AN ABSTRACT OF THE THESIS OF

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Title: Studies on Development and Flowering of *Lilium longiflorum* Thunb.

Abstract Approved: L. T. Blaney

Studies were made on 'Ace' and 'Croft' Easter lilies, *Lilium longiflorum* Thunb., to determine (1) the interactions between date of harvest and bulb storage temperatures upon growth and flowering, and (2) the effects of duration of vernalization upon leaf numbers and rate of leaf unfolding for the purpose of developing a more reliable method for timing lilies. The effects of scale removal upon growth and flowering of 'Nellie White' lilies were also studied.

The days to sprout of 'Ace' and 'Croft' bulbs, harvested monthly from February to October and given no storage, ranged from about 7 months to 2 weeks, but on a calendar date basis the earliest harvests sprouted in mid-September, the late harvests in mid-November, a range of only 2 months. This indicated that the acquisition of the ability to start another growth cycle was in phase with the changing season. Cold storage (6 weeks at 40° F), which did not hasten sprouting of February and October bulbs, accelerated greatly the

April bulbs. Warm storage (6 weeks at 70° F) accelerated sprouting of February bulbs by more than 4 months compared to no storage of these bulbs, but had no effect on October bulbs. Cold storage, which did not vernalize February bulbs, became more and more effective as the season progressed. Warm storage apparently vernalized February and March bulbs because they flowered quickly at low leaf numbers, but by April it did not vernalize and early flowering was not stimulated. These observations are discussed in terms of causes of summer-sprouting and adaptation of these cultivars to the Pacific Northwest.

Calculated growth rate curves, in terms of leaves unfolded per day for each storage treatment, were similar in shape but differed in magnitude. Leaf unfolding was slow for February bulbs, decreased to a minimum for April bulbs, and rapidly increased to a maximum with the August and later bulbs. Compared to the effects of no storage, cold storage retarded the February to May bulbs and accelerated bulbs harvested after May, while warm storage always accelerated the rate compared to no storage.

Days to emerge, leaf numbers, days to flower, numbers of flower buds, and stem lengths of 'Ace' and 'Croft' were generally inversely related to bulb storage durations of 0 to 18 weeks at 40° F, but the first 3 to 4 weeks of storage reduced all these plant characters the most. After storage for 6 weeks at 40° F, these cultivars

had formed flower buds about 6 weeks after potting, 3 weeks after emergence, at an average leaf number of 82. Leaves were unfolded at a fairly steady rate of about 1.31 to 1.35 per day. The application to timing of lilies is discussed.

Varying degrees of scale removal, ranging from 0 to 100% removal, on 'Nellie White' bulbs suggested that scales perform several physiological roles. The daughter scales, that is the young inner scales, appeared to be the seat of bulb dormancy because their removal greatly accelerated sprouting. Scale removal, especially of daughter scales, significantly reduced the number of leaves below the first flower, suggesting that the scales are inhibitory to the onset of flower bud initiation. But the number of flower buds initiated and the rates of growth were inversely proportional to the degree of scale removal.

Studies on Development and Flowering of *Lilium longiflorum* Thunb.

by

Peggy Pei-Chi Lin

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Studies on Development and Flowering of
Lilium longiflorum Thunb.

GENERAL INTRODUCTION

The Easter lily, *Lilium longiflorum* Thunb., aside from being an important horticultural specialty crop in Oregon, is a fascinating research plant. It is a perennial geophyte whose bulbs, large underground buds, remember their temperature histories so that later dramatically dissimilar plants develop from apparently similar bulbs. Horticulturists exploit these temperature responses by subjecting the bulbs to storage treatments that more or less program them to flower on the variable dates of Easter. Since the earliest Easter falls on March 21 and the latest on April 25, it can be readily understood that much skill is needed in the precise timing of the crop.

Most research on Easter lilies has concerned itself with bulb storage and greenhouse forcing as they relate to flowering, bulb handling, soils and fertilizers, watering, light and height control, timing, and insect and disease control. These were reviewed in 1967 by a number of authorities in the Easter lily handbook prepared for the New York and Ohio Lily Schools (Kiplinger and Langhans, eds., 1967). The influence of short-term and long-term seasonal weather factors and physiological changes associated with these as related to such phenomena as summer-sprouting, crop size, maturity, dormancy, flowering potential, response to vernalization, and greenhouse forcing performance (timing, flower production, plant conformation, etc.) have been vaguely recognized and hinted at.

Naturally, Oregon workers have been concerned with these latter facets of lily horticulture and physiology because of the importance of Easter lily bulb production in the Northwest. Almost all of the bulbs are sold to greenhouse growers in other parts of the United States for forcing into bloom at Easter.

This dissertation reports on and discusses three related Easter lily problems. First, the interactions between date of harvest and bulb storage temperatures were studied. This was done primarily to throw more light on the problems of summer sprouting, dormancy, maturity, and induction of flowering. A bonus from the experimental results was the gaining of more insight into Easter lily crop adaptation. Secondly, the roles of duration of vernalization upon leaf numbers and rate of leaf unfolding were studied in order to gain a firmer foundation for a Leaf Remainder Method for timing lilies proposed earlier by Blaney, Roberts and Lin (1967). Thirdly, the effects of scale removal upon growth and flowering were studied.

GENERAL REVIEW OF LITERATURE

The growth of a plant can be divided into vegetative and reproductive phases. Genetic characteristics and environmental factors, especially photoperiod and temperature, play dominant roles in the onset of the latter phase. Chouard (1960) stated that Kilppart found in 1857 that cold induced winter cereals to flower in spring. And Gassner in 1918 extended our understanding by showing that biennials also have a cold requirement for flowering. Lyssenko coined in 1928 the term 'jarovization', 'vernalization' in English, to describe the flower inducing effects of cold temperature treatment on seeds of winter cereals. Chouard (1960) emphasized that processes preparatory to flowering occur during vernalization and not flower initiation itself, therefore, vernalization is an inductive process because flower initiation occurs later. Povar (1959) has also applied the term to describe the flowering and yield responses of wheat to warm temperature treatment, but his paper does not convince that warmth truly acted to vernalize.

Vernalization either induces flower bud formation or promotes flowering in plants. In the first case, no reproductive growth is approached unless sufficient cold is given, such as in biennial plants and the Easter lily; in the second, the time required for flowering is shortened.

Some three decades ago several workers (Shippy, 1937; Brierley, 1941a, 1941b; Brierley and Curtis, 1942; Stuart, 1943, 1946a, 1946b, 1946c, 1949, 1953a, 1953b, 1954, 1957; Blaney, Hartley, and Roberts, 1963; Hartley, Blaney, and Roberts, 1965; Merritt, 1963; Miller and Kiplinger, 1963, 1966a, 1966b) reported that cold storage accelerated flowering of Easter lilies and suggested that this was a vernalization effect, and Smith reactivated this concept (1963). The commercial practices of precooling bulbs to assure flowering at Easter were largely based on the work of U.S.D.A. workers, among whom Stuart was most productive. As early as 1943, Stuart reported that 45° to 50° F storage for up to 4 to 6 weeks was best for early flowering of the 'Croft' lily, at that time the principal commercial cultivar in the Northwest. Langhans and Weiler (1967) from their review of the literature concluded that temperatures of 35°-40° F were the best vernalization temperatures for west coast cultivars and 45°-50° F for southern cultivars. Weiler and Langhans (1967) have reported 70° F to be the upper temperature limit for vernalization.

Several authors (Hartley, Blaney and Roberts, 1965; Miller, Kiplinger and Tayama, 1964; Miller and Kofranek, 1966) have suggested that soil temperatures in the field should affect the forcing of the greenhouse lily, but they have no experimental evidence. Blaney and Roberts (in press) kept the soil in a field plot from

July to mid-September at 70° - 75° F and found that this did not appreciably affect the response to vernalization of bulbs growing in the warmed soil. They earlier implicated seasonal temperature patterns as responsible for summer-sprouting (Roberts, Blaney and Garren, 1955). Miller and Kiplinger (1966a, 1966b) have conducted devernalization experiments to erase assumed vernalization of the bulbs acquired before they were dug in the fall.

Timing of Easter lilies is one of the most important of the many activities involved in having plants in flower at Easter. Kiplinger (1967) recently reviewed a great body of literature bearing on this. Weiler and Langhans (1967) summarized his remarks and wrote in the same handbook,

> Many factors cause forcing variability in the lily crop: variability in the date of Easter each year, soil temperatures in the bulb fields, the date of bulb digging, conditions during handling, temperatures in transit and storage or natural cooling, duration of storage or natural cooling, moisture content of the bulb packing medium, storage atmosphere, and greenhouse forcing practices.
>
> After cool storage, the major factor influencing the time from planting to flowering is forcing temperature. Both night and day temperatures are influential, but night temperature has the greatest effect. Higher forcing temperatures cause faster flowering. For normally cooled northwest bulbs, greenhouse temperatures of 60° F at night and 60° -80° F during the day results in plants forcing 120 days after planting.
>
> Flowering is sometimes hastened under long daylength conditions obtained with supplemental, low intensity light, but the plants are taller.
>
> During the later stage of forcing, measurement of flower bud size can be used to determine the optimum forcing temperature for timing the Easter crop.

A Leaf Remainder Method for timing lilies, based upon the rate at which leaves unfolded on plants with predictable leaf numbers, has been proposed (Blaney, Roberts and Lin, 1967).

Scales have recently been shown to be important in the flowering of Dutch iris (Rodrigues Pereira, 1962, 1964) and Star-of-Bethlehem (Halaban, Galun and Halevy, 1965). The role of scales in the physiology of the Easter lily have largely been ignored. Yet growers accept as a truism that loss of scales is harmful to flowering and general forcing performance. Scale removal was reported to be harmful to the speed of flowering (Post, 1941; White, 1940). But these early studies left many questions unanswered.

GENERAL MATERIALS AND METHODS

'Ace', 'Croft' and 'Nellie White' lily bulbs, grown on the Pacific Bulb Growers' Research and Development Station, Harbor, Oregon, were used in these experiments. Commercial cultural practices of the area were followed in growing the bulbs. Except for Experiment I, the bulbs were harvested September 7-10, 1966, and shed stored in open boxes for about 10 days at Harbor before being brought to the laboratory at Corvallis. The bulbs were packed in sawdust before shipment to prevent bruising. Immediately upon arrival, they were weight graded, and prepared for the experimental treatments outlined below. Their weights ranged from 85-125 g, approximately 7-8 inch sizes.

Stored bulbs were placed in sealed polyethylene bags with one gram peat (about 52% moisture content) per five grams of bulb at either 40° F or 70° F for the durations outlined in the presentation of the individual experiments; nonstored bulbs were potted immediately in 6-inch clay pots in well-composted soil. The pots were randomly distributed on benches in a greenhouse maintained at 60° F night and 70° F day minimum temperatures and grown to flowering. When most of the bulbs in a treatment had emerged, a 1% Standard Colorado Mixture (1.5 lb ammonium nitrate, 1 lb potassium chloride, 0.5 lb magnesium sulfate, 0.5 oz iron chelate, 0.5 oz manganese sulfate, 0.25 oz Borax) was applied to the soil with a fertilizer injector three times a week throughout the growing season.

Dates of shoot emergence and opening of first bloom, number of leaves per stem below the lowermost flower, number of flower buds per plant, and plant height above the soil were recorded. Recording of these data terminated each experiment. Treatments peculiar to individual experiments are described in the presentation of experimental results for that experiment.

Analysis of variance within and among treatments was calculated by using F-distribution and t-test to determine least significant difference in all treatments.

RESULTS AND DISCUSSION

Experiment I. Effect of Date of Bulb Harvest and Storage upon Growth and Development of 'Croft' Lilies

This experiment was suggested by a number of observations of plant responses in the field and in the greenhouse. The widespread occurrence of summer-sprouting some years has been attributed to seasonal temperature conditions (Roberts, Blaney and Garren, 1955). Greenhouse grown plants also summer sprout if they stand long enough in the greenhouse. The daughter bulbs of these plants, unlike those in the field, have never experienced low temperatures. Furthermore, plants of 'Ace' and 'Croft' in the field growing in soil warmed from April to July (before bloom) were all summer-sprouted at harvest in September (Blaney and Roberts, in press). No control bulbs nor those warmed from July to September (after bloom) were sprouted. In later experiments (Blaney and Roberts, unpublished data), the field soil was warmed for successive 3-month periods starting at monthly intervals in February and so on to July and terminating in May and so on to October. At the end of each warming period bulbs were harvested from the warmed and control plots beginning May and so on to October. Half of the bulbs were repotted in a greenhouse immediately and half were stored 6 weeks at 40° F and then repotted. Briefly, bulbs from plots warmed during the late winter and early spring sprouted quickly and flowered early at low leaf numbers without any vernalizing storage. The sprout and flower inducing effects of warm soil gradually disappeared with later soil warming periods until those warmed in the summer and fall behaved like those from unheated soil.

The foregoing observations and experimental results suggested that the response of lilies to cold and to warm temperatures varied according to the stage of development of the bulb at the time they experienced the temperature. The experiment reported here, therefore, was done to study the effects of storage temperatures and date of bulb harvest, that is, the stage of bulb development.

Thirty 'Croft' lily bulbs were harvested at monthly intervals from mid-February to mid-October, 1966. At harvest the bulbs were divided into three treatment lots of 10 each. The bulbs were either potted without any storage or were stored for 6 weeks at 40° F or at 70° F. At potting each 10-bulb lot was subdivided into two 5-bulb replicates.

Table 1 shows the average weight of the bulbs at each harvest date. During the spring months the bulbs did not increase in weight, but from June to October their weight increased rapidly. In the field flower initiation occurs in late February and early March, all leaves are expanded by May, flowering occurs in July, and the shoots are senescing in late September and October (Blaney and Roberts, 1966).

Table 1. Average weight in grams of bulbs at harvest.

Date	Weight	Date	Weight
Feb. 21	45.7	July 19	79.7
Mar. 16	42.3	Aug. 19	121.9
Apr. 13	41.5	Sept. 18	140.1
May 18	42.3	Oct. 16	134.0
June 20	61.5		

Days to Emerge

Figures 1-1(A), 1-1(B) and 1-3(A) present families of curves for days to emerge; Appendix Ia presents the results in tabular form. In general, the later the bulbs were harvested the more quickly they sprouted in the greenhouse (Fig. 1-1(A)). The curve for non-stored bulbs was quite smooth but those for stored bulbs were much more irregular. Cold storage in February and October acted much like no storage, but from February to April it rapidly accelerated sprouting. With the May and June harvests, cold storage retarded sprouting considerably compared with its effects the preceding month and the succeeding months. Warm storage in February, however, accelerated sprouting. It became less accelerating with later harvests until by October its effect was like no storage.

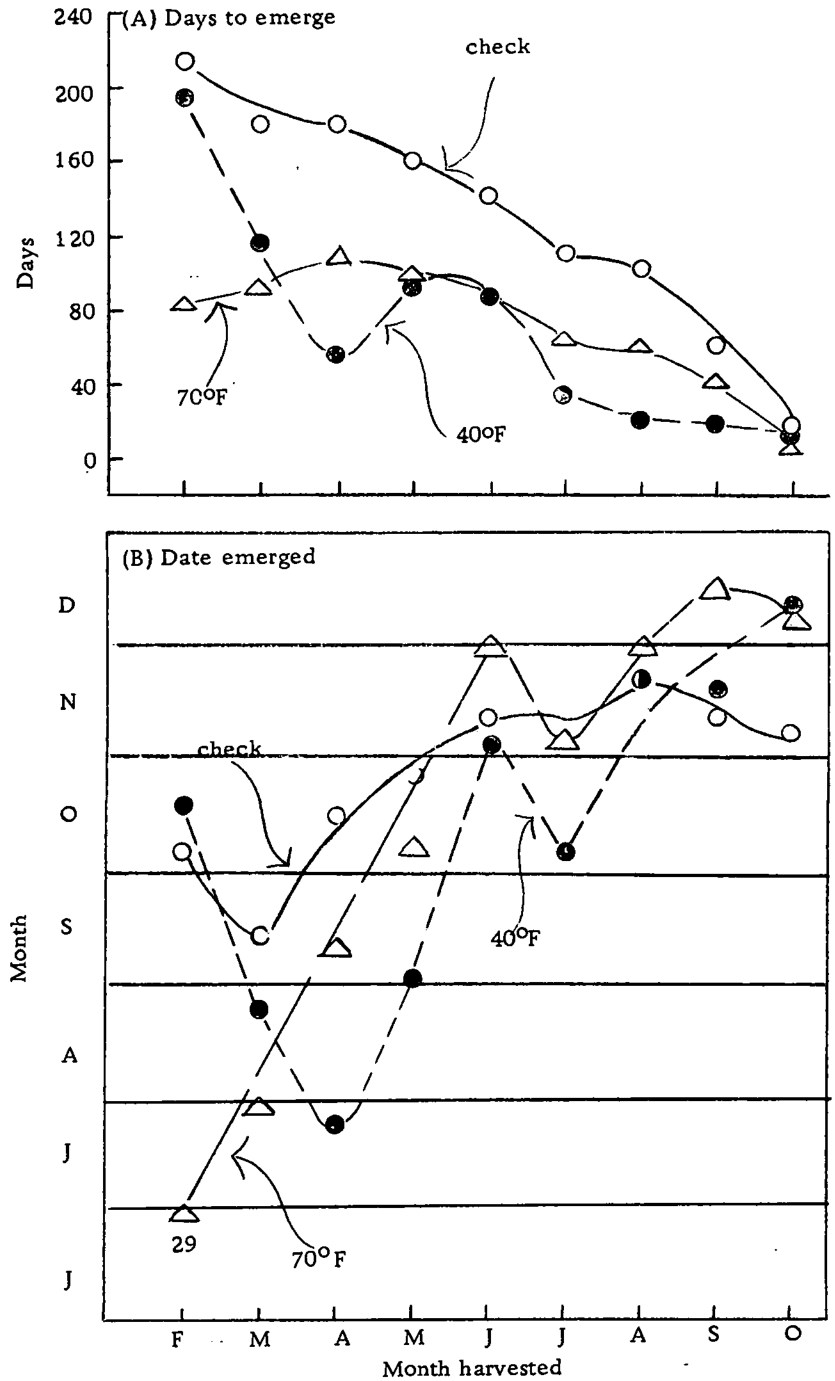

Fig. 1-1. Effect of date of bulb harvest and 6 weeks of storage on (A) days to emerge and (B) date emerged of 'Croft' lily. (Ten plants per treatment)

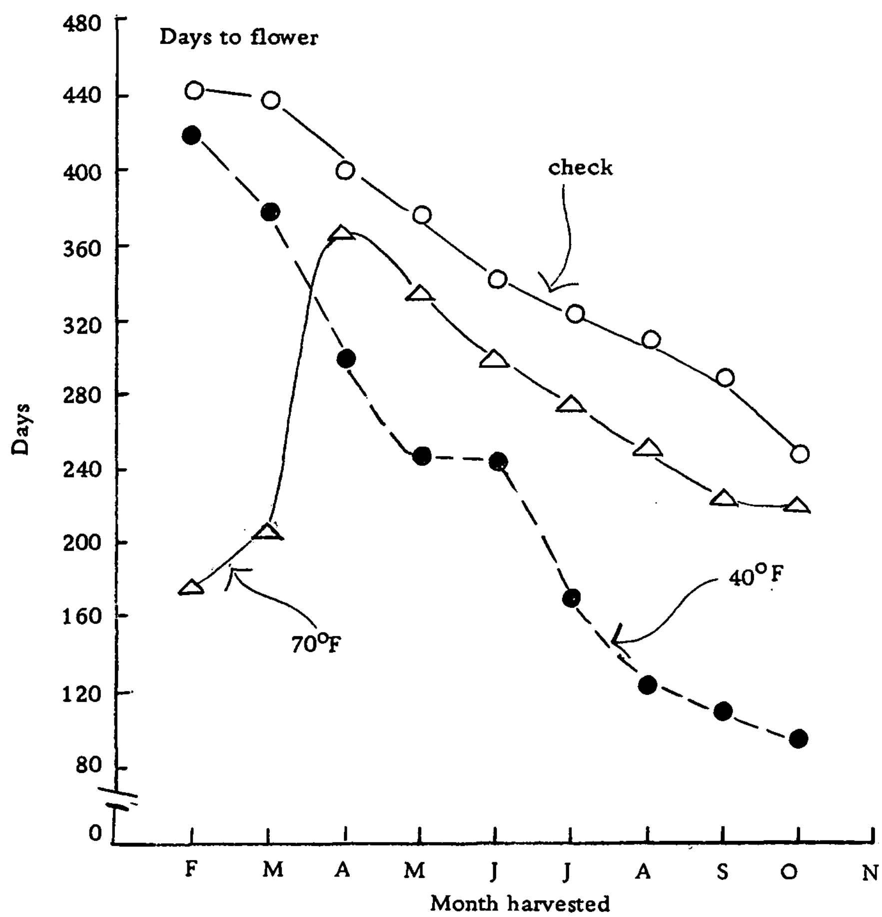

Fig. 1-2. Effect of date of bulb harvest and 6 weeks of storage on days to flower of 'Croft' lily. (Ten plants per treatment)

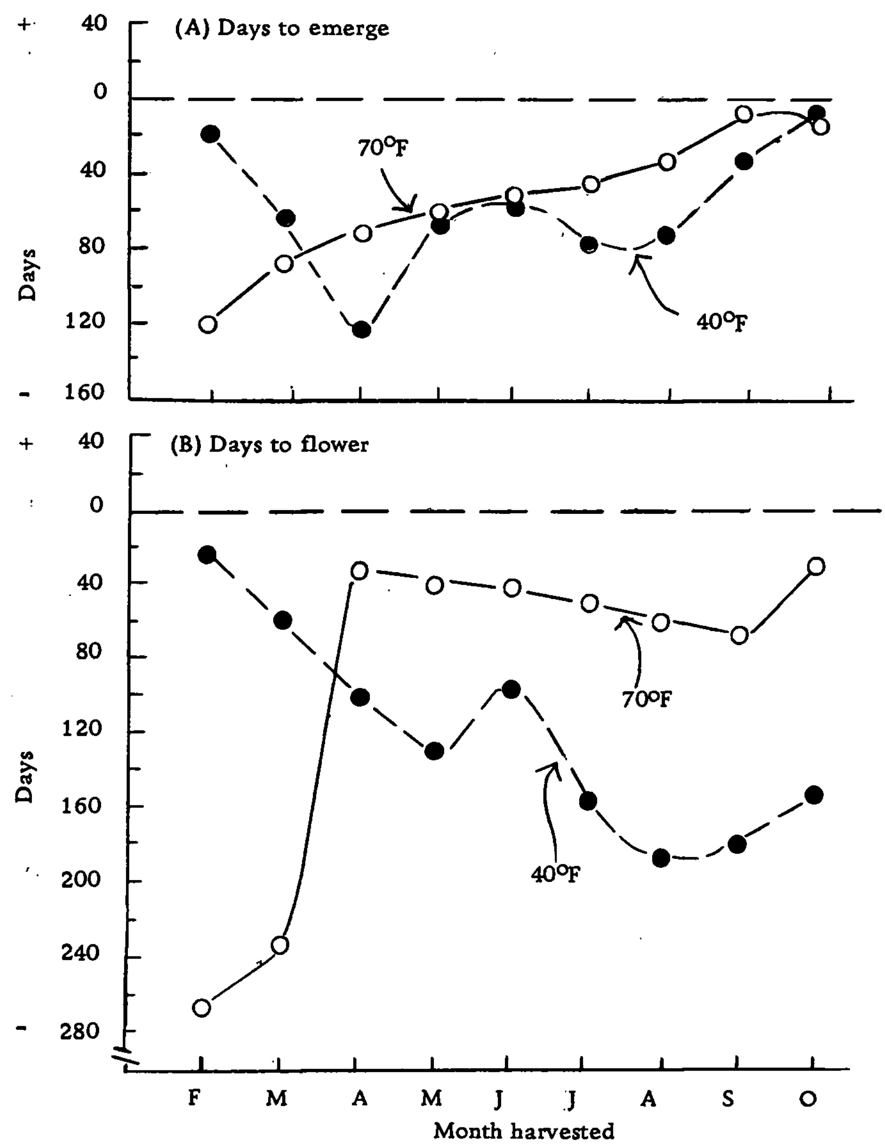

Fig. 1-3. Differences in (A) days to emerge and (B) days to flower between nonstored bulbs (dash line at zero days) and bulbs stored for 6 weeks of 'Croft' lily harvested the same date. (Ten plants per treatment)

The curves in Figure 1-1(A) obscure important phenomena related to sprouting. Although the bulbs emerged in progressively shorter times calculated on the basis of the time elapsing from potting until emergence, Figure 1-1(B) shows that the non-stored bulbs tended to emerge later the later the harvest, with the date of emergence varying from mid-September for an early harvest to mid-November for late harvests. The 40° F curve resembled the check curve except for wide divergences where the April-harvested bulbs emerged in late June; the June-harvested, in early November; and the July-harvested, in early October. Thus the date of emergence for bulbs stored at 40° F varied from late June to early December. The 70° F curve shows the most consistent trend of early harvests emerging early and late harvests emerging late. The February-harvested bulbs emerged in late June, the earliest emergence date for all treatments; the October-harvested, in early December. As with the 40° F curve, harvesting in June greatly retarded sprouting and harvesting in July greatly accelerated it.

Figure 1-3(A) helps clarify further the relationships between harvest date and storage treatment with the days to emerge. In this figure, the differences in days to emerge for the 40° and 70° F bulbs and the days for the non-stored bulbs harvested at the same time were calculated. Storage at 40° F, which little affected sprouting when given to February-harvested bulbs, was stimulating to the

April-harvested ones. It became less and less stimulating with harvests between April and June, more stimulating by July and August, and rapidly lost its influence by October. But 70°F storage, which was extremely stimulating in February, became steadily less so and by September its influence was almost nil.

These results are probably related to the developmental physiology of the Easter lily as mediated by natural growth regulating substances. Furthermore, they help explain the adaptability of this crop to the climate of the Northwest and help clarify also the problems of dormancy and summer-sprouting.

The Easter lily is adapted to the Northwest because its response to temperature varies during the course of the year. Since the daughter bulb starts to develop in late November and early December and grows continuously until the bulbs are harvested in September or October, one should expect cold and warmth to elicit different responses at different times of the year. If cold always stimulated sprouting, then summer-sprouting would occur every year and the crop would be damaged because of winter temperatures. If warmth always stimulated sprouting, then summer-sprouting also would occur because of summer temperatures. Fortunately, this does not happen. Soil temperatures of 70°F are never encountered in winter and 40°F probably rarely in April. It may well be that intermediate soil temperatures prevailing at critical times during the bulbs development are responsible for severity of the sprout problem some seasons.

Perhaps the daughter bulb is weakly dormant in the winter and thus is readily stimulated to sprout by warm temperature. Dormancy deepens as the season progresses, warmth becomes less able to stimulate sprouting, and a chilling requirement develops that wanes in the early summer in connection with the events leading to anthesis in July. After anthesis, cold temperature again becomes less and less a requirement for breaking dormancy. The response of non-stored bulbs suggests that the daughter has been steadily acquiring the ability to start another cycle of growth and flowering.

Days to Flower

Figures 1-2, 1-3(B) and Appendix Ia present days to flower data. The families of curves are particularly striking. Here we see that warm storage of February and March bulbs led to very much earlier flowering compared to no storage and 40° F storage. But by April, warm storage, although conducive to earlier flowering, was much less so. Cold storage, on the other hand, which affected little the February bulbs, rapidly became more and more stimulating as the season progressed. In June, when the flowers were developing rapidly, 40° F lost some of its stimulating power.

It would appear that warmth acted like a vernalizing temperature in the late winter. This is intriguing because Povar (1959), a Ukrainian, reported that he vernalized wheat by warmth.

Leaf Number

Figures 1-4, 1-5, and Appendix Ib show the effect of treatment on leaf numbers. Stress is laid on leaf number because it is one of the most reliable indexes of the transition between a strictly vegetative state and a flowering one (Lang, 1965). On the basis of leaf number one can say that this or that treatment was more or less capable of inducing flowering.

The increased leafiness with later harvests shows the continued leaf initiating activity of the stem apex after flowering of the mother plants in July (Blaney and Roberts, 1966). Leaf numbers for February to June harvests reflect the fact that no primordial leaves were in the bulbs then. The 40° F and 70° F curves reflect the changing ability of cold and warmth to vernalize. Figure 1-5 better clarifies this. The 40° F curve shows clearly that cold was non-inductive early in the year and that its inductive power increased steadily with the progressing season, except for a decrease in June prior to flowering of the mother plants in July. The 70° F curve shows that warmth was highly capable of inducing flowering in February and March, was quite inhibitory in June, and was again inductive in the autumn. The shape of the days to flower and leaf number curves tended to

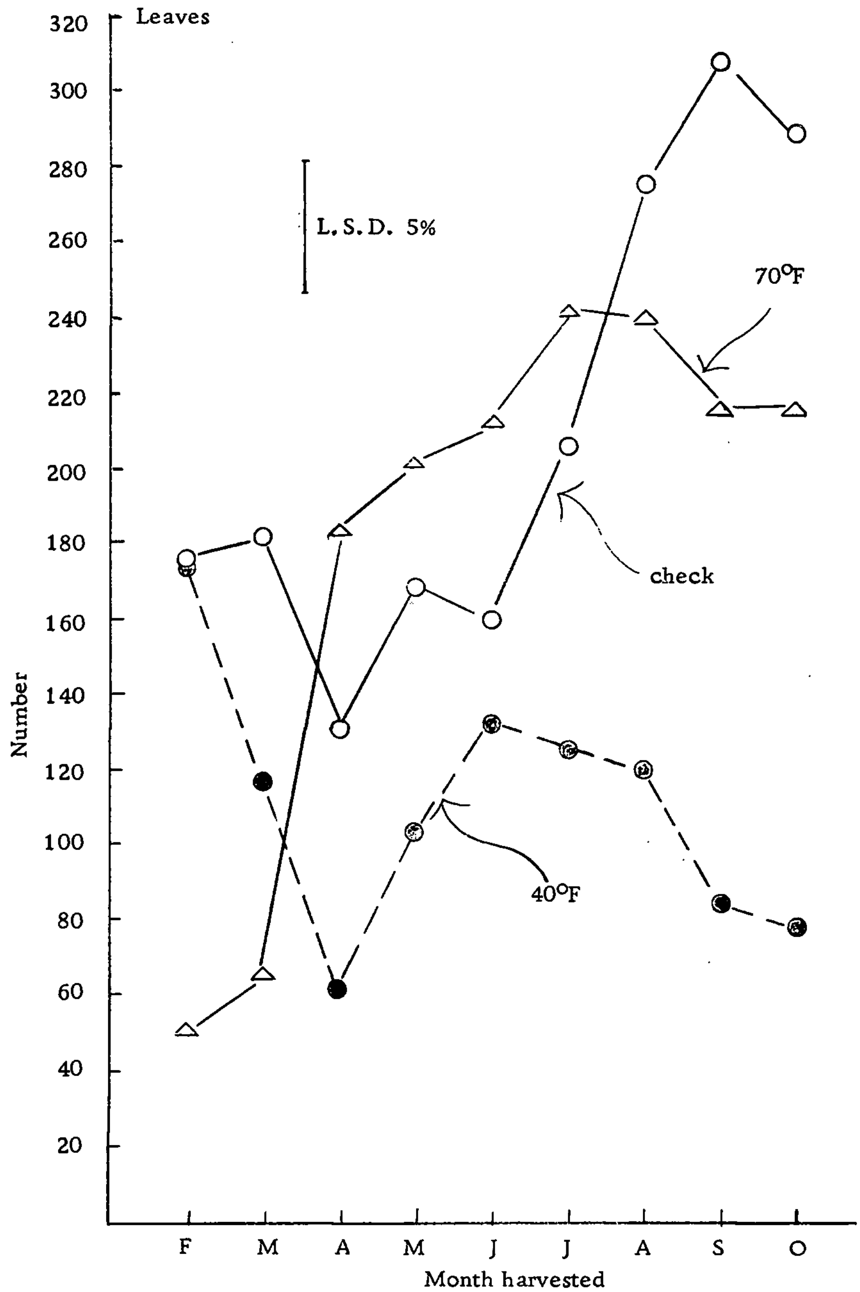

Fig. 1-4. Effect of date of bulb harvest and 6 weeks of storage on leaf numbers of 'Croft' lily. (Ten plants per treatment)

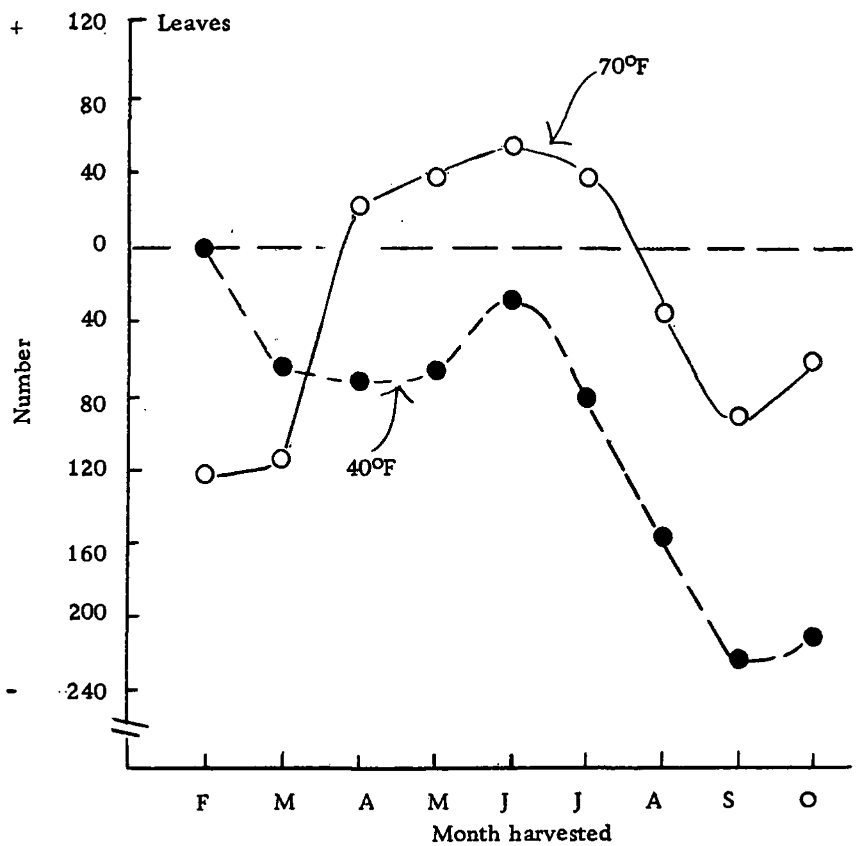

Fig. 1-5. Differences in leaf numbers between nonstored bulbs (dash line at zero days) and bulbs stored 6 weeks of 'Croft' lily harvested the same date. (Ten plants per treatment)

parallel one another.

The three responses reported in the foregoing agree remarkably well with those from soil warming experiments of Blaney and Roberts (unpublished). They cast doubt on the report of Weiler and Langhans (1967) that the Easter lily has an obligate requirement for temperatures below 70°F for floral induction, perhaps the maximum temperature for vernalization depends on the developmental stage of the bulb. How the field soil temperatures prior to harvest and temperatures in the greenhouse are related to these responses awaits further research. Certainly the bulbs experienced cold temperatures in the field and a 60°F minimum in the greenhouse.

Flower Bud Initials

Figures 1-6(A), 1-7, and Appendix Ib present the data for flower bud initiation. Figure 1-6(A) graphs flower bud initiation on the basis of flower buds per 10 gram units of bulb weight. In general, the check curve (Fig. 1-6(A)) reflected the weight of the bulbs (cf. Table 1) and the leafiness of the plants (cf. Fig. 1-4). The 70°F curve (Fig. 1-6(A)) shows warm temperature storage of February and March bulbs was deleterious to flower bud initiation, but it rapidly approached and equalled the check curve by summer. October bulbs were not favorably acted upon by 70°F. The 40°F curve (Fig. 1-6(A)) paralleled the check curve from February to

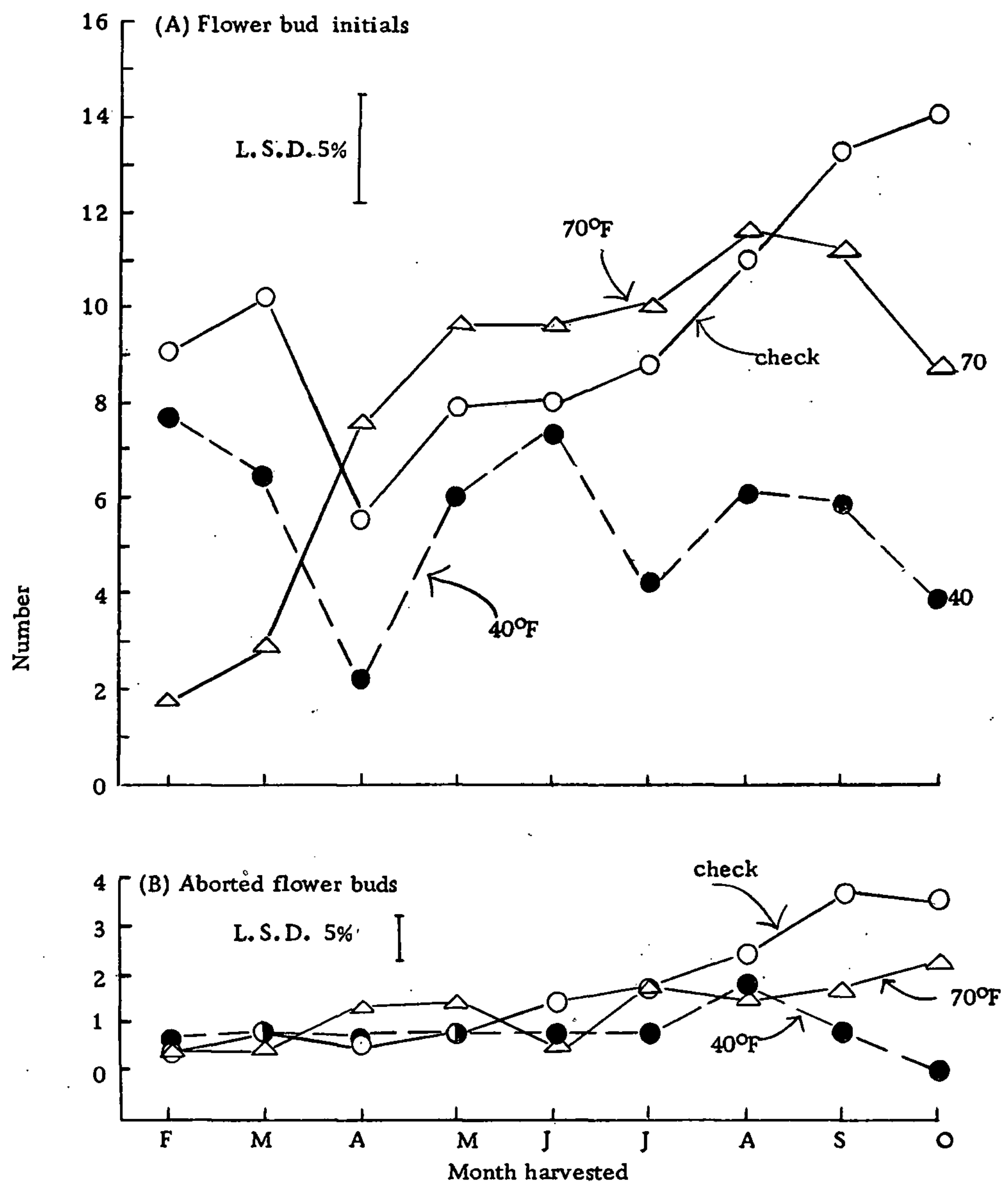

Fig. 1-6. Effect of date of bulb harvest and 6 weeks of storage on (A) flower bud initiation and (B) flower bud abortion by 'Croft' lily. (Ten plants per treatment)

June, after which 40° F became more and more deleterious to flower bud initiation.

Perhaps the curves of Figure 1-7 give a better picture of the effect of storage temperatures and dates of harvest because here differences in bulb weight were eliminated. The check and 40° F curves suggest that small bulbs are more productive of flowers than are large bulbs. The cold storage curve, although always inferior to flower bud initiation than no storage, paralleled the latter curve except for the February bulbs which were indifferent to cold storage. Warm storage varied greatly in its effects, being extremely deleterious in February and March, but by June on it was innocuous. The low points in April for no storage and 40° F storage and the peaks in May for the three storages imply that something very important was happening in the bulbs that might be related to the rapid development of the plant in April, and the rapid development of the flower buds in May. Further research is needed to clarify these phenomena.

The family of curves for aborted flower buds (Fig. 1-6(B)) show the inability of the plants to carry large numbers of flower bud initials to anthesis.

Stem Length

In general, the length of the stems (Fig. 1-8) reflected the leaf complement, that is, the number of internodes (cf. Fig. 1-4).

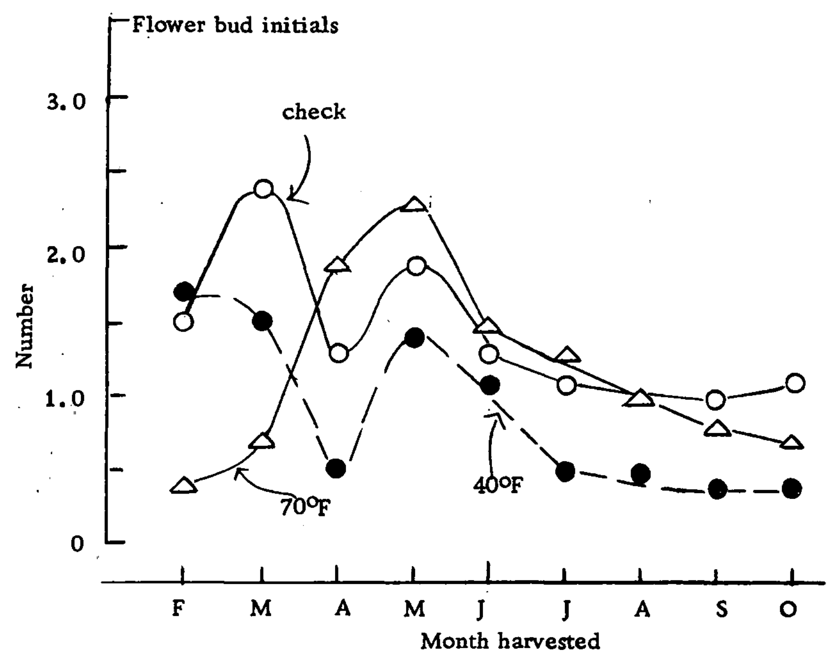

Fig. 1-7. Effect of date of bulb harvest and 6 weeks of storage on flower buds initiated per ten gram units of bulb weight by 'Croft' lily. (Ten plants per treatment)

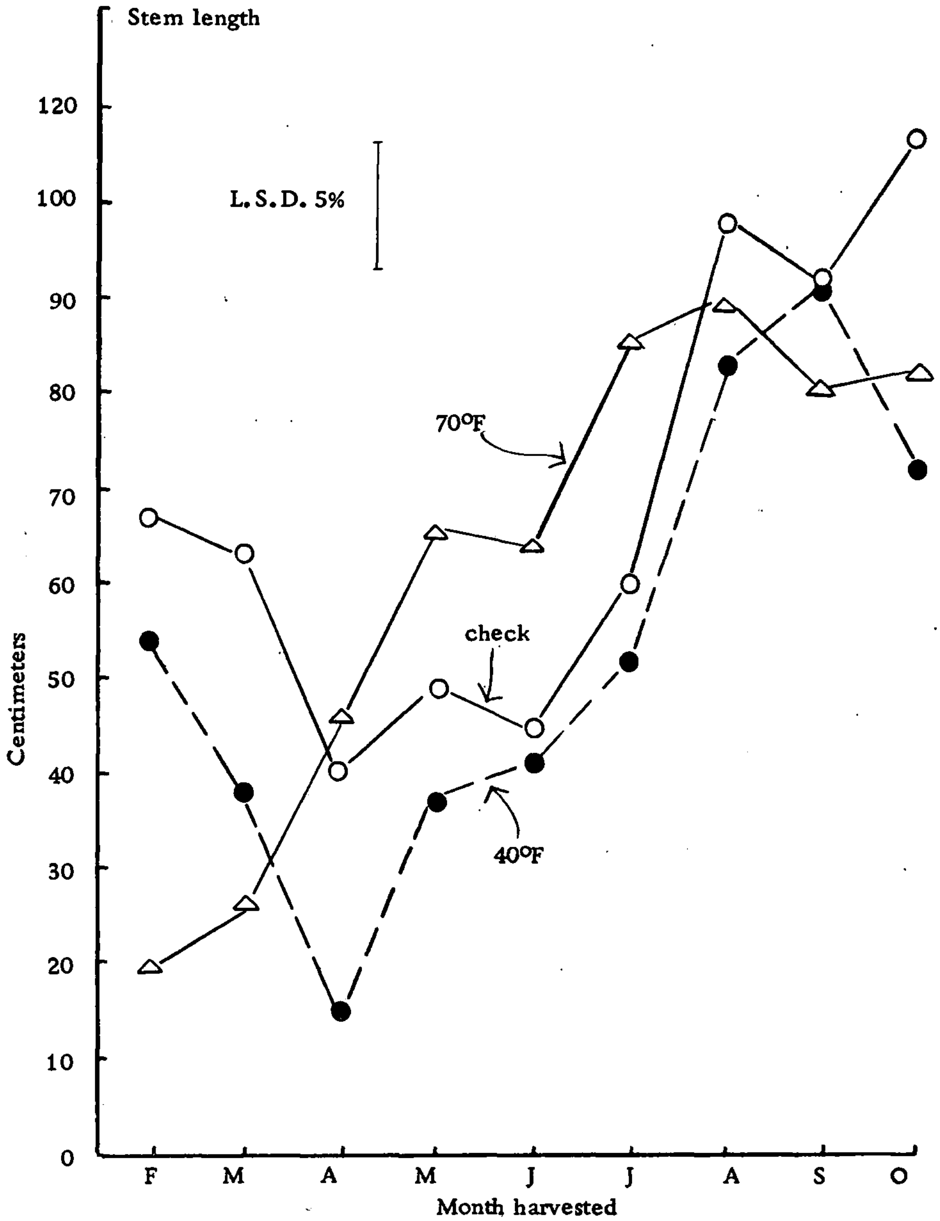

Fig. 1-8. Effect of date of bulb harvest and 6 weeks of storage on stem length of 'Croft' lily. (Ten plants per treatment)

Growth Rate

Figure 1-9 presents growth rates for plants grown from bulbs harvested at different dates and given several storage treatments.

Growth rate is expressed on the basis of the rate at which leaves unfolded from the spindle. Several assumptions were made in calculating it: 1) the growth period constituted the time elapsing from shoot emergence to when the last leaves unfolded to first reveal the flower buds, and 2) 42 days were arbitrarily assigned to the time elapsing from first bud visibility to anthesis. Therefore, the growth rate was calculated by means of the following formula:

$$\text{Growth rate} = \frac{\text{number of leaves per stem}}{\text{days to flower} - (\text{days to emerge} + 42)^{*}} = \text{leaves unfolded per day}$$

The shapes of the three curves are similar but differ in magnitude. In general, the unfolding of leaves started at a low level with the February harvest, decreased to a minimum with the April harvest, then rapidly increased to level off or decrease with the August and later harvests. Cold storage tended to retard the February to May plants and to accelerate the May and later plants compared with check plants. Warm bulb storage tended to accelerate except for

*Observations over several years have shown 42 days to be a fairly accurate estimate for the days elapsing from first bud visibility to anthesis at 70° F day and 60° F night minimum temperatures.

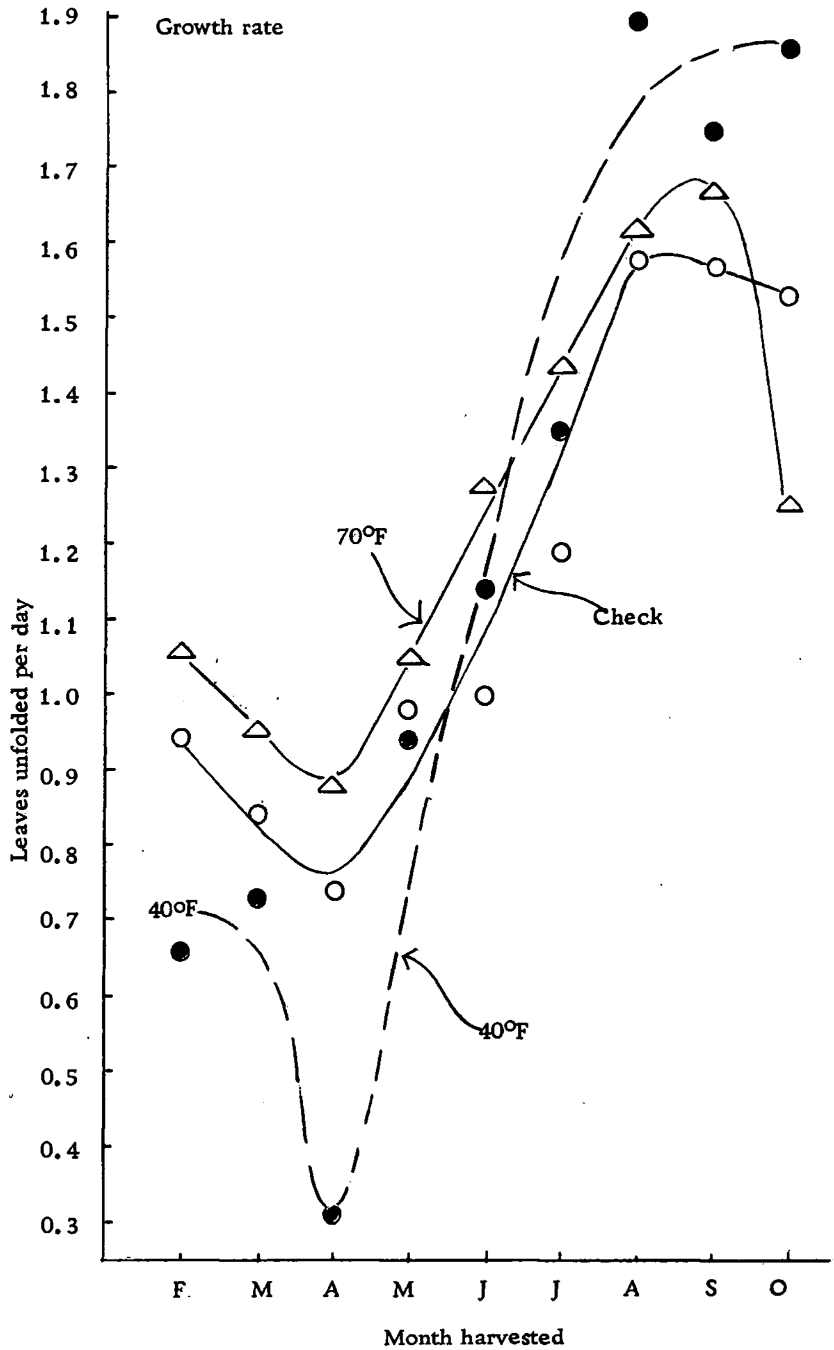

Fig. 1-9. Effect of date of bulb harvest and 6 weeks of storage on the growth rate, expressed as leaves unfolded per day, of 'Croft' lily. (Ten plants per treatment)

the October plants which were much retarded.

It is evident that one cannot categorically state that temperature acts specifically at all times. So much depends upon when the bulbs were harvested, that is, upon the phase of development of the plant. Further research is needed to explain the bulbs varying responses because of the importance of understanding crop adaptability to climate, crop behavior in the greenhouse, and the need for developing cultural practices to avoid summer-sprouting, to aid maturation of the bulbs, to break bulb dormancy, and to prepare bulbs for predictable greenhouse forcing performance.

Experiment II. Easter Lily Timing

Because Easter can occur from March 21 to April 25, precise timing of Easter lilies requires skill and detailed knowledge of the crops behavior. Traditionally, growers have used plant height at various dates before the plants are to flower as a guide as to whether or not the crop is growing too fast or too slow (Laurie, Kiplinger, and Nelson, 1958). But the height plants attain at any time during the forcing period can be very variable.

Knowledge of when flowers are formed is essential for the development of procedures for the precise timing of flowering of florist crops. In some bulbous plants, Hartsema (1961) stated that flower formation occurred long before actual flowering, in others, flower formation occurred almost simultaneously with the emergence of leaves and was immediately followed by the extension growth of flower stalks and floral parts. The time of flower bud formation in the Easter lily depends, however, mainly on bulb storage temperatures; flower primordia differentiation occurs from a few weeks after planting or months later in the case of bulbs given warm or no storage (Blaney and Roberts, unpublished data). Hence, time of flower formation depends greatly upon storage treatment.

Because lilies, whose bulbs and plants were kept at 70°F after bulb harvest and during forcing, remained vegetative for more than a year, Weiler and Langhans (1967) classified the Easter lily as having an obligate requirement for temperatures below 70°F for flowering.

Blaney, Roberts and Lin (1967) proposed a Leaf Remainder Method for timing lilies, because mature bulbs after certain storage regimes tended to produce predictable numbers of leaves. The days to force, moreover, were directly proportional to the leaf count (Blaney, Hartley and Roberts, 1963). Blaney, Roberts and Lin (1967) reported that the plants unfolded leaves at a fairly constant rate, about 1.3 leaves per day during the forcing period, if the bulbs had been adequately precooled.

This method of timing was based upon several assumptions:

1) A predictable leaf number on plants grown from adequately

precooled bulbs,

2) A high correlation between leaf number and days to flower,

3) An elapsed time of about 6 weeks between the time the terminal spindle of leaves unfold to reveal the buds and anthesis.

Many researchers (Brierley and Curtis, 1942; Stuart, 1943, 1946a, 1957; Weiler and Langhans, 1967) have noted that Easter lily plants grown from precooled or vernalized bulbs bore fewer leaves at flowering than did those from non-precooled bulbs, but it was not until years later that leaf count data (Blaney, Hartley and Roberts, 1963) were published. Hartley (1967) found that 'Ace' and 'Croft' bulbs initiated leaf primordia during storage, but the numbers initiated during 6 weeks at 40° F were small, about eight and five leaves for 'Ace' and 'Croft', respectively.

The objectives of this study, therefore, were:

A. To determine the effect of duration of vernalizing storage (precooling at 40° F) on leaf number primarily and on other physiological and morphological characteristics,

B. To determine the effect of storage on the growth rate, as measured by the leaves unfolding per day, and

C. To determine the effect of several forcing temperatures on the days to anthesis after the leaves unfolded to first reveal the flower buds.

Two hundred fifty bulbs each of 'Ace' (7-9 inch, 91-142 g) and

'Croft' (7-9 inch, 83-122 g) were used. The total number of scales and primordial scales and leaves in the bulbs at the beginning of storage were counted on ten bulbs of each cultivar. The remainder of the bulbs were divided into two groups: group a, 110 bulbs; group b, 130 bulbs.

A. The Effect of Duration of 40°F Vernalizing Bulb Storage.

Eleven 10-bulb lots (totaling 110 bulbs) were stored at 40°F commencing September 21, 1966, for 0, 1, 2, 3, 4, 5, 6, 7, 9, 13, and 18 weeks before being planted in pots in the greenhouse.

Figures 2-1 through 2-7 and Appendix II show the general inverse relationships between several growth and developmental responses and the duration of vernalizing bulb storage. The first week of storage tended, however, to increase or not to affect each response, depending upon the cultivar, except for days to emerge.

Days to Emerge

Cold storage stimulated the emergence of 'Croft' more than of 'Ace'. Although non-stored 'Ace' emerged about 2 weeks earlier than similar 'Croft', emergence time in 'Croft' was reduced about 50% by the first week of storage while about seven weeks were required to effect the same percentage reduction in 'Ace'. Emergence

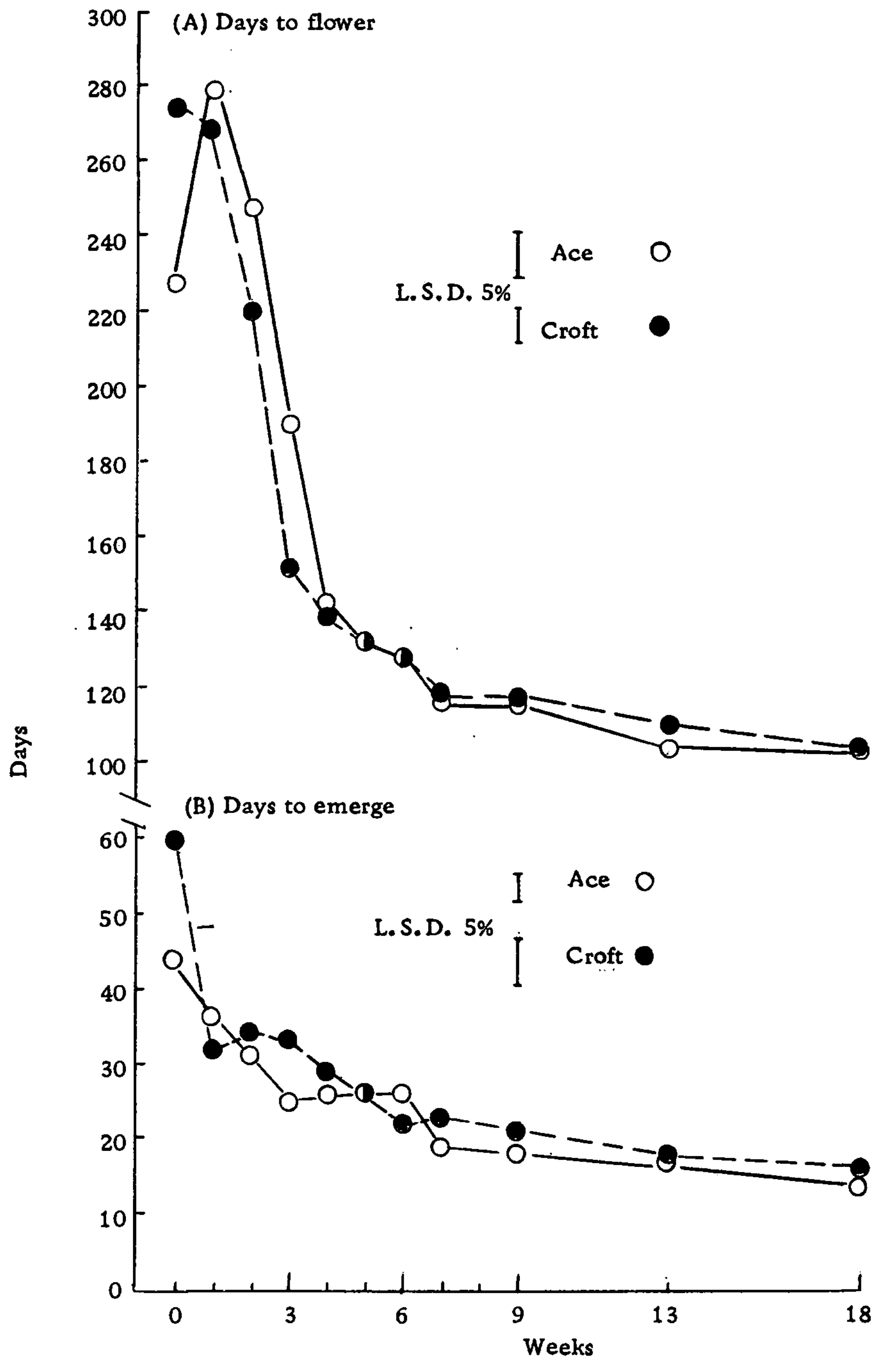

Fig. 2-1. Effect of storage duration at 40° F on (A) days to flower and (B) days to emerge of 'Ace' and 'Croft' lilies. (Ten plants per treatment)

was stimulated little further by storage beyond 6 to 7 weeks duration.

Leaf Number

Although leaf numbers were generally inversely related to the duration of storage, they did not decrease uniformly with the increases in storage duration. The first week tended to increase leaf number very significantly in 'Croft' but not in 'Ace'. The greatest reductions in leaf number followed the first three to four weeks of storage. The decrease in leaf number was more gradual between these storage durations and the 13 weeks duration and was very minor between 13 and 18 weeks.

Leaf numbers after the two longest storages probably represented those leaves already present as primordia in the bulbs at the start of storage (Blaney and Roberts, 1966). Therefore, one can assume that 13 weeks storage completely vernalized these bulbs and that they proceeded immediately to initiate flower buds after sprouting without first passing through a strictly vegetative phase, however, short, in the greenhouse.

Days to Flower

The curves for days to flower for the two cultivars are similar in shape but differ greatly in magnitude at those points on the curves

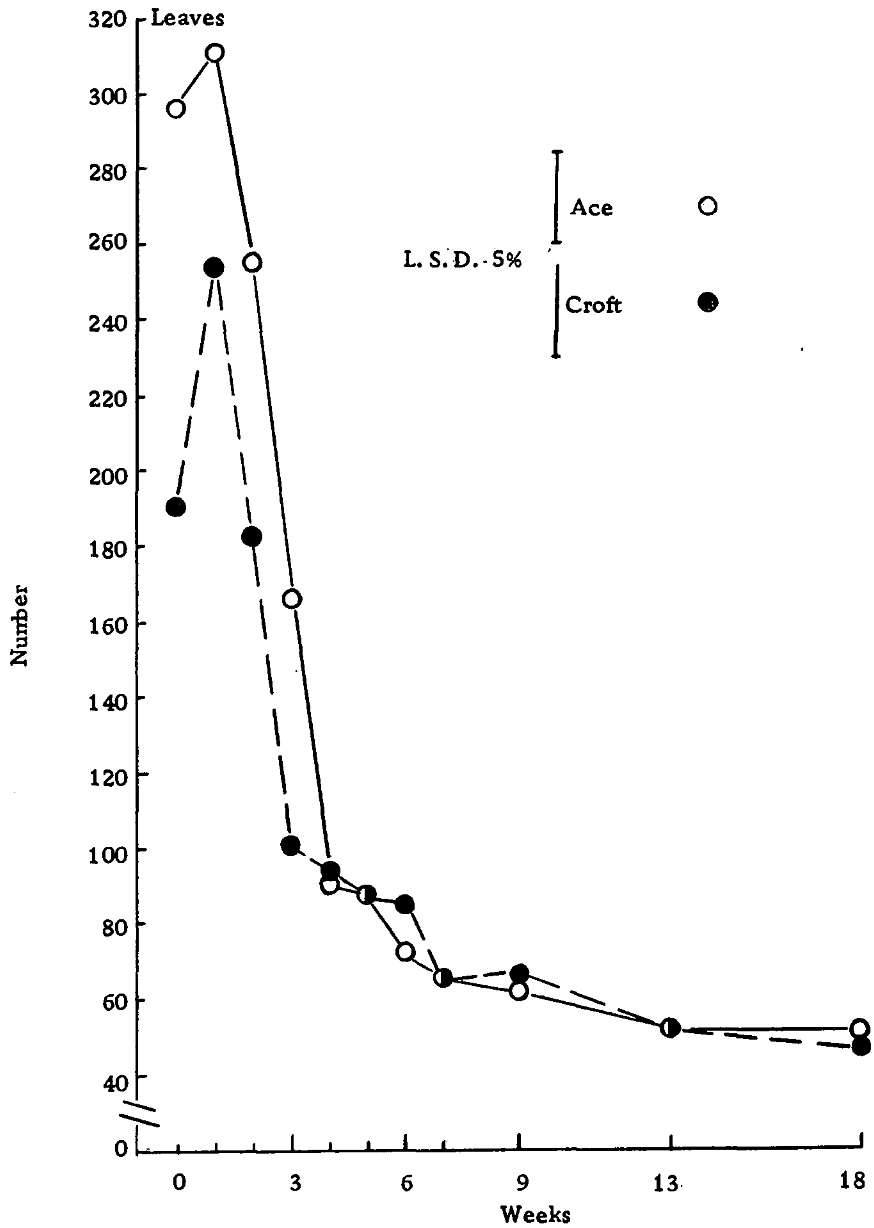

Fig. 2-2. Effect of storage duration at 40° F on leaf numbers of 'Ace' and 'Croft' lilies. (Ten plants per treatment)

representing zero to 3 weeks of storage. The 'Ace' curve suggests that non-stored 'Ace' were able to grow faster than non-stored 'Croft' because 'Ace' flowered 47 days earlier than 'Croft' even though the former bore 106 more leaves. The data for days to emerge showed also that the non-stored 'Ace' had an initial growth advantage because they emerged 16 days earlier than similar 'Croft'.

The days to flower decreased rapidly with storage up to 4 weeks long, less precipitiously between 4 and 7 weeks, and very slowly between 7 and 9 weeks.

Comparison of the days to flower and leaf number curves show that the former curve generally paralleled the latter. The two curves emphasize the importance of giving the bulbs of both cultivars at least 6 or 7 weeks of cold storage if the plants are to flower within an economically acceptable time. They also point out the great probability of plants failing to flower at Easter because of excessive leafiness if the bulbs were stored for too short a time.

Flower Buds

The curves for flower buds show that the first 3 to 4 weeks of storage were most destructive to the flowering potential of the bulbs, the next 5 to 6 weeks had little further effect, but the destructive action accelerated somewhat during the final 9 weeks. These curves also tended to parallel closely the curves for leaf numbers. The

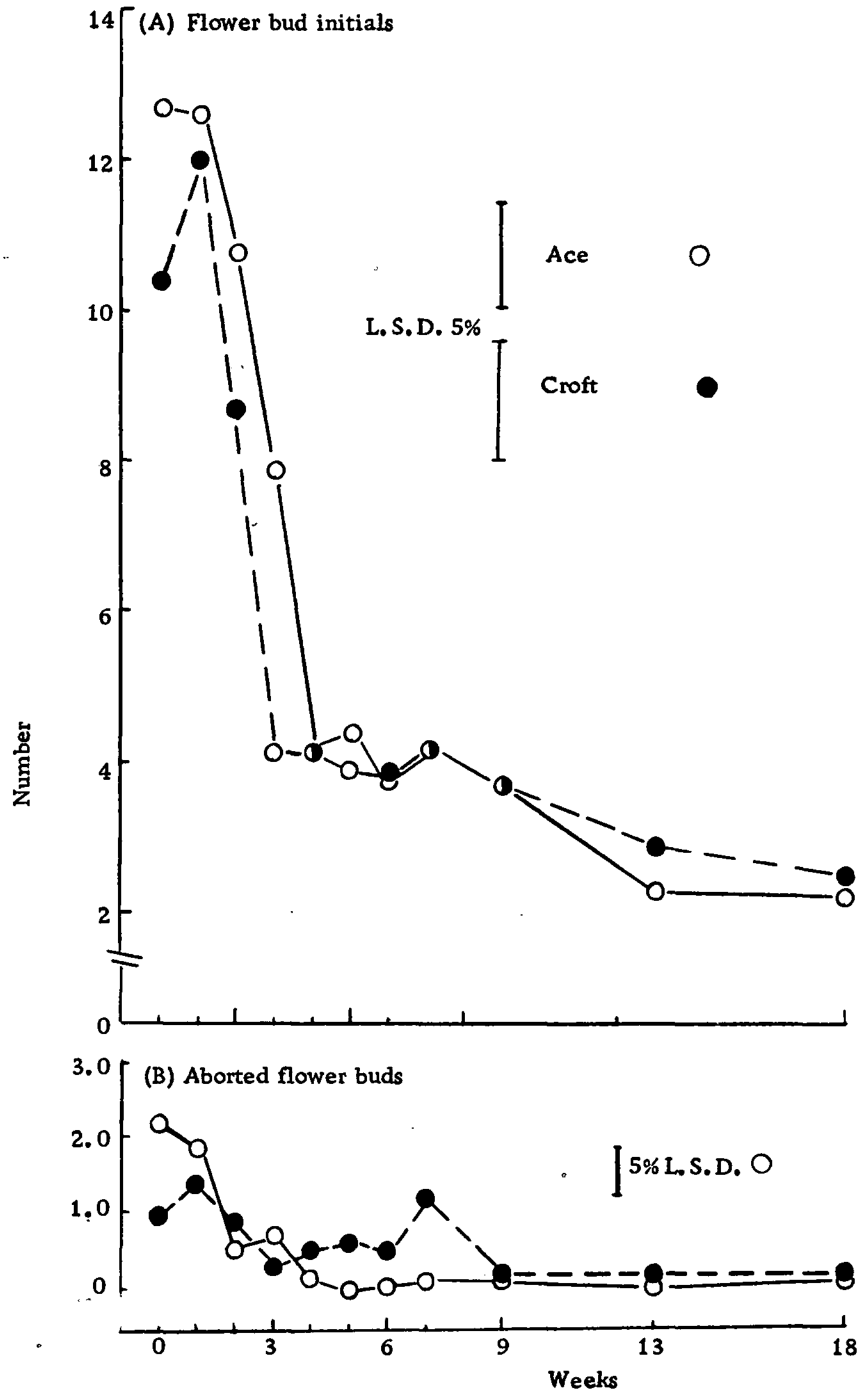

Fig. 2-3. Effect of storage duration at 40°F on numbers of flower buds (A) initiated and (B) aborted by 'Ace' and 'Croft' lilies. (Ten plants per treatment)

shorter storage durations were less destructive to the flowering potential of 'Ace' than of 'Croft'. The data suggest that one week of storage enhanced rather than diminished the ability of 'Croft' to initiate large numbers of flowers.

The curves for flower bud abortion point up the inability of the plants that initiated large numbers of flower buds to carry all of the buds to anthesis.

Stem Length

In general, the length of the stems reflected the number of leaves, that is, the number of internodes that elongated.

Growth Rate

One of the most striking observations gleaned from this experiment was the difference in growth rates between 'Ace' and 'Croft' when subjected to a range of storage durations. Non-stored 'Ace' surprisingly exhibited the most rapid growth rate, but with storage durations from 1 to 13 weeks it decreased precipitously. The first week had the greatest reducing effect. A lengthening of storage by five more weeks from 13 to 18 did not further decrease the rate of growth.

The curve for 'Croft', however, showed an initial slow rate of growth which rose rapidly to peak at about 4 to 5 weeks of storage

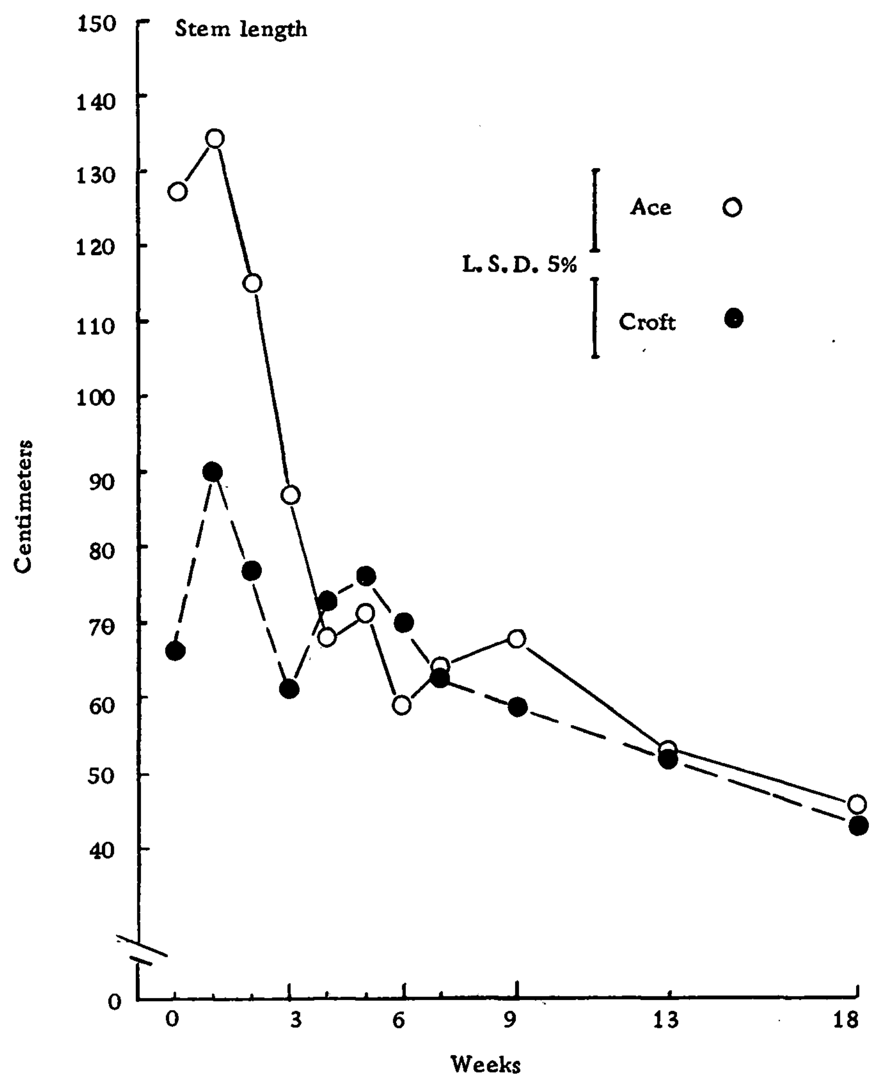

Fig. 2-4. Effect of storage duration at 40 ° F on stem length of 'Ace' and 'Croft' lilies. (Ten plants per treatment)

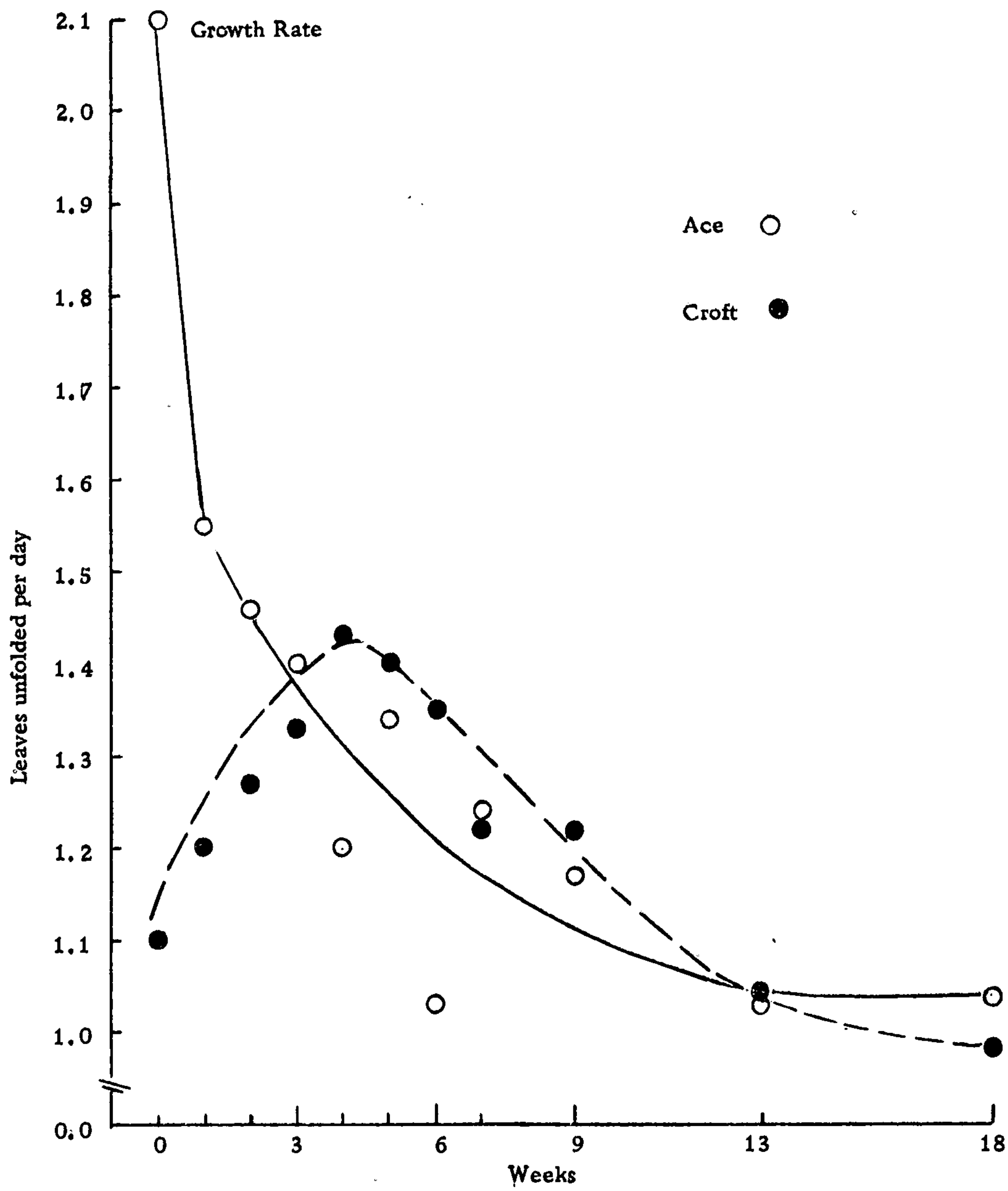

Fig. 2-5. Effect of storage duration at 40° F on growth rate, expressed as leaves unfolded per day, of 'Ace' and 'Croft' lily. (Ten plants per treatment)

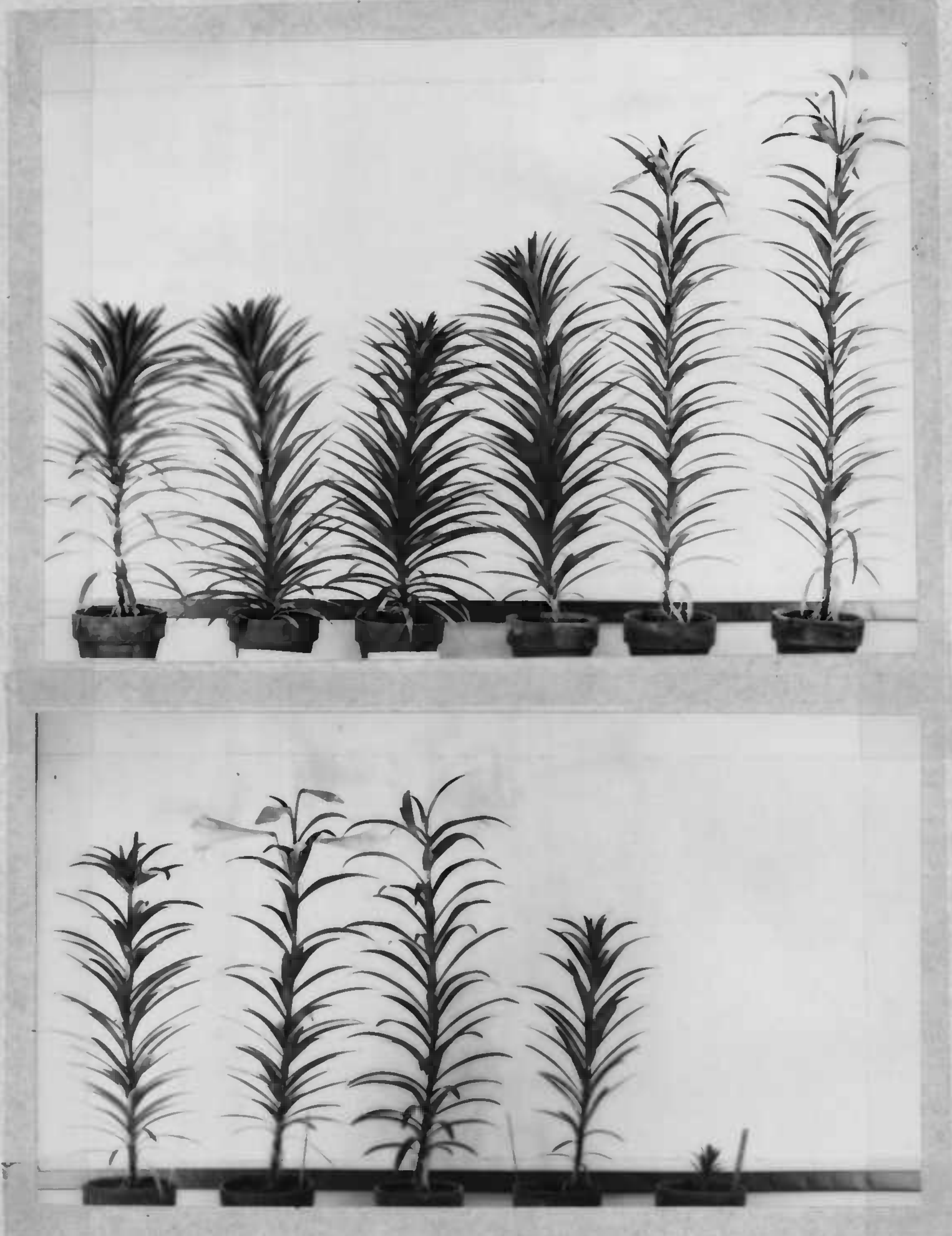

Fig. 2-6. Typical 'Ace' plants on February 23, 1967, 103 days from potting the bulbs of the 8th plant from the left which had been stored 7 weeks at 40°F. Storage durations, from left to right: 0, 1, 2, 3, 4, 5, 6, 7, 9, 13, and 18 weeks.

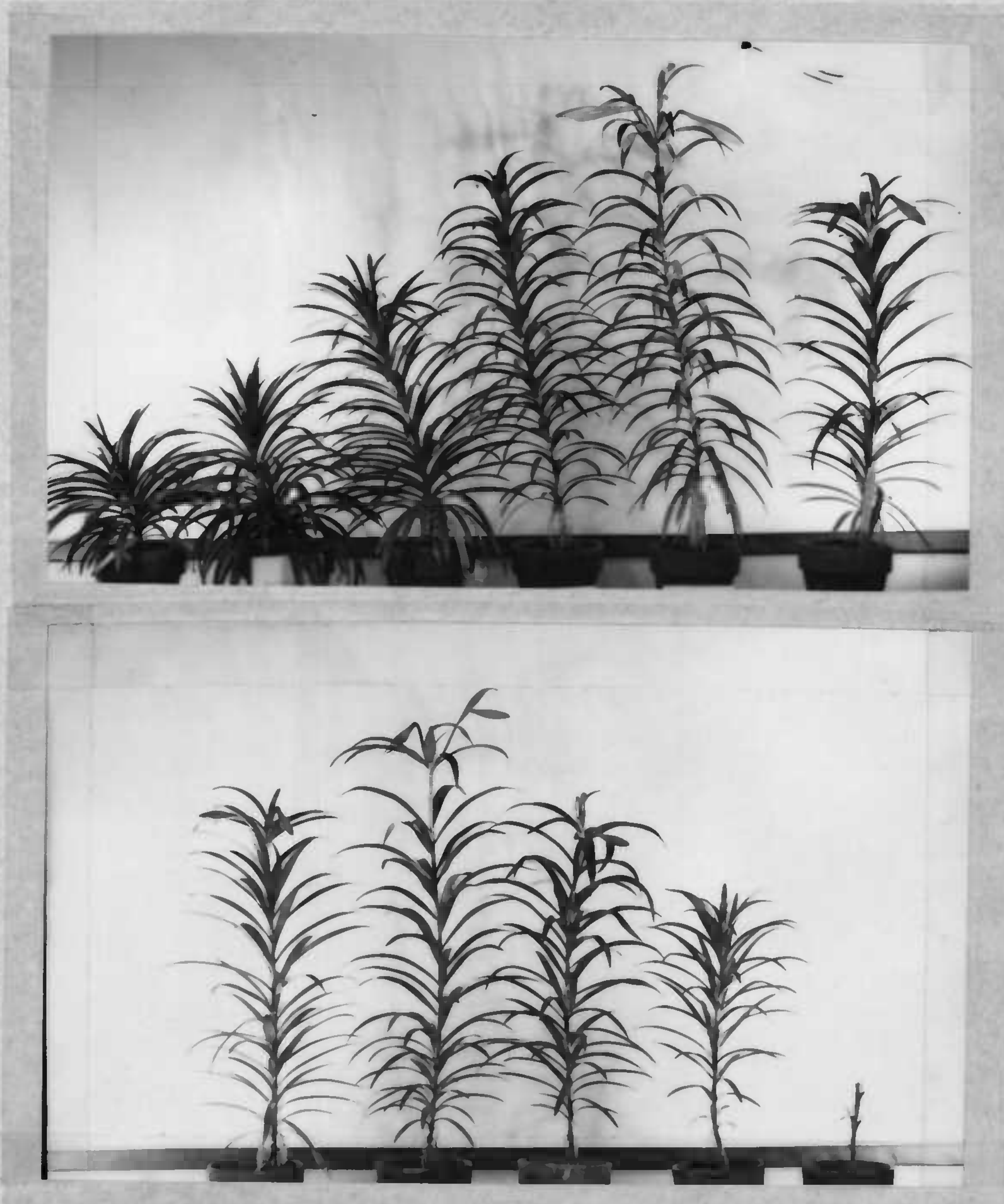

Fig. 2-7. Typical 'Croft' plants on February 23, 1967, 126 days from potting the bulbs of the 5th plant from the left which had been stored 4 weeks at 40°F. Storage durations, from left to right: 0, 1, 2, 3, 4, 5, 6, 7, 9, 13, and 18 weeks.

and then decreased rapidly after 13 weeks of storage. The change in rate between the thirteenth and eighteenth weeks was about the same as for 'Ace'. Interestingly, the growth rate at zero and at 13 weeks did not differ greatly.

Figures 2-6 and 2-7 show typical 'Ace' and 'Croft' plants from each storage treatment on February 23, 1967, 103 days from potting the 7-week bulbs of 'Ace' and 126 days from potting the 4-week bulbs of 'Croft' whose plants bloomed first. The days in the greenhouse on February 23 for each of the progressively longer storage treatments were: 0 wk, 154 days; 1 wk, 147 days; 2 wks, 140 days; 3 wks, 133 days; 4 wks, 126 days; 5 wks, 119 days; 6 wks, 112 days; 7 wks, 103 days; 9 wks, 91 days; 13 wks, 63 days; and 18 wks, 28 days.

B. The Effect of 6 Weeks Storage on the Rate of Growth of Easter Lily Plants as Measured by the Rate of Leaf Unfolding

One hundred thirty bulbs were stored 6 weeks at 40° F, commencing September 21, 1966, before being planted in pots in the greenhouse on November 3. Figure 2-8 and Appendix IIb show the results. On December 10, 20, 27, and on January 3, 10, 17, 24, and 31, that is, 37, 47, 54, 61, 68, 75, 82, and 89 days from November 3, the average date of emergence, ten plants were selected randomly and microscopically examined for first formation of flower buds. At the same time, the last leaf unfolding from the terminal leaf spindle was marked on ten plants.

'Ace' and 'Croft' plants averaged 81.1 and 82.0 leaves, respectively, below the lowermost flower. Almost all the plants had flower primordia when sampled December 20, 47 days from potting and 20 days from emergence. These results agree well with unpublished data of Blaney and Roberts. Their 'Ace' and 'Croft' after 6 weeks storage at 40° F emerged in about 3 weeks and showed flower bud initials about 3 weeks later, that is, about 6 weeks from potting in a 60-70° greenhouse.

Figure 2-8 graphs leaf unfolding by 'Ace' and 'Croft' as percentages of total leaves per plant and as actual numbers unfolded at weekly intervals from emergence to bud visibility except for two 10-day intervals immediately following emergence. During the 62 days elapsing from emergence to bud visibility, the rates of leaf unfolding for 'Ace' and 'Croft' were 1.31 and 1.35 leaves per day, respectively. These rates agree perfectly with those reported earlier by Blaney, Roberts and Lin (1967). 'Ace' unfolded leaves at a more regular rate than did 'Croft' in this experiment. The unevenness of 'Croft' might have been due to error in sampling.

Because flower bud initiation had occurred by 3 weeks from emergence (6 weeks from potting), growers who would hope to increase the bud count must be prompt in their cultural applications. To delay would be futile because the flower bud count would have

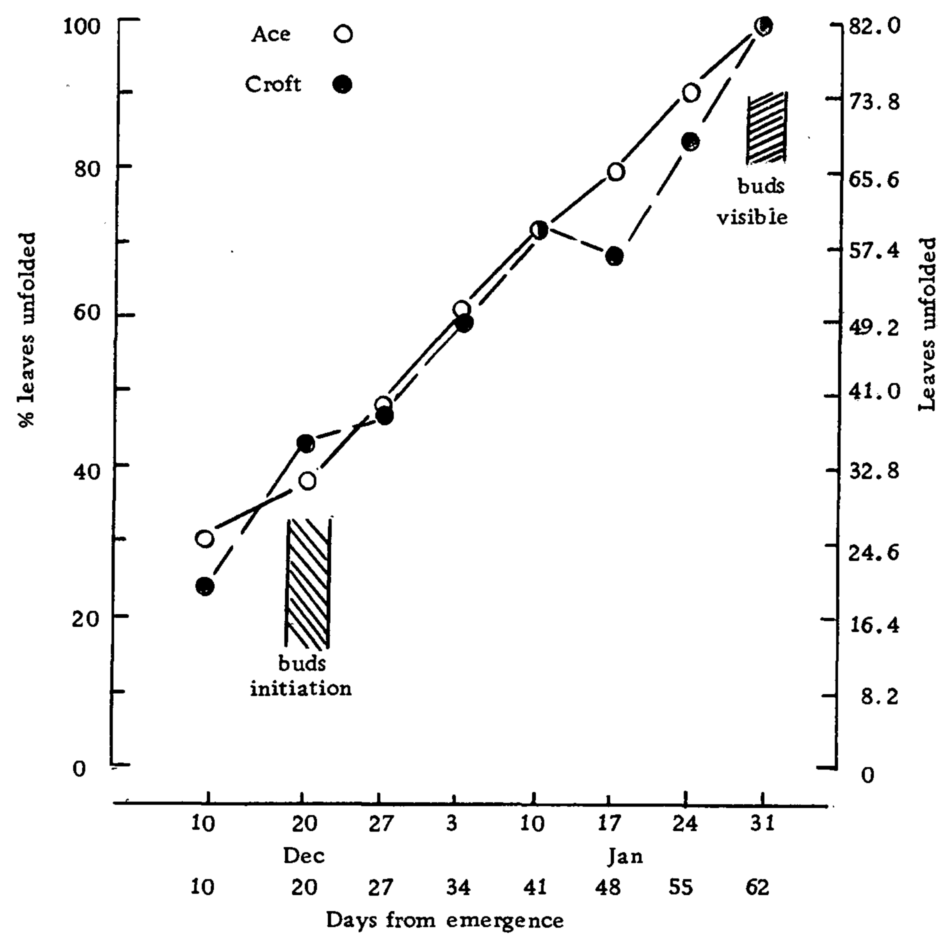

Fig. 2. 8. Leaf unfolding by 'Ace' and 'Croft plants, expressed as percentages of total leaves per plant and as actual numbers unfolded, at weekly intervals from emergence to bud visibility, except for two 10-day intervals immediately following emergence.

been irrevocably determined already.

C. The Effect of 50° and 80° F Temperatures on the Time for Flower Buds to Develop from Bud Visibility to Anthesis.

The buds became visible about 62 days from emergence. Because after this event growers commonly raise or lower greenhouse temperatures to accelerate or retard the progress of the buds toward anthesis, the following experiment was done to determine the effect of temperature during this stage of flower development. On February 1, 1967, ten plants each of 'Ace' and 'Croft' were moved to each of two temperatures, 50° F and 80° F minimum, and ten plants of each were kept in the 60° F minimum greenhouse in which they had been growing.

Table 2 presents the results. Both cultivars flowered in about 138 days, somewhat slower than expected. (This might have been due to a brief time shortly after potting when excessively high temperatures prevailed in the greenhouse because of thermostat breakdown.)

Table 2. The relative effects of 50°F and 80°F compared to 60°F minimum forcing temperatures on the development of 'Ace' and 'Croft' flower buds from bud visibility to anthesis. (Ten plants of each cultivar per temperature)

	Days to anthesis[a]			Deviation from 60°F	
	50°F	60°F	80°F	50°F	80°F
Ace	163.3	138.3	121.3	+25.0	-17.0
Croft	163.4	138.1	116.2	+25.3	-21.9

[a]Days from potting.

The low temperature retarded equally both cultivars. High temperature accelerated 'Croft' more than it did 'Ace'. Figure 2-9 shows typical plants on February 23, 1967, 112 days from potting.

These results do not solve the problem of predicting leaf numbers. But they show that the first 3-4 weeks of storage play a crucial role. 'Ace' tends to be leafier than 'Croft' but fortunately leaf numbers were about equal after 4 weeks or longer of 40°F storage. That handlers of bulbs have a considerable margin of safety in bulb storage is shown by the fact that the aftereffects of prolonged periods of storage were much less dramatic, especially with storage durations in excess of 9 weeks. Further research is needed before one will be able to accurately predict leaf numbers. The effect of such factors as cultivar, date of harvest, bulb size, growing season weather conditions, and storage conditions--duration,

Fig. 2-9. Typical plants of 'Ace' and 'Croft' forced at 60° F minimum temperature from potting to bud visibility and then forced at the temperatures shown in the photograph. 'Ace' always on the left of each pair of plants. Photographed: February 23, 1967.

temperature, atmosphere, moisture, etc.--need to be determined over a period of several years to increase the accuracy of leaf number prediction.

The growth rate curves of 'Ace' and 'Croft' in relation to the duration of storage at 40°F (Fig. 2-5) differed considerably. 'Ace' exhibited initially a much higher growth rate than did 'Croft', but the rate declined rapidly after the first several weeks of storage. The decline was quite gradual after about 9 weeks storage. 'Croft' exhibited initially, however, a relatively slow rate of growth which rapidly peaked after 5-6 weeks storage and then rapidly declined to the equal of that of 'Ace' after about 9 weeks storage. These curves help explain the differences in forcing time shown by 'Ace' and 'Croft' in the greenhouse. Additionally, they add another dimension to the problem of predicting the timing of lilies. If duration of storage at a carefully controlled temperature can elicit such diverse growth rates, it can be readily seen that the unpredictable hazards of mass commercial handling and storage might so confuse the issue that accurate prediction or interpretation of plant response would be quite difficult.

Figure 2-8 showed, however, that after 6 weeks of storage, a generally recommended storage duration, the growth rates of 'Ace' and 'Croft' were comparable and amazingly uniform. Utilization of such uniform growth rates by the greenhouse grower will first require the cooperation of others in the chain leading from the field to the greenhouse. Bulbs will need to be dissected and scale plus scale and leaf primordia counts made and storage durations and conditions will need to be carefully controlled so that the grower can be assured that his plants will bear a reliably predictable leaf count. Then he by means of index plants strategically scattered through his greenhouse can determine whether or not his plants have unfolded the proper number of leaves during the time between emergence and bud visibility. Greenhouse temperatures can be adjusted to accelerate or retard leaf unfolding.

These results, as is so often the case, ask new research questions. What is happening during the first several weeks of storage to so dramatically affect so many plant characteristics? What underlies the growth rate and why do 'Ace' and 'Croft' differ? What is the physiology of flowering in these plants?

Experiment III. The Role of Scales in Growth and Flowering of 'Nellie White' Easter Lily.

It is common knowledge that large bulbs produce more flowers than small ones, if the different sizes have been treated the same. It is commonly assumed also that loss of scales reduces the flowering potential of bulbs. But little experimental evidence has been published for the Easter lily on these points. Post (1941) either broke off at the base up to one-half of the scales or cut off the tips of scales of 'Giganteum' Easter lily and found these treatments reduced the flower count and retarded the rate of bloom in proportion to the amount of scales removed.

Although first-year lily seedlings, whose bulbs are quite small, often produce from one to perhaps six flowers (Roberts and Blaney, unpublished data), the minimum bulb size for flowering is not known. Nor does the data from this experiment resolve the question. Hartsema (1961) in her review states that Dutch Iris (Iris xiphium praecox 'Imperator') bulbs smaller than a certain size do not flower, and that tulips do not initiate flowers if the bulbs weigh less than eight grams.

The effects of scale removal on growth and flowering of 'Nellie White' lilies are reported here.

One hundered 'Nellie White' bulbs ($9\frac{1}{2}$-11 inch, 150-190 g) were divided into ten 10-bulb lots of approximately equal weight on September 23, 1966. Each lot was vernalized at 40° F for 3 weeks. This vernalization time was chosen to hasten emergence and at the same time avoid too great a reduction in flowering potential that would have resulted from longer vernalization. Five degrees of scale removal were made on five lots of bulbs. Scales amounting to 0, 25, 50, and 75% of the original weight of each bulb were removed from four lots. From the fifth lot, called hereafter 100%

scale removal, all the scales were removed so that only the growing point surrounded by leaf primordia, basal plate, and roots remained. The mean individual bulb weights after the scales were removed for each degree of scale removal were: 0%, 173 g; 25%, 129 g; 50%, 87 g; 73%, 43 g; and 100%, 16 g. All of the mother scales and one or two daughter scales were removed at the 50% level, daughter scales were removed above this level. Bulbs were potted on October 15, 1966.

The results are presented in Figures 3-1, 3-2, 3-3, 3-4 and Appendix III.

Days to Emerge

Removal of mother scales (25% and 50% scale removal) did not affect days to emerge, but removal of daughter scales (75% and 100% scale removal) before vernalization accelerated emergence, especially when the scales were removed before vernalization.

Leaves Per Stem

Leaf number is a most reliable parameter of the extent of vegetativeness (Lang, 1965). Since the Easter lily is indeterminate and bears individual flowers in the axils of leaves inserted progressively higher on the stem, the leaf number bearing the lowermost flower marks morphologically the transition from vegetative to the flowering phase.

Reduction in leaf numbers roughly paralleled the severity of scale removal, except that removal of daughter scales (75 and 100% scale removal) reduced leaf numbers most drastically. Leaf

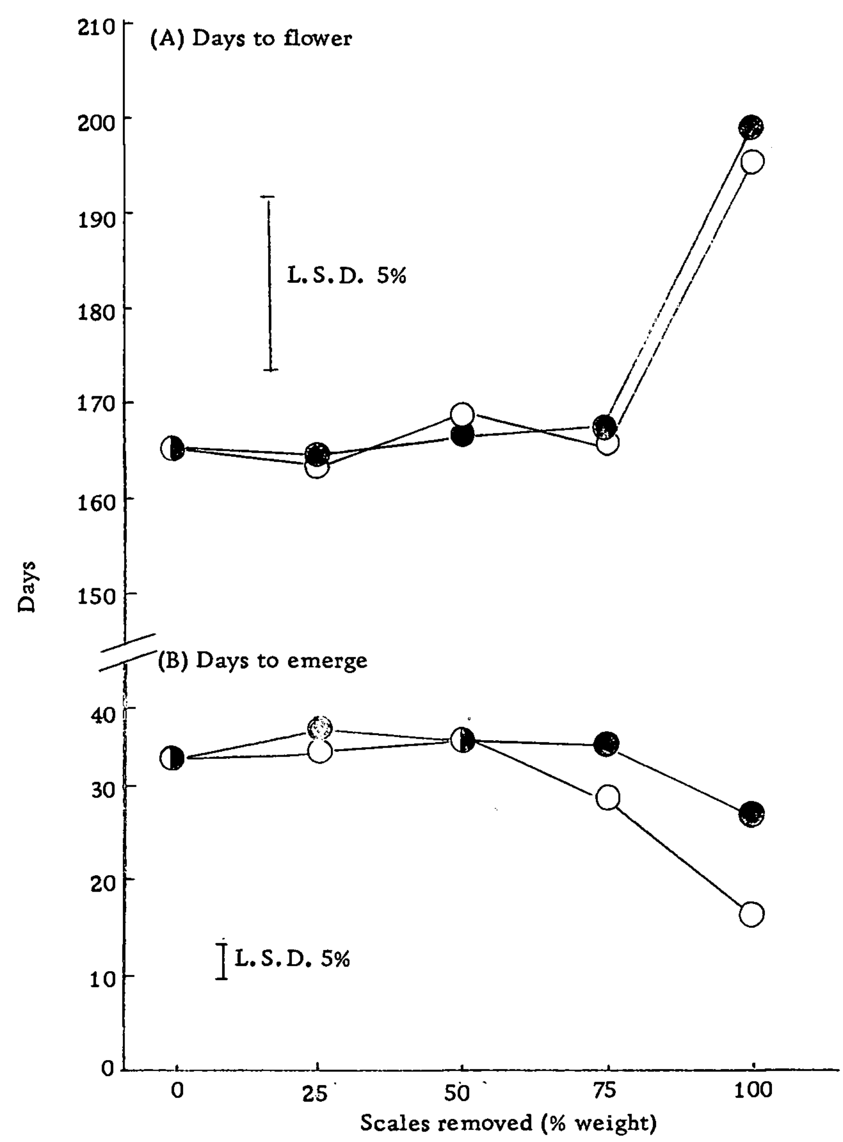

Fig. 3-1. Effect of scale removal on (A) days to flower and (B) days to emerge of 'Nellie White' lily. Open symbols: scales removed before 3 weeks storage at 40° F; closed symbols, after 3 weeks storage at 40° F. (Ten plants per treatment)

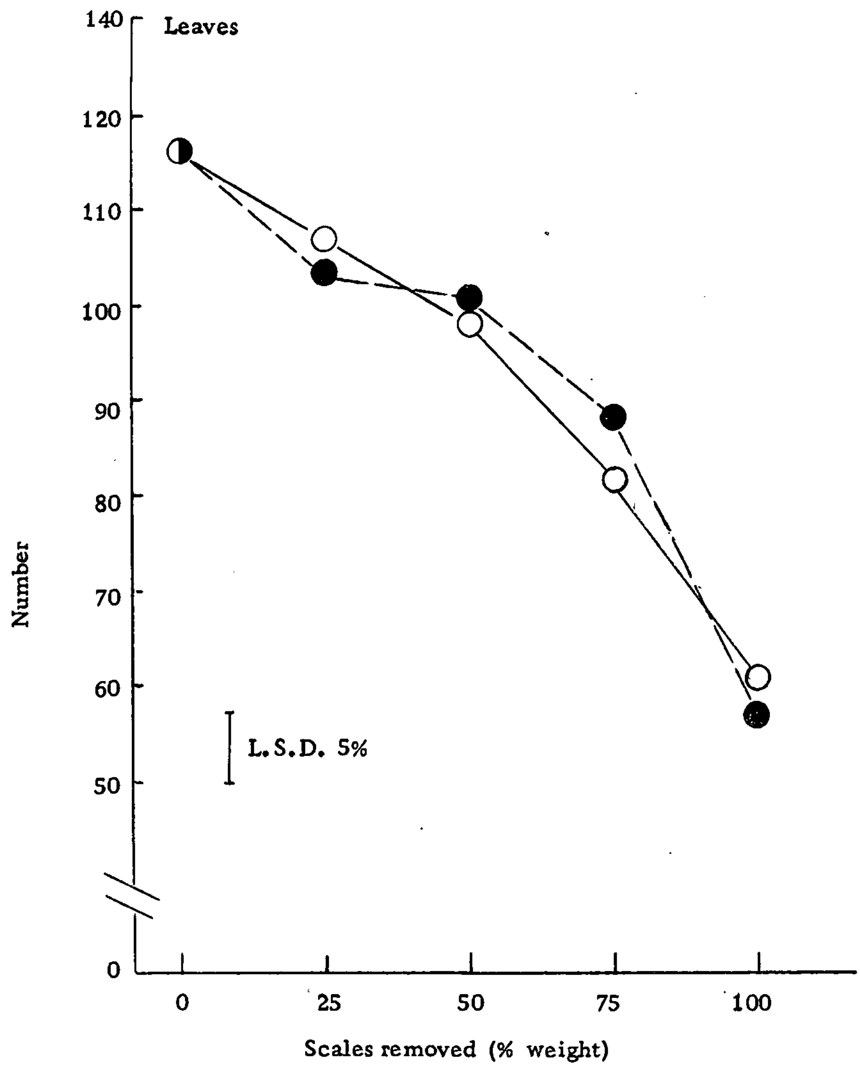

Fig. 3-2. Effect of scale removal on leaf numbers of 'Nellie White' lily. Open symbols: scales removed before 3 weeks storage at 40° F; closed symbols, after 3 weeks storage at 40° F. (Ten plants per treatment)

numbers were not affected by the time of scale removal.

Days to Flower

Removal of scales tended to increase slightly the days to flower, but between 0 and 75% scale removal this tendency was not significant. On the other hand, removal of the last 25% of the scales (100% scale removal) drastically delayed flowering. The time of scale removal did not affect the days to flower.

Number of Flower Buds Initiated

Flower buds per plant decreased in proportion to the amount of scales removed, but at least one flower bud was initiated by plants grown from bulbs without any scales. None of the buds aborted. Time of scale removal did not affect the number of flower buds initiated.

Stem and Internode Length

The length of the stem was inversely proportional to the amount of scales removed. Removal of the first 25% of scales did not affect internode length, but above this level internode length tended to decrease proportional to the severity of scale removal. Removal of the last 25% of the scales shortened the internodes severely, and the plants grown from these bulbs were rosetted during much of their life. Time of scale removal did not affect internode length.

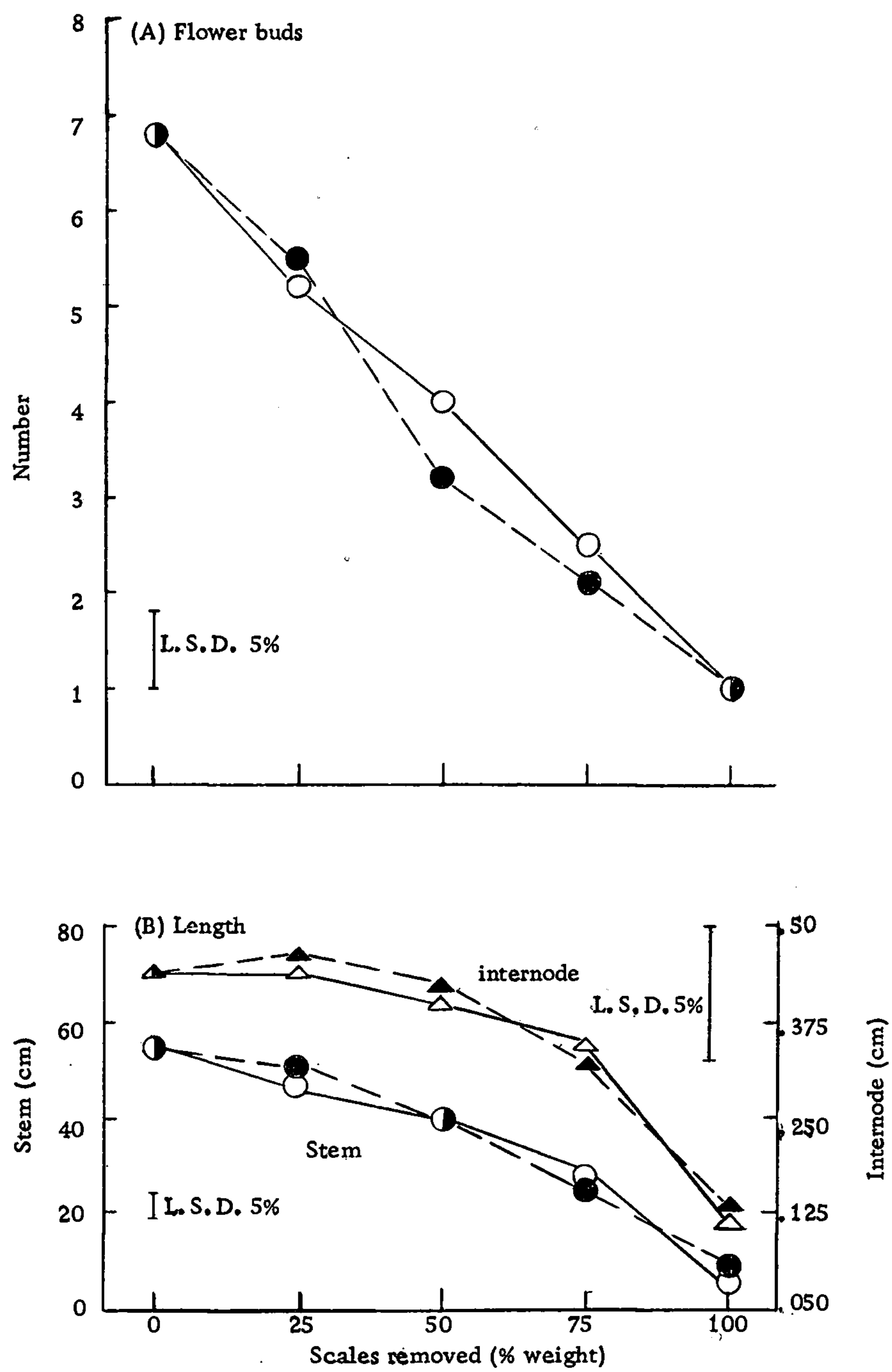

Fig. 3-3. Effect of scale removal on (A) number of flower buds and (B) length of stems and internodes of 'Nellie White' lily stored 3 weeks at 40° F. (Ten plants per treatment)

Fig. 3-4. Plants grown from 'Nellie White' bulbs whose weights were reduced by 0 to 75% by scale removal. The plant labelled 100% was grown from a bulb from which all the scales were removed. The bulbs were vernalized for 3 weeks at 40° F after the scales were removed and were grown to flower at 70° day and 60° F night minimum temperatures. Photographed March 30, 1967.

The data suggest that the scales perform several physiological roles. The daughter scales appear to be a source of dormancy, because the shoots emerged earlier after these scales were removed. Perhaps the daughter scales contain a thermolabile and diffusable substance that promotes dormancy. Comparison of the results for 100% scale removal before and after vernalization suggests that during vernalization this substance might have diffused from the youngest of the daughter scales to the shoot retarding its sprouting because removal of these scales before vernalization accelerated emergence by about ten days. Rodrigues Pereira (1962, 1964) reported in Iris that during cold storage a substance was transported from the scales which prevented or delayed growth of the bud. The primordial leaves, however, were necessary for floral induction.

That the scales are inhibitory to physiological earliness, that is, early flower initiation versus anthesis, is shown by the progressively lesser leaf numbers with each increment of scale removal. Removal of mother scales (up to 50% scale removal) reduced leaf number by 17 leaves, while removal of daughter scales (75 to 100% scale removal) reduced it by 40 more leaves. This suggests that the daughter scales are especially inhibitory to the onset of flower bud initiation. An alternative explanation would be that the scales furnish substrate for growth and, therefore, the greater the weight of scales, irrespective of their age, the more leaves the growing point will initiate before it initiates the first flower bud in response to the flower inducing action of vernalization. Further research is needed to resolve this question.

Although the earliness of onset of flower bud initiation was inversely related to the weight of scales, the quantity of flower buds initiated was directly related to the weight of bulbs. The latter relationship suggests that the scales provided substrate necessary for continued initiatory activity by the growing point. Contrarily, the present results would not assign the scales the role of promoting induction of the reproductive stage as Rodriques Pereira (1964) reported for Iris xiphium. The primordial leaves in Easter lily, as in Iris, might perform this role because primordial leaves still surrounded the growing point even after all the scales had been removed. Halaban, Galun and Halevy (1965) cultured in vitro stem tips of Ornithogalum Arabicum L., a liliaceous plant, and concluded that bulb leaves and scales promoted the transition to the reproductive phase. The scales promoted further development of the inflorescence.

The days to flower should have paralleled the number of leaves (Blaney, Hartley and Roberts, 1965). My results suggest that the growth rate was progressively retarded with each increment of scale removal so that the expected reduction in days to flower with progressively lesser leaf numbers was counterbalanced by the slower growth rates. When all the scales were removed, flowering was much retarded in spite of an extremely low leaf number, the 59 leaf number on these plants probably represented the leaf initials present at bulb harvest (Blaney and Roberts, 1966). The flower buds on these plants were also very slow in their development, taking several weeks to open after they had reached the white stage that normally precedes by a day or so the opening of the flower.

The length of the stems reflected not only the number of internodes present to elongate but also the average length of individual internodes. For example, the extremely short plant from the 100% scale removal bulbs had few internodes to elongate and these internodes were extremely short. The scales apparently supplied substrate necessary for internode elongation as was suggested earlier for rapidity of growth and development toward opening of the flowers.

In summary, the scales appear to play inhibitory and promotive roles in the life of the Easter lily. The daughter scales inhibit sprouting, that is, they are the seat of dormancy, and they inhibit the transition of the growing point from the vegetative to the reproductive stage. On the other hand, the scales promote a rapid growth rate and development of the flower buds. Once flower bud initiation commences the scales promote the initiation of large numbers of flowers. They also promote the elongation of the internodes. Further research is needed to separate the role of the scales as the source of plant regulating hormones from their role as storage organs of reserve foods. The relative plant regulatory activity of mother versus daughter scales needs to be clarified also.

SUMMARY

The days to sprout of 'Ace' and 'Croft' bulbs, harvested monthly from February to October and given no storage, ranged from about 7 months to 2 weeks, but on a calendar date basis the earliest harvests sprouted in mid-September, the late harvests in mid-November, a range of only 2 months. This indicated that the acquisition of the ability to start another growth cycle was in phase with the changing season. Cold storage (6 weeks at 40° F), which did not hasten sprouting of February and October bulbs, accelerated greatly the April bulbs. Warm storage (6 weeks at 70° F) accelerated sprouting of February bulbs by more than 4 months compared to no storage of these bulbs, but had no effect on October bulbs. Cold storage, which did not vernalize February bulbs, became more and more effective as the season progressed. Warm storage apparently vernalized February and March bulbs because they flowered quickly at low leaf numbers, but by April it did not vernalize and early flowering was not stimulated. These observations are discussed in terms of causes of summer-sprouting and adaptation of these cultivars to the Pacific Northwest.

Calculated growth rate curves, in terms of leaves unfolded per day for each storage treatment, were similar in shape but differed in magnitude. Leaf unfolding was slow for February bulbs, decreased

to a minimum for April bulbs, and rapidly increased to a maximum with the August and later bulbs. Compared to the effects of no storage, cold storage retarded the February to May bulbs and accelerated bulbs harvested after May, while warm storage always accelerated the rate compared to no storage.

Days to emerge, leaf numbers, days to flower, numbers of flower buds, and stem lengths of 'Ace' and 'Croft' were generally inversely related to bulb storage durations of 0 to 18 weeks at 40° F, but the first 3 to 4 weeks of storage reduced all these plant characters the most. After storage for 6 weeks at 40° F, these cultivars had formed flower buds about 6 weeks after potting, 3 weeks after emergence, at an average leaf number of 82. Leaves were unfolded at a fairly steady rate of about 1.31 to 1.35 per day. The application to timing of lilies is discussed.

Varying degrees of scale removal, ranging from 0 to 100% removal, on 'Nellie White' bulbs suggested that scales perform several physiological roles. The daughter scales, that is the young inner scales, appeared to be the seat of bulb dormancy because their removal greatly accelerated sprouting. Scale removal, especially of the daughter scales, significantly reduced the number of leaves below the first flower, suggesting that the scales are inhibitory to the onset of flower bud initiation. But the number of flower buds initiated and the rates of growth were inversely proportional to the degree of scale removal.

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APPENDIX

Appendix Ia. Effect of date of bulb harvest and 6 weeks of storage on (A) days to emerge and (B) days to flower of 'Croft' lily. (Ten plants per treatment)

	DAYS TO EMERGE			DAYS TO FLOWER		
	Storage Treatment					
	no storage	6 weeks at		no storage	6 weeks at	
Harvest date	check	40° F	70° F	check	40° F	70° F
Feb. 21	214.2	195.2	84.4	443.3	417.7	174.8
Mar. 16	180.1	117.3	92.8	438.6	378.6	206.2
Apr. 13	179.9	57.1	108.0	399.6	298.0	366.8
May 18	161.5	93.3	99.5	376.0	245.7	334.6
June 20	142.7	86.5	90.1	341.6	244.3	299.2
July 19	111.2	33.5	65.5	325.0	169.0	274.5
Aug. 19	93.6	21.8	61.1	309.9	123.2	250.7
Sept. 18	52.0	20.4	44.0	289.9	109.6	223.7
Oct. 16	18.5	12.0	4.9	248.5	96.0	219.7
L.S.D. 5% - 22.7				L.S.D. 5% - 13.8		

Appendix Ib. Effect of date of bulb harvest and 6 weeks of storage on (A) leaf number and (B) flower buds initiated and aborted of 'Croft' lily. (Ten plants per treatment)

	LEAF NUMBER			FLOWER BUDS INITIATED			FLOWER BUDS ABORTED		
	Storage Treatment								
Harvest date	no storage check	6 weeks at 40° F	6 weeks at 70° F	no storage check	6 weeks at 40° F	6 weeks at 70° F	no storage check	6 weeks at 40° F	6 weeks at 70° F
Feb. 21	175.0	172.7	52.3	7.0	7.70	1.8	0.4	0.7	0.4
Mar. 16	180.9	117.4	66.6	10.3	6.5	3.0	0.9	0.9	0.5
Apr. 13	131.2	60.6	184.2	5.5	2.2	7.5	0.5	0.7	1.3
May 18	168.1	103.1	203.0	7.9	6.1	9.6	0.8	0.8	1.4
June 20	159.0	131.4	213.0	8.0	7.3	9.5	1.3	0.8	0.5
July 19	205.2	125.4	241.7	8.8	4.2	10.1	1.8	0.8	1.7
Aug. 19	274.9	119.0	240.1	12.1	6.1	11.6	2.3	1.8	1.5
Sept. 18	307.1	84.2	216.9	13.4	5.9	11.2	3.7	0.8	1.7
Oct. 16	288.4	78.4	216.6	14.1	3.9	8.8	3.6	0.0	2.3
L.S.D. 5% - 36.9				L.S.D 5% - 2.3			L.S.D. 5% - 1.0		

Appendix Ic. Effect of date of bulb harvest and 6 weeks of storage on (A) stem length and (B) growth rate of 'Croft' lily. (Ten plants per treatment)

	Storage Treatment					
	STEM LENGTH (cm)			GROWTH RATE[a]		
Harvest date	no storage check	6 weeks at 40°F	6 weeks at 70°F	no storage check	6 weeks at 40°F	6 weeks at 70°F
Feb. 21	66.7	54.3	19.7	0.94	0.66	1.06
Mar. 16	63.2	38.1	26.1	0.84	0.73	0.95
Apr. 13	40.2	14.8	46.4	0.74	0.31	0.88
May 18	48.7	36.7	65.2	0.98	0.94	1.05
June 20	45.3	41.5	63.8	1.00	1.14	1.28
July 19	60.1	51.6	84.8	1.19	1.35	1.44
Aug. 19	97.7	83.2	89.3	1.58	1.99	1.62
Sept. 18	91.9	90.6	80.4	1.57	1.75	1.57
Oct. 16	105.9	72.1	81.8	1.53	1.86	1.25
L.S.D. 5% - 13.3						

[a] $\text{Growth rate} = \dfrac{\text{leaves per stem}}{\text{days to flower} - (\text{days to emerge} + 42^{b})} = \text{leaves unfolded per day}$

[b] Observations over several years have shown 42 days to be a fairly accurate estimate for the days elapsing from first bud visibility to anthesis at 70°F day and 60°F night minimum temperatures.

Appendix Id. Effect of date of bulb harvest and 6 weeks of storage on length of 'Croft' lily leaves three and six inches above the soil line. (Ten plants per treatment)

	LEAF LENGTH (cm)					
	AT 3-INCH LEVEL			AT 6-INCH LEVEL		
	Storage Treatment					
Harvest date	no storage check	6 weeks at 40°F	6 weeks at 70°F	no storage check	6 weeks at 40°F	6 weeks at 70°F
Feb. 21	18.5	16.5	11.1	16.3	15.5	11.8
Mar. 16	16.8	14.5	12.5	17.9	13.7	10.3
Apr. 13	14.5	10.1	13.7	12.0	7.7	12.3
May 18	15.8	13.0	17.1	14.7	11.0	16.2
June 20	15.2	13.1	18.8	12.5	11.1	17.0
July 19	16.7	17.2	20.4	15.4	18.1	19.0
Aug. 19	17.1	18.9	22.0	19.5	21.9	19.8
Sept. 18	17.2	13.3	19.1	17.8	17.3	18.9
Oct. 16	14.1	12.3	9.9	19.8	18.4	16.2
L.S.D. 5% - 2.6				L.S.D. 5% - 2.5		

Appendix II. Effect of duration of storage at 40° F on leaf number and other characteristics of 'Ace' and 'Croft' lilies. (Ten bulbs per treatment)

A. ACE

Storage (weeks)	Days to emerge	Days to flower	Leaf numbers	Flower numbers initiated	Flower numbers aborted	Stem length (cm)	Growth rate
0	44.1	227.3	295.7	12.7	2.2	126.8	2.10
1	36.2	279.4	311.6	12.6	1.8	134.2	1.55
2	30.6	247.9	254.7	10.8	0.5	114.9	1.46
3	31.1	190.2	165.8	7.9	0.7	86.5	1.40
4	25.3	141.7	89.7	4.1	0.1	68.3	1.20
5	26.3	132.7	87.2	4.4	0.0	71.2	1.34
6	26.3	127.7	71.5	3.7	0.0	59.2	1.03
7	19.1	114.7	67.2	4.3	0.1	64.4	1.24
9	18.3	114.4	63.3	3.6	0.1	68.3	1.17
13	16.7	104.4	51.4	2.3	0.0	53.2	1.03
18	13.5	105.4	51.3	2.2	0.1	44.8	1.04
L.S.D. 5%	3.5	12.5	24.0	1.5	0.6	10.9	

(Continued)

Appendix II. (Continued)

B. CROFT

Storage (weeks)	Days to emerge	Days to flower	Leaf numbers	Flower numbers initiated	Flower numbers aborted	Stem length (cm)	Growth rate
0	59.8	273.9	190.2	10.4	1.0	66.1	1.10
1	31.9	267.7	254.1	12.0	1.4	89.6	1.20
2	33.7	218.8	181.7	8.7	0.9	77.4	1.27
3	33.1	150.6	101.4	4.1	0.3	61.3	1.33
4	28.6	138.8	97.2	4.1	0.5	72.7	1.43
5	25.9	131.4	87.6	3.9	0.6	76.1	1.40
6	22.3	127.1	85.4	3.9	0.5	70.2	1.35
7	22.6	118.7	65.6	4.2	1.2	62.5	1.22
9	20.6	117.8	66.9	3.7	0.2	58.9	1.22
13	18.0	110.3	52.3	2.9	0.2	52.2	1.04
18	16.4	106.2	46.9	2.5	0.2	43.0	0.98
L.S.D. 5%	6.2	9.7	23.2	1.7	N.S.[a]	10.5	

[a]N.S. - not significant

Appendix III. Effect of scale removal on growth and flowering of 'Nellie White' Easter lily. A, Scales removed before; B, scales removed after 3 weeks bulb storage at 40°F. Means of ten bulbs per treatment. Average bulb weight at planting corresponding to percentage of scales removed: 0%, 173 g; 25%, 129 g; 50%, 87 g; 75%, 43 g; and 100%, 16 g.

% scale re-moved	Treatments											
	Days to				Number of				Lengths of			
	Emerge		Flower		Leaves		Flower buds		Stems		Internodes	
	A	B	A	B	A	B	A	B	A	B	A	B
0	32.7	32.7	165.2	165.2	116.2	116.2	6.8	6.8	54.3	54.3	0.45	0.45
25	33.3	32.5	163.3	164.7	103.5	107.0	5.2	5.5	46.5	50.2	0.45	0.47
50	34.8	34.9	168.3	166.7	101.0	98.0	4.0	3.1	39.9	40.6	0.37	0.41
75	28.3	34.0	165.7	167.3	88.8	81.8	2.5	2.1	28.9	25.4	0.32	0.31
100	16.5	26.7	195.0	198.1	56.2	61.2	1.0	1.0	6.5	9.5	0.11	0.15
L.S.D. 5%	3.5		18.4		7.1		0.8		5.0		0.18	