Scale Function in Growth and Flowering of *Lilium longiflorum*, Thunb. 'Nellie White'[1]

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Abstract. Response of cold-treated 'Nellie White' Easter lily bulbs to various degrees of scale removal, ranging from 0 to 100%, showed that scales can perform inhibitory and promotive roles at various times. The scales were not necessary for flower induction, but the number of leaves and flowers initiated was proportional to the number of scales retained. Daughter scale removal accelerated daughter sprouting by increasing internode elongation, but subsequently reduced the rate of organ formation and expansion. Daughter scale removal reduced the number of leaves and flowers initiated and anthesis was delayed because of the reduction in rate at which these organs expanded.

Our desire to control flower number in lilies is second only to that of controlling speed of flowering. Time to flower is the sum or function of time required for shoot emergence, flower initiation, and leaf and flower unfolding. Bulb size is known to influence these, but whether this is due to scale number or apex size is not known.

Hartsema stated that Dutch Iris *(Iris xiphium praecox* 'Imperator') plants did not flower if from bulbs smaller than a certain size. Tulips also failed to initiate flowers if the bulbs weighed less than 8 g (4). Easter lilies will often flower the first year from seed. Kohl (5) found that large lily bulbs produced more flowers than small ones, and the number of leaves produced by the apex per unit of time was likewise directly proportional to bulb size. It has been assumed that loss of scales would also reduce the growth and flowering potential of bulbs, but little evidence on these points has been published for the Easter lily. Post (7) found a reduction in flower count and retardation in bloom development of 'Giganteum' Easter lily in proportion to the amount of scales removed.

In this study, the effects of bulb scale removal, before and after cold treatment (40°F), on shoot emergence, leaf number, growth rate, and flower number were used to determine the function of bulb scales in growth and flowering of the daughter axis.

Materials and Methods

As used here the mother bulb is the old portion of the bulb whose axis is currently flowering and producing a daughter bulb in the axil of the scale directly subtending the base of the flowering shoot. The old mother scales encompass the new daughter apex that initiates new scales, leaves, and the following year flowers.

One hundred 'Nellie White' Easter lily bulbs (9½–11 inches in circumference, 150–190 g) were harvested and divided into 10-bulb lots of approximately equal weight on September 23, 1966. Each lot was stored at 40°F for 3 weeks to hasten emergence and flowering, while minimizing the reduction in flowering potential from excessive cold treatment. Scales amounting to 0, 25, 50, 75 and 100% of the original weight of each bulb, were removed either before or after cold treatment from 5 lots. In the case of 100% scale removal, only the growing point surrounded by leaf primordia, basal plate and roots remained. At 75% removal, only a portion of the daughter scales remained. With 50% removal, all of the mother scales and 1 or 2 daughter scales were removed. The mean individual bulb weights after the scales were removed were: 0%, 173g; 25%, 129g; 50%, 87g; 75%, 43g; and 100%, 16g. Bulbs were potted on October 15, 1966, and grown in a greenhouse with 60°F night and 70°F day temperatures.

Leaf number was used as an index of vegetativeness (6). For a given bulb size, the number of leaves below the lowest flower normally reflects the earliness of transition from the vegetative to flowering phase.

Results and Discussion

In general, scale removal reduced the number of leaves and flowers and the length of the internodes in proportion to the amounts removed (Figs. 1 and 2).

Days to emerge. Removal of mother scales only (25% and 50%) did not affect time required for shoot emergence (Fig. 2-A). Removal of both daughter and mother scales (75% and 100%) however, accelerated emergence, particularly when removed before cold treatment. It

Fig. 1. Plants grown from 'Nellie White' bulbs whose weights were reduced by 0 to 75% by scale removal. The plant labelled 100% was grown from a bulb from which all the scales were removed. The bulbs were vernalized for three weeks at 40°F before the scales were removed and were grown to flower at 70°F day and 60°F night temperature. Photographed March 30, 1967.

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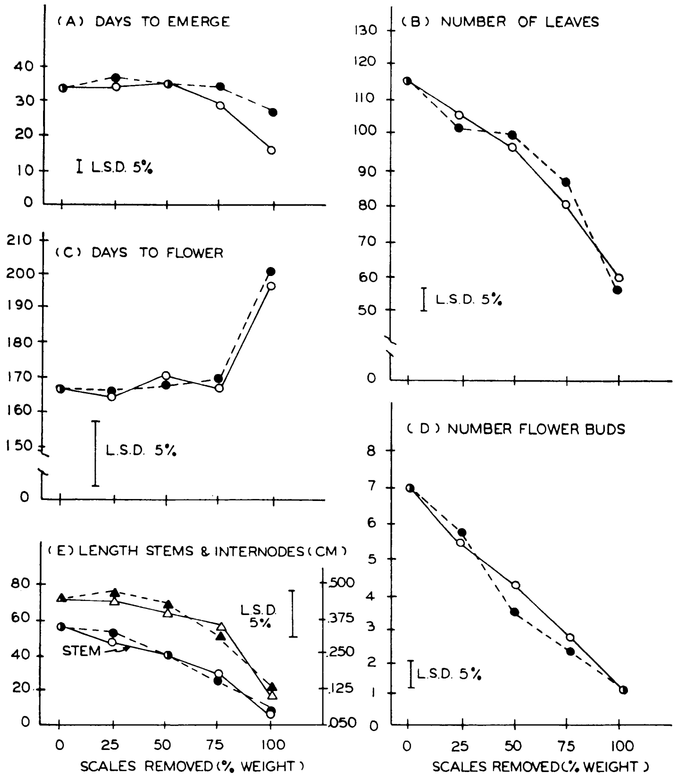

Fig. 2. Effect of scale removal on days to emerge (A), number of leaves (B), days to flower (C), number of flowers (D), and length of stems and internodes (E) of 'Nellie White' lily. Open symbols: scales removed before 3 weeks storage at 40°F; closed symbols: after 3 weeks storage at 40°F. (10 plants per treatment).

appeared, therefore, that the daughter scales were a source of inhibition to daughter axis elongation.

Time of scale removal (before or after cold treatment) did not significantly affect time of shoot emergence, unless daughter scales were removed with the mother scales. Emergence was accelerated by 16 days when all scales were removed before cold treatment, but only by 6 days when removed subsequently. Since the daughter scales appeared to be the principal source of inhibition, and their removal should be as effective as cold treatment in removing inhibitors, the earlier emergence resulting from scale removal before cold treatment must reflect an effect of early scale removal rather than one associated with cold treatment. Recent research has shown that little dormancy or delay in sprouting occurs in bulbs after August, and cold treatment is not needed to accelerate the sprouting of September-harvested bulbs.[3]

Leaves per stem. The reduction in the number of leaves per plant roughly paralleled the severity of scale removal, except that removal of daughter scales in addition to mother scales reduced leaf numbers drastically (Fig. 2-B).

That scales were inhibitory to early flower initiation was shown by the progressively fewer leaves with each increment of scale removal. Removal of mother scales only reduced leaf number by 17, while removal of both mother and daughter scales reduced it by 40 or more leaves (Fig. 2-B). This suggests that the daughter scales are especially inhibitory to the onset of flower bud initiation. An alternative explanation would be that the scales furnish substrate for growth and therefore, the greater the weight of scales, the more leaves the growing point will initiate before initiation of the first bud in response in cold induction.

Rate of leaf unfolding. Growth rate declined progressively with increasing amounts of scale removal to 75%, and was significantly reduced when all scales were removed. The number of leaves unfolded per day was 1.3, 1.2, 1.0, 0.9 and 0.4 for 0, 25, 50, 75 and 100% scale removal, respectively (Table 1). This reduction in leaf initiation and rate of development is logical in view of Kohl's (5) observation that large bulbs initiated more leaves in a given time than small ones.

Days to flower and number of flowers. As much as 75% of the scales could be removed without significantly increasing the time required to flower. However, when all the scales were removed, flowering was drastically delayed. The time of scale removal did not affect the days to flower (Fig. 2-C).

The number of flower buds per plant decreased in proportion to the amount of scales removed, but at least one flower bud was initiated by plants grown from bulbs without any scales. None of the buds aborted (Fig. 2-D).

The number of flower buds initiated was directly related to the weight of bulbs. This relationship suggests that scales provided substrate necessary for continued initiatory activity by the growing point. Contrarily, the present results would not assign to the scale the role of promoting induction of the reproductive stage as Rodrigues Pereira (8) reported for *Iris xiphium.* The primordial leaves in Easter lily, as in *Iris,* might perform this role because primordial leaves still surrounded the growing point after all the scales had been removed. Halaban, Galun and Halevy (3) cultured *in vitro* stem tips of *Ornithogalum arabicum* L., a lilaceous plant and concluded that both bulb leaves and scales promoted the transition to the reproductive phase, while the scales promoted further development of the inflorescence.

Growth rate was progressively retarded with each increment of scale removal (Table 1). Thus, the expected reduction in days to flower with progressively fewer leaves was counter-balanced by slower rate of leaf unfolding. When all the scales were removed, flowering was much retarded in spite of an extremely low leaf number. The flower buds on these plants also developed slowly. Several weeks were required for flower opening after they had reached the white stage that normally precedes by a day or two the opening of the flower.

The days required for flowering should have paralleled the number of leaves (1). The 56–61 leaves on the plants whose bulb scales were all removed probably represented the leaf primordia present at bulb harvest (2). As Kohl (5) observed, leaf initiatory activity by the apex per unit of time is proportional to bulb size, and as scales are removed bulb size, leaf numbers, and growth rate are reduced accordingly.

Stem and internode length. The length of the stem was inversely proportional to the amount of scales removed (Fig. 2-E). The 25% scale removal did not affect internode length, but above this level it decreased as more scales were removed. Removal of the last 25% of the scales shortened the internodes severely. The plants grown from these bulbs were rosetted during much of their life. There was no significant difference with time of scale removal.

The length of the stems was determined not only by

[3]Wang, S. Y. 1969. The physiology of dormancy in Easter lily, *Lilium longiflorum* Thunb. Ph.D. Thesis, Oregon State University. Corvallis.

Table 1. Effect of scale removal on growth responses of 'Nellie White' Easter lily. (A) Scales removed before and (B) scales removed after 3 weeks bulb storage at 40°F. (Means of 10 bulbs per treatment).

Scales removed %	To emerge		To flower		Leaves		Emergence to buds visible		Rate leaf unfolding	
	A	B	A	B	A	B	A	B	A	B
	Days		Days		Number		Days		Leaves/Day	
0	33	33	165	165	116	116	90	90	1.3	1.3
25	33	33	163	165	104	107	88	90	1.2	1.2
50	35	35	168	167	101	98	91	90	1.1	0.9
75	28	34	166	167	89	82	96	91	0.9	0.9
100	17	27	195	198	56	61	137	129	0.4	0.4
LSD 5%[a]	3.5		18.4		7.1		—		—	

[a]For columns and rows.

the number of internodes but also their average length. For example, the extremely short plants from bulbs without scales had few internodes and these were extremely short. Scales apparently supply substrate necessary for internode elongation, as previously suggested for rapidity of growth and development toward opening of the flowers.

Conclusions

It is concluded that the scales are not necessary for the transition of the growing point from the vegetative to the reproductive condition. However, as observed by Kohl (5) in studying the influence of bulb size, the number of leaves and flowers initiated by the lily apex per unit of time is directly proportional to the number of scales retained on the bulb.

It also appears that daughter scale removal accelerates the sprouting of the daughter regardless of the time of cold treatment. This rapid emergence of the daughter axis following scale removal appears to result from more rapid or greater basal internode elongation, since such stems averaged fewer and shorter internodes, and were slower in unfolding leaves. Separating the number and length of internodes below and above ground could have established one of these relationships.

Probably the most significant observation made in this study, because of its implications in lily forcing, was the striking reduction in growth rate (leaf and flower unfolding) following the initial acceleration in sprouting. This illustrates the need for evaluating bulb treatments on the basis of their effects not only on speed of emergence and leaf and flower numbers, but also on growth rate. Growth rate is determined not only by the number of organs initiated, but by the rate at which they are expanded.

The results also point out the complexity of using leaf number as an index of earliness in the transition from vegetative to reproductive state. We now know that leaf number reflects not only time of flower induction but also the rate of initiatory activity. Also, that in determining days to flower, it is necessary to consider not only speed of emergence and number of leaves to be unfolded following flower initiation, but also the rate at which these leaves will be unfolded. Thus, as in this experiment, daughter scale removal significantly accelerated sprout emergence, and reduced the number of leaves (and flowers) to be unfolded, but anthesis was actually delayed because there was a reduction in the rate at which these organs expanded.

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