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Nathan E. Lange

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Royal D. Heins
Major professor

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# MODELING FLOWER INDUCTION IN *LILIUM LONGIFLORUM*

By

Nathan E. Lange

A THESIS

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## ABSTRACT

## MODELING FLOWER INDUCTION IN *LILIUM LONGIFLORUM*

By

Nathan E. Lange

The effectiveness of long photoperiods and cold temperature in inducing flowering of *Lilium longiflorum* Thunb. 'Nellie White' was determined by comparing flower induction index (FII) values. FII was calculated by multiplying the relative effectiveness of a treatment in reducing total leaf number by the fraction of flowering plants resulting from the treatment. FII increased as the storage duration increased from 0 to 8 weeks and as the storage temperature decreased from 17.5 to 5C. Nonlinear regression analysis was used to model FII as a function of storage duration and temperature. The resulting model yielded an estimated optimum vernalization temperature of 4.0C. The surface generated by the model resembled an asymmetric hill. LDs during vernalization were not effective above 20C or below 10C and were not as effective as cold temperatures in inducing flowering. LDs induced flowering best at 17.5C. Substituting LDs for cold temperatures resulted in lower FII values. Plants were more responsive when LDs were preceded by cold temperatures. LDs alone were least effective in inducing flowering.

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# LITERATURE REVIEW

## Introduction

*Lilium longiflorum* Thunb. is the most economically valuable species in the genus *Lilium* (Weiler, 1992). The common name for *L. longiflorum* is Easter lily because the majority of the plants produced in the United States are marketed each year during the 14 days prior to Easter. Easter lilies are the third most important flowering potted floricultural crop in the United States. In 1990, at least 9.5 million pots were sold with a wholesale value of 36.9 million dollars (USDA National Agricultural Statistics Service, 1990).

The Easter lily (*Lilium longiflorum* Thunb.) is a member of the Liliaceae family and is native to the Japanese islands of Amami, Erabu, and Okinawa. The species is tropical and experiences an average annual temperature of 21C in its natural habitat on Erabu island which is at a latitude of 27°N (Wilkins, 1980). The species has also escaped cultivation and has established itself on mainland China, Taiwan, and the nearby islands.

Production of Easter lily bulbs in the United States occurs primarily along the West Coast of the United States between Harbor, Oregon and Smith River, California. The two most widely grown greenhouse forcing cultivars in the United States and Canada are 'Nellie White' and 'Ace' (Weiler, 1992).

Field production of bulbs large enough for greenhouse forcing requires two to four years. Bulbs can be propagated from scales of other bulbs, from bulblets formed along the stems of mature plants, and from tissue culture. Bulbs harvested in September and October are planted in the field in November and grown until the following September and October when the bulbs are harvested for sale to greenhouse forcers.

Bulbs received by the greenhouse forcer consist of outer mother scales and inner daughter scales. The current year's outer mother scales are the previous year's inner daughter scales. The bulb's current inner daughter scales initiate from a meristem located near the base of the mother shoot on the basal plate during the previous December. These new daughter scales form the daughter bulb after the primary shoot of the mother bulb begins to unfold leaves above the soil surface. The daughter bulb meristem has formed all of its scales and begins to initiate leaf primordia by the time the mother bulb flowers in July. The primary shoot of the mother bulb begins to senesce in September and the entire bulb, consisting of outer mother scales surrounding the newly formed daughter bulb, is harvested for sale in September and October for commercial greenhouse production. The shoot from the daughter bulb is the plant that is forced for greenhouse production (Wilkins, 1980).

The daughter shoot can elongate prematurely and emerge prior

to harvest from the field. Premature elongation is referred to as "summer sprouting" (Roberts et al., 1955; Van Tuyl, 1985). The percentage of premature emergence varies from year to year. Once a bulb has prematurely sprouted in the field, harvesting the sprouted bulb becomes extremely difficult because the shoot is easily damaged or desiccated when the bulb is processed and shipped to a greenhouse lily forcer. Conversely, the daughter shoot may not elongate on schedule and remain dormant for weeks after harvest. Unpredictable, delayed shoot emergence in the greenhouse causes the lily crop to be behind schedule. An understanding of what triggers the daughter shoot to elongate is needed in order for lily forcers to accurately schedule their lily crops for Easter sales.

## Bulb Dormancy

Dormancy of the lily bulb can be measured by the amount of time from planting until the daughter bulb shoot elongates and emerges from the soil (De Hertogh et al., 1971). The temperature during field production has a major influence on the degree of dormancy in field grown lilies. Artificially varying field soil temperatures during the six months prior to harvest can dramatically influence the degree of dormancy of the bulbs at the time of harvest. Wang and Roberts (1970) studied the effect of artificially heating the field soil to 21-24C, using heating cables before and after flowering of the mother shoot, on daughter shoot dormancy. Heating the soil prior to anthesis of the mother shoot caused 100% daughter

shoot emergence in the field within 70 days of mother shoot anthesis. Non-heated control plants did not emerge before harvest. Heating the soil to 21-24C from July 15 to September 24 after anthesis of the mother shoot delayed emergence of the daughter bulb by seven days compared to non-heated controls. Roh and Wilkins (1976b) demonstrated that exposure of the mother shoot to 21C or short days (SDs) hastened shoot emergence of the daughter bulb by delaying flowering of the mother shoot compared to plants exposed to long days (LDs) consisting of 35 night interruptions of incandescent light from 2200 to 0200 or from 2000 to 0400 at 16C.

The amount of time a lily bulb spends in the field prior to harvest can significantly influence the dormancy of the daughter bulb. Wang and Roberts (1970) found that emergence time of the daughter shoot in the greenhouse at 16C night and 21C day temperatures decreased from 220 days to 40 days as the harvest date progressed from February to October. Lin and Wilkins (1975) reported that the time from planting to shoot emergence in the greenhouse with 16C night and 21C day temperatures progressively decreased as harvest date progressed from July to October.

The decrease in emergence time with later harvest dates could be caused by exposure of the bulbs to increasingly cool field conditions as harvest date is delayed. Roberts and Moeller (1971) found that emergence time of August- and September-

harvested bulbs was decreased by six weeks storage at 5C, 10C, or 16C, but no decrease in emergence time from planting was observed in October-harvested bulbs. Lin and Wilkins (1975) concluded that temperatures less than 10C in the field decrease dormancy of late harvested bulbs and promotes emergence of the daughter shoot.

The degree of dormancy in a bulb is cultivar dependent. Roberts and Moeller (1971) found that daughter shoot elongation of 'Nellie White' bulbs was consistently slower than 'Ace' or 'Croft' bulbs when evaluated over different harvest dates and different years although clear data as to what "slower" means was not presented. Van Tuyl (1985) evaluated 27 cultivars of Easter lilies and reported 20 to 60 percent summer sprouting depending on the cultivar.

The absence of leaves on the mother plant affects sprouting of the daughter shoot. Roberts and Blaney (1968) reported that removal of 25 percent of the total leaf canopy increased the sprouting percentage of daughter shoots. They further found that leaf removal increased daughter shoot sprouting of partially vernalized plants more than fully vernalized plants.

## Bulb Maturity

Much attention has been given to the concept of maturity in the lily bulb at the time of harvest (Roberts and Moeller, 1971; Roh and Wilkins, 1977a and 1977e; Lin and Wilkins, 1975;

Brierley, 1941b). Lin and Wilkins (1975) defined maturity as, "the ability or readiness of the bulb shoot to perceive cold stimuli (for flower induction) either directly or from the scales." Maturity is not well understood and is difficult to study because of the inability to control the environment during field production. Maturity of the lily bulb increases as harvest is delayed (Lin and Wilkins, 1975). Previous work has considered maturity to be independent of dormancy and is measured by the time to flower in response to a bulb vernalization treatment (Brierley, 1941b; Roberts and Moeller, 1971; Roh and Wilkins, 1977h). Roberts and Moeller (1971) concluded that harvest date influenced the temperature and vernalization duration required for flowering.

Field temperatures influence the growth and development of the daughter bulb. Roberts, et al. (1983) found that the change from scale to leaf initiation and development of the daughter bulb was favored at 12C and delayed at 24C. Daughter scale filling after anthesis of the mother shoot was greatest at 18 and 24C. Meristem size of the daughter bulb was increased by 12C or lower temperatures after anthesis of the mother bulb. Unseasonably warm weather in late summer after anthesis of the mother shoot would increase bulb size while decreasing the size of the daughter meristem and reduce the number of leaf primordia at harvest.

## Bulb Scales

The scales of the lily bulb influence the bulb's state of dormancy. Previous work has demonstrated that removal of daughter scales accelerates daughter shoot elongation and suggested that the location of daughter shoot inhibition is in the daughter scales (Lin and Roberts, 1970; Wang and Roberts, 1970; Roh and Wilkins, 1977a, 1977e). Lin and Roberts (1970) reported that removing only the mother scales had no effect on daughter shoot emergence, but removal of all mother and daughter scales accelerated emergence. Wang and Roberts (1970) concluded that the daughter scales were a source of inhibition to the daughter shoot because removal of only the daughter scales accelerated emergence of the daughter shoot. Roh and Wilkins (1977a and 1977b) reported that removal of daughter scales and the presence of the mother scales accelerated daughter shoot emergence.

Bulb scale removal affects the growth and development of the daughter shoot. Lin and Roberts (1970) reported that the number of leaves and flowers initiated by the shoot was proportional to the number of scales left on the bulb. Scale removal reduced the number of leaves and flowers and delayed anthesis by decreasing the rate of leaf and flower initiation. The presence of scales was not necessary for flower induction. Roh and Wilkins (1977a) found that removal of the mother scales reduced flower bud number more than removal of the daughter scales.

## Vernalization

Vernalization has been defined as the induction of ripeness to flower by temperatures below the optimum for growth (Napp-Zinn, 1984). Exposing a plant that requires a cold treatment for flower induction to low temperatures is defined as thermoinduction (Zeevart, 1983). The effect of cold on plants is inductive. Plants do not undergo morphological changes in the shoot meristem at higher temperatures until after the cold treatment (Zeevart, 1983).

Vernalization is an aerobic process that will not take place in an atmosphere of nitrogen. The process is a cumulative process because most plants that require vernalization for flowering gradually become more effectively vernalized with increased exposure to cold temperatures. However, vernalization is an unusual biological process because within a given temperature range it has a negative $Q_{10}$ value (Bidwell, 1979).

Plants which require a cold treatment for flower induction require either a quantitative cold treatment or a qualitative cold treatment (Hillman 1969). Plants with a quantitative cold requirement eventually initiate flowers without a cold treatment, but flower initiation is greatly accelerated when plants are exposed to a cold treatment. For example, the flowering time of winter rye is accelerated as the duration of cold increases (Purvis and Gregory, 1937). Plants with a

qualitative cold requirement will not flower unless exposed to cold temperatures (Lang, 1965).

Many species which require a cold treatment for flower induction also have a photoperiodic requirement. Plants with a combination of cold and long day (LD) responses are most common (Chouard, 1960; Lang, 1965). Many plants from temperate zones respond to a cold treatment followed by exposure to LDs after vernalization which imitates naturally occurring conditions (Napp-Zinn, 1965).

Vernalization has been demonstrated in several species to modify a plant's response towards photoperiod (Lang, 1965). Sugar beets which normally require both cold and LDs for flower initiation can flower under SDs if exposed to an extended cold treatment (Owen et al., 1940). Tashima (1957) reported that non-vernalized *Raphanus sativus* plants flowered only in long days, but vernalized plants flowered regardless of the photoperiod.

Previous work has suggested the involvement of gibberellins in vernalization (Pharis and King, 1985). Lang (1956) first reported that exogenous application of gibberellin to non-thermoinduced *Hyoscyamus niger* plants could induce flowering thereby replacing the vernalization requirement for flower induction. Many other species that require vernalization for

flowering have since been treated with GA with varying results. Application of GA to *Oenothera biennis* does not replace the requirement for cold for flower induction (Picard, 1965). However, Picard (1965) found that applying GA to *O. biennis* after first exposing the plants to a subthreshold cold treatment induced flowering. The additve effect of GA and the cold treatment suggests that GA and cold act through some common mechanism (Zeevart, 1983).

There are many examples of plants, including all caulescent plants, in which a GA application will not induce flower formation (Zeevart, 1983). There are at least two possible explanations to account for the failure of exogenous GA to promote flower induction (Zeevart, 1978). First, there are over 60 different known GAs, and flower induction may require the application of a particular combination of GAs. Michniewicz and Lang (1962) demonstrated that applying $GA_7$ to *Myosotis alpestris* caused both flower induction and stem growth, but application of $GA_3$ caused only stem growth. Second, GAs are not the only factors that regulate flower induction in plants. Inhibitory substances may be present which are inactive or not produced at lower temperatures (Zeevart, 1978).

Endogenous concentrations of GA have been shown to increase during the change from vegetative to reproductive growth. Radley (1975) reported that endogenus gibberellin

concentrations increased in sugar beets following vernalization. Pocock and Lenton (1979) reported that the endogenous concentration of GA in the apex of sugar beets increased during the transition from the vegetative to the reproductive state following vernalization. There is no conclusive evidence that the observed changes in endogenous GA concentrations following vernalization cause flower intiation or are a result of floral development (Zeevart, 1983).

The effect of cold temperature on Easter lilies is similar to the effect of exogenous gibberellin applications. Aung et al. (1969) demonstrated the presence of gibberillin-like substances in Easter lily bulbs. Kays et al. (1971) reported that two 1000 ppm applications of $GA_3$ applied as soil drenches following five weeks vernalization at 4C increased average internode length of 'Ace' Easter lilies. De Hertogh and Blakely (1972) found that exogenous application of $GA_3$ and $GA_{4+7}$ applied as soil drenches following six weeks of vernalization increased internode length of 'Ace' Easter lilies. De Hertogh and Blakely (1972) concluded that the response of Easter lily to gibberillin is dependent on the stage of plant development and the specific gibberillin.

## Modeling Vernalization

Little work has been done on modeling the effect of temperature on vernalization of plants. The effect of a cold treatment on the vernalization of a plant depends on how the

duration of the cold period and the temperature during the cold period interact (Hillman, 1969). Syme (1973) modeled flowering time in wheat cultivars as a function of vernalization and photoperiod sensitivities. Others have since modeled the growth and development of wheat as a function of vernalization temperature and photoperiod (Weir et al., 1984; Travis and Day, 1988). Brewster (1987) modeled the daily vernalization rate of onion seedlings as a function of temperature to predict inflorescence development. Brewster proposed a peak-shaped function relating vernalization rate to temperature. Atherton et al. (1987) modeled the effect of constant temperature on the reciprocal of total leaf number at curd initiation of cauliflower and developed a triangular model of vernalization. Wiebe and Liebig (1989) modeled hourly vernalization and devernalization of kolhrabi and developed a temperature control algorithm for controling bolting.

Easter lilies have a qualitative cold requirement for flower initiation, which occurs after plants have been exposed for a minimum period to temperatures below a maximum vernalization temperature. The temperature and time required for vernalization interact. As the temperature decreases below the maximum vernalization temperature and/or as the vernalization duration increases, flower induction is accelerated. Commercial Easter lily forcers have historically

stored bulbs at 7 to 10C for six weeks to initiate flowering (Stuart, 1954).

## Effect of Vernalization on Flowering

Cold storage of Easter lily bulbs for increasing periods of time decreases the total number of flowers present at anthesis. A bulletin by the Bermuda Department of Agriculture (1935) reported that the total flower number decreased from 5.8 to 2.9 flowers per plant as the duration of cold storage at 3C increased from zero to four months. Shippy (1937) reported that total flower number decreased from 4.8 to 1.9 flowers per plant as the length of cold storage at 4C increased from zero to eight weeks. Brierley (1941a) found a consistent decrease in total flower number as the duration of cold storage at 4 or 10C was increased from five to ten weeks. In the same year, Brierley (1941b) further reported that flower number deceased as the duration of cold storage at 0C increased from zero to sixty weeks. Miller and Kiplinger found (1966) that flower number decreased from 10.1 to 4.3 flowers per plant as the amount of time at 4C increased from zero to seven weeks. Weiler and Langhans (1972b) reported that flower number decreased from 6.1 to 4.6 flowers per plant as the duration of cold storage at 5C increased from five to ten weeks. De Hertogh and Wilkins (1971) reported that flower number decreased from 10.6 to 5.9 flowers per plant as the number of weeks at 2C increased from zero to six weeks.

Previous studies of Easter lilies have shown that the temperature during cold storage of lily bulbs affects the number of flowers present at anthesis. Brierley (1941b) reported that total flower number decreased from 5.1 to 3.6 flowers per plant as the five-week storage temperature increased from 0 to 10C and that total flower number decreased from 4.8 to 1.8 flowers per plant as the temperature during 15 weeks cold storage increased from 0 to 10C. However, Blaney et al. (1963) reported that flower number increased from 4.0 to 11.5 as the temperature during twelve weeks of storage increased from 4 to 27C. Merritt (1964) found no effect of temperatures between -1 and 10C during twelve weeks of cold storage on flower bud number. Miller and Kiplinger (1966) found that total flower number increased from 4.4 to 7.1 flowers per plant as the temperature during six weeks of storage increased from 4 to 13C. De Hertogh and Einert (1969) reported that bulbs stored for nine weeks at 4C produced plants with 6.0 buds per plant while bulbs stored for nine weeks at 17C produced plants with 7.4 buds per plant.

The temperature and duration of bulb storage affects the percentage of plants that flower within a given storage treatment. Weiler and Langhans (1968a) found that the percentage of plants that flowered within a temperature treatment after ten weeks of storage decreased from 100 to 0 percent as the storage temperature increased from 16 to 21C. They further reported that flowering percentage decreased from

100 to 0 percent as the duration of storage at 2C decreased from six to zero weeks and as the duration of storage at 7C decreased from four to two weeks.

The variability in the number of days to flower is influenced by the amount of cold storage. De Hertogh and Wilkins (1971) reported that the number of days between the first flowering plant and the last flowering plant decreased from 34 to 13 days as the storage time at 2C increased from zero to six weeks.

**Effect of Vernalization on Leaf Number and Forcing Time**

The temperature and duration of lily bulb cold storage affects the total number of leaves formed before flower initiation. The range where temperature influences leaf number is from approximately 0C to approximately 21C. The total duration of greenhouse forcing time to flower is affected by the total number of leaves a plant produces prior to anthesis. Brierley (1941a) reported that total leaf number on plants stored for five weeks decreased from 103 to 70 leaves as the storage temperature increased from 0 to 10C. Brierley further found that the number of days from planting bulbs in the greenhouse to anthesis paralleled the decline in total leaf number as the storage temperature increased from 0 to 10C. Numerous studies since 1941 have found that total plant leaf number and time to anthesis decrease as storage temperature decreases and as duration of cold storage increases. Blaney et al. (1963)

reported that total leaf number and the number of days of forcing decreased as the temperature during twelve weeks of forcing decreased from 27 to 4C. They further reported that forcing times were proportional to the number of leaves. Merritt (1964) found that total leaf number decreased from 96 to 81 leaves per plant as the storage temperature during ten weeks of cooling decreased from 10 to 4C. Weiler and Langhans (1968a) reported that leaf number decreased from 111 to 60 leaves per plant and that the number of days of forcing to flower decreased from 99 to 74 days as the storage duration at 2C increased from two to twelve weeks. De Hertogh and Wilkins (1971) reported that total leaf number decreased from 180 to 85 leaves per plant and that the number of days to flower decreased from 135 to 104 days as the length of cold storage at 2C increased from zero to six weeks. Roh and Wilkins (1977c) found that total leaf number decreased from 83 to 57 leaves per plant and that the number of days from shoot emergence to flower decreased from 133 to 108 days as the duration of cold storage at 2C increased from three to six weeks.

Emsweller and Pryor (1943) reported that flower buds were visible sooner if the bulbs were stored at 10C than at 0 or 21 to 29C. Miller and Kiplinger (1966) found that the number of days of greenhouse forcing to flower decreased from 281 to 111 days as the duration of cold storage at 4C increased from zero to seven weeks. They further reported that forcing time

decreased from 208 to 117 days as the temperature during six weeks of cold storage decreased from 21 to 4C.

### Influence of Forcing Temperatures on Vernalization

Previous studies have shown that cool temperatures during forcing can contribute to vernalization by decreasing final leaf and flower number. Kohl (1958) indicated that plants forced under night temperatures of 8C during the first 14 days of forcing had significantly fewer leaves than plants forced under 16 or 20C night temperatures during the first 14 days of forcing. Smith and Langhans (1962b) found that flower number on plants from bulbs stored for 4.5 weeks at 2C decreased from 4.5 to 1.7 flowers per plant as the forcing temperature increased from 16 to 27C.

### Effect of Suboptimal Temperatures on Plant Growth

Staurt (1954) reported that plants from bulbs stored for eight weeks at -1C flowered 31 days later than plants from bulbs stored for eight weeks at 7C. Merritt (1964) found that the incidence of plant injury and death increased as the temperature during the two weeks preceding ten weeks of cold storage at -1C increased from 13 to 21C. Bulbs stored for twelve weeks at -1C with no high temperature storage period were not damaged but flowered twelve days later than bulbs stored at 2C for twelve weeks.

### Effect of Non-vernalizing Temperatures on Plant Growth

Weiler and Langhans (1968a) concluded that the Easter lily has a qualitative vernalization requirement for flowering. Plants with a qualitative vernalization requirement will not flower unless exposed to temperatures below a critical temperature. The critical temperature for the qualitative vernalization requirement for Easter lilies is less than 21C because plants grown at 21C did not flower unless cooled at temperatures below 21C (Weiler and Langhans, 1968a).

### Photoperiod

The Easter lily is considered to be a LD plant in that it undergoes flower induction after exposure to LDs (Waters and Wilkins, 1967). LDs can affect the qualitative vernalization requirement of Easter lilies. This means that exposing plants that are not fully vernalized to LDs after the plants have received a vernalization treatment can cause the plants to flower in less time than if the plants were grown under SDs after the vernalization treatment. The amount of vernalization required for LDs to be effective in inducing flowering is unclear. LDs have a similar effect on plant growth and development as vernalization. Both LDs and vernalization have been reported to decrease forcing time from planting to flower, decrease total leaf and flower number, and increase flowering percentage.

## Influence of Photoperiod on Flowering

Exposure of Easter lilies to LDs alters flower induction by affecting flower number, the duration of forcing time to flower, and the percentage of plants that flower. Smith and Langhans (1962a) reported that plants exposed to 18 hour photoperiods from nine hours of natural lighting and nine hours of incandescent lighting consistently flowered earlier with a reduced number of flowers than plants exposed to nine hour photoperiods at constant forcing temperatures from 10C to 27C. Waters and Wilkins (1967), using histological studies, found that the number of weeks of LDs required for floral differentiation of plants from non-vernalized bulbs decreased from nine to two weeks as the duration of incandescent lighting per night increased from zero to five hours per night. They further reported that time to flowering and total flower number were reduced by lighting periods consisting of five hour night interruptions of incandescent lighting. The effect of temperature on their results is unclear because all of their experiments were conducted in the field. Weiler and Langhans (1968b) found that plants grown from bulbs vernalized for three to six weeks and exposed to LDs flowered in less time than plants grown under SDs. LDs consisted of either four or ten hours of night incandescent lighting and SDs consisted of 8.5 hours of natural lighting.

LDs affect the time from potting to flower (forcing time) of plants grown from non-vernalized bulbs more than plants grown

from vernalized bulbs (Wilkins et al., 1968a). The number of LDs also affected the forcing time and the time from the start of LDs to flower bud differentiation of plants from non-vernalized bulbs more than plants grown from vernalized bulbs. Wilkins et al. (1968a) found that exposing plants grown at day and night temperatures of 21 and 16C from bulbs cooled for three or six weeks at 10C, to 30 or 45 LDs consistently decreased forcing time by 15 days regardless of the duration of cold storage or number of long days. LDs did not affect the time from the start of LDs to flower bud differentiation in plants grown from vernalized bulbs. Exposing plants grown from non-vernalized bulbs to 30 or 45 LDs decreased forcing time by 32 and 55 days, respectively, and decreased the time from the start of LDs to flower bud differentiation by 80 and 52 days, respectively.

Carlson and Carpenter (1970) confirmed that LDs have a greater effect on the forcing time of non-vernalized bulbs than on the forcing time of vernalized bulbs. LDs decreased the forcing time of plants grown from non-vernalized bulbs from 220 to 160 days. LDs decreased the forcing time of plants grown from bulbs vernalized at 4C for three and six weeks from 148 to 129 days and from 154 to 139, respectively. LDs consisted of continuous 16 hour photoperiods including artificial lighting from 0500 to 1100 from coolwhite fluorescent lamps. SDs consisted of natural lighting ranging from nine to eleven hours per day.

Pertuit and Link (1971) found that continual exposure of plants grown from bulbs vernalized for six weeks at 8C and forced in a 16C minimum night temperature greenhouse, to LDs until anthesis, decreased forcing time by 15 days as compared to plants grown under SDs. LDs consisted of nine hours of natural lighting supplemented with six hours of incandescent lighting from 2000 until 0200. SDs consisted of nine hours of natural daylight achieved by pulling black cloth from 1630 until 0730 over the plants.

Wilkins and Waters (1971) reported that as plants grown from non-vernalized bulbs forced at constant 16C were exposed to an increasing number of LDs from 0 to 28, the number of days to flower decreased from 245 to 141 days. Increasing the number of LDs from 28 to 52 days did not significantly reduce forcing time any further. LDs consisted of natural photoperiods supplemented with night interruptions of incandescent lighting for five hours from 2200 to 0300 hours. Plants were forced under natural day lengths after LD treatments.

Intercalating LDs with natural day lengths (SDs) does not lessen the effectiveness of the LDs to reduce total forcing time. Roh and Wilkins (1977e) reported that exposing plants grown from non-vernalized bulbs to 30 LDs intercalated with as many as 20 natural day lengths decreased total forcing time from 167 to 131 days. LDs consisted of night interruptions of incandescent lighting from 2200 to 0300 hours. Plants were

forced at day and night temperatures of 21 and 16C, respectively.

### Effect of Light Source and Timing on Flowering

The timing of night artificial lighting and the source of lighting used to simulate LDs can determine the effectiveness of the LDs in reducing forcing time. Roh and Wilkins (1977a) found that exposing plants from non-vernalized bulbs to a four hour night interruption of either incandescent, fluorescent, or BCJ-ruby incandescent from 2200 to 0200 hours was more effective in reducing time to flower than a day extension from 1600 to 2000 hours or from 0400 to 0800 hours. They further reported that plants exposed to a four hour day extension from 1600 to 2000 hours of incandescent or BCJ-ruby flowered in less time than plants exposed to a four hour day extension of fluorescent lighting. There was no difference in forcing time between plants exposed to different light qualities as night interruptions from 2200 to 0200 hours or as day extensions from 0400 to 0800 hours.

### Effect of Photoperiod on Flower Number

LDs affect the number of flowers at anthesis of plants grown from both vernalized and non-vernalized bulbs. LDs decreased flower number of plants grown from vernalized and non-vernalized bulbs by 1.5 and 1.3 flowers per plant, respectively (Wilkins et al., 1968b). Carlson and Carpenter (1970) confirmed that LDs during forcing decreases flower

number of vernalized bulbs. Exposing plants form bulbs vernalized for three and six weeks at 4C to LDs decreased flower number from 5.6 to 4.5 and from 7.0 to 6.0 flowers, respectively. Pertuit and Link (1971) found that continual exposure of plants grown from bulbs vernalized for six weeks at 8C to LDs did not affect total flower number as compared to plants grown under SDs. Wilkins and Waters (1971) found that as plants grown from non-vernalized bulbs forced at constant 16C were exposed to an increasing number of LDs from 0 to 28, flower bud number decreased from 15.4 to 6.3 buds. Increasing the number of LDs from 28 to 52 days did not have any additional effect on bud number. Roh and Wilkins (1977e) further reported that exposing plants grown from non-vernalized bulbs to 30 LDs intercalated with as many as 20 natural day lengths decreased total flower number from 15 to nine flowers per plant.

Simulating LDs with an eight hour day extension does not require continuous lighting for the extension to be effective in reducing flower number. Roh and Wilkins (1977d) reported that three minutes of incandescent light within each 30 minute cycle during an eight hour day extension from 1630 to 0030 hours for 30 days reduced total flower number from 7.4 to 5.2 flowers per plant. Increasing the duration of lighting within each 30 minute cycle to 30 minutes did not have any additional effect on flower number. All plants were grown from bulbs vernalized for three weeks at 4C and forced at day and night

temperatures of 21 and 16C, respectively.

### Influence of Photoperiod on Flowering Percentage

The percentage of plants that flower in a given population of plants is affected by the number of LDs given to the population during forcing. Weiler and Langhans (1968b) found that the flowering percentage of plants grown from bulbs vernalized for zero to five weeks and forced at 21C was greater when exposed to LDs than when the plants were grown under SDs. Wilkins and Waters (1971) found that the percentage of plants grown from non-vernalized bulbs that flowered increased from 0 to 100 percent as the number of LDs increased from 0 to 16 days. Plants were forced at 16C through the end of the photoperiod treatments and were forced at 21C from the end of the photoperiod treatments to flower. When the plants were forced at a constant 21C from the beginning of forcing to flower, forty-four LDs were required for 100 percent of the plants to flower.

The number of plants which flower in a population is influenced by the photoperiod the bulbs are exposed to during vernalization (Pertuit, 1973 and 1987). Using unsprouted bulbs, Pertuit found that the percentage of flowering plants grown from bulbs vernalized for six weeks at 7C and exposed to LDs during the last two weeks of cooling was 55 percent. The percentage of plants that flowered which were grown from bulbs exposed to SDs during storage was 25 percent. LDs consisted

of 18 hours per day of incandescent lighting and SDs consisted of twelve hours per day of incandescent lighting. All plants were forced in a 21C minimum greenhouse under natural day lengths.

### Influence of Photoperiod on Leaf Number

LDs have been reported to decrease the total number of leaves initiated prior to flower initiation. Weiler and Langhans (1968b) found that plants from bulbs vernalized at 4C for three to six weeks, forced at 21C, and exposed to LDs had consistently fewer leaves than plants grown under SDs. LDs consisted of either four or ten hours of night incandescent lighting and SDs consisted of 8.5 hours of natural lighting. Carlson and Carpenter (1970) found that LDs decreased leaf number of plants from bulbs vernalized for three weeks at 4C from 100 to 87 leaves. Wilkins and Waters (1971) found that as plants grown from non-vernalized bulbs forced at constant 16C were exposed to an increasing number of LDs from 0 to 28, total leaf number decreased from 254 to 101 leaves. Increasing the number of LDs from 28 to 52 days did not have any additional effect on leaf number. Roh and Wilkins (1977e) further reported that exposing plants grown from non-vernalized bulbs to 30 LDs intercalated with as many as 20 natural day lengths decreased total leaf number from 150 to 98 leaves per plant.

Exposing unsprouted bulbs to LDs during vernalization has been

shown to decrease final leaf number at flower (Pertuit, 1973). Pertuit reported that exposing bulbs to LDs during the last two weeks of six weeks of vernalization at 7C decreased final leaf number from 71 to 57 leaves per plant.

There are two reports that indicate that LDs do not affect leaf number. Smith and Langhans (1962a) reported that there was no difference in total leaf number between plants exposed to 18 hour photoperiods from nine hours of natural lighting and nine hours of incandescent lighting, and plants exposed to nine hour photoperiods, at constant forcing temperatures ranging from 10 to 27C. Pertuit and Link (1971) found that continual exposure of plants grown from bulbs vernalized for six weeks at 8C to LDs did not affect total leaf number as compared to plants grown under SDs.

The length of photoperiod during forcing can affect final leaf number. Weiler and Langhans (1972a) reported that total leaf number decreased from 95 to 84 leaves as the daylength increased from 8.5 to 18 hours per day. All day lengths consisted of 8.5 hours of natural light from 0815 to 1645 hours with additional light provided by incandescent lights after 1645 hour. Plants were exposed to photoperiod treatments from the start of forcing to anthesis.

The timing of night artificial lighting and the quality of lighting used to simulate LDs can affect total leaf number.

Roh and Wilkins (1977a) found that exposing plants from non-vernalized bulbs to a four hour night interruption of either incandescent, fluorescent, or BCJ-ruby incandescent from 2200 to 0200 hours was more effective in reducing total leaf number than a day extension from 1600 to 2000 hours or from 0400 to 0800 hours. They further reported that plants exposed to a four hour day extension from 1600 to 2000 hours of incandescent or BCJ-ruby produced 200 and 199 leaves, respectively, while plants exposed to a four hour day extension of fluorescent produced 235 leaves. There was no difference in leaf number between plants exposed to different light qualities as night interruptions from 2200 to 0200 hours or as day extensions from 0400 to 0800 hours.

Simulating LDs with an eight hour day extension does not require continuous lighting for the extension to be effective in reducing leaf number. Roh and Wilkins (1977d) reported that three minutes of incandescent light within each 30 minute cycle during an eight hour day extension from 1630 to 0030 hours for 30 days reduced total leaf number from 107 to 72 leaves per plant. Increasing the duration of lighting within each 30 minute cycle to 30 minutes did not have any additional effect on leaf number. All plants were grown from bulbs vernalized for three weeks at 4C and forced at day and night temperatures of 21 and 16C, respectively.

## Effect of the Interaction of Photoperiod and Vernalization on Leaf Number

The effect of photoperiod to decrease leaf number is not linear as the amount of vernalization received by the bulb increases. Weiler and Langhans (1968b) reported that the ability of LDs to decrease leaf number lessened from 27 to 9 leaves as the duration of cold storage at 4C increased from four to six weeks. LDs consisted of either four or ten hours of night incandescent lighting and SDs consisted of 8.5 hours of natural lighting. Carlson and Carpenter (1970) found that exposure to LDs decreased leaf number of plants from bulbs vernalized for three weeks at 4C from 100 to 87 leaves while LDs had no significant effect on leaf number of plants from bulbs vernalized for six weeks at 4C.

The temperature during forcing can affect the effectiveness of LDs in reducing total leaf number. Roh and Wilkins (1977b) reported that LDs decreased the total leaf number of plants forced at day and night temperatures of 18 and 16C from 157 to 90 leaves per plant while LDs reduced the total leaf number of plants forced at day and night temperatures of 10 and 7C from 127 to 105 leaves per plant. All plants were grown from non-vernalized bulbs. LDs consisted of an eight hour day extension of fluorescent lighting from 1600 to 2400 hours for 30 days, 25 days after shoot emergence.

LDs cannot totally substitute for vernalization to reduce leaf

number. Wilkins and Waters (1971) reported the total leaf number increased from 65 to 96 leaves as the duration of vernalization at 4C decreased from six to zero weeks and as the duration of LDs during forcing simultaneously increased from zero to six weeks. Plants were forced at day and night temperatures of 19 and 16C, respectively.

### Influence of Photoperiod on Plant Height

Smith and Langhans (1962a) reported that plants grown from bulbs stored for 4.5 weeks at 2C and exposed to 18 hour photoperiods from nine hours of natural lighting and nine hours of incandescent lighting were consistently taller during forcing and at flower than plants exposed to nine hour photoperiods at constant forcing temperatures ranging from 10 to 27C. Weiler and Langhans (1968b) found that plants from bulbs vernalized at 4C for three to six weeks, forced at 21C, and exposed to LDs were nearly twice as tall as plants grown under SDs. LDs consisted of either four or ten hours of night incandescent lighting and SDs consisted of 8.5 hours of natural lighting. Wilkins et al. (1968a) observed that exposing plants, grown at day and night temperatures of 21 and 16C from bulbs cooled for six weeks at 14C, to 30 LDs increased final height from 41 to 61 cm. Carlson and Carpenter (1970) confirmed that LDs increase final plant height at anthesis. Total height at anthesis of plants forced from bulbs cooled at 4C for three or six weeks and exposed to continuous LDs increased from 68 to 83 cm and from 70 to 92

cm, respectively. Pertuit and Link (1971) found that continual exposure of plants grown from bulbs vernalized for six weeks at 8C and forced in a 16C minimum night temperature greenhouse, to long days, increased final plant height from 21 to 53 cm, compared to plants grown under SDs.

Exposure of plants to LDs has been shown to increase the height of plants forced from non-vernalized bulbs. Continual exposure of plants to LDs increased the height of plants forced from non-vernalized bulbs at constant 17C from 72 to 126 cm (Carlson and Carpenter, 1970). However, Wilkins et al. (1968a) reported that LDs decreased final plant height of non-vernalized plants from 84 to 52 cm. Plants were forced with day and night temperatures of 21 and 16C, respectively. Wilkins and Waters (1971) further found that as plants grown from non-vernalized bulbs forced at constant 16C were exposed to an increasing number of LDs from 0 to 16, total plant height decreased from 71 to 38 cm. Increasing the number of LDs from 16 to 52 days did not have any additional effect on plant height.

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# CHAPTER 2

# MODELING TEMPERATURE-CONTROLLED FLOWER INDUCTION IN *LILIUM LONGIFLORUM* THUNB. 'NELLIE WHITE'

**Abstract**

Effects of storage duration and temperature on vernalization and subsequent development of *Lilium longiflorum* Thunb. 'Nellie White' were determined by cooling potted bulbs under forty combinations of storage duration and temperature. Storage durations were either two, four, six, or eight weeks, and storage temperatures ranged from 0 to 22.5C at increments of 2.5C. After termination of the storage treatments, plants were grown at 20C in a glass greenhouse with a nine-hour photoperiod under natural light conditions. The percentage of plants which flowered increased as storage duration increased from two to eight weeks at 0 to 15C. The number of days of greenhouse forcing decreased and internode lengths of plants that emerged after storage increased as the storage duration increased from two to eight weeks. The total number of flowers on plants stored for six or eight weeks increased as the storage air increased from 0 to 12.5C. The effectiveness of a treatment in promoting flowering was determined by multiplying its relative effectiveness in reducing total leaf number by its flowering percentage to produce a flower induction index (FII) value for each plant. Nonlinear regression analysis was used to model FII as a function of storage duration and temperature. The resulting model yielded an estimated optimum vernalization temperature of 4.0C.

## Introduction

Easter lilies have a qualitative cold requirement for flower initiation which occurs after plants have been exposed for a minimum period to temperatures below a maximum vernalization temperature. The temperature and time required for vernalization interact. As the temperature decreases below the maximum vernalization temperature and/or as the vernalization duration increases, flower induction is accelerated. Previous research with Easter lilies has established that cool temperatures are required for flower induction and subsequent initiation (Shippy, 1937; Brierley, 1941a, 1941b; Merritt, 1964; Miller and Kiplinger, 1966; Weiler and Langhans, 1968a; De Hertogh and Wilkins, 1971; Roh and Wilkins, 1977a). A clear relationship has not been established between vernalization temperature and duration effect on flower induction.

Present cooling practices used by lily forcers to vernalize Easter lilies for flower induction are often inadequate. Lily bulbs are commercially induced to flower by exposure to temperatures from 1.7 to 7.2C for 1000 hours (Weiler, 1992). Bulbs are occasionally cooled at higher or lower temperatures for variable periods of time, particularly if the bulbs are cooled outside under prevailing weather conditions, or if available cooling facilities are used for additional purposes and have less-than-optimal temperature settings. A relationship between flower induction as a function of

temperature and duration could be used by lily forcers to objectively determine how effective a particular forcing regime is for flower induction.

Little research has been conducted on modeling temperature effects on vernalization. The effect of a cold treatment on the vernalization of a plant depends on the interaction between the duration and temperature of the cold period (Hillman, 1969). Syme (1973) modeled flowering time in wheat cultivars as a function of vernalization and photoperiod sensitivities. Others have since modeled the development of wheat as a function of vernalization temperature and photoperiod (Weir et al., 1984; Travis and Day, 1988). Brewster (1987) modeled the daily vernalization rate of onion seedlings as a function of temperature to predict inflorescence development. Brewster proposed a peak-shaped function relating vernalization rate to temperature. Atherton et al. (1987) modeled the effect of constant temperature on the reciprocal of total leaf number at curd initiation of cauliflower and developed a peak-shaped model of vernalization. Wiebe and Liebig (1989) modeled hourly vernalization and devernalization of kolhrabi and developed a temperature-control algorithm for controlling bolting. They concluded that vernalization of kolhrabi was a function of temperature and followed a peak-shaped curve. Trione and Metzger (1970) reported that vernalization in winter wheat and barley was a function of temperature and vernalization time.

Their data resembled peak-shaped functions, but a mathematical model relating vernalization to temperature and vernalization time was not presented. A mathematical model describing the relationship between flower induction and temperature and duration of vernalization in Easter lilies has not been previously reported. The objective of this research was to model this relationship.

## Materials and Methods

*Lilium longiflorum* Thunb. 'Nellie White' bulbs 20 to 23 cm in circumference were obtained from a commercial grower and potted in 15-cm (1850 ml) standard plastic pots using a commercial peat-based medium (Baccto Pro Plant Mix, Michigan Peat Co.). Potted bulbs were irrigated and held in a glass greenhouse for three weeks at 18±2C for rooting, after which they were placed in growth chambers in 1 of 11 constant air temperatures ranging from -2.5 to 22.5C (increments of 2.5C). The plants were held at each temperature for two, four, six, or eight weeks. Shoots which emerged during the temperature treatments were exposed to a PPF at canopy level of 10 $\mu mol \cdot m^{-1} \cdot s^{-2}$ supplied from incandescent lamps for 9 hours per day. After termination of the temperature treatments, plants were grown at 20±2C in a glass greenhouse under short days (SD) consisting of a nine-hour photoperiod under natural light. Plants were maintained under SD conditions to prevent additional flower induction. Blackcloth was pulled over the plants from 1700 to 0800 to provide a daily 15-hour dark span.

Control plants were not exposed to a temperature treatment prior to being placed in the greenhouse.

The experiment was conducted during both the 1987-88 and 1988-89 Easter lily seasons. Leaf number, flower number, plant height, inflorescence stalk length, and date of anthesis were recorded for all flowering plants. The percentage of plants which flowered was calculated for each treatment. Because the results were similar, data are presented only from 1988-89.

The number of leaves produced below the inflorescence is an indication of how quickly the plant initiated flowers and, therefore, how effective a treatment was in inducing flower initiation (Brierley, 1941a; Blaney et al., 1963; Weiler and Langhans, 1968a; De Hertogh and Wilkins, 1971; Roh and Wilkins, 1977b). The effectiveness of each temperature treatment in reducing leaf number was determined by calculating a relative leaf number for each plant (Fig. 1). This number was obtained by dividing the number of leaves below the inflorescence by the mean number of leaves on plants in the treatment that yielded the lowest average number of leaves. Means of calculated relative leaf number values were less than or equal to 1.0 for each treatment.

A treatment's effectiveness in inducing flowering could be biased if based only on leaf number of flowering plants. Many treatments included both flowering and vegetative plants.

Treatments that result in plants with relatively few leaves, but with low flowering percentages, would be incorrectly judged as highly effective in inducing flowering if based only on leaf number. A quantitative measurement of flower induction in Easter lilies should incorporate both total leaf number and flowering percentage. A flower induction index (FII) was calculated by multiplying the relative leaf number by the fraction of plants that flowered in a treatment. Means of calculated FII values ranged from 0 to 1.0 for each treatment.

The majority of biological rate (R) responses to temperature follow an asymmetric, peak-shaped curve. Therefore, FII was modeled using the asymmetric function (Reed et al., 1976; Landsberg, 1977):

$$FII = A(T - T_{min})(T_{max} - T)^{B} \quad (1)$$

where

$$A = FII_{max}/(T_{opt} - T_{min})(T_{max} - T_{opt})^{B} \quad (2)$$

and

$$B = (T_{max} - T_{opt})/(T_{opt} - T_{min}) \quad (3)$$

to develop temperature-response curves for the observed data. All four parameters (Table 1), $T_{opt}$, $T_{max}$, $T_{min}$, and $FII_{max}$, have biological meaning, and the B value defines the skew. $T_{opt}$ is the temperature at which FII equals $FII_{max}$, and $T_{min}$ and $T_{max}$ are the temperatures below and above $T_{opt}$, respectively, at which FII equals 0. Initial estimates for nonlinear parameters are readily made since they can be read from a graph of the

observed data. It should be noted that for $T < T_{min}$, FII will become negative and that for $T > T_{max}$, equation (1) cannot be calculated unless B is an integer (Landsberg, 1977).

$FII_{max}$ was modeled as a function of storage duration using the function:

$$FII_{max}=H_o^{-b^{-kD}}$$

where D represents storage duration (0-8 weeks), $H_o$ represents the predicted maximum FII, b represents the inflection point, and k defines the slope.

Previous research established that vernalization does not occur above 21C (Weiler and Langhans, 1968a). The percentage of experimental plants that flowered decreased rapidly to nearly zero as the storage temperature increased above 15C (Fig. 2). As $T_{max}$ would not be expected to change with storage duration, it was fixed at 18C for all storage durations based on visual inspection of Figure 2. Equation (4) was substituted for $FII_{max}$ in (2) and $T_{max}$, $T_{min}$, $T_{opt}$, $H_o$, b, and k were estimated simultaneously using the nonlinear regression procedure (NLIN) of the Statistical Analysis System (SAS Institute, 1987).

Means and 95% confidence intervals were calculated for time of forcing, plant height, inflorescence stalk length, internode length, and total flower number. Plant height is defined as

the height from the soil surface to the bottom of the inflorescence. Heights were recorded only for plants that emerged in the greenhouse after the storage treatments. The low light level (10 $\mu mol \cdot m^{-1} \cdot s^{-2}$) in each growth chamber caused plants that emerged during the storage treatments to elongate, making meaningful inter-treatment comparisons of these plant heights and internode lengths impossible.

## Results

Plants held at 5C for eight weeks during 1988-89 averaged the fewest number of leaves (77.4). Leaf number decreased as storage duration increased from two to eight weeks (Fig. 1). As the storage temperature decreased below 2.5C or increased above 5C, the leaf number of plants stored for four, six, and eight weeks increased. Leaf number remained constant for plants from bulbs stored for two weeks regardless of storage temperature.

The percentage of plants that flowered increased as storage duration increased from two to eight weeks at 0 to 15C (Fig. 2). No plants flowered when stored above 15C for four weeks or above 17.5C for six or eight weeks. Five percent or more of plants stored for only two weeks flowered. The percentage decreased at increasingly higher temperatures as the storage duration increased from two to eight weeks. Flowering percentage decreased to 5% or less at 17.5C as the temperature during four, six, and eight weeks of storage exceeded 7.5, 10,

and 12.5C, respectively. The flowering percentage of plants from bulbs held for two weeks decreased from a maximum of 65% at 2.5C and 5C to 5% at 17.5C. None of the control plants, which received no cooling prior to greenhouse forcing, flowered.

Fitting equation (1) to the calculated FII values resulted in a highly significant model fit (Figs. 3 and 4, Table 2) with an $R^2$ value of 0.91. The FII did not respond linearly to either vernalization temperature or storage duration. The surface generated by the model resembled an asymmetric hill. $T_{opt}$ and $T_{min}$ were estimated at 4.0 and -6.7C, respectively (Table 2). Although $T_{min}$ was estimated at -6.7C, plants cooled for just two weeks at -2.5C froze and died (data not presented).

The number of days from the end of the storage treatments until flower decreased as storage duration increased from two to eight weeks (Fig. 5) and increased as the temperature during two, four, six, and eight weeks of storage increased above 10, 7.5, 5, and 5C, respectively, or decreased below 5C.

At anthesis, the height of plants that emerged after storage did not follow any discernible trend with respect to cooling temperature (Fig. 6). Height increased as storage duration between 0 and 10C increased from two to six weeks. Height of plants stored for eight weeks from 0 to 10C was consistently

equal to or less than that of plants stored for six weeks. Inflorescence stalk length increased as the storage duration increased from two to eight weeks and decreased as the storage temperature decreased from 2.5 to 0C and exceeded 7.5C (Fig. 7).

Internode lengths of plants that emerged after storage increased as the storage duration increased from two to six weeks (Fig. 8). As the six- and eight-week storage temperatures increased from 2.5 to 10C and as the four-week storage temperature increased from 5 to 12.5C, mean internode length decreased.

The total number of flowers on plants stored for six or eight weeks increased as the storage temperature increased from 0 to 12.5C (Fig. 9). There were no other discernible trends.

## Discussion

The FII includes both the number of leaves on a plant and the percentage of plants that flower in a treatment population. The FII is increased by either a decrease in leaf number per plant or an increase in the flowering percentage of a given population. Increased FII values result as the treatment duration increases from two to eight weeks and as treatment temperature decreases from 17.5 to 2.5C. Increased exposure to cooling obtained by either decreasing the treatment temperature from 17.5 to 2.5C or lengthening the treatment

duration decreases the number of leaves per plant and increases the flowering percentage of a given population of plants.

Although, abundant research has been published pertaining to the influence of cold-temperature storage on Easter lily flowering, a quantified relationship relating flower induction to temperature and its duration has not been previously reported. Equation (1) was selected to describe temperature and storage duration-dependent vernalization accumulation rates (Figs. 3 and 4) because the equation readily describes typical asymmetrical peak-shaped temperature-response curves, and all parameters have biological significance.

$T_{opt}$ and $T_{min}$ were estimated at 4.0 and -6.7C, respectively (Table 2). Researchers have found that the optimum temperature for vernalization of Easter lilies is 4C (Miller et al.,1963; Miller and Kiplinger, 1966). Although $T_{min}$ was estimated at -6.7C, plants cooled for just two weeks at -2.5C (data not presented) froze and died. Flower induction cannot be predicted by the FII model for plants exposed to subzero temperatures that cause freeze injury.

Investigators of vernalization in other species have proposed models similar to the FII model. Weibe and Liebig (1989) concluded that the vernalization of kohlrabi, measured as the bolting percentage, was a function of temperature and followed

a peak-shaped curve with a $T_{opt}$ of 5C, $T_{min}$ of 0C, and $T_{max}$ of 12C. Atherton et al. (1987) reported that the rate of vernalization in cauliflower, measured as the reciprocal of the number of leaves initiated by curd initiation, was a function of temperature and followed a triangular curve with a $T_{opt}$ of 5.5C, $T_{min}$ of -1.25C, and $T_{max}$ of 24.5C. Brewster (1987) proposed a peak-shaped function relating temperature to the vernalization rate, measured as the reciprocal of the amount of time to 50% flower initiation, with a $T_{opt}$ of 9C, $T_{min}$ of 2C, and $T_{max}$ of 16C. Trione and Metzger (1970) reported that vernalization in winter wheat and barley, measured as the elongation of the primary culm, was a function of temperature and vernalization time. Their data resembled peak-shaped functions similar to the FII for Easter lily, but no mathematical functions were presented. No previous mathematical models of vernalization that relate both temperature and its duration to vernalization have been reported for any species.

Although no previous models have been published for Easter lily vernalization, data have been reported on the effect of vernalization on flowering percentage and leaf number. Weiler and Langhans (1968a) found that, after 10 weeks of storage, the percentage of plants that flowered within a temperature treatment decreased from 100 to 0% as the storage temperature increased from 16 to 21C. However, all of the plants in their study were grown under naturally occurring, progressively

longer photoperiods, a factor which probally contributed to flower induction at 18C. Previous research has established that LDs during forcing increase the percantage of flowering plants (Weiler and Langhans, 1968b, 1970; Wilkins and Waters, 1971). In this study, percent flowering decreased rapidly from 95 to nearly 0 as the eight-week storage temperature increased from 15 to 17.5C. Weiler and Langhans (1968a) reported that flowering percentage decreased from 100 to 0 as the duration of storage at 2C decreased from six to zero weeks. The data reported here are in agreement with these results (Figs. 3 and 4).

Previous research that reports the influence of vernalization time and temperature on total leaf number is in agreement with the FII model of Easter lily vernalization (Figs. 3 and 4). Merritt (1964) found that total leaf number decreased from 96 to 81 leaves per plant as the storage temperature during 10 weeks of cooling decreased from 10 to 4C. Weiler and Langhans (1968a) reported that leaf number decreased from 111 to 60 leaves per plant as the storage duration at 2C increased from 2 to 12 weeks. Hill and Durkin (1968) reported that leaf number decreased from 90 to 77 leaves per plant as the storage duration at 10C increased from four to six weeks. Roh and Wilkins (1973) found that leaf number decreased from 169 to 72 leaves per plant as the vernalization duration at 4C increased from zero to six weeks. De Hertogh and Wilkins (1971) reported that total leaf number decreased from 180 to 85

leaves per plant as the length of cold storage at 2C increased from zero to six weeks. Roh and Wilkins (1977b) found that total leaf number decreased from 83 to 57 leaves per plant as the duration of cold storage at 2C increased from three to six weeks. The results of the current study and others (Merritt, 1964; Blaney et al., 1963) contradicted the findings of Brierley (1941a), who reported that total leaf number on plants stored for five weeks decreased from 103 to 70 leaves as the storage temperature increased from 0 to 10C. Wang et al., (1970) reported that the number of leaves was inversely related to the length of vernalization at 4C and concluded that reductions in leaf numbers corresponding to increasing storage durations were associated with reductions in stem apex diameter at the time of flower initiation.

Although the same general vernalization effect on leaf number has been observed, the absolute number of leaves per plant within a given vernalization treatment has varied between studies. Plants grown from identically vernalized bulbs, but from different years, can produce different numbers of leaves. Many other factors besides vernalization influence leaf number, such as cooling method (De Hertogh and Einert, 1969), bulb source (Widmer, 1965), bulb size (Langhans and Smith, 1966; De Hertogh et al., 1969; Lange and Heins, 1990), photoperiod during forcing (Weiler and Langhans, 1968b; Carlson and Carpenter, 1970; Wilkins and Waters, 1971; Roh and Wilkins, 1977a; Roberts et al., 1978), photoperiod of bulbs

during vernalization (Pertuit, 1973; Pertuit and Kelly, 1987), forcing temperature (Kohl, 1958; Smith and Langhans, 1962), exogenous gibberellin and abscisic acid treatments (Lin et al., 1975; Kays et al., 1971; De Hertogh and Blakely, 1972), harvest date (Roberts et al., 1978), cultivar (De Hertogh et al., 1969), bulb scale number (Lin and Roberts, 1970), and preheating treatment (Blaney et al., 1963; Durkin and Hill, 1968; Weiler and Langhans, 1972). The reported influence of temperature on leaf number before cooling suggests that the field's soil temperature prior to bulb harvest can affect subsequent leaf numbers. Discrepancies between reported leaf numbers of identically treated plants may be partly explained by yearly fluctuations in soil temperatures prior to harvest.

Greenhouse forcing time decreased as storage duration increased from two to eight weeks (Fig. 5), which agrees with previous findings (Weiler and Langhans, 1968a; De Hertogh and Wilkins, 1971; Roh and Wilkins, 1977b). The observed increase in forcing time as the temperature during two, four, six, and eight weeks of storage increased above 10, 7.5, 5, and 5C, respectively, is in agreement with results reported by Blaney et al. (1963). Forcing time increased as the temperature during storage decreased below 5C. Stuart (1954) reported that plants from bulbs stored for eight weeks at -1C flowered 31 days later than those from bulbs stored for eight weeks at 7C. The number of days of greenhouse forcing was directly proportional to the total number of leaves, which is in

agreement with previous research (Emsweller and Pryor, 1943; Blaney et al., 1963; Brierley, 1941a; Weiler and Langhans, 1968a; De Hertogh and Wilkins, 1971; Roh and Wilkins, 1977b). Forcing time increased as leaf number increased presumably because a greater number of leaves required longer to unfold prior to flower development.

Plant height is determined by the number of nodes and internode lengths. The height of plants that emerged after storage did not follow any discernible trend (Fig. 6). Miller and Kiplinger (1966) found that plant height increased with increasing storage temperature from 4 to 24C and decreased with increased exposure time at any temperature, but no data were reported on leaf numbers or internode lengths. The plants in Miller and Kiplinger's study were grown under naturally occurring, progressively longer photoperiods without regard for the effect of long photoperiods on plant development; as the storage duration increased, the photoperiods during forcing lengthened. Numerous studies have shown that long photoperiods decrease total leaf number (Weiler and Langhans, 1968b; Carlson and Carpenter, 1970; Wilkins and Waters, 1971; Lange, 1992a). Decreasing the number of leaves and consequently the number of internodes by using progressively longer photoperiods leads to decreased plant height when storage duration is simultaneously extended. The observed height increase with increasing storage temperature in Miller and Kiplinger's study can be explained

as above. Research has shown that long photoperiods are only effective if cold vernalization has preceded them (Lange, 1992b). As the storage temperature in Miller and Kiplinger's study was increased prior to greenhouse forcing under LDs, the effectiveness of LDs in reducing total leaf number and, therefore, final plant height was diminished proportionally. The plants in the current study were maintained under short photoperiods throughout the experiment to eliminate interactions between vernalization and photoperiod.

Inflorescence stalk length increased as the storage duration increased from two to eight weeks and as temperature increased from 0 to 2.5C (Fig. 7). The length decreased as the temperature during four, six, and eight weeks of storage exceeded 7.5C (Fig. 7). No data have previously been reported on the influence of storage temperature or duration on inflorescence stalk length of Easter lilies.

Internode lengths increased on plants that emerged after storage as the storage duration increased from two to eight weeks. Blaney and Roberts (1966) reported that the lengths of the 10 lowest internodes increased as the storage duration at 4C increased from 0 to 85 days and as the bulb harvest date was delayed from 14 Jul to 10 Oct. Roberts et al. (1978) reported that internode lengths of plants maintained under SDs increased as the 5 or 10C storage duration increased from 6 to 12 weeks. Wang et al. (1970) found that internode length

increased as the vernalization duration at 4C increased from 0 to 18 weeks. As the six- and eight-week storage temperatures decreased from 10 to 2.5C and as the four-week storage temperature decreased from 12.5 to 5C, the mean internode length increased. These results contradict data reported by Merritt (1964); bulbs cooled at 10C for 10 weeks produced plants with shorter internodes than those of plants from bulbs cooled at four or 7C.

Many researchers have reported that flower number is decreased by increasing the duration of cold storage (Bermuda Department of Agriculture, 1935; Shippy, 1937; Brierley, 1941a and 1941b; Miller and Kiplinger, 1966; Weiler and Langhans, 1972). However, in all of these previous studies, the plants were grown from case-cooled bulbs and forced under naturally occurring, progressively longer photoperiods; as the storage duration increased, the photoperiods during forcing lengthened. LDs have been shown to decrease total flower number of vernalized plants (Smith and Langhans, 1962; Wilkins et al., 1968; Carlson and Carpenter 1970). Increasing the cooling time of case-cooled bulbs, which have relatively few roots during cooling compared to controlled-temperature forced bulbs, could decrease the total flower number. Cooling duration may not affect flower number of controlled-temperature forced bulbs, which usually have a well-developed root system during cooling. All plants in the present study were from controlled-temperature forced bulbs and were

maintained under short photoperiods throughout greenhouse forcing. No effect of storage duration on total flower number was observed in the present study (Fig. 9). Roh and Wilkins (1973) reported that flower number was not affected as the storage duration at 4C increased from zero to six weeks. These results were consistant with those of Roberts et al. (1978) who found that vernalization temperature and duration did not affect the number of flower initials of plants forced under short photoperiods. The total number of flowers on plants stored for six or eight weeks marginally increased as the storage temperature increased from 0 to 12.5C (Fig. 9). These results are similar to those reported by Blaney et al. (1963) and Miller and Kiplinger (1966), and are in contrast to results published by Brierley (1941b), who was studying Creole lilies.

The effect of cold temperature on the internode lengths of Easter lilies is similar to that of exogenous gibberellin applications. Aung et al. (1969) demonstrated the presence of gibberellin-like substances in Easter lily bulbs from flowering plants. Aung and De Hertogh (1967) reported that *Tulipa* bulbs cooled for four weeks at 9C had 92 times more endogenous gibberellin-like substances than non-cooled bulbs. Endogenous concentrations of GA increase during the change from vegetative to reproductive development in other species (Radley, 1975; Pocock and Lenton, 1979). Vernalization could cause transport and/or production of GA in the bulb to the

stem causing stem elongation. Kays et al. (1971) reported that two 1000-ppm applications of $GA_3$ applied as soil drenches following five weeks' vernalization at 4C increased average internode length of 'Ace' Easter lilies. De Hertogh and Blakely (1972) found that exogenous application of $GA_3$ and $GA_{4+7}$ applied as soil drenches following six weeks of vernalization increased internode length of 'Ace' Easter lilies. A similar effect of gibberellin on inflorescence stalk length would explain the observed increase in stalk length with increasing vernalization (Fig. 7). De Hertogh and Blakely (1972) concluded that the response of Easter lily to gibberellin is dependent on the stage of plant development and the type of gibberellin used. Although gibberellins have been associated with vernalization in Easter lily, the relationship between GA and vernalization has not been established. There are over sixty different known GAs, and flower induction in the Easter lily may require the presence of a particular combination and concentration at a specific time during development.

Previous investigations have concluded that $GA_3$ and $GA_{4+7}$ applications following vernalization mimic the effect of vernalization in Easter lily by decreasing total flower number (Kays et al., 1971; De Hertogh and Blakely, 1972; Laiche and Box, 1970). However, in all of these previous studies, plants were grown under naturally occurring, progressively longer photoperiods. The GA may have interacted with the LDs in a

manner similar to its interaction with vernalization in other species. Application of GA to *Oenothera biennis* does not replace cold requirement for flower induction (Picard, 1965). However, Picard found that applying GA to *O. biennis* after first exposing the plants to a subthreshold cold treatment induced flowering. Zieslin and Geller (1983) have reported similar results working with *Liatris spicata*. The additive effect of GA and the cold treatment suggests that the two act through some common mechanism (Zeevaart, 1983).

The mathematical relationship that resulted from this study allows lily forcers to predict the effect of constant temperatures and storage durations during vernalization on subsequent development. Further research is necessary to determine whether temperatures are equally effective throughout the vernalization duration, or how the effect of temperature is dependent on previous exposures to other temperatures. The model does not allow lily forcers to predict absolute plant responses based solely on vernalization treatments because lily bulbs' maturity and previous vernalization accumulation vary from year to year (Roberts and Moeller, 1971; Roberts et al., 1983; Lin and Wilkins, 1975; Roh and Wilkins, 1977a, 1977c; Kays et al., 1971; Wang and Roberts, 1983). The model does allow lily forcers to predict the relative responses of different vernalization treatments. Additional research is necessary to understand the impact of

environmental conditions prior to bulb harvesting on subsequent vernalization and forcing.

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Table 1. Parameters used in this study.

| Parameter | Description | Units |
|---|---|---|
| $T_{opt}$ | Optimum temperature | C |
| $T_{max}$ | Maximum temperature | C |
| $T_{min}$ | Minimum temperature | C |
| FII | Flower Induction Index | none |
| $FII_{max}$ | Maximum Flower Incuction Index | none |

Table 2. Nonlinear regression results from fitting equation (1) to the FII model. $R^2$ was calculated as $1-SS_{residual}/SS_{corrected\ Total}$. N is the number of observations in the data set.

| Parameter | Estimate | Asymptotic 95% confidence interval | | N | $R^2$ |
|---|---|---|---|---|---|
| | | Upper | Lower | | |
| $T_{min}$ | -6.6 | -7.4 | -5.9 | 430 | 0.91 |
| $T_{opt}$ | 4.0 | 3.8 | 4.2 | | |
| $H_o$ | 1.06 | 1.03 | 1.09 | | |
| b | 5.9 | 4.9 | 7.0 | | |
| k | 0.63 | 0.57 | 0.69 | | |

Figure 1. Total leaf number of 'Nellie White' Easter lily as a function of temperature and vernalization duration. Vertical bars represent 95% confidence intervals.

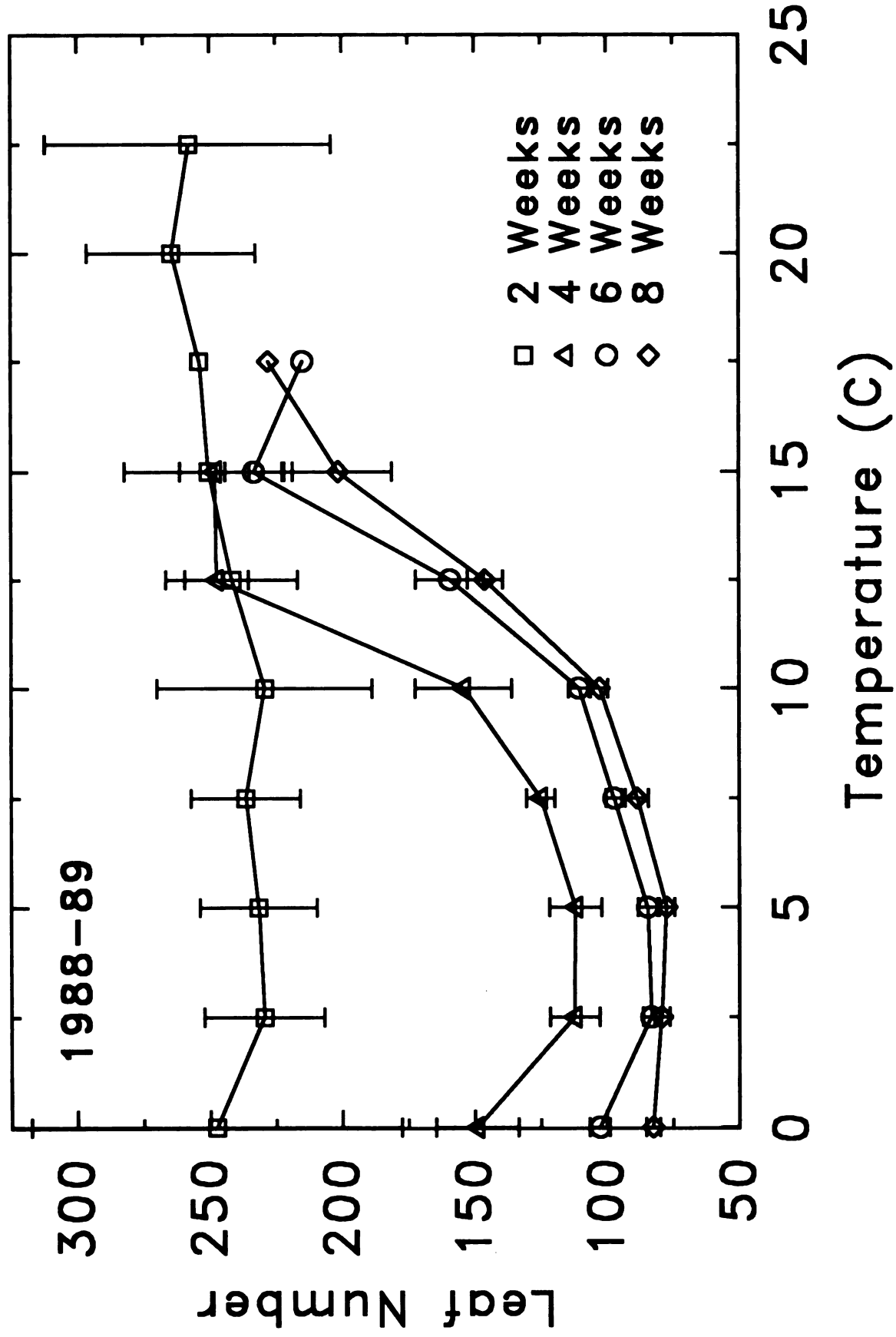

1988-89
2 Weeks
4 Weeks
6 Weeks
8 Weeks
Leaf Number
300
250
200
150
100
50
0
5
10
15
20
25
Temperature (C)

Figure 2. Flowering percentage of 'Nellie White' Easter lily as a function of temperature and vernalization duration.

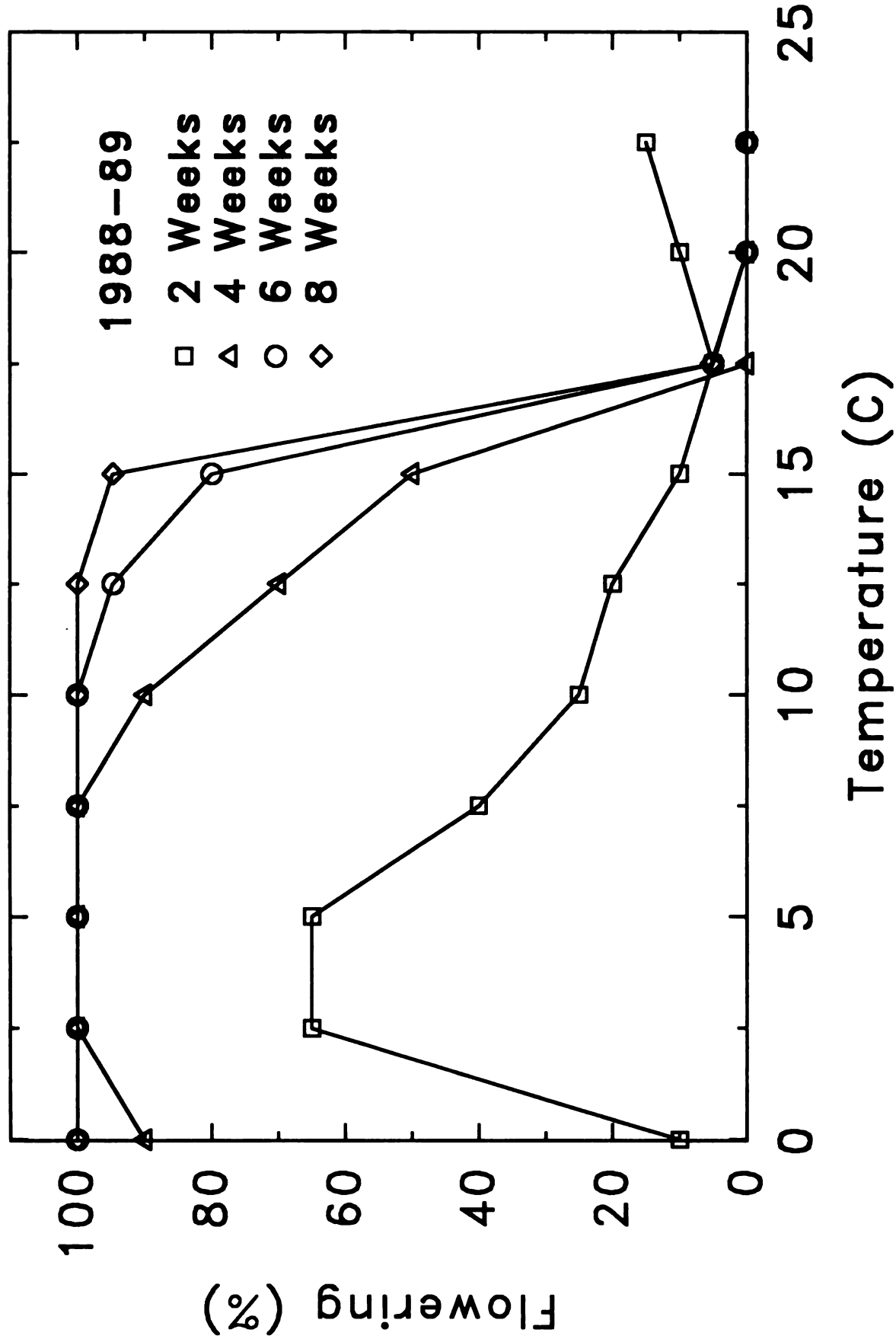

1988–89
2 Weeks
4 Weeks
6 Weeks
8 Weeks
Flowering (%)
0
20
40
60
80
100
Temperature (C)
0
5
10
15
20
25

Figure 3. Observed (symbols) and predicted (lines) vernalization indices of 'Nellie White' Easter lily in response to temperature and vernalization duration. Predicted FII values are from equation (1) and parameter estimates from Table (2). Vertical bars represent 95% confidence intervals.

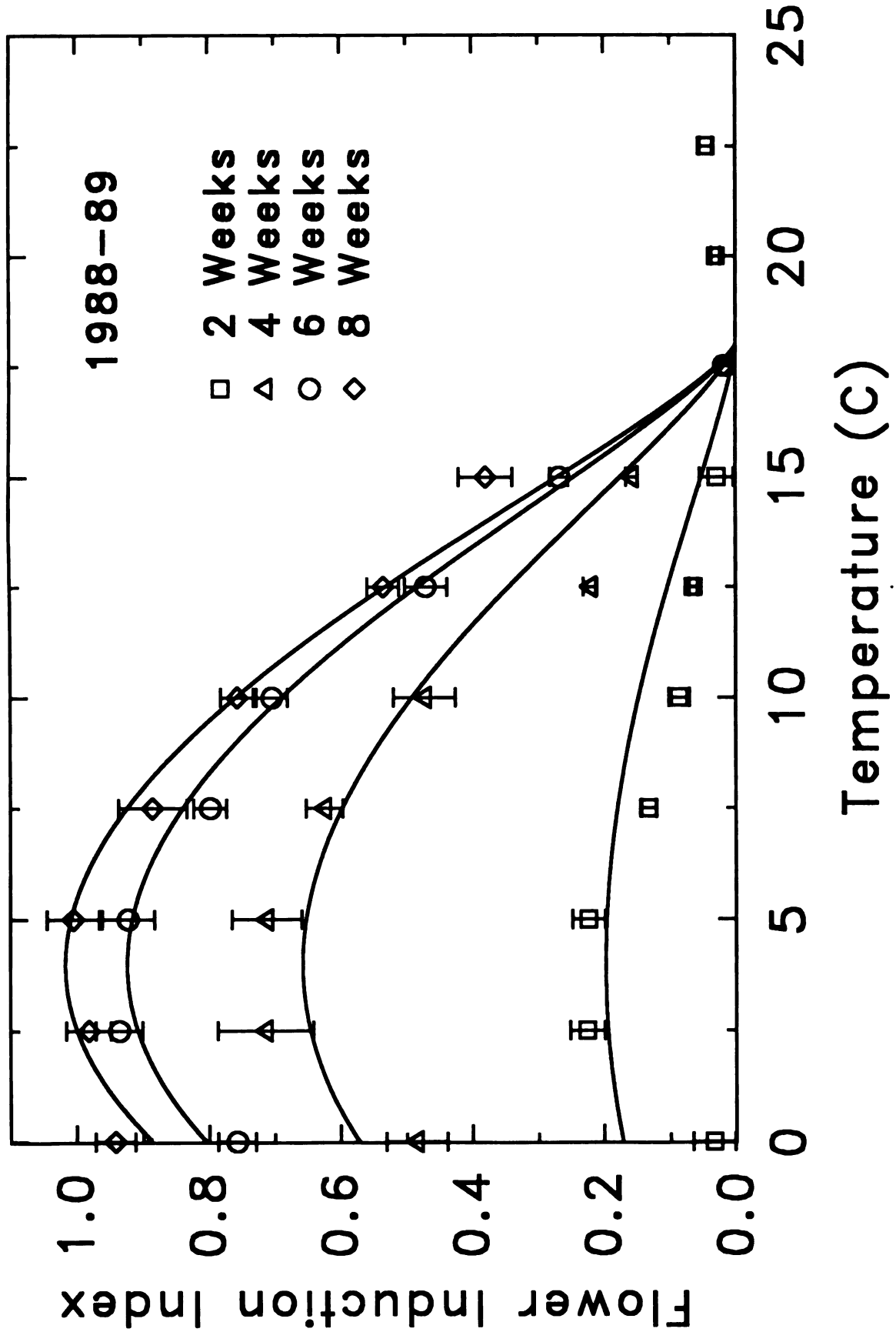

1988–89
2 Weeks
4 Weeks
6 Weeks
8 Weeks
Flower Induction Index
0.0
0.2
0.4
0.6
0.8
1.0
Temperature (C)
0
5
10
15
20
25

Figure 4. Predicted FII response surface of 'Nellie White' Easter lily in response to temperature and vernalization duration. Predicted FII values are from equation (1) and parameter estimates from Table (2).

Flower Induction Index
0.0
0.2
0.4
0.6
0.8
1.0
Time (weeks)
0
2
4
6
8
Temperature (C)
2.5
5.0
7.5
10.0
12.5
15.0
17.5

**Figure 5. Greenhouse forcing time of 'Nellie White' Easter lily as a function of temperature and vernalization duration. Vertical bars represent 95% confidence intervals.**

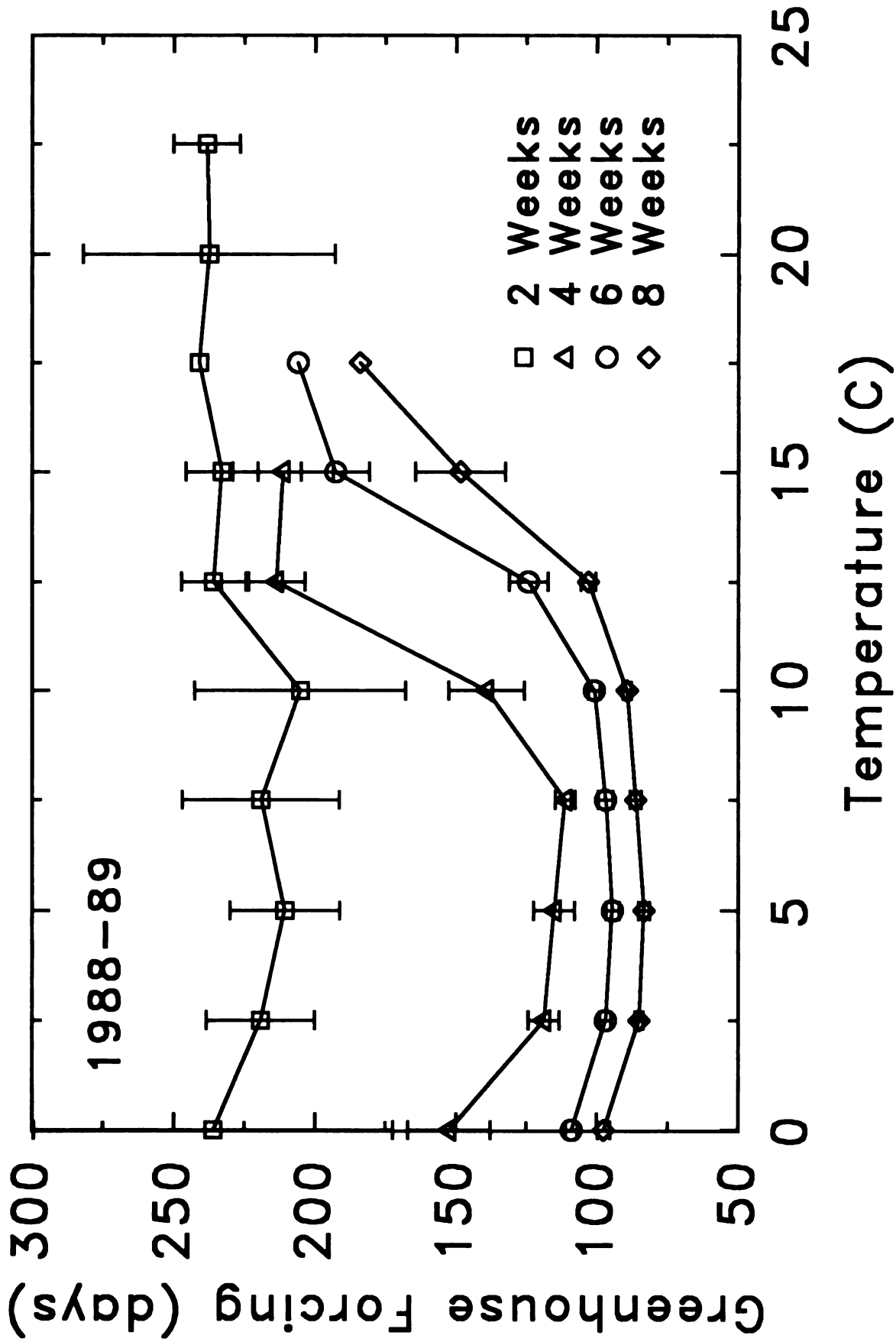

Greenhouse Forcing (days)
300
250
200
150
100
50
0
5
10
15
20
25
Temperature (C)
1988-89
2 Weeks
4 Weeks
6 Weeks
8 Weeks

Figure 6. Height of inflorescence of 'Nellie White' Easter lily as a function of temperature and vernalization duration. Data are from plants which emerged after vernalization treatments. Vertical bars represent 95% confidence intervals.

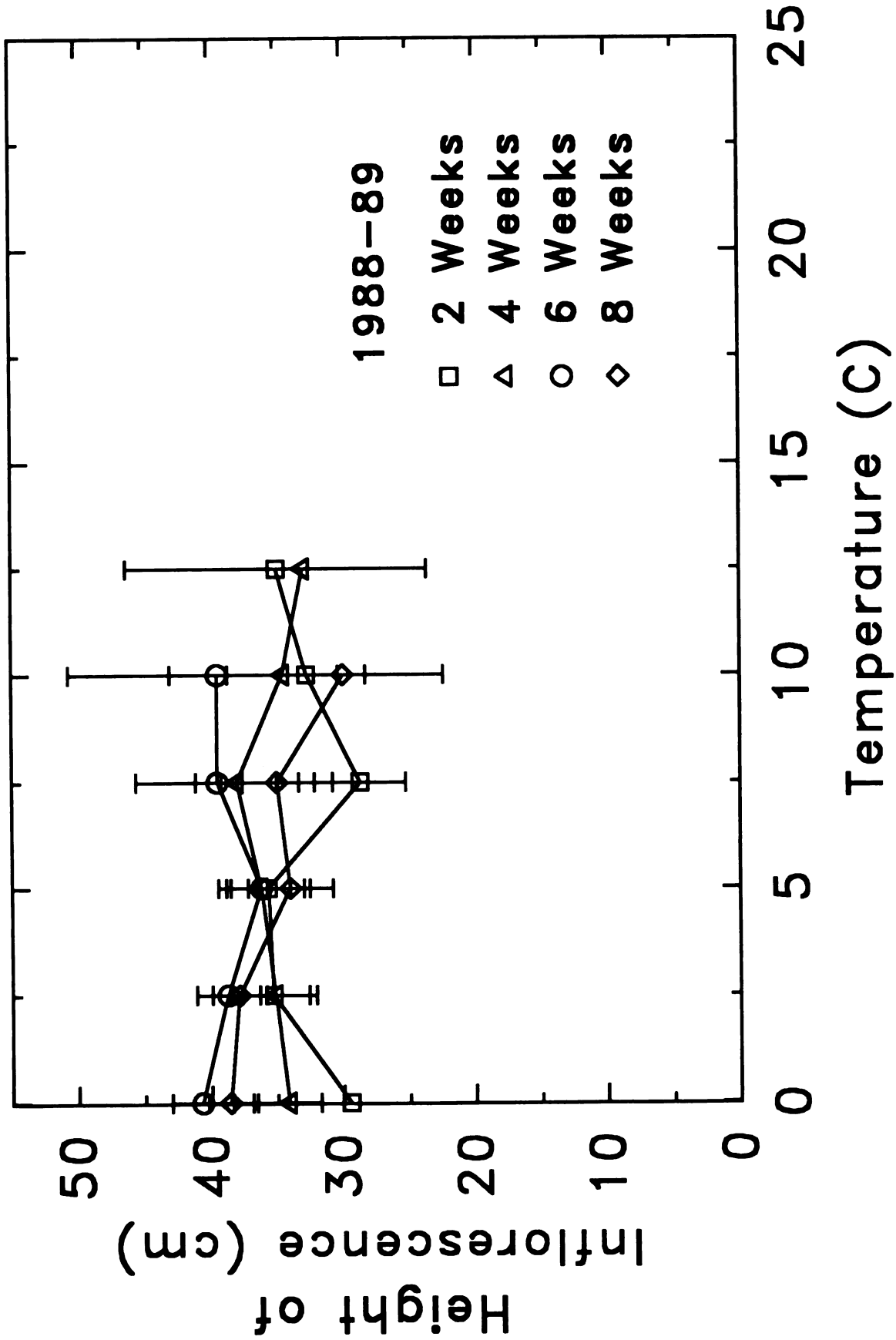

Height of Inflorescence (cm)
50
40
30
20
10
0
0
5
10
15
20
25
Temperature (C)
1988-89
2 Weeks
4 Weeks
6 Weeks
8 Weeks

Figure 7. Length of inflorescence stalk of 'Nellie White' Easter lily as a function of temperature and vernalization duration. Vertical bars represent 95% confidence intervals.

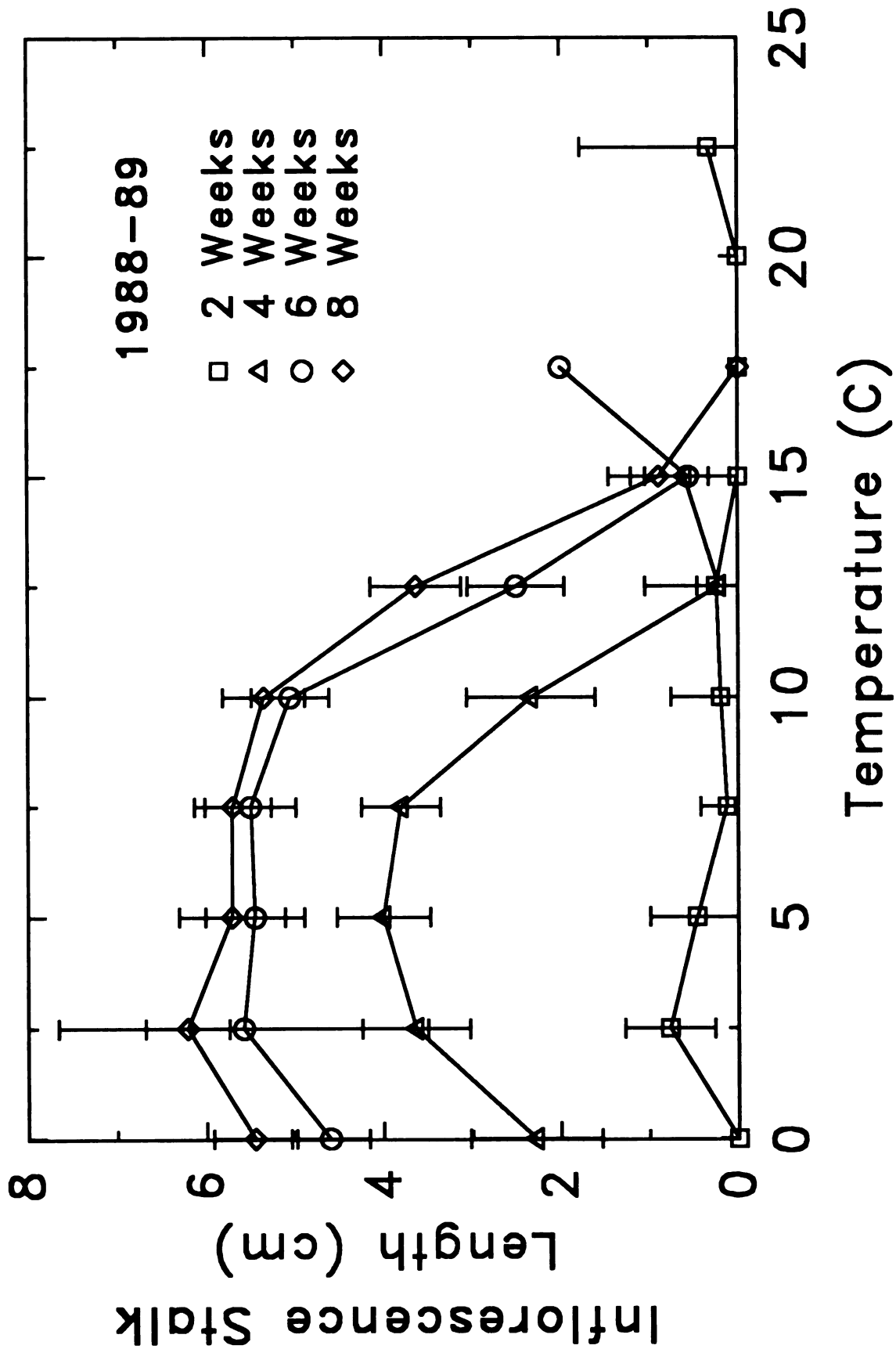

Inflorescence Stalk
Length (cm)
Temperature (C)
1988-89
2 Weeks
4 Weeks
6 Weeks
8 Weeks
0
2
4
6
8
0
5
10
15
20
25

Figure 8. Internode length of 'Nellie White' Easter lily as a function of temperature and vernalization duration. Data are from plants which emerged after vernalization treatments. Vertical bars represent 95% confidence intervals.

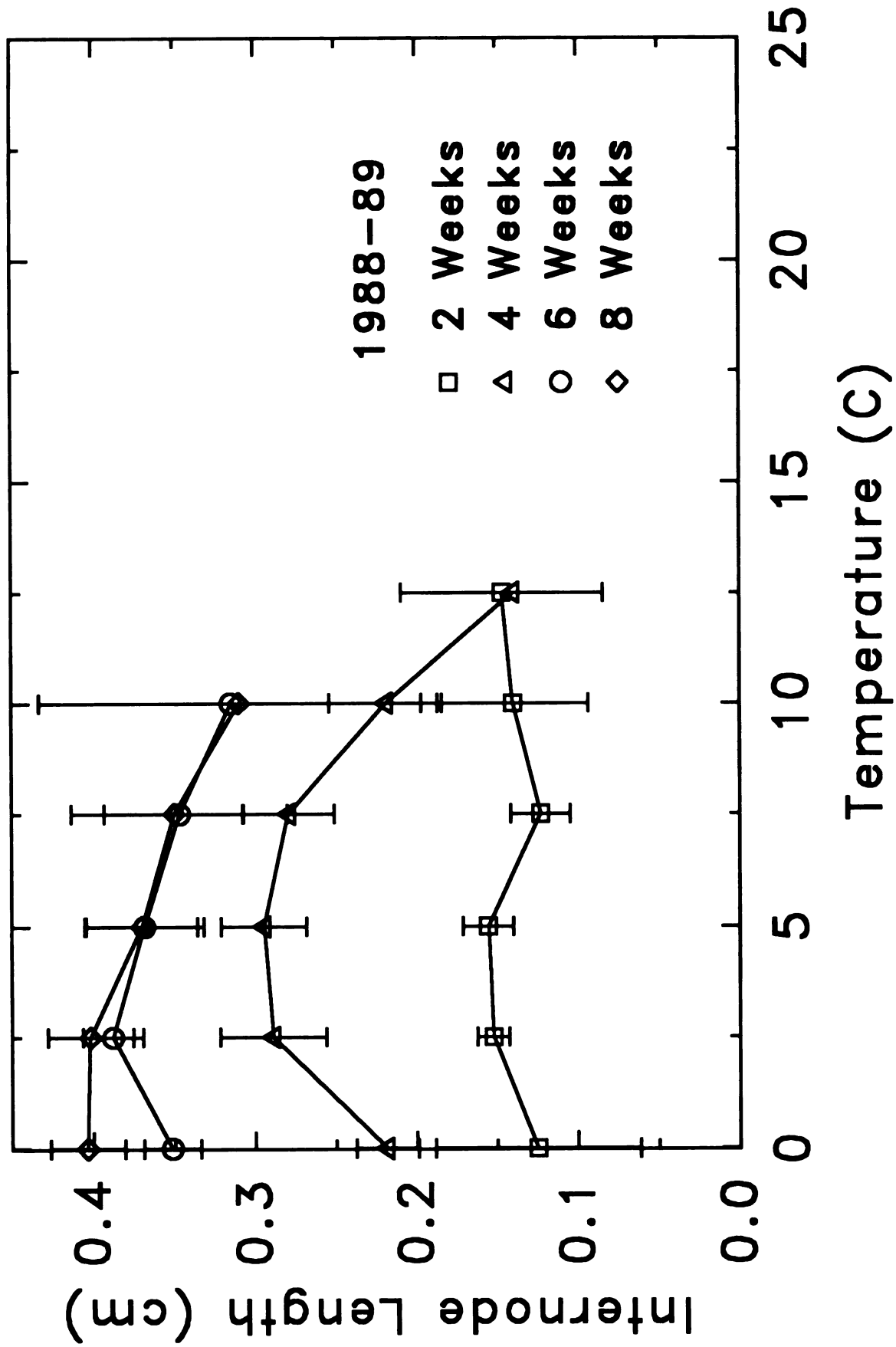
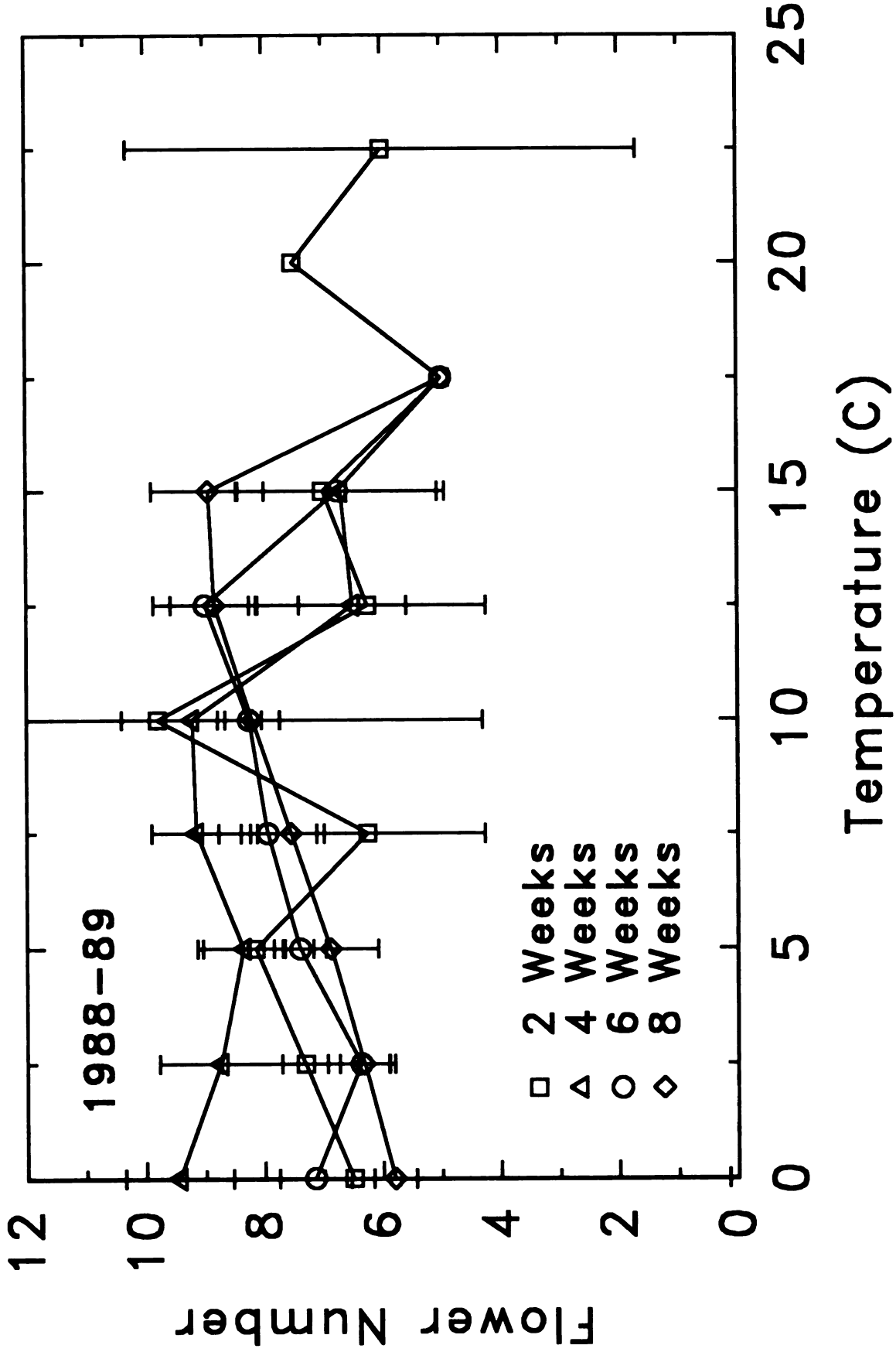

1988–89
2 Weeks
4 Weeks
6 Weeks
8 Weeks
Internode Length (cm)
0.0
0.1
0.2
0.3
0.4
Temperature (C)
0
5
10
15
20
25

Figure 9. Flower number of 'Nellie White' Easter lily as a function of temperature and vernalization duration. Vertical bars represent 95% confidence intervals. The 95% confidence interval for the two week, 20C treatment was not plotted because the mean (7.5) was based on two data points, 5 and 10.


Flower Number
0
2
4
6
8
10
12
0
5
10
15
20
25
Temperature (C)
1988-89
2 Weeks
4 Weeks
6 Weeks
8 Weeks

# CHAPTER 3

## TEMPERATURE AND PHOTOPERIOD DURING VERNALIZATION INTERACT TO AFFECT FLOWER INDUCTION IN *LILIUM LONGIFLORUM* THUNB. 'NELLIE WHITE'

**Abstract**

Effects of photoperiod and storage temperature during vernalization and subsequent development of *Lilium longiflorum* Thunb. 'Nellie White' were determined by exposing emerged plants to 20 combinations of photoperiod and temperature for 6 weeks. Emerged plants were held under short (SD) or long days (LD) at temperatures of 0 to 22.5C at 2.5C increments. After termination of the storage treatments, plants were grown at 20C in a glass greenhouse with a 9 h photoperiod under natural light conditions. The percentage of plants which flowered decreased and the leaf number on flowering plants increased as storage temperature increased above 10C. Leaf number and flowering percentage did not vary below 10C. The effect of LDs above 10C on flowering percentage, leaf number, greenhouse forcing time, and flower number was greater in 1987-88 than 1988-89. The effectiveness of a treatment in promoting flowering was determined by multiplying the relative effectiveness of a treatment in reducing total leaf number by the flowering percentage of the treatment to produce a flower induction index (FII) value for each plant. FII values decreased, representing less effective flower induction, in both years as the treatment temperature increased from 2.5 to 22.5C. LDs were more effective in increasing the FII in 1987-88 than in 1988-89 which may reflect a difference in the maturity or pretreatment vernalization status of the bulbs.

## Introduction

The Easter lily (*Lilium longiflorum*) is considered to be a long day plant that undergoes flower induction during exposure to long photoperiods (Waters and Wilkins, 1967; Rees, 1985). LDs have a similar effect on lily growth and development to vernalization. Flowering percentage increases when plants or bulbs are exposed to LDs during forcing or vernalization (Weiler and Langhans, 1968b; Wilkins and Waters, 1971; Pertuit, 1973; Roberts et al., 1978). Exposure of plants to LDs following vernalization decreases greenhouse forcing time (Smith and Langhans, 1962; Waters and Wilkins, 1967; Weiler and Langhans, 1968b; Wilkins et al., 1968; Carlson and Carpenter, 1970; Pertuit and Link, 1971). Weiler (1973) reported that the cold requirement of *L. speciosum* Thunb. 'Superstar' also decreased when forced under LDs. Many have documented that LDs during forcing decreases total leaf number (Weiler and Langhans, 1968b; Carlson and Carpenter, 1970; Wilkins and Waters, 1971; Lin and Wilkins, 1973; Roh and Wilkins, 1973, 1977a, 1977e) and the number of flower initials on *L. longiflorum* (Wilkins et al., 1968; Carlson and Carpenter, 1970; Lin and Wilkins, 1973; Wilkins and Waters, 1971; Roh and Wilkins, 1977a, 1977b, 1977d, 1977e).

The timing of night artificial lighting and the source of lighting used to simulate long days can determine the effectiveness of the long days in reducing forcing time. Roh

and Wilkins (1977a) found that exposing plants from non-vernalized bulbs to a four-hour night interruption of incandescent, fluorescent, or BCJ-ruby incandescent light from 2200 to 0200 h was more effective in reducing time to flower than a day extension from 1600 to 2000 h or from 0400 to 0800 h. They further reported that plants exposed to a four-hour day extension from 1600 to 2000 h of incandescent or BCJ-ruby light flowered in less time than plants exposed to a four-hour day extension with fluorescent lighting. There was no difference in forcing time between plants exposed to different light qualities as night interruptions from 2200 to 0200 h or as day extensions from 0400 to 0800 h.

Simulating LDs with an eight-hour day extension does not require continuous lighting during the extension in order to be effective in reducing flower number. Roh and Wilkins (1977d) reported that an eight-hour day extension for 30 days consisting of 3 minutes of incandescent light within each 30-minute cycle was as effective in reducing forcing time as an eight-hour day extension of continuous incandescent light. Intercalating thirty LDs with twenty SDs does not lessen the effectiveness of the LDs in reducing total forcing time (Roh and Wilkins, 1977e).

The interaction of vernalization and photoperiod is difficult to clarify, in part because temperature effects can never be excluded in studies of the effects of LDs. The majority of

studies on photoperiodicity in Easter lilies have examined the effects of LDs only during forcing. Pertuit and Kelly (1987) examined the effects of two-week periods of LDs during vernalization on unsprouted bulbs at 7.2C. No known investigations have been made on the effects of LDs on sprouted Easter lily plants during vernalization at different temperatures.

Potted Easter lily bulbs that have been vernalized at higher than normal vernalization temperatures (>5C) can be exposed to continuous lighting to control excessive etiolation. Elongation of the primary axis during vernalization is undesirable because it increases final plant height and because leaves that unfold under low irradiance during vernalization senesce during greenhouse forcing (personal observation). The effects of LDs during vernalization on flower induction of sprouted plants are unclear. The objective of this study was to determine the effects of photoperiod on flower induction of sprouted plants during vernalization at different temperatures.

## Materials and Methods

*Lilium longiflorum* Thunb. 'Nellie White' bulbs 20 to 23 cm in circumference were obtained from a commercial grower and potted into 11-cm (600 ml) plastic pots using a commercial peat-based medium (Baccto Pro Plant Mix, Michigan Peat Co.). Potted bulbs were held in a glass greenhouse at 18C with a

nine-hour photoperiod until shoots emerged. The emerged plants were sorted by emergence date so that the first and last 25% of the plants to emerge were discarded. All of the plants selected for experimentation emerged within a six-day period. The twenty plants selected for each treatment included an equal distribution of emergence dates. The emerged plants were placed in growth chambers at each of eleven constant air temperatures ranging from -2.5C to 22.5C (2.5C increments). The plants were held at each constant air temperature for 6 weeks. All plants were exposed to a PPF of 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at canopy level during the temperature treatments. Lighting was supplied from incandescent lamps for 9 h per day or for 24 h per day. Plants were repotted into 15-cm (1850 ml) standard plastic pots after termination of the treatments and grown at 20±2C in a glass greenhouse with a nine-hour photoperiod under natural light conditions. Black cloth was pulled over the plants from 1700 to 0800 h to provide a daily 15-h dark span. Control plants were not exposed to a temperature treatment prior to greenhouse forcing. The experiment was conducted in both the 1987-88 and 1988-89 Easter lily seasons. Leaf number, flower number, plant height, and date of anthesis were recorded for all flowering plants. The percentage of plants which flowered was calculated for each treatment. Means and 95% confidence intervals were calculated for leaf number, time of greenhouse forcing, and total flower number.

The number of leaves on a lily plant below the inflorescence is an indication of how quickly the plant initiated flowers and therefore, how effective a treatment is in inducing flower initiation (Brierley, 1941a; Blaney et al., 1963; Weiler and Langhans, 1968a, 1968b; De Hertogh and Wilkins, 1971; Roh and Wilkins, 1977c). The effectiveness of each temperature treatment in reducing leaf number was determined by calculating a relative leaf number for each plant (Fig. 1). The relative leaf number was calculated for each plant by dividing the mean number of leaves on plants in the treatment which resulted in the lowest average number of leaves by the number of leaves on that plant. Means of calculated relative leaf number values were equal to or less than 1.0 for each treatment.

A treatment's effectiveness in inducing flowering could be biased if based only on leaf number of flowering plants. Many treatments produced both reproductive and vegetative plants. Treatments that result in plants with relatively few leaves and low flowering percentages would be incorrectly judged as highly effective in inducing flowering if judged only on leaf number. A quantitative measurement of flower induction in Easter lilies should incorporate both total leaf number and flowering percentage.

The fraction of flowering plants was calculated for each treatment. A flower induction index (FII) was calculated by

multiplying the relative leaf number by the fraction of plants flowering in a given treatment. Means of calculated FII values ranged from 0 to 1.0 for each treatment.

## Results

For 1987-88, plants held at 2.5C under long photoperiods had the fewest number of leaves (91.7±2.7). For 1988-89, plants held at 5C under long photoperiods had the fewest number of leaves (93.5±2.7). In 1987-88, the leaf number of LD plants was consistently less than that of SD plants (Fig. 1). Leaf number of SD and LD plants from 1987-88 increased from 96 to 300 and from 95 to 161 as the storage temperature increased from 0 to 17.5C and from 0 to 15C, respectively. However, the leaf number of LD plants then decreased to 103 as the temperature increased from 15 to 22.5C. The trends of leaf numbers from 1988-89 were less clear from those of 1987-88. The leaf number of both SD and LD plants increased below 2.5C and generally tended to increase above 5C. In 1988-89, the leaf number of SD and LD plants increased from 114 to 254 and from 98 to 132, respectively, as the storage temperature increased from 10 to 15C.

One hundred percent of the plants treated with temperatures of 0 to 10C flowered (Fig. 2). The flowering percentage of SD and LD plants from 1987-88 decreased from 100 to 0% and from 100 to 5%, respectively, as the treatment temperature

increased from 10 to 20C and from 12.5 to 22.5C, respectively. Plants from 1988-89 under SDs or LDs decreased in flowering percentage from 100 to 0% as the treatment temperature increased from 10 to 17.5C.

The FII of LD plants was consistently greater than the FII of SD plants (Fig. 3). The FII of SD and LD plants from 1987-88 decreased from 0.96 to 0 and from 1.00 to 0.04, respectively, as the treatment temperature increased from 0 to 20C and from 2.5 to 22.5C, respectively. The difference between the FII of SD and LD at any treatment temperature in 1988-89 was less than in 1987-88. The FII of SD and LD plants from 1988-89 decreased as the treatment temperature decreased below 2.5 and 5C, respectively, and generally decreased as the treatment temperature increased above 2.5 and 5C, respectively. The most rapid decrease in the FII for either SD or LD plants in 1988-89 was as the treatment temperature increased from 10 to 12.5C.

There was little difference in the mean number of days from the end of the storage treatments to flower (100±4 days) between years or photoperiod treatments with treatment temperatures from 0 to 7.5C (Fig. 4), except for SD plants at 0C from 1988-89 (115 days). Greenhouse forcing time of SD plants in 1987-88 and 1988-89 increased to 227 days at 17.5C and 199 days at 15C, respectively, as the treatment temperature increased above 7.5C. Days to flower of LD plants

in 1987-88 and 1988-89 increased to a maximum of 126 days at 15C and 164 days at 12.5C, respectively, and decreased at higher treatment temperatures.

The mean number of flowers in the temperature-photoperiod treatments did not follow any consistent trend in either year (Fig. 5). SD plants tended to have more flowers than LD plants, especially in 1987-88. The number of flowers on LD plants from both years decreased as the treatment temperature increased from 12.5 to 22.5C. No other discernable trends were detected.

## Discussion

The total plant leaf number and the flowering percentage of a treatment population are the two most important and objectively measurable variables directly related to flower induction in Easter lilies. The FII is a quantitative measure of flower induction in Easter lilies that takes into account both the number of leaves on a plant and the percentage of plants that flowered in a treatment population. Populations of plants that are less than fully induced to flower have less than 100% flowering. Of those plants that do flower, further flower induction decreases total leaf number. Combining flowering percentage and leaf number into one multiplicative variable estimates the level of flower induction in a given population of plants.

The FII was decreased either by a increase in leaf number per plant or by a decrease in the flowering percentage of a given population. Decreased FII values from both years, representing less effective flower induction, resulted as the treatment temperature increased from 2.5 to 22.5C. When flowering of a treatment population was at 0%, the FII of a plant in that population was, by definition, equal to 0, regardless of leaf number, representing the total absence of flower induction. When flowering was at 100% from 0 to 10C in both years, the FII of a plant was equivalent to the plant's relative leaf number.

Increasing the vernalization temperature from 2.5 to 22.5C has been shown to decrease flowering percentage (Weiler and Langhans, 1968b). Weiler and Langhans concluded that the critical vernalization temperature was near 21C. However, all of the plants in their study were grown under naturally occurring, progressively longer photoperiods, a factor which probably contributed to equivocal results at temperatures above 17.5C. Previous research has established that LDs during forcing increase the percentage of flowering plants (Weiler and Langhans, 1968b, 1970; Wilkins and Waters, 1971). The present study indicates that LDs can also increase the percentage of flowering plants during vernalization of emerged plants. LDs during 22.5C-storage induced 5% of the plants to flower in the 1987-88 experiment (Fig. 2). Roberts et al. (1978) reported that plants forced under continuous SD from

bulbs held at 15C in the dark for 10 weeks failed to flower. Plants in the current study were maintained under SDs after the temperature-photoperiod treatments preventing additional flower induction by naturally occurring LDs. These results indicate that the critical vernalization temperature for Easter lilies is between 17.5 and 20C.

Merritt (1964) reported that total leaf number increased as the vernalization temperature increased from 4 to 10C. The results of the current study are in agreement with Merritt's findings. Total leaf number of plants vernalized under SDs increased as the vernalization temperature increased from 2.5 to 17.5C (Fig. 1). Lower vernalization temperatures more effectively induce flowering, therefore, the meristematic apex initiates flowers in less time following vernalization, thereby limiting the total number of leaves initiated by the apex prior to floral differentiation.

The effect of LDs in reducing leaf number and increasing flowering percentages on plants following vernalization above 10C was greater in 1987-88 than in 1988-89 (Fig. 1 and 2). This observation could reflect differences in the vernalization states of the bulbs prior to the experiments between the 1987-88 and 1988-89 seasons. Previous studies have indicated that Easter lilies are more responsive to long photoperiods following some initial level of vernalization (Pertuit and Kelly, 1987; Lange, 1992). If the bulbs used in

the 1987-88 experiment were partially vernalized prior to the start of the experiment either in the field or during shipping, then LDs would be more effective in inducing flowering than in 1988-89. Vernalization has been demonstrated in several species to modify a plant's response towards photoperiod (Lang, 1965).

LDs during the 0 to 7.5C temperature treatments had no effect on subsequent greenhouse forcing time in either year (Fig. 4). Either these temperatures saturated the plants' flower induction mechanism precluding any additional effect of LDs on flower induction or LDs were not perceived by the plants at low temperatures. LDs were increasingly effective in reducing forcing time in both years as the vernalization temperature increased from 10 to 22.5. These results are in agreement with Smith and Langhans (1962) who reported that plants exposed to 18-hour photoperiods from 9 h of natural lighting and 9 h of incandescent lighting consistently flowered earlier than plants exposed to nine-hour photoperiods at constant forcing temperatures from 10C to 27C. Waters and Wilkins (1967) reported that time to flowering was reduced by lighting periods consisting of five-hour night interruptions of incandescent lighting. The effect of temperature on their results was unclear because all of their results were based on experiments conducted in the field. Weiler and Langhans (1968b) found that plants grown from bulbs vernalized for 3 to 6 weeks and exposed to long days flowered in less time than

plants grown under short days.

The effect of LDs above 7.5C on forcing time was greater in 1987-88 than 1988-89 (Fig. 4). The difference probably reflects a higher vernalization state in the 1987-88 bulbs prior to the start of the experiment. The number of days of greenhouse forcing was directly proportional to the total number of leaves which is in agreement with previous research (Emsweller and Pryor, 1943; Blaney et al., 1963; Brierley, 1941a; Weiler and Langhans, 1968a; Hill and Durkin, 1968; De Hertogh and Wilkins, 1971; Roh and Wilkins, 1977c). Plants with more leaves required additional greenhouse forcing time. Leaf unfolding rates of plants from bulbs of equal size are a function of average daily forcing temperatures (Karlsson et al., 1988).

There is evidence that gibberellins are involved in flower induction. Endogenous concentrations of GA increase during the change from vegetative to reproductive growth in other species (Radley, 1975; Pocock and Lenton, 1979). Aung and De Hertogh (1967) reported that *Tulipa* bulbs cooled for 4 weeks at 9C had 92 times more endogenous gibberellin-like substances than non-cooled bulbs. Aung et al. (1969) demonstrated the presence of gibberellin-like substances in Easter lily bulbs from flowering plants. Tsukamoto (1971) found that the concentration of growth-promoting substances increased in lily bulbs following vernalization.

The results from the current study suggest that LDs during vernalization consistently decrease total flower number (Fig. 5). Long photoperiods have been reported to affect the number of flowers at anthesis of plants grown from both vernalized and non-vernalized bulbs. Wilkins et al. (1968) documented that long days decrease flower number of plants grown from vernalized and non-vernalized bulbs by 1.5 and 1.3 flowers per plant, respectively. Carlson and Carpenter (1970) confirmed that long days during forcing decrease flower number of vernalized bulbs.

The different responses of the plants to LDs between the two years suggests that the initial maturity and/or vernalization states of the bulbs were important factors in determining the total effect of LDs. Previous work has established that bulbs can accumulate the cold stimulus in the field prior to harvest and that field soil temperatures may influence the perception of bulbs to vernalization (Miller and Kofranek, 1966; Hill and Durkin, 1968; Roberts and Moeller, 1971; Lin and Wilkins, 1975). The effectiveness of LDs to accelerate flower induction has been demonstrated to be influenced by prior exposure to vernalization (Lange, 1992). Temperature conditions in the field, after harvest, and during shipping may partially account for the yearly variations observed in this experiment in the response of plants to LDs.

This study indicates that the effect of LDs during

vernalization on the subsequent growth and development of Easter lilies is dependent on the vernalization temperature. LDs had the most effect on growth and development as the vernalization temperature increased above 10C. This effect on plant growth and development was additive to the effect of vernalization but was not a complete substitute for cold vernalization.

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Figure 1. Total leaf number of 'Nellie White' Easter lily from 1987-88 and 1988-89 as a function of temperature under SD and LD during temperature treatment. Vertical bars represent 95% confidence intervals.

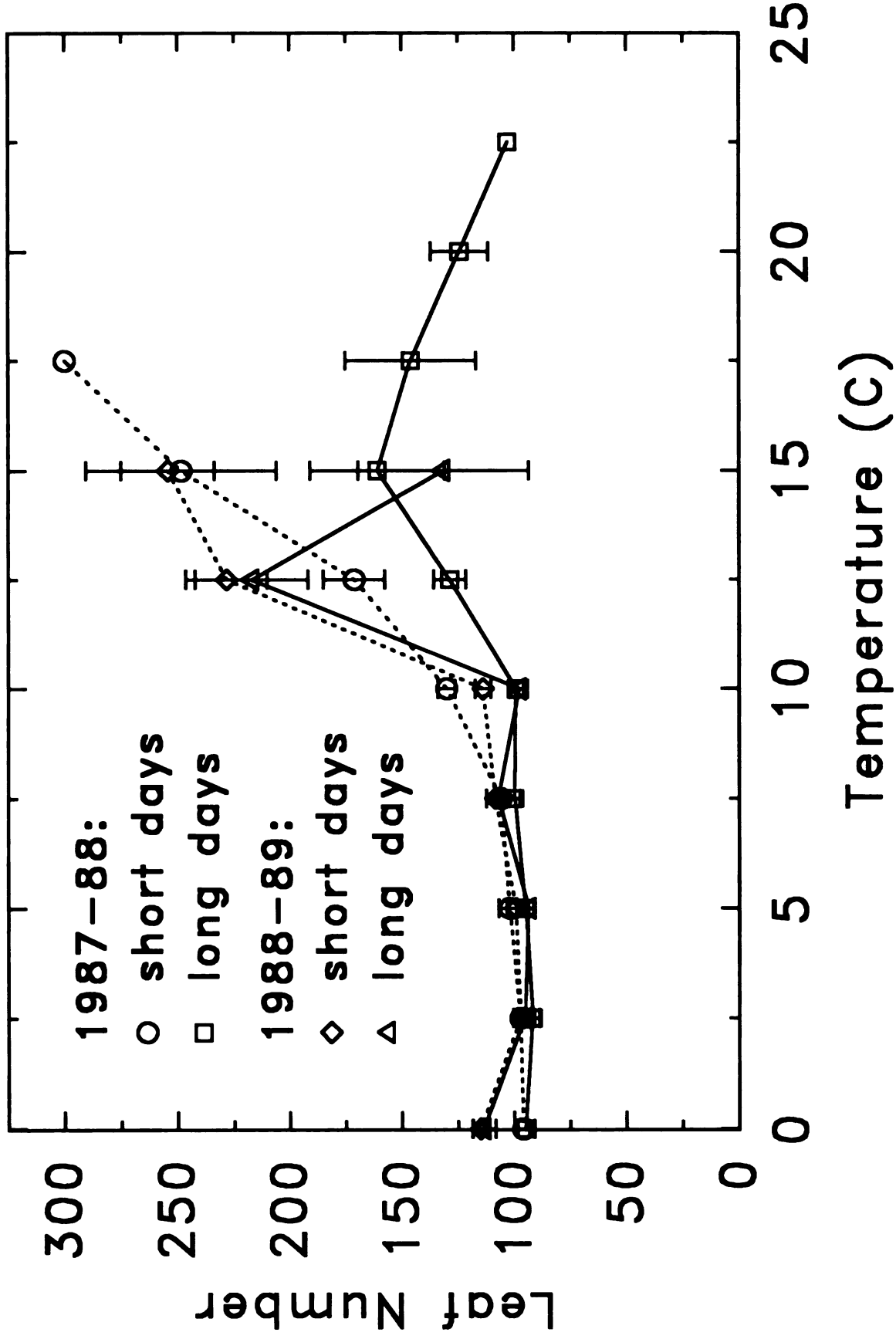

Leaf Number
300
250
200
150
100
50
0
0
5
10
15
20
25
Temperature (C)
1987–88:
short days
long days
1988–89:
short days
long days

**Figure 2. Flowering percentage of 'Nellie White' Easter lily from 1987-88 and 1988-89 as a function of temperature under SD and LD during temperature treatment.**

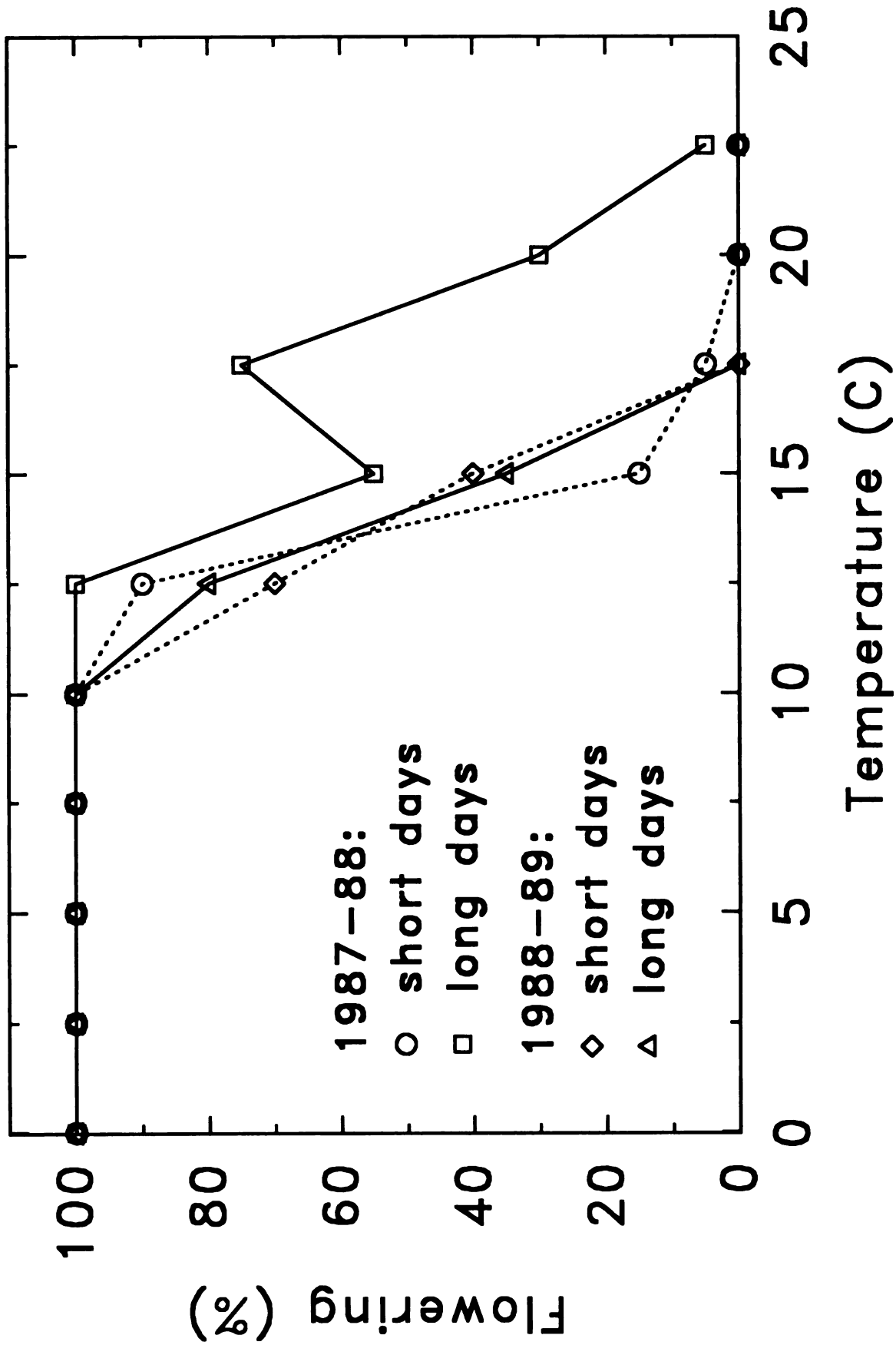

Flowering (%)
100
80
60
40
20
0
0
5
10
15
20
25
Temperature (C)
1987–88:
short days
long days
1988–89:
short days
long days

Figure 3. Flower induction indices of 'Nellie White' Easter lily from 1987-88 and 1988-89 in response to temperature and photoperiod during temperature treatment. Vertical bars represent 95% confidence intervals.

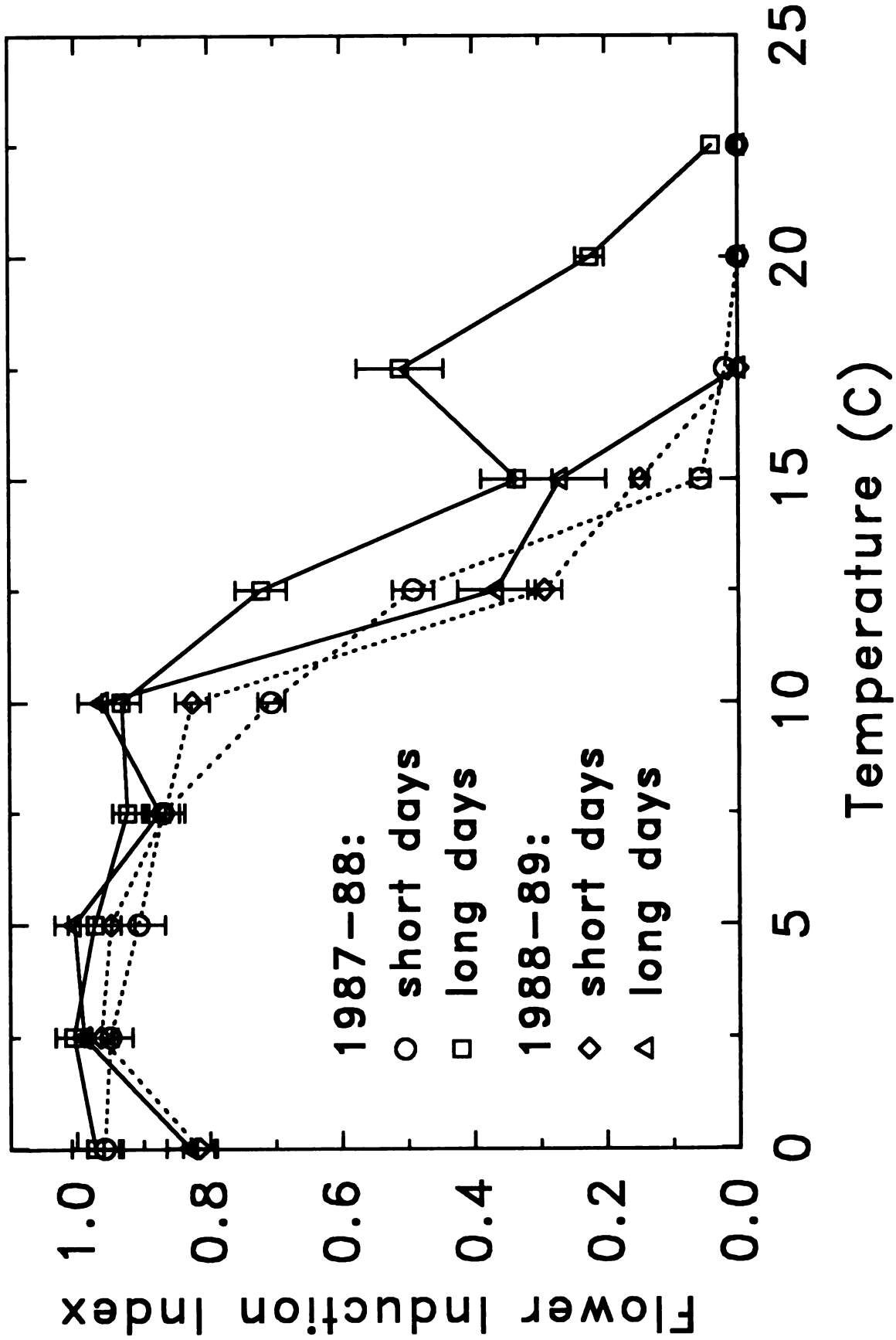

Flower Induction Index
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
Temperature (C)
1987–88:
short days
long days
1988–89:
short days
long days

**Figure 4. Greenhouse forcing time of 'Nellie White' Easter lily from 1987-88 and 1988-89 as a function of temperature under SD and LD during temperature treatment. Vertical bars represent 95% confidence intervals.**

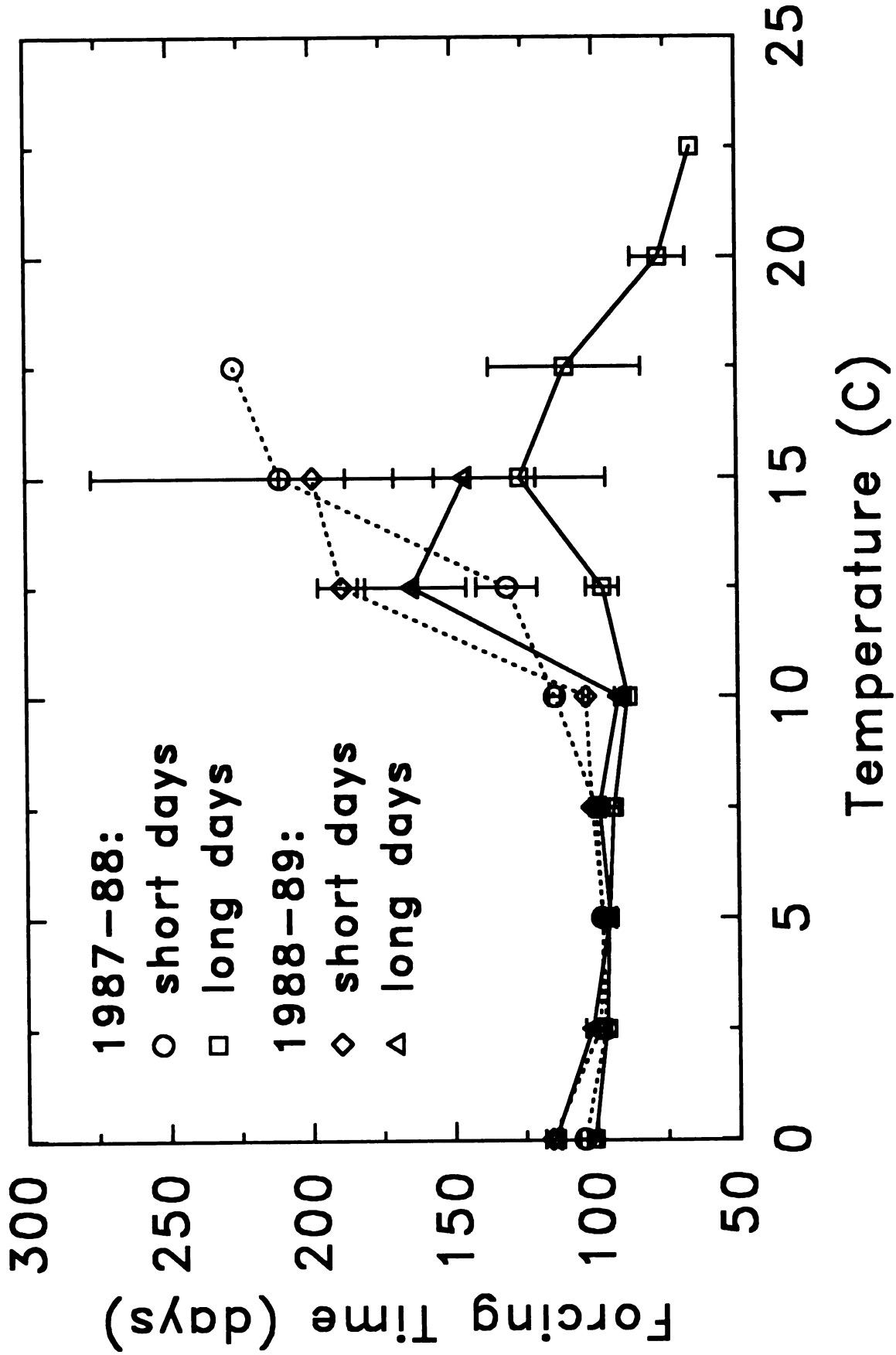
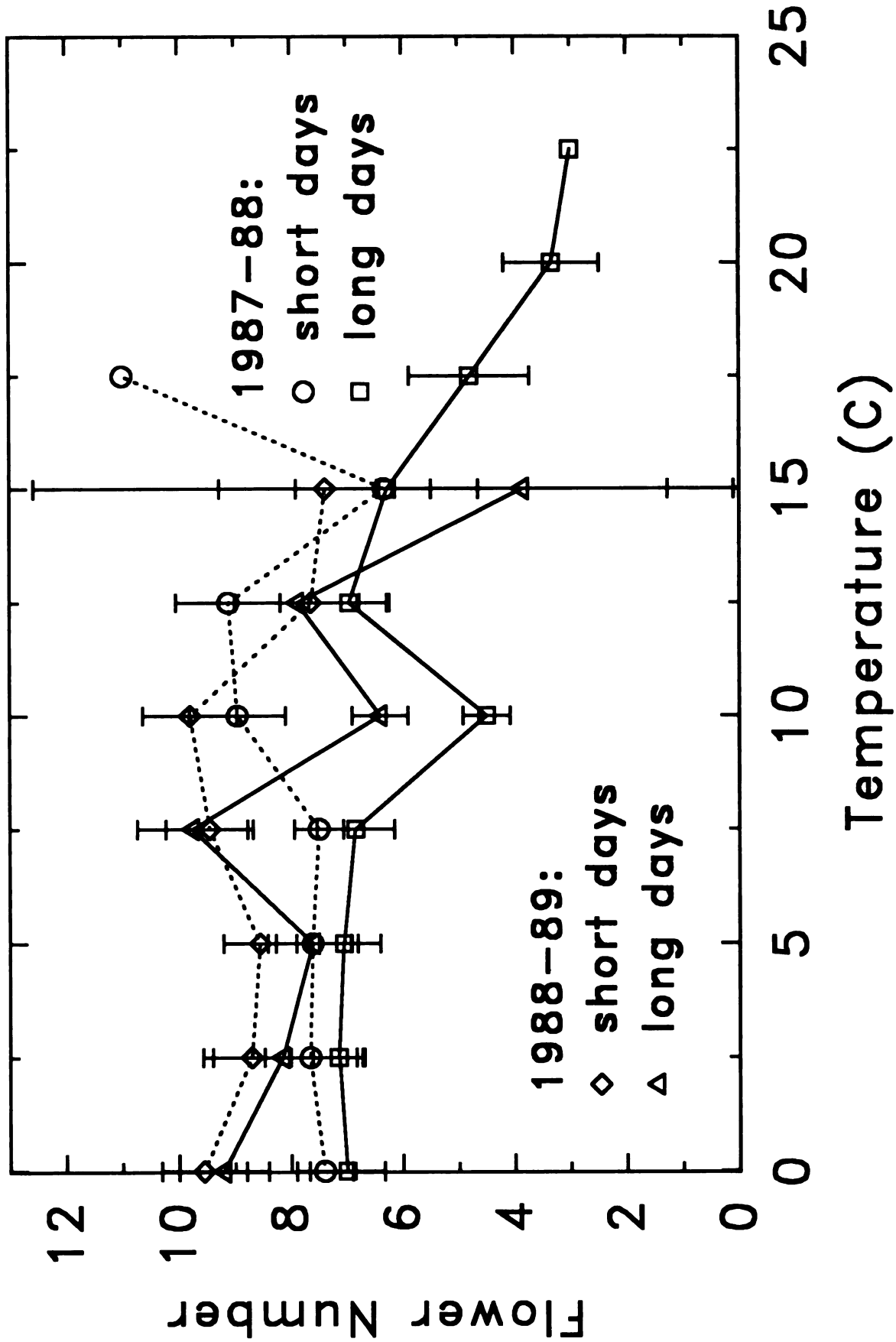

Forcing Time (days)
300
250
200
150
100
50
0
5
10
15
20
25
Temperature (C)
1987-88:
short days
long days
1988-89:
short days
long days

Figure 5. Flower number of 'Nellie White' Easter lily from 1987-88 and 1988-89 as a function of temperature under SD and LD during temperature treatment. Vertical bars represent 95% confidence intervals.


Flower Number
0
2
4
6
8
10
12
0
5
10
15
20
25
Temperature (C)
1987–88:
short days
long days
1988–89:
short days
long days

# CHAPTER 4

## THE EFFECT OF LONG DAYS ON FLOWER INDUCTION IN *LILIUM LONGIFLORUM* THUNB. 'NELLIE WHITE' IS DEPENDENT UPON PRIOR VERNALIZATION

**Abstract**

The effects of substituting durations of long days (LDs) for vernalization at the beginning and end of cold treatments on the subsequent development of *Lilium longiflorum* Thunb. 'Nellie White' were determined by exposing emerged plants to 18 combinations of LDs and to temperatures at 5C. Plants were exposed to 1, two, three, four, five, or six weeks of LDs at 17.5C or cold at 5C under short days (SDs). Plants were then moved either to a glass greenhouse at 20C under SDs until anthesis, or moved to the other floral-inductive environment (cold or LD) so that the total inductive treatment time was six weeks. After termination of the treatments, plants were grown under natural light conditions and a nine-hour photoperiod at 20C in a glass greenhouse. LDs were most effective in decreasing leaf number on flowering plants when preceded by a period at 5C, but were most effective in increasing the percentage of plants which flowered when followed by a period at 5C. The time from the start of the treatments until flower was proportional to the leaf number. There was no consistent treatment effect on flower number. The effectiveness of a treatment in promoting floral induction was determined by multiplying its relative effectiveness in reducing total leaf number by its flowering fraction to produce a flower induction index (FII) value for each plant. FII increased when the duration of cold increased from one to six weeks. LDs were, at most, 49% as effective as cold in inducing flowering.

## Introduction

The Easter lily is considered an LD plant that undergoes flower induction after exposure to LDs (Waters and Wilkins, 1967; Rees, 1985). Long photoperiods and vernalization have similar effects on plant development; both reportedly decrease the number of forcing days from planting to flower, decrease total leaf and flower number, and increase flowering percentage.

Exposure of Easter lilies to LDs alters flower induction by affecting flower number, the duration of forcing time to flower, and the percentage of plants that flower. Smith and Langhans (1962) reported that plants exposed to 18-hour photoperiods from 9 h of natural lighting and 9 h of incandescent lighting consistently flowered earlier and had fewer flowers than plants exposed to nine-hour photoperiods at constant forcing from 10 to 27C. Using histological studies, Waters and Wilkins (1967) found that the number of weeks of LDs required for floral differentiation of plants from nonvernalized bulbs decreased from nine to two as the duration of incandescent lighting per night increased from zero to five h. They also reported that time to flowering and total flower number were reduced by incandescent lighting periods consisting of five-hour night interruptions. Weiler and Langhans (1968b) found that plants grown from bulbs vernalized for three to six weeks and exposed to LDs flowered in less time than those grown under SDs. LDs consisted of either four

or 10 h of incandescent lighting at night, and SDs consisted of 8.5 h of natural lighting.

Long photoperiods affect the time from potting to flower (forcing time) of plants grown from nonvernalized bulbs more than that of plants grown from vernalized bulbs (Wilkins et al., 1968a). The number of LDs also affected the forcing time and the time from the start of LDs to flower-bud differentiation of plants from nonvernalized bulbs more than that of plants grown from vernalized bulbs. Wilkins et al. (1968a) found that exposing plants to 30 or 45 LDs consistently decreased forcing time by 15 days regardless of the duration of cold storage or number of LDs if the plants were grown at a 21/16C day/night cycle from bulbs cooled for three or six weeks at 10C. LDs did not affect the time from the start of LDs to flower-bud differentiation of plants grown from vernalized bulbs. Exposing plants grown from nonvernalized bulbs to 30 or 45 LDs decreased greenhouse forcing time by 32 and 55 days, respectively, and decreased the time from the start of LDs to flower-bud differentiation by 80 and 52 days, respectively.

Carlson and Carpenter (1970) confirmed that LDs have a greater effect on the forcing time of nonvernalized bulbs than on that of vernalized bulbs. LDs decreased the forcing time of plants grown from nonvernalized bulbs from 220 to 160 days. LDs decreased the forcing time of plants grown from bulbs

vernalized at 4C for three and six weeks from 148 to 129 days and from 154 to 139 days, respectively. LDs consisted of continuous 16-hour photoperiods with artificial lighting provided by cool white fluorescent lamps from 0500 to 1100. SDs consisted of natural lighting from 9 to 11 h per day.

Pertuit and Link (1971) found that continually exposing plants to LDs until anthesis, if the plants were grown from bulbs vernalized for six weeks at 8C and forced in greenhouse with a minimum night temperature of 16C, decreased forcing time by 15 days compared to that of plants grown under SDs. LDs consisted of 9 h of natural lighting supplemented with 6 h of incandescent lighting from 2000 until 0200 h. SDs consisted of 9 h of natural daylight, and was achieved by pulling blackcloth from 1630 until 0730 over the plants.

Wilkins and Waters (1971) reported that as plants grown from nonvernalized bulbs forced at constant 16C were exposed to an increasing number of LDs from 0 to 28, the number of days to flower decreased from 245 to 141. Increasing the number of LDs from 28 to 52 did not further significantly reduce forcing time. LDs consisted of natural photoperiods supplemented with night interruptions of incandescent lighting for 5 h from 2200 to 0300 h. Plants were forced under natural day lengths after LD treatments.

Roh and Wilkins (1973) claimed that LD treatments could

substitute for cold treatments on a day-for-day basis to initiate flower induction. However, plants in their study were forced at 16C, which is known to induce flowering (Lange, 1992a). Pertuit and Kelly (1987) reported that exposing bulbs to LDs was only effective in decreasing leaf number during the last two weeks of a six-week vernalization treatment at 7.2C. Their study suggested that vernalization is necessary for LDs to influence photoinduction. There are no known reports on the effect of prevernalization LDs on flower induction. The purpose of this experiment was to determine whether vernalization affects the responsiveness of plants to LDs.

## Materials and Methods

*Lilium longiflorum* Thunb. 'Nellie White' bulbs 20 to 23 cm in circumference were obtained from a commercial grower in October, 1988, and potted in 11-cm (600 ml) plastic pots with a commercial peat-based medium (Baccto Pro Plant Mix, Michigan Peat Co.). Potted bulbs were held in a glass greenhouse at 18C with a nine-hour photoperiod until shoots emerged. The emerged plants were sorted by emergence date so that the first and last 25% of the plants to emerge were discarded. All of the plants selected for experimentation emerged within a six-day period. The twenty plants selected for each treatment included an equal distribution of emergence dates.

The emerged plants selected for the experiment were placed for two, three, four, five, or six weeks in either a cooler at 5C

under SDs or under LDs in a greenhouse at 17.5C (Fig. 1). SDs consisted of 9 h of incandescent lighting from 0800 to 1700. LDs consisted of 9 h of natural lighting from 0800 to 1700 plus 4 h of incandescent lighting from 2200 to 0200. The PPF of the incandescent lighting at canopy level was 10 $\mu mol \cdot s^{-1} \cdot m^{-2}$. Half of the plants placed at 5C were then moved to LDs over time and vice versa so that the total treatment time was six weeks. These treatments were abbreviated 2C/4L, 3C/3L, 4C/2L, 5C/1L, and 6C/0L (weeks cold / weeks LDs) and 2L/4C, 3L/3C, 4L/2C, 5L/1C, and 6L/0C (weeks LDs / weeks cold). The other half of the plants were moved directly into a greenhouse under SDs at 20±2C until anthesis. These treatments were abbreviated 2C/0L, 3C/0L, 4C/0L, 5C/0L, 6C/0L, 2L/0C, 3L/0C, 4L/0C, 5L/0C, and 6L/0C.

Plants were repotted into 15-cm (1850 ml) standard plastic pots after termination of the treatments and grown at 20±2C in a glass greenhouse with a nine-hour photoperiod under natural light. Blackcloth was pulled over the plants from 1700 to 0800 to provide a daily 15-hour dark span. Control plants were not exposed to a temperature or photoperiod treatment prior to placement in the greenhouse. Leaf number, flower number, and date of anthesis were recorded for all flowering plants. The percentage of plants which flowered was calculated for each treatment.

The number of leaves produced below the inflorescence is an

indication of how quickly the plant initiated flowers and, therefore, how effective a treatment was in inducing flower initiation (Brierley, 1941a; Blaney et al., 1963; Weiler and Langhans, 1968a, 1968b; De Hertogh and Wilkins, 1971; Roh and Wilkins, 1977d). The effectiveness of each temperature treatment in reducing leaf number was determined by calculating a relative leaf number for each plant (Fig. 1). The relative leaf number for a plant was calculated by dividing the mean number of leaves on plants in the treatment that resulted in the lowest average number of leaves by the number of leaves below the inflorescence on that plant. Means of calculated relative leaf-number values were equal to or less than 1.0 for each treatment.

A treatment's effectiveness in inducing flowering could be biased if based only on leaf number of flowering plants; many treatments produced both reproductive and vegetative plants. Treatments that result in plants with relatively few leaves and low flowering percentages would be incorrectly judged as highly effective in inducing flowering if the conclusion were based only on leaf number. A quantitative measurement of flower induction in Easter lilies should incorporate both total leaf number and flowering percentage.

The fraction of flowering plants was calculated for each treatment. A flower induction index (FII) was calculated by multiplying the relative leaf number by the fraction of plants

that flowered in a given treatment. Means of calculated FII values ranged from 0 to 1.0 for each treatment. Means and 95% confidence intervals were calculated for time of greenhouse forcing and total flower number.

## Results

Leaf number was affected by the type of flower induction stimulus and the order of stimuli (Fig. 1). Leaf number decreased from 244 to 101 as the treatment series changed from 2C/0L to 6C/0L, but only decreased from 241 to 212 as the treatment series changed from 2L/0C to 6L/0C (Fig. 1). As the sequence of treatments progressed from 2C/4L to 6C/0L, leaf number decreased from 114 to 101. However, when cold followed LDs, leaf number increased from 116 to 212 as the treatment series changed from 2L/4C to 6L/0C.

The flowering percentage was influenced primarily by the duration of vernalization; it increased from 65 to 100% as the treatment series changed from 2C/0L to 4C/0L (Fig. 2). The flowering percentage of plants held under LDs for less than five weeks was variable and less than fifty. Seventy percent of the plants flowered when held for five or six weeks under LDs. As the sequence of treatments progressed from 2C/4L to 5C/1L, flowering percentage increased from 55 to 100. However, when cold followed LDs, flowering percentage decreased from 100 to 70 as the sequence of treatments progressed from 6L/0C to 4L/2C. Zero percent of the control

plants flowered.

Flower induction always increased as the duration of vernalization increased, and was least effected by LDs alone. The FII increased from 0.3 to 1.0 as the treatment progressed from 2C/0L to 6C/0L, but it only increased from 0.2 to 0.4 as the treatment progressed from 2L/0C to 6L/0C (Fig. 3). As the treatment changed from 2C/4L to 6C/0L, the FII increased from 0.5 to 1.0. However, when cold followed LDs, the FII linearly decreased from 0.9 to 0.4 as the treatment series changed from 2L/4C to 6L/0C.

The time to flower from the start of the treatments was shortest with the maximum duration of vernalization and when LDs followed cold. The time to flower decreased from 219 to 125 days as the treatment sequence changed from 2C/0L to 6C/0L, but only decreased from 229 to 206 days as the treatment sequence changed from 2L/0C to 6L/0C (Fig. 4). As the treatment sequence changed from 2C/4L to 6C/0L, the time to flower from the beginning of the treatments did not vary by more than seven days. However, when cold followed LDs, the time until flower linearly increased from 134 to 206 days as the treatment series changed from 2L/4C to 6L/0C.

Plants from treatments which resulted in 100% flowering consistently had eight or more flowers. There were no other discernible trends in the total number of flowers among

treatments (Fig. 5).

## Discussion

The total leaf number per plant and the flowering percentage of a treatment population are the two most important and objectively measurable variables directly related to flower induction in Easter lilies. The FII is a quantitative measure of flower induction that takes into account both variables and is decreased either by a decrease in the flowering percentage of a given population or by a increase in leaf number per plant. Populations of plants that are not fully induced to flower have less than 100% flowering. Of those plants that do flower, further flower induction decreases total leaf number. Combining flowering percentage and leaf number into one multiplicative variable allows estimation of the level of flower induction in a given population of plants.

The air setting of 17.5C used during LD treatments was chosen because of previously reported results that suggested that LDs were most effective in inducing flowering at that temperature (Lange, 1992b). Lin and Wilkins (1973) found that exposing plants from nonvernalized bulbs to zero and ten LDs at 16C following emergence and continuing forcing at 21C resulted in 0 and 100% flowering, respectively. LD treatments consisted of five-hour night interruptions of incandescent light.

Flower induction increased as the treatment series changed

from 2C/0L to 6C/0L (Fig 3). Increasing the vernalization duration increased the flowering percentage and simultaneously decreased leaf number (Figs. 1 and 2). Weiler and Langhans (1968a) reported that flowering percentage decreased from 100 to 0 as the duration of storage at 2C decreased from six to zero weeks. Weiler and Langhans (1968b) reported that leaf number decreased from 111 to 60 as the storage duration at 2C increased from two to twelve weeks. Hill and Durkin (1968) reported that leaf number decreased from 90 to 77 as the storage duration at 10C increased from four to six weeks. De Hertogh and Wilkins (1971) reported that total leaf number decreased from 180 to 85 as the length of cold storage at 2C increased from zero to six weeks. Roh and Wilkins (1977d) found that total leaf number decreased from 83 to 57 as the duration of cold storage at 2C increased from three to six weeks. The results of the current study and others (Merritt, 1964; Blaney et al., 1963) contradicted the findings of Brierley (1941a), who reported that total leaf number on plants stored for five weeks decreased from 103 to 70 as the storage air increased from 0 to 10C. Wang et al. (1970) reported that the number of leaves was inversely related to the length of vernalization at 4C and concluded that reductions in leaf numbers corresponding to increasing storage durations were associated with reductions in stem apex diameter at the time of flower initiation.

Increasing the duration of LDs in this experiment from two to

six weeks was not as effective in inducing flowering as increasing the duration of vernalization (Fig. 3). LDs were not as effective as vernalization in reducing leaf number or increasing flower percentage (Figs. 1 and 2). Wilkins and Waters (1971) reported that plants vernalized for six weeks at 4.4C and forced under natural day lengths produced 65 leaves, while nonvernalized plants exposed to six weeks of LDs produced 96 leaves. Roh and Wilkins (1973) reported that plants vernalized for three, four, five, or six weeks at 4.4C consistently produced fewer leaves than those exposed to LDs for identical periods. There are two reports that indicate that LDs do not affect leaf number. Smith and Langhans (1962) reported that there was no difference in total leaf number between plants exposed to 18-hour photoperiods from 9 h of natural lighting and 9 h of incandescent lighting, and those exposed to nine-hour photoperiods at constant forcing from 10 to 27C. Pertuit and Link (1971) found that continually exposing plants to LDs did not affect total leaf number compared to plants grown under SDs, provided that the plants were grown from bulbs vernalized for six weeks at 8C.

LDs during forcing affected flowering percentage less in this study than in others (Waters and Wilkins, 1967; Wilkins et al., 1968a and 1968b; Roh and Wilkins, 1973, 1977a, 1977b, 1977d, 1977e). However, all of the plants in previous studies were grown under naturally occurring, progressively longer photoperiods, a factor that in combination with the LD

treatments used probably contributed to additional flower induction. Other research involved forcing below 18C, which can induce flowering (Lange, 1992a). Plants in the current study were maintained under SDs at 20C after the temperature-photoperiod treatments preventing additional flower induction by naturally occurring LDs or low temperatures. Wilkins and Waters (1971) found that the percentage of plants grown from nonvernalized bulbs that flowered increased from 0 to 100 as the number of LDs increased from 0 to 16. Their plants were forced at 16C through the end of the photoperiod treatments and at 21C from that point to flower. When the plants were forced at a constant 21C from the beginning of forcing to flower, 44 LDs were required for 100 percent of the plants to flower (Wilkins and Waters, 1971). The fact that 100% flowering was obtained without any vernalization by only 16 LDs suggests that the bulbs in their study were at least partially induced to flower prior to the start of their experiments or that the plants were highly responsive to LDs. Roberts and Moeller (1971) found that plants from nonvernalized bulbs were unable to flower after 120 LDs. Only 70% of the plants exposed to six weeks of LDs flowered in the present study, which suggests that they were relatively insensitive to LDs, or fewer were induced to flower prior to the start of the experiment.

Leaf number increased and the flowering percentage decreased as the treatment sequence changed from 6C/0L to 2C/4L (Figs.

1 and 2). Plants in the treatment sequences from 2C/4L to 4C/2L had lower flowering percentages and fewer leaves than those that were held at 2C/0L to 4C/0L. Wilkins and Waters (1971) reported that leaf number increased from 65 to 96 as the duration of LDs following vernalization increased from zero to six weeks and the duration of vernalization decreased from six to zero weeks but incorrectly concluded that LDs can be substituted for effective flower induction. The data from the present study demonstrated that LDs cannot be substituted for equal durations of vernalization for flower induction based on leaf number (Fig. 3).

LDs were more effective in reducing leaf number when preceded by at least two weeks of vernalization (Fig. 1). Leaf number increased from 100 to 113 as the treatment sequence changed from 6C/0L to 2C/4L. When LDs preceded vernalization, leaf number increased from 116 to 212 as the treatment sequence changed from 2L/4C to 6L/0C. Prior exposure to cold increased the responsiveness of the plants to LDs, accelerating flower induction. These results are similar to those obtained by Pertuit and Kelly (1987), who found that exposing bulbs to LDs was effective in decreasing leaf number only during the last two weeks of a six-week vernalization treatment at 7.2C. Roberts and Fuchigami (1972) found that bulbs are more responsive to vernalization when the aging mother shoot is exposed to SDs. There are no other reports discussing plant exposure to LDs prior to vernalization.

Although LDs following cold increased the FII of plants more than LDs that preceded cold did (Fig. 3), LDs increased flowering percentage more when before cold than when following cold (Fig. 2). The percentage of 2C/4L flowering plants was 55 with 114 leaves whereas the percentage of 4L/2C flowering plants was 100 with 159 leaves.

The time from the beginning of the treatments until flower was directly proportional to the total number of leaves, which is in agreement with previous research (Emsweller and Pryor, 1943; Blaney et al., 1963; Brierley, 1941a; Weiler and Langhans, 1968a; De Hertogh and Wilkins, 1971; Roh and Wilkins, 1977d). Plants with more leaves to unfold required additional forcing time. Leaf-unfolding rates of plants from bulbs of equal size are a function of average daily forcing temperatures (Karlsson et al., 1988). There is no evidence to suggest that LDs or the synchronization of LDs and vernalization affects leaf-unfolding rates.

Greenhouse forcing time decreased as vernalization duration increased from two to six weeks (Fig. 4), which agrees with previous findings (Weiler and Langhans, 1968a; De Hertogh and Wilkins, 1971; Roh and Wilkins, 1977a; Lange, 1992a). Increasing the duration of LDs from two to six weeks was less effective in reducing the amount of time to flower than increasing the vernalization duration (Fig. 4). LDs were more effective in reducing the time until flower when preceded by

cold than when followed by cold (Fig. 4). Weiler and Langhans (1968b) found that plants grown from bulbs vernalized for three to six weeks and exposed to LDs flowered in less time than vernalized plants grown under SDs. LDs consisted of either 4 or 10 h of night incandescent lighting and SDs consisted of 8.5 h of natural lighting.

There was no consistent treatment effect on flower number. Wilkins et al. (1968a) reported that exposing plants from commercially vernalized bulbs to 45 LDs did not affect flower-bud number compared to plants exposed to zero LDs. Carlson and Carpenter (1970) reported that exposing plants from nonvernalized bulbs to continuous LDs did not affect flower number compared to exposing plants to natural photoperiods. Lange (1992a) reported that the duration of vernalization at 0 to 17.5C did not affect flower number of plants forced under SDs. Others have reported that LDs during forcing decrease flower number. Waters and Wilkins (1967) reported that LDs decreased flower numbers of plants from nonvernalized bulbs. Roh and Wilkins (1973) found that the flower number of plants from nonvernalized bulbs decreased from 11.2 to 7.2 as the duration of LDs increased from zero to six weeks. Roh and Wilkins (1977a) also reported that LDs decreased flower number of plants from nonvernalized bulbs.

This experiment has demonstrated that LDs alone are not equivalent to vernalization in inducing flowering on a day-

for-day basis. Plants are more responsive to LDs after an initial exposure to cold temperatures. FII is an effective measure of the flower induction response of plants to an inductive treatment, and is independent of the floral-induction stimulus. As a result of pretreatment with cold, LDs increase the flower-induction response by decreasing the total leaf number at flower. However, LDs are not as effective as cold after partial vernalization because they cannot substitute for it in increasing the flowering percentage of partially vernalized plants. Current recommendations that advocate exposing partially vernalized plants to LDs during forcing, called the "insurance policy", may be deleterious since this study suggests that the flowering percentage is decreased by LDs following vernalization. By decreasing leaf number, LDs following vernalization consequently decrease the time until flower. Flower number was not affected by the order or type of floral-induction stimulus.

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Figure 1. Total leaf number of 'Nellie White' Easter lily from 1988-89 as a function of vernalization (5C) and photoperiod (LD) treatments prior to forcing under SD. Vertical bars represent 95% confidence intervals.

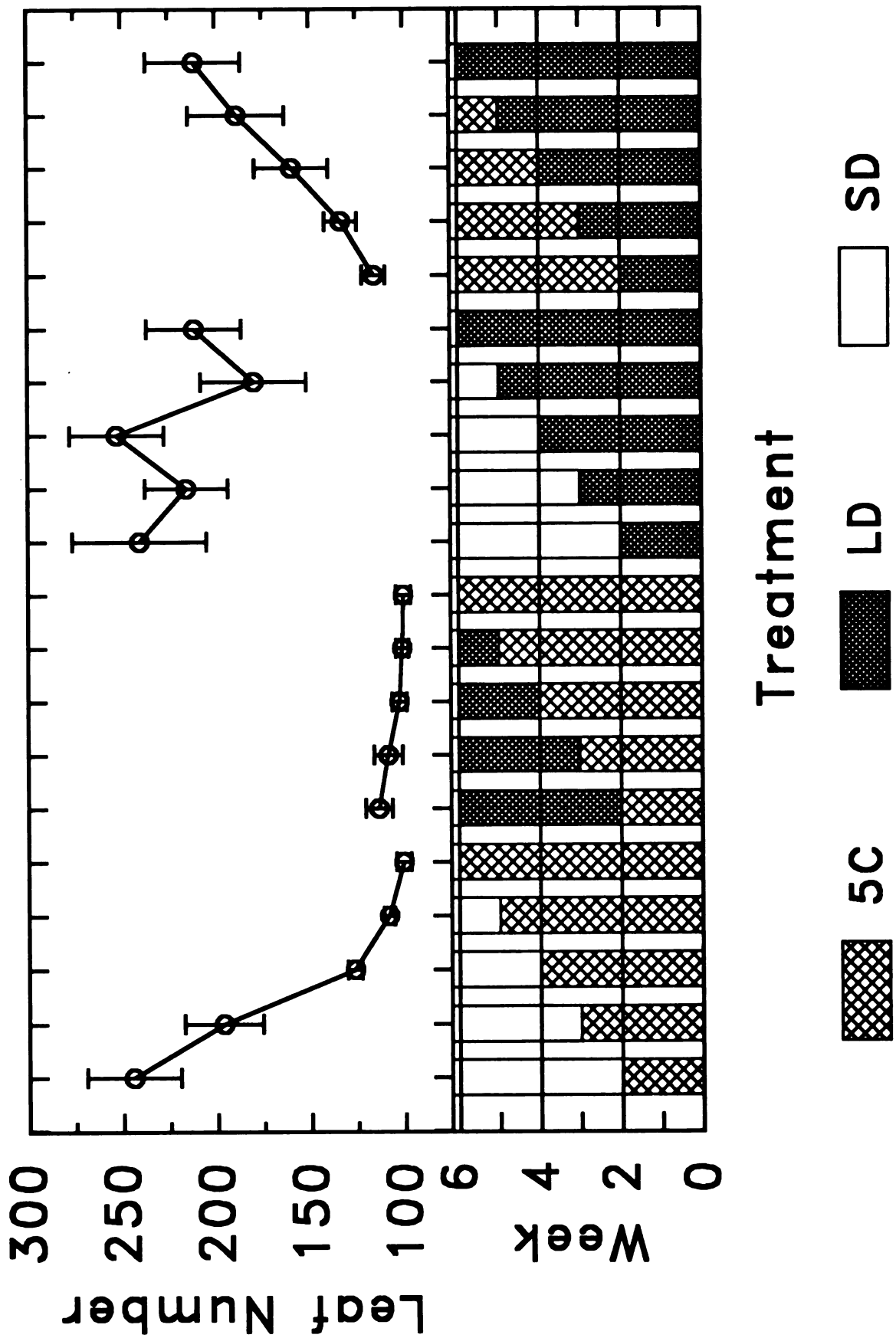

Leaf Number
300
250
200
150
100
Week
6
4
2
0
Treatment
SD
LD
SC

Figure 2. Flowering percentage of 'Nellie White' Easter lily from 1988-89 as a function of vernalization (5C) and photoperiod (LD) treatments prior to forcing under SD.

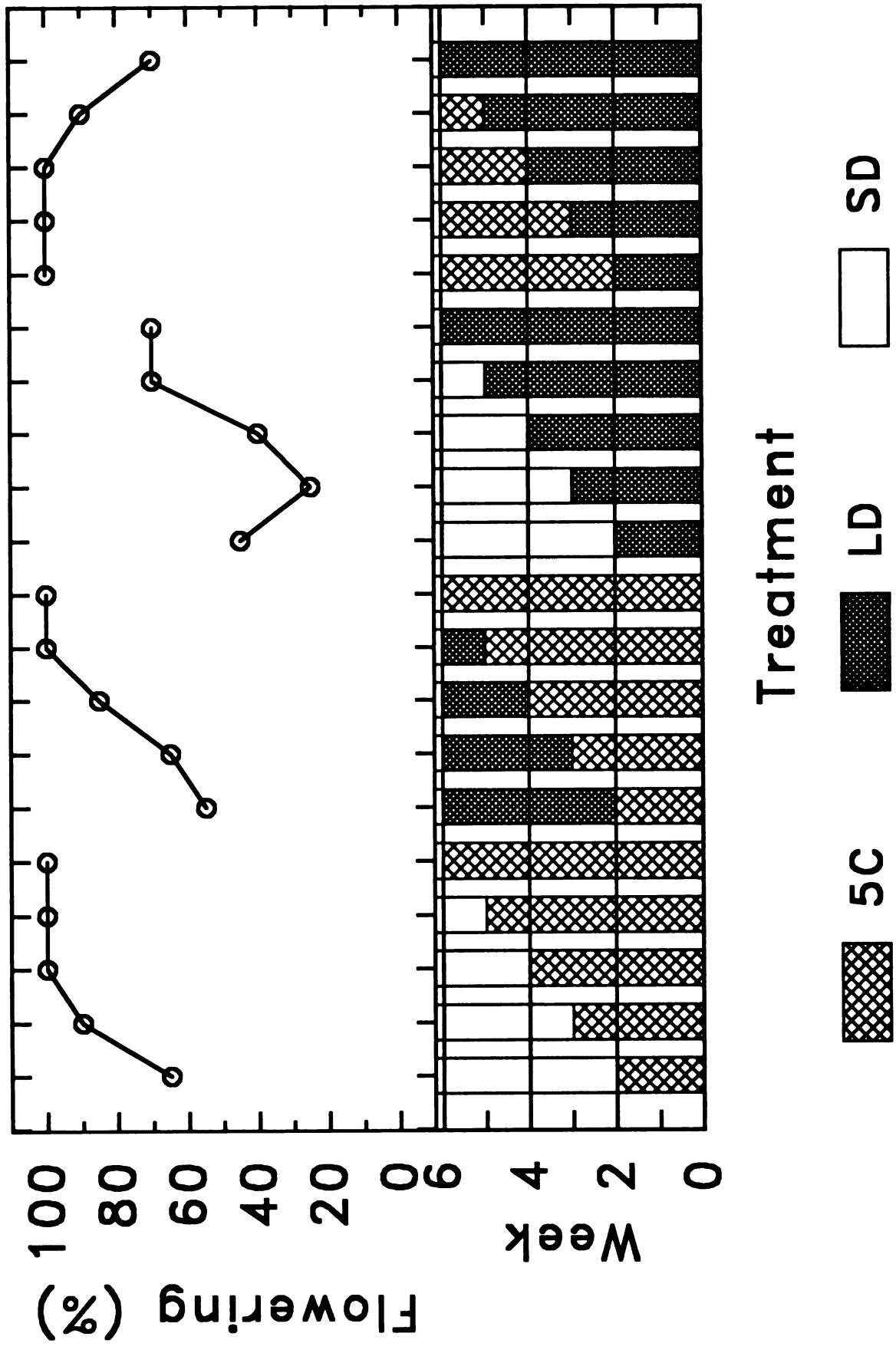

Flowering (%)
100
80
60
40
20
0
Week
0
2
4
6
Treatment
SD
LD
SC

Figure 3. Flower induction indices of 'Nellie White' Easter lily from 1988-89 as a function of vernalization (5C) and photoperiod (LD) treatments prior to forcing under SD. Vertical bars represent 95% confidence intervals.

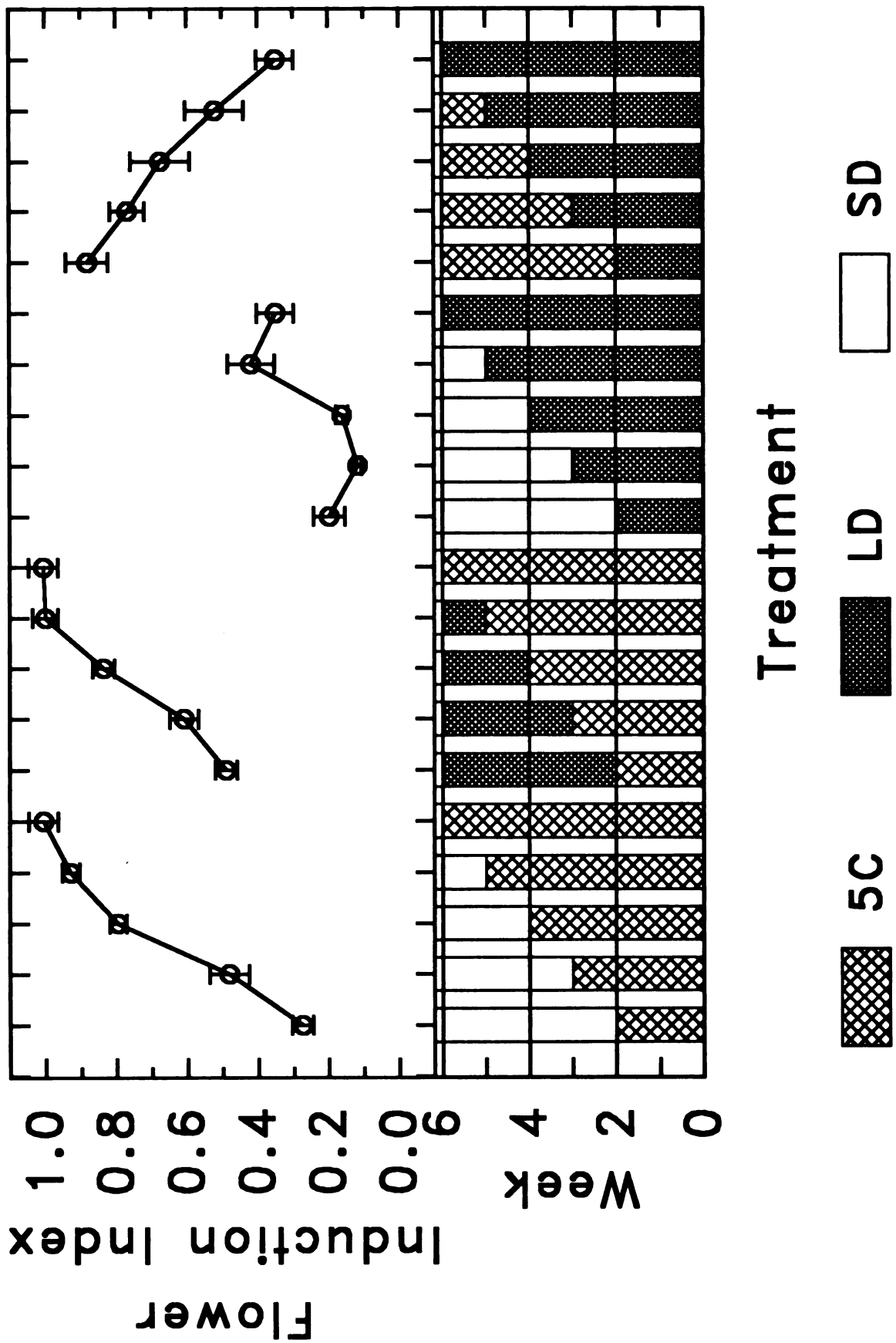

Flower
Induction Index
1.0
0.8
0.6
0.4
0.2
0.0
Week
0
2
4
6
Treatment
SD
LD
SC

Figure 4. Forcing time of 'Nellie White' Easter lily from 1988-89 as a function of vernalization (5C) and photoperiod (LD) treatments prior to forcing under SD. Vertical bars represent 95% confidence intervals.

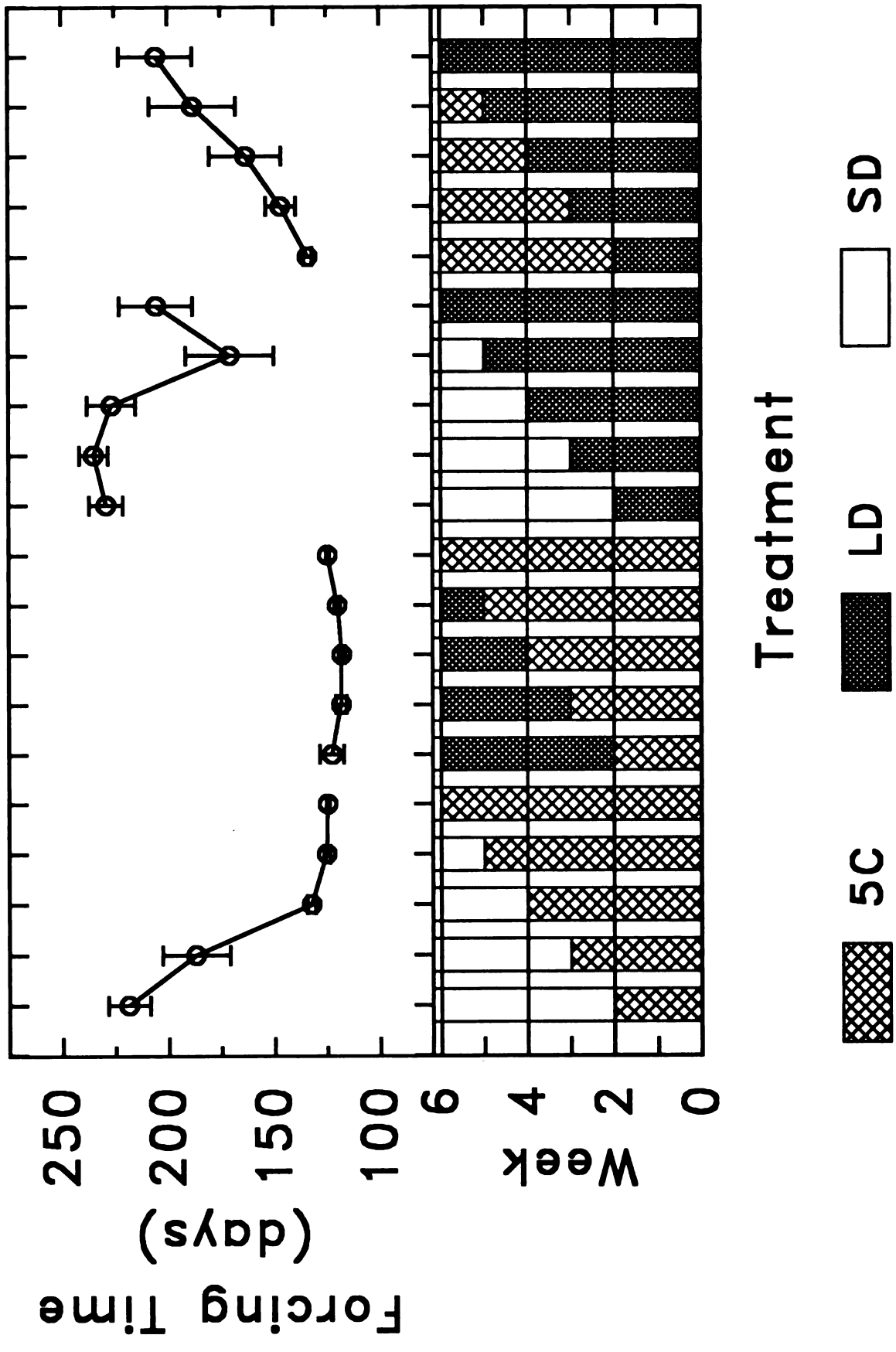
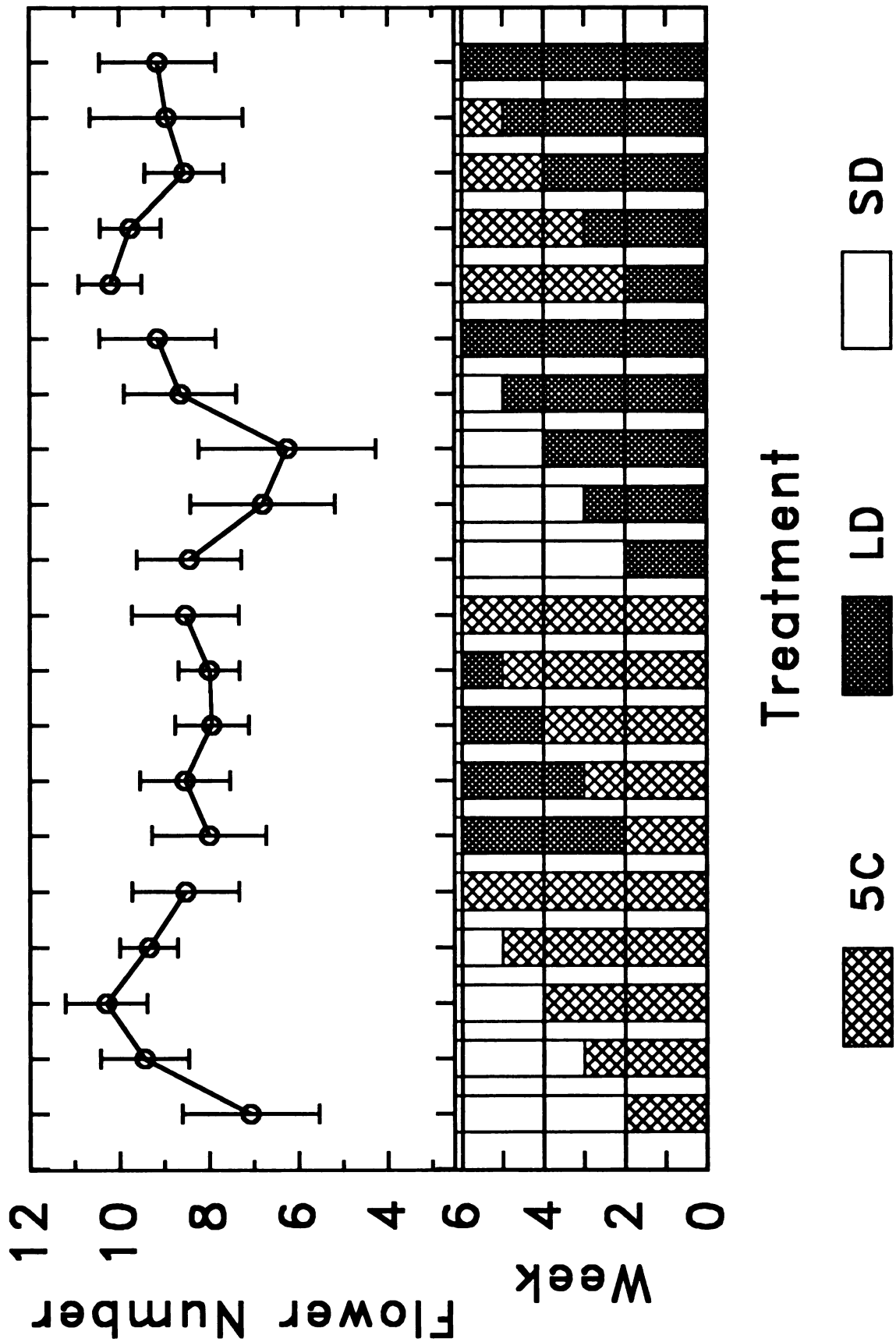

Forcing Time
(days)
250
200
150
100
Week
6
4
2
0
Treatment
5C
LD
SD

Figure 5. Flower number of 'Nellie White' Easter lily from 1988-89 as a function of vernalization (5C) and photoperiod (LD) treatments prior to forcing under SD. Vertical bars represent 95% confidence intervals.


Flower Number
12
10
8
6
4
2
0
Week
6
4
2
0
Treatment
SD
LD
SC