Physiology of Dormancy in *Lilium longiflorum* 'Ace', Thunb.[1]

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Abstract. The physiology of dormancy in *Lilium longiflorum* 'Ace' was studied by determining the relationships between plant growth and composition and treatments such as bulb scale removal, cold treatment, field soil heating and chemical stimuli. Initiatory activity was continuous in the daughter bulb until its anthesis, but elongation of daughter axis leaves and internodes were normally inhibited until autumn. Inhibition of the daughter axis was high during the spring prior to anthesis of the mother, but progressively decreased following anthesis and disappeared completely by autumn. Balances of inhibitor-promoter growth substances were found in the bulb scales. Daughter scales were found to be the principal source of inhibitors. Treatments conducive to breaking dormancy included 40°F storage, GA_3 treatment and field soil heating in early spring. Dormancy-breaking cold treatments were followed by changes in nitrogenous substances characteristic of dormancy removal in other species. The period of dormancy in the daughter portion of the lily bulb is of the correlated type and involves scale inhibition of axis elongation rather than initiatory activity in the apex.

Forcers of the Easter lily, *Lilium longiflorum,* contend that in some seasons the bulbs are immature or dormant as indicated by delay in sprouting or elongation of the daughter axis of healthy bulbs. It has been questioned whether dormancy is the best term for describing this delay. According to Vegis' review (18), Blaauw and co-workers have shown that in the garden forms of hyacinths, tulips, and daffodils, there is no true dormancy.

Doorenbos (4) used the term dormancy in woody plants for all instances in which a tissue predisposed to elongate did not do so. This concept seems to separate initiatory activity from that of primordial organ expansion or elongation in describing the dormant state.

Blaney and Roberts (2) found that the daughter bulb of the Easter lily started its growth and development as early as mid-November and continued to initiate scales, leaves or flowers during the rest of its growth cycle at a rate regulated by temperature. These primordia and internodes, however, did not normally elongate until the following November with the advent of short days and low temperatures. The correlated inhibition of the daughter by the mother axis in non-chilled or only partially chilled plants appeared dependent in great measure on the young expanding leaves to supply the necessary inhibitors (11).

The onset of dormancy in lily bulbs in greenhouse soils was reported by Thornton (14) as due to poor aeration, but this appears to be an unusual rather than normal situation. Lin[3] found dormancy in the lily bulb daughter increased with progressive development, and a chilling requirement developed in the spring that decreased in early summer in connection with events leading to anthesis in July. Cold treatment became progressively less a requirement for breaking dormancy after anthesis, and the daughter axis steadily acquired the ability to elongate rapidly. Lin concluded that the daughter scales were the seat of inhibition because their removal greatly accelerated sprouting.

Naylor (9) reported amino acids to be sensitive indicators of dormancy changes in plants. Marked changes in levels of the basic amino acids, arginine, histidine and lysine were found to be associated with vernalization of wheat by Trione et al. (16). Asen and Stuart (1) reported that dormant *Hydrangea macrophylla* leaves showed approximately a 4-fold increase in free amino acids in the leaves after 6 weeks storage at 41–43°F. The concentration of free amino acids in the buds doubled during the same period. El-Mansy and Walker (5) observed that the total amino acid content of peach buds increased just prior to completion of rest.

The experiments reported here were designed to determine the nature of growth inhibition in the Easter lily daughter bulb, so that its type of dormancy could be more precisely defined and overcome by treatment. Changes in bulb composition associated with the development and removal of this dormancy were also determined.

Materials and Methods

'Ace' bulbs, grown at the Pacific Bulb Growers' Research and Development Station, were used in these experiments. Bulbs to be stored were sealed in polyethylene bags with 1 g of dry peat moss per 5 gms of bulb weight. Non-stored bulbs were potted immediately after specific treatments. After treatment and potting, all bulbs were distributed randomly on benches in a greenhouse maintained at 60°F night and 70°F day temperatures and grown to flowering. Days to shoot emergence was used to indicate the degree of dormancy remaining in the bulbs.

Bulb and scale growth and development. To determine seasonal changes in fresh and dry weight and ratio of daughter (new) to mother (old) scales, 20 bulbs were harvested and dissected monthly from February through October 1967. Another 20-bulb sample, harvested at the same time, was potted immediately upon arrival at Corvallis and used to determine speed of shoot emergence.

Relation of scales to dormancy. To determine scale influence at progressively later stages of development on daughter dormancy, 40 bulbs were harvested monthly from June through October, 1967, and 10 bulbs each given one of the following scale removal treatments: 1) mother scales removed, 2) daughter scales removed, 3) all scales removed, and 4) no scales removed.

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[3]Lin, P. 1968. Studies on development and flowering of *Lilium longiflorum* Thunb. Masters thesis, Corvallis, Oregon State University.

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Breaking dormancy. Two types of treatments were used for breaking dormancy. I. Field soil heating and storage treatments. One-year-old 'Ace' bulbs of 40–50 g size were planted in the autumn of 1964, 4 inches apart in single rows between two strands of thermostatically controlled heating cables laid in the bottom of the planting trench. The soil was heated to 70–75°F for specific periods of time: a) April 15 to July 15, b) July 15 to September 24 and compared with c) natural soil temperatures without heating. Since full bloom occurred near July 15, the soil treatments henceforth will be referred to as "heated before bloom", "heated after bloom" and "control". The bulbs from each field treatment were divided into four 5-bulb lots of about equal weight. Individual lots were then stored at 40°F for 0, 3, 6 or 9 weeks before potting and greenhouse forcing. Bulbs receiving no cold treatment were potted within two days of harvest.

II. Storage and chemical treatments. 'Ace' bulbs, harvested on June 15, 1967, and averaging 70 g in size, were divided into five 10-bulb lots and given the following storage and chemical treatments for breaking dormancy: a) no storage, potted immediately after harvest, b) 6 weeks' 70°F storage, c) 6 weeks' 40°F storage, d) bulbs soaked 2 hours in gibberellic acid (GA_3) 2500 ppm, followed by 6 weeks' 70°F storage, e) bulbs soaked 2 hours in GA_3 2500 ppm, followed by 6 weeks' 40°F storage.

Changes in bulb composition with dormancy. Samples of daughter and mother scales from the 1967 storage treatments were used to study changes in nitrogenous substances associated with the removal of dormancy. The samples were ground through a food chopper, thoroughly mixed, extracted with 95% ethanol and heated to boiling. After cooling, the samples were homogenized in a Waring blender at high speed for 3 minutes, then filtered through Whatman #2 filter paper into volumetric flasks for final washing of the residues 4–5 times with 80% ethanol. Suitable aliquots of these extracts were used in determining free amino acids. Total alcohol insoluble nitrogen was determined on the dried residues.

The individual free amino acids contained in the ethanol extracts were purified and separated into basic, neutral and acidic fractions according to the procedures of Thompson et al. (13), and then run through the Technicon Amino Acid Autoanalyzer.

The basic amino acids were retained on a Dowex 50W-X4 ion exchange resin in the NH^+_4 form, and were eluted with 3 N NH_4OH. Neutral and acidic amino acids were retained on a Dowex 50W-X4 resin in the H^+ form, and were also eluted with 3 N NH_4OH, followed by deionized water. The combined eluates were then evaporated at 150°F until no odor of ammonia could be detected. The individual amino acids in each sample were then separated and quantitatively determined by the Technicon Amino Acid Autoanalyzer. The amino acid peaks on the Autoanalyzer charts were identified by comparison with a known standard and by the characteristic absorption maximum of its ninhydrin reaction product. An estimate of peak area was obtained by triangulation.

Total nitrogen in the dried alcohol insoluble residues was determined by the Kjeldahl method (8).

A method similar to that described by Liao[4] and Nitsch and Nitsch (10) was used to determine the presence of naturally occurring growth substances. One-hundred gram samples of both mother and daughter scales were extracted with methanol at 32°F for 2 hours. The methanol extract was evaporated to dryness under reduced pressure. The residue was taken up in acetonitrile and hexane (1:1) then shaken in a separatory funnel. The hexane fraction was discarded and the acetonitrile fraction reduced to dryness. The residue was dissolved in 2 ml absolute methanol and separated by paper chromatography using Whatman No. 1. The paper was equilibrated for at least 10 hours before the solvent (isopropanol/ammonia-28%/water, 8:1:1, v/v) was added. After the solvent had descended about 20 cm the paper was removed from the chamber and dried at room temperature. After drying the paper was cut into 10 equal segments including the original spot. An additional segment of equal width was taken above the origin as a control. The pieces of paper were then placed in small vials (15.5 × 50 mm) with 1 ml of a phosphate-citrate buffer (pH 5.0) and 2% sucrose. The oat ('Forkedeer', obtained from Tennessee Seed Production, Inc.) coleoptile straight growth test was used for the bioassay. Oat seeds were soaked 2 hours in distilled water and then germinated in vermiculite for 4 days in the dark at 75°F with 90–100% relative humidity. The 4 mm coleoptile sections were cut 3 mm below the tip and transferred to the vials containing the chromatography strips and phosphate-citrate buffer. The vials were then shaken at about 140 cycles per minute in the dark. After 22 hours, the length of the coleoptile sections was measured with the aid of a photographic enlarger. Growth of coleoptile section was expressed as percent of elongation of control sections. A 30 ppm solution of indoleacetic acid (IAA) in absolute methanol was given the same procedure in extraction and chromatography to verify its R_f value and the color reaction to Salkowski and Ehrlich reagents.

Results and Discussion

The data show (Table 1) that the bulbs did not increase significantly in fresh weight during the early spring (February–April), but increased progressively from 47 g in May to 170 g in October, similar to the observations of Blaney and Roberts (2). Dry weight increased in a similar manner. On a dry weight basis the ratio of daughter/mother scales increased from 0.5% in April to 1% in May, 60% in August and 100% in September (daughter and mother scales equal in dry weight).

The ability of the daughter axis to elongate increased progressively during the growing season and with delay of harvest (Fig. 1). The time required for the untreated daughter bulbs to sprout decreased progressively with later harvest, except for a short period during anthesis,

Table 1. Progressive increase in fresh weight, dry weight and ratio of new/old scales with time of harvesting 'Ace' lily bulbs.

Harvest date	Fresh weight (g)	Dry weight (g)	Ratio new/old scale (on dry weight basis)
February 14	41	—	—
March 15	42	—	—
April 14	43	5	0.5%
May 16	47	8	1%
June 19	62	12	19%
July 21	80	18	40%
August 18	112	25	60%
September 12	150	35	100%
October 11	170	44	—

[4]Liao, T. 1966. Quantitative changes of growth-promoting and inhibiting substances in peach seeds receiving various chilling treatments. Thesis, M.A. degree, Utah State University, Logan.

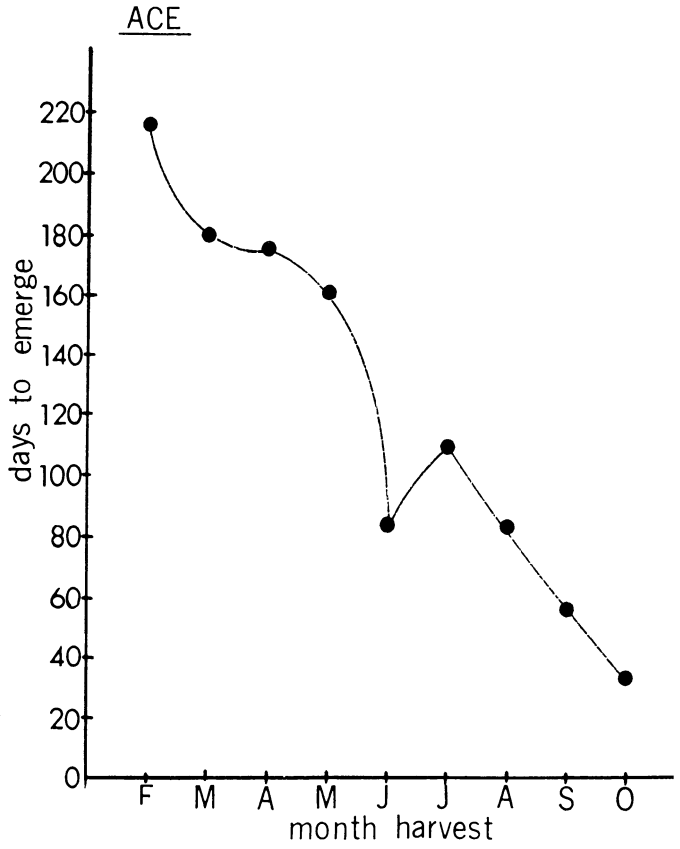

Fig. 1. Progressive increase in speed of emergence of 'Ace' lilies with delay in harvest date (1967).

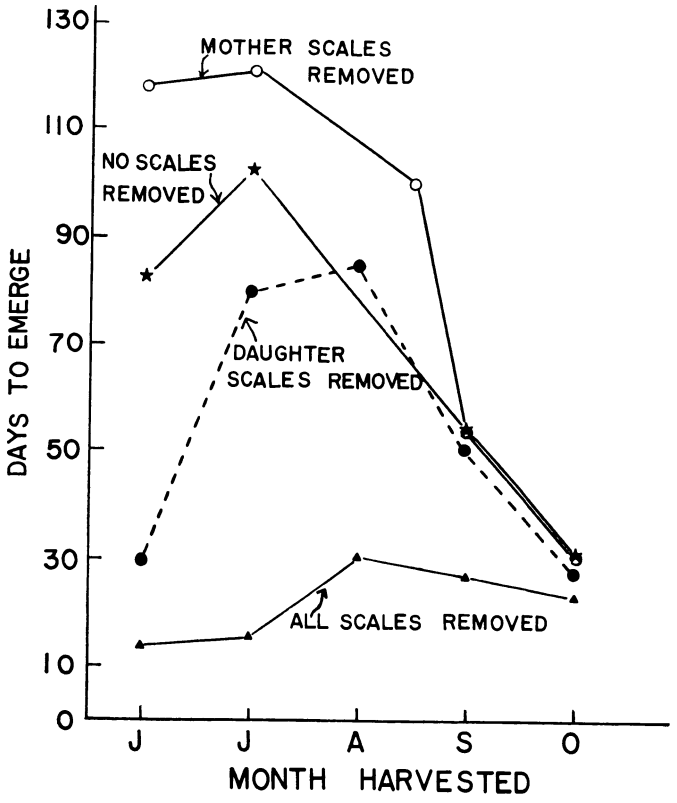

Fig. 2. Effects of scale removal at progressively later harvest dates on speed of shoot emergence in 'Ace' lily (1967).

when this trend was reversed. The most dormant, nontreated, July-harvested bulbs required 125 days to emerge when mother scales were removed, 83 days when daughter scales were removed, but only 19 days when all scales were removed (Fig. 2). September-harvested bulbs with mother or all scales removed emerged in 54 and 27 days, respectively. Emergence was delayed when mother scales were removed from bulbs harvested before September, while emergence was accelerated by removal of daughter scales harvested before August. These results are in agreement with those of Lin[3] and support her hypothesis that the daughter scales were a source of inhibition to the daughter apex before and immediately following anthesis of the mother axis.

All bulbs grown with soil heating before flowering of the mother axis had daughter bulbs with sprouts, while those without this treatment were still dormant (Table 2). The bulbs warmed in the field after bloom tended to emerge later than the controls. These responses to soil heating are perhaps similar to those reported by Ticknor (15) and Tsukamoto and Suzuki (17), where immersion of lily bulbs in hot water (110° and 116°F) for one hour overcame dormancy. Molisch (7) developed a warm water treatment for breaking the dormancy of leafless branches, using water at temperatures of 86° to 104°F. High temperature treatment has also been effective in breaking the dormancy of gladiolus corms (6).

The content of protein nitrogen in the scales increased with storage and GA_3 treatment, indicating an active net synthesis of protein during storage and GA_3 treatment (Table 3). In general, the higher the scale protein content, the less dormant the bulb and fewer days required for emergence. Cotrufo and Levitt (3) suggested that dormancy removal may be a result of increased protein synthesis.

Twenty amino acids in the free state were identified from the daughter and 18 from the mother scales before cold treatment (Table 4). After 6 weeks storage at 40°F, glycine, valine, and methionine disappeared in daughter scales while cysteic, gama-amino-butyric acid, valine, and isoleucine appeared in mother scales. Phenylalanine, tyrosine, alanine, cystine and glutamic were the predominant amino acids in the daughter scales of 'Ace' bulbs, while alanine, phenylalanine, glutamic and aspartic were the predominant ones in mother scales at the beginning of storage. Cysteic, aspartic, threonine, serine, glutamic, alanine, alpha-amino-butyric acid, lysine, tryptophan, histidine, arginine and an unidentified amino acid increased in concentration in the daugh-

Table 2. Effects of field soil heating and 40°F storage on speed of emergence of 'Ace' lily bulbs.

Treatment	Weeks at 40°F	Days to emerge (Ace)
No soil heating	0	46
	3	40
	6	28
	9	29
Heating after bloom	0	57
	3	43
	6	35
	9	35
Heating before bloom	0	0[a]
	3	0[a]
	6	0[a]
	9	0[a]

[a]Summer sprouted before harvest.

Table 3. Changes in level of protein-nitrogen in scales of 'Ace' bulbs following 40°F and 70°F storage and GA_3 treatment and its relation to dormancy (bulbs dug on June 15, 1968).

Treatment	Protein-N (mg/10 g fresh weight)	Degree of dormancy (days to emerge)
No storage, sample taken immediately after harvest	30.5	80
6 weeks 70°F storage	35.1	66
6 weeks 40°F storage	45.2	37
2500 ppm GA_3 followed by 6 weeks 70° storage	50.4	10
2500 ppm GA_3 followed by 6 weeks 40°F storage	47.0	18

ter scales after 6 weeks' 40°F storage. All amino acids increased in concentration in the mother scales after 40°F storage. Differences in concentration of each amino acid before and after 6 weeks of 40°F storage are shown in Table 5. Certain amino acids in the scales tended to increase in concentration, while others decreased after 6 weeks' storage at 40°F (Table 6). The increased content of free amino acids associated with cold treatment may be due to the presence of certain enzymes involved in converting carbohydrates to free amino acids. Alanine, serine, glycine, glutamic and aspartic acids have been reported to increase in concentration at the end of completion of rest in peach and apricot (5). The 2-fold increase in total amino acids in the bulbs after 6 weeks' storage at 40°F is similar to that reported by Asen and Stuart (1) in the bud of *Hydrangea macrophylla*. The relationship between dormancy and individual amino acids warrants further investigation.

The presence of growth substances in the scales of unchilled bulbs was established by bioassay. The daughter scales were shown to be lower in IAA and higher in inhibitor content than the mother scales during the period of inhibited growth or dormancy (Fig. 3). The

Table 4. Free amino acids in new and old scales of 'Ace' bulbs before and after 6 weeks storage at 40°F (bulbs dug on June 19, 1967).

Peak number	Amino acid	Scales from bulbs not stored[a]		Scales from bulbs stored 6 weeks at 40°F	
		New scales μ M/10 g	Old scales μ M/10 g	New scales μ M/10 g	Old scales μ M/10 g
1	Cysteic	0.268	0.000	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	0.000	11.450
7	Alanine	8.350	10.785	8.455	12.610
8	αNH_2 butyric	0.067	1.630	6.655	10.815
9	Valine	0.618	0.000	0.000	0.344
10	Cystine	4.550	0.627	1.200	4.300
11	Methionine	0.097	0.135	0.000	0.205
12	Isoleucine	2.325	0.000	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	γNH_2butyric	0.000	0.000	0.000	1.060
17	Unknown #1	0.000	0.329	0.000	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	0.788	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 5. Difference in concentration of each amino acid before and after 6 weeks storage at 40°F (bulbs dug on June 19, 1967).

Peak number	Amino acid	Difference in concentration before and after storage	
		New scales μ M/10 g	Old scales μ M/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	αNH_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	γNH_2 butyric	0.000	1.060
17	Unknown #1	0.000	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 indicates decreased concentration after storage (6 weeks at 40 F).

identity of the inhibitors (R_f 0.8∼1.0) has not been determined. These results help explain the adaptability of this crop to seasonal temperature changes and the nature of the correlated inhibition of the daughter axis by its scales (Figs. 1 and 2). Treatments conducive to breaking this dormancy, such as 40°F storage, GA_3 treatment, and field soil heating may be associated with reduced inhibitor content. Bulb storage at 40°F was effective in breaking dormancy, as reflected in the reduced time required for emergence (Table 2).

These experiments substantiate the earlier observa-

Table 6. Free amino acids in scales of 'Ace' bulbs before and after 6 weeks storage at 40°F (bulbs dug on June 19, 1967).

Peak number	Amino acid	Scales from bulbs not stored[a]	Scales from bulbs stored 6 weeks at 40°F
		μ M/10 g	μ M/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	αNH_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	γNH_2 butyric	0.000	0.530
17	Unknown #1	0.164	0.524
18	Unknown #2	0.390	0.780
19	Lysine	1.424	2.498
20	Tryptophan	0.894	1.007
21	Histidine	1.826	2.735
22	Arginine	0.521	7.225
	Total Amount	40.953	85.943

[a]Samples taken immediately after harvest.

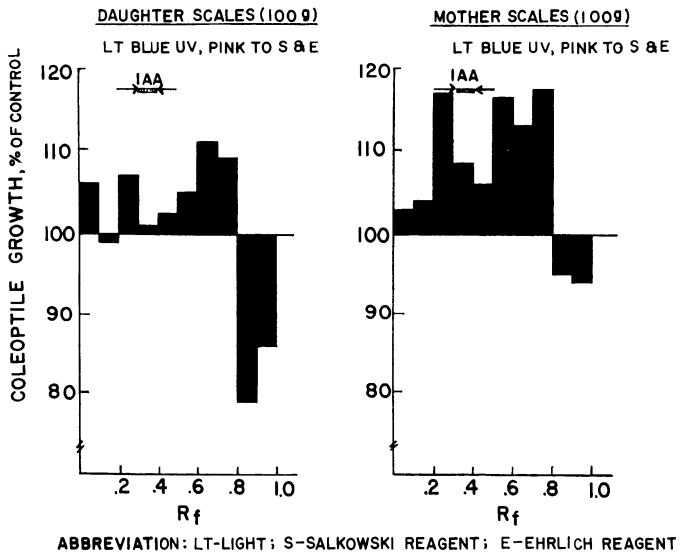

Fig. 3. Oat coleoptile assays of extracts of 'Ace' scales chromatographed in isopropanol, ammonium hydroxide, and water (8:1:1 by volume). The cross-hatched inserts represent the location of IAA on chromatograms developed in the same solvent system (bulbs were dug on September 1, 1966).

tions of Blaney and Roberts (2) that the daughter apex in the *L. longiflorum* bulb is continually initiating either scales, leaves, or flower primordia and in that order. With increased numbers of organs and amounts of storage reserves there is a progressive increase in weight of the daughter until it equals the mother portion in weight at harvest. Although initiatory activity is continuous in the bulb, the expansion and elongation of the daughter axis' leaves and internodes is normally inhibited through most of the year. This correlated inhibition of the daughter axis, attributed to the young leaves by Roberts and Blaney (11) and to the daughter scales by Lin[3], has been shown in this study to be high during the spring months prior to anthesis of the mother axis, and to progressively decrease following anthesis and disappear completely by autumn. It appears that inhibitors accumulate in the daughter scales, but following anthesis of the mother axis they gradually disappear as a result of the aging leaves ceasing to be a source of supply, or their being inactivated by cold weather.

The evidence obtained in this study, and that cited in the literature, supports the conclusion that the period of dormancy in the lily daughter bulb is of the correlated type referred to by Samish (12), and involves inhibition of axis expansion rather than initiatory activity in the apex.

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