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The Influence of Light on Lily (*Lilium longiflorum* Thunb.). II. Influence of Photoperiod and Light Stress on Flower Number, Height, and Growth Rate¹

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Abstract. Placing lily plants in complete darkness, with or without 12 hr per day of low intensity incandescent (Inc) lighting for 5 days at 5 day intervals during the first 40 days of growth after emergence (E) had no influence on final flower bud number. Low intensity Inc lighting given as a 4 hr night interruption under natural daylight (ND) conditions for 10 days at various intervals during the first 40 days after E had no horticulturally significant influence on flower bud number. Final lily plant heights were controlled by photoperiod. Heights were reduced when plants were forced under 8 hr photoperiods (SD) when compared to ND forced plants. Heights of 'Ace' and 'Nellie White' plants were reduced by 29% and 45% when forced under SD from E to flower (F), by 19% and 42% when forced from 30 days after E to F, and by 20% and 20% when forced from visible bud to F. Repetitive light/dark cycles of 4, 6 or 12 hr had no effect on lily flower bud development rate from the time buds were 6–12 cm in length to anthesis.

Forcing the lily for Easter requires precise scheduling, proper height control, as well as a high bud count for maximum pricing. Historically, high light was thought to be needed for this. Furthermore, the use of high intensity discharge (HID) lamps to supplement natural daylight (ND), or to replace ND for photosynthesis, is becoming more commonplace in greenhouses. On the other hand, most greenhouse energy conservation systems reduce light available for plant growth. Double layer polyethylene over glass

reduces light intensity by 18% of the exterior light level above the light reduction due to the glass and structure (2). Retractable thermal curtains drawn at night to conserve energy to a degree cast shadows during the day. These curtains may also be used to shorten the photoperiod for crops. What influence do these new factors have on forcing of the Easter lily?

Several studies have been conducted on light intensity and flower abortion in lily. Einert and Box (7) observed that when 'Georgia' lilies were grown under 50% shade, the number of flowers initiated was reduced by 10%, but there were no differences in number of aborted flowers on plants when compared to plants grown under normal day conditions. Mastalerz (12) found 35–80% bud abortion on 'Croft' lilies stored in darkness at 27°C for 10 days and 15% bud abortion when held at 18°. Buds were approximately 0.6 to 1.2 cm in length. Weiler (19) found 70% shading from emergence to flower reduced bud number by 22% when bulbs were programmed by the CTF method (5).

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Kamerbeck and Durieux (10) observed that 'Enchantment' lilies were very susceptible to flower bud abortion due to low light during the 5th to 7th week after shoot emergence. This period concurred with meiosis of the pollen mother cells. Mor and Halevy (13) have shown that the critical period for rose flower bud abortion is about 15 days after lateral bud break. Flower bud abortion could at least in part be prevented by night lighting with incandescent lamps. Their results indicated that incandescent lighting increased the sink strength of the developing bud which therefore was able to compete more strongly with other sinks for a limited source of metabolites. Shillo and Halevy (17) have shown with the gladiolus that natural short days of winter reduced the percentage of gladiolus corms that flowered and that a low intensity incandescent light extension of the natural winter daylength could reverse this by altering source/sink strengths between the flowering shoot and corm.

Height of lily plants, when grown continuously under short photoperiods, is significantly less than when plants are grown under long photoperiods of incandescent light (11, 14, 18, 22). Plants grown under long photoperiods of incandescent light can be as much as two times taller than plants grown under short photoperiods (18). Roh and Wilkins (15) have shown that high temperatures ($>21^{\circ}\text{C}$) from at least the visible bud to open flower stage increased height. The use of thermal curtains for energy conservation may allow the lily forcer to conserve energy at night, moderate greenhouse temperature increases during the day and economically control height by creating short days (SD), and perhaps eliminate the need for chemical growth retardants.

Thus, we wished to determine for the Easter lily: a) if there were a developmental stage especially sensitive to low light stress which resulted in reduced flower initiation or increased abortion, b) if low intensity night lighting during the vegetative and early reproductive growth period would increase the number of flower buds initiated by increasing shoot sink strength, and c) if short photoperiods influence lily plant height during different developmental stages of the lily.

Materials and Methods

General conditions. 'Nellie White' lily bulbs (20–23 cm in circumference) were grown, harvested and subsequently shipped by non-refrigerated truck on October 10, 1979, from the Pacific Bulb Growers Research Farm in Brookings, Oregon to Michigan State University (MSU) and the University of Minnesota (UM). Bulbs were received on October 25 (MSU) or October 29 (UM), and planted on October 27 (MSU) or November 1 (UM) in 15 cm clay pots. Bulbs had on the average 43 mother scales plus 76 daughter scales and leaves. Meristem diameter averaged 0.56 mm. Bulbs received 6 days (MSU) or 0 days (UM) of 4°C prior to potting. All bulbs were programmed by the CTF method (5) by maintaining them at 17° after potting until November 9 for rooting purposes and then at 5° for 6 weeks for vernalization. All bulbs received one week of "insurance policy" (IP) incandescent (Inc) lighting (nightly from 2200–0200) upon emergence (E) except where noted. Average night/day (N/D) temperatures were $17\text{--}18^{\circ}/18\text{--}20^{\circ}$. Standard cultural procedures were followed throughout forcing (20).

Light stress experiment (MSU). At E, 5 plants per treatment were shifted from ND to darkness with $2\ \mu\text{Em}^{-2}\text{sec}^{-1}$ of Inc light for 12 hr a day on a) the entire plant, b) the expanded leaves by covering the upper leaves with an aluminum foil cone, c) the upper unexpanded leaves by covering the lower foliage with a black cloth, or d) the plants were in total darkness. Different groups of plants were each light stressed for 5 days, starting at E

and continued every 5 days for up to 45 days. Air temperatures in the dark chambers and in the greenhouse were similar ($17^{\circ}/20^{\circ}\text{C}$, N/D). Date of visible bud (VB) and flower (F), plant height, and number of flower buds were recorded.

Incandescent lighting experiment (UM). Plants were irradiated with Inc light for 4 hr from 2200 to 0200 with $11\ \mu\text{Em}^{-2}\text{sec}^{-1}$ during the following periods after E: E to 10, 10 to 20, 15 to 25, 20 to 30, 25 to 35, 30 to 40, or E to 40 days. Five plants per treatment were used. Plants did not receive 1 week of lighting on E as described under general conditions. Height, number of days to F and number of primary, secondary or tertiary flower buds (15) were recorded at anthesis.

Photoperiod experiment (MSU). 'Ace' and 'Nellie White' bulbs (13–15 cm in circumference) were planted on October 14 and treated as described under general conditions except they were placed under SD for 8 hr light/16 hr darkness from a) E to F, b) 30 days after E (which is the approximate time of floral initiation (FI) to F, or c) from VB to F. These 3 respective treatment time spans were approximately 90, 60 or 30 days in length, respectively. Five plants per treatment were used. Visible bud and F dates, number of flowers, and height were recorded for each plant.

Bud opening experiment (MSU). Lily plants were forced in the greenhouse under conditions already described above until the largest bud was at least 12 cm in length. Five plants per treatment were then placed in chambers to provide a) continuous Inc light, b) continuous dark or c) repetitive light/dark cycles of 4, 6, or 12 hr. Plants were therefore held under continuous Inc light, continuous dark or under 1, 2 or 3 light/dark cycles during any one 24 hr time cycle. Light was provided by a 100 W Inc bulb placed 90 cm above the pot rim ($11\ \mu\text{Em}^{-2}\text{sec}^{-1}$). Temperatures ranged from 21° to 26°C during the experiment but temperatures were generally $21\text{--}22^{\circ}$. When the lamps were on, the chamber temperature increased about 1° . The four largest buds on each plant were measured at the time the experiment commenced and every 24 hr thereafter until the 4 flower buds had opened on each plant.

Results and Discussion

Light stress experiment (MSU). No significant differences in total number of flowers bud either differentiated or aborted were observed as a result of light-stress (Table 1). In addition, no time differences were observed in days from E to VB, E to F, or VB to

Table 1. Influence of 5-day time spans of dark or of low light intensities on total flowers and aborted buds on Easter lily 'Nellie White' plants (MSU).

Time span of light-stress after emergence (days)	Total flowers formed			
	Dark whole plant	Inc ^Z whole plant	Inc ^Z apex only	Inc ^Z base only
0-5	7.6 (0) ^Y	7.4 (0) ^Y	7.8 (0) ^Y	8.2 (0) ^Y
5-10	7.6 (0)	8.2 (0)	7.8 (0)	7.0 (0)
10-15	8.4 (0)	7.8 (0)	8.2 (0)	8.0 (0)
15-20	7.8 (0)	7.4 (0)	8.0 (0.2)	7.6 (0)
20-25	7.6 (0)	7.8 (0.2)	8.0 (0)	7.0 (0)
25-30	8.2 (0)	7.6 (0)	8.4 (0.2)	7.4 (0)
30-35	8.2 (0)	7.4 (0.6)	8.2 (0)	8.2 (0)
40-45	7.4 (0.4)	8.4 (0)	8.4 (0.2)	6.6(0.2)
No light-stress NS ^X	8.2 (0)			

^Z $2\ \mu\text{Em}^{-2}\text{sec}^{-1}$

^YNumber of aborted flower buds in parentheses.

^XF-test for all variables nonsignificant.

Table 2. Influence of lighting Easter lily 'Nellie White' plants with incandescent lighting during the vegetative (leaf unfolding) and early reproductive (floral initiation) phase of plant development (UM).

Lighting period ^z (days from emergence)	No. of buds			Days to flower	Height (cm)
	Primary	Secondary	Total		
No lighting	5.0	0.8	5.8	84	32
0-10	5.0	1.1	6.1	79	38
10-20	4.9	1.1	6.0	82	39
15-25	5.0	1.4	6.4	81	39
20-30	5.0	1.4	6.4	83	40
25-35	4.9	0.9	5.8	85	38
30-40	5.0	1.7	6.7	83	39
0-40	4.8	1.0	5.8	78	39
HSD (5%)	0.7	0.4	0.7	5.6	6.5

^z11 μ Em⁻²sec⁻¹.

F. At anthesis, all plants were acceptable and heights were similar (data not presented).

'Nellie White' appear to be less sensitive to light stress related flower bud abortion than 'Enchantment' lilies (10). Likewise, no increase in flower bud number occurred. Source/sink relationships apparently were not altered sufficiently to affect flower bud number. A longer light stress (>5 days in the dark) may have induced bud abortion if given.

Incandescent lighting experiment (UM). If the lily were to respond to Inc light like the rose (13) and gladiolus (17), increased lily flower bud number or a decrease in abortion would occur. However, differences in total flower bud number were small with a maximum increase for only 0.9 flower buds when plants were lighted from 30–40 days after E (Table 2). Heins, et al. (9) found that during vegetative or early reproductive growth, neither continuous supplemental high intensity discharge (HID) lighting, nor 50% saran shading, influenced flower bud number. However, long term (30 day) Inc lighting reduced bud number (9). We note that temperatures were not lowered as reported by Roh and Wilkins (16) during floral initiation to possibly increase flower bud numbers.

Photoperiod experiment (MSU). Significant height reductions occurred when plants were placed under SD and final plant height decreased as the number of SD increased. Final 'Ace' height was reduced 29% and 'Nellie White' 45% when plants were grown continuously under SD compared with plants grown under ND (Table 3). This is in agreement with Smith and Langhans (18)

who found a 38% reduction in plant height when grown from E to F under SD. Short days had no effect on time to F from E or from VB. Height from the top leaf to top of the plant was significantly reduced on 'Nellie White' plants in all SD treatments but only on the E to F treatment in 'Ace'.

Using the observation that final height of a lily grown under ND will be at least double that of the VB height (9), a SD treatment starting at VB should significantly reduce subsequent shoot elongation. This photoperiodic control could also be combined with a thermal blanket for night heat conservation purposes and be used during the day to decrease solar induced high day temperatures. High temperatures have been associated with increased height during the last stages of growth (15).

Bud opening experiment (MSU). If bud opening in the lily were related to the number of light/dark cycles in a given time period as in many other plants (3), then by increasing the number of light/dark cycles the opening of a lily bud could be hastened. However, no differences in bud growth rates were observed among any of the photoperiod treatments or light/dark cycles (Fig. 1). At the 21°C temperatures at which these plants were held, bud elongation rate was an almost constant 11.3 mm per day from the time the buds were 11 cm in length until they opened. Both Erickson (8) and Wilkins et al. (21) have reported uniform bud growth rate at uniform temperatures.

Conclusions from these data and those previously published (9) were: a) light intensity or duration did not control the rate of lily plant development (9) (Table 1, 2, 3; Fig. 1), b) light intensity had no influence on the number of lily buds initiated within the range from 2 μ Em⁻²sec⁻¹, to 50% reduction of ND by saran, to ND, to ND plus Inc supplemental (11 μ Em⁻²sec⁻¹ for 4 hr), to ND plus HID (85 μ Em⁻²sec⁻¹ for 16 hr) (9) (Table 1, 2, 3; Fig. 1), c) the 'Nellie White' lily was not susceptible to flower bud abortion due to light stress for 5–day intervals during the first 45 days of growth after E (Table 1) or SD during the various phases of growth (Table 3), d) the number or length of repetitive light/dark cycles did not influence rate of lily bud development after the buds were 12 cm or greater in length (Fig. 1), e) SD significantly reduced plant height without reducing rate of plant development (Table 3), the maximum SD effect was during the 30–35 day span from VB to F where the lily elongated to at least twice its height under ND conditions, and f) short term (5–10 days) photoperiodic lighting during vegetative and early reproductive growth did not increase number of flower buds initiated on the meristem

Table 3. Influence of natural daylight (ND) and short photoperiods (SD, 8hr light) at different time spans during the growth and development of Easter lily plants (Michigan State University).

Treatment: ^z photoperiod time spans	Days from:			Total buds	Height		
	E to VB	VB to F	E to F		Apical leaf to top of plant (cm)	Total (cm)	% Total reduction in height from ND
				<i>Ace</i>			
ND	66.4	32.6	99.0	4.4	13.2b ^y	40.8b	0
SD: E to F	65.2	33.4	98.6	3.0	9.2a	28.8a	29
SD: FI to F	63.4	31.8	95.2	4.4	12.6ab	33.0ab	19
SD: VB to F	66.3	32.5	98.8	3.4	11.2ab	32.5ab	20
	NS	NS	NS	NS			
				<i>Nellie White</i>			
ND	68.6	30.0	98.6	2.0	16.2b	36.8b	0
SD: E to F	69.8	33.6	103.4	1.8	8.2a	20.4a	45
SD: FI to F	69.0	31.8	100.8	2.2	9.4a	21.4a	42
SD: VB to F	71.0	31.3	102.3	1.4	10.8	29.6b	20
	NS	NS	NS	NS			

^z(E)=Emergence, (FI)=Floral initiation, (VB)=Visible bud, (F)=Open flower.

^yMean separation within columns by Tukey's HSD test, 5% level.

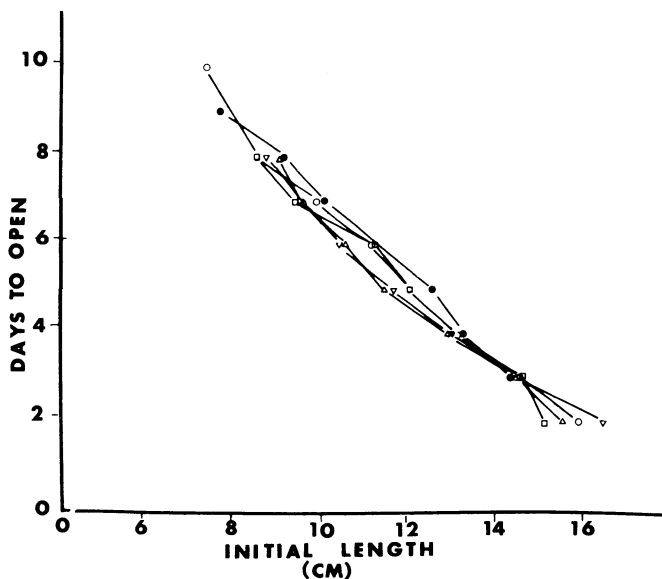


Fig. 1. Influence of light on rate of *Lilium longiflorum* flower bud development at various initial lengths. Light treatments were continuous dark ○—○ continuous light ●—● 12 hr light/dark □—□, 6 hr light/dark Δ—Δ, 4 hr light/dark ▽—▽ at 21°C (MSU).

from fully programmed lily bulbs (Table 2). Thus, the rate of development is not dependent on light but apparently is a function of temperature (9, 15, 21).

The statement that light intensity does not influence rate of plant development or influence flower bud development rate should not be confused with the effect of light on plant quality. To maintain plant quality, light intensity must also increase as temperature increases. However, light does not hasten these physiological processes; temperature is responsible (9, 15, 21). Our past work on lily did not show a hastening or retarding of flowering from increased or decreased light quantity at a uniform temperature during flower bud elongation (9). This probably is not true with all plants. Flowering of the seed geranium has been correlated with total accumulated light (4). However, Armitage and Carlson (1) have shown that once a geranium reached VB, light intensity had no effect on days to F when plants were grown under constant temperatures; at higher temperatures flowering was hastened.

Greenhouse operators discuss the "need" for a sunny day to hasten their crop development, theorizing that high light hastens development. The real cause may indeed be temperature rather than light. Under high light conditions, the leaf is warmed above air temperature (6). Therefore, higher temperatures speed development while high light increases photosynthesis which maintains quality.

Care must be taken in future research to insure uniform temperatures, and to monitor air and leaf temperatures in experiments where light intensity is involved.

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