Temperature and Photoperiod Influence Flowering and Morphology of Four *Petunia* spp.

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Abstract. Flowering and morphology of four *Petunia* Juss. spp. [*P. axillaris* (Lam.) Britton et al., *P. exserta* Stehmann, *P. integrifolia* (Hook.) Schinz & Thell., and *P. ×hybrida* Vilm.] were evaluated in response to photoperiod and temperature. Photoperiod responses were evaluated under 9-h short days (SD), 9-h photoperiod plus 4-h night-interruption lighting (NI), or a 16-h photoperiod supplemented with high-pressure sodium lamps (16-h HPS). All species flowered earlier under NI than SD and were classified as facultative (quantitative) long-day plants. Increasing the daily light integral within long-day treatments increased flower bud number for *P. axillaris* only. In a second experiment, crop timing and quality were evaluated in the temperature range of 14 to 26 °C under 16-h HPS. The rate of progress toward flowering for each species increased as temperature increased from 14 to 26 °C, suggesting the optimal temperature for development is at least 26 °C. The calculated base temperature for progress to flowering varied from 0.1 °C for *P. exserta* to 5.3 °C for *P. integrifolia*. Flowering of *P. axillaris* and *P. integrifolia* was delayed developmentally (i.e., increased node number below the first flower) at 14 °C and 17 °C or less, respectively, compared with higher temperatures. *Petunia axillaris* and *P. integrifolia* flower bud numbers decreased as temperature increased, whereas *P. ×hybrida* flower bud number was similar at all temperatures. The differences in crop timing and quality traits observed for these species suggest that they may be useful sources of variability for petunia breeding programs.

Petunia (*Petunia ×hybrida*) has long been a popular bedding plant with a wholesale value of \$110 million in 2008 (U.S. Department of Agriculture–National Agricultural Statistics Service, 2009). *Petunia* is a facultative long-day plant for flowering (Adams et al., 1998; Piring and Cathey, 1960), although *Petunia* ‘Wave Purple’ has been described as an obligate long-day plant (Erwin, 2006). *Petunias* are often produced in northern climates during the late winter and early spring months, when light levels are low and ambient photoperiods are short, necessitating the use of supplemental lighting to promote flowering. Breeding efforts have been successful in reducing the strength of the photoperiodic response (i.e., reducing the delay in flowering for plants grown under short days compared with night-interruption long days) of some cultivars (Pemberton and Roberson, 2006), although no day-neutral cultivars are known. In addition to photoperiod, daily light integral (DLI) can influence earliness of flowering by reducing node

number below the first flower (Armitage and Tsujita, 1979; Erwin and Warner, 2002; Warner and Erwin, 2003), referred to as a facultative irradiance response (Mattson and Erwin, 2005). A survey of 40 herbaceous ornamental species identified 10 species with a facultative irradiance response, 28 species that were irradiance indifferent, and two species in which node number below the first flower increased with increasing DLI (Mattson and Erwin, 2005). Adams et al. (1999) determined that increasing DLI reduced the length of the juvenile phase of *petunia* ‘Express Blush Pink’.

The time required for developmental processes to occur in plants is primarily a function of accumulated thermal time, often quantified as degree-days (Bonhomme, 2000). The rate of progress toward a developmental event (such as appearance of a new node, or flowering) increases linearly between a species-specific base temperature (T_{base}), in which development rate is nil, and an optimum temperature (Adams et al., 1997). At temperatures above the optimum, development rate declines. Growing plants at the optimum temperature for development rate, resulting in minimum production time, may be undesirable because it often results in reductions in crop quality. For example, increasing temperature from 14 to 26 °C decreased *Campanula carpatica* Jacq. time to flower, but also decreased flower number and flower size (Niu et al., 2001).

The genus *Petunia* consists of 14 currently recognized species (Stehmann et al., 2009)

native to temperate and subtropical South America. Wild relative species may hold potential for improvement of the cultivated *petunia* (*P. ×hybrida*). *Petunia ×hybrida* is derived from a cross between *P. axillaris* and *P. integrifolia* (Stehmann et al., 2009), and *Petunia* spp. are generally cross-compatible (Ando et al., 2001; Watanabe et al., 1996, 2001), although fertility varies widely between parental species combinations. Little information is available concerning the influence of light and temperature on floral timing and crop quality characteristics of wild *Petunia* spp. Therefore, the objectives of work presented here were to: 1) determine the photoperiodic response group for *P. ×hybrida* ‘Mitchell’ and three wild relative species; and 2) evaluate the influence of photoperiod and temperature on crop timing and quality parameters.

Materials and Methods

Expt. 1: Photoperiod treatments. *Petunia axillaris* (PI 28546; obtained from the USDA Ornamental Plant Germplasm Center, Columbus, OH), *P. exserta* (provided by Dr. Robert Griesbach, USDA-ARS), *P. ×hybrida* ‘Mitchell’ (provided by Dr. David Clark, Univ. of Florida), and *P. integrifolia* (Diane’s Flower Seeds, Ogden, UT) seeds were sown in 128-cell (10 mL cell volume; one seed per cell) trays on 3 Feb. 2008 and placed in a greenhouse at 23 ± 1.0 °C (24-h mean ± SD) under intermittent mist. When two true leaves had unfolded, seedlings were transplanted into 10-cm diameter round pots (450 mL) containing (v/v) 70% peatmoss, 21% vermiculite, and 9% perlite (Sure-Mix; Michigan Grower Products, Galesburg, MI) and placed into one of three treatments. Treatments were: short days (SD; a truncated 9-h photoperiod obtained by covering plants with opaque cloth from 1700 to 0800 HR daily), long days provided as night interruption lighting (NI; 9-h photoperiod obtained by covering plants with opaque cloth from 1700 to 0800 HR daily plus 3 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ night-interruption lighting from incandescent lamps from 2200 to 0200 HR), or a 16-h photoperiod (16-h HPS; ambient light plus 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from high-pressure sodium lamps from 0600 to 2200 HR) at 20 ± 1 °C (24-h mean ± SD) until flowering. Photosynthetic photon flux at the top of the plant canopy was measured in each treatment every 10 s with a 10-photodiode line quantum sensor (Apogee Instruments, Logan, UT) connected to a data logger (CR10; Campbell Scientific, Logan, UT). Hourly averages were stored and used to calculate DLI. The mean DLI for the SD, NI, and HPS treatments was 11.4, 11.5, and 16.5 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, respectively.

Expt. 2: Temperature effects on crop timing and quality. Seeds of the same species were sown and transplanted as described previously and then were placed into one of five greenhouse compartments set to a constant temperature of 14, 17, 20, 23, or 26 °C under a 16-h photoperiod supplemented with HPS lamps as described for Expt. 1. Air temperature in each treatment was measured

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by a Type E thermocouple (TT-E-40; Omega Engineering, Stamford, CT) placed in an aspirated tube. Thermocouples were connected to a data logger (CR10) and data were recorded every 10 s. Hourly averages were stored. Actual mean temperatures $\pm$ SD during the experimental period were 14.0 ± 0.75 , 17.0 ± 0.50 , 20.0 ± 1.1 , 22.6 ± 0.64 , and 25.7 ± 0.60 °C. Vapor pressure deficit was maintained between 0.7 and 1.0 kPa at each temperature by steam injection.

Plant culture. Plants were irrigated as needed with reverse osmosis-treated well water supplemented with (mg·L⁻¹): 125 nitrogen, 13 phosphorus, 125 potassium, 15 calcium, 1 iron, 0.1 boron and molybdenum, and 0.5 manganese, zinc, and copper (MSU Special; GreenCare Fertilizers, Kankakee, IL).

Experimental design, data collection, and analysis. Both experiments were fully factorial split plot designs with plants arranged in two replicated blocks of 10 plants each per species per main plot. In Expt. 1, photoperiod treatment constituted the main plot with three levels, whereas in Expt. 2, temperature was the main plot with five levels. Species was the subplot in each experiment. Block effects were not significant in any case. Therefore, data were pooled for subsequent analysis. In both experiments, at anthesis of the first flower, the date was recorded and the number of nodes on the primary shoot below the open flower, number of visible flower buds (greater than 3 mm in length), and the number of lateral branches (greater than 5 cm in length) were determined. Flowering rate in response to temperature was calculated as 1/days to flower. Analyses of variance and means separations [Tukey's HSD_(0.05)] were conducted using the general linear model procedure of the SPSS 17.0 for Windows statistical software package (SPSS Inc., Chicago, IL). Regression analyses were performed with Sigmaplot 8.0 (Systat Software, Chicago, IL). Linear regression analysis was conducted on flowering rate as a function of temperature. The slope (b_1) and y-intercept (b_0) of each equation were used to calculate T_{base} ($-b_0/b_1$) and degree-days to flowering ($1/b_1$) for each species.

Results

Species and photoperiod treatment interacted to impact time to flower, number of nodes below the first flower, and flower bud number (Table 1). All species flowered earlier in time and with fewer nodes under NI than SD (Table 1). The increase in node number below the first flower under SD compared with NI ranged from 14 nodes for *P. exserta* (from 12 to 26 nodes) to 22 nodes for *P. integrifolia* (from 18 to 40 nodes). *Petunia exserta* formed the fewest nodes below the first flower regardless of treatment. Growing under 16-h HPS did not reduce node number below the first flower or time to flower for any species compared with NI (Table 1). Although *P. exserta* formed fewer nodes below the first flower than *P. axillaris* or *P. integrifolia* under NI, time to flower was

Table 1. Influence of short days (SD; 9-h photoperiod), long days provided as a 4-h night interruption (NI), or long days provided by 16-h lighting with high-pressure sodium lamps (16-h HPS) on time to flower (in days), number of nodes below the first flower (nodes), number of visible flower buds at first flowering (buds), and the number of lateral branches at first flowering (branches; greater than 5 cm in length) for four *Petunia* spp.^z

Species	Photoperiod	Time to flower (d)	Nodes (no.)	Buds (no.)	Branches (no.)
<i>P. axillaris</i>	SD	70 b	37.6 b	36.7 b	10.0 b
	NI	49 a	17.7 a	14.2 a	8.4 a
	16-h HPS	45 a	20.0 a	33.7 b	7.7 a
<i>P. exserta</i>	SD	64 b	25.8 b	24.9 b	8.8 b
	NI	52 a	12.3 a	13.4 a	7.2 b
	16-h HPS	53 a	13.0 a	14.9 a	4.9 a
<i>P. ×hybrida</i>	SD	71 b	36.5 b	39.3 b	16.4 a
	NI	63 a	22.3 a	23.1 a	15.1 a
	16-h HPS	59 a	24.1 a	28.4 a	12.0 a
<i>P. integrifolia</i>	SD	70 b	40.3 b	30.9 a	13.2 b
	NI	49 a	18.3 a	25.7 a	6.8 a
	16-h HPS	48 a	19.1 a	31.7 a	8.4 a
Source		Significance			
Species		****	***	***	***
Photoperiod		***	***	***	***
Species × photoperiod		***	*	*	NS

^zValues followed by different letters indicate significant differences across photoperiod treatment within a species as determined by Tukey's HSD_(0.05). Means are based on two blocks of 10 plants each.

^yNS, * and *** indicate nonsignificance or significance at $P < 0.05$ or 0.001, respectively.

similar for all three species (Table 1), indicating a lower node appearance rate for *P. exserta*.

Species and photoperiod treatment interacted to impact flower bud production. All species except *P. integrifolia* produced more flower buds at first flowering under SD than NI (Table 1). Growing plants under 16-h HPS increased flower bud number compared with NI for *P. axillaris* only. Branch number at first flowering varied by species and by photoperiod treatment. *Petunia axillaris* and *P. integrifolia* produced more branches under SD than under NI or 16-h HPS (Table 1). Photoperiod treatment did not significantly influence *P. ×hybrida* branch production, whereas *P. exserta* produced fewer branches under 16-h HPS than SD or NI.

Increasing temperature from 14 to 26 °C decreased time to flower for all species (Fig. 1). The time to flower response to temperature was best fit by a quadratic polynomial equation for each species. The rate of progress toward flowering increased as a linear function of temperature between 14 and 26 °C for all four species (Table 2). Species varied in calculated T_{base} , ranging from 0.1 °C for *P. exserta* to 5.3 °C for *P. integrifolia* (Table 2). Because the flowering rate continued to increase throughout the range of temperatures evaluated, the optimum temperature for rate of progress to flowering is at least 26 °C for all species.

The effect of temperature on node number below the first flower varied by species (Table 3). *Petunia axillaris* node number was similar as temperature decreased from 26 to 17 °C, but increased as temperature further decreased to 14 °C. *Petunia integrifolia* node number was similar from 26 to 20 °C, but increased as temperature declined to 17 or 14 °C. In contrast, *P. exserta* node number was greater at 26 than 14 °C (Table 3).

Flower bud number response to temperature varied by species (Table 3). For example,

P. axillaris and *P. integrifolia* flower number declined as temperature increased, whereas *P. ×hybrida* flower number was similar at all temperatures. *Petunia axillaris* bud number was more temperature-sensitive than the other species, declining from 42.5 buds at 14 °C to 20.1 buds at 26 °C, a 53% decrease. *Petunia ×hybrida* and *P. integrifolia* branch number decreased as temperature increased from 14 to 26 °C (Table 3). *Petunia exserta* branch number was lower at 20 and 23 °C than at 14 °C.

Discussion

All four species responded as facultative (quantitative) long-day plants, forming fewer nodes below the first flower under NI compared with SD (Table 1), although flowering occurred under all photoperiods. The similar photoperiodic responses of the evaluated *Petunia* spp. are perhaps not surprising considering that the genus is small with only 14 species and occurs naturally in a relatively narrow geographic area. In contrast, species of the genus *Hibiscus* L., with 250 to 300 species (Bates, 1965) distributed widely throughout the world, exhibit a wide range of photoperiodic responses, including obligate and facultative short-day, day-neutral, and facultative and obligate long-day species (Warner and Erwin, 2001). However, despite the similar and relatively strong photoperiodic response of the *Petunia* spp. evaluated here, it may be possible to use these species to breed for petunia cultivars with reduced photoperiod sensitivity, because interspecific hybrid populations derived from these species exhibited wide variation for floral timing traits such as node number below the first flower and days to flower (Warner and Walworth, 2010). Also, evaluation of 51 seed-propagated trailing petunia cultivars revealed that although flowering time of all cultivars was accelerated by night-interruption lighting compared with ambient

Fig. 1. Influence of temperature on days to flower for (A) *Petunia axillaris*, (B) *P. exserta*, (C) *P. xhybrida* 'Mitchell', and (D) *P. integrifolia*. Also shown are the significance levels of linear (L) and quadratic (Q) regressions of the data with ** and *** representing significance at $P < 0.01$ and 0.001 , respectively, and predictive models for days to flower (DTF) in response to temperature (T). Error bars represent se about the mean.

Table 2. Linear regression coefficients and calculated values for base temperature (T_{base}) for progress to flowering and thermal time (in degree-days) to flowering for four *Petunia* spp.²

Species	b_0	b_1	Degree-days to flowering	T_{base} (°C)
<i>P. axillaris</i>	-0.0048	0.0013	769	3.7
<i>P. exserta</i>	-0.0010	0.0010	1000	0.1
<i>P. xhybrida</i>	-0.0015	0.0010	1000	1.5
<i>P. integrifolia</i>	-0.0080	0.0015	667	5.3

²Time to flower data were converted to rate of progress to flowering (1/days to flower) for linear regression analysis with temperature as the independent variable. Equations are in the form $\text{Rate} = b_0 + b_1 T$ where b_0 is the y-intercept, b_1 is the slope, and T is temperature. Degree-days to flowering and T_{base} values are calculated from linear regression models for data from plants grown between 14 and 26 °C.

short photoperiods, the acceleration ranged from 32 d for 'Tidal Wave Hot Pink' to only 4 d for 'Ramblin' Burgundy Chrome' (Pemberton and Roberson, 2006).

Within the long-day treatments, increasing the DLI from the NI (11.5 mol·m⁻²·d⁻¹) to 16-h HPS (16.5 mol·m⁻²·d⁻¹) treatment increased flower bud number for *P. axillaris* only, from 14.2 to 33.7 buds. Increasing flower bud numbers with increased DLI have been observed in other species, although the DLI resulting in the maximum flower production varies widely. Increasing DLI from 6.7 to 8.9 mol·m⁻²·d⁻¹ increased *Hibiscus radiatus* flower bud number from seven to 10 buds (Warner and Erwin, 2003), although further increasing DLI (up to 16.7 mol·m⁻²·d⁻¹) did not further increase flower bud number. Faust et al. (2005) evaluated several bedding plant species under mean DLIs of 5, 12, 19, and 43 mol·m⁻²·d⁻¹. *Begonia xsemperflorens-cultorum* L. 'Vodka Cocktail' flower number was highest at a DLI of 19 mol·m⁻²·d⁻¹ or higher, whereas *Catharanthus roseus* L. 'Pacific Lilac', *Petunia xhybrida* 'Apple Blossom', *Tagetes erecta* L.

'American Antigua Orange', and *Zinnia elegans* L. 'Dreamland Rose' flower numbers were highest at 43 mol·m⁻²·d⁻¹.

The optimal temperature for minimizing time to flower appears to be at least 26 °C for each *Petunia* species evaluated here, because time to flower decreased with increasing temperature from 14 to 26 °C, similar to results for *P. xhybrida* 'Snow Cloud', which had an optimum temperature of 25 °C (Kaczperski et al., 1991). Differences in time to flower across species at a given temperature were explained by interactions between degree-days to flower and T_{base} . For example, both *P. exserta* and *P. xhybrida* required 1000 degree-days to flower (Table 2). However, *P. exserta* T_{base} is lower and consequently accumulates more degree-days per day than *P. xhybrida*. Similarly, although *P. axillaris* had a higher degree-day requirement for flowering than *P. integrifolia*, days to flower at a given temperature were generally higher for *P. integrifolia* because it had a higher T_{base} . Although T_{base} is a useful variable for modeling crop timing responses to temperature, it

is not a good predictor for low-temperature stress tolerance. For example, *P. exserta* had the lowest T_{base} of the four species evaluated here; however, it was also the most freezing-sensitive of the four species after cold acclimation (Walworth and Warner, 2009).

The increase in time to flower at low temperatures for *P. axillaris* (at 14 °C) and *P. integrifolia* (14 and 17 °C), compared with warmer temperatures, was attributable both to slower leaf unfolding rates and an increase in the number of nodes formed below the first flower. Mattson and Erwin (2003) previously noted that increasing temperature from 12 to 24 °C decreased petunia 'Avalanche Pink', 'Dreams Rose', and 'Wave Purple' node number below the first flower. In contrast, *Salvia splendens* F. Sello ex Roem & Schult. 'Vista Red' and *Tagetes patula* L. 'Bonanza Yellow' developed a similar number of nodes below the first flower, regardless of temperature between 14 and 26 °C (Moccaldi and Runkle, 2007). *Petunia exserta* node number below the first flower was greater at 26 than 14 °C, indicating that not all *Petunia* spp. experience developmental delay in flowering at cool temperatures.

Increasing temperature reduced flower bud number of *P. axillaris* and *P. integrifolia* (Table 3). Similarly, flower bud number of nine grandiflora-type *P. xhybrida* cultivars declined as temperature increased from 14 to 26 °C (Warner, unpublished data). In contrast, *P. xhybrida* 'Mitchell' exhibited much greater thermal stability for floral production across the evaluated temperature range, because flower bud number did not decline with increasing temperature (Table 3). This

Table 3. Effect of temperature on the number of nodes below the first flower (nodes), number of visible flower buds at first flowering (buds), and number of lateral shoots (branches) for four *Petunia* spp. grown under a 16-h photoperiod.^z

Species	Temperature (°C)	Nodes (no.)	Buds (no.)	Branches (no.)
<i>P. axillaris</i>	14	29.1	42.5	11.1
	17	21.0	39.4	8.8
	20	20.1	31.7	7.7
	23	19.4	24.9	9.1
	26	19.3	20.1	8.2
Significance		***y	***	***
<i>P</i> _{linear}		NS	***	NS
<i>P</i> _{quadratic}		*	*	NS
<i>P. exserta</i>	14	12.6	22.7	11.1
	17	13.1	16.4	8.4
	20	14.6	22.2	6.5
	23	14.1	30.3	6.8
	26	15.0	24.0	9.0
Significance		*	***	***
<i>P</i> _{linear}		*	NS	NS
<i>P</i> _{quadratic}		NS	NS	**
<i>P. ×hybrida</i>	14	24.3	32.2	12.4
	17	23.7	33.5	12.7
	20	25.7	39.7	11.1
	23	22.9	37.6	9.9
	26	21.9	42.6	8.9
Significance		*	***	***
<i>P</i> _{linear}		NS	*	*
<i>P</i> _{quadratic}		NS	NS	*
<i>P. integrifolia</i>	14	25.3	39.0	10.6
	17	24.7	31.9	10.1
	20	17.4	32.6	6.0
	23	15.5	24.3	6.5
	26	14.6	20.9	6.6
Significance		***	***	***
<i>P</i> _{linear}		*	**	NS
<i>P</i> _{quadratic}		NS	NS	NS

^zMeans are based on two blocks of 10 plants each.

^yNS, *, ** and *** indicate nonsignificance or significance at $P < 0.05$, 0.01, or 0.001, respectively.

genotype may be a useful genetic source for improving floral production of modern *P. ×hybrida* cultivars at higher temperatures.

Collectively, these results indicate that although all four species were classified as facultative long-day plants, considerable variation exists in crop timing and quality traits in response to light and temperature, and these species may therefore be useful sources of genetic variation that can be used in *Petunia* breeding programs.

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