Flowering of Herbaceous Perennials under Various Night Interruption and Cyclic Lighting Treatments

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Abstract. Six long-day species of herbaceous perennials were grown under six night-interruption (NI) photoperiod treatments to determine their relative effectiveness at inducing flowering. Photoperiods were 9-hour natural days with NI provided by incandescent lamps during the middle of the dark period for the following durations: 0.5, 1, 2, or 4 hours; 6 minutes on, 54 minutes off for 4 hours (10% or 6/54 cyclic lighting); or 6 minutes on, 24 minutes off for 4 hours (20% or 6/24 cyclic lighting). For five species, the experiment was repeated with more mature plants; for the sixth, *Rudbeckia fulgida* Ait. 'Goldsturm', following a cold treatment of 8 weeks at 5 °C. The species generally showed a quantitative flowering response to the NI duration until a saturation duration was reached; as the length of the uninterrupted night break increased, flowering percentage, uniformity, and number and plant height increased and time to flower decreased. Minimum saturation durations of NI were 1 hour for *Coreopsis grandiflora* Hogg ex Sweet 'Early Sunrise' and *Hibiscus moscheutos* L. 'Disco Belle Mixed', 2 hours for *Campanula carpatica* Jacq. 'Blue Clips' and *Coreopsis verticillata* L. 'Moonbeam', and 4 hours for unchilled *R. fulgida* 'Goldsturm'. *Echinacea purpurea* Moench 'Bravado' flowered similarly across all lighting treatments. The 6/24 cyclic lighting regimen induced flowering comparable to that under a continual 4-hour NI for four of the six species and the cold-treated *R. fulgida* 'Goldsturm'. Flowering under the 6/54 regimen was generally incomplete, nonuniform, and delayed compared to that under saturation duration treatments. Three of five species flowered earlier when more mature plants were placed under the NI treatments. Cold-treated *R. fulgida* 'Goldsturm' flowered more rapidly than unchilled plants and the saturation duration of NI decreased to 1 hour.

In the floriculture industry, photoperiod often is manipulated artificially to keep plants vegetative or induce flowering. For most photoperiodic plants, the duration of the uninterrupted dark period determines whether plant development is vegetative or reproductive (Vince-Prue, 1975). Under natural short days (SD), night-interruption (NI) lighting effectively breaks up the long dark period (Vince-Prue and Canham, 1983). In general, NI more effectively induces flowering than the same quantity or duration of light added to the end of the photoperiod (Thomas and Vince-Prue, 1997).

A 4-h NI (e.g., from 2200 to 0200 HR) generally is recommended for long-day plants (LDP) (Mastalerz, 1977) and is adequate to

induce flowering in several genera of long-day (LD) herbaceous perennials, including *Campanula*, *Coreopsis*, and *Lavandula* (Damann and Lyons, 1996; Whitman et al., 1996, 1997). Durations of NI longer than 4 h may not improve flowering: a 7-h NI induced flowering similar to that induced by a 4-h NI in six species of herbaceous perennials (Hamaker et al., 1996), and *Asclepias tuberosa* L. flowered similarly under a 4- or 8-h NI (Albrecht and Lehmann, 1991). The efficacy of shorter NI durations or cyclic lighting in inducing flowering of LD herbaceous perennials has not been investigated.

Most short-day plants (SDP) remain vegetative when illuminated for 0.5 h or less during the middle of the night (Vince-Prue, 1994). To promote flowering, LDP often require longer durations of light, higher intensities, or both (Thomas and Vince-Prue, 1997). For example, in the LDP carnation (*Dianthus caryophyllus* L.), a 0.5-h NI with incandescent lamps during the middle of 16-h dark periods failed to promote flowering, whereas a 2-h NI produced an LD flowering response (Harris, 1968). In another study, 15-min light breaks interrupting 16-h dark periods did not induce flowering in the LDPs: sugar beet (*Beta vulgaris* L.), henbane (*Hyoscyamus niger* L.), dill (*Anethum graveolens* L.), dandelion (*Lolium*

temulentum L.), and petunia (*Petunia ×hybrida* Vilm.-Andr.) (Lane et al., 1965).

Cyclic, or intermittent, lighting consists of lamps being flashed on and off so that light and dark cycles are provided throughout the usual lighting period. The primary advantage of cyclic lighting is an energy savings of 60% to 80% (Bickford and Dunn, 1972; Canham, 1966). Furthermore, when the supply of electricity is limited, one may light a much larger area by alternating the light cycles among greenhouse sections. The total period of illumination during cyclic lighting regimens varies from 2% up to 50% of the total dark period (Bickford and Dunn, 1972; Vince-Prue and Canham, 1983).

Hume (1939), one of the first to study the effects of cyclic lighting on flowering of SDP and LDP, found that efficacy varied with species and the timing and duration of lighting during the cycle. Some SDP, such as *Dendranthema* spp., remained vegetative under a cyclic regimen of lights on for a minimum of 5% to 40% of a 4-h dark period (Smith and Langhans, 1962a). When fluence was kept constant, short cycles (3 s·min⁻¹) were more effective than ones with longer light periods and cycle times (Borthwick and Cathey, 1962; Cathey and Borthwick, 1961). Flowering response of LDP to cyclic lighting varies considerably and has been investigated only in a few species.

Our objective was to identify how various NI treatments induced flowering in six LD herbaceous perennial species. We wanted to determine: 1) the minimum duration of NI lighting for complete, rapid, and uniform flowering; 2) the effectiveness of cyclic lighting at promoting flowering; and 3) if more mature plants responded differently to light-break treatments than did younger plants.

Materials and Methods

Plant material. The species studied, plug size, and age of plant material are provided in Table 1. The experiment was replicated in time, with Expts. 1 and 2 beginning on 20 Dec. 1995 and 16 Feb. 1996, respectively. Plants in Expt. 2 were propagated on the same date as those in Expt. 1. Except for *R. fulgida* 'Goldsturm', plants were grown under natural short-day photoperiods (≤11.5 h of light) until the beginning of the experiment, so plants in Expt. 2 were more mature (higher node count) than those used in Expt. 1 (Table 1).

Cold treatment. *Rudbeckia fulgida* 'Goldsturm' with an average of 11 nodes (leaves) either received no cold treatment (Expt. 1) or were placed in a controlled-environment chamber for 8 weeks at 5 °C (Expt. 2); the chamber was illuminated from 0800 to 1700 HR at ≈10 μmol·m⁻²·s⁻¹ from cool-white fluorescent lamps (VHO96T12; Philips, Bloomfield, N.J.), as measured with a LI-COR quantum sensor (model LI-189; LI-COR, Lincoln, Neb.). No other species received a cold treatment.

Light treatments. For each species, 70 plants in plugs were removed from their containers, thinned to one plant per plug, and transplanted

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Table 1. Species studied, characteristics of starting material, and average air temperatures from date of forcing to average date of flowering for each species under each night interruption treatment.

Species and cultivar	Propagation ^z		Plug size ^x	Initial nodes	Expt.	SD ^w	Average air temperature during forcing (°C)					
	Date (1995)	Environment ^y					Night interruption (h)					
							0.5	1	2	4	6/54 ^v	6/24 ^u
<i>Campanula carpatica</i> ‘Blue Clips’	7 Aug.	a	70	16.0 23.5	1 2	--- ¹ ---	--- ---	20.4 ---	20.6 20.4	20.4 20.1	20.3 20.4	20.3 20.0
<i>Coreopsis grandiflora</i> ‘Early Sunrise’	25 June	b	50	6.3 8.4	1 2	--- ---	20.7 20.6	20.4 20.2	20.6 20.4	20.4 20.1	20.3 20.4	20.4 20.0
<i>Coreopsis verticillata</i> ‘Moonbeam’	14 Aug.	a	70	≈3 ≈3	1 2	--- ---	20.7 20.6	20.3 20.1	20.5 20.3	20.4 19.9	20.3 20.4	20.3 19.9
<i>Echinacea purpurea</i> ‘Bravado’	9 Oct.	c	128	4.1	1	---	20.7	20.3	20.5	20.3	20.3	20.2
<i>Hibiscus moscheutos</i> ‘Disco Belle Mixed’	30 Oct.	c	128	4.8 8.8	1 2	20.4 20.1	20.6 20.7	20.2 20.1	20.4 20.4	20.2 19.9	20.3 20.3	20.2 19.7
<i>Rudbeckia fulgida</i> ‘Goldsturm’	1 June	b	50	11.0 11.0	1 2	--- ---	--- 20.7	20.3 20.0	20.4 20.3	20.4 19.9	20.3 20.4	20.3 19.8

^zAll plants were propagated by seed, except for 'Moonbeam', which was propagated by stem cuttings.

^ya = natural photoperiods (41°N lat.), no exposure to temperatures below 12 to 15 °C; b = natural photoperiods (40°N lat.), minimum temperatures of 19 °C until last two weeks, when minimum temperatures decreased to 13 °C; c = natural photoperiods (42°N lat.), temperatures beginning at 24 °C and gradually decreasing to 19 °C.

^xVolume of 128-, 70-, or 50-cell trays are 10, 50, or 85 mL, respectively.

^wNine-hour photoperiods.

^vLights on and off for 6 and 54 min, respectively, for 4 h.

^uLights on and off for 6 and 24 min, respectively, for 4 h.

^tNo plants flowered.

into 13-cm square containers (1.1-L volume). Ten plants were apportioned to each treatment and treatments were assigned randomly 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 $\approx 50 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant level when the ambient greenhouse PPF was lower than $400 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. During the middle of the dark period, benches were lighted with incandescent lamps at 1 to $3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the following durations: continual for 0, 0.5, 1, 2, or 4 h; 6 min on, 54 min off for 4 h (10% or 6/54 cyclic lighting); or 6 min on, 24 min off for 4 h (20% or 6/24 cyclic lighting).

Plant culture. Plants were grown in a commercial soilless medium composed of composted pine bark, horticultural vermiculite, Canadian sphagnum peat moss, processed bark ash, and washed sand (MetroMix 510; Scotts-Sierra Horticultural Products Co., Marysville, Ohio). Plants were top-watered with acidified well water (two parts H_3PO_4 plus one part H_2SO_4 , which provided P at $\approx 2.5 \text{ mol}\cdot\text{m}^{-3}$) to a titratable alkalinity of $\approx 130 \text{ mg CaCO}_3/\text{L}$ and fertilized with 14N-0P-5K ($\text{mol}\cdot\text{m}^{-3}$) (36% ammoniacal N) from KNO_3 (13N-0P-39K) (Vicksburg Chemical Co., Vicksburg, Miss.) and NH_4NO_3 (34N-0P-0K) (Cargill, Lexington, Ky.).

Greenhouse temperature control. All plants were grown in a glass greenhouse at 20 °C. Air temperatures on each bench were monitored with 36-gauge (0.127-mm diam) type E thermocouples connected to a CR10 datalogger (Campbell Scientific, Logan, Utah). 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. Actual average

daily air temperatures from the beginning of forcing to the average date of flowering under every photoperiod were calculated for each species and varied within 1 °C (Table 1).

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

A completely randomized design with 10 observations for each treatment and experiment was used. Data were analyzed using SAS's (SAS Institute, Cary, N.C.) analysis of variance (ANOVA) and general linear models (GLM) procedures.

Results

Campanula carpatica 'Blue Clips'

Experiment 1. No plants flowered with ≤ 0.5 h of NI (Table 2). As the NI duration increased from 1 to 4 h, days to flower decreased from 79 to 49 and flowering uniformity improved (Fig. 1B). Flower number (Fig. 1C), node count (Table 2), and plant height (Fig. 1D) were similar on plants exposed to 2 or 4 h of NI or the 6/24 cyclic lighting treatment; they developed 17 to 20 nodes, averaged 17 or 18 cm tall, and had an average of 38 or 39 flowers. Compared with that of plants under a continual 4-h NI, flowering under 6/54 cyclic lighting was incomplete, nonuniform, and delayed by 6 weeks. Statistically, night inter-

ruption treatment did not affect time from visible bud to flower.

Experiment 2. For plants exposed to 2 or 4 h of NI or 6/24 cyclic lighting, time to flower, and the number of new nodes formed were similar to those in Expt. 1 (Table 2, Fig. 1). Although plants were more mature, they had approximately half the number of flowers produced by plants in Expt. 1 (Fig. 1C). Few or no plants flowered with 1 h of NI or 6/54 cyclic lighting.

Coreopsis grandiflora 'Early Sunrise'

Experiment 1. No plants flowered without NI and all plants flowered with ≥ 0.5 h of NI or 6/54 or 6/24 cyclic lighting (Table 2). Flowering was delayed under 0.5 h of NI or 6/54 or 6/24 cyclic lighting compared with that of plants under 4-h NI (Fig. 2A and B). Plants under 0.5 h of NI had the fewest flowers (Fig. 2C). Plant height at flower increased from 21 to 31 cm as the duration of NI increased (Fig. 2D).

Experiment 2. All plants that received NI flowered (Table 2). Plants flowered more uniformly and ≈ 10 d faster than those in Expt. 1 (Fig. 2B). Under 0.5 h of NI or 6/54 or 6/24 cyclic lighting, time to visible bud and flower was delayed compared to that under 4-h NI. Flower number was reduced (by five to seven) (Fig. 2C), and time from visible bud to flower was longest (by at least 2 d), for plants under 0.5-h or 6/54 cyclic lighting.

Coreopsis verticillata 'Moonbeam'

Experiment 1. No plants flowered without NI (Table 2). Percentage of flowering increased from 40 to 100, days to flower decreased from 114 to 68, and plant height increased from 31 to 77 cm as the duration of NI increased from 0.5 to 4 h (Fig. 3). Furthermore, the variability in time to flower decreased dramatically as the NI duration increased, as indicated by the reduction in the

Table 2. The effects of night-interruption duration and cyclic lighting on flowering of six species of herbaceous perennials.

Night interruption ²	Expt. 1		Expt. 2	
	Flowering (%)	Increase in node count	Flowering (%)	Increase in node count
<i>Campanula carpatica</i> 'Blue Clips'				
0 h	0	---	0	---
0.5 h	0	---	0	---
1 h	70	27 a*	0	---
2 h	100	20 b	83	20 a
4 h	100	17 b	100	16 a
6/54 cyclic ^w	40	29 a	17	17 a
6/24 cyclic ^y	100	20 b	89	19 a
<i>Coreopsis grandiflora</i> 'Early Sunrise'				
0 h	0	---	0	---
0.5 h	100	8 b	100	9 a
1 h	100	9 a	100	8 b
2 h	100	9 ab	100	8 b
4 h	100	8 ab	100	8 b
6/54 cyclic	100	9 ab	100	8 ab
6/24 cyclic	100	8 ab	100	8 b
<i>Coreopsis verticillata</i> 'Moonbeam'				
0 h	0	---	0	---
0.5 h	40	5.3 b	80	5.3 a
1 h	90	6.0 a	100	5.9 a
2 h	100	5.9 a	100	5.6 a
4 h	100	6.2 a	100	5.7 a
6/54 cyclic	80	6.1 a	100	5.9 a
6/24 cyclic	100	6.1 a	100	5.9 a
<i>Echinacea purpurea</i> 'Bravado'				
0 h	0	---		
0.5 h	100	17 a		
1 h	100	14 b		
2 h	90	14 b		
4 h	100	14 b		
6/54 cyclic	100	14 b		
6/24 cyclic	100	13 b		
<i>Hibiscus moscheutos</i> 'Disco Belle Mixed'				
0 h	10	21 a	70	14 a
0.5 h	50	19 a	100	14 a
1 h	90	15 a	100	14 a
2 h	90	17 a	100	14 a
4 h	90	15 a	100	12 a
6/54 cyclic	80	17 a	100	13 a
6/24 cyclic	90	15 a	100	12 a
<i>Rudbeckia fulgida</i> 'Goldsturm'				
0 h	0	---	0	---
0.5 h	0	---	100	22 a
1 h	100	23 a	100	18 c
2 h	100	23 a	100	15 de
4 h	100	18 b	100	13 e
6/54 cyclic	60	24 a	100	20 b
6/24 cyclic	90	22 a	100	16 d

²Nine-hour natural days with night-interruption lighting during the middle of the dark period.³--- = no plants showed visible bud after 105 d of forcing.^{*}Mean separation within each species and column by Duncan's multiple range test ($P = 0.05$).^wLights on and off for 6 and 54 min, respectively, for 4 h.^yLights on and off for 6 and 24 min, respectively, for 4 h.

95% confidence interval (Fig. 3B). All flowering characteristics measured under 6/24 cyclic lighting were similar to those under 4-h NI. Flowering under 6/54 cyclic lighting was incomplete and delayed by ≈ 4 weeks compared with that of plants under 4-h NI. Flowering of plants under 2-h NI was delayed by ≈ 17 d compared with that of plants under 4-h NI.

Experiment 2. No plants flowered without NI. All plants flowered under ≥ 1 h of NI or either cyclic lighting treatment. Duration of NI did not influence time to flower as it did with younger plants. Flower number increased from 27 to 63 as the NI duration increased from 0.5 to 4 h. Plants were shortest under 0.5 h of NI or

6/54 cyclic lighting. Flowering under 6/24 cyclic lighting was similar to that of plants under 4 h of NI.

Echinacea purpurea 'Bravado'

Many plants in Expt. 2 died, so only results of Expt. 1 are presented. No plants flowered without an NI treatment and all but one plant flowered with NI (Table 2). All NI durations and cyclic lighting regimens induced plants to flower at about the same time (Fig. 4B). Flower count decreased (Fig. 4C) and plant height increased (Fig. 4D) as the NI duration increased from 0.5 to 4 h.

Hibiscus moscheutos 'Disco Belle Mixed'

Experiment 1. Ten percent of the plants flowered without NI, 50% flowered with 0.5 h of NI, and $\geq 80\%$ flowered with ≥ 1 h of NI or 6/54 or 6/24 cyclic lighting for 4 h (Table 2). Days to flower decreased from 154 to 114 (Fig. 5B) and flower number increased from 5 to 17 (Fig. 5C) as the NI duration increased from 0 to 4 h. Cyclic lighting induced flowering at approximately the same time as that of plants under 4-h NI.

Experiment 2. Plants flowered more uniformly and 25 to 40 d earlier than plants in Expt. 1. Seventy percent of plants flowered without NI, and all plants flowered with it. All plants flowered at about the same time and developed about the same number of nodes.

Rudbeckia fulgida 'Goldsturm'

Experiment 1. No plants flowered without NI or with 0.5 hours of NI (Table 2). All plants that received ≥ 1 h of NI flowered, and 60% or 90% of plants flowered under 6/54 or 6/24 cyclic lighting, respectively. Plants under 4 h of NI flowered earlier (≥ 19 d) (Fig. 6B) and developed at least four fewer nodes than plants under other lighting treatments. Flowering of plants under all other photoperiods was delayed (by 3 to 4 weeks) compared to that under the 4-h NI. Flower number and plant height were unaffected by NI treatment.

Experiment 2. No plants flowered without NI and all plants flowered with it. The cold treatment shifted the minimum NI duration necessary for flowering from 1 to 0.5 h and hastened flowering by more than 2 weeks. Plants flowered earliest under 2-h NI, ≈ 5 or 6 d earlier than plants under 1- or 4-h NI or 6/24 cyclic lighting. Flowering under 6/54 cyclic lighting or 0.5-h NI was delayed by ≈ 12 or 20 d, respectively. Plants under 0.5- or 1-h NI or 6/54 cyclic lighting had the most flowers (Fig. 6C).

Discussion

Thirty minutes of light during the middle of 15-h dark periods induced a complete LD flowering response in *E. purpurea* 'Bravado'. The other five species required longer durations of NI lighting to induce the most rapid, complete, uniform flowering. One hour of NI appeared to saturate the response for *C. grandiflora* 'Early Sunrise' and *H. moscheutos* 'Disco Belle Mixed', whereas *C. carpatica* 'Blue Clips' and *C. verticillata* 'Moonbeam' required at least 2 h of NI lighting. For unchilled *R. fulgida* 'Goldsturm', no other lighting treatment induced as complete and rapid flowering as the continual 4-h NI. A longer NI may have accelerated flowering.

Some LDP show a quantitative response to the duration of NI (Vince-Prue and Canham, 1983). In the LDP sweet clover (*Melilotus alba* Desr.), days to first flower decreased at a decreasing rate from >60 to 32 and average flower number increased as the NI duration increased from 2 to 16 h (Kasperbauer et al., 1963). The species we studied generally

Fig. 1. Flowering of *Campanula carpatica* 'Blue Clips' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-h dark periods. For the cyclic lighting treatments, lights were on for 6 min every 30 or 60 min for a 4-h period during the middle of the night. Error bars are 95% confidence intervals and were offset to the right of data points in Expt. 2 for clarity.

Fig. 2. Flowering of *Coreopsis grandiflora* 'Early Sunrise' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-h dark periods. For the cyclic lighting treatments, lights were on for 6 min every 30 or 60 min for a 4-h period during the middle of the night. Error bars are 95% confidence intervals and were offset to the right of data points in Expt. 2 for clarity.

showed a quantitative flowering response to the duration of NI until a saturation duration was reached; as the length of the uninterrupted night break increased, flowering percentage and uniformity and flower number increased and time to flower decreased.

Coreopsis grandiflora 'Early Sunrise', *C. verticillata* 'Moonbeam', and *H. moscheutos* 'Disco Belle Mixed' flowered earlier when plants were more mature (i.e., those in Expt.

2). Sixteen- or twenty-four-node *C. carpatica* 'Blue Clips' flowered in the same time. *Coreopsis grandiflora* 'Early Sunrise' was the only species in which more mature plants (by about two nodes) produced more flowers.

The cold treatment increased the responsiveness of *Rudbeckia* to shorter durations of NI. Cold-treated plants with 1 h of NI and those under longer durations of NI flowered similarly, which suggests that cold

treatment of some herbaceous perennials may improve response to short NI. In Expt. 2, all *R. fulgida* 'Goldsturm' under 4 h of NI and some under 6/24 cyclic lighting had an atypical flowering phenotype: the tip of the inflorescence died and flowering shoots became branched at the base of the inflorescence, which may explain why time from visible bud to flower was delayed under these two lighting treatments.

Except for that of *E. purpurea* 'Bravado' and *H. moscheutos* 'Disco Belle Mixed', flowering under 6/54 cyclic lighting for 4 h was incomplete and delayed compared to that under a continual 4-h NI. Kasperbauer et al. (1963) found that a cyclic lighting regimen induced flowering of sweet clover, but the effectiveness varied with the lighting treatments. During 16-h dark periods, five different 10% cyclic lighting treatments were provided, with incandescent lamps delivering $8.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Sweet clover provided with either shorter (1.5 min) but more frequent (every 15 min) cyclic lighting cycles or continual light flowered similarly. The flowering response decreased as the duration of light during each cycle increased and cycle frequency decreased. Cyclic lighting also hastened flowering in the facultative LDP snapdragon (*Antirrhinum majus* L.); plants provided with at least 10 s of light per min (16.6% cyclic lighting) for 4 h and those provided with a continual 4-h NI flowered simultaneously (Maginnes and Langhans, 1967).

In our experiments, the 6/24 cyclic lighting treatment induced flowering comparable to that under a continual 4-h NI for *C. carpatica* 'Blue Clips', *C. verticillata* 'Moonbeam', *E. purpurea* 'Bravado', *H. moscheutos* 'Disco Belle Mixed', and cold-treated *R. fulgida* 'Goldsturm'. A 4-h cycle [5 min of light and 10 min of dark (33% cyclic lighting)] with incandescent lamps, which provided $2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, induced flowering in the LDP baby's-breath (*Gypsophila paniculata* L. 'Bristol Fairy'), as did a continual 4-h NI (Shillo and Halevy, 1982).

Some LDP flower in response to less frequent cyclic lighting regimens. Five seconds of light every minute (8.3% cyclic lighting) and continual illumination during a 4-h NI yielded similar flowering responses in the LDP Easter lily (*Lilium longiflorum* Thunb.) (Smith and Langhans, 1962a). Smith and Langhans (1962b) showed that lighting for 2 s every minute (3.3% cyclic lighting) from 2200 to 0200 HR at a minimum intensity of 1 to $2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ could induce an LD effect similar to that of a continual 4-h NI in the LDP cornflower (*Centaurea cyanus* L. 'Blue Boy'), feverfew (*Chrysanthemum parthenium* Bernh. 'Ball Double White Improved'), and 'Pink Magic' petunia. In two cultivars of the qualitative LDP China aster (*Callistephus chinensis* Nees), cyclic lighting cycles of 1 min every hour (1.6% cyclic lighting) during 16-h dark periods induced flowering faster than 1 h of continual NI, but not as rapidly as continual light (Cockshull and Hughes, 1969).

Five of the six species, *C. carpatica* 'Blue Clips', *C. grandiflora* 'Early Sunrise', *C.*

Fig. 3. Flowering of *Coreopsis verticillata* 'Moonbeam' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-h dark periods. For the cyclic lighting treatments, lights were on for 6 min every 30 or 60 min for a 4-h period during the middle of the night. Error bars are 95% confidence intervals and were offset to the right of data points in Expt. 2 for clarity.

Fig. 4. Flowering of *Echinacea purpurea* 'Bravado' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-h dark periods. For the cyclic lighting treatments, lights were on for 6 min every 30 or 60 min for a 4-h period during the middle of the night. Error bars are 95% confidence intervals.

verticillata 'Moonbeam', *E. purpurea* 'Bravado', and *R. fulgida* 'Goldsturm', require NI for flowering and thus are qualitative LDP. The results of our study illustrate the variation among LD species in response to different durations of NI and cyclic lighting. *Echinacea purpurea* 'Bravado' required only 30 min to saturate its flowering response, whereas at least 4 h of NI was required to saturate the response of *R. fulgida* 'Goldsturm'. The 6/54 cyclic lighting treatment effectively induced

flowering in *E. purpurea* 'Bravado', while the 6/24 cyclic lighting treatment failed to induce a rapid and complete flowering response in unchilled *R. fulgida* 'Goldsturm'.

Although some species of herbaceous perennial LDP flower completely and rapidly with as little as 1 h of NI, 4 h of continual NI assures complete, rapid, and uniform flowering of a variety of LD perennials. A 4-h NI of 6/24 cyclic lighting promotes flowering of some, but not all, LD perennials, as does

continual NI. A cyclic lighting treatment may induce flowering of a variety of LD perennials, as does a continual one, but the frequency of such a regimen has to be determined.

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Fig. 5. Flowering of *Hibiscus moscheutos* 'Disco Belle Mixed' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-h dark periods. For the cyclic lighting treatments, lights were on for 6 min every 30 or 60 min for a 4-h period during the middle of the night. Error bars are 95% confidence intervals and were offset to the right of data points in Expt. 2 for clarity.

Fig. 6. Flowering of *Rudbeckia fulgida* 'Goldsturm' under various durations of night interruption or cyclic lighting. Night interruption was provided by incandescent lamps that were turned on during the middle of 15-h dark periods. For the cyclic lighting treatments, lights were on for 6 min every 30 or 60 min for a 4-h period during the middle of the night. Error bars are 95% confidence intervals and were offset to the right of data points in Expt. 2 for clarity.