AN ABSTRACT OF THE THESIS OF

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in HORTICULTURE (Major) presented on March 4, 1969 (Date)

Title: PHYSIOLOGY OF DORMANCY IN LILIUM LONGIFLORUM THUNB.

Abstract approved: [redacted]
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Responses in growth and plant composition to bulb scale removal, vernalization, field soil heating, and chemical stimuli were used to study the physiology of dormancy in Lilium longiflorum Thunb.

Responses suggested that daughter scales are the main source of dormancy up to time of bulb maturity. Ratio of new/old scales may be used as index of bulb maturity. When new and old scales are equally distributed, the bulb is approaching maturity. The source of dormancy is equally distributed in new and old scales at this time.

Dormancy could be overcome by cold storage (40° F), hot water (1-1/2 hours at 100° F), heating soil before bloom (75° F), gibberellic acid (GA), indole acetic acid (IAA), Ethrel (2 chloroethane phosphonic acid) or ethylene treatment.

Cold storage, while overcoming dormancy and inducing flowering, was deleterious to flowering potential. The longer the bulbs

were stored, the greater the reduction in number of flowers initiated. The size of the stem apex may be directly related to flower number in this case.

High temperatures tended to devernalize plants from vernalized bulbs, while low temperatures tend to vernalize plants from non-vernalized bulbs.

Plant responses to various degrees of scale removal, ranging from 0 to 100% with 'Ace' bulbs, suggested that scales perform different roles in dormancy (vegetative) and floral induction (reproductive). Removing old scales (25% and 50%) had little or no significant effect on dormancy, but new scale removal (75% and 100%) accelerated emergence and broke dormancy. Removal of up to 50% of the scales of bulbs hastened flowering, but removing all of the scales delayed flowering drastically.

Bulbs harvested "immature", that is, with only 20 new daughter scales, required 71 days to emerge and 85 days to flower from emergence without special treatment but emerged in 51 days with GA treatment. However, these GA treated bulbs required 92 days to flower, indicating that dormancy and flowering while associated are independent phenomena.

The presence of and changes in certain free amino acids in old and new scales before and after vernalization treatment were indicative of metabolic changes during chilling and overcoming dormancy.

Most of the free amino acids, as well as, protein nitrogen tended to increase with chilling.

The content of inhibitors was higher in new than old scales, and storage decreased these while increasing the content of unknown growth promoters. One of the inhibitors was found to be very similar to that of abscisic acid in R_f value and ultraviolet absorption spectra, and one of the promoters was similar to indole acetic acid (IAA) in color reactions with Salkowski and Ehrlich reagents, and R_f value.

Physiology of Dormancy in Lilium longiflorum Thunb.

by

Shiow-ying Wang

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

June 1969

APPROVED:

Professor of Horticulture
in charge of major

Head of Department of Horticulture

Dean of Graduate School

Date thesis is presented March 4, 1969

Typed by Donna L. Olson for Shiow-ying Wang

ACKNOWLEDGEMENTS

I am deeply indebted to the late Dr. L. T. Blaney for originally sparking my interest in this research and guiding me during the initial phase of this investigation.

I would like to express my sincere gratitude to Drs. A. N. Roberts and E. Hansen for their suggestions and guidance throughout this investigation and during the preparation of this thesis.

Much appreciation is also extended to Dr. H. K. Phinney, Dr. N. I. Bishop, Dr. M. N. Westwood, and Dr. W. S. McGuire for serving on my graduate committee.

The financial assistance of the Pacific Bulb Grower's Association is deeply appreciated.

Special appreciation goes to my parents, Mr. and Mrs. Keng-hsin Shyr for giving me the courage and confidence to begin and the fortitude to complete this endeavor. To my husband, Chien-yi, for his help during the course of the experimental work and constant encouragement, I express my sincere gratitude.

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PHYSIOLOGY OF DORMANCY IN *LILIUM LONGIFLORUM* THUNB.

INTRODUCTION

The Easter lily (*Lilium longiflorum* Thunb.) is one of the more important potted plants and cut flowers grown in commercial greenhouses. For many decades greenhouse forcers of Easter lilies have on occassion experienced difficulty in accelerating growth during greenhouse forcing. Under certain circumstances bulbs have been observed to remain dormant for long periods of time after planting. There has been little work done on the physiology of bulb dormancy in Easter lily. The onset of dormancy in lily bulbs in greenhouse soil has been reported by Thornton (78), as due to poor aeration, but this might be regarded as an unusual, rather than the normal situation. The object of this research was to determine certain aspects of dormancy in Easter lily bulbs. First, attempt to define dormancy and develop a concept of its development and removal by temperature, chemical, and mechanical treatment. Secondly, attempt to separate dormancy responses (vegetative) from floral induction (reproductive) to treatments. Thirdly, determine some of the biochemical changes taking place during the development and removal of dormancy. Endogenous growth substances may play an important direct role in this regard, and information of free amino acids and nitrogen as

biosynthetic precursors of proteins, coenzymes and many other substances may be of importance in better understanding the nature and control of dormancy. Therefore, the qualitative and quantitative changes in growth substances, free amino acids, and nitrogen fractions in the bulbs were considered.

LITERATURE SURVEY

Among horticulturists the state in which growth does not proceed whether as a result of unsuitable environment or internal physiology within the organism or organ is referred to as dormancy. Specifically, when internal conditions are such that growth would not occur, even though external conditions were favorable is termed a state of rest. Winter chilling is responsible for the termination of rest in nature. The amount of chilling and the optimum temperature vary with species (12). During dormancy the frequency of mitosis decreases correlatively with the inhibition of growth.

Smith and Kefford (70) characterized the onset of dormancy as a phase of increasing cell division and decreasing cell enlargement.

Onset of Dormancy

As is evident by the amount of literature on the subject, considerable attention has been and is being focused on the study of dormancy in both buds and seeds (85), but, little work has been done on factors responsible for the onset and removal of dormancy in bulbs. Our understanding of the nature of dormancy seems to have begun in the mid-1930's with the proposal that the dormant state was a consequence of auxin shortage. Avery et al. (2), studying growth hormones in Aesculus and Malus, detected auxins in increasing

amounts during the period of the swelling of ternminal buds. The peak hormone content was reached just prior to the period of the most rapid spring growth.

Dormancy in bulbs has been described by some as the condition of the bulb after the leaves have died down and before extension growth is resumed in the autumn. Others have objected to the use of the term "dormancy" in this context since, flower initiation may be taking place, as in the tulip (33, 90). Rees (65) indicated that there is no dehydration of bulbs as occurs in the ripening of seeds, but there is a cessation of extension growth at the time of flowering. When the main axis is growing the lateral buds are suppressed by an apical dominance mechanism, which is effective even when the main bulb axis is no longer active and is thus carried over into the autumn when growth is resumed (65). Clark and Heath (14) also showed there to be an increase in indoleacetic acid following long-day induction of bulbing in onion, even before visible signs of leaf-base swelling. Bulb dormancy resembles most closely the summer dormancy category suggested by Doorenbos (21) for wood plants, i.e. dormancy in which the environmental effect was less important than that of internal causes and which disappeared with time. Contrary to popular belief low temperatures are not essential to overcoming dormancy in tulip and narcissus bulbs.

There is no evidence of photoperiodic control of dormancy in

bulbs, as has been demonstrated in the buds of many woody plants, although Magruder and Allard (49), Bremer (9), and Holdsworth and Heath (40) showed that day-length had an effect on bulb-formation in onion, bulbing occurring only under long days. Day-length effects appear to have been recorded only for species of Allium.

Temperature, Flowering and Dormancy

Chouard (13) 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 in 1928 coined the term 'jarovization', or 'vernalization' in English, to describe the flower inducing effects of cold temperature treatment on seeds of winter cereals. Chouard (13) emphasized that processes preparatory to flowering occur during vernalization and not flower initiation itself, therefore, vernalization was an inductive process. Wellensiek(87) stated that vernalization, in the sense of removal of inhibitions, was not always sufficient for flower bud formation. An illustration was seed vernalization, which must always be followed by long days in order to obtain flowering, perhaps with the exception of Silene. Povar (64) has also the opinion that flowering in wheat can be induced by warm temperature treatment, but his paper did not convince that warmth truly acted to vernalize.

Chouard (13) indicated that the breaking of dormancy as induced by chilling, often removed growth inhibition and allowed active growth as soon as favorable conditions returned, but did not directly cause the formation of new kinds of organs as did vernalization. The breaking of dormancy belonged to the physiology of growth or vegetative development; vernalization to the physiology of reproductive development. As an example, chilling potatoes to increase tuber yield, though commonly, but wrongly named "vernalization", merely utilizes an after effect of cold on vegetative vigour, and has nothing to do with the specific aim of vernalization, which is, to induce the capacity for flowering.

Inhibitors and Dormancy

In recent years there have been an increasing number of observations which lead us to believe that naturally occurring growth inhibitors may play an important role in the origin and control of dormancy in seeds, tubers, and buds. The inhibitors in buds have usually been found in the bud scales, while none could be found in the meristem proper in peach (19), potato tuber (34) and Fraxinus (35, 36). Hemberg reported evidence of the existence of growth-inhibiting materials of significance to the rest period. Large amounts of inhibitors were extracted from resting terminal buds, while similar extracts made in early spring showed much reduced

inhibitor concentrations. Ethylene chlorohydrin or rindite treatment have both been reported as effective in reducing the inhibitor content of Faxinus buds and thereby breaking the rest (35, 36).

Numerous studies subsequent to Hemberg's, have shown that as dormancy was broken buds showed a marked lowering of extractable inhibitor content. Extraction of resting peach flower buds yielded a specific inhibitor, present in large amounts between November and February, which decreased in concentration until it disappeared from the buds two weeks prior to bloom (37, 38, 86). Blommaert (6, 7) measured the auxin and inhibitor contents of peach buds in South Africa and found that during the dormant period the auxin content was low and inhibitor content high, but the situation was reversed as dormancy was broken. This led him to postulate that dormancy may be conditioned by an auxin-inhibitor relationship. He also separated the effect of a cold (7° to 2° C) and a warm (10 to 26° C) dormant period on the auxin and inhibitor contents of buds. He found that with breaking of dormancy the inhibitor content dropped more rapidly in the former than in the latter case, and confirmed that adequate cold stimulated inactivation of the inhibitor. On the other hand, delayed inactivation of the inhibitor during a relatively warm dormant period may disturb the auxin/inhibitor balance, thus giving rise to prolonged rest or delayed foliation in spring. Similar results have been found by Hendershott and Bailey

in peach (37).

Phillips and Wareing (60) studied the inhibitor content of leaves, stems, and buds of Acer pseudoplatanus and found the inhibitor accumulated in both leaves and stem tips during the growing period, reaching their highest levels at cessation of growth. The dormant buds then showed quite high inhibitor levels, which declined in February and March as dormancy passed. They (61) also found that the production of the inhibitor in the leaves was followed by significant translocation to and accumulation of inhibitor in the apical region. The active growing shoot tolerated the inhibitor, which never disappeared completely from the apical region during the year, but underwent quantitative changes with a significant drop in content occurring at the time of breaking dormancy. An objection to the inhibitor explanation of bud dormancy has been raised by Von Guttenberg and Leike (29). They found that while the decline of inhibitors coincided with the passing of dormancy in Fraxinus, it occurred considerably later in Syringa and Acer buds. Similar objections have been raised by Buch and Smith (11), and Housley and Taylor (41) working with the inhibitor content of potato tuber-buds.

Inhibitors have been identified as parasorbic acid, ammonia, hydrogen cyanide, mustard oil, unsaturated lactones (coumarin and parasorbic acid) (1, 81), naringenin (5, 7, 4-trihydroxy flavanone) (39) and Abscisin II (dormin) (15, 16).

Auxin and Dormancy

In 1935 Boysen-Jensen (8) first proposed that dormancy was a consequence of a shortage of auxins necessary for the progress of growth. In 1937 Avery et al. (2) measured the auxin content of apple buds as they started growth in the spring and found there was indeed a surge in auxin formation at the commencement of growth. But if a shortage of auxin were responsible for dormancy, then auxin applications should be generally effective in relieving dormancy, and they are not. Samish (68) in his review has summarized the results of various workers. In accordance with the theory of polar inhibition of lateral buds due to excessive auxin concentration (84), Kassem (43) was able to extract a much larger amount of "total" auxin from pear shoots at the beginning of rest than later on. Toward the end of the rest period, the auxin concentration continuously declined. Eggert (24) showed that rest was terminated when the auxin concentration in apple buds dropped below about 0.25 μg. But this theory was questioned by Skoog (69) and Thom (76) who showed that an auxin concentration would have to be above 10^{-3} M in order to inhibit growth in pear, an amount much greater than that found in these buds at any time. As against these findings with "total" auxin, Bennett and Skoog (3) did not find any diffusible heteroauxin in resting pear buds, but it rather increased when the rest was ending in the cold

room. Similar results have also been obtained by other workers (43, 76) and clearly indicate that the auxin content of the resting bud was at a minimum and this situation was reversed during the breaking of rest by chilling and auxin levels increased. The application of low concentrations of indoleactic acid or of tryptophane or even sprays with zinc sulphate resulted in breaking of rest.

Other growth substances as kinetin (25, 50), ethylene chlorohydrin or rindite (34, 35, 36) and dimethyl sulfoxide (DMSO) (88) are also effective in breaking dormancy in some species.

Gibberellin Action and Dormancy

Gibberellic acid (GA) applied to resting buds has been substituted for the normal cold treatment in breaking dormancy of some species. The dormancy of inadequately chilled buds and seeds can also be overcome with GA applications (20). Application of either GA or IAA solutions to Hydrangea effectively broke dormancy and induced flowering without exposure to low temperature (73). Stuart and Cathey (74) applied GA to partially replace the cold requirement of seeds requiring low temperature to break their dormancy. For example, the partially cold-treated seeds of sweet cherry and peach showed germination with GA treatment, but the unchilled seeds did not germinate with GA treatment. GA also replaced the light requirement in germinating lettuce seeds. Eagles and Wareing (22, 23)

postulated that winter chilling may overcome dormancy by increasing endogenous GA levels rather than reducing the inhibitor content, thus balance between GA and inhibitors may regulate dormancy. GA can also increase the amount of diffusible auxin (46), controlling apical dominance. For example, Jacobs and Case (42) found auxin applications restored apical dominance for no more than a few days, while GA plus IAA significantly increased the duration of the inhibition of side shoots. Gibberellins may also increase the translocation of endogenous auxin. In 1958, Brian (10) suggested that gibberellin might alleviate the action of some growth inhibitors and Kato (44) reported that the inhibition of pea-stem sections by coumarin was alleviated by adding gibberellin. Similarly, Phillips (62) reported that the dormancy of lettuce seed imposed by treatment with naringenin was overcome by additions of gibberellin.

Miscellaneous Treatments

Stuart (72) treated Louisiana-grown 'Estate' lilies with hot water (75° to 120° F) and found that it reduced the number of days to emergence and flowering compared to cold storage. Ticknor (79) and Tsukamoto (83) also reported that the immersion of bulbs in hot water (110 and 166.6° F for 1 hour) overcame dormancy. Post (63) found that removal of one-third to one-half the scales or the top one-eighth to one-half of each scale delayed flowering one week over

that of bulbs with intact scales. Scales were also important in the flowering of Dutch iris (66, 67) and star-of-Bethlehem (31).

Effect of Treatments on Nitrogen Metabolism

Fine and Barton (26) showed the dormant seeds of peony to have very low levels of amino acid, but during the cold stratification their amino acid content increased. Pauli and Mitchell (59) found that total free amino acids in winter wheat plants increased during the first two weeks of cold treatment. Qualitative studies of free amino acids in winter grown wheat plants by Kirillova (45) showed that some acids increased while others decreased. Moskov and Bozova (55) found that glutamic acid increased in a winter variety of barley during cold treatment but decreased in a spring variety; proline increased only in the winter variety. Grzesiuk and Kulka (28) found the free amino acids glutamic acid and lysine in highest concentrations in young vernalized rye seedlings, whereas aspartic acid was highest in non-vernalized rye seedlings. Trione E. J. et al. (82) also found that certain free amino acids changed with vernalization of wheat. They found 17 known and at least seven unidentified ninhydrin positive components in winter and spring wheat. Only glutamic acid and lysine were more abundant at 25° than at 2°. At 2° the spring variety contained higher quantities of 14 of the amino acids, and the winter wheat contained higher quantities of alanine,

glutamic acid, proline and arginine; at 25° the differences were not so marked. Toshevikova (80) indicated the appearance of catalase and proteinase during rest-breaking.

TERMINOLOGY

Certain terms take on slightly different meanings as they are used by laymen in the culture of certain crop plants and by certain professional research groups. The following terms are defined to indicate the sense in which they are used in this investigation.

New or daughter scales. Scale initiated by and developing below and around the new daughter apex arising from a bud in the axil of the scale subtending the old or mother axis. Constitute approximately half of the dry weight of the bulb at maturity. Initiated and start their development shortly after mother axis starts elongation (Figure 1) (4).

Old or mother scales. That portion of the bulb carried over from the previous year's initiatory activity. No new scales possible, but the younger innermost scales of this portion of the bulb continue to expand and accumulate reserves although the contents of the outermost scales are being hydrolyzed and transported to mother axis for utilization during early stages of leaf unfolding (Figure 1) (4).

Bulb maturity. Two year old bulbs from bulblets (bulblet $\xrightarrow{1st}$ yearling $\xrightarrow{2nd}$ commercial) are usually harvested in September for commercial greenhouse forcing. Maturity cannot be based on calendar date or plant appearance, but on daughter bulb's ability to commence its growth cycle. Daughter sprouting after potting is

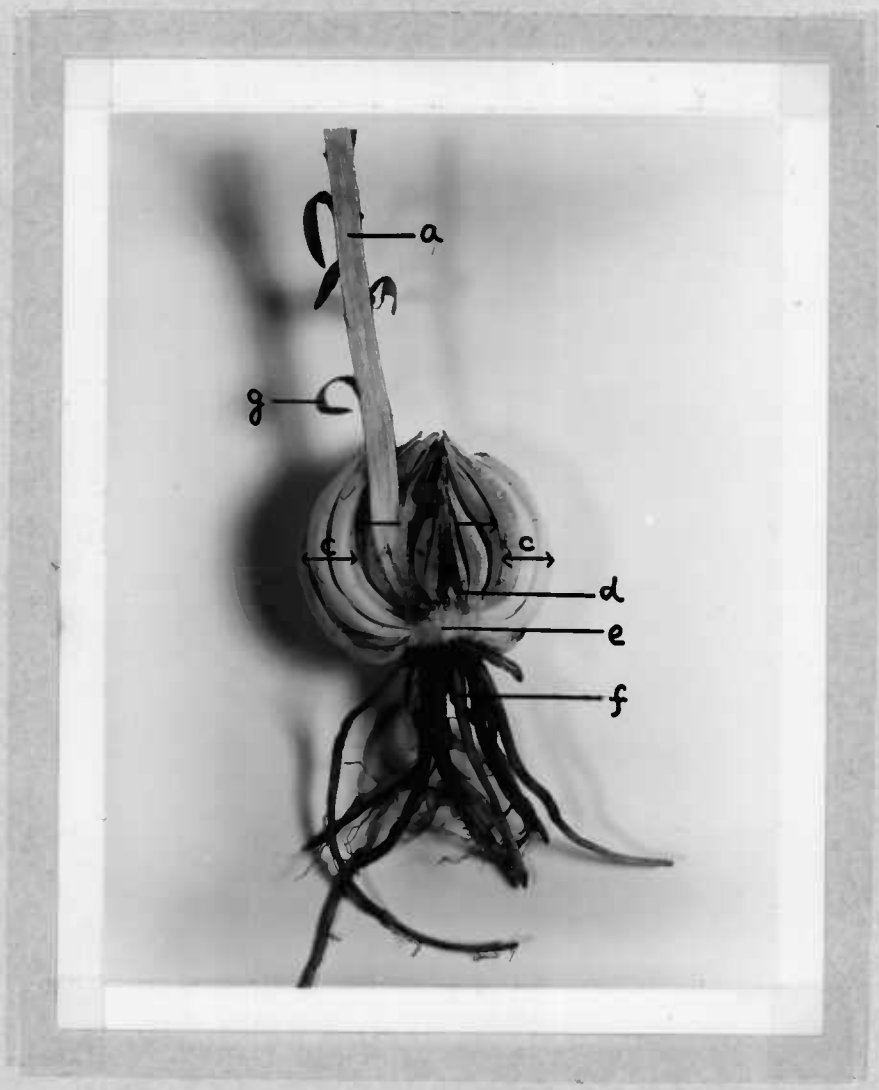


Figure 1. Position of new scales, old scales, flowering shoot, daughter apex and basal plate in a commercial bulb.

a. flowering shoot
b. new scales (daughter scales)
c. old scales (mother scales)
d. apex (next season's plant arises)
e. basal plate
f. root
g. leaves

only sure measure at present of daughter maturity and loss of dormancy.

The first year small bulbs, the stem-bulblets, are produced on the below-ground portion of the flower stem. During the first year of independent growth, which is the second year in the life of the bulb, they are called bulblets. At the end of the second year and during the third year, they are called yearlings. At the end of the third year they are harvested as commercials and are sold for greenhouse forcing. The growers have no name for the bulb which develops within the mother bulb at the base of the flower stem, usually as the result of growth by the bud in the axil of the innermost scale. We have termed it the daughter bulb or daughter. At maturity the daughter is largely enclosed by the imbricated scales of the mother bulb (4).

Dormancy. Undue delay in sprouting or elongation of daughter axis after bulb is dug and mother axis (flower shoot) is removed. Measured on basis of days to shoot emergence, which is determined by growth rate (rate of initiatory activity and organ expansion) and internode elongation.

Vernalization (cold storage, precooling, chilling, cold-moist treatment, 40° F storage). A cold-moist treatment used to accelerate elongation of daughter axis (overcome dormancy), and induce early flowering. While these are often associated phenomena, they

are not necessarily interdependent and dormancy can be removed by treatments that do not induce subsequent flowering. 40° F vernalization is most effective in bringing about rapid floral induction in fall treated bulbs, but 60° F treatment is most effective in bringing about early shoot emergence. 70° F is considered non-vernalizing in fall treated bulbs, but brings about rapid elongation of daughter axis and flowering in early spring.

Growth rate. Growth rate is expressed on the basis of the rate at which leaves unfolded from the spindle, and calculated according to the following formula.

$$\text{Growth rate} = \frac{\text{Number of leaves per stem}}{\text{Days to flower - (days to emerge + 42)}}$$

Observations over several years have shown that 42 days is a fairly accurate estimate of the time lapse between buds visible and anthesis at 70° F day and 60° F night minimum temperature (5).

MATERIALS AND METHODS

Source of Material, General Handling Methods, and Measurement of Growth and Dormancy

'Ace' and 'Croft' lily bulbs, grown on the Pacific Bulb Growers' Research and Development Station, Harbor, Oregon, were used in these experiments. Bulbs were stored in sealed polyethylene bags with one gram of peat moss (52% moisture content) per five grams of bulb. Non-stored bulbs were potted immediately after treatment. The potted plants were randomly distributed on benches in a greenhouse, maintained at 60° F night and 70° F day temperatures, and grown to flowering. Days to shoot emergence, opening of first flower, number of leaves per stem below the lowest flower, number of flower buds per plant, and plant height from soil to lowest flower were determined. Days to emerge was used as an index of the degree of dormancy.

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

Bulb and Scale Growth and Development

Twenty 'Ace' bulbs were harvested monthly from February through October 1967. Total fresh weight, dry weight, and ratio of

new to old scales were recorded (Experiment 1).

Twenty 'Ace' bulbs were harvested monthly from February through October 1967. Bulbs were potted immediately after arrival at Corvallis (Experiment 2).

Relation of Scales to Development of Dormancy

Fifty 'Ace' bulbs (157~200g) were divided into ten-bulb lots of approximately equal weights, on September 12, 1967, and 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, all the scales were removed, so that only the growing point surrounded by leaf primordia, basal plate, and root remained. The mean individual bulb weights after the scales were removed for each degree of scale removal were: 0%, 151g; 25%, 108g; 50%, 76g; 75%, 38g; and 100%, 12g. All of the old scales and one or two new scales were removed at the 50% weight level. Bulbs were potted on September 12, 1967 (Experiment 3).

Forty bulbs were harvested each month from June through October, 1967. Three degrees of scale removal were made on four 10-bulb lots, (1) Old scales removed (2) new scales removed (3) all scales removed (100% scales removed), as in Experiment 3. The mean individual bulb weights after the scales were removed were:

Table 1. Average weight in grams of bulb after scale removal. (Experiment 4)

Harvest dates (1967)	Weight (g) of bulb after removed scales Degree or portion of scales removed			
	0%	New scales	Old scales	100%
June 19	71	57	24	13
July 21	80	70	37	14
August 18	112	86	45	13
Sept. 12	151	124	67	12
October 11	170	85	80	14

Breaking Dormancy

Temperature and Mechanical Treatments

Vernalization and scale removal. Each unit in Table 1 above was further divided into three treatment groups: (1) no storage, (2) six weeks storage at 40° F, and (3) six weeks storage at 70° F (Experiment 5).

Vernalization, hot water and scale removal. One hundred and sixty 'Ace' bulbs were harvested on June 19, 1967. The bulbs were divided equally into four groups, each containing ten entire bulbs: ten with new scales removed, ten with old scales removed and ten with all scales removed. The four groups are treated as follows:

1. Soaked in 100° F water 1-1/2 hours.

2. Soaked in 100°F water 1-1/2 hours → vernalized six weeks at 40° F.

3. Vernalized six weeks at 40° F → soaked in 100° F water 1-1/2 hours.

4. Soaked in tap water (about 60° F) 1-1/2 hours.

The experiment was repeated on bulbs harvested on September 12, 1967 (Experiment 6).

Degree of vernalization and hot water treatment. Twelve 10-bulb lots of 'Croft' were harvested on October 16, 1966. The treatments were as follows:

Group I: No hot water treatment.

Treatment 1. Non-vernalized

Treatment 2. Vernalized 2 weeks at 40° F

Treatment 3. Vernalized 6 weeks at 40° F

Treatment 4. Vernalized 19 weeks at 40° F

Group II: Vernalized for various lengths of time at 40° F → soaked in 100° F hot water 1-1/2 hours.

Treatment 5. Non-vernalized → soaked in 100° F hot water 1-1/2 hours.

Treatment 6. Vernalized 2 weeks at 40° F → soaked in 100° F hot water 1-1/2 hours.

Treatment 7. Vernalized 6 weeks at 40° F → soaked in 100° F hot water 1-1/2 hours.

Treatment 8. Vernalized 19 weeks at 40° F → soaked in 100°F hot water 1-1/2 hours.

Group III: Soaked in 100°F hot water 1-1/2 hours → vernalized for various length of time at 40° F.

Treatment 9. Soaked in 100° F hot water 1-1/2 hours → non-vernalized.

Treatment 10. Soaked in 100° F hot water 1-1/2 hours → vernalized 2 weeks at 40° F.

Treatment 11. Soaked in 100° F hot water 1-1/2 hours → vernalized 6 weeks at 40° F.

Treatment 12. Soaked in 100° F hot water 1-1/2 hours → vernalized 19 weeks at 40° F.

Bulbs in all above experiments were potted in the greenhouse after treatment (Experiment 7).

Field soil heating. One-year-old bulbs of 40~50 gm size, were planted in the autumn about four inches apart in single rows between two strands of thermostatically-controlled heating cables laid in the bottom of the rows. Soil temperatures (70~75° F) were checked daily and the thermostates were adjusted when necessary to maintain the desired temperatures. Cultural practices were those commonly followed by commercial growers in the area.

In the 1964 experiment, soils were heated at various specific periods from (a) April 15 to July 15, (b) July 15 to September 24,

(c) natural soil temperature. Because full bloom occurred about July 15, the soil treatments were referred to hereafter as "warmed before bloom", "warmed after bloom," and "control". The bulbs in each treatment were divided into four five-bulb lots of about equal weights. Individual lots of both cultivars were then vernalized at 40° F for 0, 3, 6, and 9 weeks before planting. The non-vernalized bulbs were potted within two days after harvest (Experiment 8).

Chemical Treatments

2-Chloroethane phosphonic acid (Ethrel). Eighty 'Ace' bulbs, harvested on September 26, 1967, were divided into eight 10-bulb lots, and treated with 0, 1000, 2000, 4000 ppm 2-chloroethane phosphonic acid for 30 seconds. Bulbs in group I were planted in the greenhouse without storage. Bulbs in group II were treated the same as in group I, but stored for ten days at 70° F prior to growing in greenhouse (Experiment 9).

Ethylene (C_2H_4). Ninety bulbs, harvested on September 26, 1967, were divided into two groups, group I containing five 10-bulb lots were treated with 500 ppm ethylene for 0, 2, 4, 6 and 13 days. Bulbs were planted in greenhouse without storage. Group II contained four 10-bulb lots, and were treated the same as in group I, but vernalized at 40° F for four weeks prior to growing in greenhouse (Experiment 10).

Other growth substances. Eleven 10-bulb lots harvested on September 13, 1967, were soaked in various concentrations of the following growth substances for two hours:

(1) Gibberellic acid (GA) 2500 ppm

(2) N, N dimethylamino succinamic acid (B-995, B-9, Alar) 2500 ppm, 5000 ppm

(3) Indoleacetic acid (IAA) 1250 ppm, 2500 ppm

(4) Kinetin 1250 ppm

(5) Abscisic acid (Ab II) 5 ppm

(6) Dimethyl sulfoxide (DMSO) 20 ppm

(7) Control, no chemical treatment (Experiment 11).

Effect of number of new scales in daughter portion, vernalization and GA_3 treatment on dormancy. 'Ace' yearling bulbs harvested October 6, 1967 and potted in the greenhouse soil bench were maintained at approximately 70° F. Bulbs were lifted at specific stages of development as follows:

(1) When approximately 20 new scales were formed (February 29, 1968).

(2) When approximately 40 new scales were formed (May 3, 1968).

(3) With anthesis of mother axis (July 20, 1968).

After lifting, the flowering shoots were removed. The bulbs then received:

a) 1. No storage, no GA_3

2. No storage, soaked in 2500 ppm GA_3 two hours

b) 1. Stored at 70° F for six weeks, no GA_3 treatment

2. Stored at 70° F for six weeks then soaked in 2500 ppm GA_3 two hours

c) 1. Stored at 40° F for six weeks, no GA_3 treatment

2. Stored at 40° F for six weeks, then soaked in 2500 ppm GA_3 two hours

After each treatment, the bulbs were potted and grown in the greenhouse (60~70° F) (Experiment 12).

Apex Size and Flower Number

Ninety uniform 'Ace' bulbs, averaging 123g in size, were dug on August 18, 1967. Fifteen bulbs were stored at 40° F for 0, 6, and 18 weeks before planting in the greenhouse. Immediately after each storage period and at time of flower bud initiation the diameter (mm) of each bulb apex was determined under a dissecting microscope. Days to flower bud initiation from potting following these storage regimes were estimated to be (5).

0 week storage - 115~155 days

6 weeks storage - 20~50 days

18 weeks storage - 10~30 days (Experiment 13)

Plant Vernalization and Devernalization

Eighty 'Ace' bulbs, were dug on August 1st, 1966, and divided into two groups, each containing four 10-bulb lots. Group I was stored at 40° F, and group II at 70° F. After six weeks' storage, all were potted in the greenhouse. After emergence, plants of group I were moved to storage at 70° F for 0, 1, 2, and 3 weeks; plants of group II were moved to storage at 40° F for 0, 1, 2, and 3 weeks. After each treatment, plants were returned to the greenhouse to grow at 70° F day and 60° F night temperature (Experiment 14).

Chemical Analyses

Preparation of Samples

Samples of new and old scales were separated from 15 bulbs in a lot to provide a total weight of 300~350 grams. After cleaning, the scales were ground through a food chopper and thoroughly mixed. Duplicate 50-gram samples were weighed into 600 ml pyrex beakers, covered with 270 ml of 95 percent alcohol and heated to boiling. After cooling, the samples were transferred quantitatively to a waring blender, ground at high speed for three minutes, then filtered through Whatman #2 filter paper into 500 ml volumetric flasks, finally washing the residues 4~5 times with 80 percent alcohol. The extracts were adjusted to volume with 80 percent alcohol.

Suitable aliquots of these solutions were used for determination of free amino acids, the dried residues were used for determination of total alcohol insoluble nitrogen (protein nitrogen).

Free Amino Acid

The individual free amino acids contained in the extracts were separated by Technicon Amino Acid Autoanalyzer. The instrument used was equipped with a 140 centimeter x 6.3 millimeter I.D. glass column. Column packing was Technicon Chromobeads, Type A. The colorimeter unit consisted of two colorimeters equipped with narrow band interference filters providing 470 millimicron and 400 millimicron light respectively. An elution gradient of buffer ranged in pH from 2.875 to 5.0. The three buffers used were of pH 2.875, 3.80 and 5.0 and the gradient attained in a nine chambered "Autograd" (75).

The free amino acids in the extracts were partially purified and separated into basic and neutral and acidic fractions according to the procedures of Thompson et al. (77). The basic amino acids were retained on a Dowex 50 W-X4 ion exchange resin in the NH_4^+ form and were eluted with about 3 ml of 3N NH_4OH. Neutral and acidic amino acids were retained on a Dowex 50 W-X4 resin in the H^+ form, and were also eluted with about 3 ml 3N NH_4OH, followed by 45 ml deionized water. The combined elutes were then evaporated

under reduced pressure at 65° C until no odor of ammonia could be detected. The final solution was 5 ml. The individual amino acids in each sample were then separated and quantitatively determined by Technicon Amino Acid Autoanalyzer.

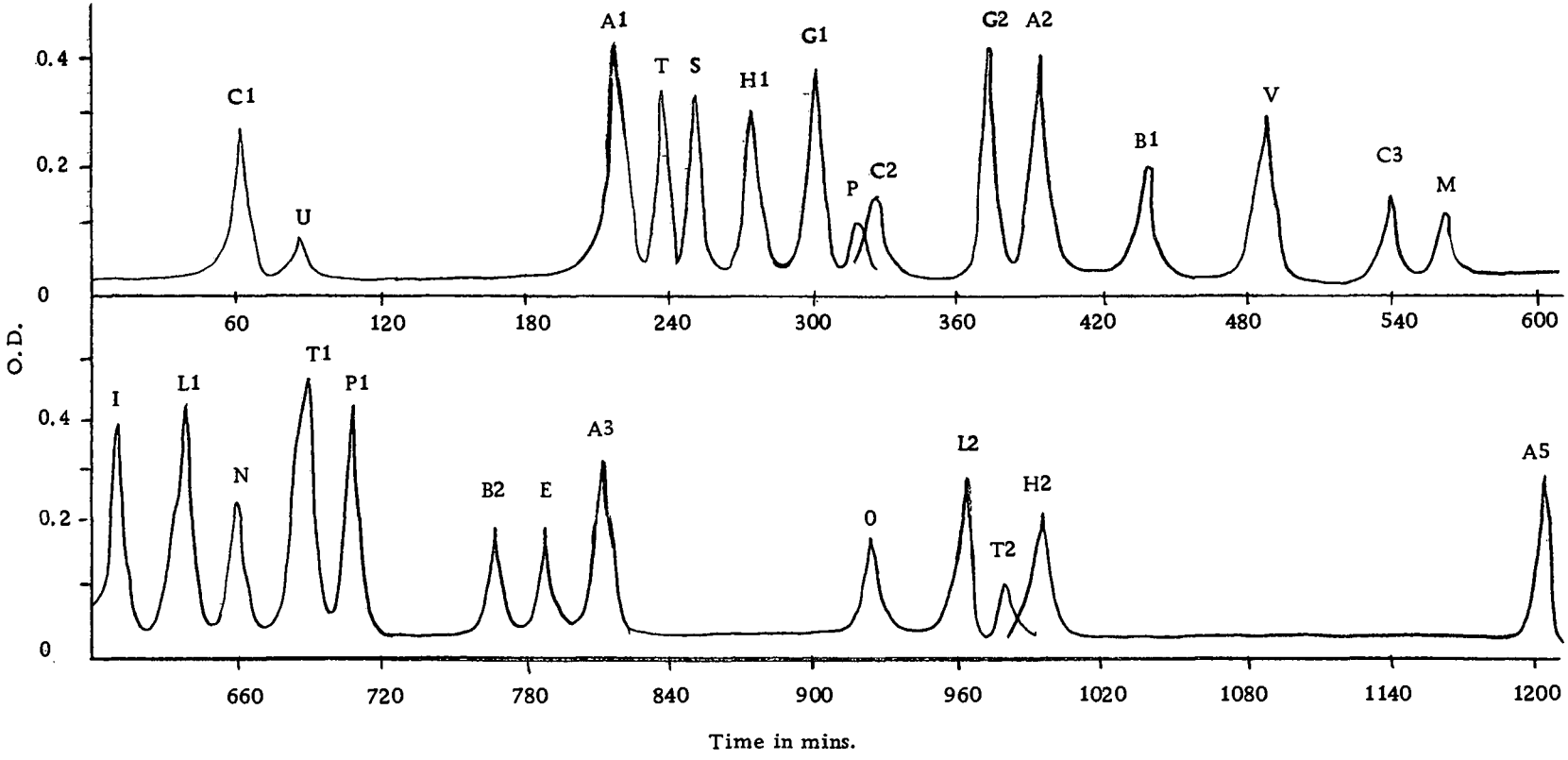
The amino acid peaks on the Auto Analyzer charts were identified by comparison with a known standard and by the characteristic absorption maxium of its ninhydrin reaction product as shown in Figure 2. An estimate of peak area was obtained by triangulation (Experiment 15).

Total Alcohol Insoluble Nitrogen (Protein-N)

Total nitrogen in the residues, total alcohol insoluble nitrogen, was determined by the Kjeldahl Gunning Arnold method (56) (Experiment 16).

Growth Substances

New and old scales were separated from 'Ace' bulbs and extracted with methanol. Oat seeds (cv. 'Forkedeer') were used in the bioassay. The principle of the method is similar to that described by Liao (47) and Nitsch and Nitsch (58). The acidic fraction was used for inhibitor study. The identity of the abscisic acid was determined by the ultraviolet absorption spectra and the Rf value by comparing with synthetic acid and also by paper chromatography (48).



C1 - Cysteic
U - Urea
A1 - Aspartic
T - Threonine
5 - Serine
H1 - Homoserine
G1 - Glutamic
P - Proline
C2 - Citrulline
G2 - Glycine
A2 - Alanine
B1 - ∝ NH2 Butyric
V - Valine
C3 - Cystine
M - Methionine
I - Isoleucine
L1 - Leucine
N - Norleucine
T1 - Tyrosine
P1 - Phenylalanine
B2 - γ NH2 Butyric
E - Ethanolamine
A3 - Ammonia
O - Ornithine
L2 - Lysine
T2 - Tryptophan
H2 - Histidine
A5 - Arginine
O. D. - Optical Density

Figure 2. Position of ninhydrin reactive substances on the chromatogram.

Salkowski and Ehrlich reagents (30) were used for indole acetic acid identification studies.

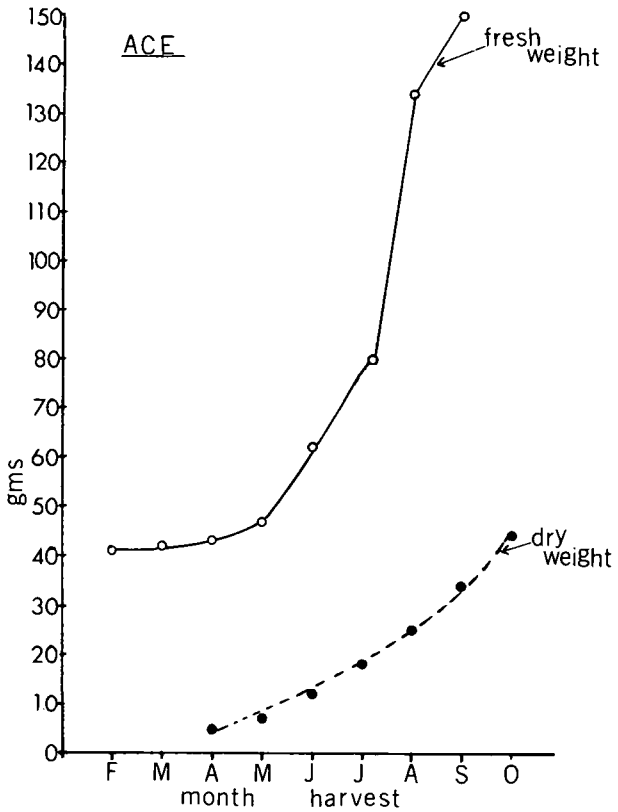
RESULTS

Plant and Scale Growth and Development

Experiments were conducted in 1967 to study plant and scale growth and development in commerical fields. During the spring months (February-April) the bulbs did not increase significantly in fresh weight (from 41g in February to 43g in April), but from June to October increased rapidly from 62g in June to 150g in September. Dry weight also increased from 5g in April to 44g in October (Figure 3).

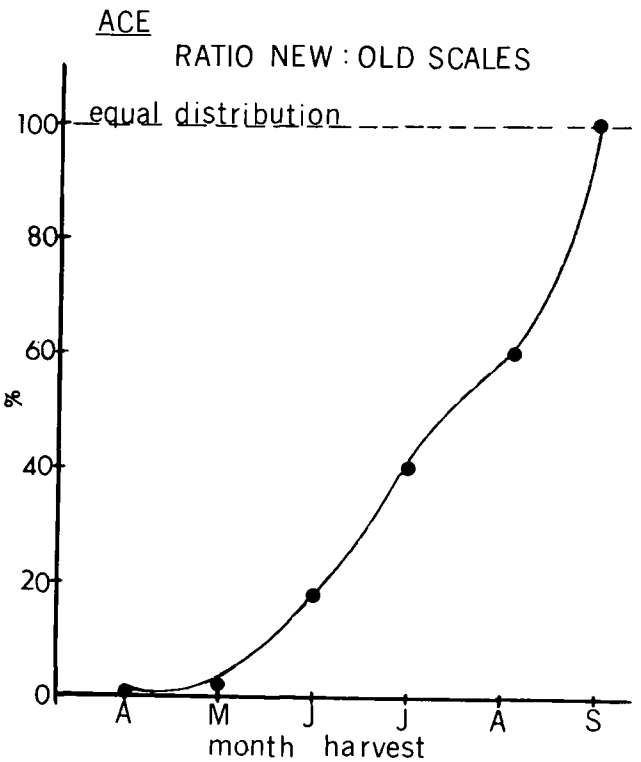
Ratio of new/old scales (on dry weight basis) increased from 0.5% in April to 1% in May, but increased from 60% in August to 100% in September, i.e., in September new and old scales were equally distributed (Figure 4).

The data obtained in Experiment 2 (Figure 5) show that the daughter bulb's ability to start another cycle of growth increases progressively during the growing season and with delay of harvest. With the exception of a short period during anthesis when the trend is reversed, the days required for the non-vernalized daughter bulbs to sprout after harvest and greenhouse potting decreased progressively with later digging dates.



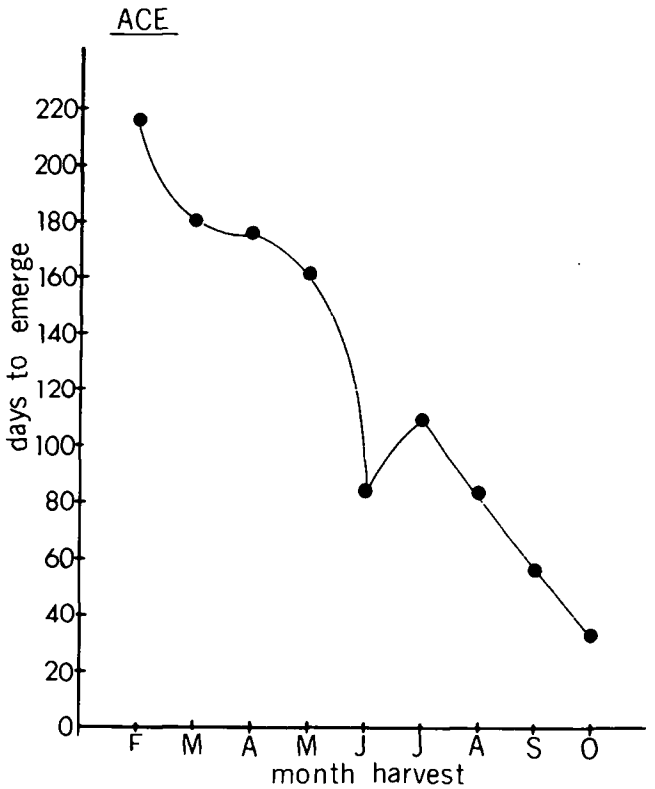
fresh weight---L.S.D. 5% - 28.6
dry weight ---L.S.D. 5% - 9.1

Figure 3. Fresh and dry weight increase of 'Ace' lily bulbs at successive harvests during the growing season.



L.S.D. 5% - 18.4

Figure 4. Progressive increase in ratio of new/old scales (on dry weight basis) with time of harvesting 'Ace' lily bulbs.



L.S.D. 5% - 18.1

Figure 5. Progressive increase in speed of emergence of 'Ace' lilies with delay in harvest date.

Relation of Scales to Development of Dormancy

Removal of old scales (25% and 50% scale removal on September harvested bulbs) had little or no significant effect on days to emerge, but removal of new scales (75% and 100%) accelerated emergence (Figures 6 and 7). Non-vernalized bulbs, July dug 'Ace' bulbs required 83 days to emerge when daughter scales were removed, but 125 days after removal of mother scales. When both were removed, emergence occurred in only 19 days. September dug bulbs with old and all scales removed emerged in 54 and 27 days, respectively (Figures 8 and 9, Table 2). These data indicate that new scales are the principal source of dormancy up to the time of bulb maturity in September. Thus dormancy in the scales progressively decreased during the growing season.

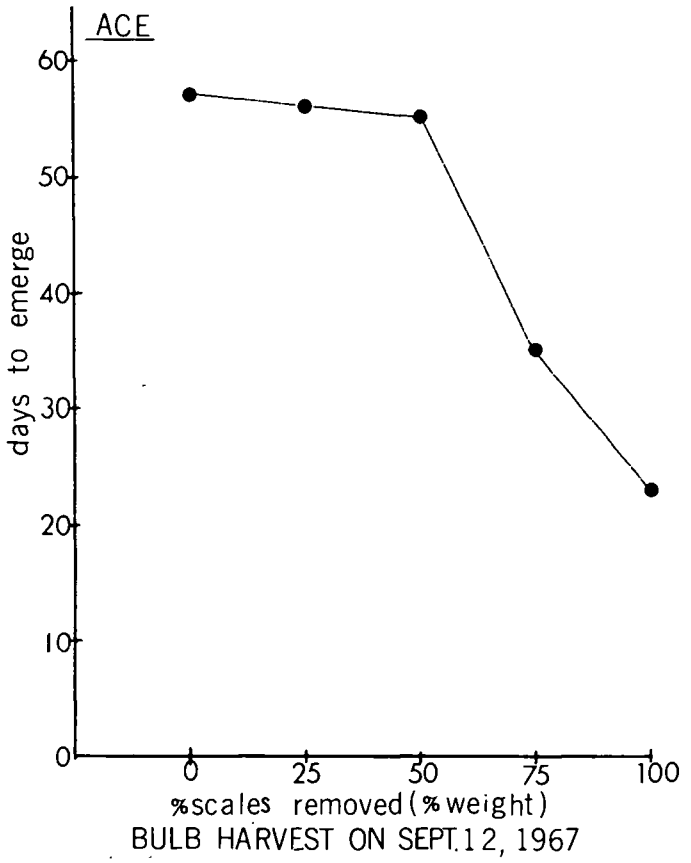
Table 2. Effect of scale removal treatments following various harvest dates on speed of emergence of 'Ace' lily bulbs.

Harvest dates	Days to emerge[a] Treatments			
	Entire bulb	New scales removed	Old scales removed	All scales removed
June 19	84	33	121	15
July 21	110	83	125	19
Aug. 18	84	87	99	32
Sept. 12	57	54	55	27
Oct. 11	33	31	33	23

L. S. D. 5%---9.0

[a]Bulbs were potted immediately and placed in greenhouse at $60^{\circ}\sim70^{\circ}$.

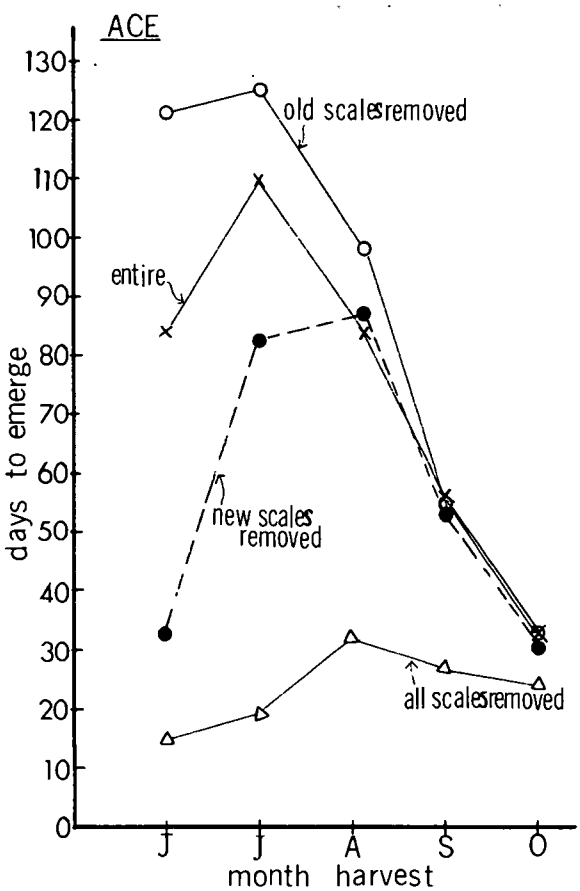
Figure 6. 'Ace' bulbs whose weights were reduced by 100%, 75%, 50%, 25%, 0% (left to right) by scale removal. Photographed September 1967.



L.S.D. 5% - 3.3

Figure 7. Effect of scale removal on days to emerge of 'Ace' lily.

Figure 8. 'Ace' bulbs with all scales removed; old scales removed; new scales removed; entire bulb (left to right). Photographed September 1967.



L.S.D. 5% - 9.0

Figure 9. Effects of scale removal at progressively later harvest dates on speed of shoot emergence in 'Ace' lily.

Removal of up to 50% of the scales of mature bulbs hastened flowering, but removing all of the scales delayed flowering drastically (Table 3).

Table 3. Effect of scale removal on flowering of non-vernalized 'Ace' lily. Means of ten bulbs per treatment, average bulb weight at planting reflecting the percentage of scales removed: 0%, 151g; 25%, 108g; 50%, 76g; 75%, 38g; and 100%, 12g.

% Scales removed	Days to emerge	Days to flower after emergence
0	57	185
25	56	170
50	55	110
75	35	166
100	27	201
L.S.D. 5%---	3.3	15.7

Immature bulbs developed to flowering stage sooner with old scales removed than with new scales removed. The reverse situation, however, was found in mature bulbs. Removal of all scales also drastically reduced flowering (Table 4).

Reduction in leaf numbers roughly paralleled the severity of scale removal, except that removing 75 and 100% of the scales reduced leaf numbers most severely (Table 5). The old scales may play an important role in leaf initiation, because their removal drastically reduce leaf number (Table 6). Flower buds per plant decreased in proportion to the amount of scales removed, but at

Table 4. Effect of scale removal treatments following various harvest dates on speed of flowering of 'Ace' lily bulbs.

Harvest dates	Days to flower after emergence[a] Treatments			
	Entire bulb	New scales removed	Old scales removed	All scales removed
June 19	252	299	241	375
July 21	206	240	208	369
Aug. 18	175	171	166	236
Sept. 12	185	118	110	199
Oct. 11	207	194	215	224
L.S.D. 5%---10.7				

[a]Bulbs were potted immediately and placed in greenhouse at 60°~70°F.

Table 5. Effect of scale removal on growth of non-vernalized 'Ace' lily. Means of ten bulbs per treatment, average bulb weight at planting reflecting the percentage of scales removed: 0%, 151g; 25%, 108g; 50%, 76g, 75%, 38g; and 100%, 12g.

% scales removed	No. of leaves	No. of flower buds	Length of stem (cm)	Length of internodes (cm)	Growth rate
0	239	12.2	70	0.61	2.1
25	180	10.2	60	0.55	1.8
50	102	5.0	35	0.35	1.3
75	87	2.7	32	0.33	1.0
100	51	1.2	31	0.11	0.33
L.S.D. 5%---7.5		0.6	3.6	0.11	0.10

Table 6. Effect of scale removal treatments at progressively later harvest dates on number of leaves of 'Ace' lily.

Harvest dates	Treatments			
	Entire bulb	New scales removed	Old scales removed	All scales removed
June 19	149	113	77	19
July 21	139	129	87	51
Aug. 18	137	124	72	57
Sept. 12	239	138	102	51
Oct. 11	268	207	167	67

L.S.D. 5%---8.01

Bulbs were potted immediately and placed in greenhouse at 60°~70°F.

Table 7. Effect of scale removal treatments at progressively later harvest dates on (A) number of flower buds (B) number of flowers aborted of 'Ace' lily.

Harvest dates		Treatments			
		Entire bulb	New scales removed	Old scales removed	All scales removed
June 19	A	9.4	6.8	3.8	1.0
	B	0.2	0.2	0.2	0.0
July 21	A	8.8	7.8	2.0	1.4
	B	0.0	0.0	0.0	0.2
Aug. 18	A	8.5	8.3	2.8	1.5
	B	0.0	0.0	0.0	0.0
Sept. 12	A	12.2	8.6	5.0	1.2
	B	0.8	0.2	0.0	0.0
Oct. 11	A	11.0	10.2	8.0	1.0
	B	2.5	3.0	2.0	0.0

L.S.D. 5% A---0.98 B---0.30

Bulbs were potted immediately and placed in greenhouse at 60°~70°F.

least one flower bud was initiated by plant grown from bulbs without any scales (Table 4). Old scales may also play an important role in flower bud initiation, because their removal drastically reduced number of flower buds initiated. The data for flower bud abortion show the inability of the plants initiating large numbers of flowers to develop all of them to anthesis (Table 7). In general, the length of the stems reflected the number of leaves and the length of their internode. The length of the stem was inversely proportional to the amount of scales removed. 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 (Table 8). Growth rate decreased in proportion to the amount of scales removed, removal of the last 25% of the scales decreased growth rate severely. Old scales may play an important role in growth rate, because their removal reduced growth rate when compared to removal of new scale (Table 9A).

Table 8. Effect of scale removal treatments following various harvest dates on lengths of stem (cm) of 'Ace' lily.

Harvest dates	Treatments			
	Entire bulb	New scales removed	Old scales removed	All scales removed
June 19	44	36	35	12
July 21	42	40	21	12
Aug. 18	50	48	32	36
Sept. 12	75	68	35	31
Oct. 11	104	121	76	44

L.S.D. 5%---2.58

Bulbs were potted immediately and placed in greenhouse at 60°~70°F.

Table 9. Effect of scale removal treatments at progressively later harvest dates on (A) growth rate (leaves unfolded per day) (B) leaf length (cm) of 'Ace' lily.

Harvest dates		Treatments			
		Entire bulb	New scales removed	Old scales removed	All scales removed
June 19	A	0.70	0.40	0.37	0.06
	B	14.1	14.7	13.1	12.1
July 21	A	0.84	0.63	0.52	0.15
	B	15.3	15.7	15.3	14.5
Aug. 18	A	1.0	1.0	0.58	0.29
	B	16.8	16.9	16.8	15.5
Sept. 12	A	1.1	1.27	1.3	0.33
	B	14.0	17.5	15.0	13.2
Oct. 11	A	1.3	1.3	0.97	0.36
	B	14.8	15.9	14.9	14.5

L.S.D. 5% A---0.56 B---0.18

Bulbs were potted immediately and placed in greenhouse at 60°~70°F.

Breaking Dormancy

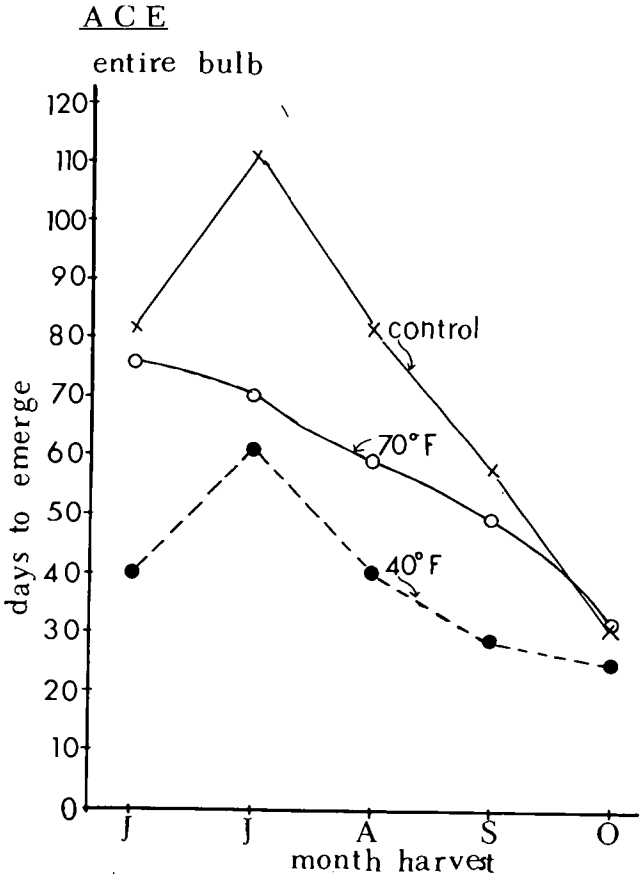
Temperature and Mechanical Treatments

Vernalization and scale removal. As shown previously, the later the bulbs were harvested the sooner they sprouted after planting in the greenhouse. Storage at 70° and 40° reduced time required for sprouting, the latter temperature being most effective. The vernalization effect gradually decreased during the growing season; in October mature bulbs showed only a slight response to temperature treatment. Differences in days to emerge between bulbs stored

at 40° and 70° and those non-stored, but harvested at the same time are shown in Figures 10 and 11. Storage at 40° F was most stimulating to July harvested bulbs, but progressively lost its influence to October. 70° F storage, which had little affect on sprouting of bulbs harvested in June, was extremely stimulating in July. Thereafter, the difference in emergence between bulbs stored at 70° and those not stored decreased steadily until October when no significant difference was evident.

The effects of temperature and scale removal treatments on bulbs harvested at progressively later dates on days to emerge are shown in Figures 12 and 13. In general, the shoots emerged earlier when new scales were removed. 40° or 70° storage delayed sprouting in June-harvested bulbs when new scales were removed, but was stimulating to the July-, August- and September-harvested bulbs. Storage became less and less stimulating with delay in harvest from September to October. 70° storage even delayed the sprouting of October harvested bulbs. The removal of old scales from June-harvested bulbs stimulated sprouting, especially if stored at 40° F. This stimulation became progressively less evident and by October the removal of old scales had little effect on bulbs stored at 70° F.

The differences in days to emerge between bulbs stored at 40°, 70° and those not stored and with old or new scales removed after several harvest dates are shown in Figures 14 and 15. Storage



L.S.D. 5% - 10.4

Figure 10. Effect of storage temperature at progressively later harvest dates on speed of emergence of 'Ace' lily bulbs. Controls potted immediately and placed in greenhouse at 60°~70° F.

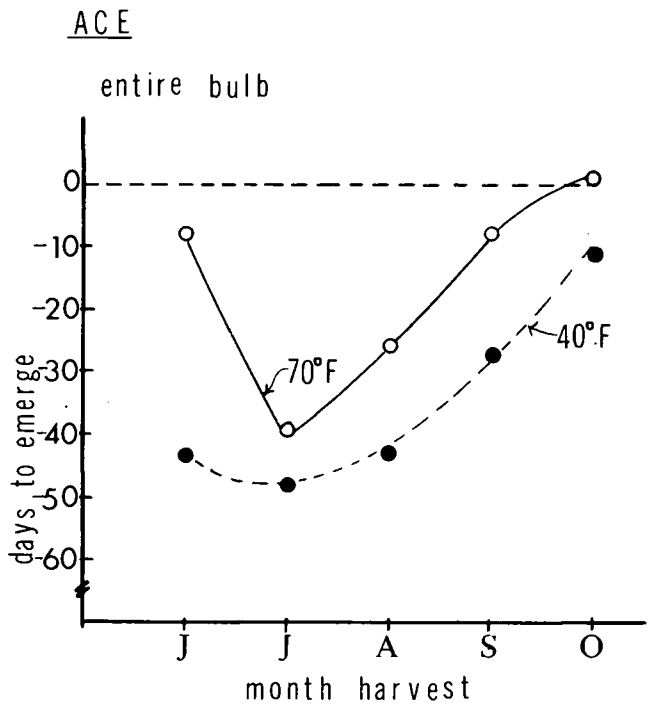
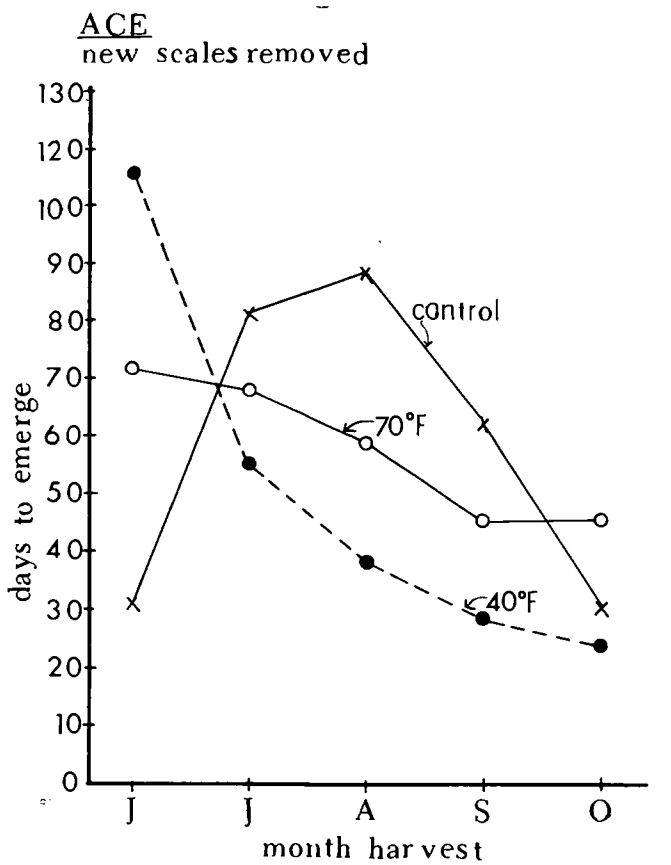
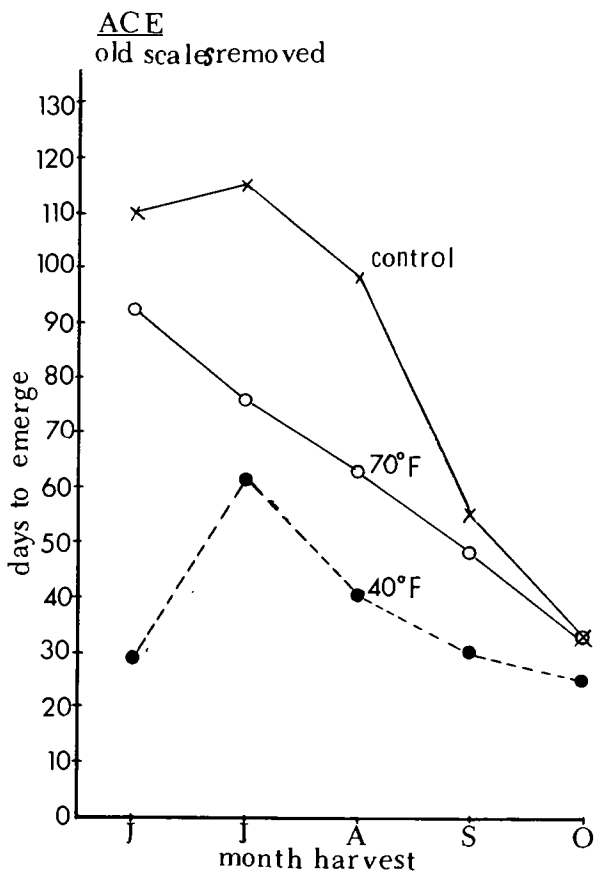


Figure 11. Differences in days to emerge between non-stored 'Ace' lily bulbs (dotted line as zero days control) and those harvested at the same date but stored six weeks at 40° or 70° F.



L.S.D. 5% - 10.6

Figure 12. Effect of storage temperature and new scale removal following various harvest dates on speed of emergence of 'Ace' lily bulbs. Controls potted immediately and placed in greenhouse at 60°~70° F.



L.S.D. 5% - 9.7

Figure 13. Effect of storage temperature and removal of old scales following various harvest dates on speed of emergence of 'Ace' lily bulbs. Controls potted immediately and placed in greenhouse at $60^{\circ} \sim 70^{\circ}$ F.

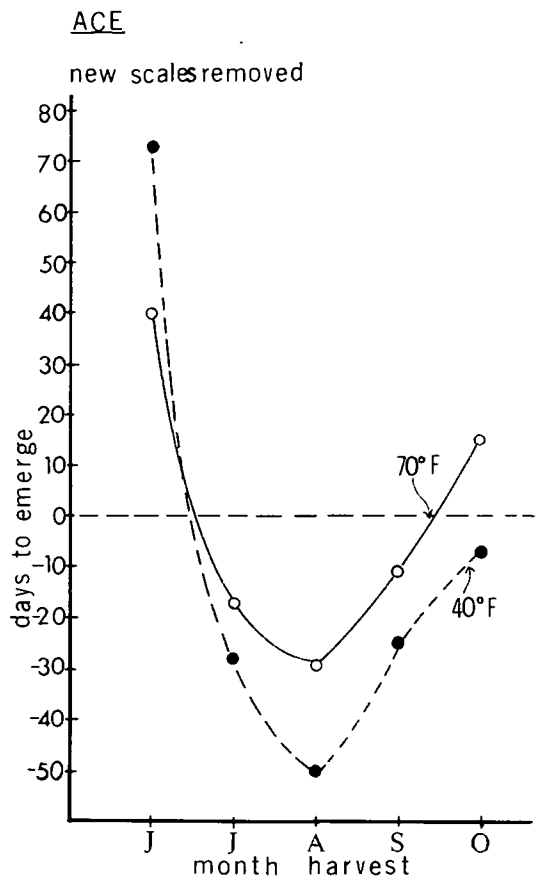


Figure 14. Differences in speed of emergence of non-stored 'Ace' lily bulbs (dash line at zero days for control) and those stored for six weeks at 40° and 70° F following new scale removal on several harvest dates.

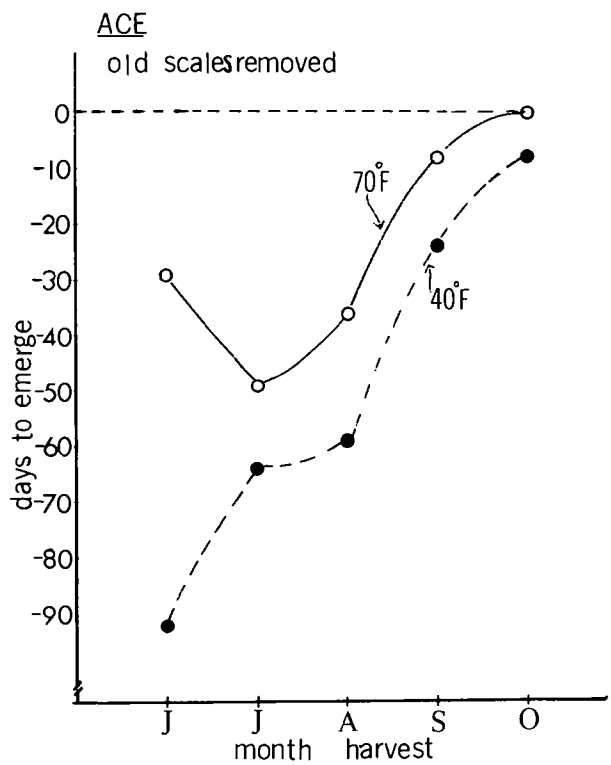


Figure 15. Differences in speed of emergence of non-stored 'Ace' lily bulbs (dash line at zero days for control) and those stored for six weeks at 40° and 70° F following old scale removal on several harvest dates.

at 40° and 70° was most stimulating to the bulbs harvested in June and with the old scales removed, and was most inhibiting to the same bulbs when new scales were removed, especially following 40° F storage. These influences declined gradually to approximately zero in October.

Figures 16, 17, and Table 10 show the delay in emergence caused by retention of old scales or new scales following various harvest dates and six weeks of storage. The same phenomena discussed above was evident also in further experiments involving 'Ace' bulbs, in which comparable differences in days to emerge for 'Ace' bulbs with new scales, old scales, or all scales removed are shown in Figures 18 and 19.

40° and 70° storage inhibited the sprouting of the daughter apex when all the scales were removed and especially with June harvested bulbs (Figures 20 and 21).

Warm and cold storage tended to speed emergence and flowering regardless of scale removal treatment, cold being more effective than warm storage in this regard (Table 11).

The 40°F storage reduced, while 70° F storage increased leaf number in July, August and September harvested bulb. Earlier and later dug bulbs produced less leaves if stored six weeks at 70° F (Table 12). 40° storage reduced the number of flower initials more than 70° F storage (Table 13), whether cold or warm, tended to

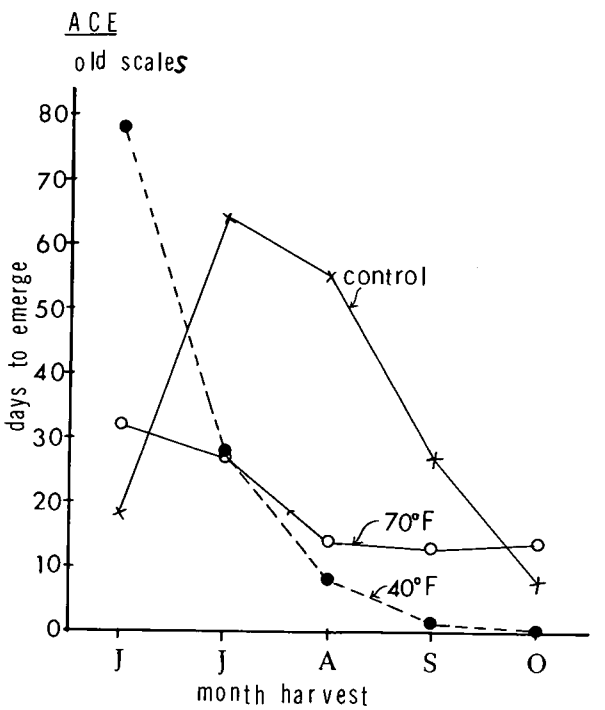
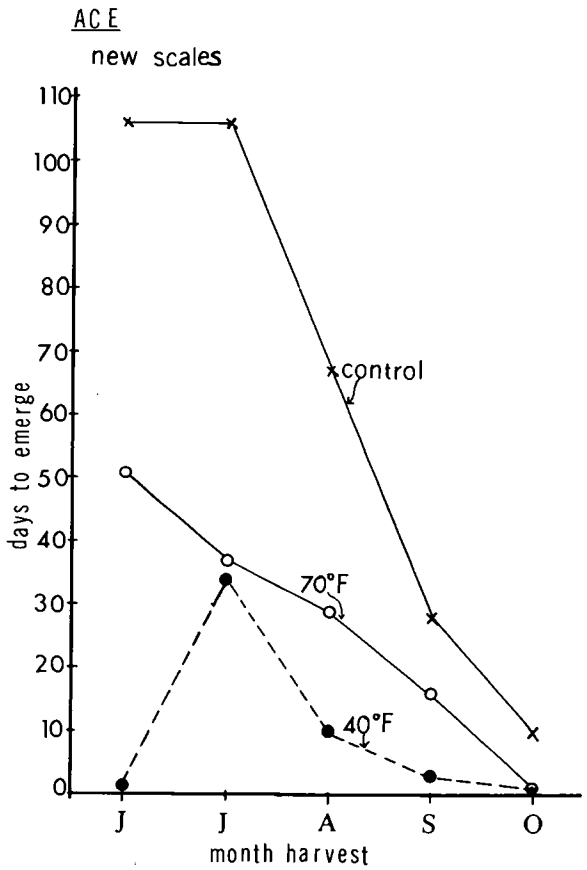


Figure 16. Delay in emergence resulting from presence of old scales on 'Ace' bulbs harvested on several harvest dates and receiving no storage (control) or storage for six weeks at 40° or 70° F.



L.S.D. 5% - 18.5

Figure 17. Delay in emergence resulting from presence of new scales on 'Ace' bulb harvested on several harvest dates and receiving no storage (control) or storage for six weeks at 40° F or 70° F.

Table 10. Delay in emergence resulting from presence of (A) old scales or (B) new scales on 'Ace' bulbs following on several harvest dates and receiving no storage (control) or storage for six weeks at 40° or 70°F.

Harvest dates	(A) Old scales			(B) New scales		
	non-stored bulbs	6 weeks at 40°F	6 weeks at 70°F	non-stored bulbs	6 weeks at 40°F	6 weeks at 70°F
June 19	18	78	32	106	1	51
July 21	64	28	27	106	34	37
Aug. 18	55	8	14	67	10	29
Sept. 12	27	1	13	28	3	16
Oct. 11	8	0	14	10	1	1
L.S.D. 5% = 8.5				L.S.D. 5% - 18.5		

The influence of old scales or new scales on speed of shoot emergence was calculated by means of the following formula:

(A) Days to emerge of bulbs with new scales removed - Days to emerge of bulbs with all scales removed
(only old scales plus shoot apex remaining) (shoot apex only)
= Delay in emergence resulting from presence of old scales

(B) Days to emerge of bulbs with old scales removed - Days to emerge of bulbs with all scales removed
(only new scales plus shoot apex remaining) (shoot apex only)
= Delay in emergence resulting from presence of new scales

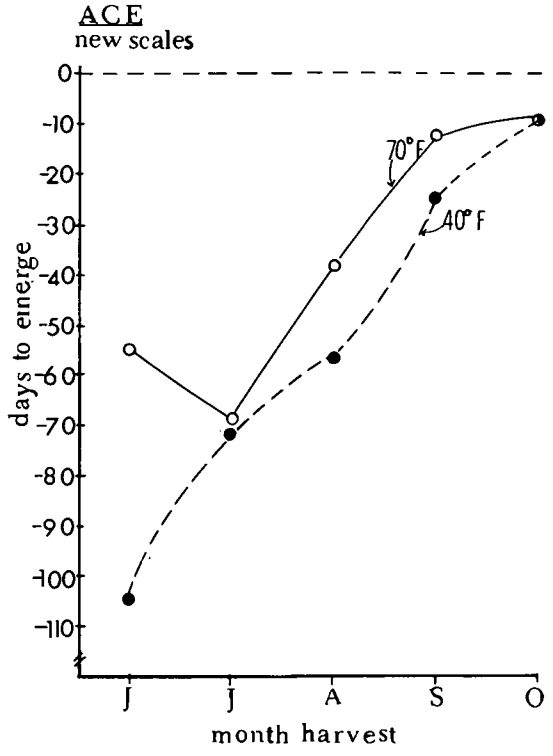


Figure 18. Effectiveness of six weeks of 40° and 70° F storage in shortening the emergence time of 'Ace' lilies on various harvest dates where only new scales were retained. Non-stored bulbs with new scales retained served as control and basis for zero line in graph.

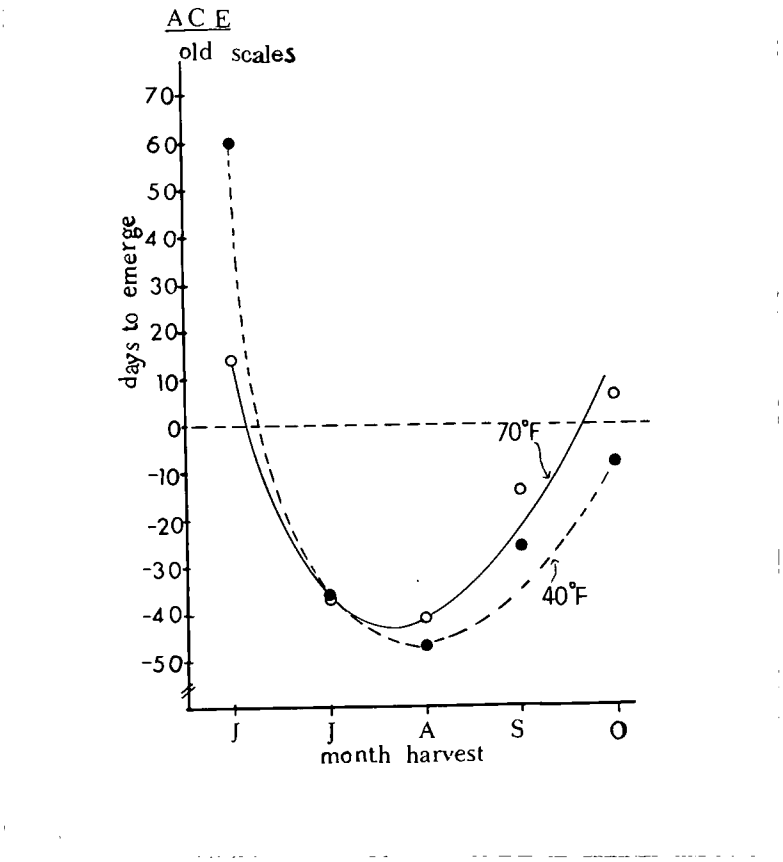
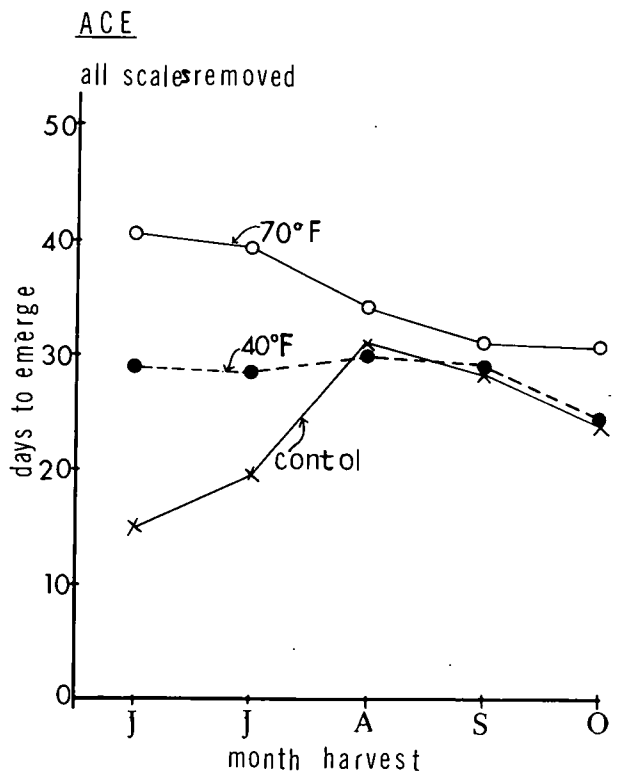


Figure 19. Effectiveness of six weeks at 40° and 70° F storage in shortening the emergence time of 'Ace' lilies following various harvest dates where only old scales were retained. Non-stored bulbs with old scales retained served as control and basis for zero line in graph.



L.S.D. 5% - 4.1

Figure 20. Effects of six weeks of 40° and 70° F storage on speed of elongation of 'Ace' daughter axis without scales (all scales removed from basal plate) following various harvest dates. Non-stored 'Ace' bulbs with all scales removed used as control.

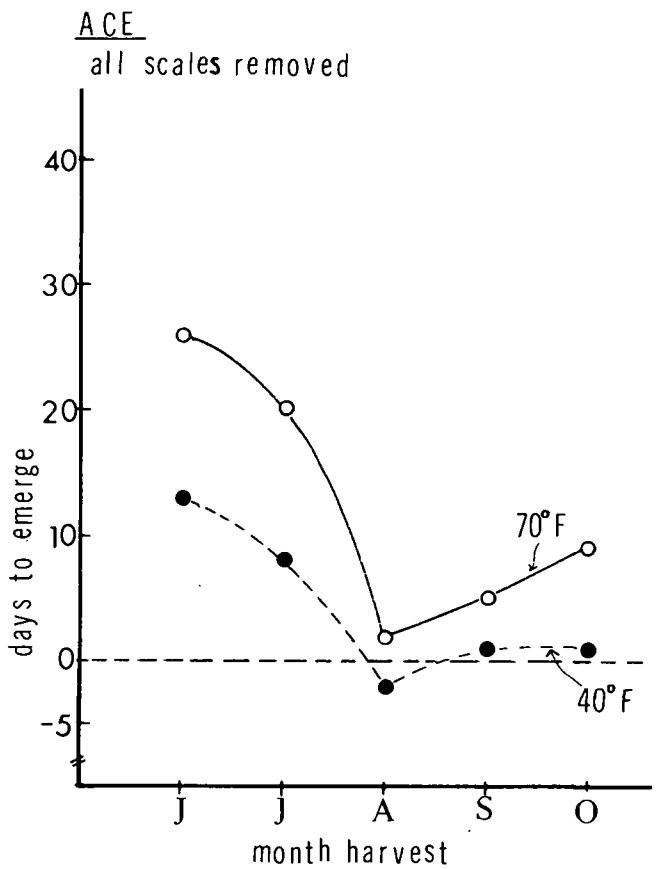


Figure 21. Differences in speed of elongation of 'Ace' daughter axis without scales and given six weeks storage at 40° and 70° F from non-stored bulbs with all scales removed following various harvest dates.

Table 11. Effect of storage temperature and scale removal treatments at progressively later harvest dates on days to flower after emergence of 'Ace' lily.

Harvest dates	SCALE REMOVAL TREATMENTS											
	Entire bulb			New scales removed			Old scales removed			All scales removed		
	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F
June 19	252	165	250	299	242	268	241	116	250	375	303	321
July 21	206	179	192	240	200	104	208	168	195	369	264	283
Aug. 18	175	121	160	171	125	163	166	126	160	236	162	224
Sept. 12	185	92	187	118	101	164	110	86	183	199	111	185
Oct. 11	207	101	157	194	102	161	215	104	168	224	130	182

L.S.D. 5% - 20.70

*Controls were potted immediately and placed in greenhouse at 60°~70°F.

Table 12. Effect of temperature and scale removal treatments at progressively later harvest dates on number of leaves of 'Ace' lily.

Harvest dates	Scale removal treatments											
	Entire bulb			New scales removed			Old scales removed			All scales removed		
	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F
June 19	149	115	124	113	103	129	77	40	58	19	49	64
July 21	139	100	259	129	107	-	87	80	-	51	-	-
Aug. 18	137	98	238	124	89	125	72	70	85	57	28	-
Sept. 12	239	82	256	138	79	248	102	80	128	51	45	36
Oct. 11	268	67	212	207	69	197	167	72	162	67	-	-

L.S.D. 5% - 25.02

*Controls potted immediately and placed in greenhouse at 60°~70° F.

Table 13. Effect of temperature and scale removal treatments at progressively later harvest dates on (A) number of flower buds (B) number of flowers aborted of 'Ace' lily.

Harvest dates		Scale removal treatments											
		Entire bulb			New scales removed			Old scales removed			All scales removed		
		Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F
June 19	A	9.4	4.8	6.3	6.8	5.8	7.6	3.8	1.0	1.2	1.0	1.0	2.2
	B	0.2	0.4	1.5	0.2	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2
July 21	A	8.8	4.0	7.5	7.8	6.0	7.1	2.0	2.5	2.0	1.4	8.8	1.4
	B	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Aug. 18	A	8.5	4.8	8.5	8.3	3.6	7.0	2.8	2.2	3.5	1.5	1.0	1.0
	B	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sept. 12	A	12.2	4.6	13.0	8.6	4.0	12.3	5.0	4.0	8.3	1.2	1.0	1.0
	B	0.8	0.6	3.3	0.2	0.2	2.5	0.0	0.8	1.3	0.0	0.0	0.0
Oct. 11	A	11.0	5.0	12.2	10.2	5.7	8.3	8.0	5.0	8.5	1.0	1.0	1.0
	B	2.5	0.3	2.0	3.0	0.0	1.3	2.0	0.0	1.7	0.0	1.0	0.0

L.S.D. 5% A - 1.28, B - 0.30

*Controls potted immediately and placed in greenhouse at 60°~70°F.

accelerate the growth rate of plants harvested after June (Table 14A). Stem length reflected the leaf complement of the plants, that is, the number of leaves and the length of their internodes (Table 15).

Vernalization, hot water and scale removal. Bulbs harvested in June and September showed different responses to hot water treatment. June bulbs soaked in 100° F water for 1-1/2 hours were made more dormant, while September bulbs so treated were stimulated slightly. Hot water significantly delayed the sprouting of June harvested bulbs when their new scales were removed, but slightly enhanced sprouting of these bulbs if the old scales were removed. Hot water treatment before or after six weeks of 40° F storage accelerated emergence, especially when hot water treatment preceded the 40° F storage. Soaking the bulbs in tap water at 60° F for 1-1/2 hours also accelerated emergence of entire bulbs or those having only the old scales removed. Hot water, tap water and hot water followed by six weeks storage at 40° F all slightly hastened the emergence of September dug bulbs. The removal of all scales and hot water plus six weeks storage at 40° F also accelerated the emergence of September dug bulbs (Table 16, Figures 22 and 23).

June and September bulbs without scale removal, or not stored six weeks at 40° or 70° F tended to flower earlier when treated with hot water. Results are presented in Table 17.

Reduction in leaf numbers followed hot water and tap water

Table 14. Effect of temperature and scale removal treatments at progressively later harvest dates on (A) growth rate (leaves unfolded per day) (B) average leaf length (cm) of 'Ace' lily.

Harvest dates		Scale removal treatments											
		Entire bulb			New scales removed			Old scales removed			All scales removed		
		Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F
June 19	A	0.70	0.90	0.59	0.40	0.50	0.57	0.37	0.50	0.37	0.06	0.18	0.23
	B	14.1	13.8	16.1	14.7	14.7	17.0	13.1	12.7	15.5	12.1	13.0	15.0
July 21	A	0.84	0.92	1.00	0.63	0.67	1.60	0.52	0.63	0.70	0.15	-	-
	B	15.3	14.2	15.4	15.7	14.3	16.5	15.3	15.1	16.0	14.5	-	-
Aug. 18	A	1.00	1.20	1.20	1.00	1.00	1.10	0.58	0.83	0.72	0.29	0.85	0.13
	B	16.8	17.1	16.7	16.9	17.4	15.7	16.8	14.7	16.1	15.5	-	-
Sept. 12	A	1.10	1.4	1.75	1.27	1.50	1.75	1.30	1.70	1.60	0.33	0.65	0.25
	B	14.0	16.5	14.4	17.5	16.7	13.6	15.0	15.3	14.7	13.2	18.5	16.7
Oct. 11	A	1.30	1.50	1.69	1.30	1.60	1.65	0.97	1.10	1.28	0.36	-	0.38
	B	14.8	15.7	15.5	15.9	17.9	13.3	14.9	15.5	14.2	14.5	-	10.8

L. S. D. 5% A - 0.56, B - 0.18

*Controls potted immediately and placed in greenhouse at 60°~70° F.

Table 15. Effect of temperature and scale removal treatments at progressively later harvest dates on stem length (cm) of 'Ace' lily.

Harvest dates	Scale removal treatments											
	Entire bulb			New scales removed			Old scales removed			All scales removed		
	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F	Control*	6 weeks at 40°F	6 weeks at 70°F
June 19	44	51	45	36	44	52	35	12	24	12	12	19
July 21	42	30	61	40	36	52	21	16	28	12	15	21
Aug. 18	50	74	68	48	63	53	32	49	32	36	14	25
Sept. 12	75	70	118	68	65	106	35	74	58	31	11	26
Oct. 11	104	53	93	121	62	91	76	62	65	44	19	27

L.S.D. 5% 8.58

*Controls potted immediately and placed in greenhouse at 60°~70°F.

Table 16. Effect of scale removal, 40° and 70° F storage, hot water (100° F 1-1/2 hours) treatments on speed of emergence of 'Ace' bulbs following June and September harvest dates.

	Days to emerge											
	Entire bulb			New scales removed			Old scales removed			All scales removed		
Treatment	No storage*	6 weeks at 40°F	6 weeks at 70°F	No storage*	6 weeks at 40°F	6 weeks at 70°F	No storage*	6 weeks at 40°F	6 weeks at 70°F	No storage*	6 weeks at 40°F	6 weeks at 70°F
June bulbs - dug on June 19, 1967[c]												
None*	84	41	76	33	106	73	121	29	92	15	28	41
Hot water	129	18[a] 24[b]	-	136	18[a] 34[b]	-	109	19[a] 20[b]	-	22	19[a] 16[b]	-
Tap water (60°F, 1-1/2 hours)	61	-	-	37	-	-	50	-	-	17	-	-
September bulbs - dug on September 12, 1967[d]												
None*	57	29	49	54	29	45	55	31	48	27	28	32
Hot water	58	21[a] 22[b]	-	51	28[a] 20[b]	-	48	26[a] 21[b]	-	24	16[a] 16[b]	-
Tap water (60°F, 1-1/2 hours)	56	-	-	52	-	-	52	-	-	26	-	-

[a] Soaked in hot water (100°F 1-1/2 hours) followed by six weeks at 40°F storage.

[b] Six weeks at 40°F storage followed by hot water soak (100°F 1-1/2 hours).

[c] L.S.D. 5% - 21.0

[d] L.S.D. 5% - 8.0

*Control bulbs potted immediately without soaking and placed in greenhouse at 60°~70°F.

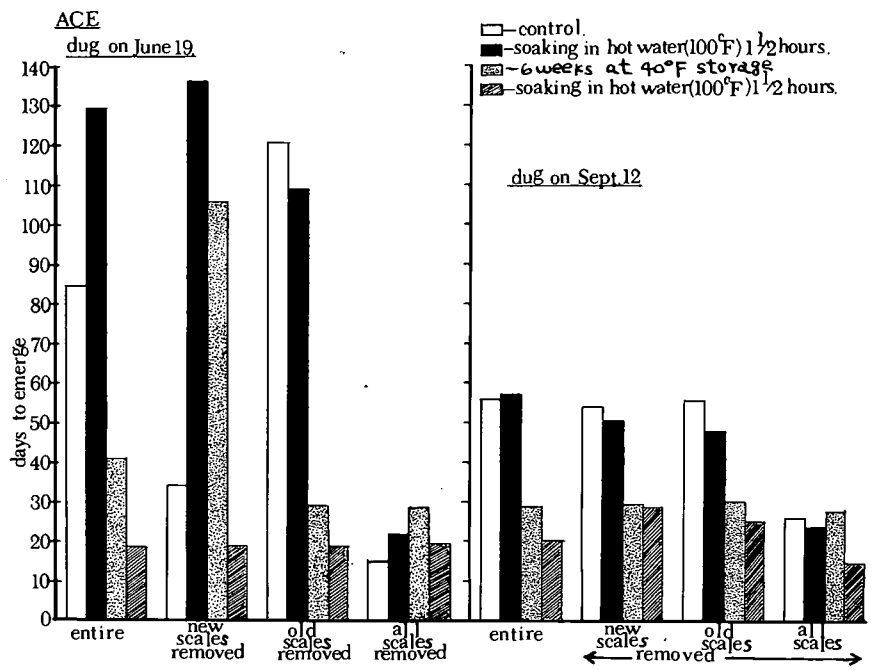


Figure 22. Effect of scale removal, 40° F storage and hot water treatments (100° F 1-1/2 hours) on speed of emergence of 'Ace' bulbs following June and September harvest dates. Controls potted immediately and placed in greenhouse at 60°~70° F.

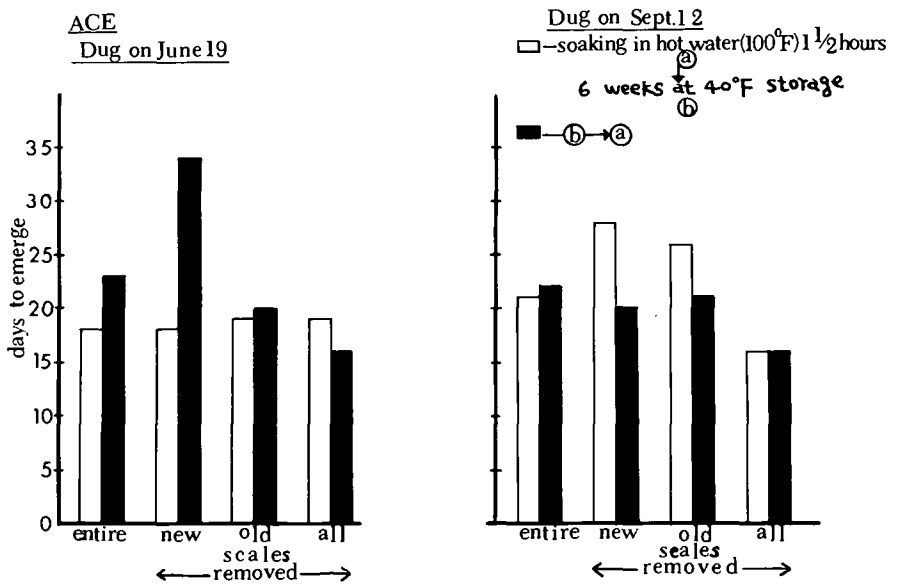


Figure 23. Effect of date of bulb harvest, hot water (100° F 1-1/2 hours), vernalization and scale removal treatments on days to emerge of 'Ace' lily.

Table 17. Effect of 40° and 70° F storage, scale removal, hot water (100° F 1-1/2 hours) treatments on days to flower of 'Ace' lily plants from (A) bulbs dug on June 19, 1967 (B) bulbs dug on September 12, 1967.

		Scale removal treatments											
		No scales removed			New scales removed			Old scales removed			All scales removed		
Bulb Treatments	Date Dug	No storage*	6 weeks at 40°F	6 weeks at 70°F	No storage*	6 weeks at 40°F	6 weeks at 70°F	No storage*	6 weeks at 40°F	6 weeks at 70°F	No storage*	6 weeks at 40°F	6 weeks at 70°F
Soak:													
None*	June	252	165	250	299	242	268	241	116	250	375	303	321
	Sept.	185	92	187	118	101	164	110	86	183	199	111	185
Hot water	June	214	102[a] 132[b]	-	205	103[a] 184[b]	-	269	113[a] 174[b]	-	366	241[a] 298[b]	-
	Sept.	120	90[a] 94[b]	-	138	87[a] 93[b]	-	136	91[a] 94[b]	-	174	213[a] 219[b]	-
Tap water (60°F, 1-1/2 hours)	June	278	-	-	303	-	-	306	-	-	327	-	-
	Sept.	146	-	-	124	-	-	117	-	-	166	-	-

L.S.D. 5% - 15.9

[a]Soaked in hot water (100° F 1-1/2 hours) followed by six weeks 40° F storage.

[b]Six weeks at 40° F storage followed by hot water soak (100° F 1-1/2 hours).

*Control bulbs potted immediately without soaking and placed in greenhouse at 60°~70° F.

treatments, but if bulbs were given 40° F storage immediately following hot water treatment leaf numbers were increased (Table 18). Hot water and 40° F storage were deleterious to flower bud initiation, but warm (70° F) storage increased flower bud initiation (Tables 19 and 20). The length of the stems seemed to reflect the number of leaves, that is, the number of internodes that elongated. Hot water treatment tended to decrease the length of the stem and leaf number, but increase the length of internodes (Tables 21 and 22).

Degree of vernalization and hot water treatment. In general, vernalization and hot water treatment stimulated early emergence of 'Ace' and 'Croft' bulbs. Maximum acceleration was achieved by six weeks storage at 40° F, emergence being stimulated but little by longer 40° F storage. Hot water treatment of 'Ace' bulbs immediately following 19 weeks storage, caused sprouting in storage before potting, but 19 weeks storage following hot water treatment increased dormancy (Figure 24). Leaf numbers in 'Ace' and 'Croft' were generally inversely related to 40° F storage duration. Hot water treatment again decreased leaf numbers, stem and internode length and thus hastened flowering. Vernalized 'Croft' bulbs were not further stimulated by hot water treatment except in speed of emergence. Although 18 weeks of 40° F storage further reduced days to flower, six weeks of 40° F storage was responsible for most of the time reduction. Six weeks of 40° storage also reduced the number of

Table 18. Effect of 40° and 70° F storage, scale removal, hot water (100° F 1-1/2 hours) treatments on leaf numbers of 'Ace' lily plants from (A) bulbs dug on June 19, 1967 (B) bulbs dug on September 12, 1967.

		Scale removal treatments											
		No scales removed			New scales removed			Old scales removed			All scales removed		
Bulb Treatment	Date Dug	No storage*	6 weeks at 40°F	6 weeks at 70°F	No storage*	6 weeks at 40°F	6 weeks at 70°F	No storage*	6 weeks at 40°F	6 weeks at 70°F	No storage*	6 weeks at 40°F	6 weeks at 70°F
Soak													
None*	June	149	115	124	113	103	129	77	40	58	19	49	64
	Sept.	239	82	256	138	79	248	102	80	128	51	45	36
Hot water	June	91	54[a] 116[b]	-	86	58[a] 119[b]	-	58	37[a] 54[b]	-	17	23[a] 66[b]	-
	Sept.	155	73[a] 84[b]	-	168	71[a] 83[b]	-	103	78[a] 83[b]	-	50	32[a] 69[b]	-
Tap water (60° F 1-1/2 hours)	June	135	-	-	102	-	-	79	-	-	35	-	-
	Sept.	187	-	-	98	-	-	101	-	-	49	-	-

L. S. D. 5% - 20.7

[a] Soaked in hot water (100° F 1-1/2 hours) followed by six weeks at 40° F storage.

[b] Six weeks at 40° F storage followed by hot water soak (100° F 1-1/2 hours).

*Control bulbs potted immediately without soaking and placed in greenhouse at 60°~70° F.

Table 19. Effect of 40° F and 70° F storage, scale removal, hot water (100° F 1-1/2 hours) on number of flower buds of 'Ace' lily plants from (A) bulbs dug on June 19, 1967 (B) bulbs dug on September 12, 1967.

		Scale removal treatments											
		No scales removed			New scales removed			Old scales removed			All scales removed		
Bulb Treatment	Date Dug	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F
Soak													
None*	June	9.4	4.8	6.3	6.8	5.8	7.6	3.8	1.0	4.2	1.0	1.0	2.2
	Sept.	12.2	6.6	13.0	8.6	5.0	12.3	5.0	4.0	8.3	1.2	1.0	1.0
Hot water	June	5.8	2.0[a] 3.8[b]	-	4.2	1.8[a] 4.5[b]	-	1.2	1.0[a] 1.4[b]	-	1.0	1.0[a] 1.6[b]	-
	Sept.	9.4	5.4[a] 6.0[b]	-	9.8	4.8[a] 5.0[b]	-	6.6	2.4[a] 3.8[b]	-	1.4	1.2[a] 1.3[b]	-
Tap water (60° F 1-1/2 hours)	June	8.3	-	-	7.2	-	-	3.4	-	-	3.0	-	-
	Sept.	11.0	-	-	9.4	-	-	4.8	-	-	1.4	-	-

L.S.D. 5% - 1.3

[a] Soaked in hot water (100° 1-1/2 hours) followed by six weeks at 40° F storage.

[b] Six weeks at 40° F storage followed by hot water soak (100° F 1-1/2 hours).

*Control bulbs potted immediately without soaking and placed in greenhouse at 60°~70° F.

Table 20. Effect of 40° F and 70° F storage, scale removal, hot water (100° F 1-1/2 hours) treatments on number of flowers aborted of 'Ace' lily (A) bulbs dug on June 19, 1967, (B) bulbs dug on September 12, 1967.

		Scale removal treatments											
		No scales removed			New scales removed			Old scales removed			All scales removed		
Bulb Treatments	Date Dug	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F
Soak													
None*	June	0.2	0.4	1.5	0.2	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2
	Sept.	0.8	0.6	3.3	0.2	0.2	2.5	0.0	0.8	1.3	0.0	0.0	0.0
Hot water	June	0.0	0.0[a] 0.0[b]	-	0.0	0.4[a] 0.0[b]	-	0.0	0.2[a] 0.0[b]	-	0.0 0.0	0.0[a] 0.0[b]	-
	Sept.	0.2	0.2[a] 0.25[b]	-	0.2	0.0[a] 0.0[b]	-	0.2	0.6[a] 0.2[b]	-	0.0	0.0[a] 0.0[b]	-
Tap water (60° F 1-1/2 hours)	June	0.25	-	-	0.0	-	-	0.0	-	-	0.0	-	-
	Sept.	0.5	-	-	0.0	-	-	0.0	-	-	0.0	-	-

L.S.D. 5% - 0.24

[a]Soaked in hot water (100° F 1-1/2 hours) followed by six weeks at 40° F storage.

[b]Six weeks at 40° F storage followed by hot water soak (100° F 1-1/2 hours).

*Control bulbs potted immediately without soaking and placed in greenhouse at 60°~70° F.

Table 21. Effect of 40° and 70° F storage, scale removal, hot water (100° F 1-1/2 hours) treatments on stem length (cm) on 'Ace' lily (A) bulbs dug on June 19, 1967, (B) bulbs dug on September 12, 1967.

		Scale removal treatments											
		No scales removed			New scales removed			Old scales removed			All scales removed		
Bulb Treatments	Date Dug	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F
Soak													
None*	June	44	51	45	36	44	52	35	16	24	12	12	19
	Sept.	75	70	118	68	65	106	49	74	58	31	11	26
Hot water	June	35	38[a] 41[b]	-	27	39[a] 45[b]	-	25	15[a] 16[b]	-	3	3[a] 9[b]	-
	Sept.	74	67[a] 63[b]	-	69	63[a] 61[b]	-	48	61[a] 62[b]	-	31	7[a] 9[b]	-
Tap water (60° F, 1-1/2 hours)	June	43	-	-	38	-	-	29	-	-	19	-	-
	Sept.	63	-	-	70	-	-	44	-	-	26	-	-

L.S.D. 5% - 8.3

[a]Soaked in hot water (100° F 1-1/2 hours) followed by six weeks at 40° F storage.

[b]Six weeks at 40° F storage followed by hot water soak (100° F 1-1/2 hours).

*Control bulbs potted immediately without soaking and placed in greenhouse at 60°~70° F.

Table 22. Effect of 40° and 70° F storage, scale removal, hot water (100° F 1-1/2 hours) treatments on internode length (cm) of 'Ace' lily (A) bulbs dug on June 19, 1967 (B) bulbs dug on September 12, 1967.

		Scale removal treatments											
		No scales removed			New scales removed			Old scales removed			All scales removed		
Bulb Treatments	Date Dug	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F	No storage*	6 weeks at 40° F	6 weeks at 70° F
Soak													
None*	June	0.29	0.44	0.36	0.32	0.42	0.40	0.45	0.30	0.41	-	0.49	0.49
	Sept.	0.34	0.86	0.46	0.49	0.82	0.43	0.34	0.93	0.45	0.61	0.25	0.39
Hot water	June	0.39	0.67[a] 0.52[b]	-	0.12	0.66[a] 0.38[b]	-	0.42	0.47[a] 0.32[b]	-	0.18	0.13[a] 0.42[b]	-
	Sept.	0.48	0.91[a] 0.74[b]	-	0.17	0.95[a] 0.89[b]	-	0.47	0.98[a] 0.74[b]	-	0.56	-	-
Tap water (60° F, 1-1/2 hours)	June	0.31	-	-	0.31	-	-	0.34	-	-	0.54	-	-
	Sept.	0.34	-	-	0.49	-	-	0.45	-	-	0.53	-	-

L.S.D. 5% - 0.08

[a]Soaked in hot water (100° F 1-1/2 hours) followed by six weeks at 40° F storage.

[b]Six weeks at 40° F storage followed by hot water soak (100° F 1-1/2 hours).

*Control bulbs potted immediately without soaking and placed in greenhouse at 60°~70° F.

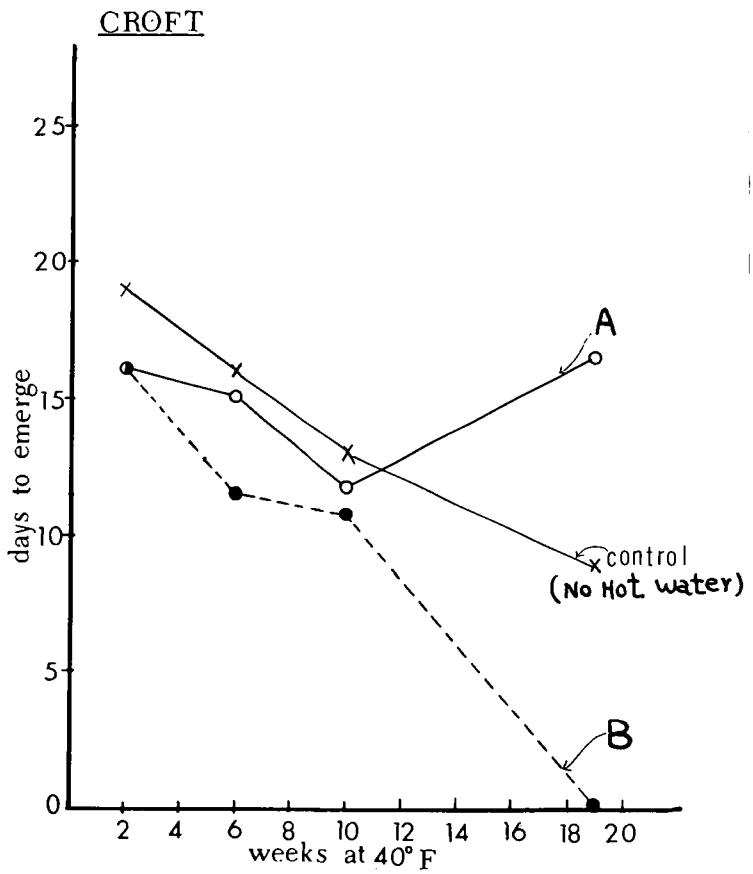


Figure 24. Effect of 40° F storage before (A) and after (B) hot water treatments (1-1/2 hours at 100° F) on speed of emergence of 'Croft' lily bulbs.

leaves of 'Ace', and increased internode length, so that such plants were taller than non-stored (50 cm vs. 74 cm). Extending the 40° storage to 18 weeks drastically reduced leaf number but did not further increase internode length, so the plants were shorter than those from non-vernalized bulbs. Vernalization reduced the number of leaves of 'Croft' in proportion to the length of the 40° F storage to 19 weeks. Vernalization influenced growth rate (leaves unfolding/day). The growth rate of 'Ace' bulbs was increased from 1.16 for non-vernalized bulbs to 1.62 leaves per day by six weeks storage at 40° F. However, prolonging the 40° F storage to 18 weeks significantly reduced growth rate (0.80 leaves per day). Growth rate increase of 'Croft' plants was proportional to the weeks of 40° F storage up to 19 weeks (Tables 23 and 24).

Field soil heating. The results are presented graphically in Figures 25, 26, 27, and 28. All bulbs warmed in the field before bloom were summer-sprouted at harvest, while those without soil heating were not. The 'Ace' bulbs warmed after bloom tended to emerge later than the control. 'Croft' bulbs always emerged earlier than comparable 'Ace', irrespective of previous soil heating or 40° F vernalization treatments (Figures 25 and 26). Plants grown from bulbs warmed in the field before bloom flowered earliest during greenhouse forcing, the 'Croft' being earlier than 'Ace'. Although the days to flower in forcing were inversely related to the duration

Table 23. Effect of vernalization on speed of emergence and other characteristics of 'Ace' lily.

No. weeks of storage	Days to emerge	Days to flower	Leaf number	Number of flowers	Length of stem (cm)	Internode length (cm)	Growth rate
0 weeks at 40° F	90	267	157	9.4	50	0.32	1.16
6 weeks at 40° F	42	146	101	5.0	74	0.73	1.62
18 weeks at 40° F	29	132	48	3.0	34	0.70	0.80
L. S. D. 5%	7.2	13.0	29.0	0.2	19.6	0.02	0.07

Table 24. Effect of vernalization and hot water treatments (100° F 1-1/2 hours) on speed of emergence and other characteristics of 'Croft' lily.

Treatments	Days to emerge	Days to flower after emergence	No. of leaves	No. of flowers	Length of stem (cm)	Internode length (cm)	Growth rate
No hot water treatment							
0 weeks at 40°F	21	174	188	9.0	74	0.39	1.4
2 weeks at 40°F	16	100	90	5.0	52	0.57	1.5
6 weeks at 40°F	13	86	72	4.4	56	0.78	1.6
19 weeks at 40°F	10	66	59	2.8	34	0.74	2.5
40°F storage before hot water							
Hot water only	16	146	150	6.4	67	0.42	1.5
2 weeks at 40°F then hot water	15	100	91	5.6	51	0.55	1.6
6 weeks at 40°F then hot water	12	83	72	4.0	52	0.73	1.7
19 weeks at 40°F then hot water	16	69	59	3.0	42	0.70	2.2
40°F storage after hot water							
Hot water only	16	146	150	6.4	67	0.44	1.5
Hot water then 2 weeks at 40°F	12	93	86	4.6	53	0.62	1.6
Hot water then 6 weeks at 40°F	11	80	70	3.4	48	0.68	1.9
Hot water then 19 weeks at 40°F	0	68	58	2.2	40	0.69	2.2
L.S.D. 5% -	4.4	30.3	37.1	1.6	10.1	0.11	0.29

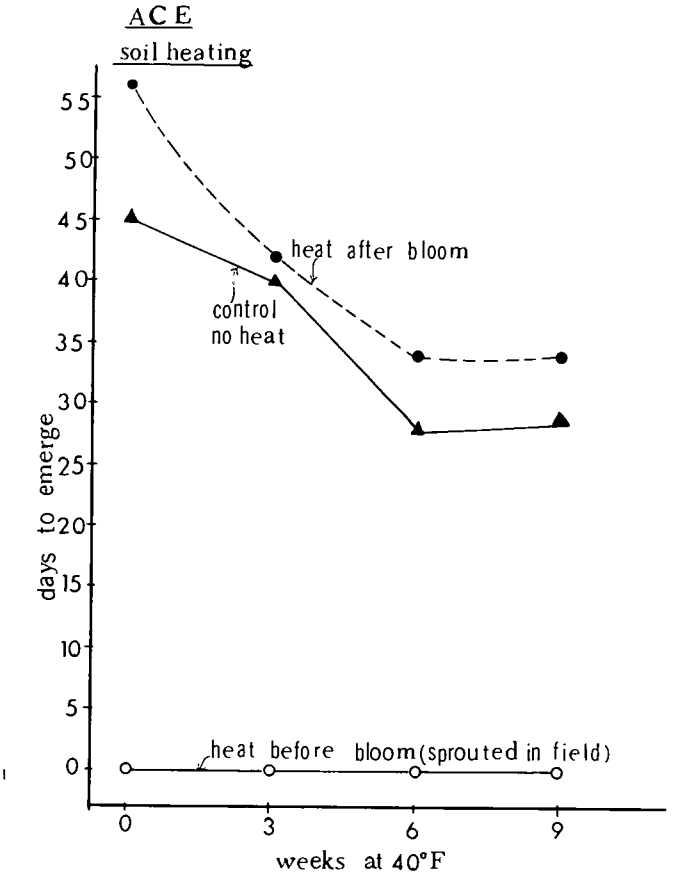


Figure 25. Effect of field soil heating (ca. 75° F) and weeks vernalization in storage at 40° F on speed of emergence of 'Ace' lily bulbs.

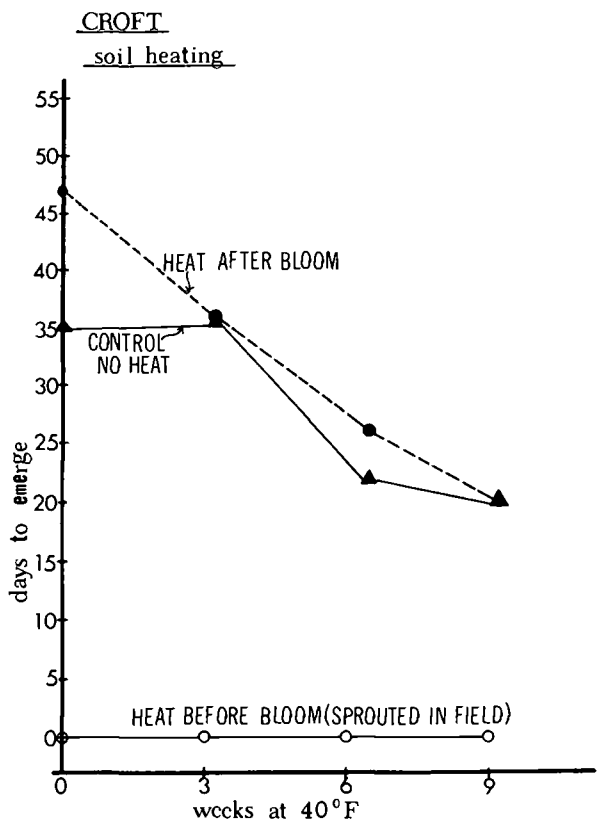


Figure 26. Effect of field soil heating (ca. 75° F) and weeks vernalization in storage at 40° F on speed of emergence of 'Croft' lily bulbs.

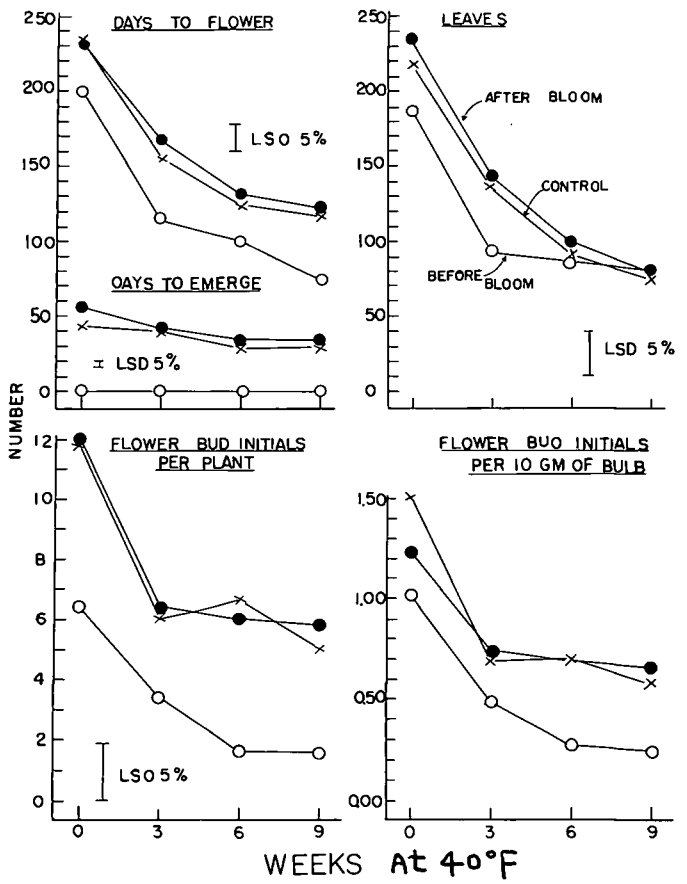


Figure 27. Effects of warming soil around 'Ace' lilies (ca. 75° F) before and after bloom in field on subsequent responses to vernalization treatment and greenhouse forcing.

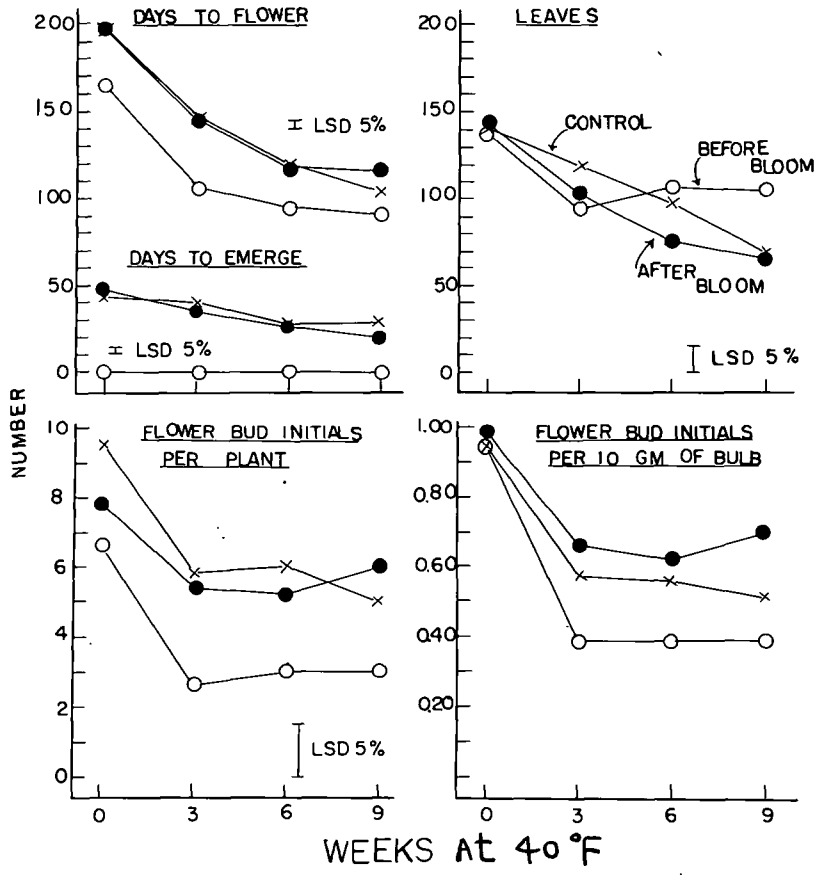


Figure 28. Effects of warming soil around 'Croft' lilies (ca. 75° F) before and after bloom in field on subsequent responses to vernalization treatment and greenhouse forcing.

of vernalization, the first three weeks of 40° vernalization always accelerated flowering the most. Days to flower generally reflected the number of leaves produced. Warming the soil for 'Croft' in the field, either before or after bloom, had no flower inducing effect, and consequently no leaf reducing effect on plants later forced from non-vernalized bulbs. But bulbs warmed in field before bloom needed less vernalization in forcing for induction of flowering as reflected in leaf numbers. Leaf reduction from 40° vernalization was maximum with three weeks treatment of these bulbs. In contrast, six and nine weeks of 40° vernalization were required for bulbs warmed after bloom and the non-heated controls, respectively. Similarly, 'Ace' bulbs receiving soil heating required at least nine weeks of vernalization for maximum acceleration in flowering.

The plants from bulbs warmed before bloom in the field initiated fewer flower buds during greenhouse forcing than did those from bulbs warmed after bloom, and the control bulbs. The number of flower buds initiated by the latter two differed little. Non-vernalized 'Ace' bulbs that had been warmed after bloom in the field and the controls initiated more flower buds during greenhouse forcing than did similarly treated 'Croft' bulbs.

Chemical Treatments

Various growth substances. 2-Chloroethane phosphonic acid

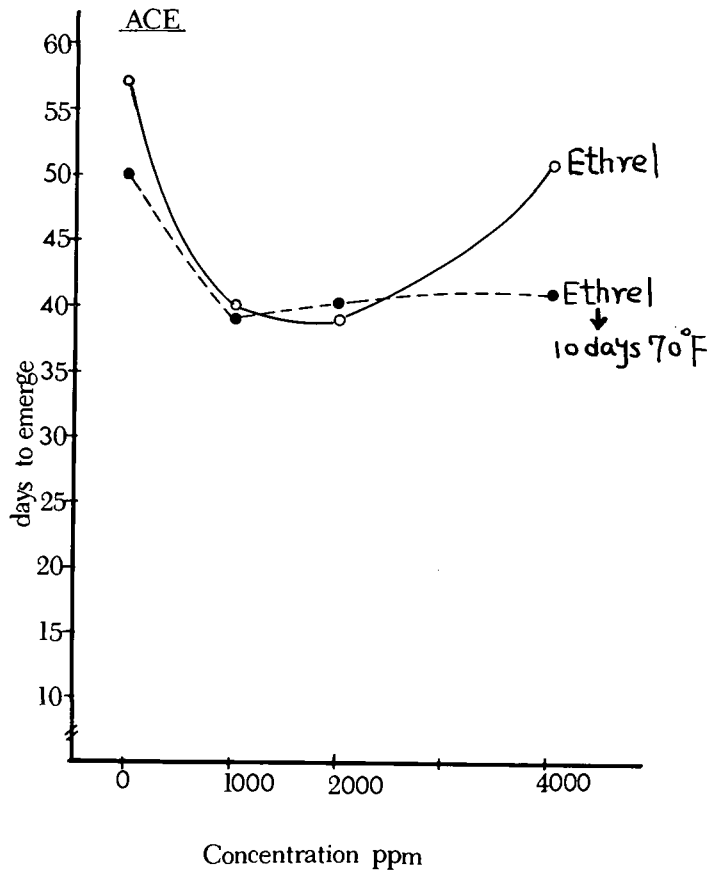
(Ethrel), ethylene, gibberellic acid (GA_3), N, N-dimethylamino-succinamic acid (B-9, Alar), indoleacetic acid (IAA), kinetin, abscisic acid, dimethyl sulfoxide (DMSO) were tested for effectiveness in accelerating daughter emergence and growth rate.

Ethrel at 1000~2000 ppm hastened the emergence of the daughter, while higher concentrations (4000 ppm) were less effective Ethrel treated bulbs were further accelerated in emergence by ten days storage at 70° F (Figure 29).

Ethylene treatment was most effective in hastening the emergence of 'Ace' when the bulbs were exposed to 500 ppm for four days, further treatment not being significantly more effective. Ethylene treated bulbs were further accelerated in emergence by four weeks storage at 40° F (Figure 30).

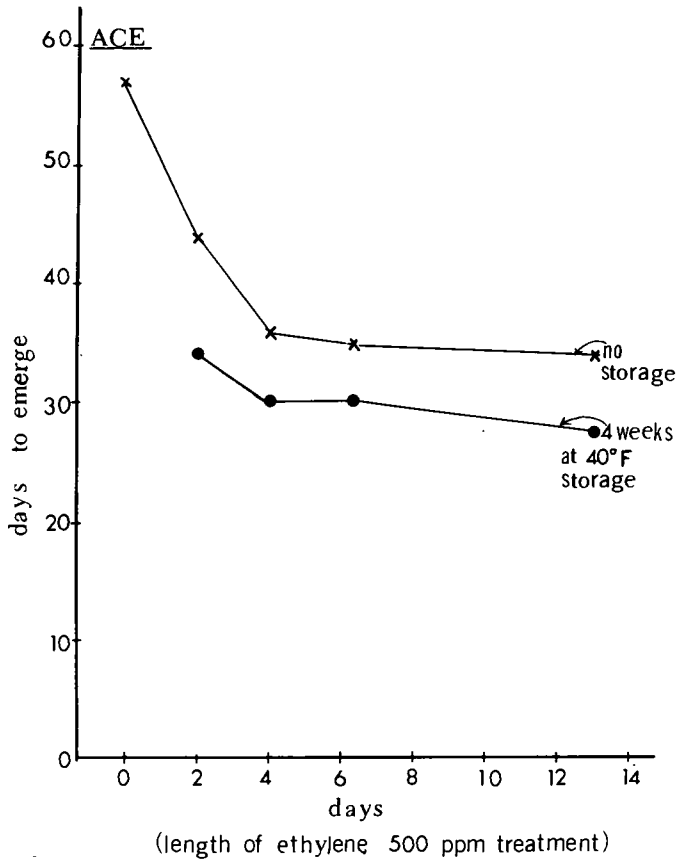
The data in Table 25 give evidence that 2500 ppm of GA_3 enhanced early emergence, the bulbs emerging in 23 days as compared with 56 days for controls. IAA (1250 ppm) was only slightly stimulating to emergence. B-9 showed no inhibitory effects even at higher concentrations (5000 ppm). The other growth substances used did not significantly affect speed of emergence.

Flowering was delayed by Ethrel, especially at the higher concentration (4000 ppm). Prolonging ethylene treatment up to six days delayed flowering, unless followed by six weeks storage at 40° F, in which case it hastened flowering. Although GA_3 and IAA treatments



L.S.D. 5% - 6.0

Figure 29. Effect of 2-chloroethane phosphonic acid (Ethrel) treatment prior to ten days storage at 70° F on speed of emergence of 'Ace' lily.



L.S.D. 5% - 5.9

Figure 30. Effect of 500 ppm ethylene treatment prior to four weeks storage at 40° F on speed of emergence of 'Ace' lily.

Table 25. Effect of various growth substances on days to emerge of 'Ace' lily.

TREATMENT		DAYS TO
CHEMICAL	CONC(PPm)	EMERGE
GA_3	2500	23
B-9	2500	56
B-9	5000	63
ALAR-85	2500	58
ALAR-85	5000	66
IAA	1250	47
IAA	2500	54
KINETIN	1250	55
Ab 11	5	58
DMSO	20	56
CONTROL	0	56

L.S.D. 5% - 8.0

Bulbs planted immediately after chemical treatment.

hastened emergence, they delayed flowering thus separating the vegetative (sprouting) and flowering response. B-9 (2500 ppm, 5000 ppm), Alar-85 (2500 ppm, 5000 ppm) hastened flowering but had no significant effect on emergence. Treatments with 1000-2000 ppm Ethrel, ethylene, GA_3 (2500 ppm), IAA (1250, 2500 ppm) and DMSO (20 ppm) increased leafiness. In general, the length of the stems reflected the number of leaves, and the extent of internode elongation. Ethrel and ethylene treatments slightly increased the number of flower buds initiated, 2000 ppm of Ethrel and six days of 500 ppm of ethylene treatment were especially effective. GA_3, B-9, Alar-85, IAA, kinetin, Abscisic acid, and DMSO showed no significant effect on the number of flower buds initiated (Tables 26, 27, and 28).

Effect of number of new scales in daughter portion, vernalization and GA_3 treatment on dormancy. The results are presented in Figure 31. Bulbs harvested and replanted when the daughter portion contained 20 and 40 new scales emerged in 70 and 37 days, respectively, while those lifted and replanted at time of anthesis of mother axis were found to contain sprouted daughter bulbs. Six weeks at 70° F of storage of these bulbs lifted from the soil in the greenhouse bench increased their dormancy (85 days vs. 70 days for bulbs with 20 new daughter scales and 46 days vs. 37 days for those with 40 new scales). But, storage for six weeks at 70° F preceded by GA_3 2500 ppm treatment effectively broke dormancy. Bulbs with 20 new scales

Table 26. Effect of Ethrel on growth and flowering of 'Ace' lily.

Treatments	Days to emerge	Days to flower after emergence	Length of stem (cm)	No. of leaves	No. of flowers	Average length of leaf (cm)	Internode Length (cm)	Growth rate
Control	57	170	75	165	9.5	17.3	0.45	1.28
Ethrel 1000 ppm	39	179	56	181	11.3	14.1	0.31	1.32
Ethrel 2000 ppm	38	182	58	191	11.6	15.5	0.30	1.36
Ethrel 4000 ppm	45	193	56	153	10.4	13.2	0.37	1.01
10 days at 70°F storage	45	189	72	163	10.7	14.2	0.44	1.11
Ethrel 1000 ppm followed by 10 days at 70°F	38	186	59	176	10.6	14.3	0.34	1.21
Ethrel 2000 ppm followed by 10 days at 70°F	41	181	70	203	12.5	14.6	0.34	1.46
Ethrel 4000 ppm followed by 10 days at 70°F	41	196	62	177	10.5	14.4	0.52	1.15
L.S.D. 5% -	6	8	12	17	0.9	1.35	0.07	0.12

Table 27. Effect of ethylene (C_2H_4) on growth and flowering of 'Ace' lily.

Treatment	Days to emerge	Days to flower after emergence	Length of stem (cm)	No. of leaves	No. of flowers	Average of length leaf (cm)	Internode length (cm)	Growth rate
No storage no ethylene	57	161	61	142	17.1	9.5	0.43	1.10
Ethylene 2 days no storage	44	161	62	154	15.1	8.8	0.40	1.20
Ethylene 4 days no storage	36	158	69	171	14.8	7.0	0.40	1.40
Ethylene 6 days no storage	35	185	74	176	14.7	13.0	0.42	1.20
Ethylene 13 days no storage	34	196	111	112	16.1	10.7	0.99	0.72
Ethylene 2 days followed by 4 weeks at 40°F storage	34	128	60	96	17.9	6.6	0.63	1.10
Ethylene 4 days followed by 4 weeks at 40°F storage	30	123	61	109	17.3	8.4	0.56	1.30
Ethylene 6 days followed by 4 weeks at 40°F storage	30	109	66	111	17.9	9.6	0.56	1.65
Ethylene 13 days followed by 4 weeks at 40°F storage	28	97	69	114	17.0	9.2	0.61	2.00
L.S.D. 5% -	9	9	16	30	1.3	1.9	0.18	0.37

Table 28. Effect of various growth substances on growth and flowering of 'Ace' lily.

Treatment	Days to emerge	Days to flower after emergence	Length of stem (cm)	No. of leaves	No. of flowers	Average length of leaf (cm)	Internode length (cm)	Growth rate	No. of flowers aborted
GA_3 2500 ppm	23	239	77	225	10.1	13.1	0.35	1.1	1.5
B-9 2500 ppm	56	188	59	161	9.0	13.7	0.37	1.1	0.5
B-9 5000 ppm	63	183	64	181	10.5	13.7	0.35	1.2	0.1
Alar-85 2500 ppm	58	185	65	167	9.8	14.9	0.39	1.2	0.4
Alar-85 5000 ppm	66	176	65	172	9.0	14.8	0.38	1.3	0.3
IAA 1250 ppm	47	230	95	246	10.6	13.0	0.38	1.3	2.8
IAA 2500 ppm	54	216	76	215	9.6	13.0	0.35	1.2	2.0
Kinetin 1250 ppm	55	204	68	196	9.8	13.9	0.35	1.2	1.3
Abscisic acid 5 ppm	58	208	69	209	10.6	13.8	0.33	1.2	1.4
DMSO 20 ppm	56	216	84	228	11.2	14.1	0.37	1.3	1.4
Control	56	206	78	199	10.1	14.8	0.39	1.2	1.6
L.S.D. 5% -	8	11	9	24	0.82	0.5	0.02	0.1	0.7

in daughter portion emerged in 33 days following such treatment, while those with 40 emerged during storage. Six weeks storage at 40° F with or without GA_3 (2500 ppm) treatment or GA_3 2500 ppm alone, effectively increased speed of emergence (Figure 31).

Apex Size and Flower Number

The results obtained in the Experiment 14 designed to relate apex size to flower number indicate a high negative correlation between apex size and length of vernalization period (Figure 32). In general 40° F vernalization of 'Ace' bulbs was destructive of flowering potential, the longer the storage period the greater the reduction in flower initials. This may be the result of a number of factors, but it is probable that size of apex is a major one. The size of the apex did not change during storage, but decreased significantly during axis extension and flower bud initiation. The longer the vernalization period the smaller the diameter of the apex. The average of size of apex during the estimated period of flower bud initiation was 3.37, 2.91 and 2.49 mm (x44) for 0, 6, and 18 weeks of 40° F vernalization, respectively (Table 29).

Plant Vernalization and Devernalization

The effects of temperature treatment on bulb as opposed to plant are presented in Table 30. These results indicate that 70° F

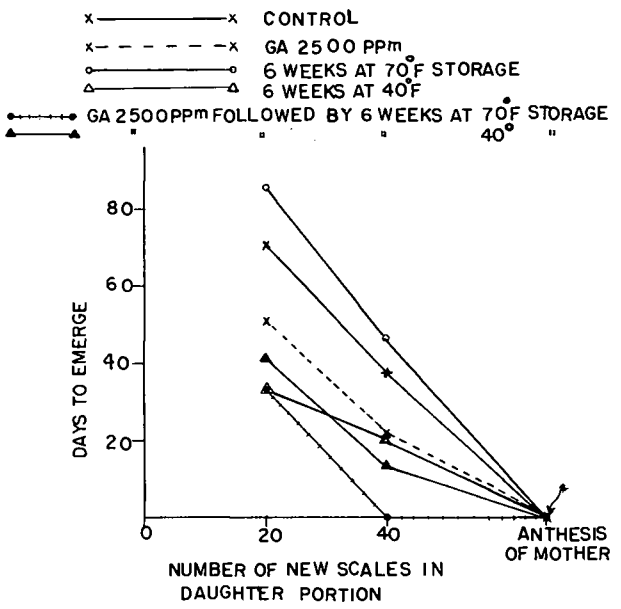


Figure 31. Effect of new scale number in daughter portion, vernalization and GA_3 treatment on speed of emergence of 'Ace' lily.

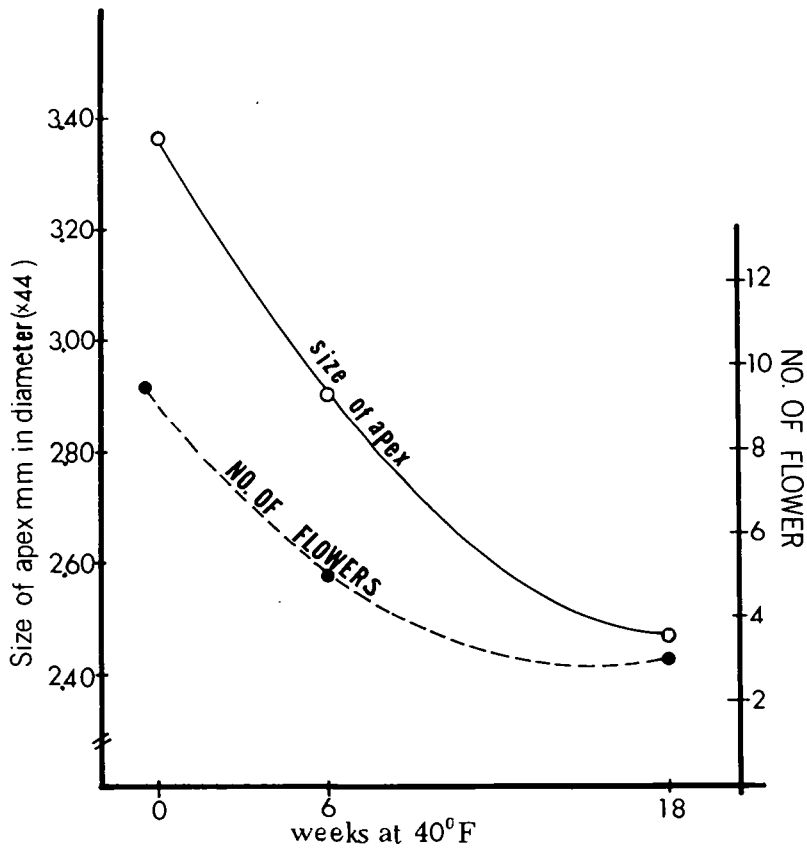


Figure 32. Effect of vernalization at 40° F on apex size and flower numbers of 'Ace' lilies.

Table 29. Effect of vernalization at 40° F on apex size after storage and during flower initiation time.

No. of weeks of storage	Diameter of size of apex mm (x44)	
	After storage	During flower initiation time
0 week	2.0	3.37
6 weeks at 40° F	2.2	2.91
18 weeks at 40° F	2.2	2.47

L.S.D. 5% - 0.35

Table 30. Effect of plant vernalization (40° F) and devernalization (70° F) on growth and flowering of 'Ace' lily.

	Treatment: Temperature Bulb storage ⟶ Temperature Plant exposure	Days to emerge	Days to flower after emergence	Length of stem (cm)	No. of leaves	No. of flowers	Average length of leaf (cm)	Internode length (cm)	Growth rate
Group I	6 weeks at 40°F ⟶ 0 weeks at 70°F	23	159	95	123	6.2	19.3	0.77	1.3
"	" ⟶ 1 "	21	151	105	136	5.8	19.0	0.77	1.3
"	" ⟶ 2 "	22	161	112	139	6.6	18.5	0.81	1.4
"	" ⟶ 3 "	25	173	130	168	5.8	18.6	0.77	1.5
Group II	6 weeks at 70°F ⟶ 0 weeks at 40°F	49	283	120	264	13.8	16.1	0.45	1.4
"	" ⟶ 1 "	48	277	125	272	13.0	14.9	0.46	1.4
"	" ⟶ 2 "	46	261	119	223	13.4	17.0	0.54	1.2
"	" ⟶ 3 "	47	224	75	145	8.0	16.7	0.52	1.0
	L. S. D. 5% - On group I	5	10	8	21	0.15	5.8	-	-
	On group II	5	10	5	19	0.91	4.0	-	-

had a devernalizing effect on previously vernalized bulbs. Plants from bulbs vernalized at 40° required at least three weeks of 70° F to retard flowering, while plants from bulbs stored at 70° F required at least two weeks exposure to 40° F to accelerate flowering. Plants from bulbs stored at 40° F were made progressively taller by 70° F plant forcing temperature treatment, while plants from bulbs stored at 70° required three weeks exposure to 40° to shorten them significantly. On the basis of leaf count, plants from bulbs stored at 40° appeared to have been devernalized by 70° treatment, because leaf numbers trended upward with progressively longer exposures of plant to 70° F greenhouse temperature. Bulbs stored initially at 70° were strongly vernalized by 40° F treatment, because leaf numbers decreased greatly with increasing length of 40° F exposure of plants. Flower numbers of plants from bulbs stored at 70° F was greatly reduced by plant exposure to 40° F. Bulbs stored previously at 70° F produced roughly twice as many flowers as compared to 40° F bulbs. Temperature treatment of plants had little effect on leaf length.

Chemical Analyses

Changes in nitrogen metabolism during storage

Free Amino Acids

Identification of free amino acids. The amino acids occurring

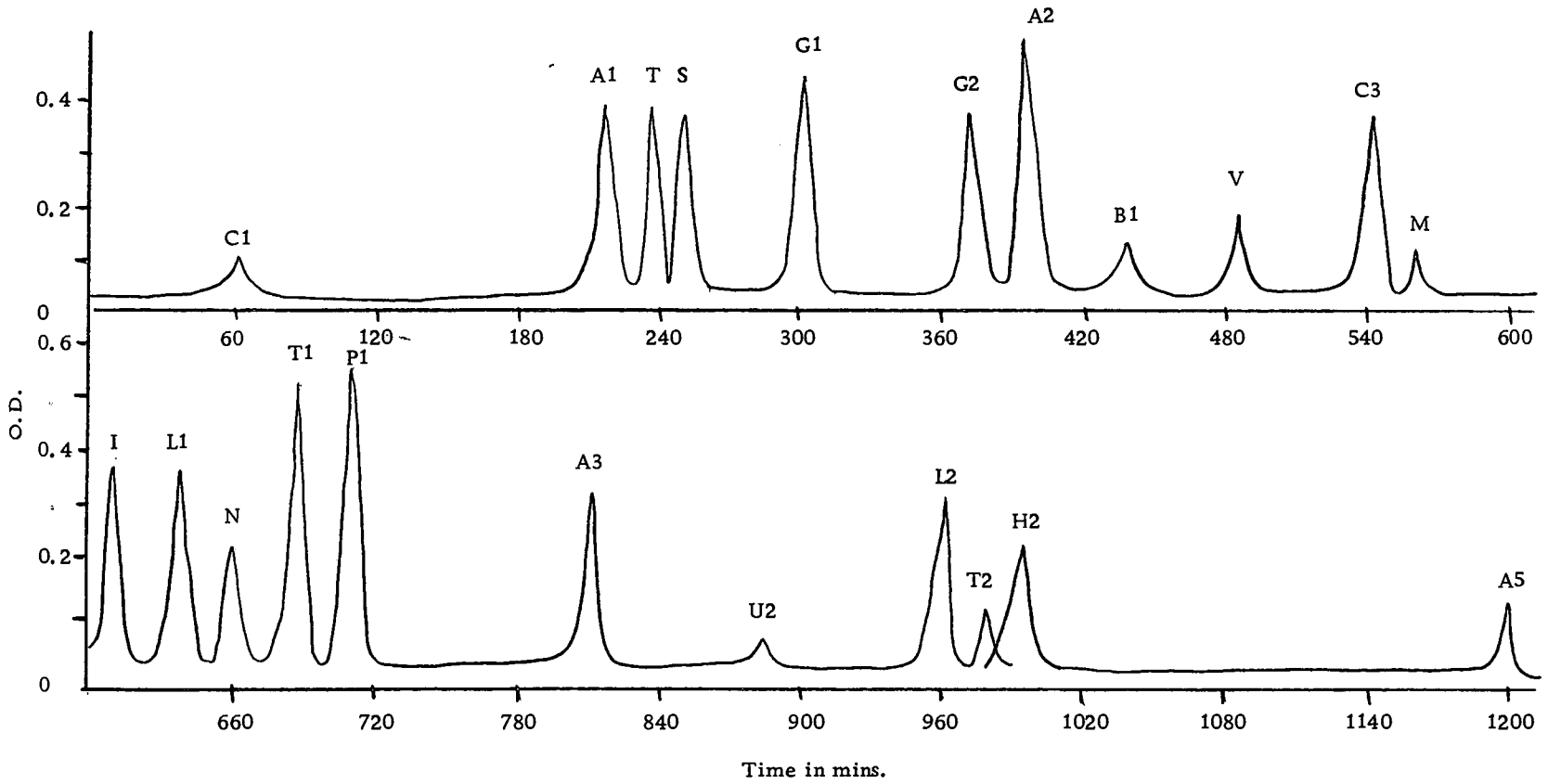
in the scales of 'Ace' bulbs before and after storage are listed in Table 31. Twenty amino acids in the free state were identified from the new scales of 'Ace' bulbs before storage as cysteic, aspartic, threonine, serine, glutamic, glycine, alanine, alpha-amino-butyric acid, valine, cystine, methionine, isoleucine, leucine, tyrosine, phenylalanine, lysine, tryptophan, histidine, arginine and an unidentified #2 (Figure 33). Those present in highest concentration were phenylalanine, tyrosine, alanine, cystine, glutamic, leucine, isoleucine, glycine and aspartic.

Prior to storage, the old scales of 'Ace' bulbs contained 18 amino acids: aspartic, threonine, serine, glutamic, glycine, alanine, alpha-amino-butyric acid, cystine, methionine, leucine, tyrosine, phenylalanine, two unidentified #1, #2, lysine, tryptophan, histidine, and arginine (Figure 34). Those present in highest concentration were alanine, phenylalanine, glutamic, aspartic, threonine, histidine and glycine. After six weeks storage at 40° F, glycine, valine, methionine disappeared in new scales (Figure 35), and cysteic, gama-amino-butyric acid, valine, isoleucine appeared in old scales (Figure 36). There were no changes in other amino acids during the six weeks of 40° F storage with the exception of an increase or decrease in the amount of certain amino acids.

Quantitative changes in individual amino acids during storage. Phenylanine, tyrosine, alanine, cystine and glutamic were the

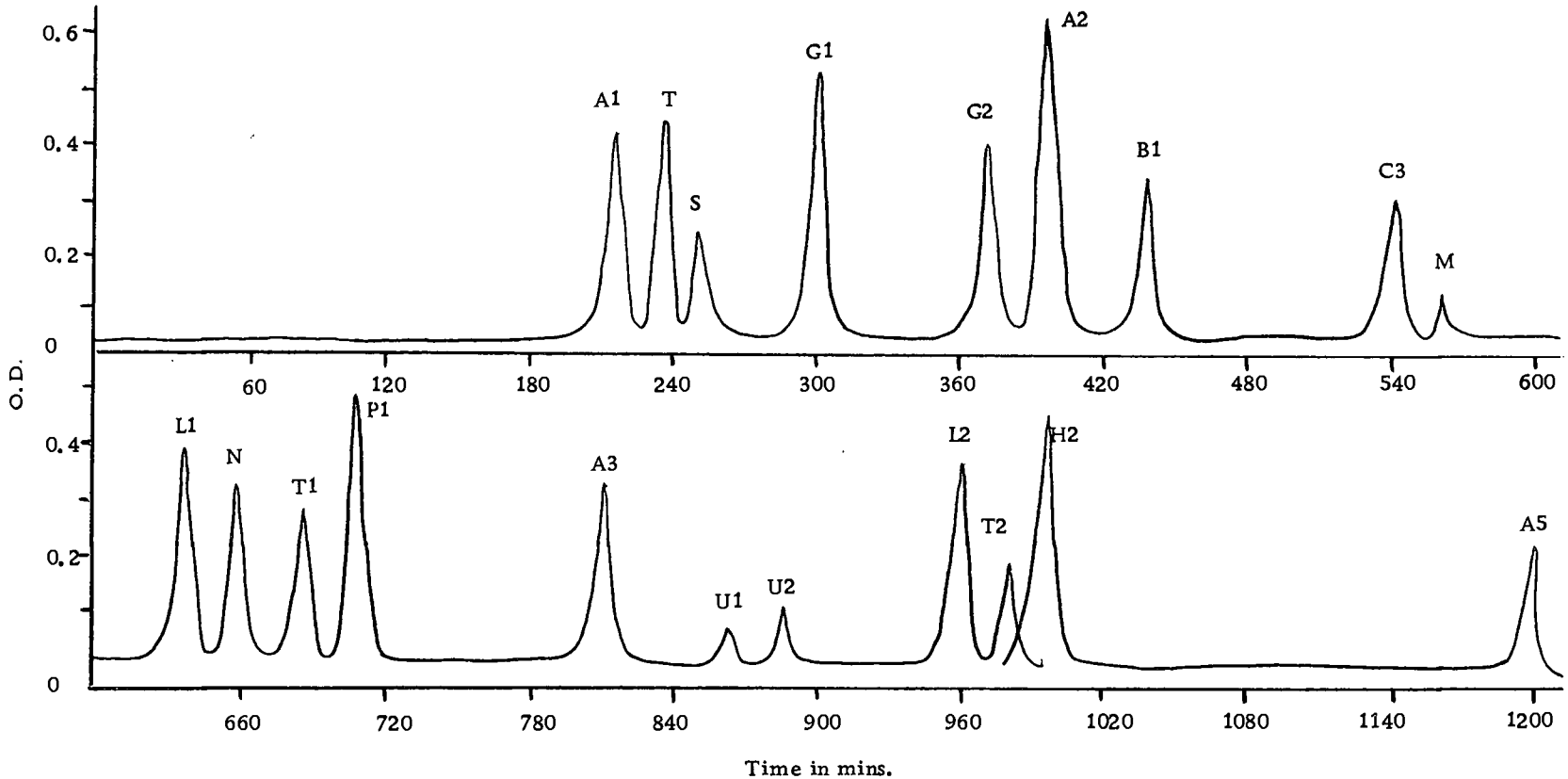
Table 31. Free amino acids in new and old scales of 'Ace' bulbs before and after storage.

Amino acid	Before storage		After 6 weeks of 40°F storage	
	New scales	Old scales	New scales	Old scales
Cysteic	x	-	x	x
Aspartic	x	x	x	x
Threonine	x	x	x	x
Serine	x	x	x	x
Glutamic	x	x	x	x
Glycine	x	x	-	x
Alanine	x	x	x	x
α NH_2 butyric	x	x	x	x
Valine	x	-	-	x
Cystine	x	x	x	x
Methionine	x	x	-	x
Isoleucine	x	-	x	x
Leucine	x	x	x	x
Tyrosine	x	x	x	x
Phenylalanine	x	x	x	x
γ NH_2 butyric	-	-	-	x
Unknown #1	-	x	-	x
Unknown #2	x	x	x	x
Lysine	x	x	x	x
Tryptophan	x	x	x	x
Histidine	x	x	x	x
Arginine	x	x	x	x



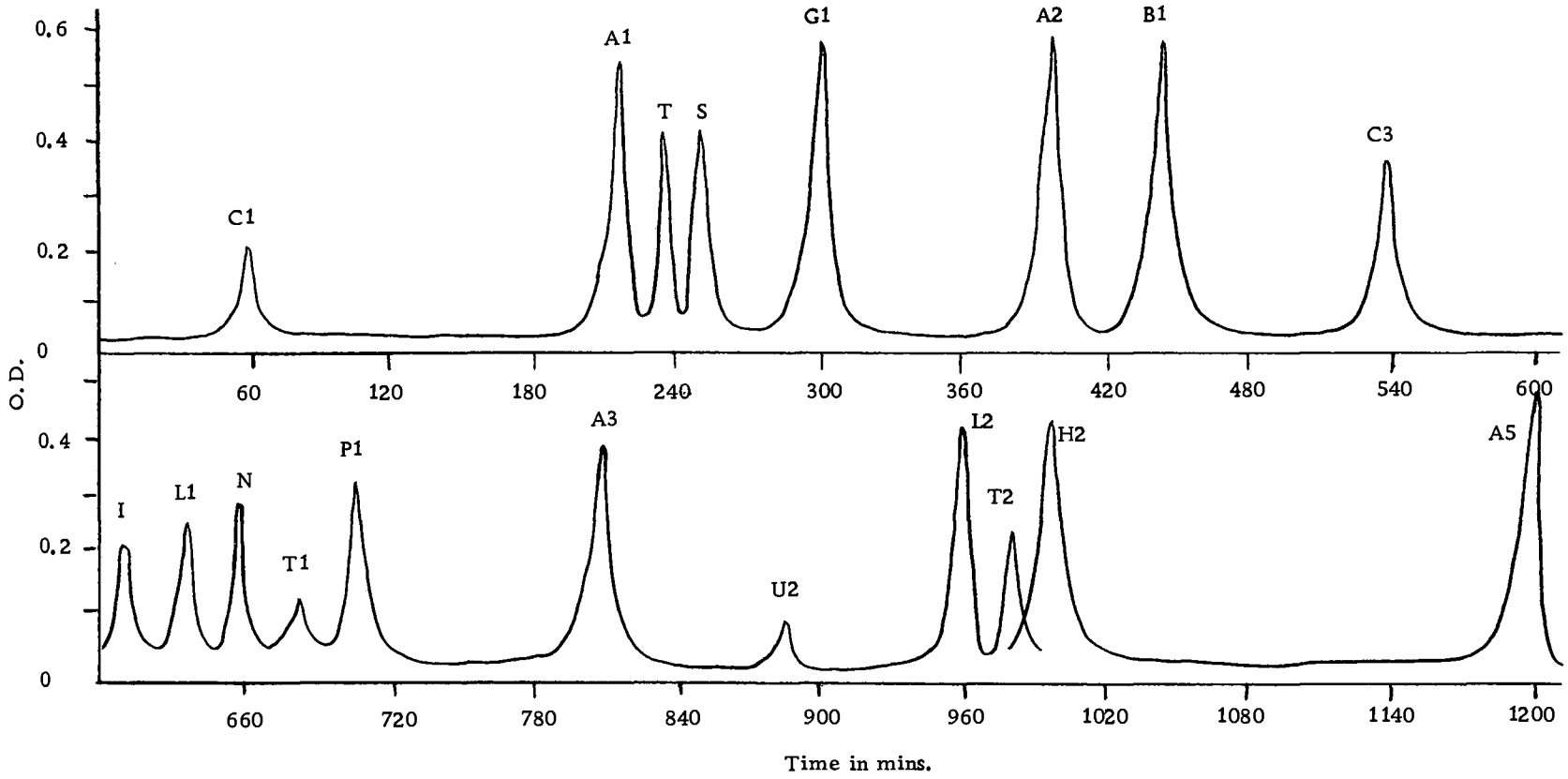
C1 - Cysteic
A1 - Aspartic
T - Threonine
S - Serine
G1 - Glutamic
G2 - Glycine
A2 - Alanine
B1 - αNH_2 Butyric
V - Valine
C3 - Cystine
M - Methionine
I - Isoleucine
N - Norleucine
L1 - Leucine
T1 - Tyrosine
P 1 - Phenylalanine
A3 - Ammonia
U2 - Unknown #2
L2 - Lysine
T2 - Tryptophan
H2 - Histidine
A5 - Arginine
O. D. - Optical Density

Figure 33. Amino acids in new scales of 'Ace' bulbs before storage.



A1 - Aspartic
T - Threonine
S - Serine
G1 - Glutamic
G2 - Glycine
A2 - Alanine
B1 - ∝ NH2 Butyric
C3 - Cystine
M - Methionine
L1 - Leucine
N - Norleucine
T1 - Tyrosine
P1 - Phenylalanine
A3 - Ammonia
U1 - Unknown #1
U2 - Unknown #2
L2 - Lysine
T2 - Tryptophan
H2 - Histidine
A5 - Arginine
O.D. - Optical Density

Figure 34. Amino acids in old scales of 'Ace' bulbs before storage.



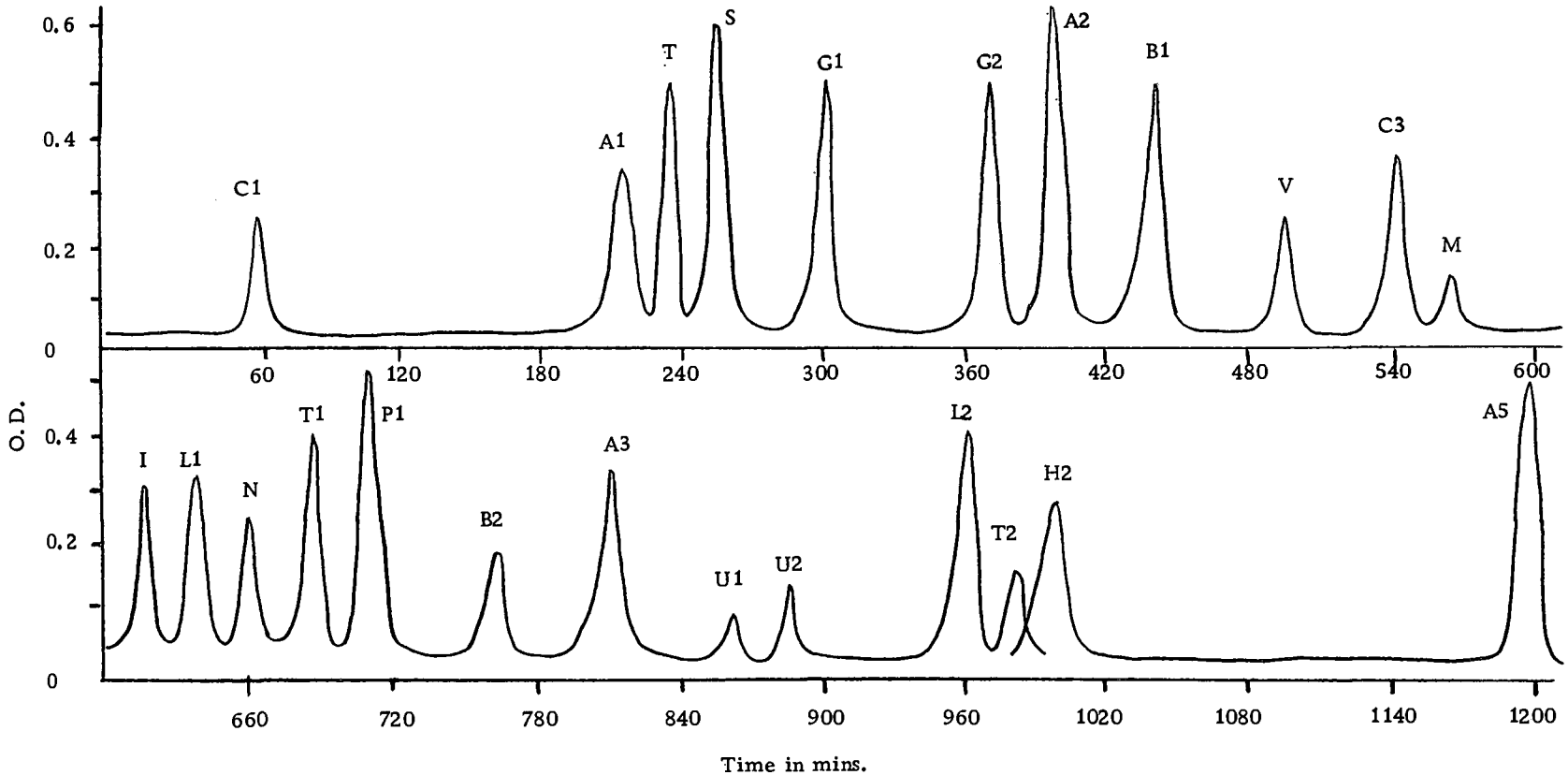
C1 - Cysteic
A1 - Aspartic
T - Threonine
S - Serine
G1 - Glutamic
A2 - Alanine

B1 - ∝ NH2 Butyric
C3 - Cystine
I - Isoleucine
L1 - Leucine
N - Norleucine
T1 - Tyrosine

P1 - Phenylalanine
A3 - Ammonia
U2 - Unknown #2
L2 - Lysine
T2 - Tryptophan
H2 - Histidine
A5 - Arginine

O. D. - Optical Density

Figure 35. Amino acids in new scales of 'Ace' bulbs after six weeks of 40°F storage.



C1 - Cysteic
A1 - Aspartic
T - Threonine
S - Serine
G1 - Glutamic
G2 - Glycine

A2 - Alanine
B1 - ∝NH2 Butyric
V - Valine
C3 - Cystine
M - Methionine
I - Isoleucine

L1 - Leucine
N - Norleucine
T1 - Tyrosine
P1 - Phenylalanine
B2 - γ NH2 Butyric
A3 - Ammonia

U1 - Unknown #1
U2 - Unknown #2
L2 - Lysine
T2 - Tryptophan
H2 - Histidine
A5 - Arginine
O.D. - Optical Density

Figure. 36. Amino acids in old scales of 'Ace' bulbs after six weeks of 40° F storage.

predominant amino acids in the new scales of 'Ace' bulbs, with concentrations of 19.05, 10.70, 8.35, 4.55 and 2.41 μM/10 gm fresh weight respectively. Alanine, phenylalanine, glutamic and aspartic were the predominant amino acids in old scales with concentrations of 10.79, 3.46, 2.99 and 2.49 μM/10 gm fresh weight, respectively, at the beginning of storage. Cysteic, aspartic, threonine, serine, glutamic, alanine, alpha-amino-butyric acid, unknown #2, lysine, tryptophan, histidine and arginine increased in concentration in the new scales after six weeks of 40° F storage. After six weeks of 40° F storage, all amino acids also increased in concentration in the old scales (Table 32).

Difference in concentration of each amino acid before and after six weeks of 40° F storage as indicated by the data are shown in Table 33.

Certain amino acids contained in the scales tended to increase in concentration after six weeks storage at 40° F. These were cysteic, aspartic, threonine, serine, glutamic, glycine, alanine, α NH_2 butyric, valine, cystine, isoleucine, unknown #1, unknown #2, γNH_2 butyric, lysine, tryptophan, histidine and arginine. Other amino acids tended to decrease in concentration; methionine, leucine, tyrosine and phenylalanine (Table 34).

Table 32. Free amino acids in new and old scales of 'Ace' bulbs before and after storage.

Peak number	Amino acid	Scales from bulbs not stored[a]		Scales from bulbs stored 6 weeks at 40°F	
		New scales μM/10 g	Old scales μM/10 g	New scales μM/10 g	Old scales μM/10 g
1	Cysteic	0.268	-	0.598	2.070
2	Aspartic	1.860	2.490	4.900	3.705
3	Threonine	1.460	2.325	3.635	11.650
4	Serine	1.055	0.092	3.060	13.050
5	Glutamic	2.405	2.990	6.200	11.050
6	Glycine	1.900	2.290	-	11.450
7	Alanine	8.350	10.785	8.455	12.610
8	α NH_2 butyric	0.067	1.630	6.655	10.815
9	Valine	0.618	-	-	0.344
10	Cystine	4.550	0.627	1.200	4.300
11	Methionine	0.097	0.135	-	0.205
12	Isoleucine	2.325	-	0.485	1.885
13	Leucine	2.350	1.375	0.531	2.240
14	Tyrosine	10.700	0.116	0.166	7.850
15	Phenylalanine	19.050	3.460	0.982	11.100
16	γ NH_2 butyric	-	-	-	1.060
17	Unknown #1	-	0.329	-	1.049
18	Unknown #2	0.280	0.500	0.500	1.061
19	Lysine	1.369	1.480	1.536	3.460
20	Tryptophan	0.878	1.000	0.902	1.112
21	Histidine	1.302	2.350	2.645	2.825
22	Arginine	0.483	0.560	6.600	7.850

[a]Samples taken immediately after harvest.

Table 33. Difference in concentration of each amino acid before and after storage.

Peak Number	Amino Acid	Difference in concentration before and after storage	
		New scales μM/10 g	Old scales μM/10 g
1	Cysteic	0.330	2.070
2	Aspartic	3.040	1.215
3	Threonine	2.175	9.325
4	Serine	2.005	12.958
5	Glutamic	3.795	9.060
6	Glycine	-1.900	9.160
7	Alanine	0.105	1.825
8	α NH_2 butyric	6.588	9.185
9	Valine	-0.618	0.344
10	Cystine	-3.350	3.673
11	Methionine	-0.097	0.070
12	Isoleucine	-1.840	1.885
13	Leucine	-1.819	0.865
14	Tyrosine	-10.534	7.734
15	Phenylalanine	-18.068	7.640
16	γ NH_2 butyric	-	1.060
17	Unknown #1	-	0.720
18	Unknown #2	0.220	0.561
19	Lysine	0.167	1.980
20	Tryptophan	-0.114	0.112
21	Histidine	1.343	0.475
22	Arginine	6.117	7.290

- sign indicated decreased concentration after storage (six weeks at 40°F)

Table 34. Free amino acids in scales of 'Ace' bulbs before and after storage.

Peak number	Amino acid	Scales from bulbs not stored[a] μM/10 g	Scales from bulbs stored 6 weeks at 40°F μM/10 g
1	Cysteic	0.134	1.334
2	Aspartic	2.180	4.302
3	Threonine	1.892	7.642
4	Serine	0.574	8.055
5	Glutamic	2.697	8.625
6	Glycine	2.095	5.725
7	Alanine	2.567	10.533
8	α NH_2 butyric	0.849	8.785
9	Valine	0.309	0.172
10	Cystine	2.588	2.750
11	Methionine	0.117	0.102
12	Isoleucine	1.162	1.185
13	Leucine	1.862	1.385
14	Tyrosine	5.408	4.008
15	Phenylalanine	11.255	6.041
16	γ NH_2 butyric	-	0.530
17	Unknown #1	0.164	0.524
18	Unknown #2	0.390	0.780
19	Lysine	1.424	2.498
20	Tryptophan	0.939	1.007
21	Histidine	1.826	2.735
22	Arginine	0.521	7.225

[a]Samples taken immediately after harvest.

Total Alcohol Insoluble Nitrogen (Protein-Nitrogen)

Changes occurring in the protein nitrogen fraction during 40° F and 70° F storage, GA_3 treatment and their relation to dormancy are outlined in Table 35. Protein nitrogen in scales of 'Ace' bulbs increased from 1.25% to 1.33% with six weeks storage at 70° F, increased to 1.45% with six weeks storage at 40° F, to 1.49% with the same 40° F storage preceded by 2500 ppm GA_3 treatment, and further increased to 1.56% with six weeks 70° F of storage preceded by 2500 ppm GA_3.

Growth Substances

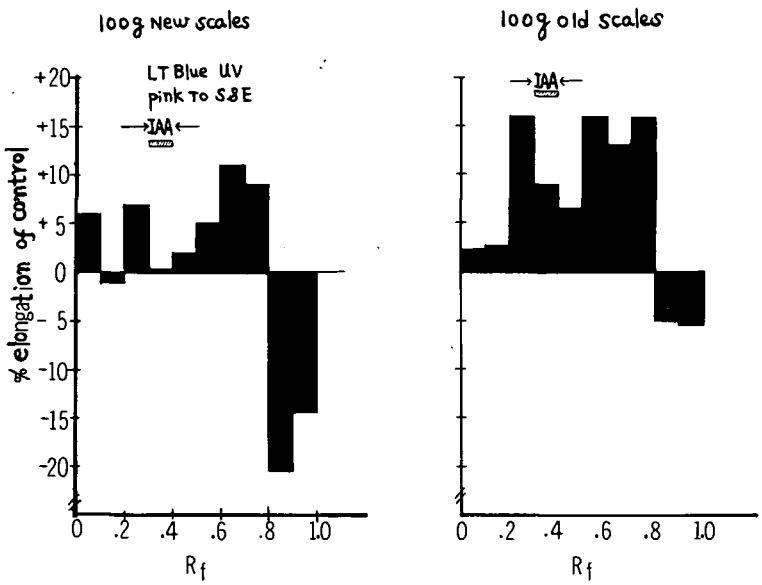
Oat (var. 'Forkedeer') coleoptile assays of chromatographic fractions of extracts from unchilled new and old scales revealed zones of inhibition at R_f 0.8-0.9 and R_f 0.9-1.0 (Figure 37). The content of these two inhibitors was higher in new than old scales. The presence of indole acetic acid (IAA) was established by typical color reactions with Salkowski and Ehrlich reagents, co-chromatography with IAA, and by bioassay. The amount of IAA in old scales was approximately 7.5% (based on % oat coleoptile elongation) higher than that found in the new scales (Figure 37). There was a 6.0% increase in quantity of IAA in the scales after six weeks storage at 40° F (Table 36). Total amount of promoter also increased in

Table 35. Effect of 40° F and 70° F storage and GA_3 treatment on total alcohol insoluble nitrogen in scales of 'Ace' bulbs.

Treatment	Total alcohol insoluble nitrogen (% protein nitrogen per g dry weight)	Dormancy (Days to emerge)
1. No storage, sample taken immediately after harvest	1.25	80
2. Six weeks 70° F of storage	1.45	37
3. Six weeks 40° F of storage	1.33	66
4. 2500 ppm GA_3 followed by six weeks 70° F of storage	1.56	10
5. 2500 ppm GA_3 followed by six weeks 40° F of storage	1.49	18

Table 36. Effect of 40° F storage on indole acetic acid content of 'Ace' scales.

Treatment	Growth of coleoptile section, expressed as percent of the elongation of control sections
1. No storage, sample taken immediately after harvest	3.7%
2. Six weeks at 40° F storage	9.7%



Abbreviation: LT - Light; S - Salkowski reagent; E - Ehrlich reagent

Figure 37. Oat coleoptile assays of extract of 'Ace' scales chromatographed in isopropanol, ammonium hydroxide, and water (8:1:1 by volume). The crosshatched inserts represent the location of indole acetic acid on chromatograms developed in the same solvent system. 0% -- control. (Bulbs were dug on Sept. 1, 1966).

scales with storage, while that of the inhibitor decreased. Old scales contained about 3.6% (% elongation of control) of promoter, while new scales had about 6.0% of inhibitor. After six weeks at 40° F storage, the amount of promoter in old scales increased from 3.6% to 8.6%. In new scales, inhibitor disappeared, and contained about 7.4% of promoter (Table 37). Total amount of inhibitor (2.0%) in scales decreased, while total amount of promoter increased to 8.5% (Table 38).

Abscisic acid and scale extracts (acid fraction) were chromatographed simultaneously in an isopropanol, ammonium hydroxide, and water (8:1:1 by volume) system. The R_f of the inhibitor in the scale extract was similar to that of abscisic acid (R_f 6.0~7.0).

The inhibitor zone at R_f 0.60 to 0.70 was eluted with absolute ethanol from several chromatograms.

The ultraviolet absorption spectra of the elutant in absolute ethanol were compared with and found to be very similar to those of abscisic acid (Figure 38).

Table 37. Effect of 40° F storage of new and old scales of 'Ace' bulbs on total promoter and inhibitor content.

Treatment	Growth of coleoptile sections, expressed as percent of the elongation of control sections
1. No storage, sample taken immediately after harvest	
(a) Old scales (100g)	+3.6%
(b) New scales (100g)	-6.0%
2. Six weeks at 40° F storage	
(a) Old scales (100g)	+8.6%
(b) New scales (100g)	+7.4%

- inhibition
+ promotion

Table 38. Effect of 40° F storage of scales of 'Ace' on total promoter and inhibitor content.

Treatment	Growth of coleoptile sections, expressed as percent of the elongation of control sections
1. No storage, sample taken immediately after harvest (100g)	-2.0%
2. Six weeks at 40° F storage (100g)	+8.5%

- inhibition
+ promotion

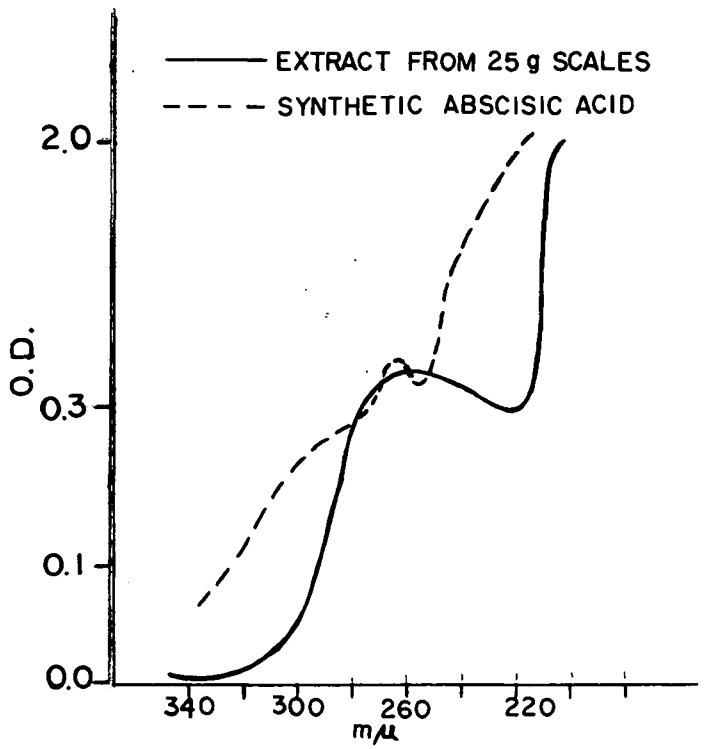


Figure 38. Ultraviolet absorption spectra of synthetic abscisic acid and the inhibitor extracted from scales. Each was measured in 100% ethanol. (Bulb scales were harvested in June 1968.)

DISCUSSION

The concept which this thesis appears to support, on the basis of the data presented, is that dormancy in the Easter lily bulb is a specific expression of growth suppression by inhibitors in the bulb scales, and is associated with but independent of the subsequent phenomena of stem elongation and floral induction.

Development of Dormancy in the Scales and Role of Scales

As expected from previous experience, the daughter bulb's ability to start another cycle of growth increases progressively during the growing season and with delay of harvest. The days required for the non-vernalized daughter bulbs to sprout after harvest and greenhouse potting decreased progressively with later digging dates.

Removal of old scales had little or no significant effect on days to emerge, but removal of new scales accelerated emergence. This would indicate that new scales are the principal source of dormancy up to the time of bulb maturity normally in September. Thus the dormancy factor in the scales decreased progressively during the growing season. These results are probably related to the developmental physiology of the Easter lily, as mediated by natural growth regulating substances. Stewart and Stuart (71) studied the distribution

of auxins in lily bulbs. They found large differences in the amount of auxin in different parts of Easter lily bulbs. The apical 3 mm of the stem axis contained about 1000 times the concentration of auxin present in the scales and basal plate. These bulbs had been stored for four and one-half months in moist peat at $70^{\circ}\sim85^{\circ}$ before the auxin determinations were made.

DeHertogh and Carlson (17) reported the presence of Gibberellin-like substances in some bulbous crops. In studies with tulip, they found the amount of both free and bound Gibberellin-like substances increased during the obligatory low temperature treatment. At the end of 13 weeks the amount of freely extractable Gibberellin-like substances increased approximately 370 fold. They concluded from these results that a great proportion of this increase was the result of biosynthesis of these compounds.

The evidence obtained in Experiment 17 with 'Ace' lily scales from unchilled bulbs revealed zones of inhibition of R_f 0.8~0.9 and R_f 0.9~1.0 (Figure 37). The content of these two inhibitors was higher in new than old scales. The amount of indole acetic acid (IAA) in old scales was approximately 7.5% higher than that found in the new scales (Figure 37). There was a 6.0% increase in quantity of IAA in the scales after six weeks storage at 40° F (Table 36). The total amount of promoter also increased in scales with storage, while that of the inhibitor decreased. Old scales contained about

3.6% of promoter, while new scales had about 6.0% of inhibitor. After six weeks at 40°F storage, the amount of promoter in old scales increased from 3.6% to 8.6%. In new scales, the inhibitor disappeared and they contained about 7.4% of promoter (Table 37). Total amount of inhibitor (2.0%) in scales decreased, while total amount of promoter increased to 8.5% (Table 38). This tends to explain the adaptability of this crop to seasonal temperature changes and helps clarify also the problem of dormancy. Bulb storage at 40° was effective in breaking dormancy as reflected in reduced time required for sprouting (Figures 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 23, 24, 25, 26, and Tables 23 and 24).

Changes in nitrogen metabolism also occurred during the development and removal of dormancy. In addition to the twenty known amino acids which were identified, at least two unidentified ninhydrin positive compounds were detected. These two unknown compounds came off the column about 80~105 min before lysine, and calculations of their quantity were based on the norleucine standard. The amides, glutamine and asparagine, nearly always emerge together and are particularly difficult to resolve from other compounds with present chromatographic systems. In the standardized procedure used here, the amides eluted about same with serine. Fowden and Steward (27) found the γ-substituted glutamic acid were conspicuous in Lilium, but glutamine was not detected. Serine

values for plants are commonly of the same order of magnitude as threonine and glycine (82). Such information coupled with the values obtained for soluble serine and possibly amide content of bulb scales under different temperature conditions seems to indicate that amide is not the predominant constituent in our serine peak.

The free amino acid content differed in the two ages of scales and changed with temperature. These may be regarded as evidence of the widespread existence of metabolic pathways which had not previously been suspected.

Tryptophan as precursor of indole acetic acid was in higher concentration in old scales and increased in concentration after six weeks of 40° F storage. The content of indole acetic acid also followed this pattern. The importance and direct relationship of each amino acid to dormancy is still unclear. Trione et al. (82) studied the amino acid patterns in the spring wheat grown at 25° C. They found the spring wheat was induced to flower, whereas the winter wheat remained vegetative. The physiological difference as not reflected in the levels of the neutral and acidic amino acids, but marked differences were observed in the levels of the basic amino acids, arginine, histidine and lysine. Naylor (57) also has suggested that these basic amino acids play a leading role in dormancy and senescence, or at least are sensitive indicators.

The content of alcohol insoluble nitrogen in 'Ace' scales

increased with storage and GA_3 treatment. Protein nitrogen increased indicating an active net synthesis of protein during storage and GA_3 treatment. In general, the higher the scale protein content, the less the bulb dormancy and days required for emergence. Dormancy was also overcome with hot water treatment (1-1/2 hours at 100° F), by heating the soil before bloom (70° F), or chemical treatment with indole acetic acid (IAA), 2-chloroethane phosphonic acid (Ethrel) or ethylene. This may be the result of changes in certain metabolic processes and levels of natural growth regulating substances.

The increased content of free amino acids associated with cold treatment may be due to presence of certain enzymes involved in converting sugar to free amino acid.

Dormancy, Flowering and Growth

Dormancy and flowering while associated are independent phenomena. Differences in responses to treatment as related to dormancy and floral induction are summarized diagramatically in Table 39.

Although GA_3, scale removal, Ethrel and IAA treatments induced earlier emergence, they did not induce earlier flowering. Days to flower was measured from time of shoot emergence rather than potting date to separate, if possible, dormancy (vegetative) from

Table 39. Summary of the effect of various treatments on speed of emergence and other growth and flowering characteristics of Easter lily.

Treatment	Days to emerge	Days to flower from emergence	No. of leaves	Length of stem	Length of internode	Growth rate
1. Scale removal (Ace)						
(a) 0% →100% (by weight)	-	+	-	-	-	-
(b) New scales removed bulb	-	+	-	-		-
(c) Old scales removed bulb	+	-	-	-		-
2. Six weeks at 40° F storage (Ace)						
(a) Entire bulb	-	-	-	-		+
(b) New scales removed bulb	-	-	-	-		+
(c) Old scales removed bulb	-	-	-	-		+
(d) All scales removed bulb	+	-	-	-		+
3. Six weeks at 70°F storage (Ace)						
(a) Entire bulb	-	-	a	+		+
(b) New scales removed bulb	-	-	a	+		+
(c) Old scales removed bulb	-	a	a	a		+
(d) All scales removed bulb	+	-	a	a		a
4. Hot water (1-1/2 hrs. at 100°F)						
A. June bulb (Ace)						
(a) Entire bulb	+	-	-	-	+	
(b) New scales removed bulb	+	-	-	-	-	
(c) Old scales removed bulb	-	-	-	+	*	
(d) All scales removed bulb	+	-	*	+	-	
B. September bulb (Ace)						
(a) Entire bulb	*	-	-	*	+	
(b) New scales removed bulb	-	-	+	*	-	
(c) Old scales removed bulb	-	-	*	+	+	
(d) All scales removed bulb	-	-	*	+	-	
C. Croft bulb	-	-	-	-	+	+
5. 40°F storage (6 weeks →18 weeks)	-	-	-	-	+then-	+then-
6. Field soil heating						
A. Ace						
(a) Heat after bloom	+	+	+			
(b) Heat before bloom	-	-	-			

Continued

Table 39 Continued.

Treatment	Days to emerge	Days to flower from emergence	No. of leaves	Length of stem	Length of internode	Growth rate
B. Croft						
(a) Heat after bloom	+	*	*			
(b) Heat before bloom	-	-	-			
7. Growth substances						
(a) Ethrel	-	+	+	-	-	+
(b) Ethylene	-	+	+	+	+	+
(c) Gibberellic acid	-	+	+	*	-	-
(d) B-9 (2500 ppm)	*	-	-	-	-	-
" (5000 ppm)	+	-	-	-	-	*
(e) Alar-85 (2500 ppm)	*	-	-	-	*	*
" (5000 ppm)	+	-	-	-	*	*
(f) IAA (1250 ppm)	-	+	+	+	*	*
(2500 ppm)	*	+	+	*	-	*
(g) Kinetin (1250 ppm)	*	*	*	-	-	*
(h) Abscisic acid (5 ppm)	*	*	*	-	-	*
(i) DMSO (20 ppm)	*	*	+	+	-	*

\+ increase
\- decrease
* no significant effect
a inconsistence result, depend upon bulb harvest dates

flowering (reproductive) responses. Differences in speed of emergence did not necessarily reflect differences in speed of flowering. This is evident particularly in Table 40, where "immature" bulbs, that is those with only 20 new daughter scales when harvested and receiving no special treatment, required 71 days to emerge and 85 days to flower, but when soaked in 2500 ppm GA_3 these bulbs emerged in only 51 days, although they required 92 days to flower. Hence, it is evident that GA_3 treatment increased leaf number (Table 28) and accelerated emergence (removal dormancy) without affecting flower induction.

There has been little work done to relate scale development to onset of dormancy in bulbs. The results obtained in Experiment 3 with various degrees of scale removal suggest that the scales perform different roles in controlling dormancy (vegetative) and in floral induction (reproductive). Removing old scales (25% and 50%) had little or no significant effect on dormancy but the removal of new scales (75% and 100%) accelerated emergence and broke dormancy. Leaf number is one of the most reliable indices of the transition from the strictly vegetative to flowering state (87). On the basis of leaf number, one can say that a certain treatment was more or less capable of inducing flowering. Reduction in leaf numbers roughly paralleled the severity of scale removal, except that removing 75 and 100% of the scales reduced leaf numbers most severely.

Table 40. Effect of various treatments on speed of emergence and flowering of 'immature' 'Ace' bulb.

Treatment	Days to emerge	Days to flower after emergence
(a) Only 20 new daughter scales bulb		
(1) No storage, no GA_3 treatment	70	85
(2) 2500 ppm GA_3	51	92
(3) Stored in six weeks at 70° F	85	148
(4) 2500 ppm GA_3 followed by six weeks at 70° F storage	33	119
(5) Stored in six weeks at 40° F	33	88
(6) 2500 ppm GA_3 followed by six weeks at 40° F storage	41	90
(b) Only 40 new daughter scales bulb		
(1) No storage, no GA_3 treatment	37	102
(2) 2500 ppm GA_3	21	104
(3) Stored in six weeks at 70° F	46	162
(4) 2500 ppm GA_3 followed by six weeks at 70° F storage	0	95
(5) Stored in six weeks at 40° F	20	96
(6) 2500 ppm GA_3 followed by six weeks at 40° F storage	13	100
(c) Anthesis of mother bulb	0[a]	54

[a]Summer sprouted in soil bench.

Removal of up to 50% of the scales hastened flowering with a lower leaf number, but removing all of the scales delayed flowering drastically even with a lowest leaf number, suggesting that the scales furnish substrate for growth and, therefore, the greater the weight of scales the more leaves the growing point will initiate before it initiates the first flower bud. The old scales may play an important role in leaf initiation, because their removal drastically reduces leaf number.

The days to flower paralleled the number of leaves. 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. Scales also have been shown to be important in the flowering of Dutch iris (66, 67) and star-of-Bethlehem (31), scale removal was also reported to be harmful to the speed of flowering (63, 89).

40° vernalization is most effective in bringing about rapid floral induction in fall treated bulbs, 70° was found to be non-vernalizing in fall treated bulbs, but brought about rapid elongation of daughter axis and flowering in early spring. It would appear that warmth acted like a vernalizing temperature in the late winter. This is intriguing because Povar (64) reported vernalization in

wheat with warmth. Several authors (32, 51, 54) have suggested that soil temperatures in the field should affect the forcing of the greenhouse lily, but have presented no experimental evidence. 70° F hastens emergence of late summer and fall harvested bulbs also, but probably does not induce at that temperature unless cumulative 60° exposure in field will accomplish it. Further research is needed to resolve this question.

Heating the soil in the field to 70°~75° from July to mid-September (Experiment 8) did not appreciably affect the response of the bulbs to subsequent vernalization treatment. Miller and Kiplinger (52, 53) conducted devernalization treatments to erase any field vernalization acquired by the bulbs prior to autumn harvest. They concluded time to flower was controlled by the last temperature to which the bulbs were exposed, indicating a reversal of vernalization. High temperature caused devernalization, devernalized bulbs were again vernalized when exposed to cold temperature. Under certain conditions, end products of vernalization are stabilized and high temperatures do not result in devernalization. That vernalization and devernalization occur, not only in the bulb but also in the plant, is shown in the results presented in Table 30. These data substantiate the 70° F treatment had a devernalizing effect on previously vernalized bulbs. Plants from bulbs vernalized at 40° required at least three weeks exposure to 70° F to retard

flowering, because leaf numbers trended upward with progressively longer exposures of plant to 70° F greenhouse temperature. Plants from bulbs previously stored at 70° F required at least two weeks exposure to 40° F to accelerate flowering, because leaf numbers decreased greatly with increasing length of 40° F exposure of plants.

Cold storage, as well as, scale removal was deleterious to flowering potential (number flowers). The longer the bulbs were stored, the greater the reduction in number of flowers initiated. Flower number may be directly related to stem apex size in this case (Figure 32).

Cold storage reduces leaf number, and 18 weeks of 40° F storage is sufficient to completely vernalize the bulb, bringing about immediate flower bud initiation when planted, and the leaf complement is essentially that derived from primordia in the bulb at harvest and before storage.

Significance of New Findings

The conclusions drawn from this study are as follows:

1. A daughter stem apex is always actively initiating new scales, leaves or flowers at varying speeds. The new daughter scales contain the dormancy factor, keeping the daughter suppressed up to time of normal field

maturity, when new and old scales are equally distributed in weight in the bulb. The dormancy factor is equally distributed in new and old scales when the bulb is approaching maturity.

2. The stem apex and scales respond differently to 40° and 70° F storage. In general, cold (40° F) and warm (70° F) storage seemed to remove dormancy factors present in the scales, but increased the amount of inhibiting substances in the stem apex. Cold and warm may change some metabolic processes in scales or increase or decrease certain growth substances which alter sprouting.

3. Dormancy (vegetative) and floral induction (reproductive) are two associated but independent phenomena, since certain treatments can hasten sprouting without hastening flower initiation.

4. Cold storage, which is deleterious to flowering potential (number flowers), appears to have its effects through reducing apex sizes which is directly correlated to flower number.

5. High temperature (70° F) tends to devernalize plants from vernalized bulbs, while low temperature (40° F) tends to vernalize plants from non-vernalized bulbs.

6. Vernalization tends to increase the amounts of most free amino acids and protein nitrogen in the new and old scales of the bulb.

7. The content of inhibitors is higher in new than old scales, and their total content decreases with 40° and 70° F storage, while that of promoters is increasing. One of the inhibitors was found to be very similar to that of abscisic acid, and one of the promoters was similar to indole acetic acid (IAA).

Some interesting questions can be asked regarding the action of GA and other treatments in promoting sprouting in Easter lily. Eagles and Wareing (46, 47) postulated that in Betula pubescens winter chilling may overcome dormancy by increasing the endogenous GA level. Is it possible that under cold storage conditions the GA levels in Easter lily would increase, and that warm (70° F) induction is required to decrease the level of GA? Yet, accepting this hypothesis, bulbs following cold storage emerge faster than in the case of non-storage ones, and warm (70° F) storage causes slower emergence than no storage. The former case is true, but the latter has never been observed in Easter lily. 40° F and 70° F storage accelerated earlier emergence of June through October harvested bulbs (Figures 10 and 11).

Does cold storage (40° F) reduce the level of endogenous

gibberellin and warm storage (70° F) increase it? If so, 70° F storage should promote earlier emergence than 40° F storage, but this has been observed to occur only in bulbs harvested in early winter and late fall (5). From recent experiments it is found that 60° F promotes earlier emergence of September and October bulbs after dormancy gone, and 40° retards.

Does a natural inhibitor and promoter play an important role in altering sprouting? Does cold and warm storage cause the production of naturally occurring growth substances, or change certain metabolic processes which interfere with the action of the inhibitor? Application of exogenous GA to lily bulbs increases speed of emergence. DeHertogh (18) found endogenous GA decreased following cold treatment. It seems more likely that cold decreases the amount of inhibitor present rather than increasing the endogenous GA level. Application of exogenous GA may be antagonizing the action of endogenous inhibitors in the bulb, resulting in early emergence.

Is the auxin-inhibitor balance important in regulating dormancy? With the passing of natural dormancy, the inhibitor content dropped more rapidly with cold than warm treatment. Exposure to cold may bring about inactivation of the inhibitor.

Such questions and explanations, which are highly hypothetical, must be tested thoroughly before the mode of action of temperature

and chemical treatments on bulb dormancy or quiescence can be fully elucidated.

We know nothing as to the quantity or nature of growth substances that are transported to the stem apex from the bulb scales. It is possible that substantial quantities of inhibitors in the scales are derived from the leaves. Future work with various isotopically labelled inhibitors, such as abscissic acid will provide data on translocation, penetration, and metabolism of such substances during such treatments.

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