The Effect of Day/Night Temperature on *Pharbitis nil* Chois. Flowering

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Abstract. The interaction between day/night temperature (DT/NT) and irradiance during the photoperiod prior to the inductive night on *Pharbitis nil* (L.) cv. Violet flower induction was studied. Plants exposed to 12 or 18 °C NT did not flower regardless of DT. When NT was 24 or 30 °C, percent flowering plants increased progressively as DT increased from 12 to 30 °C. Percent flowering plants and total flower bud number per plant was greatest when seedlings were induced with a 24 or 30 °C DT/30 °C NT regime. DT/NT did not affect the node number to first flower. Irradiance did not affect flowering. Temperature effects on *P. nil* flowering could be described as a function of average daily temperature, where flowering increased as temperature rose from 22 to 30 °C.

Day and/or night temperature (DT and/or NT, respectively) affects flower initiation of many plant species (Erwin and Kovanda, 1990; Karlsson et al., 1989; Langhans and Larson, 1960; Went, 1952). For example, in *Euphorbia pulcherrima* Willd. ex. Klotzsch, NT above 26 °C delays flower initiation (Kristoffersen, 1969; Langhans and Larson, 1960). In contrast, DT above 20 °C delays flower initiation in *Fuchsia ×hybrida* Hort. ex Vilm. (Erwin and Kovanda, 1990). Flowering of *Dendranthema ×grandiflorum* Ramat. cv. Bright Golden Anne is DT and NT sensitive, with 30 °C DT/NT delaying flower initiation (Karlsson et al., 1989).

Pharbitis nil Chois. (L.) cv. Violet (Japanese morning glory) is used as a model plant to study photoperiodic flower induction for four reasons: 1) it can be induced to flower with one inductive day/night cycle (Imamura and Marushige, 1976); 2) cotyledons are sensitive to photoperiodic induction (Vince-Prue and Gressel, 1985); 3) seed germination occurs easily and rapidly (≈ 2 d at 25 °C) (Vince-Prue and Gressel, 1985); and 4) flowers develop rapidly allowing data collection 3–4 weeks after flower induction.

Limited research has been conducted on temperature effects on *P. nil* flower induction/initiation. Ikeda (1965), and Takimoto and Hamner (1964) studied DT or NT effects on *P. nil* flowering independently and reported that

optimal NT for flower induction was 25–30 °C and that NT >32 or <19 °C inhibited flowering. DT had little effect on flowering. *P. nil* flower induction was, therefore, reported to be NT-sensitive. Our objective was to determine whether *P. nil* flowering is DT/NT-sensitive by studying DT and NT effects on flower induction simultaneously. We also studied the interaction between DT, NT, and irradiance immediately prior to a photoperiodically inductive night.

Materials and Methods

Pharbitis nil cv. Violet seed (Marutane Seed Co., Kyoto, Japan) were scarified in 250 mL of concentrated H₂SO₄ (Baker Analyzed Reagent, 96.8% H₂SO₄ by acidimetry) for 45 min, then rinsed in distilled water for 15 min and soaked in 350 mL of distilled water for 16 h (Takimoto, 1967). Rinsed seed were planted in 10-cm-wide standard plastic pots (454 cm³) in a soilless growing medium (Michigan Peat Co., Houston) composed of 2 sphagnum peat : 1 perlite : 1 vermiculite. Seedlings were germinated and grown under continuous light [$250 \pm 10 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$, cool-white fluorescent lamps (Phillips VHO, Phillips Lighting Co., Somerset, N.J.)] for 5 d at 24 ± 1 °C in chambers.

Five-day-old seedlings were exposed to 16 different DT/NT regimes during an inductive 8-h day/16-h night cycle. DT/NT treatments were achieved by rotating seedlings among four chambers (0.74 m² growing area) maintained at 12, 18, 24, or 30 ± 1 °C at 0700 and 1900 hr each day. Moving the plants required 5 min. Seedlings were exposed to 150, 250, or $350 \pm 10 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ irradiance levels during the 8-h day prior to the 16-h inductive night. Different irradiance levels were achieved by adjusting the distance between the seedlings and lamp. Seedling tissue temperature did not vary among irradiance treatments.

Following DT/NT treatments, seedlings were grown under continuous $220\text{--}270 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ at 24 °C until visible bud (bud length ≥ 5 mm) [28 d (rep 1) and 32 d (rep 2)]. Plants were fertilized weekly through irrigation water with 65.8 mM Ca(NO₃)₂ and 97.6 mM KNO₃. Data were collected at visible bud on the number of flowering plants, the number of plants with axillary flower buds, and the number of plants with terminal flower buds. In addition, total, axillary, and terminal flower bud number per plant and the node position of the first axillary flower bud were recorded. Node position of the first axillary flower bud was identified using '1' as the cotyledonary node, with node numbers increasing distally.

A $4 \times 4 \times 3$ factorial statistical design was used, with DT (4 levels), NT (4 levels), and irradiance (3 levels) as the main factors (Montgomery, 1991). Data were analyzed using an analysis of variance (ANOVA) procedure (Systat 5.2.1, Evanston, Ill.). The experiment was replicated twice over time with 8–9 and 7–10 plants per treatment for the first and second replicates, respectively. Arcsine square root transformation was performed on percent data before ANOVA and multiple comparison tests (Tukey's HSD). An alpha level of 0.05 was used throughout the experiment to determine significance.

Results

Percent of plant flowering. DT and NT interacted to affect percent flowering plants and percent plants with axillary and terminal flower buds (Table 1). Percent flowering plants increased as DT increased from 12 to 30 °C when NT was 24 or 30 °C (Fig. 1a). For example, percent flowering plants increased

Table 1. Analysis of variance (ANOVA) table showing the effects of day temperature (DT), night temperature (NT), and irradiance on flowering of *Pharbitis nil* (L.) Chois. 'Violet'. Arcsin square root transformations were conducted on percent data before ANOVA. Unreported interactions were nonsignificant.

Characteristic	Term			
	DT	NT	Irradiance	DT × NT
Percent of plants				
Flowering	***	***	NS	**
Axillary	**	***	NS	**
Terminal (%)	***	***	NS	**
Number of flowers per plant				
Total	***	***	NS	*
Axillary	**	***	NS	**
Terminal	**	***	NS	**
Node position to first axillary flower	NS	NS	NS	NS

NS, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

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Fig. 1. Main effects of day and night temperature on flowering of *Pharbitis nil* (L.) Choisy, cv. Violet across irradiance treatments. Vertical bars indicate standard errors about the treatment means. Flowering did not occur at 12 or 18 °C NT.

from 4% to 56% and from 77% to 96% as DT increased from 12 to 30 °C when NT was 24 or 30 °C, respectively (Fig. 1a). No flowering occurred when NT was less than 24 °C, regardless of DT. Irradiance did not affect the percentage of flowering plants (Table 1).

The percentage of plants with axillary flower buds increased from 4% to 52% and from 72% to 96% as DT increased from 12 to 30 °C when NT was 24 or 30 °C, respectively (Fig. 1b). Response was greatest (96%) with a 30/30 °C DT/NT regime (Fig. 1b). The percentage of plants with terminal flowers increased from 0% to 21% and from 47% to 86% as DT increased from 12 to 30 °C when NT was 24 or 30 °C, respectively (Fig. 1c).

Number of flower buds per plant. DT and NT interacted to affect total, axillary, and terminal flower bud number per plant (Table 1). Total flower buds per plant increased from 0.1 to 2.5 and from 3.9 to 6.3 as DT increased from 12 to 30 °C with a 24 or 30 °C NT, respectively (Fig. 2a). Seedlings exposed to DT/NT regimes of 24/30 °C or 30/30 °C had the greatest flower bud number per plant (6.2 and 6.3, respectively) (Fig. 2a). Irradiance did not affect the response (Table 1).

The number of axillary flower buds per plant increased from 0.1 to 2.0 when DT increased from 12 to 30 °C with a 24 °C NT (Fig. 2b). Response was not affected by DT when NT was 30 °C (Fig. 2b) and was greatest (3.3) with a 30 °C NT regardless of DT (Fig. 2b). Number of terminal flower buds per plant increased from 1.4 to 2.7 as DT increased from 12 to 30 °C with a 30 °C NT

(Fig. 2c). Response was greatest (2.6 and 2.7, respectively) with a 24 or 30 °C DT when NT was 30 °C (Fig. 2c). Very few terminal flower buds were produced on plants grown at 24 or 30 °C DT when NT was 24 °C (0.7 and 0.5 per plant, respectively) (Fig. 2c).

Position of the first axillary flower bud. DT, NT, or irradiance did not affect the node position of the first axillary flower bud (Table 1).

Average daily temperature. DT and NT affected *P. nil* flowering in a similar manner in our study; we found no significant difference between DT and NT effects on flowering on a per hour basis (analysis not shown). Therefore, the effect of average daily temperature (ADT) on *P. nil* flowering was analyzed. ADT affected percent flowering plants and total and terminal flower bud number per plant (Table 2). Percent flowering plants increased from 2% to 96% as ADT increased from 20 to 30 °C (Fig. 3a). Plants did not flower when ADT was below 22 °C (Figure 3a). Total flower bud number per plant increased from 0.0 to 6.3 and terminal flower bud number per plant increased from 1.0 to 2.7 as ADT increased from 22 to 30 °C (Fig. 3 b and c).

Discussion

In *P. nil*, strong flower induction is characterized by more plants flowering, high flower bud number, and more terminal flower buds, whereas weak induction is characterized by axillary flower bud formation with little or no terminal flowering (Imamura and Marushige, 1976). We found that *P. nil* flowering was greatest when plants were induced with a 24/30 or 30/30 °C DT/NT regime. Our results differ from those of Ikeda (1965), who concluded that flowering was only NT-sensitive. Ikeda (1965) observed that *P. nil* flowered when induced with a single 16-h night at 25 °C regardless of whether plants were exposed to a 12 or 28 °C DT. We found that flowering increased as DT increased from 12 to 30 °C when NT was 24 or 30 °C (Figs. 1 and 2). Two factors that differed between our experiment and Ikeda's (1965) were seedling age at induction and light quality; Ikeda (1965) used 3-d-old seedlings grown under fluorescent and incandescent lamps, whereas we used 5-d-old seedlings grown under fluorescent lamps only.

Flowering of *P. nil* was not observed in our experiment when NT was 12 or 18 °C. Takimoto and Hamner (1964) demonstrated that as NT decreased, the length of the critical dark period increased. Three timing mechanisms were suggested concerning photoperiodic flowering in *P. nil* (Takimoto and Hamner, 1964). One mechanism resembled an hourglass, i.e., the flowering response increased as dark period was prolonged. This timer was/would be temperature sensitive (Takimoto and Hamner, 1964). Flowering occurred with an 18 °C NT and a 48-h dark period, but did not occur with a 16-h dark period at 18 °C NT, indicating that, as NT decreased, critical dark period length increased (Takimoto and Hamner, 1964). *P. nil* flowering may not have occurred when NT was 12 or 18 °C in our experiment because the dark period was not long enough.

Fig. 2. Main effects of day and night temperature on flowering of *Pharbitis nil* (L.) Choisy, cv. Violet across irradiance treatments. Vertical bars indicate standard errors about the treatment means. Flowering did not occur at 12 or 18 °C NT.

Table 2. Analysis of variance (ANOVA) table showing effects of average daily temperature (ADT) and irradiance on flowering of *Pharbitis nil* (L.) Chois. 'Violet'. Arcsin square root transformations were conducted on percent data before ANOVA. Unreported interactions were nonsignificant.

Characteristic	Term		
	ADT	Irradiance	ADT × Irradiance
Flowering plants (%)	***	NS	NS
Number of flower buds per plant			
Total	***	NS	NS
Terminal	***	NS	NS

NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Fig. 3. Effect of average daily temperature on flowering of *Pharbitis nil* (L.) Chois. cv. Violet across irradiance treatments. Vertical bars indicate standard errors about the treatment means.

Prolonged cool temperature (15 °C) reportedly can induce flowering in *P. nil* under long-day conditions (Kimura, 1966). Kimura (1966) hypothesized that 1) *P. nil* flowering may be insensitive to the normal inhibitory effect of long-day conditions when temperatures are cool, or 2) low temperatures promote *P. nil* flowering. We did not observe promotion of *P. nil* flowering by a similar low temperature (12 °C) when low temperature was imposed for one short-day cycle (Figs. 1 and 2).

Irradiance reportedly affects *P. nil* flowering (King and Vince-Prue, 1978; Shinozaki, 1972; Takimoto and Ikeda, 1959). Irradiance prior to induction did not affect *P. nil* flowering in our study (Table 1); however, the irradiance range applied in our study may not have been large enough to observe differences. Alternatively, our treatments may not have been applied long enough. Adding strength to this hypothesis is the fact that Shinozaki (1972) was able to induce flowering in *P. nil* seedlings by irradiating them continuously (224 or 364 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$) for 30 d using metal halide lamps alone.

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