

AN ABSTRACT OF THE THESIS OF

Kim Diane Gray for the Master of Science
(Name of student) (Degree)

in Horticulture presented on June 8, 1973
(Major) (Date)

Title: Initiation and Development of *Lilium longiflorum* Thunb.

Bulb Scales as Affected by Temperature and Daylength.

Abstract approved: _____

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The development of Easter lily *Lilium longiflorum* Thunb. 'Ace' bulblets from scales was used to study the influence of scale pre-cooling, growing temp, and daylength on scale initiation, scale "filling" (bulbing), and scale leaf formation. The development of 'Croft', 'Ace', and 'Nellie White' daughter bulbs in field-grown yearlings was also used to study scale filling and "feathering."

Scale bulblet formation and development is a gradual process which proceeds at a fairly constant rate. Since bulblets formed at all temp (12° , 22° , and 27°C) and daylengths (8, 12, and 16 hr) in this study, it was concluded that there is no critical temp or daylength requirement for bulbing. Temp exerted a stronger influence on bulblet development than did daylength, a 10°C increase (from 12° to 22°C) nearly always doubling the growth response.

A further increase in temp (to 27°C) seldom increased the growth response, and frequently decreased growth as compared with 22°C.

Scale initiation and wt increase was near optimum at 22°C. Pre-cooling (0°C for 6 weeks) the scales from which the bulblets formed reduced the no. of new scales initiated and their wt.

Scale leaves formed most readily at 22°C and under short days (8 hr). Pre-cooling the scales from which the bulblets formed reduced the no. of bulblets with scale leaves and their length.

Daughter bulb scales of field-grown yearlings fluctuated in wt in a consistent manner and in proportion to their age and position in the bulb. The outer daughter scales had larger wt increases and filled a month longer than the inner scales. At the time of daughter axis elongation (sprouting), the inner scales either lost wt or ceased to gain wt before the outer scales responded.

The no. and position of abnormally long feathered scales of 'Nellie White' were fairly constant in the 1972 season studied. Based on scale complement of the daughter bulbs, those that feathered were the 12th-27th scales and were in the outer half of the bulb.

Initiation and Development of Lilium longiflorum Thunb.
Bulb Scales as Affected by Temperature
and Daylength

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

June 1974

APPROVED:

Professor of Horticulture
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Date thesis is presented June 8, 1973

Typed by Maryolive Maddox for Kim Diane Gray

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Initiation and Development of Lilium longiflorum Thunb.
Bulb Scales as Affected by Temperature
and Daylength

INTRODUCTION

Japan and the United States lead the world in lily bulb production, and within the United States production is centered in California and Oregon (16). About 500 acres in southern Oregon and northern California produce Easter lily bulbs for commercial greenhouse forcing. This represents a gross income of approximately \$3,000,000 annually to bulb growers. In addition, Oregon is the leading U.S. producer of colored lily bulbs with an estimated crop value in excess of \$1,000,000 (32).

Easter lily research in the United States has been mainly concerned with greenhouse forcing and pre-planting handling and storage, because those practices relate directly to the flowering and sale of the crop. Consequently, the physiology of flowering and dormancy is well understood. Although some research on bulb development has been done, it is neither complete nor extensive. This is unfortunate because determining the relationship of scale no. and wt to the total bulb size should enable the production of larger bulbs and the prediction of bulb size. Since

bulbs should be as large as possible to produce high quality potted plants, research on bulb development will eventually improve Easter lily production.

The research described in this thesis deals with certain processes of Easter lily bulb development. Scale bulblets and daughter bulbs in field-grown yearling bulbs were used. The major objectives were to study the influence of temp and daylength on scale initiation, scale filling (wt gain), scale leaf formation, and scale "feathering".

REVIEW OF LITERATURE

Influence of Temperature and Daylength
on Bulb and Tuber Formation

Onion Bulbs

Garner and Allard (13) were the first to point out the photo-periodic effect on bulb formation. Working with a silver skin onion cv., they reported that the plants did not show signs of bulbing when grown under short days (SD - 10 hr) with full sunlight (10,500 ft-c), but bulbing did occur under long days (LD - 14.9 hr), even when the light intensity was reduced to 1/3 that of sunlight (3,500 ft-c). Extending these studies in 1923 (14), they grew sets of common silver skin onions under 4 different daylengths: 10 hr, 13 hr, natural daylength (ND - 14.9 hr) and 14.9 hr plus 5 hr of illumination at 3-5 ft-c. Plants grown under ND plus 5 hr of artificial light developed bulbs to the same extent as those under ND; those under a 13-hr day eventually formed bulbs of considerable size. The plants failed to form bulbs under a 10-hr day. Garner and Allard concluded that onion bulb development and subsequent rest are induced by LD.

Thompson and Smith (36) and Heath and Holdsworth (20) found a temp-daylength interaction in bulb formation. In one

experiment plants were grown under SD and LD with 3 temp regimes, (50° - 60° F, 60° - 70° F, and 70° - 80° F). Under SD no bulbing occurred. Under LD no bulbing occurred at 50° - 60° F, but did occur at 60° - 70° F and at 70° - 80° F, and the bulbing began a month earlier at 70° - 80° F than at 60° - 70° F (36). Therefore, under LD, high temp accelerate bulb formation while lower temp delay or prevent it.

Shallot Bulbs

Jenkins (21), working with shallots, found that, as in onions, LD and high temp were necessary for bulb formation. In his experiments, shallot plants grown at 70° F quickly produced bulbs when placed under a 15-hr day, but when placed under a 10-hr day bulbing was greatly delayed. When grown at low temp (28° - 40° F), bulbs did not form at either daylength.

Garlic Bulbs

Mann (28) found that garlic also requires LD and high temp for bulbing. Garlic plants were grown under 18- and 11-hr photoperiods at 70° F. The LD plants bulbed, but the SD plants did not. Bulbs also formed more quickly under warm (50° - 60° F) than cool (40° - 50° F) temp.

Mann and Minges (29) showed that pre-planting storage temp also affected bulbing. For storage periods of 1-2 months, bulbing occurred more quickly in plants exposed to 0° or 5° C than in plants stored at warmer temp (10° - 15° C). Plants never exposed to temp below 20° C failed to form bulbs, even when grown under LD.

Tulip Bulbs

Le Nard and Cohat (25) studied the influence of storage temp on tulips normally harvested after maturity of the mother plant. They found that low temp were necessary to induce bulbing i. e., the transformation of an axillary bud into a daughter bulb. The induction of bulbing was stronger at $2-3^{\circ}$ C than at 10° C, and increased with longer storage at low temp. No induction occurred at $18-20^{\circ}$ C. This low-temp induction of bulbing could occur only in bulbs which had reached a certain stage of "physiological maturity" (22).

Potato Tubers

In the formation of potato tubers the most important environmental factor is low temp. Tuber production occurs optimally at low temp and high light intensity, and is strongly governed by photoperiod at higher temp. At high temp tuber formation is

possible to a limited extent in SD, whereas at lower temp tuberizing can occur under both LD and SD (17, 42, 43).

Experiments conducted by Bushnell (5) involving the lifting of potato tubers after 2 months of growth at temp ranging from 20° to 29°C showed that tuber wt decreased with increasing temp, and no tubers were formed at 29°C. Beaumont and Weaver (1) obtained lower tuber wt with potato seedlings grown at 15°C than at 10°C in an experiment carried out in winter under low light intensity. Werner (43) found, without controlled conditions, an unfavorable influence of high temp (24°-33°C) on tuber yield.

Tuber formation starts earlier at low than at high temp. However, Borah and Milthorpe (4), found the optimum temp to be 20°C; at 15° and 25°C tuber formation started 1 and 3 weeks later, respectively. There are more tubers per plant at low than at higher temp, especially at low night temp (3, 4, 17). High night temp also seem to decrease tuber yield more than high day temp, thus Gregory (17) obtained a much higher yield at 30° day-10°C night than at 23° day-23°C night temp.

Light intensity also affects tuber production. Tuber yields were larger at higher (1488 ft-c and 744 ft-c) than at lower (279 ft-c) light intensities when grown at 16°C (3). Light intensity can also influence the optimum temp. In low light intensity

experiments, max tuber wt were obtained at 12^o-14^oC, while at high light intensities the optimum was found at 18^o-20^oC (3). Thus, with an unfavorably low light intensity, a lower temp favors tuberizing.

Although European varieties initiate tubers at any daylength, their development is very much accelerated by SD (3). There is a range of daylengths between LD and SD which is inexactly termed the 'critical daylength', below which the plants develop SD characteristics, above it LD characteristics. Temp and light intensity influence the critical daylength (3). A shorter day is required if there is an increase in temp or a decrease in light intensity.

Dahlia Tubers

Zimmerman and Hitchcock (45) and Moser and Hess (31) found SD enhanced tuberization in dahlia. Daylength determined the type of root system formed, heavy storage roots being correlated with SD and a fibrous root system with LD (45). Daylength experiments showed that the critical daylength was 11-12 hr (31). Very little tuberization occurred with longer daylengths. Daylengths of less than 11-12 hr produced 4 times the wt of tubers obtained under LD. The effect of night interruptions was also studied. Tuberization was inhibited by any interruption which

prevented the plants receiving a continuous dark period of more than 12 hrs. These night interruptions were as effective in preventing tuber development as extended photoperiods (31).

Investigations by Moser and Hess (31) revealed that max tuberization occurred at 60° and 70°F, whereas it was inhibited at either 50° or 80°F. The tuberous roots of plants grown under LD failed to develop at any of the night temp used. These results indicate that the SD requirement for tuberization is not altered by night temp.

Tuberous-rooted Begonias

Tuber formation in tuberous-rooted begonias is a response to short photoperiods (8, 9, 11, 24, 25). Lewis (24) showed the critical photoperiod to be between 12 and 14 hr.

The effects of temp on tuber formation were studied by Esashi et al. (10). The optimum temp for tuberization was 23°C. Lower (11°C) or higher (35°C) temp delayed tuberization. Night temp were found to affect tuberization more than day temp. The optimum night temp was 23°C regardless of day temp.

Artichoke Tubers

Tickner (37, 38, 39) showed that a 10-12 hr daylength

accelerated the growth of artichoke tubers. Extending the day-length, however, decreased the rate of development of the tubers.

Summary of Bulb and Tuber Formation

In general, bulbs and tubers form in response to photoperiodic stimuli; bulbs induced by LD and tubers by SD. Temp also influences bulb and tuber formation. In onion, garlic, and shallot plants grown under LD, high temp accelerate and low temp delay or prevent bulb formation. In dahlia and tuberous-rooted begonia plants grown under SD, intermediate temp are optimum for tuber formation and high or low temp inhibit or delay tuber formation. If these bulbous or tuberous plants are grown under the improper daylength, no bulbs or tubers will be formed regardless of the temp.

Potato tubers form optimally under low temp and SD, the low temp being the more important factor. At high temp tuber formation is possible to a limited extent in SD, whereas at lower temp tuberizing can occur under both LD and SD.

Storage temp can also influence bulb formation. Garlic and tulip form bulbs most rapidly when they receive prior low temp storage ($0-5^{\circ}\text{C}$), but they never form bulbs if stored at high temp ($18-20^{\circ}\text{C}$).

Development of Lilium longiflorum Bulblets by Scaling

"Scaling" is a method of propagating lilies, whereby scales are separated from the mother bulb and placed in a favorable environment (18). Adventitious bulblets form on the adaxial side of the proximal end of the individual bulb scales regardless of the orientation of the scale when planted (15, 18, 34, 40). Depending on the species and cv., each scale will usually develop from 3 to 5 bulblets (18).

The favorable environment should be humid, moist, and warm (12). Temp of 70^oF and higher are reported to produce larger bulblets faster than lower temp (7, 12, 15, 18, 35). The mother scales can be placed directly into soil (12, 35), put in plastic bags with moist peat, vermiculite, or sphagnum (12, 35), or inserted base down in sand (7). One investigator reported that propagation was better when the scales were exposed to air (7). Light intensity is not a factor as bulb formation will occur in the dark as well as at an intensity of 100 ft-c (18).

The best time to scale lilies of many species is not definitely known. Generally it should be done soon after flowering (7, 12). However, Robb (34) reported that scaling in Lilium speciosum is successful in either spring or autumn when the mother plant is

vegetative. Emsweller (7) reported the best results from lily scaling were obtained when the larger scales of large, solid bulbs were used. In a scaling experiment with Lilium longiflorum, more and larger bulblets were obtained from the larger outer scales than from the smaller inner ones. In a scaling experiment with Lilium speciosum, however, Robb (34) reported that inner scales regenerated as easily as outer ones.

Walker (40) studied the regeneration of bulblets from Lilium longiflorum bulb scales. Following is a description of the general morphology of the developing bulblet.

The earliest indication of meristematic activity in the detached scales is the formation of a callus tissue over the cut surface. This appears within a few days after being placed in the propagating medium. Small buds appear on the basal portion of the scales 2 weeks after planting. These occur singly or in groups of 2 or 3. The buds are recognizable as small humps of meristematic tissue. A protuberance arises from the lateral surface of the meristematic hump which is immediately followed by a second one; from these develop the primordia for the first scales. Between the leaf primordia the stem tip continues to grow giving rise successively to other leaf initials.

Under ordinary conditions root development was not observed until after the formation of several leaf primordia. In the early stages of growth, root and bud primordia are independent of one another. As development continues, however, the parenchyma between the root and bud primordia becomes meristematic, and forms cells which become differentiated into vascular elements connecting the primordia. At no time is there any indication of a vascular connection between the vascular elements of the root and bud

primordia and the mother bulb scale.

New leaf primordia arise at intervals from the lateral surface of the embryonic stem tip. As these develop within the center of the rosette, the outer older primordia grow and assume the shape of mature scales. The inner leaf primordia of buds formed on mother scales planted near the surface of the propagating medium continue to grow in length and become green, whereas the primordia of buds developing on scales planted 2 to 3 inches below the surface remain scale like. In either case the developing bulblet remains attached to the mother scale until the food in the scale is exhausted.

Godden and Watson (15) studied the development of bulblets from mother scales of Olympic, Fiesta, and Bellingham hybrids. They reported, contrary to Walker's observations of Lilium longiflorum, that vascular connections did arise between the mother scale and the bulblet primordia. In addition, the bulblet was dependent upon the parent scale during its early stages of initiation.

Matsuo (30) studied the growth sequence of 3 cv. of Lilium longiflorum scale bulblets from incubation to the yearling stage. He found that there are 3 processes by which a yearling bulb can be formed. In one, the bulblets form scale leaves (blades formed on the distal end of the scale; these are mentioned by Walker as the scales which continued to grow in length and became green) and then bolt. In the second, bulblets form scale leaves but do not bolt. In the third, the bulblets bolt without forming scale leaves.

Development of Lilium longiflorum from Stem
Bulblets into Commercial Bulbs

Blaney and Roberts (2) studied the growth and development of Lilium longiflorum 'Croft' from stem bulblets to commercial bulbs. They made several important observations. One was that at anthesis of the mother plant, scale initiation at the apices of stem bulblets and daughter bulbs ceases. A second was that the rate of primordia initiation by the apex was relatively constant regardless of the fluctuations in seasonal temp. A third was that the food reserves in the old outer bulb scales were being periodically hydrolyzed and transported to the growing shoot, to the inner old scales, and to the scales of the new daughter.

Roberts et al. (33), in nutrient studies with Lilium longiflorum 'Croft' bulbs, reported that total and daughter bulb wt increases are relatively constant throughout the growing season.

ASPECTS OF SCALE FILLING AND FEATHERING IN
FIELD GROWN LILIUM LONGIFLORUM THUNB.
DAUGHTER BULBS*

Abstract

The development of 'Croft', 'Ace', and 'Nellie White' daughter bulbs in field-grown yearlings of Easter lily Lilium longiflorum Thunb. was used to study scale "filling" and "feathering."

The scales fluctuated in wt in a consistent manner and in proportion to their age and position in the bulb. The outer scales had larger wt increases and filled a month longer than the inner scales. At the time of daughter axis elongation (sprouting), the inner scales either lost wt or ceased to gain wt before the outer scales responded.

The no. and position of abnormally long feathered scales of 'Nellie White' were fairly constant in the 1972 season studied. Based on scale complement of the daughter bulbs, those that feathered were the 12th-27th scales and were in the outer half of the bulb.

* Prepared for publication in the Journal of the American Society for Horticultural Science.

Introduction

Bulb development in Easter lily has been described by Blaney and Roberts (1). They reported that scale primordia are initiated at a relative constant rate, regardless of seasonal temperature fluctuations. Roberts et al. reported that total and daughter bulb weight increases are relatively constant throughout the growing season (3). However, in these studies they made no attempt to determine which scales in the daughter bulb were filling, the order in which they were filling, or the magnitude of their individual weight increases. Accomplishing this was one of the purposes of this study.

Another purpose has been to study the phenomenon of feathering, which is poorly understood. Feathering has been described as a condition, which can occur from late spring to harvest, in which certain inner scales elongate and project out of the top of the bulb (2). Although 'Croft', 'Ace', and 'Nellie White' (the cv. used in this experiment) may all exhibit feathering, 'Nellie White' has a greater tendency to do so.

Materials and Methods

The terms used in this report to describe the various

organs, functions, and physiological events in the Easter lily bulb have been defined by De Hertogh et al. (2).

Each month from July to October and in December 1972, 10 bulbs each of 'Ace', 'Croft', and 'Nellie White' (30 to 40 g planting stock) were harvested at the Pacific Bulb Grower's Research and Development Station, Harbor, Oregon. For each cv. the following procedure was followed. The mother scales were removed and discarded, thus only daughter bulbs were considered. The scales of each daughter bulb were removed centripetally and placed into 9 groups of 5 scales each. Since the average no. of scales per bulb was 54, about 9 scales were discarded because they were too small to be handled. The first 5-scale group thus represented the outermost scales and the ninth group the innermost scales of the bulb. The scales of the 10 bulbs were then combined into their 9 respective groups, fresh wt were recorded, and an average wt per 5-scale group was calculated.

Since only 'Nellie White' bulbs had feathered scales, they were used to study feathering. Using the same 10 'Nellie White' daughter bulbs, and the same method of scale removal described for the previous experiment, the following data were recorded for each bulb: no., position, and wt of normal and feathered scales.

Data were evaluated by analysis of variance, and the

monthly group means compared using Least Significant Difference (LSD) values.

Results

Scale Filling

The combined cv. fresh wt data show that groups 1-7 increased significantly in wt from July to December while groups 8 and 9 did not (Fig. 1). The wt increases from July to December of group 1-3 (6.7, 6.9, 6.9 g, respectively) were larger than those of groups 4-7 (6.3, 5.1, 3.2, 1.4 g, respectively). By October the daughter bulbs were sprouting. This sprouting was accompanied by a cessation of significant wt increases in groups 4-7, while groups 1-3 continued to increase in wt. By December groups 1-3 had also ceased to increase in wt.

There were cv. differences in the amount of scale filling. In July the average wt of the 45 scales of each cv. was 20 g (Fig. 2). By December, however, the average wt of the 45 scales of 'Nellie White' (65 g) was greater than that of 'Ace' (58 g), which was greater than that of 'Croft' (49 g).

'Croft' and 'Nellie White' scale groups responded similarly to daughter sprouting in October (Fig. 3). Groups 1-3 of both cv. continued to increase in wt, but groups 4-7 either lost ('Croft') or

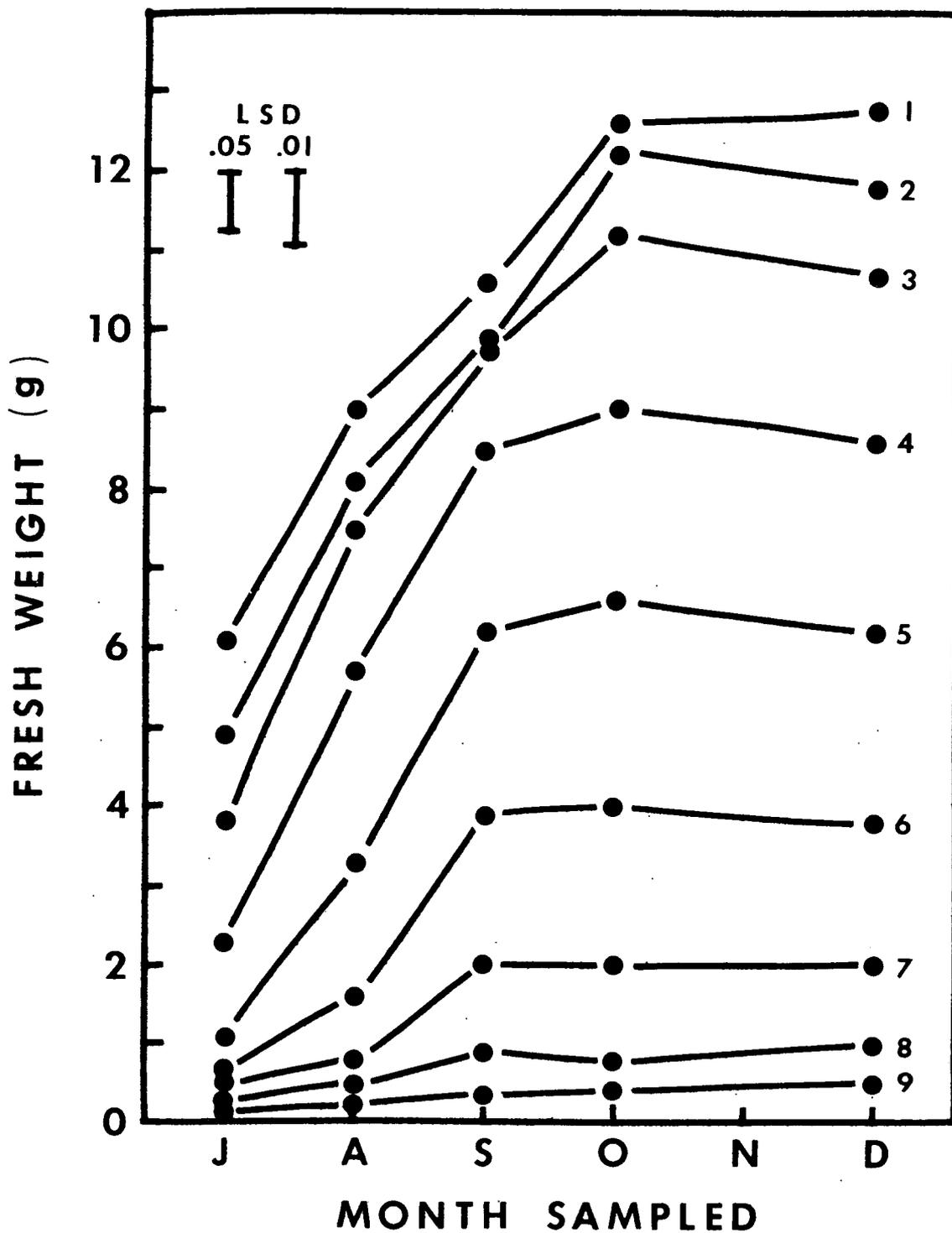


Fig. 1. Average fresh wt of the 9 groups of scales from July to December. The wt for the 3 cv. have been combined.

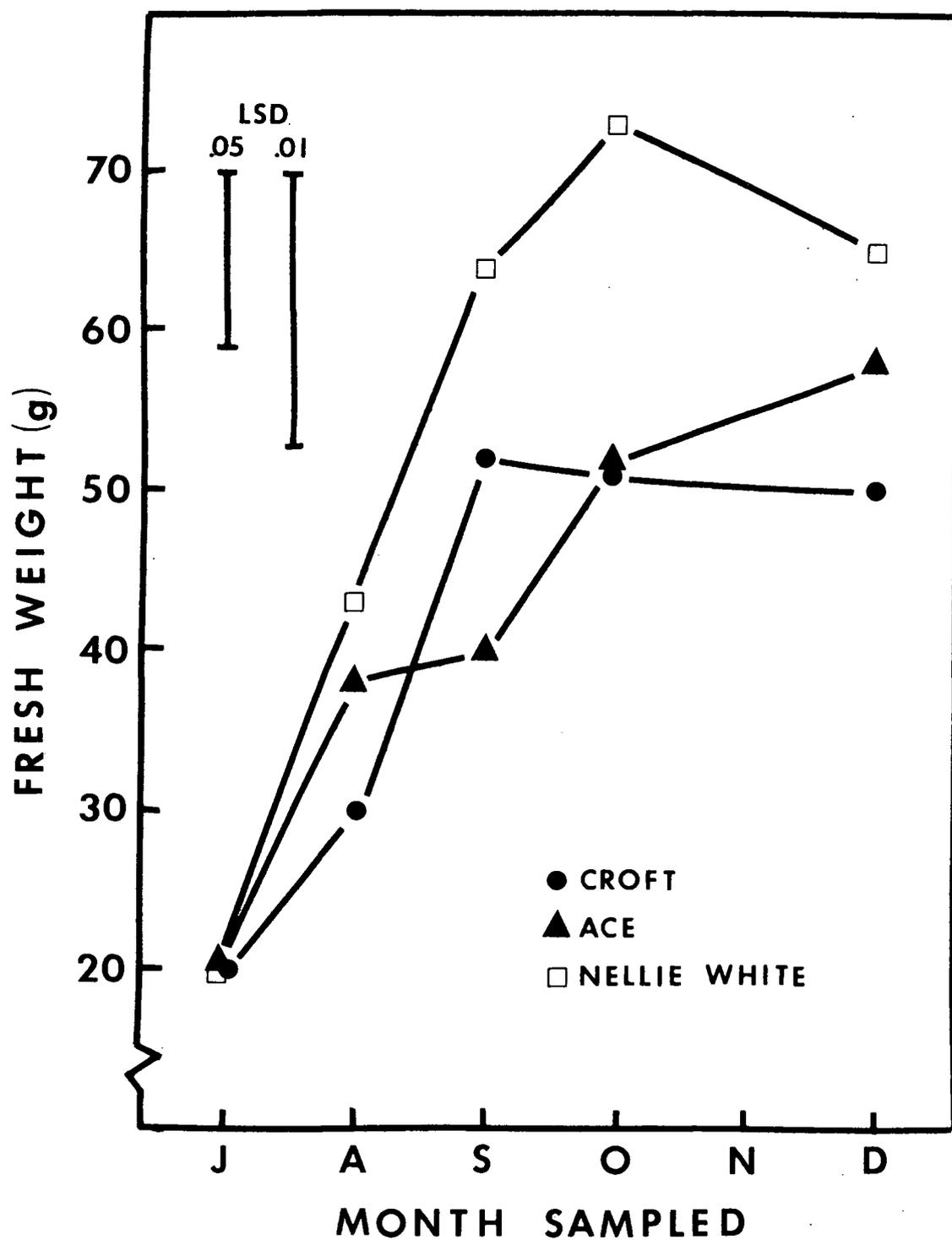
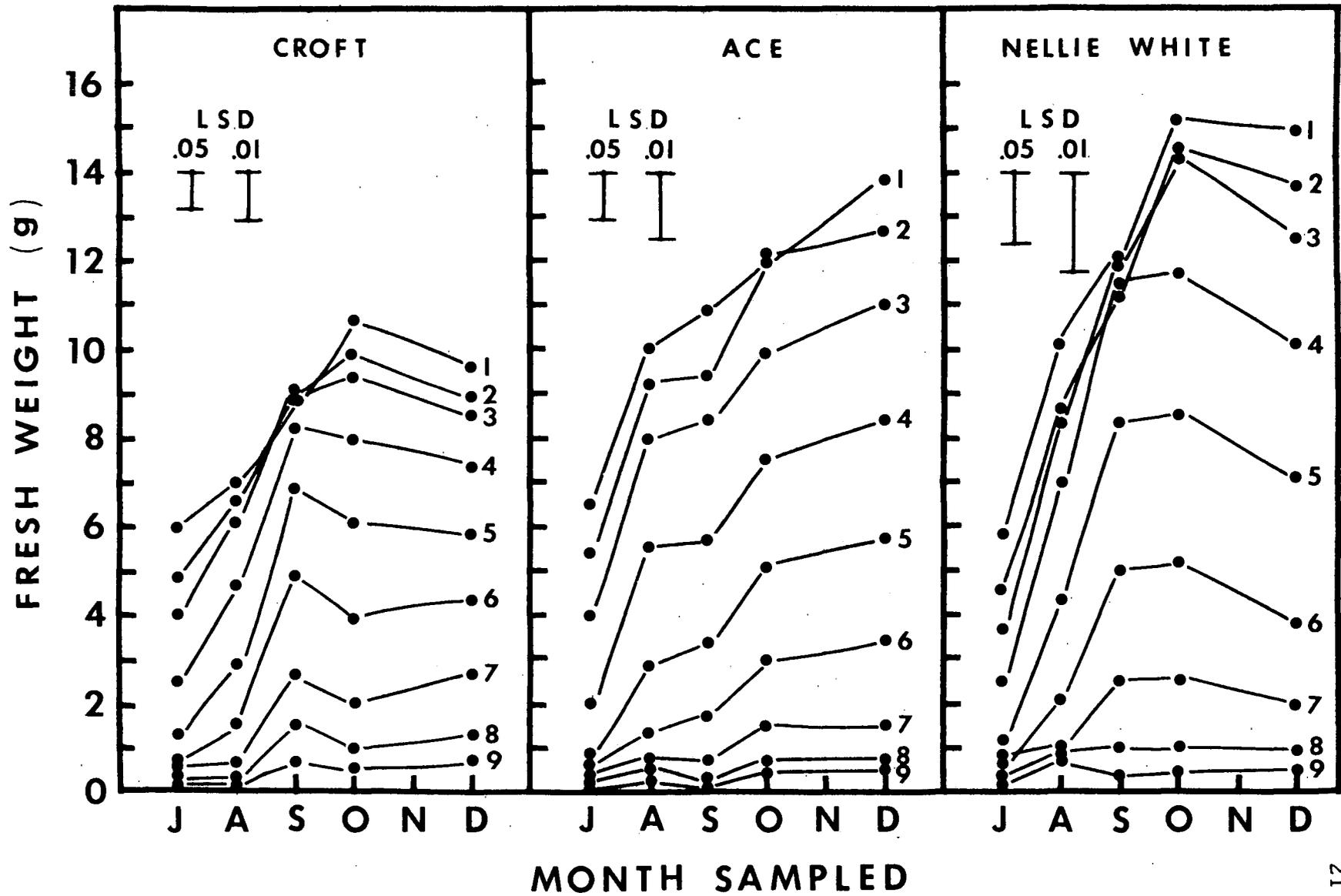


Fig. 2. Average fresh wt of the 45 scales of 'Croft', 'Ace', and 'Nellie White' from July to December.

Fig. 3. Average fresh wt of the 9 groups of scales of 'Croft', 'Ace', and 'Nellie White' from July to December.



increased only slightly ('Nellie White') in wt. However, these October wt changes in groups 4-7 were not significant. In December, groups 1-3 of both cv. lost wt and groups 4-7 either lost wt or gained only slightly in wt. In contrast, 'Ace' scales never lost wt, even after sprouting had occurred (Fig. 3).

Another cv. difference was evident in September. 'Croft' and 'Nellie White' scale groups 1-7 increased significantly in wt, but 'Ace' scale groups 1-7 did not (Fig. 3).

Feathering

'Nellie White' daughter bulbs showed feathered scales in July. When these bulbs were dissected, it was found that, only the middle scales (the 12th-27th scales) were feathered (Fig. 4). The position of these scales was fairly constant from month to month. Of the 54 scales comprising the average bulb, the normal outer scales accounted for 20%, the feathered scales for 30%, and the normal inner scales for 50%.

The feathered scales increased in wt in the same manner as the other scales in the bulb, and constituted about 50% of the total scale wt (Fig. 5). The feathered scales were essentially those of groups 3-6.

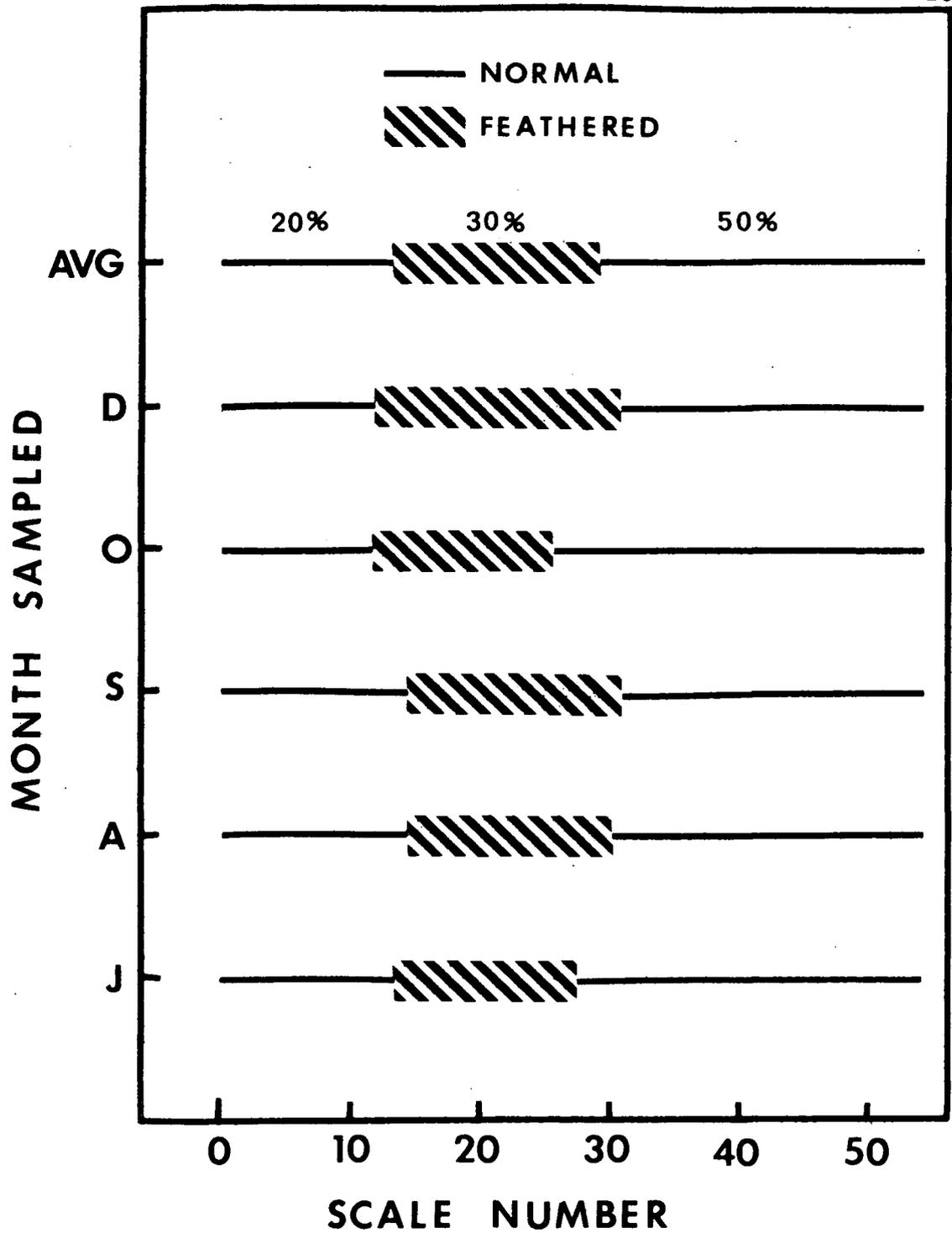


Fig. 4. No. and position of normal and feathered scales in the 'Nellie White' bulb from July to December. The average is the mean of the 5 months, and the percentages are based on 54 scales per bulb.

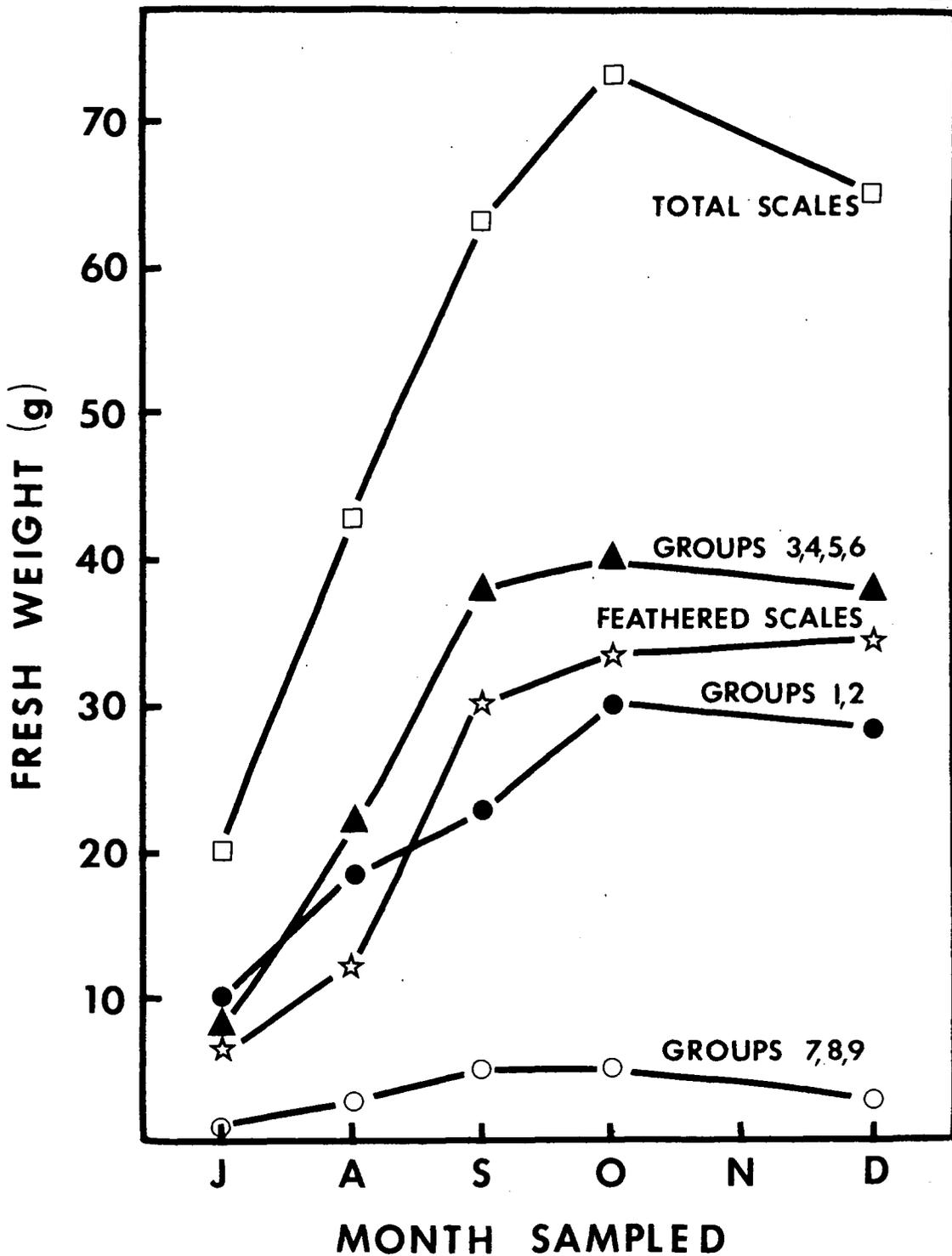


Fig. 5. Average fresh wt of the total 45 scales, feathered scales, and scales of groups 1-2, 3-6, and 7-9 of 'Nellie White'. The feathered scales are essentially those from groups 3-6.

Discussion

Scale Filling

In general, Easter lily bulb scales gain or lose wt in a consistent pattern and in proportion to their age and position in the bulb (Fig. 1). Of the scales that increased significantly in wt. (groups 1-7), the outer scales (groups 1-3) had larger wt increases and filled a month longer than the inner ones (groups 4-7). This indicates that the outer scales may be the major sites for the accumulation of food reserves being translocated from the mother plant to the daughter bulb.

Sprouting, which had occurred by October, was accompanied by wt losses in groups 1-7 in both 'Croft' and 'Nellie White' (Fig. 3). It seems reasonable to conclude that the elongation of the new daughter sprout caused stored food reserves in the scales to be translocated to the new sprout thus reducing the wt of these scales. An important new finding was that the inner scales (groups 4-7) either lost wt or stopped gaining wt before the outer scales (groups 1-3) responded. Blaney and Roberts (1) found that 'Croft' stem-bulblets (comprised of scales initiated in one season) utilized stored food reserves from the outer scales during rapid shoot growth in late February and early March. The older, outer scales of such

bulbs shrivelled and decomposed rapidly as stored food was hydrolyzed for use in the accelerated growth of the new daughter plant, or was redistributed to the younger inner scales of the stem-bulblet, which were also increasing in size and storing food. Although Blaney and Roberts reported the inner scales to increase in wt during rapid shoot growth, the present results indicate that the inner scales can also lose wt, at least from October to December. The time difference (3 months) between the 2 studies could account for the differences observed. There may also be some discrepancies in the use of the terms "inner" and "outer" scales. In this experiment outer scales were considered as those scales in groups 1-3 and inner scales as those in groups 4-7.

Feathering

The no. and position of feathered scales were fairly constant (Fig. 4). The scales that feathered were the 12th-27th scales, and according to Blaney and Roberts (1) these scales were initiated from January to March in the growing areas of the Pacific Northwest. Since no additional scales feathered during the 6 month period, it is suggested that they were induced to feather in early spring, but that expression of this feathering stimulus was not evident until July. Another possibility is that the scales were induced to feather at a

later period when they had reached a certain stage of development which made them sensitive to feathering induction. Since the no. of feathered scales did not change with time, it is suggested that once the scales feather, they do not lose the propensity to do so.

It has been suggested that feathered scales are elongated inner scales (3). Again, there is some confusion with the term "inner". Based on the total no. of daughter scales, the feathered ones in this study were in the outer half of the daughter bulb, the inner half being comprised of normal scales.

It has also been suggested that feathered scales are those that elongate faster than they fill, suggesting perhaps that feathered scales do not gain wt normally (3). The present results indicate, however, that feathered scales fill in the same manner as do normal scales (Fig. 5). Thus feathered scales must be abnormal only in the extent of their elongation.

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INITIATION AND DEVELOPMENT OF SCALES IN
LILIUM LONGIFLORUM THUNB. SCALE
BULBLETS AS AFFECTED BY
TEMPERATURE AND
DAYLENGTH *

Abstract

The development of scale bulblets of Easter lily Lilium longiflorum Thunb. 'Ace' was used to study the influence of pre-cooling the scales from which the bulblets formed, growing temp, and daylength on scale initiation, scale "filling" (bulbing), and scale leaf formation.

Scale bulblet formation and development is a gradual process which proceeds at a fairly constant rate. Since bulblets formed at all temp (12° , 22° , and 27°C) and daylengths (8, 12, and 16 hr) in this study, it was concluded that there is no critical temp or daylength requirement for bulbing. Temp exerted a stronger influence on bulblet development than did daylength, a 10°C increase (from 12° to 22°C) nearly always doubling the growth response. A further increase in temp (to 27°C) seldom increased the growth response, and frequently decreased growth as compared with 22°C .

Scale initiation and wt increase was near optimum at 22°C .

*Prepared for publication in the Journal of the American Society for Horticultural Science.

Pre-cooling (0°C for 6 weeks) the scales from which the bulblets formed reduced the no. of new scales initiated and their wt.

Scale leaves formed most readily at 22°C and under short days (8 hr). Pre-cooling the scales from which the bulblets formed reduced the no. of bulblets with scale leaves and their length.

Introduction

It has been suggested that there is a bulbing response in Easter lilies and that this bulbing or scale filling is the enlargement of the scales associated with the storage of food reserves in the bulb (5). Other bulbous plants, such as onion, exhibit a bulbing response to temp and daylength where bulbing is induced by long days and high temp (6). Tuberos plants also exhibit a tuberizing response to temp and daylength. Potatoes, for example, form tubers under short day-low temp conditions (1, 3, 4). One of the objectives of this study was to determine if Easter lily scale bulblets have a bulbing response that is influenced by temp and daylength.

Bulb development in Easter lily has been described by Blaney and Roberts (2). They reported that scale primordia are initiated at a relatively constant rate, regardless of seasonal temp fluctuations. Roberts et al. also reported that total and daughter bulb wt increases are relatively constant throughout the growing

season (10). Their studies, however, did not report how scale initiation, development, and wt gain are affected by specific temp and daylengths. Accomplishing this was another purpose of the study.

Vernalization or cold treatment (0° - 5°C) of lily bulbs to induce early flowering has been found to reduce plant ht, flower and leaf no., and leaf length (8). Bulb pre-cooling effects are also mediated through the scales themselves (9, 12). To determine if pre-cooling the scales from which the scale bulblets formed would influence subsequent bulblet development was also considered.

Materials and Methods

Commercial size 'Ace' bulbs (30-40 g planting stock) harvested in September at the Pacific Bulb Grower's Research and Development Station, Harbor, Oregon, were used to supply the scales from which scale bulblets were formed. Half of the bulbs was used immediately while the other half was stored for 6 weeks at 0°C . Mother scales were removed from these non-cooled and cooled bulbs and placed in 5-inch, square, molded fiber pots, 12 scales per pot. The scales in each pot were randomly selected so that each group of 12 contained an equal no. of both inner and outer mother scales. They were approximately the same size, turgid, and disease free. They were placed vertically in the pot so that the

proximal half of each mother scale was imbedded in the potting mixture and the distal half exposed. The potting mixture was layered so that the top inch was washed river sand and the lower 4 inches was a soil mixture of equal parts loam, sand, and sphagnum moss. This layering permitted the developing bulblets to form in the loose sand and the new roots to penetrate the soil mixture and thus sustain continued growth.

Pots of non-cooled and cooled mother scales were placed in 2 growth chambers at constant day-night temp ($27^{\circ}\text{C} \pm 2^{\circ}\text{C}$) for 2 daylength treatments (8 and 16 hr). Pots of non-cooled and cooled mother scales were also placed in 2 temp-controlled walk-in storage rooms partitioned by black plastic into 3 daylength compartments. Two constant day-night temp ($\pm 2^{\circ}\text{C}$) and 3 daylengths were used to provide the following environments:

| | |
|-----------------------------|-----------------------------|
| 12°C - 8 hr | 22°C - 8 hr |
| 12°C -12 hr | 22°C -12 hr |
| 12°C -16 hr | 22°C -16 hr |

Light in each chamber or compartment was produced by eight 40-watt, cool-white fluorescent tubes and eight 40-watt, incandescent bulbs. Light intensity in the center of the bench at pot level was 1000 ft-c, as measured with a Weston Illumination Meter-Model 756 using a quartz filter. The pots were irrigated with tap water; no fertilizer was applied.

Beginning 4 weeks after planting, the scale bulblets produced in 1 pot from each temp-daylength combination were examined weekly for 9 weeks. The bulblets were removed from the mother scales and the roots cut off. The no. of bulblets produced by the 12 mother scales and the percentage of those having scale leaves (scales with leaf blades formed on the distal end) were determined. The 10 largest bulblets were then dissected under a binocular microscope; the blades of any scale leaves were counted and removed. Growth response to the temp, light, and pre-cooling treatments was based on the no. of organs initiated and their combined fresh wt at the time of sampling. The degree of initiatory activity was evident in the total no. of organs initiated by the bulblet growing point during the period between samples. The organ counts included the no. of scales, scale leaves, and scale or leaf primordia. Scale and leaf primordia (stem leaves) could not be distinguished even microscopically, before stem or axis elongation, so were not separated in this study. Bulb yield was based on the average fresh wt of the 10 bulblets sampled.

Data were evaluated by analysis of variance. The temp-daylength interaction means (to compare the 3 daylengths at 12^o and 22^o C), temp means, and daylength means (to compare the 2 daylengths at 27^o C) were compared by Least Significant Difference

(LSD) values. The temp-daylength interaction means, the daylength means, and the corresponding LSD values for each growth response studied have been placed to the right of each individual line graph. Data for bulblets grown at 27°C were analyzed separately from those at 12°C and 22°C, because the growing environments were not identical.

Results

No. of Bulblets Produced

Significantly more bulblets were produced at 22°C than at 12°C (Table 1). Fewer bulblets formed at 27°C than at 22°C. When grown at 12°C and 27°C there was no difference in the no. of bulblets produced as a result of pre-cooling the mother scales. However, pre-cooling the mother scales increased subsequent bulblet production over those not chilled when grown at 22°C.

There was no significant effect of daylength on the no. of bulblets produced (Fig. 1 and 2).

Organ Initiation

Bulblets formed at 22°C had significantly more organs than those grown at 12°C (Table 1). At 27°C bulblets had about the same no. of organs as those grown at 22°C. At both 12°C and 22°C,

TABLE 1. Growth responses of bulblets from non-cooled and cooled mother scales to 3 temp regimes, 12^o, 22^o, and 27^o C (temp means).

| | | 12 ^o C | 22 ^o C | LSD ^y | 27 ^o C |
|----|---|-------------------|-------------------|------------------|-------------------|
| A. | No. of bulblets produced by the mother scales | | | | |
| | Non-cooled | 18.1 | 22.6 | 1.8, 2.5 | 19.0 |
| | Cooled | 17.3 | 25.4 | 1.8, 2.4 | 20.0 |
| | LSD ^z 1.6, 2.2 | | | | 1.5, 2.2 |
| B. | Average no. of organs per bulblet | | | | |
| | Non-cooled | 6.1 | 13.4 | 0.5, 0.6 | 11.4 |
| | Cooled | 5.1 | 10.7 | 0.3, 0.4 | 11.4 |
| | LSD ^z 0.4, 0.5 | | | | 0.4, 0.5 |
| C. | Percentage of bulblets produced having scale leaves | | | | |
| | Non-cooled | 46 | 38 | 10, 14 | 15 |
| | Cooled | 25 | 25 | 7, 10 | 35 |
| | LSD ^z 8, 10 | | | | 4, 6 |
| D. | Average no. of scale leaves per bulblet | | | | |
| | Non-cooled | 1.7 | 3.5 | 0.6, 0.9 | 2.9 |
| | Cooled | 1.6 | 3.5 | 0.6, 0.9 | 2.5 |
| | LSD ^z 0.4, 0.6 | | | | 0.6, 0.8 |
| E. | Average scale leaf length per bulblet (cm) | | | | |
| | Non-cooled | 2.1 | 10.5 | 0.8, 1.2 | 6.5 |
| | Cooled | 1.4 | 9.2 | 0.8, 1.1 | 5.3 |
| | LSD ^z 0.6, 0.9 | | | | 0.6, 0.8 |
| F. | Average bulblet wt (g) | | | | |
| | Non-cooled | 0.10 | 0.68 | 0.04, 0.06 | 0.55 |
| | Cooled | 0.08 | 0.49 | 0.03, 0.04 | 0.48 |
| | LSD ^z 0.03, 0.04 | | | | 0.08, 0.12 |

^yLSD_{0.05, 0.01} to compare temp within each treatment

^zLSD_{0.05, 0.01} to compare non-cooled and cooled treatments

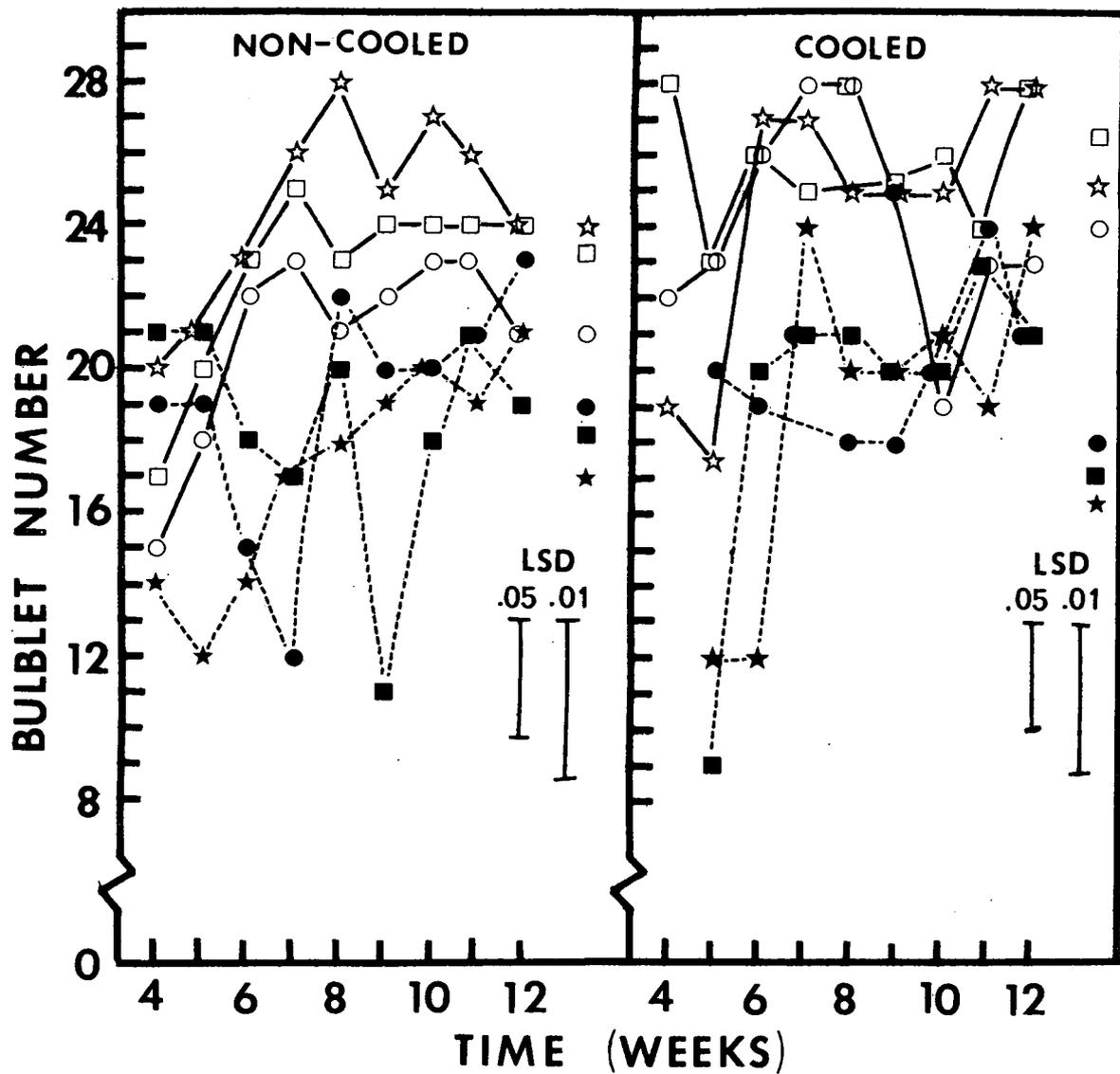


Fig. 1. Effect of temp and daylength on the no. of bulblets produced by the non-cooled and cooled mother scales at 12°C (-----, solid symbols) and 22°C (—, open symbols) and at 8 hr (★, ☆), 12 hr (■, □), and 16 hr (●, ○) daylengths.

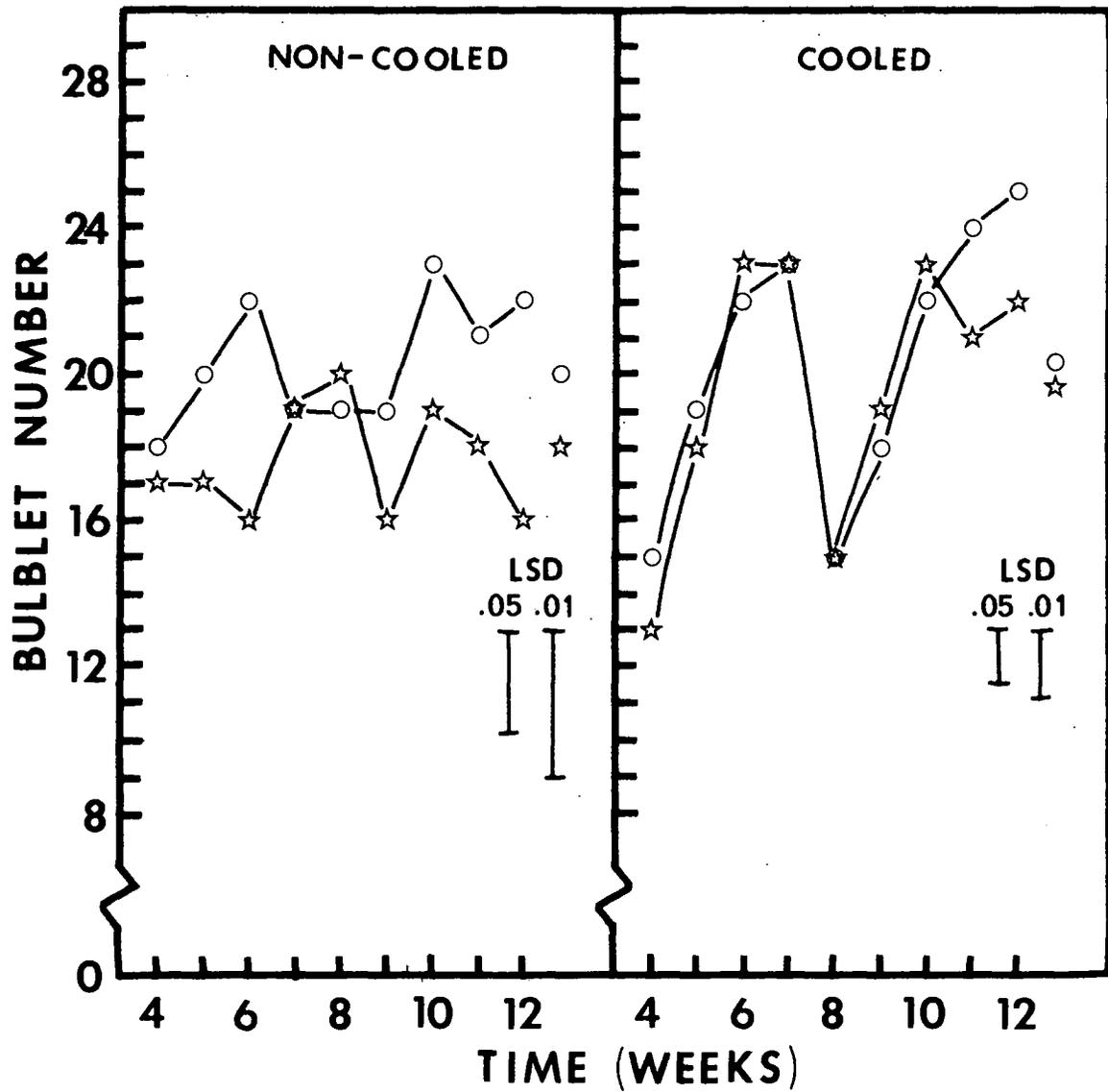


Fig. 2. Effect of daylength on the no. of bulblets produced by the non-cooled and cooled mother scales at 27°C and at 8 hr (☆) and 16 hr (○) daylengths.

cooling the mother scales significantly reduced the no. of organs per bulblet. At 27°C, however, there was no difference in organ no. attributable to the cooling of the mother scales.

Daylength influenced the no. of organs in bulblets grown at 12°C and 22°C (Fig. 3). At 12°C bulblets produced significantly more organs under 16 hr than 8 hr days. At 22°C, daylength had a significant effect on the no. of organs only if the mother scales had been previously cooled. Short days (8 hr) favored organ initiation in these bulblets. The 12 hr day had an intermediate effect on organ initiation as compared with 8 hr and 16 hr daylengths. There was no evidence of a daylength effect on organ no. when bulblets were grown at 27°C (Fig. 4).

Percentage of Bulblets with Scale Leaves

There was no significant difference in the percentage of bulblets with scale leaves between 12°C and 22°C environments (Table 1). At 27°C the percentage of bulblets with scale leaves from non-cooled mother scales was less than at 22°C, but if the mother scales had been precooled, the percentage of bulblets with scale leaves was greater than at 22°C. Temp did, however, affect when scale leaves were formed (Fig. 5 and 6). The bulblet scales formed scale leaves by the 6th, 8th, and 10th weeks when grown

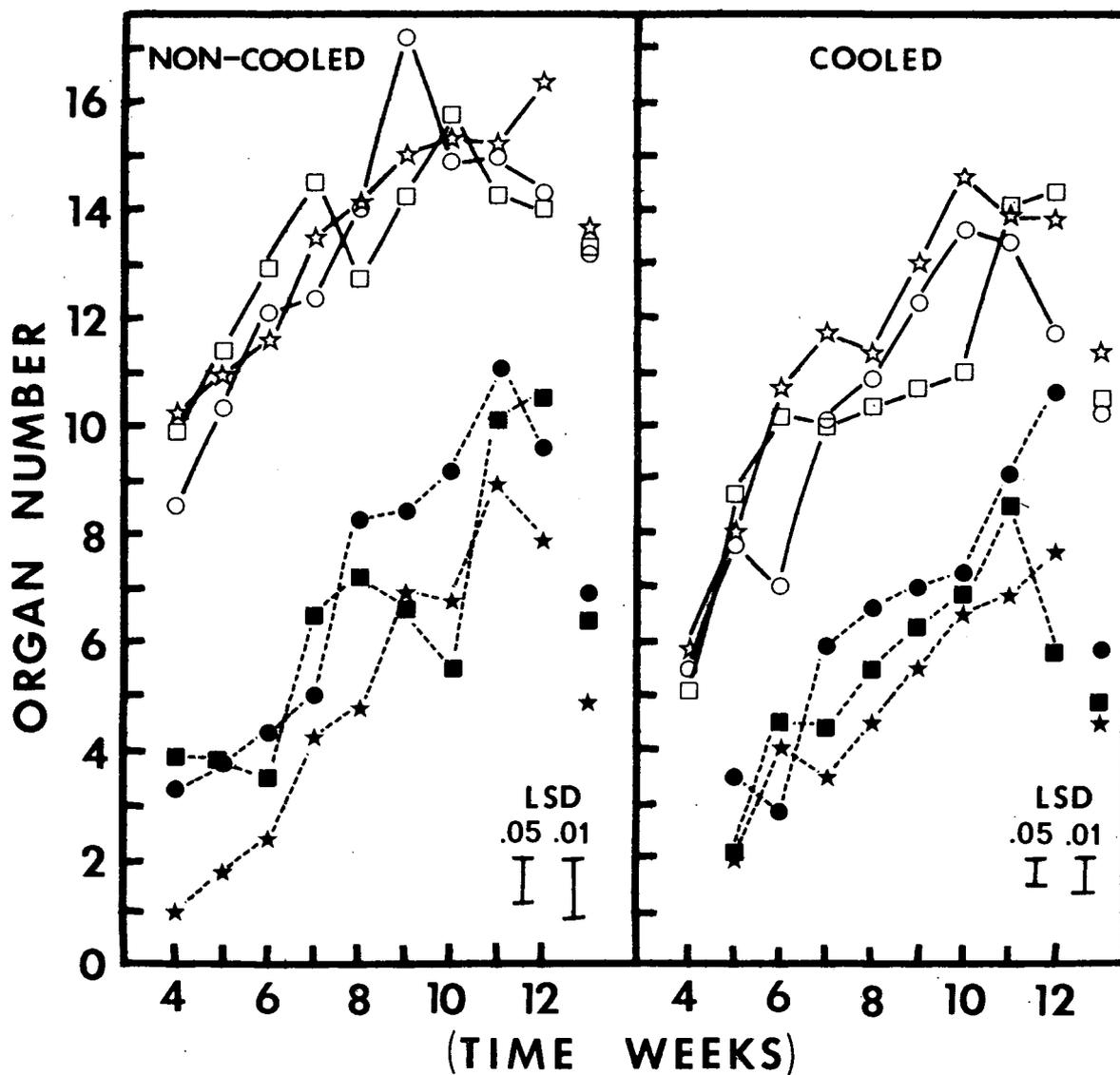


Fig. 3. Effect of temp and daylength on the average no. of organs initiated in bulblets produced by the non-cooled and cooled mother scales at 12°C (-----, solid symbols) and 22°C (—, open symbols) and at 8 hr (★, ☆), 12 hr (■, □) and 16 hr (●, ○) daylengths.

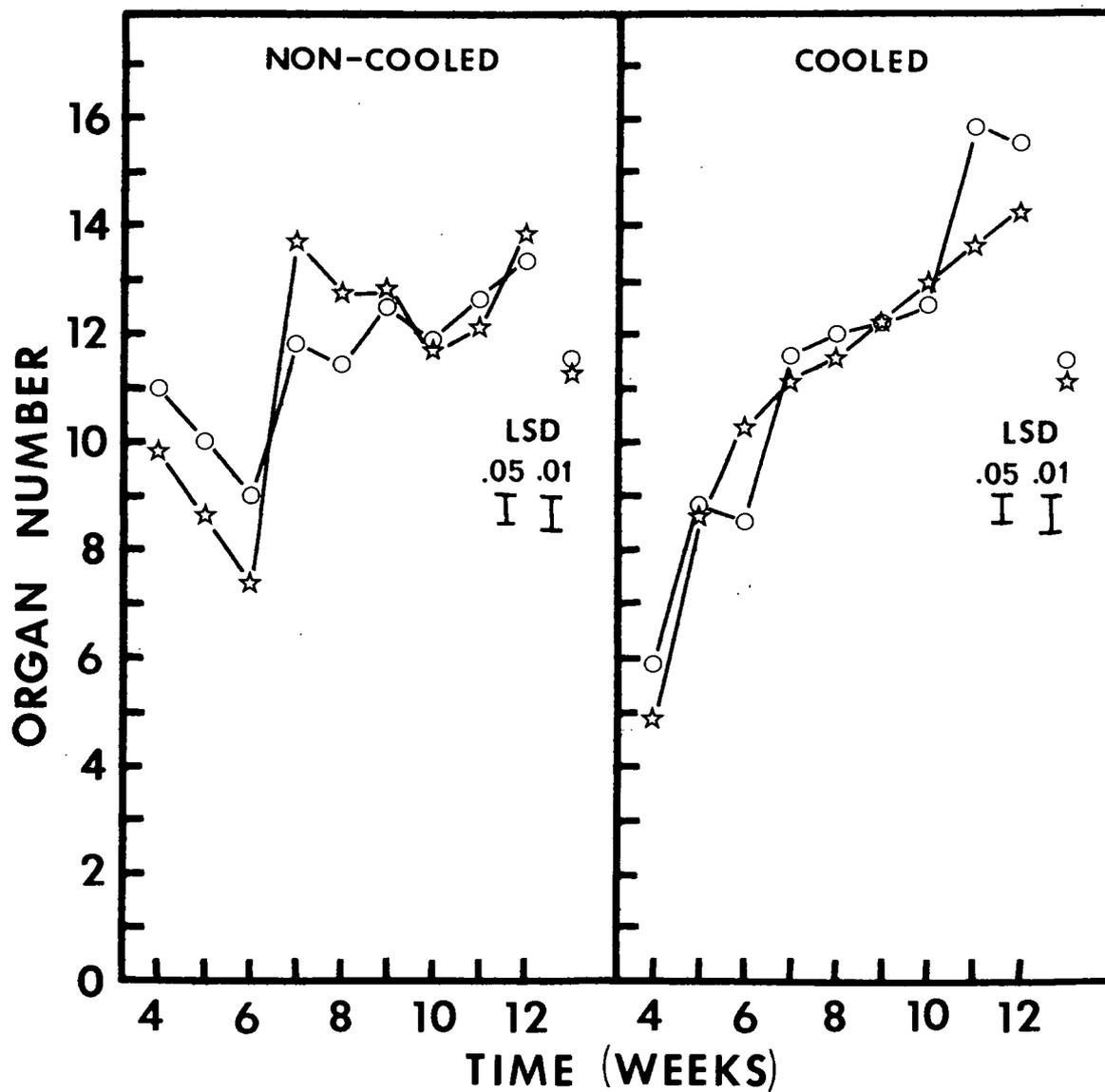


Fig. 4. Effect of daylength on the average no. of organs initiated in bulblets produced by the non-cooled and cooled mother scales at 27°C and at 8 hr (☆) and 16 hr (○) daylengths.

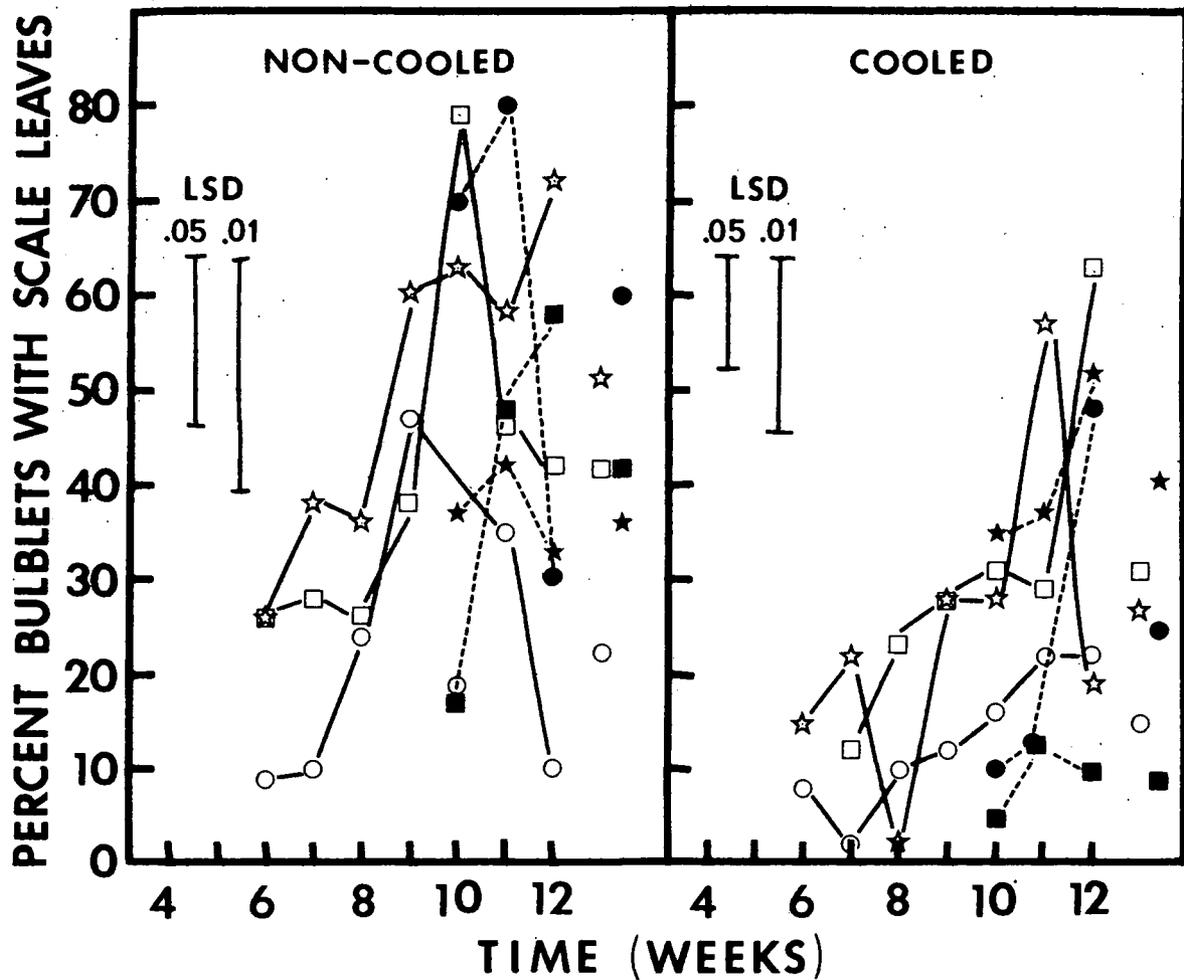


Fig 5. Effect of temp and daylength on the percentage of the bulblets produced by the non-cooled and cooled mother scales having scale leaves at 12°C (-----, solid symbols) and 22°C (——, open symbols) and at 8 hr (★, ☆), 12 hr (■, □), and 16 hr (●, ○) daylengths.

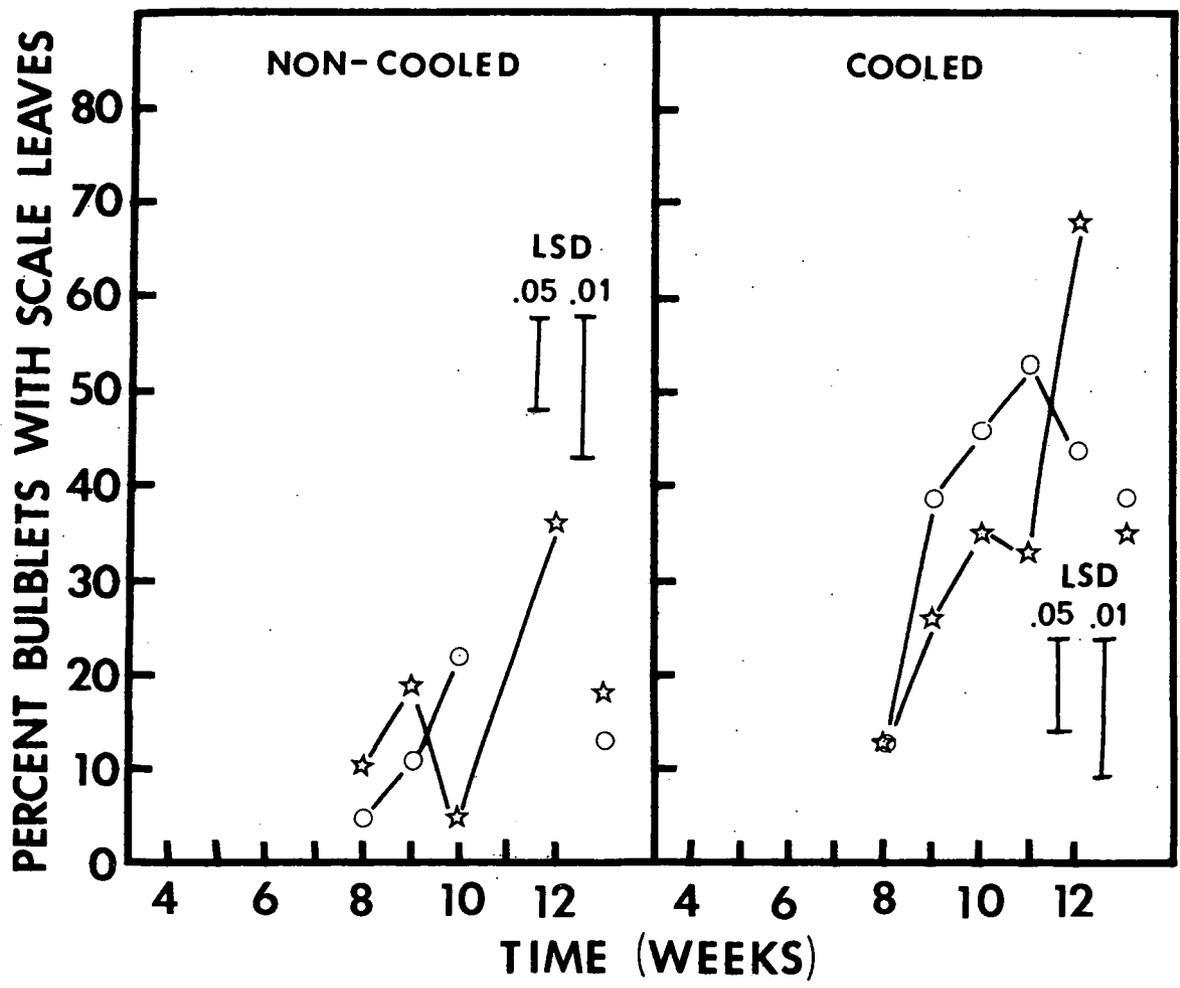


Fig. 6. Effect of daylength on the percentage of the bulblets produced by the non-cooled and cooled mother scales having scale leaves at 27°C and at 8 hr (☆) and 16 hr (○) daylengths.

at 22^o, 27^o, and 12^oC, respectively.

Cooling the mother scales prior to planting significantly reduced the no. of bulblets with scale leaves when grown at both 12^o and 22^oC (Table 1). At 27^oC, cooling the mother scales significantly increased the percentage of bulblets with scale leaves.

Daylength significantly influenced the percentage of bulblets with scale leaves at 12^o and 22^oC (Fig. 5). At 22^oC more bulblets with scale leaves were produced under 8 and 12 hr days than under a 16 hr day. At the lower temp (12^oC) non-cooled mother scales produced more bulblets with scale leaves at 16 hr than at 12 or 8 hr daylengths, and if the mother scales had been cooled before planting, there were more bulblets with scale leaves at 8 hr than at 16 hr and more at 16 hr than at 12 hr. At 27^oC there were no differences in the no. of bulblets with scale leaves that could be attributed to daylength (Fig. 6).

No. and Length of Scale Leaves Per Bulblet

Only temp affected the no. of scale leaves per bulblet (Table 1). Bulblets at 22^oC had significantly more scale leaves than did bulblets at 12^oC. Bulblets at 27^o had fewer scale leaves than did bulblets at 22^oC. Neither daylength (Fig. 7 and 8), nor cooling the mother scales (Table 1) affected the no. of scale leaves

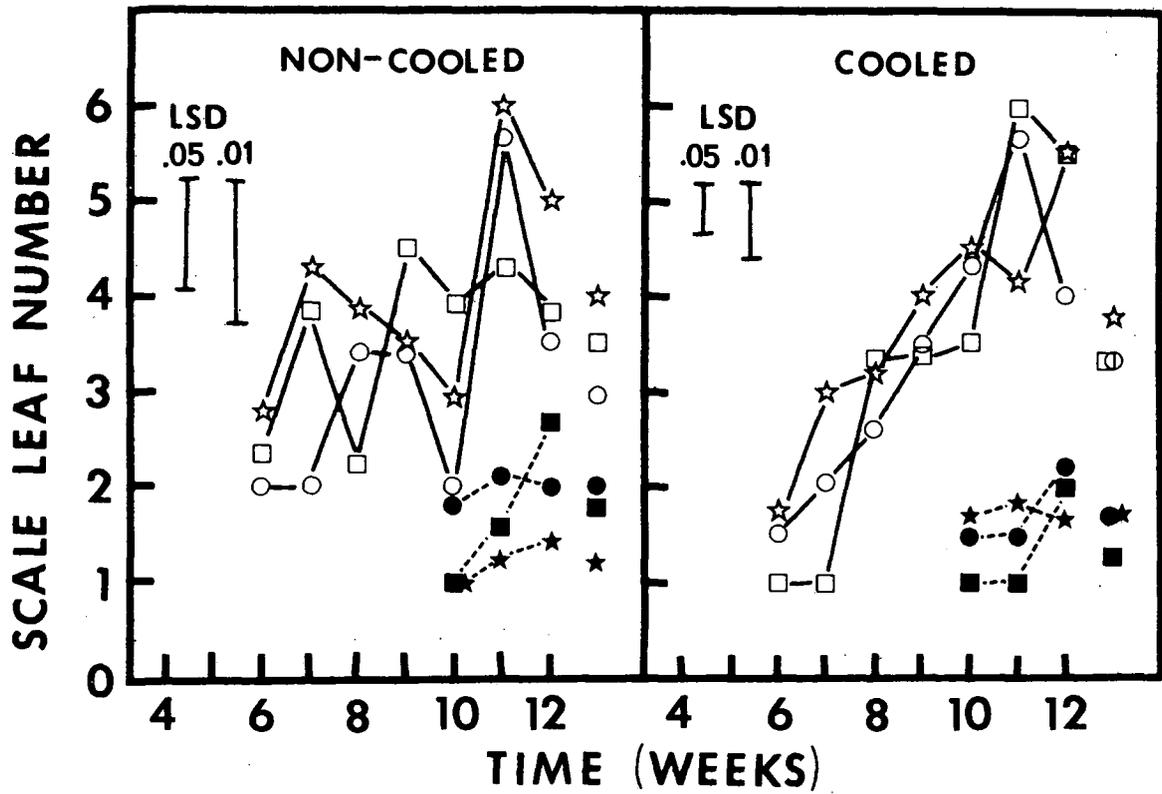


Fig. 7. Effect of temp and daylength on the average no. of scale leaves per bulblet produced by the non-cooled and cooled mother scales at 12°C (-----, solid symbols) and 22°C (—, open symbols) and at 8 hr (★, ☆), 12 hr (■, □), and 16 hr (●, ○) daylengths.

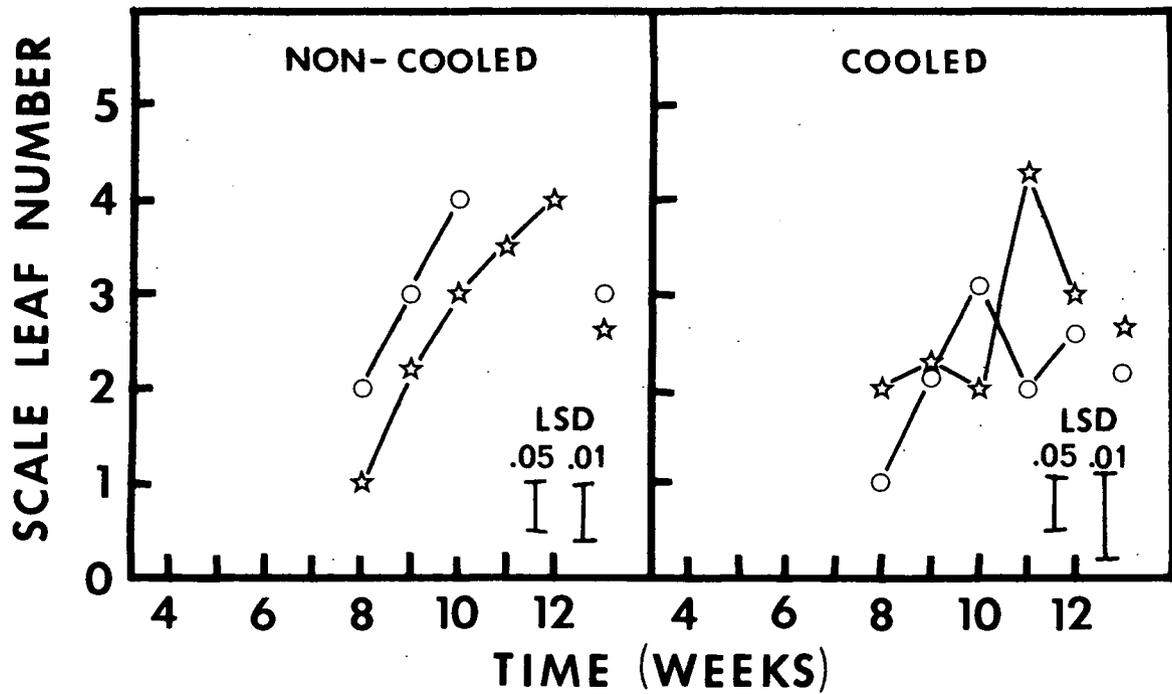


Fig. 8. Effect of daylength on the average no. of scale leaves per bulblet produced by the non-cooled and cooled mother scales at 27°C and at 8 hr (☆) and 16 hr (O) daylengths.

per bulblet.

In contrast to the above, temp, daylength, and cooling of the mother scales influenced scale leaf length. Scale leaf length was greatest at 22°C, followed by 27°C, and lastly by 12°C (Table 1). Cooling the mother scales resulted in significantly shorter scale leaves on resulting bulblets at all growing temp.

Scale leaf length was influenced by daylength only in bulblets produced by the non-cooled mother scales (Fig. 9 and 10). At 22°C the bulblets had progressively shorter scale leaves with increasing daylength. Grown at 12°C, daylength had the reverse effect with the 16 hr day producing the longest scale leaves.

Bulblet wt

The wt of the scale bulblets was significantly greater at 22°C than at 12°C without further increase at 27°C (Table 1). Cooling the mother scales reduced bulblet wt only at the 22°C growing temp.

Daylength significantly influenced the wt of only those bulblets grown at 22°C and produced from non-cooled mother scales (Fig. 11 and 12). The wt of the bulblets increased progressively from 8 to 12 to 16 hr daylengths.

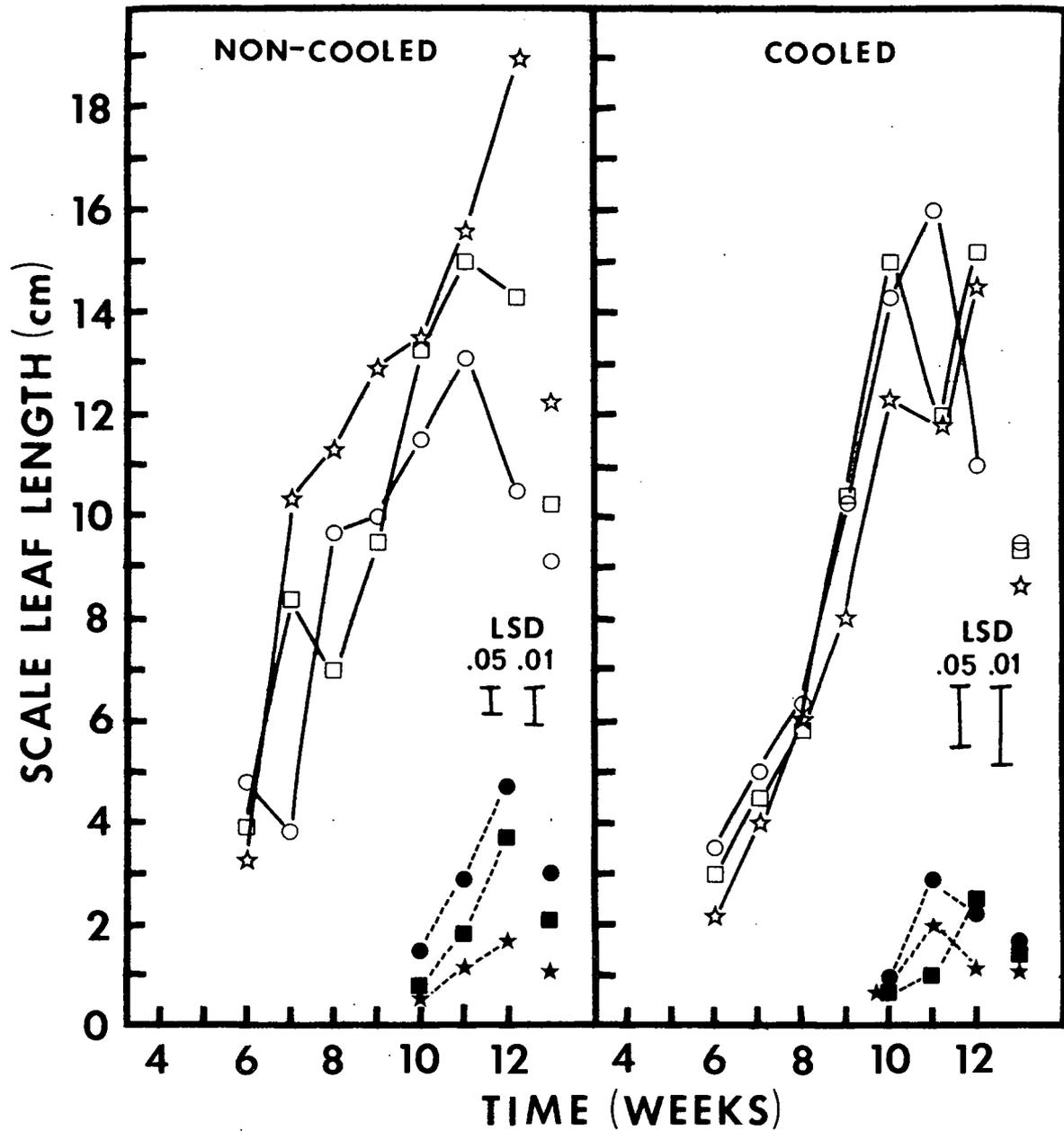


Fig. 9. Effect of temp and daylength on the average scale leaf length per bulblet produced by the non-cooled and cooled mother scales at 12°C (-----, solid symbols) and 22°C (—, open symbols) and at 8 hr (★, ☆), 12 hr (■, □), and 16 hr (●, ○) daylengths.

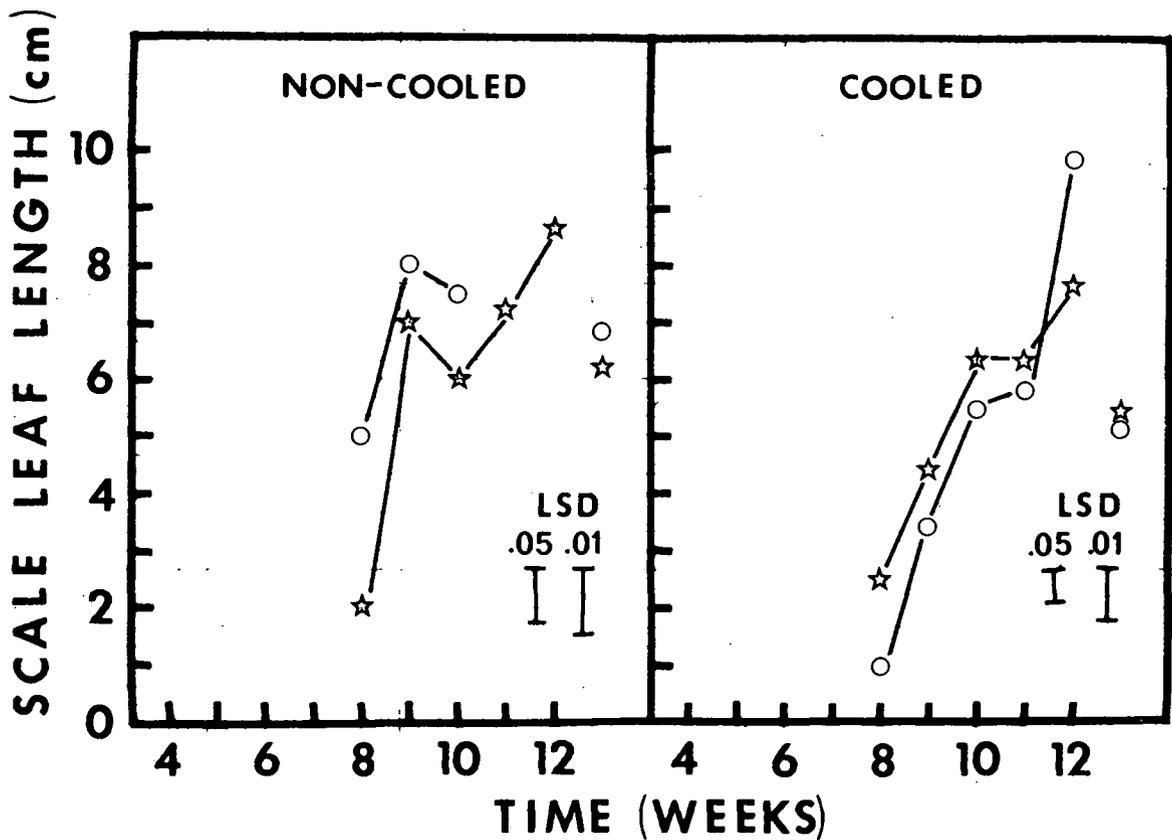


Fig. 10. Effect of daylength on the average scale leaf length per bulblet produced by the non-cooled and cooled mother scales at 27°C and at 8 hr (☆) and 16 hr (○) daylength.

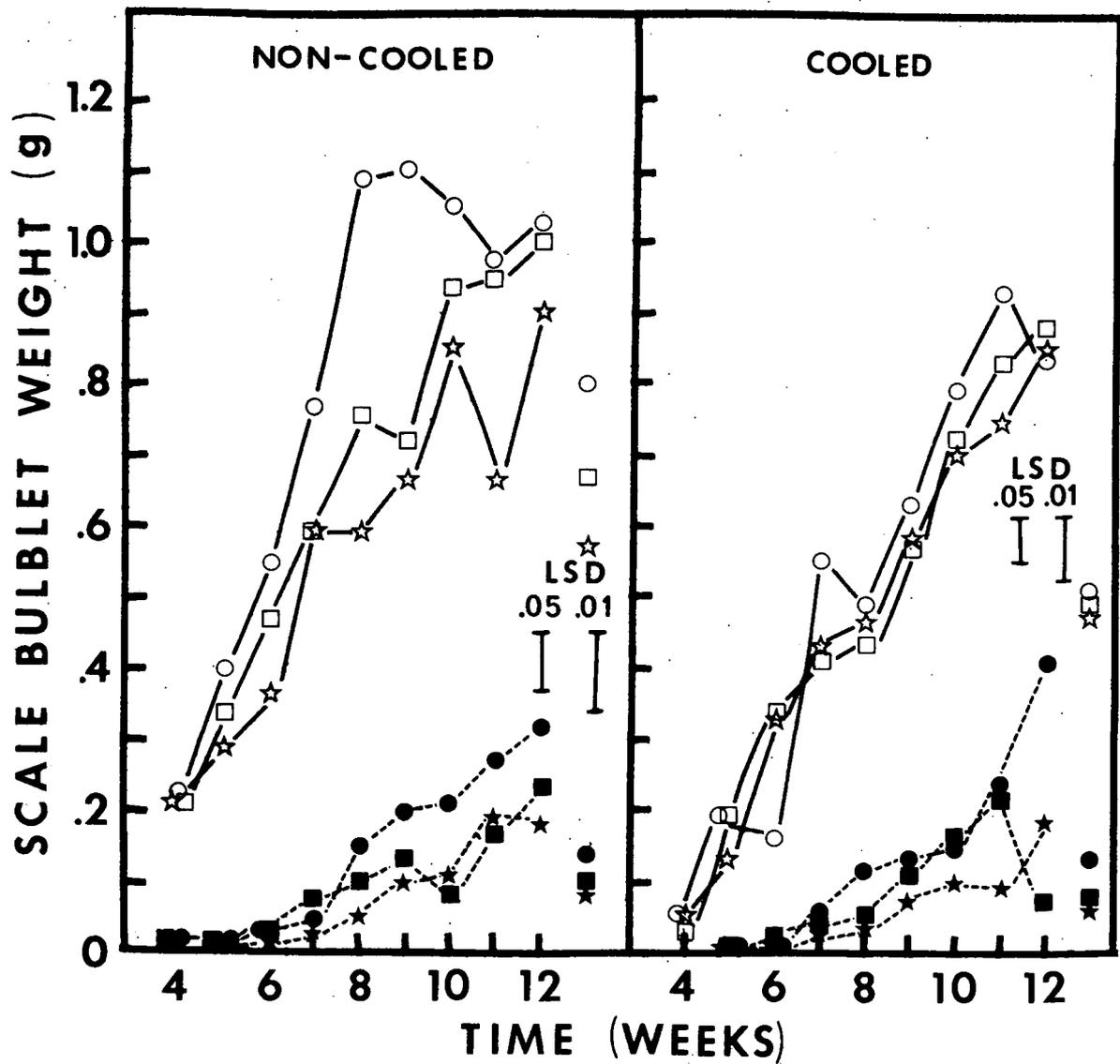


Fig. 11. Effect of temp and daylength on the average wt of scale bulblets produced by the non-cooled and cooled mother scales at 12°C (-----, solid symbols) and 22°C (——, open symbols) and at 8 hr (★, ☆), 12 hr (■, □), and 16 hr (●, ○) daylengths.

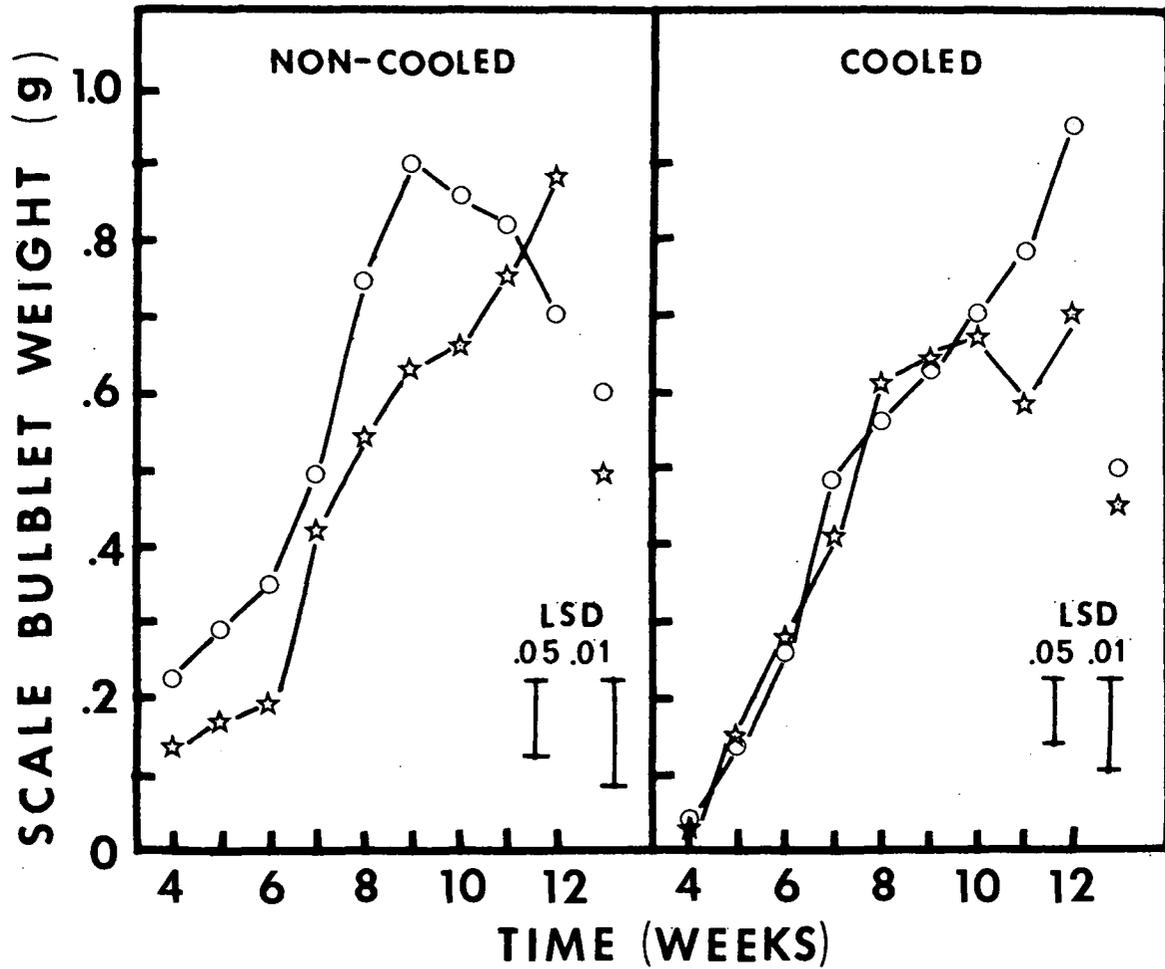


Fig. 12. Effect of daylength on the average wt of scale bulblets produced by the non-cooled and cooled mother scales at 27°C and at 8 hr (☆) and 16 hr (○) daylengths.

Discussion

Although there were some responses to daylength in these studies of the young, vegetative plants, and even interactions between temp and daylength, temp appears to play the principal role in the initiation and development of vegetative organs. Of the plant responses studied, only the percentage of bulblets with scale leaves appeared insensitive to the range of temp used (12° to 27°C). The 10°C increase in temp used (from 12° to 22°C) nearly always doubled plant growth response. In the separate but comparable experiment, increasing the temp another 5°C (from 22° to 27°C) seldom increased growth and more frequently reduced it. These data suggest that vegetative growth and development of the L. longiflorum scale bulblet is near optimum at 22°C at the light values used (1000 ft-c). Hartley (8) stored Easter lilies at temp from 30° to 80°F (-1° to 26.5°C) and found 60°F (15.5°C) to be optimum for leaf initiation. Wilkins and Roh (13) have recently shown the growth rate of lilies during forcing to be maximal from 60° to 70°F (15.5° to 21.5°C).

Bulblet growth responses to daylength are difficult to interpret in this study because they were not consistent or of sufficient magnitude. When responses did occur, they were minor

compared to those for temp. Even though the partially exposed mother scales might have been able to respond to daylength effects, it is more likely that those bulblets which formed scale leaves at an early stage would be more apt to respond to the influence of light. Since those bulblets grown at 22°C were first to form scale leaves, the early presence of scale leaves in addition to the apparent optimal growing temp may explain the larger bulblets produced at 22°C.

Since Lin (9) and Wang (12) had shown that bulb pre-cooling effects were mediated in great measure through the scales themselves, a possible carryover effect of chilling the mother scales on the developing bulblets was given consideration. Only the no. of scale leaves formed per bulblet was not affected by cooling the mother scales. In general, cooling the mother scales reduced responses to the other factors studied, and the differences between non-cooled and cooled treatments were more pronounced at 22°C than at 12°C or 27°C.

It was also apparent that the 0°C-5°C temp optimum (storage) for flower induction in L. longiflorum was not conducive to max vegetative growth responses, since this cooling significantly reduced bulblet development. This observation is interesting in light of the fact that vernalization or cold treatment of lily bulbs

to induce early flowering has been found to reduce plant ht, leaf, and flower no., and leaf length (8). These as well as bulblet development are vegetative growth responses.

The formation of scale leaves in lily bulblets is an interesting phenomenon in their developmental sequence. Walker (11) reported that the inner primordia of bulblets on mother scales planted near the soil surface continue to grow in length and become green and leaf-like, whereas the primordia of bulblets developing on scales planted 2-3 inches below the surface remain scale-like. Depth of planting and exposure to light, therefore appear to have a bearing on scale leaf formation. In general, scale leaves formed most readily at high temp (22°C) and under short days (8 hr).

Blaney and Roberts (2) and Roberts et al. (10) have reported that scale initiation and bulb wt increases are relatively constant during the growing season regardless of seasonal temp fluctuations. These results show, however, that a 10°C difference in temp (from 12° to 22°C) can produce a considerable difference in scale (or organ) no. and bulblet wt. These results suggest that warm growing seasons favor larger bulbs.

It was evident in this study that scale no. was not directly correlated to bulb wt. The largest bulblets were those grown at 22°C because they weighed more and had the most scales. However,

at this near optimum temp the non-cooled mother scales produced bulblets with the same no. of organs regardless of daylength, but there were differences in bulblet wt. Conversely, in bulblets from cooled mother scales, there was a difference in organ no. due to daylength but no difference in the wt of the bulblets. This suggests that both scale no. and wt contribute to the ultimate size of the bulb.

A purpose of this study was to determine if Easter lily scale bulblets have a bulbling response to temp and daylength similar to that for onions (induced by long days) and potatoes (induced by low temp). It appears that Easter lily bulblet formation and development is a gradual process which proceeds at a fairly constant rate that is reflective of prevailing temp, which during much of the growing season on the Oregon coast are below optimum. Onion bulb and potato tuber formation, on the other hand, are sudden occurrences. Since scale bulblets did form at all temp and daylengths in this study, it can be concluded that there is no critical temp or daylength requirement for bulbing in lily. This would account for the continuous increase in bulb size that occurs over a wide range of temp and daylengths in nature.

Some preliminary research using Easter lily seedlings, scale bulblets from mother scales which had been completely covered by the potting mixture, and the same temp-daylength combinations

as in the study was also done. Organ initiation and wt increases were similar to those described in this study. The only remarkable difference occurred in the scale bulblets from covered mother scales. They produced substantially fewer bulblets with scale leaves than did those bulblets from mother scales which had been exposed to light.

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