HORTSCIENCE 33(7):1172–1174. 1998.

Flowering of *Phlox paniculata* Is Influenced by Photoperiod and Cold Treatment

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Additional index words. critical photoperiod, herbaceous perennial, long-day plant, perennial phlox

Abstract. ***Phlox paniculata*** **Lyon ex Pursh 'Eva Cullum' plants were grown under seven photoperiods following 0 or 15 weeks of 5 °C to determine the effects of photoperiod and cold treatment on flowering. Photoperiods were a 9-hour day extended with incandescent lamps to 10, 12, 13, 14, 16, or 24 hours; an additional treatment was a 9-hour day with a 4-hour night interruption (NI). Noncooled plants remained vegetative under photoperiods ≤13 hours; as the photoperiod increased from 14 to 24 hours, flowering percentage increased from 20 to 89. Flowering of noncooled plants took 73 to 93 days. Flowering percentage was 19, 50, or 100 when cooled plants were held under photoperiods of 10, 12, or ≥13 hours or NI, respectively. Time to flower in cooled plants progressively decreased from 114 to 64 days as the photoperiod increased from 10 to 24 hours. Reproductive cooled plants had at least three times more flowers, were at least 50% taller, were more vigorous, and developed seven or eight more nodes than did noncooled plants. Photoperiod had no effect on height of flowering plants.**

Interest in forcing herbaceous perennials into flower continues to increase, creating a demand for knowledge of species-specific flowering requirements. The attractive large panicles of perennial phlox make it a popular species; in 1994, *Phlox* was one of the top 10 best-selling genera of herbaceous perennials (Rhodus and Hoskins, 1995). In many herbaceous perennials, flowering is controlled by temperature, photoperiod, or both. To our knowledge, little detailed information exists on how these conditions affect flowering of *Phlox paniculata*.

Vernalization may be defined as a cold-temperature treatment that is given to an imbibed seed or young plant and promotes flowering at subsequent higher temperatures (Thomas and Vince-Prue, 1997). The duration and effective temperature range necessary to saturate the vernalization response vary with species, but, in general, a population of plants requires several weeks of cold, with an optimum range of 1 to 7 °C (Lang, 1965). However, the classical botanical definition of vernalization ignores other flowering parameters of horticultural importance. A cold-temperature treatment, not necessarily one that vernalizes a plant, could enhance flowering in any of the following ways: higher flowering percentage, faster flowering, increased flower production, improved flowering uniformity, and increased vigor.

Photoperiod is a completely reliable environmental signal for flower induction with respect to calendar date at a given latitude. Many herbaceous perennials require long days for flowering [e.g., are qualitative long-day plants (LDP)]; *Achillea millefolium* L. 'Summer Pastels' and *Coreopsis verticillata* L. 'Moonbeam' are examples (Iversen and Weiler, 1994; Zhang et al., 1996). The effect of photoperiod on flowering of *P. paniculata* has been investigated twice, but with different results: long days had little promotive effect on flowering in one study (Roberts and Struckmeyer, 1938) but were required for flowering in another (Iversen and Weiler, 1994).

Critical photoperiod was defined by Thomas and Vince-Prue (1997) as the daylength that marks the transition between vegetative growth and flowering during an experiment, but this definition does not address the stochastic nature of flowering in an experiment in which some plants flower and others do not. Roberts and Summerfield (1987) proposed several definitions for the critical photoperiod of LDP, including that photoperiod above which time to flowering is minimal and not affected by further increases in photoperiod, and below which flowering is delayed. From this definition, an LDP that flowers most rapidly under 24-h of continuous light would have a critical photoperiod of 24 h.

In practice, flowering percentage, time to flower, and flowering uniformity are all important to a commercial grower. We define the critical photoperiod of LDP as the photoperiod that, if met or exceeded, induces a population of plants to flower completely, rapidly, and uniformly. Daylengths shorter than the critical daylength may induce incomplete or delayed flowering.

Roberts and Summerfield (1987) also proposed an additional flowering photoperiod concept for qualitative plants, the base photoperiod, which for LDP is that photoperiod at which, if shortened, plants remain vegetative. For horticulturists, strictly vegetative growth is useful for increasing plant size or producing cuttings for propagation. Transitional photoperiods, those that induce only part of a population to flower, are perhaps horticulturally least desirable.

The objectives of these experiments with *P. paniculata* were to identify the critical, base, and transitional photoperiods and to quantify the effects of a cold treatment on flowering to facilitate propagation and production.

Materials and Methods

Plant material. The experiment was replicated in time, beginning on 9 Nov. 1995 (Year 1) and 4 Nov. 1996 (Year 2). Experimental treatments were identical between years unless noted. Stem cuttings were propagated by a Pennsylvania wholesale grower in June 1995 and May 1996 and grown under natural daylengths (lat. 40°N) at 16 to 29 °C. Seventy-cell plug (50-mL volume) trays were received on 18 Oct. 1995 or 15 Oct. 1996; plants averaged nine or 14 nodes, respectively. Plug trays were exposed to natural daylengths at 20 °C (lat. 43°N) until the experiments began.

Cold treatment. One-half of the plug trays were placed in a controlled-environment chamber for 15 weeks at 5 °C; the chamber was illuminated from 0800 to 1700 HR at ≈10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from cool-white fluorescent lamps (VHOF96T12; Philips, Bloomfield, N.J.), as measured with a LI-COR quantum sensor (model LI-189; LI-COR, Inc., Lincoln, Nebr.). While in the cooler, plugs were watered with well water ($CaCO_3$ at 340 $mg \cdot L^{-1}$) acidified (93% H_2SO_4) to a titratable alkalinity of $CaCO_3$ at 100 $mg \cdot L^{-1}$.

Light treatments. Seventy plants without or with a cold treatment were removed from the plug trays and transplanted into 13-cm square plastic containers (1.1-L volume). Following cold treatment, stems were pruned at planting just above soil level, because shoots died during cold treatment. Ten plants were used per treatment and treatments were assigned randomly each year to greenhouse benches. Opaque black cloth was pulled at 1700 HR and opened at 0800 HR every day on all benches so plants received a similar daily light integral. From 0800 to 1700 HR, high-pressure sodium lamps provided a supplemental photosynthetic photon flux (*PPF*) of ≈50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant level when the ambient greenhouse *PPF* was <400 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Photoperiods were 10, 12, 13, 14, 16, or 24 h of continuous light or 9 h with a 4-h (2200 to 0200 HR) NI. Continuous photoperiods consisted of 9-h days completed by day-extension

Received for publication 8 Jan. 1998. Accepted for publication 10 June 1998. We gratefully acknowledge the support of the Michigan Agricultural Experiment Station and funding by greenhouse growers supportive of Michigan State Univ. floricultural research. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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lighting; lamps were turned on at 1700 HR and turned off after each photoperiod was completed. Day-extension and NI lighting (1–3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at canopy level) was provided by incandescent lamps. In Year 2, the average daily light integral during the experiment was measured at canopy level with quantum sensors (LI-COR) connected to a CR10 datalogger (Campbell Scientific, Logan, Utah) (Table 1).

Plant culture. Plants were grown in a commercial soilless medium composed of composted pine bark, horticultural vermiculite, Canadian sphagnum peat, processed bark ash, and washed sand (MetroMix 510; Scotts-Sierra Horticultural Products Co., Marysville, Ohio). Plants were fertilized at every irrigation using well water (EC of 0.65 $mS \cdot cm^{-1}$ and 105, 35, and 23 $mg \cdot L^{-1}$ Ca, Mg, and S, respectively), acidified (two parts H_3PO_4 plus one part H_2SO_4, which provided P at ≈80 $mg \cdot L^{-1}$) to a titratable alkalinity of ≈130 $mg \cdot L^{-1}$ $CaCO_3$ containing 200N–0P–155K $mg \cdot L^{-1}$ (36% ammoniacal N) from KNO_3 and NH_4NO_3 and applied by top-watering with minimal leaching. Micronutrients (Fe, Mn, Zn, Cu, B, and Mo) were added with a commercially available blended chelated material [Compound 111 (1.50 Fe–0.12 Mn–0.08 Zn–0.11 Cu–0.23 B–0.11 Mo); Scotts] at a constant 50 $mg \cdot L^{-1}$.

Greenhouse temperature control. All plants were grown in a glass-glazed greenhouse at 20 °C. Air temperatures on each bench were monitored with 36-gauge (0.127-mm diameter) type E thermocouples connected to a CR10 datalogger (Campbell Scientific). To provide uniform night temperatures, the datalogger controlled a 1500-W electric heater, which provided supplemental heat under each bench as needed throughout the night. The datalogger collected temperature data every 10 s and recorded the hourly average. Average daily air temperatures from the beginning of forcing to the average date of flowering under every photoperiod each year were calculated (Table 1).

Data collection and analysis. Nodes per plant were counted when forcing began. The date the first flower bud was visible (without dissection) and the date the first flower opened were recorded for each plant. At flowering, the visible flower buds and nodes on the main stem below the first flower were counted, and total plant height (not including the container) was measured. Plants that did not have visible buds after 15 weeks of forcing were considered nonflowering and discarded. Days to visible bud, days from visible bud to flower, days to flower, node-count increase from the start of forcing, and rate of node development (determined by dividing the increase in node number by days to visible bud) were calculated. Plants that died during the experiment were discarded and not included in the results.

Each year, a completely randomized design with eight to 10 observations for each photoperiod and cold treatment was used. Data were analyzed using SAS's (SAS Institute, Cary, N.C.) analysis of variance (ANOVA) and general linear models (GLM) procedures. Data were pooled for all measured characteristics, and when there was a significant year × treatment interaction, the comparisons were analyzed separately for each year.

Table 1. Average air temperatures and daily light integrals from date of forcing to average date of flowering of *Phlox paniculata* 'Eva Cullum' under each photoperiod.

Year	Weeks at 5 °C	Average daily light integral ($mol \cdot m^{-2} \cdot d^{-1}$)	Photoperiod (h) 10	12	13	14	16	24	NI[z]
			Average air temperature during forcing (°C)						
1995–96	0	-[y]	--[x]	--	--	20.8	20.2	20.6	20.6
	15	-	--	20.7	21.1	21.2	20.5	21.1	20.8
1996–97	0	7.7	--	--	--	20.5	20.5	21.5	20.9
	15	11.0	20.6	20.2	20.9	20.8	20.1	20.7	21.1

[z]9-h photoperiod plus 4-h night interruption.
[y]Not measured (one dash).
[x]No plants flowered (two dashes).

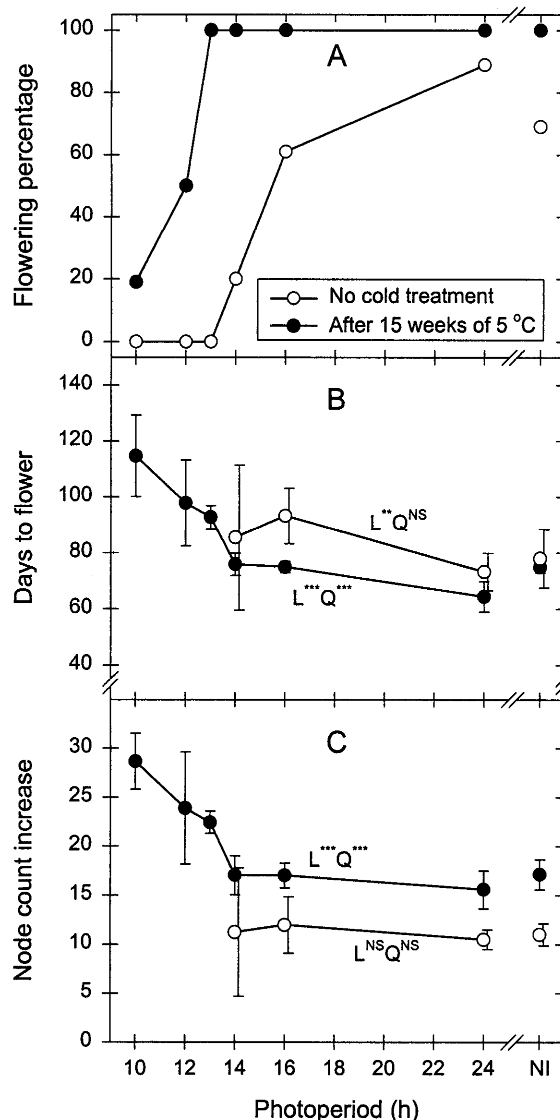

Fig. 1. Flowering of *Phlox paniculata* 'Eva Cullum' under various photoperiods after 0 or 15 weeks of 5 °C cold treatment. Continuous photoperiodic treatments consisted of 9-h natural days extended with light from incandescent lamps. NI = 9-h photoperiod plus 4-h night interruption. Error bars are 95% confidence intervals and for clarity are offset to the right of data points for noncooled plants. L = linear; Q = quadratic trends. NS, **, ***Nonsignificant or significant at $P \leq 0.01$ or 0.001, respectively.

Results

Without a cold treatment, flowering percentage never reached 100 under any photoperiod. No noncooled plants flowered under photoperiods ≤13 h, and as the photoperiod increased from 14 to 24 h, flowering percentage increased from 20% to 89% (Fig. 1A). Only 69% of plants flowered under a 4-h NI. After cold treatment, all plants flowered when photoperiods were ≥13 h or with NI.

Under the same photoperiods, plants flow-

ered sooner following cold treatment than without (Fig. 1B). After cold treatment, time to flower progressively decreased (linearly or quadratically) by nearly 50% as the photoperiod increased from 10 to 24 h (Fig. 1B). Except for the continuous light treatment, uniformity in time to flower improved at least 3-fold following cold treatment, based on the standard deviation. Mean time from visible bud to flower was 8.7 and 11.5 d (significantly different at $P < 0.001$) for noncooled and cooled plants, respectively, and was not influenced by photoperiod. Without cold treatment, time to flower was slightly delayed under NI compared with that in the 24-h photoperiod ($P < 0.01$). Cooled plants flowered most rapidly but with higher variability under continual light than did plants under 16-h photoperiods or NI; the standard deviation in days to flower was 3.8, 10.2, or 3.4 under 16 or 24 h or NI, respectively.

Cooled plants produced seven to eight more nodes, developed at least three times more flowers, and were at least 50% taller than noncooled plants (Fig. 1C, Table 2). Flower number was highly variable under all photoperiods, and no significant differences existed. For cooled plants, the number of new nodes produced decreased as the photoperiod increased from 10 to 24 h. Regardless of photoperiod, the rate of plant node development at 20 °C was 0.15 to 0.17 vs. 0.25 to 0.28 nodes/day without and after cold treatment, respectively. Photoperiod did not significantly influence final plant height of flowering plants.

Table 2. The effects of photoperiod and cold treatment on plant height and flower number of *Phlox paniculata* 'Eva Cullum'.

Weeks at 5 °C	Photoperiod (h)	No. flowering plants	Plant height at flowering (cm)	No. flowers and buds
0	10	0	---	---
	12	0	---	---
	13	0	---	---
	14	3	26	17
	16	11	25	28
	24	17	30	28
	NI[z]	10	24	22
15	10	3	53	138
	12	7	43	112
	13	16	47	99
	14	16	43	89
	16	16	50	127
	24	16	51	89
	NI	15	46	127
Significance				
Weeks cold (WC)			***	***
Photoperiod (P)			NS	NS
WC × P			NS	NS
Contrasts				
0 weeks of 5 °C				
P_{Linear}			NS	NS
$P_{Quadratic}$			NS	NS
15 weeks of 5 °C				
P_{Linear}			NS	NS
$P_{Quadratic}$			NS	NS

[z]NI = 9-h photoperiod plus 4-h night interruption.

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

Discussion

For potted plant production of *P. paniculata*, a cold treatment is required for complete, rapid, and uniform flowering and a high flower count. In this experiment, the increased flower count could be attributed to a higher average daily light integral after cold treatment (Table 1), as cold treatment and daily light integral are confounded. However, growth of cooled plants was much more vigorous than that of noncooled plants, as indicated by the accelerated rate of node development.

The most rapid and complete flowering of *P. paniculata* occurred under continuous light; thus, the critical photoperiod based on our definition is 24 h. The base photoperiod is ≈13 h for noncooled plants and <10 h for cooled plants. After cold treatment, transitional photoperiods were >10 and <13 h. Fourteen- or 16-h photoperiods or a 4-h NI induced the most uniform flowering. Flowering was incomplete, nonuniform, and delayed in cooled plants under photoperiods ≤12 h. Providing plants with a cold treatment and photoperiods <10 h (perhaps 8 or 9 h) should produce stock plants for vigorous, vegetative cuttings.

In a study by Iversen and Weiler (1994) on *P. paniculata* 'Fairy's Petticoat', a cold treatment was not required for complete flowering. However, they found similar beneficial effects of cold treatments on flowering: plants stored for 12 weeks at 4.5 °C flowered more uniformly and 10 to 15 d sooner, and were more "robust" and about one-third taller than noncooled plants. Furthermore, no plants flowered under 8-h photoperiods, whereas all flowered under 16- or 24-h photoperiods. We also found that *P. paniculata* 'Tenor' responded to cold treatment and photoperiod similarly to 'Eva Cullum' (Runkle, 1996), which suggests that these responses could be applied to other cultivars of the same species. Roberts and Struckmeyer (1938) found little effect of photoperiod on flowering. However, no data were presented, and the short-day photoperiod consisted of natural photoperiods (≤12 h) and was relatively uncontrolled, which makes comparisons difficult.

Recommendations for propagation of vegetative *P. paniculata* cuttings include cold-treating plants and providing photoperiods <10 h. For commercial production of flowering plants, we suggest cold-treating material and forcing under photoperiods ≥14 h or using a 4-h NI.

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