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The Influence of Light on Lily (*Lilium longiflorum* Thunb.). I. Influence of Light Intensity on Plant Development¹

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Abstract. Lily plants were exposed to natural daylight (ND), 50% ND (50% saran), ND plus 16 hours of incandescent (Inc) or ND plus 16 hours of high pressure sodium discharge (HID) lamp light at both University of Minnesota and Michigan State University. Light intensity had no significant horticultural effect on plant development rate that could not be readily explained by temperature. The Inc or HID light source hastened flowering by 5 to 8 days over the ND plants when given from emergence to flower. However, the rate of development from visible bud to flower was not influenced by light intensity. Plant heights were increased by all light treatments when compared to the ND plants. These increases appeared due to photoperiod for the HID treated plants, photoperiod and light quality for the Inc treated plants, and light quantity for the 50% saran-treated plants. The number of flower buds initiated was not affected by light treatment but Inc lighting increased flower bud abortion. Final plant height was highly correlated with height at visible bud; final height being about double the height at visible bud when plants were grown continuously under ND, HID, or 50% saran.

All energy for growth of higher plants originates from radiant energy. Light strongly influences plant photomorphogenesis by altering plant height (13) and lateral branching (6, 7, 8), as well as

the flowering process (5). Light has been shown to influence plant shape (19), height (11, 17), flower initiation (15, 18) and flower abortion (4, 12) in the Easter lily. After several cloudy days, lily forcers often comment that sunny days will hasten plant development. This is especially true during the period from visible bud (VB) to open flower (F).

With the introduction of energy conserving devices which reduce incoming solar radiation to greenhouse plants, we had expected decreased plant quality, e.g. increased height and reduced flower number due to reduced flower initiation or increased early and late flower abortion. Traditionally, these were attributed to reduced light. However, to our surprise, these did not occur in commercial greenhouses. Further, we were told by a lily forcer that supplemental lighting with high pressure sodium discharge (HID) lamps hastened lily flower development. We attempted to duplicate these results by lighting from VB to F (1976–77) and from floral initiation (FI) to VB, FI to F or VB to F (1977–78). We were unable to increase growth rates (unpublished data).

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With the advent of energy conservation techniques, which may result in reduced light on one hand and the increased use of HID lamps on the other, we wished to reevaluate the influence of light intensity on growth rate and plant development of the Easter lily. A second paper (9) will report further effects of light stress and photoperiod on lily growth rate and plant development.

Materials and Methods

These experimental treatments (Table 1) were repeated for 2 bulb forcing seasons (1978–79 and 1979–80). This paper will be limited to the 1979–80 experiments as results were similar for both years. These experiments concurrently evaluated the effects of light levels (Table 1) during different stages of plant development at both Michigan State University (MSU) and the University of Minnesota (UM).

General conditions. ‘Nellie White’ lily bulbs (20–23 cm in circumference) were grown, harvested and shipped from the Pacific Bulb Growers’ Research Farm in Brookings, Oregon to MSU and UM on October 10, 1979. Bulbs were received at MSU on October 25 (UM – October 23), and planted in 15 cm clay pots (MSU) on October 27 or in plastic pots (UM) on October 25. On these dates, bulbs averaged 43 mother scales and 76 daughter scales and leaves. Apical meristem diameter averaged 0.56 mm. Bulbs had received 6 (MSU) or 0 (UM) days of 4°C prior to potting. Bulbs were programmed for rapid flowering by rooting at 17° until November 9 and then at 5° for 6 weeks (22). Upon shoot emergence (E), all bulbs received one week of “insurance policy” (IP) incandescent lighting (nightly from 2200 to 0200) (21) unless noted. Standard cultural procedures were followed throughout forcing (22).

Individual light treatments on a bench and individual benches were separated by opaque dividers which were pulled from 1600 to 0800 to eliminate light pollution. Date of E was recorded for each plant and individual plants were given the light treatments when they reached the appropriate stage of development (Table 1). Data collected included date of VB, date of first F, height at

VB (MSU only), height at flowering (UM recorded stem height from the rim of the pot to the lowest flower pedicel; MSU recorded height from the rim of the pot to the top of the highest flower), total leaf number, number of primary, secondary, and tertiary flower buds as defined by Roh and Wilkins (15), and number of aborted buds. Number of leaves unfolding each week (20) was recorded at MSU from January 24 (FI) to VB.

Total outdoor solar radiation was recorded during the forcing season with UM receiving 25,798 Langleys from January 1 to April 6, 1980, and MSU, 18,972 Langleys.

Plants irradiated with HID lamps received an irradiance of 85 $\mu\text{Em}^{-2}\text{sec}^{-1}$. In common units, plants under natural daylight (ND) received 25 W m^{-2} at MSU and 33.8 W m^{-2} at UM (24 hour average) while those continuously under HID averaged 36 W m^{-2} and 44.8 W m^{-2} respectively of which 11 W m^{-2} were from the HID supplementing the ND.

Greenhouse temperatures were recorded on thermographs. Average night/day temperatures were 18.5°/ 19.2°C at UM and 17.5°/22.5° at MSU. Leaf temperatures were recorded on representative plants under ND and HID lights using thermocouples pressed against the underside of leaves. During the period of HID irradiation, leaf temperature averaged 0.5° to 1° warmer than ND plant leaf temperature. The U of M is located at 45°N latitude and MSU at 43°N with the resulting daylengths at the two respective stations on January 1 being 8 hours 51 minutes or 9 hours 5 minutes; on April 6 (Easter, 1980) they were 13 hours 11 minutes or 13 hours 6 minutes.

Results

No differences in any parameter measured at either station existed between the ND control and the ND plus one week of lighting (ND+IP) which indicated that all bulbs were fully programmed to flower by cold treatment (18, 21, 22) and any differences in time to flower between treatments were due to applied light treatments and not to further induction by photoperiod.

The authors will concentrate on data from treatments administered from E to F and from VB to F in relation to the ND+IP control since all other plants received the IP treatment. Data from other treatments will be discussed when necessary to expand a point. Data from MSU are presented first, UM second.

Days from emergence to flower and from visible bud to flower. Continuous HID lighting from E hastened flowering by 6 to 11 days while Inc lighting hastened flowering by 5 to 15 days (Table 2). The 50% shade delayed flowering by 6 days at MSU but had no effect at UM.

No differences in the number of days from VB to F existed when plants were grown under the various light treatments from VB to F, at UM. Flowering of plants at MSU under 50% saran was significantly delayed when exposed to the shade treatment from VB to F and FI to F but not in the E to F treatment. The trend, however, was towards a 4–5 day delay in flowering of plants exposed to 50% shade at MSU.

Days from E to F and VB to F among treatments were very similar between locations although variations did exist in some cases.

Total flowers initiated. Flower bud number at MSU averaged 2–3 buds greater on plants in all treatments than at UM (Table 2). No significant differences in total bud number existed between the ND+IP plants and any of the light-treated plants. No reduction in bud number existed on the plants grown continuously under 50% saran or Inc.

Aborted flower buds. Few flower buds aborted at MSU while significant numbers aborted at UM, especially on the Inc treated

Table 1. Light treatments used at various stages of development during the forcing of Easter lily ‘Nellie White’ plants at Michigan State University and University of Minnesota.

Treatments consisted of all combinations of the following factors:

Stage of development

1. Emergence to Flower
2. E to Visible Bud
3. E to Floral Initiation (30 days post-emergence)
4. FI to F
5. FI to VB
6. VB to F

Light

1. HID (16 hours)^Z
2. Inc (16 hours)^Y
3. Shade (50% saran)^X
4. ND^W
5. ND + IP^V

^ZHID=400 W high pressure sodium vapor light at 175 cm above the pot rim with a supplemental intensity of 85 $\mu\text{Em}^{-2}\text{sec}^{-1}$, on from 0800 to 2400 hr.

^YInc=100W incandescent light bulb at 90 cm above the pot rim with a supplemental intensity of 5.6 $\mu\text{Em}^{-2}\text{sec}^{-1}$, on from 0800 to 2400 hr.

^X50% shade=50% reduction in natural daylight using 50% saran shade.

^WND=Natural daylight

^VND + IP = ND plus Insurance Policy for one week of night interruption (2200 to 0200) lighting from 100 W incandescent lights at 90 cm above pot rim and 90 cm apart for an intensity of 11 $\mu\text{Em}^{-2}\text{sec}^{-1}$.

Table 2. Influence of light treatments on Easter lily 'Nellie White' plants at various stages of development when forced at Michigan State University (MSU) and University of Minnesota (UM).

Light treatment ^Z	Stage of development ^Z											
	E-F		E-VB		E-FI		FI-F		FI-VB		VB-F	
	MSU	UM	MSU	UM	MSU	UM	MSU	UM	MSU	UM	MSU	UM
	<i>Days emergence to flower</i>											
HID	81.3	82.5	83.3	84.6	83.5	87.9	85.8	87.8	85.0	89.8	85.2	92.7
Inc	82.7	78.0	85.0	82.1	84.8	87.1	87.0	82.2	86.7	87.6	85.2	91.0
50% Saran	92.8	90.7	90.2	91.4	89.3	96.4	93.8	88.6	88.2	90.9	87.3	92.2
ND	86.0	90.7	HSD (5%) MSU 4.5; UM 5.5									
ND + IP	87.2	93.2										
	<i>Days visible bud to flower</i>											
HID	32.8	33.5	34.0	36.6	32.5	35.1	30.3	32.6	32.8	35.6	32.8	32.4
Inc	31.9	30.4	32.3	33.5	35.0	34.9	30.3	29.5	31.5	34.5	30.3	31.8
50% Saran	34.7	31.8	30.7	33.6	32.0	36.6	34.2	31.7	32.0	33.4	35.0	32.6
ND	30.7	35.1	HSD (5%) MSU 3.8; UM 3.3									
ND + IP	31.0	35.0										
	<i>Flowers initiated</i>											
HID	9.5	6.2	8.5	6.0	8.0	6.1	8.3	6.0	8.5	5.7	8.8	5.6
Inc	8.5	6.0	8.0	5.6	9.2	5.9	7.8	6.0	8.5	5.5	8.0	5.6
50% Saran	8.5	5.8	8.7	5.8	8.7	5.9	8.7	5.9	8.2	5.3	8.5	5.6
ND	8.2	4.9	HSD (5%) MSU 2.6; UM 2.1									
ND + IP	8.5	5.4										
	<i>Aborted flower buds</i>											
HID	0.0	1.7	0.5	1.9	0.0	1.2	0.2	0.8	0.0	1.2	0.2	0.0
Inc	0.8	3.0	1.3	2.6	0.3	1.8	0.0	1.6	0.3	1.6	0.2	0.2
50% Saran	0.0	0.4	0.0	0.6	0.2	0.4	0.0	0.9	0.0	0.5	0.2	0.8
ND	0.0	0.0	HSD (5%) MSU 1.2; UM 1.4									
ND + IP	0.0	0.0										

^ZSee Table 1 for treatment details.

plants (Table 2). The same trend under Inc existed at MSU. Light treatments had no effect on flower bud abortion when applied from VB to F. Furthermore, the 50% saran treatment had no effect on flower abortion.

Leaf number and unfolding. Average leaf number was constant over all treatments (74.4 ± 5.3 for MSU and 67.1 ± 4.3 for UM). At MSU total of leaves unfolded and rate of leaf unfolding were determined weekly for 6 weeks starting January 24 when FI occurred and continued until VB stage (Table 3). From January 24 to February 7 the average number of leaves unfolded per plant was similar among all light treatments (40–42 leaves per plant). However, from February 7 until VB, leaf unfolding rates were 1.7, 2.0, 1.9, and 1.4 leaves per day for ND, HID, Inc and 50% saran respectively. These differences in rate of leaf unfolding after February 7 resulted in treatment differences in days to flower with the ND and 50% saran-treated plants unfolding fewer leaves than the HID- or Inc-treated plants (Table 3).

Final plant height to the apical leaf. Plants grown continuously (E–F) under all light treatments (HID, Inc, 50% saran) were taller at flower than plants grown continuously under ND (Table 4). As the number of days under a lighting treatment increased, so did height, e.g., plants grown under HID at UM from E to FI, VB, or F increased in stem height to the apical leaf by 6%, 34% or 47% respectively. The percent increases in height were not as large at MSU but the control and light treatment plants were taller than at UM. Inc light treatments increased plant height more than HID or 50% saran light treatments except on plants treated during the FI and VB period.

Final total plant height. Direct height comparison between UM and MSU is not possible as UM measured final height from the rim of the pot to the base of the first flower pedicel while MSU measured to the top of the flowers. However, similar trends between total height and height to the apical leaf occurred at both MSU and UM. Actual percent increases were, however, smaller at MSU.

Table 3. Average leaf number unfolded from Easter lily 'Nellie White' plants which had been growing continuously from emergence in the indicated light treatment at Michigan State University.

Date	No. of leaves									
	Light treatment ^Z									
	ND		HID		INC		50% saran		HSD (5%)	
	Week	Sum	Week	Sum	Week	Sum	Week	Sum	Week	Sum
Jan. 24		20.5	---	21.3	---	18.3	---	20.2	---	3.4
31	9.7	30.2	10.3	31.7	10.8	29.0	10.6	30.8	1.9	4.1
Feb. 7	9.3	39.5	10.5	42.2	11.1	40.1	10.2	10.9	2.1	4.7
14	13.0	52.5	13.0	55.2	12.3	52.3	9.0	49.9	2.8	5.6
21	11.0	63.5	15.3	70.4	14.3	66.7	11.3	61.2	2.1	5.8
	---	74.3 ^Y	---	73.5 ^Y	---	77.8 ^Y	---	75.2 ^Y	---	5.5

^ZSee Table 1 for treatment details.^YValues shown are final average leaf numbers for each treatment.

Discussion

Length of top internode (UM). Elongation of the final internode below the flower is generally significantly greater than other internodes on the stem. Lighting treatments influenced final length of this internode (Table 4). When plants were under light treatments from VB to F, internode elongation was greater than the ND+IP plants although not statistically different in all cases. In contrast internodes were shorter than the ND+IP plants when plants were lighted prior to VB, although not statistically different in all cases.

Plant height at visible bud (MSU). Compared to the ND+IP controls, all plants exposed to any type lighting prior to VB, e.g., E to FI or E to VB or FI to VB, were taller to some degree at VB (Table 4). Under these light treatment conditions, VB height was a good predictor of final height. Plants maintained from E to F under ND, HID, or 50% saran increased in height 98% or more from VB to F. Plants under Inc from E to F increased in height by 82% but were taller at VB when compared to other plants. Light treatments during the VB to F period increased plant elongation by an additional 25–35% over the ND+IP grown plants.

Time to flower. While the total quantity of light received among different groups of plants varied greatly, only small differences in time to flower were observed. When standardizing the lowest light level to a base of 100, plants received the following total light energies from E to F in the 400–700 nm region of the spectrum: 50% saran, 100 MSU (140 UM); ND, 200 MSU (270 UM); Inc, 210 MSU (280 UM); HID, 270 MSU (360 UM). However, compared to plants grown under 50% saran, time to flower from E was hastened by only 6% (1% UM) under ND, 11% (16% UM) under Inc, and 12% (11% UM) under HID. Even though there are statistical differences between time to flower from E among the various light treatments, the influence on time to flower is not in relationship to the amount of total light energy received by the plants. Thus, little or no relationship between light intensity and time to flower was found to exist.

Light intensity had little effect on rate of development from VB to F (Table 2). Those trends which exist may be attributed to leaf heating from the lamps or sunlight (3, 13).

Table 4. Influence of light treatments on Easter lily 'Nellie White' plant height characteristics when forced at Michigan State University (MSU) and University of Minnesota (UM).

Light treatment ^z	Stage of development ^z									
	E-F		E-VB		E-FI		FI-F		FI-VB	
	MSU	UM	MSU	UM	MSU	UM	MSU	UM	MSU	UM
<i>Height to apical leaf (cm)</i>										
HID	42.8	40.6	42.1	37.0	38.7	29.4	41.7	39.4	41.1	31.0
Inc	58.3	51.6	57.2	48.2	47.3	33.2	51.3	45.6	40.2	33.3
50% Saran	42.6	44.8	35.5	40.6	35.0	29.8	37.1	38.4	33.3	33.4
ND	31.8	25.9								
ND + IP	30.8	27.6								
HSD (5%) MSU 8.2; UM 8.8										
<i>Height to apical leaf (% of ND controls)^y</i>										
HID	136	151	134	138	123	109	133	147	131	115
Inc	186	193	182	180	151	124	163	170	128	124
50% Saran	136	167	113	152	119	111	118	143	106	125
<i>Total height (cm)^x</i>										
HID	61.8	47.1	63.2	43.7	60.0	37.0	61.2	47.5	62.0	39.1
Inc	79.7	60.7	78.2	56.0	67.8	40.9	73.7	54.2	60.8	40.3
50% Saran	69.7	52.0	55.3	47.7	57.8	37.8	60.2	45.9	56.2	40.1
ND	54.0	32.8								
ND + IP	50.3	35.3								
HSD (5%) MSU 12.6; UM 7.6										
<i>Total height (% of ND controls)^y</i>										
HID	117	138	121	128	115	108	117	140	119	115
Inc	153	178	150	164	130	120	141	159	117	118
50% Saran	134	152	106	140	111	111	115	135	108	118
<i>Visible bud height (cm)</i>										
HID	30.7		30.0		26.8		29.0		28.7	
Inc	44.2		45.6		34.0		37.6		33.3	
50% Saran	35.3		32.5		28.2		29.2		30.2	
ND	25.2									
ND + IP	24.0									
HSD (5%) MSU 7.0										
<i>Final height as a % of VB height</i>										
HID	202		211		225		211		219	
Inc	182		172		200		198		183	
50% Saran	198		170		205		206		183	
ND	215									
ND + IP	210									
HSD (5%) MSU 58										
<i>Top internode length (cm)</i>										
HID		7.0		5.6		5.4		7.3		5.1
Inc		7.7		5.3		4.7		7.6		4.3
50% Saran		8.1		4.7		6.1		7.6		5.0
ND		6.1								
ND + IP		6.8								
HSD (5%) UM 1.7										

^zSee Table 1 for treatment details.

^yAverage of ND and ND + IP.

^xMSU measured rim of pot to top of flower cluster, UM measured from rim of pot to apical node.

We conclude light intensity cannot be considered effective in influencing development rate of a shoot from a fully programmed lily bulb. While air temperatures were similar among treatments, plant leaf temperatures were higher under HID and probably were higher under conditions of high natural irradiance (2, 3). Therefore light intensity may be confounded with plant temperatures (Table 3). Furthermore, effects of Inc or HID supplemental lighting immediately after E can also be confused with photoperiodic (floral induction) responses of the lily (18, 21). This was not the case in these experiments as the ND and ND+IP plants flowered in the same amount of time. Work by Armitage and Carlson (1) further supports this concept. They demonstrated that temperature is the factor controlling flower development rate from VB to F in the seedling geranium. In addition, lily plants forced in complete darkness elongated, unfolded leaves, reached VB, and flowered at the same time as plants grown under continuous HID lighting or ND (data not presented). Regardless, the base average temperature for maximum lily flower bud development rate from VB to F is 21°C (14, 23).

Plant height. Light is extremely important in controlling plant height. In this experiment, a photoperiodic response (HID), a light quality response (Inc), and a light quantity response (50% saran) were evident (Table 4). Plants placed under 50% shade were significantly taller than plants grown under ND. Height of plants was increased by approximately 40% throughout any stage of development when shaded. Increased plant height due to lower light intensities has been reported before by Kohl and Nelson (10).

The increase in height under continuous HID lighting is apparently a photoperiodic response (9, 13, 17). Cathey and Campbell (2) have reported that under High Pressure Sodium lighting stems elongate very slowly and extra thick stems develop; this is in contrast to Inc lighting where stem elongation is excessive. Therefore, the elongation under our HID lighting for 16 hr a day must be photoperiodic, rather than a photomorphogenic response to light quality (13, 17). Previous work by Smith and Langhans (17) showed a reduction in lily plant height due to short days.

Increases in plant height in the Inc treatments greater than those in the HID treatments can be attributed to light quality. The Inc treated plants were 28% taller than HID plants even though they both had the same photoperiod. Inc light is well known to have a higher ratio of far-red (FR) to red (R) light. Roh and Wilkins (16) have shown that FR-treated plants were taller than R-treated plants.

It is of significance to commercial lily forcers that at flower the final plant height to the top of the inflorescence was approximately double the VB height. A 110, 101, or 97% increase in height was observed from VB to F with the ND plants, the HID or 50% saran-treated plants respectively. The final height of the Inc irradiated plants was less than double the VB height. However, Inc plants were already very tall at VB and they still elongated 35.5 cm (MSU datum) which was more than any of the other treated plants. These data suggest that growth retardants could be applied shortly after VB in order to reduce stem elongation without causing excessive clustering of nodes to create the "palm tree" effect. In addition, short photoperiods could be applied to plants at VB to control final shoot elongation.

Bud number. Within the limits of the treatments in these experiments, light intensity had no influence on number of flower buds initiated (Table 2). However, Inc lighting increased flower bud abortion as previously reported (16, 17).

Einert and Box (4) reported a significant reduction in number of flower buds initiated under 50% shade on 'Georgia' lilies, from

13.3 to 11.9 buds per plant. However, flower numbers are traditionally much higher with 'Georgia' than with 'Nellie White' or 'Ace'. Mastalerz (12) also found bud abortion to be higher under high temperature and light stress. Under normal greenhouse-forcing temperatures, light reduction to 50% of natural solar radiation did not induce flower bud abortion in this study (Table 2).

While the data between the 2 universities are not comparable in all cases, the data were consistent over 2 years. These data support the following conclusions on lily plant growth in relation to light: 1) Total light quantity had essentially no effect on rate of lily plant development. Temperature appears to be the controlling factor (14). 2) Light is, however, a critical component of plant quality. On fully induced bulbs, light quantity prevents abortion, while light quantity, quality and photoperiod independently control height and are no doubt additive. 3) Under many light regimes, final plant height under standard culture will double from VB to F.

From these data we better appreciate the fact that once the lily bulb is programmed by 6 weeks of 5°C, temperature controls the growth rate of the shoot (14) in an amazingly uniform manner regardless of light conditions, even in the dark. We now ponder what is the absolute minimum light quantity and duration required for acceptable plant growth? Can light quality (red vs. far-red) effectively control plant height? Can light quantity, duration and quality be combined to better force Easter lily bulbs into quality plants in a more efficient manner?

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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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