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Flowering of *Leucanthemum* ×*superbum* 'Snowcap' in Response to Photoperiod and Cold Treatment

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Abstract. **'Snowcap' Shasta daisy [*Leucanthemum* ×*superbum* Bergmans ex. J. Ingram (syn: *Chrysanthemum* ×*superbum*, *C. maximum*)] was grown under various photoperiods and temperatures to determine their effects on flowering. In the first experiment, plants were held for 0 or 15 weeks at 5 °C and then were grown at 20 °C under the following photoperiods: 10, 12, 13, 14, 16, or 24 hours of continuous light or 9 hours with a 4-hour night interruption (NI) in the middle of the dark period. Without cold treatment, no plants flowered under photoperiods ≤14 hours and 65% to 95% flowered under longer photoperiods or NI. After 15 weeks at 5 °C, all plants flowered under all photoperiods and developed three to four or 10 to 11 inflorescences under photoperiods ≤14 or ≥16 hours, respectively. To determine the duration of cold treatment required for flowering under short photoperiods, a second experiment was conducted in which plants were treated for 0, 3, 6, 9, 12, or 15 weeks at 5 °C, and then grown at 20 °C under 9-hour days without or with a 4-hour NI. Under 9-hour photoperiods, 0%, 80%, or 100% of plants flowered after 0, 3, or ≥6 weeks at 5 °C, and time to flower decreased from 103 to 57 days as the time at 5 °C increased from 3 to 12 weeks. Plants that were under NI and received ≥3 weeks of cold flowered in 45 to 55 days. For complete and rapid flowering with a high flower count, we recommend cold-treating 'Snowcap' for at least 6 weeks, then providing photoperiods ≥16 hours or a 4-hour NI during forcing.**

Predictable flowering of herbaceous perennials has become a priority for many greenhouse and nursery growers in the United States, since flowering plants are much more marketable than vegetative plants. Species and cultivars with incomplete or nonuniform flowering within a population, or those with lengthy production schedules, are less suitable for large-scale production. Thus, there is interest in selecting desirable herbaceous perennial species for container production and identifying their flowering requirements. Shasta daisy is a widely cultivated herbaceous perennial with attractive white inflorescences. Numerous cultivars exist, most of which are seed-propagated. Often, flowering within a population is not complete and flowering variability is excessive. We chose to investigate the flowering response of a clone, 'Snowcap', a cultivar that flowers profusely and has a compact habit, making it well-suited for potted plant production.

Once capable of flowering, many herbaceous plants flower in response to a cold temperature treatment, photoperiod, or both (Heins et al., 1997). Laurie and Poesch (1932) were the first to label Shasta daisy as a long-day plant (LDP), observing that plants grown under natural days extended with lamps flowered earlier than plants grown without day-extension lighting. Shasta daisy has been labeled a qualitative LDP by Vince-Prue (1975), citing Altman and Katz (1973), who in turn reference Roberts and Struckmeyer (1938), who do not specify a particular long-day (LD) response.

The effects of photoperiod and cold treatments on flowering of Shasta daisy vary by cultivar. For example, noncooled 'Esther Read' remained vegetative under 12-h photoperiods and flowered under those 13 h or longer, but 'T.E. Killian' flowered under 15-h photoperiods and remained vegetative under daylengths ≤14 h (Griffin and Carpenter, 1964). Three studies indicate that 'G. Marconi' requires a cold treatment for flowering, but there is disagreement as to whether LD are required for flowering following exposure to cold (Damann and Lyons, 1995, 1996; Shedron and Weiler, 1982). Following an extended period of natural cold temperatures, flowering of 'G. Marconi' increased to ≥80% when plants were provided ≥8 LD and only 50% flowered under 9-h photoperiods (Damann and Lyons, 1996). In contrast, Shedron and Weiler (1982) reported complete flowering for 'G. Marconi' under 10-h photoperiods after 16 weeks at 4.5 °C. However, the plants used were considerably older at the time of treatment than those used by Damann and Lyons (1996), and for many species, larger plants are generally less sensitive to photoperiod than smaller ones (Lang, 1965).

Another seed-propagated cultivar, 'White Knight', has a slightly weaker flowering response to photoperiod and cold treatments. Without cold, 25% flowered under photoperiods ≤14 h, and 87% flowered under photoperiods ≥16 h or with a 4-h NI (Runkle, 1996). After 15 weeks at 5 °C, 69% or 100% flowered under photoperiods ≤14 h or ≥16 h, respectively. 'Snow Lady' is a quantitative LDP that has no cold requirement; 90% of 'Snow Lady' flowered under 9-h photoperiods without cold treatment. A 4-h NI induced 100% flowering, and at a faster rate (Damann and Lyons, 1995).

Experiments by Engle (1994) and Yuan (1995) indicated that 'Snowcap' was a LDP that did not require a cold treatment for flowering. However, more detailed experiments are needed to understand and quantify flowering responses to photoperiod and cold. Therefore, we conducted studies at Michigan State Univ. to determine the cold and photoperiodic requirements for complete, rapid, and uniform flowering of 'Snowcap' Shasta daisy.

Materials and Methods

Plant material. A Michigan wholesale grower propagated plants by tissue culture at ≈22 °C with 16- to 17-h photoperiods in June 1995 and May 1996; the plants were then grown under natural daylengths (lat. 43°N) at 13 to 18 °C until shipping. Plants in 8-cm pots (350-mL container volume) were received on 19 Oct. 1995 or 9 Oct. 1996 and were grown under natural daylengths (lat. 43°N) until the experiments began. Plants averaged 12 to 16 nodes at the onset of experiments.

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 $mg \cdot L^{-1}$ $CaCO_3$. The nutrient solution (200 $mg \cdot L^{-1}$ of N and 155 $mg \cdot L^{-1}$ of K from KNO_3 and NH_4NO_3) was 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 $mg \cdot L^{-1}$.

Greenhouse temperature control. All plants were grown in a glass greenhouse at 20 °C. Air

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temperatures on each bench were monitored with 36-gauge (0.127-mm-diameter) type E thermocouples connected to CR10 dataloggers (Campbell Scientific, Logan, Utah). To provide uniform night temperatures, dataloggers controlled 1500-W electric heaters under each bench, which provided supplemental heat as needed throughout the night. The dataloggers collected temperature data every 10 s and recorded the hourly averages. For each experiment, actual average daily air temperatures from the beginning of forcing until the average date of flowering under every photoperiod were calculated (Table 1).

Cold treatments. Plants were placed in a controlled-environment chamber for various durations at 5 °C; the chamber was illuminated by cool-white fluorescent lamps (VHOF96T12; Philips, Bloomfield, N.J.) from 0800 to 1700 HR at ≈10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at canopy level, 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 acidified (93% H_2SO_4) to a titratable alkalinity of $CaCO_3$ at ≈100 $mg \cdot L^{-1}$.

Light treatments. Plants without or with a cold treatment were transplanted 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 within cold treatment. 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 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The average daily light integral during experiments in 1996–97 was measured at canopy level with quantum sensors (LI-COR) connected to a CR10 datalogger (Campbell Scientific) (Table 1).

Photoperiod experiment (Expt. 1). The experiment was replicated in time, beginning on 9 Nov. 1995 (Year 1) and 4 Nov. 1996 (Year 2), and was identical in design between years. Plants received 0 or 15 weeks of cold treatment and then were placed under one of seven photoperiods: 10, 12, 13, 14, 16, or 24 h of continuous light or 9 h with a 4-h NI. Natural photoperiods were extended with incandescent lamps at 1 to 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at canopy level. For the continuous photoperiodic treatments, lamps provided day extensions; they were turned on at 1700 HR and turned off after each photoperiod was completed. The NI was delivered from 2200 to 0200 HR.

Cold-treatment experiment (Expt. 2). Beginning on 16 Nov. 1996, plants were held at 5 °C for 0, 3, 6, 9, 12, or 15 weeks and then placed on greenhouse benches under continuous short days (9 h) with or without a 4-h NI. All other experimental materials and procedures were as described above.

Data collection and analysis. Nodes per plant were counted when forcing began. The date the first inflorescence was visible (without dissection) and the date the first flower

Table 1. Average air temperatures and daily light integrals from date of forcing to average date of flowering of *Leucanthemum ×superbum* 'Snowcap'.

Year	Expt.	Weeks at 5 °C	Average daily light integral ($mol \cdot m^{-2} \cdot d^{-1}$)	Photoperiod (h)							
				9	10	12	13	14	16	24	NI[v]
				Average air temperature during forcing (°C)							
1	1	0	-[y]	--[x]	---[w]	---	---	---	20.3	20.6	20.6
		15	-	--	21.0	20.9	21.1	21.4	20.6	21.2	20.8
2		0	7.3	--	---	---	---	---	20.6	21.7	21.0
		15	11.6	--	20.6	20.4	20.9	20.7	20.1	20.8	21.1
	2	0	7.5	---	--	--	--	--	--	--	20.2
		3	8.3	20.5	--	--	--	--	--	--	20.2
		6	8.8	20.5	--	--	--	--	--	--	20.2
		9	10.9	21.0	--	--	--	--	--	--	20.4
		12	12.4	21.3	--	--	--	--	--	--	20.6
		15	13.6	21.5	--	--	--	--	--	--	21.0

[v]Four-hour night interruption.
[y]Not measured (one dash).
[x]Not included in experiment (two dashes).
[w]No plants flowered (three dashes).

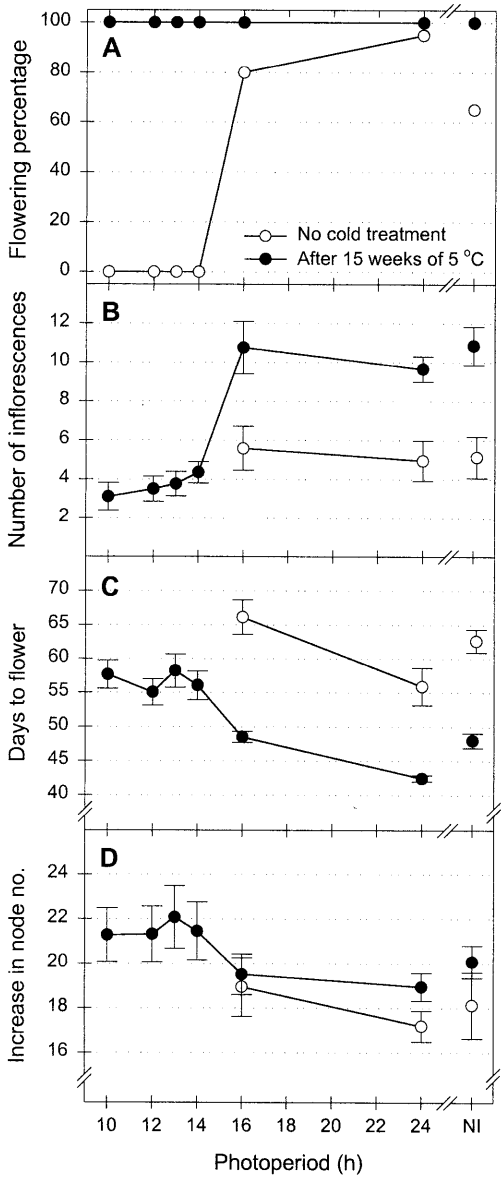

Fig. 1. Responses of *Leucanthemum ×superbum* 'Snowcap' to various photoperiods after 0 or 15 weeks of exposure to 5 °C. Continuous photoperiodic treatments consisted of 9-h natural days extended with light from incandescent lamps. NI = 4-h night interruption. Error bars represent 95% confidence intervals. Data for days to flower and increase in node number are for the period from the start of forcing until anthesis.

reached anthesis were recorded for each plant. At flowering, visible inflorescences and nodes on the main stem below the first inflorescence were counted, and total plant height (not including the container) was measured. Plants that did not have visible inflorescences after 15 weeks of forcing were considered nonflowering and discarded. Days to visible inflorescence, days from visible inflorescence to flower, days to flower, and node-count increase from the start of forcing were calculated.

For each experiment, a completely randomized design with 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. The mean separation test used was the Ryan-Einot-Gabriel-Welsch multiple F test ($P \leq 0.05$), which, compared to more traditional tests (e.g., Duncan's test), has a lower probability of making a Type I error (SAS Institute, 1994). For Expt. 1, data for both years were pooled for all measured characteristics except plant height, for which year × photoperiod and year × cold-treatment interactions were significant.

Results

Photoperiod experiment. Without a cold treatment, all plants remained vegetative under photoperiods ≤14 h (Fig. 1A), whereas 65%, 80%, or 95% flowered under NI, 16 h, or 24 h, respectively. After 15 weeks at 5 °C, all plants flowered under all photoperiods.

Table 2. The effects of photoperiod and cold treatment on plant height at flowering of *Leucanthemum ×superbum* 'Snowcap'.

Weeks at 5 °C	Photoperiod (h)	Year 1	Year 2
		Final plant height (cm)	
0	10	---[z]	---
	12	---	---
	13	---	---
	14	---	---
	16	21	16
	24	21	17
	NI[y]	19	17
15	10	10	13
	12	11	15
	13	12	15
	14	12	18
	16	15	22
	24	17	27
	NI	13	20
Significance			
Weeks cold (WC)		***	***
Photoperiod (P)		***	***
WC × P		NS	***
Contrasts			
16 h vs. NI		*	NS
24 h vs. NI		***	***
15 weeks of 5 °C			
P_{Linear}		***	***
$P_{Quadratic}$		*	***

[z]No plants showed visible bud within 105 d of forcing.
[y]NI = 4-h night interruption.
[NS, *, ***]Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

Cold-treated plants flowered 10 to 15 d faster and developed twice as many inflorescences as noncooled plants under the same photoperiods (Fig. 1 B and C). Without a cold treatment, reproductive plants flowered in 55 to 65 d and produced an average of about five inflorescences; after 15 weeks of cold, plants flowered in 57, 48, or 42 d under photoperiods ≤14, 16, or 24 h, respectively (Fig. 1C). Cold-treated plants developed three to four or 10 to 11 inflorescences under photoperiods ≤14 h or ≥16 h, respectively (Fig. 1B). Noncooled plants developed 17 to 19 nodes below the first inflorescence, whereas cooled plants developed 19 to 22 nodes (Fig. 1D). Under the same photoperiods, the rate of plant development increased 40% to 46% following cold treatment; noncooled plants developed 0.52 to 0.57 node/day and cooled plants developed 0.73 to 0.83. In Year 1, noncooled plants were taller at flowering than those that were cooled, but the reverse was true for photoperiods ≥16

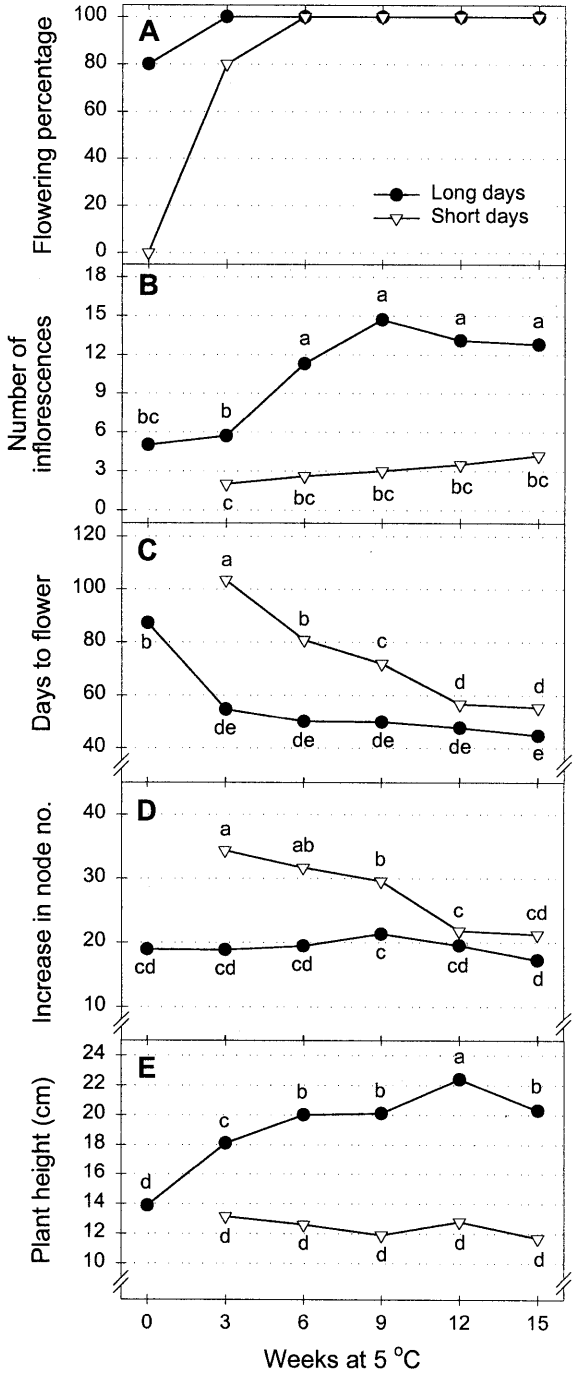

Fig. 2. Responses of *Leucanthemum ×superbum* 'Snowcap' under two photoperiods after 0, 3, 6, 9, 12, or 15 weeks of exposure to 5 °C. Photoperiods consisted of 9-h natural days without (short days) or with (long days) a 4-h night interruption with light from incandescent lamps. For each graph, letters next to symbols represent mean separation by the Ryan-Einot-Gabriel-Welsch multiple F test ($P \leq 0.05$). Data for days to flower and increase in node number are for the period from the start of forcing until anthesis.

h in Year 2 (Table 2). Following cold treatment, plant height at flowering in both years increased at least 70% as the photoperiod increased from 10 to 24 h. Plants under continuous light were always taller than those under NI. Cold-treated plants under 16 h or NI reached visible inflorescence and flowered at the same time, developed the same number of nodes and inflorescences, and were the same height ($P \leq 0.05$).

Cold-treatment experiment. Under 9-h photoperiods, noncooled plants did not flower, but all flowered after ≥6 weeks at 5 °C (Fig. 2A). Under NI, 80% of the plants flowered without a cold treatment and all flowered after ≥3 weeks at 5 °C. Plants under 9-h photoperiods developed two to four inflorescences, regardless of cold duration; plants under NI developed fewer than six or >11 inflorescences after ≤3 or ≥6 weeks at 5 °C (Fig. 2B).

Plants flowered progressively faster as duration of cold treatments increased (Fig. 2C). Plants that received ≥3 weeks of cold and were under NI flowered in 45 to 55 d. Under 9-h photoperiods, time to flower decreased from 103 to 57 d as the exposure to cold increased from 3 to 12 weeks. Time from visible inflorescence to flowering was 26 and 24 d without and with NI, respectively (data not shown).

Plants under NI developed 17 to 21 nodes below the first inflorescence regardless of cold treatment (Fig. 2D). For plants under 9-h photoperiods, the number of nodes to the first inflorescence decreased from 34 to 21 as exposure to cold increased from 3 to 15 weeks. The height of plants under 9 h of light were 12 to 13 cm at flower, regardless of cold duration (Fig. 2E). Plants under NI were 14, 18, or 20 to 22 cm in height after 0, 3, or ≥6 weeks at 5 °C. All measured flowering characteristics were similar for plants under 9-h photoperiods after 12 or 15 weeks of cold.

Discussion

'Snowcap' is a qualitative LDP without a cold treatment and a quantitative LDP after exposure to cold; plants forced under short days (≤14 h) have a qualitative cold requirement and plants under LD (≥16 h or NI) have a quantitative cold requirement. Changes in photoperiodic responses brought about by cold-temperature treatments have been well documented (Lang, 1965; Vince-Prue, 1975). Some changes are slight, with minimum photoperiods for flowering shifting from 16 to 14 h after cold (e.g., *Campanula rhomboidalis* L.), and others are more dramatic, with minimum photoperiods shifting by >4 h (e.g., *Ajuga reptans* L.) (Grossin and Mathon, 1961). For 'Snowcap', the minimum photoperiod for flowering shifted by >5 h, from between 14 and 16 h to <9 h after cold.

Flowering characteristics (e.g., flower number, flowering percentage, etc.) of 'Snowcap' are enhanced by a cold treatment. The benefits of such treatment can be divided into two categories: first, increased flowering percentage of a population, and second, desirable flowering characteristics, such as improved uniformity, reduced time to flower, and increased flower number. 'Snowcap' required between 3 and 6 weeks of cold for complete flowering of a population under 9-h photoperiods; complete flowering under NI required no more than 3 weeks of cold. In contrast, 'G. Marconi' required between 12 and 16 weeks of cold treatment for 100% flowering (Shedron and Weiler, 1982). Desirable responses to exposure to 5 °C were saturated after 6 weeks when plants subsequently were forced under NI, and after 12 weeks when forced under 9-h photoperiods.

While short exposures to cold were adequate for flowering, cold temperatures only partially substituted for LD, since even 15 weeks of cold were inadequate; cold-treated plants under photoperiods ≥16 h or NI flowered earlier, more uniformly, and had more flowers than those under shorter photoperiods.

If providing a cold treatment is not feasible, then lighting a crop 24 h per day will produce a high flowering percentage. However, the beneficial effects of cold treatment followed by LD are many: all plants within a population will flower, and will do so earlier, more uniformly, and more prolifically than noncooled plants. Our results indicate that the earliest flowering occurs when cold-treated plants are provided continual light during forcing, but plants may become undesirably tall. An alternative lighting strategy is to provide a 4-h NI when daylengths are <16 h.

Under NI, plants cold-treated for 15 weeks flowered in about the same time in Expts. 1 and 2, but there were discrepancies with noncooled plants: those in Expt. 2 flowered ≈25 d later. In addition, plants were more branched and shorter. We cannot readily explain this discrepancy. Plants in Expt. 2 were exposed to natural short photoperiods for 12 d longer than those in Expt. 1, Year 2, which could have promoted branching and vegetative growth and thus have inhibited flowering.

In Expt. 1, the increase in inflorescence count and the hastening of flowering 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, in Expt. 2, inflorescence number increased dramatically between 3 and 6 weeks of cold (Fig. 2B), even though *PPF* levels were only 0.5 $mol \cdot m^{-2} \cdot d^{-1}$ higher in the latter cold treatment (Table 1). Furthermore, inflorescence number remained statistically unchanged despite longer cold temperature durations and increased light levels during forcing. Similarly, time to flower under NI after ≥3 weeks of cold remained statistically unchanged in Expt. 2 despite higher ambient light levels. Thus, the accelerated flowering and increased inflorescence count can be associated primarily with cold treatment, not higher ambient light levels.

For forcing 'Snowcap', we recommend providing plants with a minimum of 6 weeks of cold treatment followed by photoperiods ≥16 h or a 4-h NI. The only negative aspect of 'Snowcap', like most Shasta daisies, is that its inflorescences produce an unpleasant odor, which is noticeable when plants are massed. However, the numerous positive attributes of 'Snowcap' merit its consideration as a cultivar of choice for forcing Shasta daisy as a potted plant.

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