Photoperiod and Cold Treatment Regulate Flowering of *Rudbeckia fulgida* 'Goldsturm'

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Abstract. To determine the flowering requirements of *Rudbeckia fulgida* Ait. 'Goldsturm', plants were grown under 9-hour photoperiods until maturity, then forced at 20 °C under one of seven photoperiods following 0 or 15 weeks of 5 °C. Photoperiods consisted of a 9-hour day that was 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 'Goldsturm' remained vegetative under photoperiods ≤13 hours, and essentially all plants flowered under photoperiods ≥14 hours or with a 4-hour NI. Flowering percentages for cooled plants were 6, 56, or ≥84 under 10-, 12-, or ≥13-hour daylengths and NI, respectively. Critical photoperiods were ≈14 or 13 hours for noncooled or cooled plants, respectively, and base photoperiods shifted from 13 to 14 hours before cold treatment to 10 to 12 hours following cold treatment. Within cold treatments, plants under photoperiods ≥14 hours or NI reached visible inflorescence and flowered at the same time and developed the same number of inflorescences. Fifteen weeks of cold hastened flowering by 25 to 30 days and reduced nodes developed before the first inflorescence by 28% to 37%. Cold treatment provided little or no improvement in other measured characteristics, such as flowering percentage and uniformity, flower number, plant height, and vigor.

Rudbeckia fulgida 'Goldsturm' is an attractive herbaceous perennial that produces abundant gold-colored inflorescences in temperate-climate summers and is hardy in U.S. Dept. of Agriculture zones 3 to 9. 'Goldsturm' makes an excellent landscape plant, reaching heights up to 75 cm, but is shorter in a container and is suitable for flowering potted-plant production (Nau, 1996; Yuan et al., 1996). *Rudbeckia* is one of the top 10 best-selling herbaceous perennial genera (Rhodus and Hoskins, 1995), but detailed requirements for controlled flowering of *R. fulgida* have not been published.

The photoperiodic response of *Rudbeckia* sp. was first studied in the 1920s by Garner and Allard (1931) and *Rudbeckia* are considered typical qualitative long-day plants (LDP), with minimal reproductive photoperiods ranging from 10 to 14.5 h (Kochankov and

Chailakhyan, 1985). Nau (1996) stated that *R. fulgida* does not flower in the first year from seed and requires a cold treatment for flowering. However, Yuan (1995) found 'Goldsturm' to be a qualitative LDP with a quantitative flowering response to cold-temperature treatment. In addition, Yuan (1995) recommended that, to overcome juvenility, plants have at least 10 nodes before inductive long days (LD) are provided. Four hours of lighting during the middle of 15-h nights were sufficient to induce flowering of 'Goldsturm'; shorter night interruption (NI) durations or cyclic lighting regimens were ineffective or delayed flowering for noncooled plants (Runkle et al., 1998a).

There are several useful terms that describe how photoperiod regulates vegetative or reproductive growth. For qualitative LDP, the base photoperiod is the one below which plants remain vegetative (Roberts and Summerfield, 1987). The critical photoperiod of LDP is the one that, if met or exceeded, induces a population of plants to flower completely, rapidly, and uniformly (Runkle et al., 1998b). Transitional photoperiods, or daylengths between the base and critical photoperiods, induce only part of a population to flower.

The goal of our research was to define the environmental control of flowering of *R. fulgida* 'Goldsturm' to facilitate potted-plant production. We conducted experiments to identify the critical, base, and transitional photoperiods and to quantify the effects of a cold treatment on flowering.

Plant material. Seed were sown 1 June 1995 or 9 June 1996 by a wholesale plug producer (Swift Greenhouses, Gilman, Iowa) and grown under natural daylengths (lat. 40°N) at a minimum of 19 °C. Fifty-cell plug trays (85-mL volume) were received on 25 Oct. 1995 or 31 Oct. 1996; plants averaged four to five nodes (leaves). Plug trays were exposed to 10.5- to 11-h natural daylengths (lat. 43°N) for 1 or 2 weeks before plants were removed from their containers, thinned to the largest plant per plug, and transplanted into 13-cm square plastic containers (1.1-L volume). Plants were grown under 9-h photoperiods (as described below) for ≈6 to 8 weeks at 20 °C until the population averaged ≈10 nodes, after which they were transferred to lighting or cold-temperature treatments.

Cold treatment. On 7 Dec. 1995 (Year 1) or 15 Dec. 1996 (Year 2), half the plants were placed in a controlled-environment chamber for 15 weeks at 5 °C; the chamber was irradiated 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, Nebr.). While in the cooler, plants were watered with well water (CaCO₃ at 340 mg·L⁻¹) acidified (93% H₂SO₄) to a titratable alkalinity of CaCO₃ at ≈100 mg·L⁻¹. Plants were transferred to lighting treatments upon completion of cold treatments.

Light treatments. For noncooled plants, lighting treatments commenced on 6 Dec. 1995 (Year 1) and 11 Jan. 1997 (Year 2); lighting treatments for cooled plants began on 23 Mar. 1996 (Year 1) and 30 Mar. 1997 (Year 2). Nine or 10 plants were apportioned to each 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 each year within each cold-treatment forcing period. From 0800 to 1700 HR, high-pressure sodium lamps provided a supplemental photosynthetic photon flux (PPF) of ≈50 μmol·m⁻²·s⁻¹ at plant level when the ambient greenhouse PPF was <400 μmol·m⁻²·s⁻¹.

Photoperiods were 10, 12, 13, 14, 16, or 24 h of continual light or 9 h with a 4-h (2200 to 0200 HR) NI. Continual photoperiods consisted of 9-h days completed by day-extension lighting; lamps were turned on at 1700 HR and turned off after each photoperiod was completed. Day-extension and NI lighting were provided by incandescent lamps at 1 to 3 μmol·m⁻²·s⁻¹ at canopy level. In Year 2, the average daily light integral during the experiment was measured at canopy level with LI-COR quantum sensors 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-

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Sierra Horticultural Products Co., Marysville, Ohio). Plants were fertilized at every irrigation using well water (electrical conductivity of 0.65 mS·cm⁻¹ and 105, 35, and 23 mg·L⁻¹ Ca, Mg, and S, respectively) acidified (two parts H₃PO₄ plus one part H₂SO₄, which provided P at ≈80 mg·L⁻¹) to a titratable alkalinity of ≈130 mg·L⁻¹ CaCO₃ containing 200N-0P-155K mg·L⁻¹ (36% ammoniacal N) from KNO₃ and NH₄NO₃ 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, Marysville, Ohio] at a constant 50 mg·L⁻¹.

Greenhouse temperature control. All plants were grown in a glass-glazed greenhouse at 20 °C. Air temperatures on each bench were monitored near canopy level with 36-gauge (0.127-mm diameter) type-E thermocouples connected to a CR10 datalogger. To provide uniform night temperatures, the datalogger controlled a 1500-W electric heater under each bench, which provided supplemental heat as needed throughout the night to maintain 20 °C. 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 and ranged from 20.2 to 22.4 °C in 1995–96, and 20.2 to 21.5 °C in 1996–97 (Table 1).

Data collection and analysis. Nodes per plant were counted when forcing began (Table 1). The date the first inflorescence was visible without dissection (VI) and the date the first flower opened (anthesis) were recorded for each plant. At flowering, VI and nodes on the main stem below the apical inflorescence were counted, and total plant height (not including the container) was measured. Plants that did not have a VI after 15 weeks of forcing were considered nonflowering and, except where noted, were discarded. Days to VI, days from VI to flower, days to flower, node-count increase from the start of forcing, and rate of node development (plant vigor) (determined by dividing the increase in node number by days to VI) were calculated. The few plants that died during the experiment were discarded and not included in the results.

The experiment was replicated in time. Each year, a completely randomized design with nine or 10 observations for each photoperiod and cold treatment was used. Data were analyzed using the SAS (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.

Results

Noncooled *R. fulgida* 'Goldsturm' remained vegetative under photoperiods ≤13 h and essentially all flowered under photoperiods ≥14 h or with a 4-h NI (Fig. 1A). Flowering

Table 1. Initial node count and average air temperatures and daily light integrals from date of forcing to average date of flowering of *Rudbeckia fulgida* 'Goldsturm'.

Year	Weeks at 5 °C	Initial nodes	Avg daily light integral ^z (mol·m ⁻² ·d ⁻¹)	Photoperiod (h)						NI ^y
				10	12	13	14	16	24	
				<i>Average air temperature during forcing (°C)</i>						
1995–96	0	10.0	- ^x	-- ^w	--	--	21.0	20.2	20.6	20.7
	15	10.4	-	--	21.5	21.7	21.3	21.1	22.4	20.8
1996–97	0	12.2	10.5	--	--	--	20.5	20.2	20.8	21.0
	15	11.3	10.2	20.6	20.4	21.1	20.7	20.2	20.9	21.5

^zCalculated from date of forcing to average time to flower within cold treatment.

^yFour-hour night interruption.

^xNot measured (one dash).

^wNo plants flowered (two dashes).

percentages of cooled plants were 6, 56, or ≥84 under 10-, 12-, or ≥13-h daylengths and NI, respectively. One cooled plant flowered under a 10-h daylength, but had an abnormal, incomplete inflorescence and was omitted from further statistical analysis.

Noncooled reproductive plants reached anthesis in 96 to 103 d, regardless of photoperiod (Fig. 1B). Under photoperiods ≥14 h or NI, cooled plants flowered 25 to 30 d earlier than noncooled plants. Plants under the 12-h photoperiod flowered nonuniformly, as indicated by the large 95% confidence interval. Cooled plants flowered at about the same time whether under photoperiods ≥13 h or NI. Noncooled or cooled plants flowered 5 to 6 d earlier under continual light than those under NI ($P = 0.006$ or 0.040, respectively). Time from VI to flower was 3 d earlier following cold treatment (significantly different at $P = 0.039$) and ranged from 32 to 40 d for noncooled plants and 28 to 38 d for cooled plants (data not shown).

The number of developed nodes below the first inflorescence in noncooled plants declined linearly from 19.7 to 15.6 as the photoperiod increased from 14 to 24 h (Fig. 1C). Node development under NI was similar to that for plants under 16- or 24-h photoperiods. Cooled plants developed 28% to 37% fewer nodes before flowering than noncooled plants. Node count for cooled plants decreased (linearly or quadratically) from 19.0 to 10.3 as the photoperiod increased from 12 to 24 h. Rate of node development varied with cold treatment but not with photoperiod. Noncooled and cooled plants developed 0.32 or 0.28 nodes/d, respectively (significantly different at $P = 0.003$).

Cold treatment did not influence inflorescence number under photoperiods ≥14 h or NI (Fig. 1D). For noncooled plants, inflorescence number slightly decreased linearly ($P = 0.032$) as the photoperiod increased from 14 to 24 h. Cooled reproductive plants under 12-h photoperiods developed about three inflorescences, and those under daylengths ≥13 h or NI produced >15 inflorescences. Plants under 16-h photoperiods or NI had similar numbers of inflorescences, but cooled and noncooled plants under NI developed three to four more inflorescences than those under continual light ($P < 0.04$).

Excluding flowering plants under 12-h photoperiods, noncooled plants were ≈3 cm (10%)

taller than cooled ones (significantly different at $P < 0.001$) (Fig. 1E). There was a linear ($P = 0.023$) or quadratic ($P < 0.001$) effect of photoperiod on plant height for noncooled plants; cooled plants showed similar trends ($P < 0.001$). Regardless of cold treatment, plants under NI were 6 to 8 cm shorter than those under continual light.

Discussion

Rudbeckia fulgida 'Goldsturm' is a qualitative LDP regardless of cold treatment, similar to all nine previously studied species of *Rudbeckia* (Kochankov and Chailakhyan, 1985). The critical photoperiods for noncooled and cooled plants were ≈14 and 13 h, respectively. The base photoperiod was reduced from 13 to 14 h before cold treatment to 10 to 12 h following cold. The flowering phenotype of reproductive plants under 10- or 12-h photoperiods was atypical, and in some instances, inflorescences developed incompletely. In Year 2, noncooled plants were kept on benches for ≈25 weeks under 10- to 13-h photoperiods. A few plants under 13-h photoperiods exhibited a very weak flowering phenotype after 23 to 25 weeks, but all others remained vegetative. However, all noncooled plants under 13-h photoperiods developed larger and more vertically oriented leaves than those under shorter daylengths. Similar observations were reported with the annual *R. hirta* L., and were interpreted as the first visual sign in the developmental shift from vegetative to reproductive growth (Harkess and Lyons, 1993; Murneek, 1940). For cooled plants, transitional photoperiods were between 10 and 12 h.

In agreement with Yuan (1995) and Runkle et al. (1998a), but not Nau (1996), a cold treatment was not required for flowering of 'Goldsturm' but did hasten time to flower by ≈35%. Application of a cold treatment also reduced the number of new nodes developed below the first inflorescence. A cold treatment had little or no influence on flowering percentage or uniformity, or on flower number, plant height, or vigor. Using the equations of Yuan et al. (1998), predicted time to flower for field-grown, cooled plants under a 4-h NI at the air temperatures recorded (Table 1) was 86 and 83 d for Year 1 and Year 2, respectively. These values were similar to the 80 and 76 d we observed in this study.

Fig. 1. Flowering of *Rudbeckia fulgida* 'Goldsturm' under various photoperiods after 0 or 15 weeks of 5 °C cold treatment. Continual photoperiodic treatments consisted of 9-h natural days extended with light from incandescent lamps (NI = 4-h night interruption). At flowering, the number of visible inflorescences and nodes on the main stem below the apical inflorescence were counted, and total plant height was measured. Error bars are 95% confidence intervals and are offset to the right of data points of noncooled plants for clarity (L = linear, Q = quadratic trends; NS, * , ** , *** nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively).

Cold treatment increased the sensitivity of 'Goldsturm' to photoperiod. The maximum night length for flowering increased by at least 1 h, from ≈ 10 to ≥ 11 . This phenomenon has also been reported with other species (Grossin and Mathon, 1961; Lang, 1965). Similarly, Runkle et al. (1998a) found that the saturation duration of NI for 'Goldsturm' decreased from 4 to 1 h following 8 weeks of cold. A cyclic lighting regimen, 6 min on and 24 min off for 4 h (20% or 6/24 cyclic lighting), was as effective as a continual 4-h NI for cooled plants, but not for noncooled plants (Runkle et al., 1998a).

A population of 'Goldsturm' must have an average of ≥ 10 nodes per plant for relatively complete flowering (Yuan, 1995). This conclusion is supported by a photoperiod experiment we conducted in 1994–95 similar to that described here but with plants averaging 4.3 nodes (unpublished data). Only 40% or 43% of noncooled or cooled plants flowered, respectively, under photoperiods ≥ 14 h or with a 4-h NI, and time to flower also was delayed, averaging 118 d at ≈ 20 °C regardless of cold treatment (data not shown). In this study, the few plants that did not flower under completely inductive photoperiods were probably juvenile at the start of LD. An interesting question is why these plants did not flower as they reached maturity (>10 nodes) under LD. One possibility is that mature *R. fulgida* 'Goldsturm' requires either short days (SD) or cold prior to LD for complete flowering of a population of plants. Plants maturing under LD would receive neither. Preliminary results support this hypothesis; flowering of 'Goldsturm' was more complete, rapid, and uniform when grown under SD prior to LD induction than when grown under continual LD (J. Chong, unpublished data).

Our data indicated that plants under inductive photoperiods developed at a greater rate (by $\approx 13\%$) prior to cold treatment, and the difference cannot be attributed to temperature or light levels, since conditions measured were similar (Table 1). This finding contrasts with that for some herbaceous perennials (e.g., *Phlox paniculata* Lyon ex Pursh), which develop nodes at a markedly greater rate and are more vigorous following cold treatment (Runkle et al., 1998b). Plants grown under 9-h photoperiods to overcome juvenility took ≈ 6 to 8 weeks to develop ≈ 6 to 7 nodes, which corresponds to a development rate of ≈ 0.13 nodes/d, less than half the rate of node development under inductive photoperiods. This suggests that plants may develop nodes at a slower rate under noninductive than under inductive photoperiods, but further tests are needed to support this observation.

In summary, noncooled seedlings of *R. fulgida* 'Goldsturm' should be grown under photoperiods ≤ 13 h to promote vegetative growth, until plants have at least 10 nodes. Under LD, a 15-week treatment at 5 °C hastens flowering by ≈ 4 weeks at 20 °C but provides no other horticultural benefits. To induce flowering, recommended inductive photoperiods are ≥ 14 or ≥ 13 h without or following a cold treatment, respectively, or a 4-h NI.

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