Influence of Simulated Shipping and Rooting Temperature and Production Year On Easter Lily (*Lilium longiflorum* Thunb.) Development

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ADDITIONAL INDEX WORDS. vernalization, flower induction, leaf number, light quality, phytochrome, plant height, stem elongation, flowering

ABSTRACT. Interaction between simulated shipping and rooting temperature and harvest year was studied on *Lilium longiflorum*. Bulb dormancy and maturity appear to be separate phenomenon and are affected by temperature differently. Shoot emergence (an indicator of release from dormancy) was hastened by 10 °C shipping and 10 to 20 °C rooting temperatures in both years. Flower induction was affected differently by simulated shipping and rooting temperatures during 1992 and 1993, indicating that bulb maturity differed between the 2 years. Final leaf and flower number decreased because of shipping or rooting temperature, but only when bulbs were mature and received cool temperatures (<16 °C) before a 6-week vernalization treatment. Immature bulbs (at harvest) are unresponsive to vernalizing shipping and rooting temperatures. Prevernalization handling temperature and vernalization treatment length should vary with year based on degree of bulb maturity to achieve consistency in final morphology. Internode length is associated more with the time elongation is suppressed after dormancy is broken than with flower induction (where internode length increases as the length of time elongation is suppressed after breaking of dormancy increases).

Lilium longiflorum bulbs are harvested in southwest Oregon and northwest California from 10 Sept. to 15 Oct. (De Hertogh and Wilkins, 1971; O. Hoffman and H. Harnes, personal communication). Bulbs are subsequently cleaned, stored, packaged, and shipped. The period from harvesting to arrival of bulbs at a forcer's or broker's facility requires ≈2 to 4 weeks. *Lilium longiflorum* bulbs are vernalized in the shipping case or in a pot for 6 weeks (4 to 6 °C) to induce flowering commercially. If potted before vernalization, bulbs are allowed to develop roots for 1 to 3 weeks (16 to 20 °C media temperature) (De Hertogh et al., 1969; De Hertogh and Blakely, 1972). Following vernalization, potted bulbs are placed in a glasshouse for forcing for Easter sales.

Bulb dormancy and maturity affect the induction and forcing process from year to year. Dormancy in *L. longiflorum* has been defined as "a physiological state of a healthy bulb characterized by a temporary delay of sprouting or elongation of the daughter stem axis" (De Hertogh et al., 1971). Breaking dormancy in *L. longiflorum* is identified by initiation of stem elongation of the primary stem axis in the daughter bulb (De Hertogh et al., 1971; Lin and Wilkins, 1975). Therefore, a later indicator of timing of bulb release from dormancy would be shoot emergence from the medium surface (Lin and Wilkins, 1975). How temperature affects bulb dormancy is not known. However, Roberts and Moeller (1971) suggested that optimal temperature for breaking dormancy and subsequent shoot emergence in *Lilium* is 10 to 15.5 °C.

In contrast to bulb dormancy, bulb maturity is related to the ability of a shoot meristem to induce reproductive development. Bulb maturity in *L. longiflorum* has been defined as "a measure of

capacity of a healthy daughter stem axis to sprout without delay and to respond to flower inducing (temperature) treatments" (De Hertogh et al., 1971). The degree of bulb maturity is determined by quantifying the response of a bulb to a vernalization treatment. Lily bulbs are vernalized at any temperature <16 °C with a maximum response at 4 °C (De Hertogh and Wilkins, 1971). *Lilium* leaf and flower number decrease and internode length increases as vernalization time increases (Blaney and Roberts, 1966; De Hertogh and Wilkins, 1971). Earliness of shoot emergence and a decrease in the variability in time of shoot emergence among a bulb population are also associated with increased vernalization time in *L. longiflorum* (De Hertogh and Wilkins, 1971).

Difficulties in forcing *L. longiflorum* are related to the date of Easter changing each year (often changing the length of the shipping, rooting, or forcing period) and bulb dormancy and maturity at harvest (Wang and Roberts, 1970) varies within a population and from year to year (De Hertogh and Wilkins, 1971). Research on vernalization (De Hertogh and Wilkins, 1971), irradiance, and temperature effects on *L. longiflorum* (Erwin et al., 1989; Karlsson et al., 1988; Smith and Langhans, 1962) increased the ability of a forcer to schedule a crop for a desired marketing date. Here we show how simulated shipping and rooting temperature and year interact to affect *L. longiflorum* development. The experiment was designed to identify possible environmental regimes before vernalization to increase uniformity in bulb dormancy or maturity within a crop and between years. We hypothesized that shipping and rooting temperatures affect the vernalization requirement of bulbs and breaking of shoot dormancy, and that the response of a lily bulb to shipping and rooting temperatures varies from year to year.

Materials and Methods

Lilium longiflorum 'Nellie White' bulbs (18 to 20 cm in circumference) were delivered immediately (next day air freight) after being dug on 9 Oct. 1992 and 17 Oct. 1993. Upon receipt, bulbs were divided into 27 groups of seven (1992) or six (1993) bulbs each and were repackaged in the original medium (100% milled sphagnum peat) in plastic bags with holes for aeration. The

Received for publication 2 Mar. 1997. Accepted for publication 26 June 1997. Minnesota Agricultural Experiment Station no. 21,738. We appreciate the support of the Fred C. Gloeckner Foundation, The Easter Lily Research Foundation, the Minnesota Commercial Flower Growers' Association, and the Widmer Fund. In addition, we acknowledge the efforts of Ollie Hoffman (Fred C. Gloeckner Inc.), Harry Harnes (Hastings Bulb Co.), Jerry Pierson, Dean Engleman, and Debra Schwarze. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked advertisement solely to indicate this fact.

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Table 1. Effect of simulated shipping and rooting temperatures on *Lilium longiflorum* Thunb. 'Nellie White' time from termination of vernalization to shoot emergence, anthesis and time from emergence to anthesis in days. Letters denote mean comparisons across temperature. Treatments followed by the same letter are not significantly different at $\alpha = 0.05$.

Parameter	Temp (°C)		
	10	20	30
Shipping			
Emergence	12 a	15 b	18 c
Anthesis	90 a	95 b	95 b
Emergence to anthesis	78 ab	80 b	77 a
Rooting			
Emergence	15 b	12 a	18 c
Anthesis	91 a	93 b	96 b
Emergence to anthesis	76 a	81 b	78 a

medium was kept moist by dipping bags in water periodically. Nine bags were then placed in dark growth chambers at constant 10, 20, or 30 ± 1 °C (SD $\pm 95\%$) air temperature to receive a 2-week simulated shipping treatment.

Following the shipping treatment, bulbs were removed from the packing medium, washed in water, and exposed to darkness, red light (660 nm) [R:FR (660 nm/720 to 740 nm as determined using a LICOR spectroradiometer) = 154 supplied with red supplemented Sylvania 150-W cool-white fluorescent lamps (5 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)], or far red light (720 to 740 nm) [(R:FR = 0.6 supplied with far red supplemented Sylvania 150-W cool-white fluorescent lamps (5 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)] for 15 min to study the impact of the last light exposure on subsequent lily development. Exposure occurred in a growth chamber maintained at 20°C. Bulbs were then planted 6 cm from the base of a 15.2-cm-diameter plastic pot (volume = 2.6 L) in the dark in a medium composed of 2 sphagnum peat : 1 perlite : 1 vermiculite (by volume) (Baccto, Michigan Peat Co., Houston, Texas).

Planted bulbs were then placed in growth chambers at constant 10, 20, or 30 ± 1 °C media temperature for a 2-week rooting temperature treatment, after which all bulbs were vernalized at 4 ± 1 °C air temperature for 6 weeks in a single growth chamber. Care was taken to ensure that the medium was uniformly moist at all times.

Vernalized bulbs were then placed in a glasshouse with an 18 ± 2 °C air temperature setpoint for forcing. Photoperiod was maintained at 8 h by pulling an opaque curtain over plants at 1600 HR and retracting it at 0800 HR. Irradiance levels were that for St. Paul, Minn., from January to April 1992 and 1993 (5.8 and 7.2 $\text{mol}\cdot\text{d}^{-1}$, respectively). Plants were irrigated with water plus fertilizer (14.3 mM calcium nitrate and 5.1 mM potassium nitrate) as needed. Phosphorus and micronutrients were added immediately after planting. Nutrient levels were at recommended levels during the experiment. Electrical conductivity was maintained at 0.75 to 1.0 mS (using a 1 medium : 2 water solution).

Dates of emergence and anthesis were recorded. Plant height, leaf number, and total and aborted flower number were recorded at anthesis. Plant height was defined as the distance from the surface of the planting medium to the tip of the uppermost flower bud. Aborted flower number was determined by counting the number of residual bud scars visible in the inflorescence. Internode length was calculated as total height (to top of uppermost flower bud) – 15 cm (average inflorescence height)/leaf number.

The experiment was organized as a 3 $\times$ 3 $\times$ 3 factorial statistical

design with simulated shipping temperature, light quality exposure before planting, and rooting temperature as the main factors (27 treatments). The experiment was replicated twice over time (1992 and 1993). Treatments were assigned to bulbs at random and bulbs were placed throughout the glasshouse at random. Data were subjected to an analysis of variance procedure and a Tukey's test for mean separation (HSD) (Snedecor and Cochran, 1967). Statistical significance was determined using $\alpha = 0.05$ throughout the analysis.

Results

Bulbs harvested in 1993 were considerably smaller and were believed to be less mature than bulbs harvested in 1992 (O. Hoffman and H. Harmes, personal communication). Lily development was unaffected by the quality of light the bulb was last exposed to. Because bulb size and, possibly, physiological state varied in 1992 and 1993, and because of the lack of a significant light quality effect, data were analyzed using light-quality treatments as replications to enable analysis of the interaction between simulated shipping and rooting temperature and harvest year.

TIME TO EMERGENCE, ANTHESIS, AND EMERGENCE TO ANTHESIS. Time to emergence, anthesis date, and forcing time were affected by simulated shipping and rooting temperature and year. Time to emergence increased from 12 to 18 d as shipping temperature increased from 10 to 30 °C (Table 1). In contrast, time to emergence decreased from 15 to 12 d as rooting temperature increased from 10 to 20 °C, then increased from 12 to 18 d as rooting temperature was further increased from 20 to 30 °C. Time to anthesis increased from 90 to 95 d and from 91 to 93 d as shipping and rooting temperature increased from 10 to 20 °C, respectively. The time from emergence to anthesis was greatest when shipping or rooting temperature were 20 °C. Time to emergence was earlier but time to anthesis and time from emergence to anthesis were later in 1993 than in 1992 (Fig. 1).

PLANT HEIGHT AND INTERNODE LENGTH. Rooting temperature and harvest year interacted to affect plant height. Plant height decreased as rooting temperature increased from 20 to 30 °C in 1992 but not in 1993 (Table 2).

Fig. 1. The effect of year of harvest on the time from the end of vernalization until emergence of the shoot from the media and anthesis and the forcing period of *Lilium longiflorum* Thunb. 'Nellie White'. Letters over symbols denote mean comparisons between years across rooting and shipping temperature. Treatments followed by the same letter are not significantly different at $\alpha = 0.05$.

Table 2. Interaction between rooting temperature and production year on *Lilium longiflorum* Thunb. 'Nellie White' plant height and flower and aborted flower number per plant. Letters not in parenthesis denote mean comparisons across rooting temperature. Letters in parenthesis denote mean comparisons across year. Treatments followed by the same letter are not significantly different at $\alpha = 0.05$.

Year	Rooting temp (°C)		
	10	20	30
Plant height (cm)			
1992	40.4 a (a)	42.1 a (a)	33.9 b (a)
1993	45.4 a (b)	47.2 a (b)	47.0 a (b)
Flower number per plant			
1992	3.1 a (a)	2.9 a (a)	3.0 a (a)
1993	5.5 a (b)	5.8 a (b)	6.6 b (b)
Aborted flower number per plant			
1992	0.6 a (a)	0.8 a (a)	0.8 a (a)
1993	0.6 a (a)	0.4 ab (b)	0.3 b (b)

Simulated shipping temperature, rooting temperature, and year interacted to affect internode length. Internode length decreased as simulated shipping or rooting temperature increased from 10 to 30 °C in 1992 (Table 3). For instance, internode length decreased from 0.79 to 0.63 cm as shipping temperature increased from 10 to 20 °C when bulbs were rooted at 10 °C. Similarly, internode length decreased from 0.79 to 0.64 cm as rooting temperature increased from 10 to 30 °C when bulbs received a 10 °C shipping temperature. In contrast to 1992, internode length was unaffected by shipping or rooting temperature in 1993.

LEAF NUMBER. Leaf number per plant was affected by simulated shipping and rooting temperature and harvest year. Leaf number per plant increased from 56 to 65 leaves per plant as shipping temperature increased from 10 to 20 °C in 1992 (Table 4). In contrast, leaf number per plant was unaffected by shipping temperature in 1993. Leaf number increased from 57 to 66 leaves per plant as rooting temperature increased from 10 to 20 °C. As with shipping temperature, rooting temperature did not affect leaf number per plant in 1993. Plants had more leaves in 1993 than in 1992; leaf number averaged 62 ± 1 and 71 ± 1 leaves per plant, respectively, in 1992 and 1993.

FLOWER AND ABORTED FLOWER NUMBER. Rooting temperature and year interacted to affect flower and aborted flower number per plant. Flower number per plant was unaffected by rooting temperature in 1992 but increased from 5.5 to 6.6 flowers per plant as rooting temperature increased from 10 to 30 °C in 1993 (Table 2). Similarly, aborted flower number per plant was unaffected by rooting temperature in 1992 but decreased from 0.6 to 0.3 flowers per plant as rooting temperature increased from 10 to 30 °C in 1993.

Discussion

A marked difference was evident in how simulated shipping and rooting temperatures affected *L. longiflorum* plant development in 1992 and 1993 (Tables 2–4, Fig. 1), possibly indicating different physiological states of bulbs between the 2 years. Date of shoot emergence was affected by shipping and rooting temperature in 1992 and 1993, suggesting that shipping and rooting treatments affected bulb dormancy. Specifically, shoot emergence was hastened as shipping or rooting temperature increased from 10 to 20 °C, indicating an accelerated release of bulbs from dormancy.

Further increasing shipping temperature from 20 to 30 °C hastened shoot emergence, but increasing rooting temperature

from 20 to 30 °C delayed emergence, suggesting that whether a bulb is actively rooting or not may affect the impact of temperature on shoot emergence; *L. longiflorum* root growth is most active when bulbs are grown at 21 °C (De Hertogh and Blakely, 1972). These data do not agree with results of Lin and Wilkins (1975), where a 2-week 10 °C pretreatment similar to our simulated shipping treatment did not affect earliness of shoot emergence of vernalized bulbs. Bulb dormancy may have varied between bulbs in Lin and Wilkins' experiments and the experiment presented here.

That shipping and rooting temperature affected flower and leaf number per plant in 1992 but not in 1993 could be a result of bulb maturity varying with year. This assumption is supported by the higher leaf number on plants grown in 1993 than 1992 across shipping and rooting treatments (Table 4).

The association between internode length and vernalization is not clear. We propose that internode length increases as the length of time elongation is suppressed after breaking dormancy increases rather than as a measure of degree of flower induction.

Our data support the conclusion of Lin and Wilkins (1975) that, although there is an association, bulb dormancy and maturity are different physiological phenomena. Our data do not support the suggestion by Roberts and Moeller (1971) that the degree of bulb dormancy is a measure of bulb maturity. Rather, our data show that 1) date of emergence (release from dormancy) was affected by shipping and rooting temperatures in 1992 and 1993, suggesting that temperature before vernalization is critical in the release of bulbs from dormancy regardless of the state of bulb maturity and, 2) shipping and rooting temperatures affect bulb dormancy where release was hastened by a 10 °C shipping and a 10 to 20 °C rooting temperature.

In summary, the impact of shipping or rooting temperatures on *L. longiflorum* flower induction depends on the degree of bulb maturity; cool shipping or rooting temperatures affect *Lilium* flowering when bulbs are mature when dug. Final plant quality is, therefore, decreased (leaf and flower number are reduced) when bulbs are mature and receive cool shipping and rooting temperatures (<16 °C) before vernalization (6 weeks) such as in 1992. The ability of a mature bulb to accumulate vernalization is documented (Hill and Durkin, 1968; Lin and Wilkins, 1975; Miller and Kofranek, 1966) and is confirmed here. Therefore, in essence, the bulbs are over-cooled or over-vernalized (De Hertogh and Wilkins, 1971) following a standard 6-week vernalization period when bulbs receive either vernalizing shipping or rooting temperatures.

Table 3. Interaction between simulated shipping temperature, rooting temperature and production year on *Lilium longiflorum* Thunb. 'Nellie White' internode length. Letters not in parenthesis denote mean comparisons across rooting temperature. Letters in parenthesis denote mean comparisons across rooting temperature. Treatments followed by the same letter are not significantly different at $\alpha = 0.05$.

Rooting temp (°C)	Shipping temp (°C)		
	10	20	30
1992			
10	0.79 b (a)	0.63 a (a)	0.67 a (a)
20	0.66 a (b)	0.56 a (a)	0.62 a (a)
30	0.64 b (b)	0.45 a (b)	0.49 a (b)
1993			
10	0.61 a (a)	0.67 a (a)	0.64 a (a)
20	0.63 a (a)	0.62 a (a)	0.63 a (a)
30	0.63 a (a)	0.65 a (a)	0.65 a (a)

Table 4. Interaction between simulated shipping temperature/rooting temperature and production year on *Lilium longiflorum* Thunb. 'Nellie White' leaf number per plant. Letters not in parenthesis denote mean comparisons across rooting temperature. Letters in parenthesis denote mean comparisons across year. Treatments followed by the same letter are not significantly different at $\alpha = 0.05$.

Year of bulb harvest	Temp (°C)		
	10	20	30
Shipping			
1992	56.2 a (a)	65.0 b (a)	63.5 b (a)
1993	70.4 a (b)	71.3 a (b)	72.4 a (b)
Rooting			
1992	56.8 a (a)	66.1 b (a)	62.6 b (a)
1993	69.6 a (b)	73.4 a (b)	71.4 a (b)

Communication between bulb growers, brokers, shippers, and forcers is needed to develop appropriate yearly temperature regimes between digging and vernalization. Prevernalization handling and even length of the vernalization treatment should vary with year to achieve consistency in final plant morphology from year to year.

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