 13 mol·m⁻²·d⁻¹.

It has been shown for numerous plant species (Ellis et al., 1990; Hadley et al., 1983, 1984; Roberts et al., 1985), both short (SDP) and long day plants (LDP), that the rate of progress to first flowering (1/f) can be described as a simple linear function of photoperiod and temperature:

$$1/f = a + bT + cP \quad [1]$$

where T is the mean temperature (°C), P is the photoperiod (h·d⁻¹), and a , b , and c are genotype-specific constants. For LDP, lengthening of photoperiod increases the rate of progress to flowering, so that c is positive and vice versa for SDP. The linear response to photoperiod applies between the critical (P_c) and ceiling photoperiods (P_{ce}), where

the P_c is the photoperiod above which, in LDP, the time to flowering can not be hastened any further. P_{ce} is the daylength below which, in a LDP, the time to flowering is not further delayed.

The temperature limits of the general photothermal response can be delineated with three cardinal temperatures, the base (T_b), optimum (T_o) and ceiling (T_c) temperatures. At the base and ceiling temperatures, the rate of progress to flowering is zero, whereas the maximum rate of progress to flowering occurs at the optimum temperature. The optimum temperature can be estimated using the concept of effective temperature (Pearson et al., 1993). This technique assumes that the rate of development with temperature is similar but opposite above and below T_o . Supraoptimal temperatures, for any estimated value of T_o , can then be converted into effective temperatures (T_e), which represent the suboptimal temperature equivalents of a supraoptimal temperature in terms of developmental rate:

$$T_e = T_o - |T_o - T_a| \text{ and } T_b < T_a < T_c \quad [2]$$

where T_a is the actual temperature. To estimate the optimum temperature, T_e is calculated for a range of optima. The optimized value for T_o is the one which minimizes the residual sum of squares of the regression between reciprocal of days to flowering and effective temperature. By considering effective temperatures, Eq. [1] can now be adapted to quantify the effects of both supra- and suboptimal temperatures on the rate of progress to flowering:

$$1/f = a + bT_e + cP \quad [3]$$

Interactions between the effects of temperature and photoperiod on the reciprocal of time to flowering are rare. However, Adams et al. (1997a) found a significant interaction between the effects of temperature and photoperiod on the reciprocal of time to flowering in trailing petunia, a close relative of *Petunia* × *hybrida*.

The general photothermal Eq. [3] does not consider the influence of PPF on the rate of progress to flowering. To consider this effect, Adams et al. (1997b) showed that time to flowering in *Viola* × *wittrockiana* could be described with a three parameter linear model containing terms for the effects of temperature, photoperiod, and PPF, thus

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$$1/f = a + bT_e + cP + dM \quad [4]$$

where M is the mean daily PPF and d is a genotype-specific constant.

Flowering in petunia would appear to be a complex function of temperature, photoperiod and average daily PPF , but to date there has been no attempt to synthesize these responses into a single model. The objectives of this study were to produce such a model that would have considerable commercial value to growers for designing improved sowing date schedules that minimize plant wastage. The model could also be used to forecast the maturity of crops after sowing in response to predicted future environmental conditions.

Materials and Methods

EXPERIMENT 1: THE EFFECT OF TEMPERATURE AND SOWING DATE ON TIME TO FLOWERING UNDER NATURAL PHOTOPERIODS. This experiment was designed to test the response of *Petunia ×hybrida* 'Express Blush Pink' to a range of temperature, photoperiod and PPF environments brought about by several sowing dates. Seeds were sown in seed trays containing a peat-based compost (Shamrock Special, Shamrock Horticulture, Bristol, U.K.) on three dates: 8 Feb., 1 Mar., and 22 Mar. 1993. These were germinated inside a growth chamber (Conviron S10H, Controlled environments Ltd. Winnipeg, Canada) at a temperature of $22 \pm 0.5^\circ\text{C}$ and a PPF of $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant height, provided from a 2:1 mixture of warm white fluorescent and tungsten bulbs (determined on the basis of nominal wattage) for $12 \text{ h}\cdot\text{d}^{-1}$. After 25 d, plants were pricked out into plug-trays (P84, volume of each cell, 40 mL; Plantpak Ltd. Maldon, U.K.), and transferred to the inner six of a linear array of eight temperature-controlled glasshouse compartments ($3.7 \text{ m} \times 7 \text{ m}$) set to provide minimum temperatures of 4, 10, 14, 18, 22, and 26°C , with ventilation at temperatures 4°C above these set points. Plants were grown under natural daylengths and potted on after a further three weeks into 9-cm pots (volume 370 mL) containing the same peat-based compost. They were irrigated by hand and fertilized twice weekly with a solution of Sangral 101 (SHL, William Sinclair Horticulture Ltd. Lincoln, U.K.) soluble fertilizer ($260 \text{ mg}\cdot\text{L}^{-1} \text{ N}$, $0 \text{ mg}\cdot\text{L}^{-1} \text{ P}$, and $223 \text{ mg}\cdot\text{L}^{-1} \text{ K}$). Pots were gradually re-spaced to avoid mutual shading, until they reached a final plant density of 40 pots/ m^2 . Twenty plants were used in each temperature treatment and the number of days from sowing to first flowering (petals fully reflexed) was recorded for each plant.

Mean diurnal temperatures were calculated from data recorded on a datalogger (Combine, Murdoch, 1985) using aspirated thermistors (30-s scans, logged every 5 min). Average daily PPF was obtained from a meteorological site located 300 m from the glasshouses. A measured glasshouse light transmission of 70% was used to estimate the PPF transmitted into the glasshouse. Daily photoperiods during the course of the experiment were computed using the method of Sellers (1965), this involves calculation of the declination angle (δ), from which the daylength can be calculated for any given local latitude.

EXPERIMENT 2: THE EFFECT OF TEMPERATURE AND PHOTOPERIOD ON THE RATE OF PROGRESS TO FLOWERING. The objective of this experiment was to determine the flowering response of *Petunia ×hybrida* 'Express Blush Pink' to constant photoperiods and temperatures. Seeds were sown on 3 Mar. 1995 in seed trays containing a peat-based seed and modular compost (SHL, William Sinclair Horticulture Ltd. Lincoln, UK) and germinated for 21 d at $20 \pm 1^\circ\text{C}$ in a growth room providing $90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant height from a mixture of white fluorescent and tungsten bulbs (6.3% tungsten by nominal wattage), with a $16 \text{ h}\cdot\text{d}^{-1}$ photoperiod. These were then pricked out into plug trays (Plantpak P84) containing the same peat-based compost. The

plants were then placed on movable trolleys in the same six temperature-controlled glasshouse compartments used in Expt. 1, set to provide minimum temperatures of 6, 10, 14, 18, 22, and 26°C , with ventilation at temperatures 4°C above the setpoints. Mean diurnal temperatures within each compartment were calculated from data recorded on a datalogger (Datataker, DT500; Data Electronics, Letchworth Garden City, U.K.), using aspirated PT100 temperature sensors (15-s scans, logged hourly). Each compartment was equipped with four photoperiod-controlled chambers, which were sealed from exterior light sources. Plants remained in the glasshouse for eight hours. At 1600 HR each day plants were wheeled into the photoperiod chambers where they remained until 0800 HR the following morning. Daylengths were extended inside each of the chambers by illuminating the plants with low intensity lighting at a PPF of $11 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant height, from a 40-W tungsten and a 15-W compact fluorescent light bulb. In all treatments, the lamps were switched on, automatically at 1600 HR for a duration dependent on the daylength extension required. To minimize any temperature increase, the chambers were continually ventilated, having an average air speed of $0.2 \text{ m}\cdot\text{s}^{-1}$ over the plants when inside the chambers. The daylengths were set at 8, 11, 14, and $17 \text{ h}\cdot\text{d}^{-1}$, thus, the experimental design provided a combination of six temperatures and four photoperiods.

After an additional 18 d, plants were potted into 9-cm pots (volume 370 mL) containing a peat-based potting compost (SHL, William Sinclair Horticulture Ltd.) to which 25% perlite (by volume) was incorporated. A fertigation system provided Sangral 111 liquid feed (SHL, William Sinclair Horticulture Ltd.) every watering at a conductivity of 1.5 mS ($182 \text{ mg}\cdot\text{L}^{-1} \text{ N}$; $78 \text{ mg}\cdot\text{L}^{-1} \text{ P}$; $150 \text{ mg}\cdot\text{L}^{-1} \text{ K}$), acidified to pH 5.8. Six plants were grown in each treatment and the number of days from sowing to first flowering were recorded for each plant. Data were analyzed using the FITNONLINEAR subroutine of GENSTAT 5 (GENSTAT 5, Release 3.1 Reference manual, OUP, 1993).

EXPERIMENT 3: MODEL VALIDATION. Three more crops of petunia were grown to independently validate the model. Seeds of *Petunia ×hybrida* 'Express Blush Pink' were sown on the 28 Feb. 1994, 27 Mar. 1994, and 17 Jan. 1995. Plants were raised as in Expt. 1 and grown on to flowering in the same temperature-controlled glasshouse compartments, set to provide minimum temperatures of 6, 10, 14, 18, 22, and 26°C . For each sowing date, ten plants were grown in each temperature compartment and the number of days to flowering were recorded. Temperature data were recorded using a DT500 data logger as in Expt. 2, light data were measured as in Expt. 1 and photoperiods during the course of the experiment were again estimated using the method of Sellers (1965).

Results

EXPERIMENT 1: THE EFFECT OF TEMPERATURE AND SOWING DATE ON TIME TO FLOWERING UNDER NATURAL PHOTOPERIODS. Time to first flowering was found to be highly dependent on mean temperature. Thus, plants sown on 8 Feb. 1993 and grown at 14.5°C flowered after 113 d, whereas plants grown at either 21.7 or 24.9°C flowered after 70 d (Fig. 1). The optimum temperature for promoting flowering for these crops was therefore high. In addition, flowering was hastened by sowing later in the season (Fig. 1). For example, plants sown on 8 Feb. 1993 and grown at 24.9°C flowered after 70 d compared to 57 d when sown on the 22 Mar. 1993 and grown at 24.6°C . However, in this experiment plants were grown under natural photoperiods and therefore PPF and photoperiods were confounded. The mean daily PPF increasing from 15.3 to $20.5 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ and mean daylength from 12.9 to $14.8 \text{ h}\cdot\text{d}^{-1}$ for the 8 Feb. and 22 Mar. sown crops respectively. Thus,

Fig 1. The effect of mean temperature from sowing on days to flower for *Petunia x hybrida* 'Express Blush Pink' sown on 8 Feb. 1993 (●), 1 Mar. 1993 (○), and 22 Mar. 1993 (▲). Each point represents the mean time to flower of the 20 replicate plants, vertical bars (where larger than the points) represent the 95% confidence interval of the means.

it was not clear to what extent each factor affected the rate of progress to flowering.

EXPERIMENT 2: THE EFFECT OF TEMPERATURE AND PHOTOPERIOD ON THE RATE OF PROGRESS TO FLOWERING. In this experiment, the rate of progress to flowering, estimated as the reciprocal of time to flowering ($1/f$), increased linearly with increasing photoperiod up to a critical photoperiod of $14.4 \pm 0.6 \text{ h}\cdot\text{d}^{-1}$ (Fig. 2). Extending the photoperiod beyond this resulted in no further hastening of flowering. The rate of progress to flowering also increased linearly with increasing temperature up to the optimum and declined linearly thereafter (Fig. 2). Furthermore, the optimum temperature increased linearly with increasing photoperiod from 20.7°C at $8 \text{ h}\cdot\text{d}^{-1}$, up to 24.3°C at the critical photoperiod of $14.4 \text{ h}\cdot\text{d}^{-1}$. There was no significant multiplicative interaction between temperature and photoperiod. The analysis therefore showed both temperature and photoperiod independently affected the rate of progress to flowering and showed that the general photothermal model (Eq. [3]) is appropriate in describing the flowering response in petunia, provided it is adjusted for changes in optimum temperature with photoperiod.

THE COMBINED EFFECTS OF TEMPERATURE, PHOTOPERIOD, AND PPF ON TIME TO FLOWERING. Data from both experiments were then combined in a further analysis. This enabled an additional parameter, PPF ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), to be incorporated into the model as a linear additive term. The analysis showed increasing PPF to have a significant effect in reducing the time to first flowering, however, this response was quite weak. Thus the final fitted model describing the effects of mean temperature (T), photoperiod (P), and PPF (M) on the rate of progress to flowering can be written as

$$1/f = -0.00585 + 0.000643T_e + 0.000359P + 0.000093M$$

$$(\pm 0.0013) (\pm 0.00005) (\pm 0.00008) (\pm 0.000032)$$

$$\text{and } P < P_c \text{ (} r^2 = 0.91, 35 \text{ df)} \quad [5]$$

where the optimum temperature for the calculation of T_e can be determined thus

$$T_o = 15.92 + 0.593P, \text{ where } P < P_c \text{ and } T_b < T_o < T_c$$

$$(\pm 1.15) (\pm 0.099) \quad [6]$$

and the critical photoperiod (P_c) was found to be $14.3 (\pm 0.5) \text{ h}\cdot\text{d}^{-1}$. The values in parentheses are the standard errors of the regression coefficients. Therefore, all three factors examined had significant

and independent linear effects on the rate of progress to flowering. Figure 3 shows the actual rate of progress to flowering versus those predicted from the model.

EXPERIMENT 3: MODEL VALIDATION. Independent data (excluding plants from the first sowing grown under the two coldest temperature regimes, which died at the extreme temperature) were then used to test the validity of the flowering model (Eqs. [5] and [6]). For each data set, the model was solved using an iterative procedure against running means of average daily temperature, photoperiod, and PPF , up to the day on which the product of the average daily contributions to flowering equalled one. Figure 4 shows the accuracy of the predicted time to first flowering using the model ($r^2 = 0.88$).

Discussion

The analysis presented here has indicated independent additive effects of mean temperature, photoperiod and PPF on the rate of progress to flowering in petunia. Previous studies (Piringer and Cathey, 1960; Kaczperski et al., 1992) have indicated longer photoperiods and warmer temperatures hasten flowering, however, to date, no attempt has been made to combine all these factors in a single model. The model developed here could provide the basis of a powerful decision support tool for bedding plant growers (Pearson et al., 1995). Such decision support systems are increasingly important, since U.K. growers estimate that up to 10% of their annual production is wasted due to poor plant scheduling (S. Coutts, personal communication).

The seasonal change in maturity date for plants grown at a particular temperature, although largely a function of photoperiod, was partly due to changes in PPF . Kaczperski et al. (1991) also showed an effect of PPF on the time to flower of petunia, with plants grown at $13 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ flowered up to 23 d before their respective counterparts grown at $6.5 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Furthermore, their controlled environment studies showed that the effect of PPF on flowering was greater at lower than higher average tempera-

Fig 2. The relationship between temperature, photoperiod and the rate of progress to flowering ($1/f$) of *Petunia x hybrida* 'Express Blush Pink' sown on 3 Mar. 1995, where each point represents the mean of six plants. The response surface was fitted using the FITNONLINEAR subroutine of GENSTAT 5; $1/f = -0.00248 (\pm 0.0012) + 0.000463 (\pm 0.00006)T_e + 0.000437 (\pm 0.00007)P$, where P is the mean photoperiod ($\leq$ the critical photoperiod) and the optimum temperature (T_o) for the calculation of the mean effective temperature (T_e) can be determined thus, $T_o = 16.31 (\pm 1.38) + 0.553 (\pm 0.12)P$, ($r^2 = 0.93, 18 \text{ d.f.}$).

Fig 3. The relationship between the actual rate of progress to flowering against those predicted by the flowering model (Eqs. [5] and [6]), for *Petunia × hybrida* 'Express Blush Pink' sown on 8 Feb. 1993 (●), 1 Mar. 1993 (○), and 22 Mar. 1993 (▲) and grown under natural photoperiods (Expt. 1. Seeds sown on 3 Mar. 1995 (Δ) and grown under controlled daylengths (Expt. 2). The solid line is the line of identity ($r^2 = 0.91$, 35 df).

tures. Similarly, by considering the rate of progress to flowering to be a positive additive function of mean *PPF*, the present study shows the effect of *PPF* in terms of days to flower to be greater at lower temperatures and short days, even though there are no interacting terms in the model between *PPF*, temperature or photoperiod. Further work is needed to investigate more fully the effect of *PPF* on flowering in petunia.

Spector (1956) described petunia as a LDP at high temperatures, but day neutral at low temperatures. Work by Piringer and Cathey (1960), however, showed long days to hasten flowering at all temperatures. Indeed, over the wide range of photothermal environments in this study, there was no evidence to suggest that plants became less sensitive to photoperiod at low temperatures. However, there was evidence to suggest that the plants had a critical photoperiod of $14.3 \text{ h} \cdot \text{d}^{-1}$, because extending the photoperiod beyond this level did not hasten flowering. Little other work has been conducted to quantify the critical photoperiod of petunia, although Adams et al.

Fig 4. Independent validation of the flowering model (Eqs. [5] and [6]) against flowering time of *Petunia × hybrida* 'Express Blush Pink' sown on the 28 Feb. 1994 (●), 27 Mar. 1994 (○), and 17 Jan. 1995 (▲) and grown at six different temperature regimes (minimum temperatures of 6, 10, 14, 18, 22, and 26°C). The vertical bars represent the 95% confidence intervals of the means of the 10 plants ($r^2 = 0.88$). The solid line is the line of identity.

(1997a) showed the critical photoperiod of trailing petunia to be in the region of 15 to $15.5 \text{ h} \cdot \text{d}^{-1}$, slightly higher than that shown here.

The time at which plants flowered was highly dependent on mean temperature. Kaczperski et al. (1991) found a similar curvilinear relationship between days to flower and average temperature. The optimum temperature (at which the rate of progress to flowering will be maximal) was relatively high, however, there was evidence to suggest that this decreased linearly as the photoperiod fell below the critical photoperiod. The physiological basis for this response is not fully understood, however, it may be linked to the change in growth habit with photoperiod (Piringer and Cathey, 1960).

The growth habit of plants was observed to be highly dependent on the photoperiod under which plants were grown. Plants grown under long days tended to be single stemmed, plants having an upright terminal growth habit with little basal branching. However, plants grown under short days tended to be short and compact, with numerous basal branches on which the first flowers opened, giving the plants a rosette appearance. These differences in growth habit were similarly observed by Piringer and Cathey (1960) and Adams et al. (1997a) in trailing petunia. It is possible that the optimum temperature for growth of branches is relatively low, which then effects the optimum temperature for flowering in plants grown at SD. This change in growth habit may be due to photoperiod per se as plants grown under natural LDs also tended to have an upright habit. Furthermore, Piringer and Cathey (1960) found the growth habit of petunia was similar irrespective of whether plants were given a day extension with either incandescent or fluorescent light sources (although the internodes were significantly longer under incandescent light). However, the degree to which light quality effects growth habit and flowering is unclear and further work is needed on this topic.

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