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Seasonal Changes in Leaf Emergence from Scale Bulblets during Scaling and Endogenous Plant Hormone Levels in Easter Lily (*Lilium longiflorum* Thunb.)

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Leaf emergence from scale bulblets during scaling in *Lilium longiflorum* was investigated monthly throughout the year with respect to endogenous plant hormone levels to clarify the factors inducing dormancy of bulbs and the relationship between the induction of bulb formation and the induction of dormancy. Leaf emergence behavior suggested us that the bulbs of *L. longiflorum* were induced into dormancy by low winter temperature and released by high summer temperature. These were confirmed also by changes in abscisic acid and auxin activities in the bulbs. It was also suggested that there is a close relationship between the induction of bulb formation and the induction of dormancy of autumn planting bulbous plants including *L. longiflorum*.

INTRODUCTION

Lilium longiflorum which originated in the Ryukyu Islands has summer dormancy as well as other major autumn planting bulbous plants such as *Iris*, *Hyacinthus*, *Narcissus* and *Tulipa* which originated in the Mediterranean areas. Dormancy of bulbs is a result of their adaptations to avoid severe summer environments of heat and dryness in the native habit. As induction of dormancy in these bulbs is always accompanied by a process of bulb swelling, the relationship between the induction of bulb formation and the induction of bulb dormancy has been little studied.

In the experiments in *Hyacinthus orientalis* (Okubo *et al.*, 1988), *we* showed that leaf emergence from scale bulblets during scaling was vigorous in the post-dormancy stage, at the end of the period of high summer temperature, but not during the period from winter to early summer. We also showed that auxin activity in the bulbs was high in the post-dormancy stage and then decreased while abscisic acid activity was high in winter and spring. We suggested from these results that the induction of dormancy in hyacinth is caused by low temperature and that there is a close relationship between the phenomenon of the induction of dormancy and the induction of bulb formation.

Uemoto *et al.* (1983) have shown that leaf emergence from scale bulblets during scaling in *Lilium longiflorum* 'Hinomoto' was inhibited when the scaling was started at flowering time (June 15) and that the activity of abscisic acid was high. These results suggest that the dormancy of this plant has already been induced at this time.

In this study, leaf emergence from scale bulblets during scaling in *L. longiflorum* and changes in endogenous plant hormone levels in the bulbs were investigated

monthly for one year to clarify the inducing factors for dormancy and the relationship between the induction of bulb formation and the induction of dormancy.

MATERIALS AND METHODS

Bulbs of *L. longiflorum* 'Hinomoto', 20 cm in circumference, produced in Okino-Erabu Island, Kagoshima Prefecture, Japan, were obtained on July 4, 1985 and kept at room temperature until used. One hour disinfection of the bulbs in 0.2% Benlate took place before planting. They were planted on July 18 and grown in the open fields. The growing bulbs were lifted at monthly intervals throughout the year from December 16 to November 16 of the following year and used for scaling and hormone analysis. Scales were prepared from the middle part of the bulbs, and the weight of them was 2-3 g. Therefore, the scales of mother bulbs which had been formed in 1985 were used for scaling from December to May, and new scales of daughter bulbs which had rapidly enlarged and substituted for the old scales during the period from May to June, 1986 were used from June to November. They were placed vertically in sand in plastic flats (16 X 10 X 5 cm) to a depth of about half their length and incubated for 120 days at 20°C constant temperature under natural light in the phytotron of the Biotron Institute, Kyushu University. The growth cabinet in which the temperature and the daylength were controlled to keep them similar to those in the phytotron was used from April 1 to 30 and from October 1 to 31, because the phytotron was out of service during these periods for technical maintenance. Observation of leaf emergence from the scale bulblets were made at one-week intervals.

Twenty grams fresh weight of the scales were prepared at the same dates of scaling for each extraction of plant hormones. Extraction, chromatography and bioassay procedures were identical to those described before (Okubo et al., 1988).

RESULTS

Figure 1 shows the growth of mother plants and the daughter bulbs with the average monthly temperature at Fukuoka City during the past 30 years. Plant height increased as temperature rose and the average flowering date was June 11. Accelerated growth of daughter bulbs occurred in mid-April, about one-month later than that of the shoots from mother bulbs.

As shown in Table 1, number of bulblets produced per scale ranged from 1 to 2.3 throughout the year, and fewer bulblets resulted when scalings were done during the period from May to November than from December to April.

Changes in leaf emergence from scale bulblets during scaling are shown in Fig. 2. Percentage of leaf emergence was high when scalings were started in December (100%) and January (90%), but it decreased to 30% in February-scaling. The lowest percentage of leaf emergence (10%) was observed when scalings were done in March and April, then leaf emergence was resumed and the percentage of it increased progressively from May-to November-scalings ; 30% in May- and June-, 60% in July- and 80% in August-, September-, October- and November-scalings.

Days to first leaf emergence after the start of scalings were between 27 and 30 when scalings were done in December, January and February. Scales prepared from

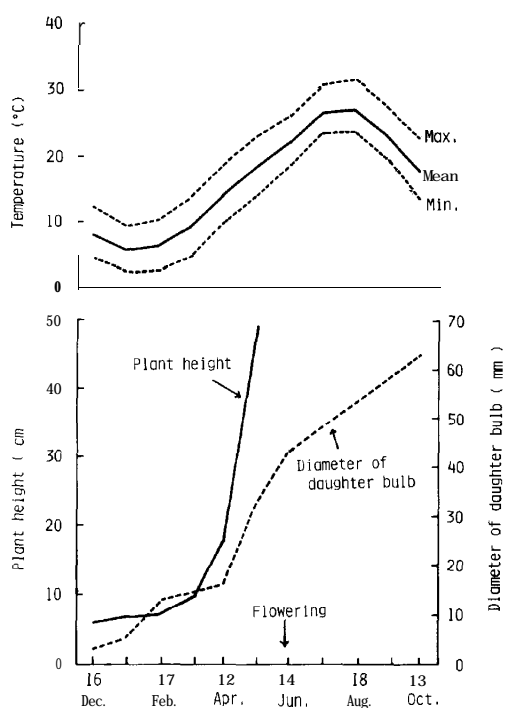


Fig. 1. Growth of mother plants and daughter bulbs with average monthly temperature at Fukuoka City during the past 30 years.

Table 1. Effect of time of scaling on number of bulblets produced per scale. Values within a column followed by different letters are significantly different at 5% level according to Duncan's new multiple range test.

Number of bulblets per scale		
December	2.3	d
January	1.9	bcd
February	2.25	cd
March	2	bcd
April	2	bcd
May	1.33	ab
June	1	a
July	1.67	abcd
August	1.63	abcd
September	1.5	abc
October	1.4	ab
November	1.25	ab

March-harvested bulbs required 86 days of incubation to emerge the first leaf from scale bulblets. Then, days to first leaf emergence decreased month by month towards autumn. The patterns of the changes in percentage of leaf emergence were quite

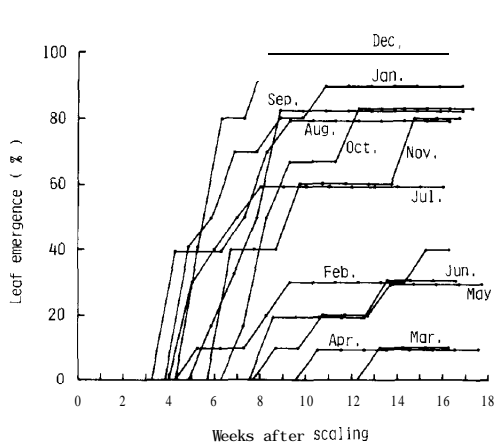


Fig. 2. Effect of time of scaling on percentage of leaf emergence from scale bulblets.

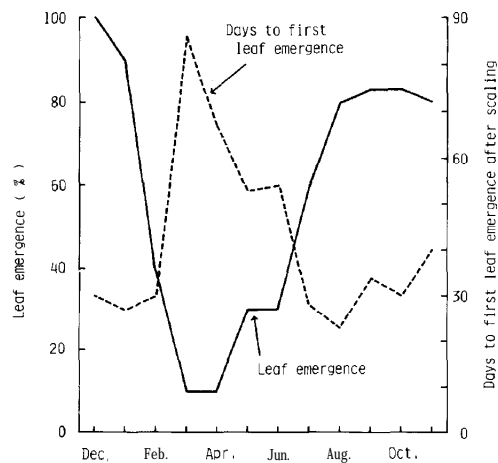


Fig. 3. Effect of time of scaling on days to first leaf emergence and percentage of leaf emergence from scale bulblets.

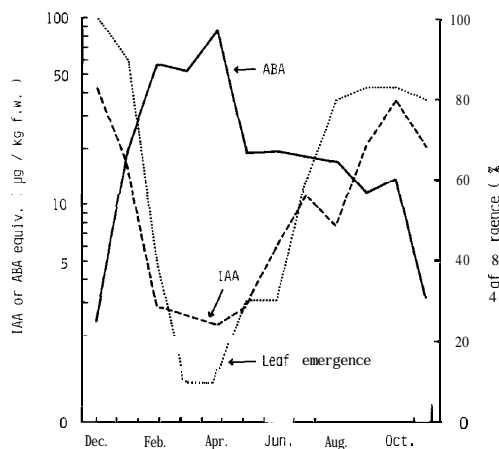


Fig. 4. Changes in auxin and abscisic acid activities in scales.

opposite to those in days to first leaf emergence (Fig. 3). Percentage of leaf emergence was higher in the month when leaf emergence occurred earlier.

As shown in Fig. 4, auxin activity was high in December and January. It dramatically decreased in February and reached the lowest level in April. A subsequent rapid increase in auxin activity occurred from May to October. In contrast, abscisic acid activity was lowest in December and then it increased in January and February. The maximum level of abscisic acid activity was attained in April. The decrease in abscisic acid activity occurred dramatically between April and May, then slowly from May to October, and dramatically again between October and November. Finally the amount of abscisic acid-like substances in November was almost the same as that in

December of the previous year. Changes in auxin activity coincided with those in percentage of leaf emergence, and were quite opposite to those in abscisic acid activity.

DISCUSSION

Changes in the rate of leaf emergence show the changes in the physiological state of bulbs. These seasonal changes in leaf emergence were quite similar to those in *Hyacinthus orientalis* (Okubo *et al.*, 1988). Matsuo and Arisumi (1979) showed that the longer the period of cold treatment during the 25°C storage of mother bulbs of *L. longiflorum* 'Hinomoto', the lower the percentage of leaf emergence from newly formed bulblets in scaling outdoors. Matsuo and van Tuyl (1984) reported that a higher storage temperature of mother bulbs of the same plant cv. White American promoted leaf emergence from scale bulblets whereas a lower temperature delayed it. Kaneko and Imanishi (1985) studied the seasonal changes of sprouting of the uppermost axillary buds of corms of Freesia cultures in vitro at different dates from February to September. They concluded that new corms have reached a state of true dormancy at flowering time of the mother plants. Their data, however, shows that percentage of sprouting already decreased in February compared to that in the period from July to September. It is considered from leaf emergence behavior that dormancy in *L. longiflorum* is induced by low winter temperature when the lateral meristems start to form new scales, and is released by high summer temperature when they had enlarged and become inner scales. On the other hand, an apical meristem, a previous year's lateral meristem, which had been induced into dormancy by the previous year's low winter temperature and released by the previous year's high summer temperature, requires current year's low temperature for flower initiation and rapid and uniform growth in the following spring. It is shown by Wang and Roberts (1970) and Lin and Roberts (1970) that removal of only the inner scales from field-grown *L. longiflorum* overcame dormancy, but removal of only the outer scales did not. This indicates that the state of dormancy in inner scales are different from that in outer scales. Thus, it should be noted that there are at least three generations in one bulb of *L. longiflorum*; outer scales (previous year's inner scales), inner scales (next year's outer scales or previous year's lateral meristems) and lateral meristems of inner scales (next year's inner scales). Times of receiving low or high temperature for them are different. The dormancy or other physiological phenomena of the bulbs not only of *L. longiflorum* but also of other bulbous plants, therefore, should be considered separately. Unless, both the opposite stimuli such as low temperature and high temperature might be considered to be effective on dormancy breaking of *L. longiflorum* (Matsuo, 1977 ; Matsuo and Arisumi, 1979 ; Stimart *et al.*, 1982 ; Matsuo and van Tuyl, 1984).

Although the temperature had already fallen in December and January, percentage of leaf emergence was still high when scalings were started in these months. Induction of bulb formation in *Oxalis* (Aoba, 1972) and *Iris* (Aoba, 1974) was shown to be caused by low temperature, but its effect was negated by high temperature if low temperature was not given enough. He concluded that this effect resembles vernalization, devernialization and revernialization in flower formation. In scaling in *L. longiflorum*, it is considered that low temperature was not yet sufficient in December and January and its inhibition of leaf emergence might be negated by a high scaling temperature of 20°C.

Difference in number of bulblets produced between the period from December-scaling to April-scaling and that from May-scaling to November-scaling does not associate with the state of dormancy. It seems to have a relation to the degree of maturity or the size of scales. Scales used for scalings from December to May were prepared from mother bulbs which had been formed and developed in the early summer of the previous year, while those from June to November were from newly developed daughter bulbs during May and June of the current year inside the mother bulbs. As Matsuo and Arisumi (1978) had proved, the inner the scale position of mother bulbs was, the lesser the number of bulblets developed. This means that the larger or more matured scales bring forth the larger number of bulblets.

In accordance with the decrease in percentage of leaf emergence from bulblets during the period from January to April, auxin activity decreased. In contrast, abscisic acid activity increased in the meanwhile. Increase in leaf emergence thereafter was also associated with the decrease in abscisic acid activity and with the increase in auxin activity. Abscisic acid is recognized that it is involved in controlling dormancy in various organs of plants. Tsukamoto and Ando (1973) showed that the breaking of the dormancy of *Iris* bulbs is due to a decrease in abscisic acid in high temperature. Abscisic acid increased in bulbous iris during growth under bulb-forming conditions (low temperature), but not under non bulb-forming conditions (Okubo and Uemoto, 1981). These results also suggest that bulbs of *L. longiflorum* are induced into dormancy by low temperature, and in the state of true dormancy by flowering time. Then the dormancy is terminated by high temperature.

The facts that low temperature induced the bulb formation in bulbous plants (Aoba, 1971, 1972, 1974, 1976; Okubo and Uemoto, 1981), that the induction of dormancy of *Iris hollandica* (Okubo and Uemoto, 1981), *Hyacinthus orientalis* (Okubo et al., 1988) and *L. longiflorum* (results obtained here) is caused by low temperature, that abscisic acid is recognized to control dormancy in various organs of plants and that abscisic acid activity increase when these bulbs receive low temperature lead us to the same conclusion as we did in *Hyacinthus orientalis* in previous paper (Okubo et al., 1988) that the induction of bulb formation and the induction of bulb dormancy in bulbous plants are the same phenomenon.

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