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## Inheritance of Bulb Dormancy and Early Flowering Ability in F<sub>1</sub> Progenies of Intra- and Interspecific Crosses of *Lilium formosanum* and *L. longiflorum*

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One-year-old seedlings of the northern populations of *Lilium longiflorum* in the Ryukyu Archipelago have deep dormancy in summer, whereas those of the southern populations of *L. longiflorum* and *L. formosanum* show lack or reduction of dormancy. Dormancy status of the F<sub>1</sub> progenies of intraspecific hybrids among *L. longiflorum* with different degrees of dormancy and interspecific hybrids between *L. formosanum* and *L. longiflorum* was studied in an open field condition. Three populations of *L. longiflorum*, Yakushima (LYA) and Kikai Jima (LKI) in the Ryukyu Archipelago, Japan and Pitouchiao (LPI), Taiwan and two populations of *L. formosanum*, Wulai (FWU), Taiwan and Fukuoka (FFU), Japan were used. FFU, FWU, LPI and hybrids of FFU × FWU, FFU × LPI and FWU × LPI continued developing leaves in summer and flowered in a year after seed sowing, while LYA and LKI and the hybrids with them did not. Since FFU, FWU and LPI are categorized as non-dormant populations and LKI and LYA as deep dormant, the bulb dormancy seems to be dominant, while early flowering ability is recessive in the F<sub>1</sub> progenies.

**Key words:** dormancy, inheritance, *Lilium formosanum*, *Lilium longiflorum*

### INTRODUCTION

*Lilium longiflorum* and its derivative, *L. formosanum* (Hiramatsu *et al.*, 2001) are among Liliaceae endemic to the subtropical Ryukyu Archipelago, Japan and Taiwan (Wilson, 1925; McRae, 1998). We previously confirmed that temperature is the important factor for differentiation in degree of dormancy in the one year old seedlings of *L. longiflorum* populations through the geographic gradient of the Ryukyu Archipelago (Mojtahedi *et al.*, 2011, 2012). In those experiments, dormancy in the one year old seedlings of northern populations of *L. longiflorum* was induced by high summer temperature wherein those populations stopped leaf development when the temperature reached to 25°C in the middle of June and showed deep dormant status till the end of following January without producing any leaf and flower, while those of *L. formosanum* and *L. longiflorum* populations growing in the southern part of the Archipelago showed no or weak dormancy even in high temperature (25 and 30°C) in July and August, and can produce flowers in the first year (Mojtahedi *et al.*, 2011, 2012).

Inheritance of dormancy and/or bulb formation has been reported only in a few species (Tashiro, 1984; Tashiro *et al.*, 1995; Xiao *et al.*, 2010), due to the difficulties of obtaining dormant and non-dormant phenotypes in the same species or fertile progenies between them. Induction of early-flowering traits has been

achieved in many horticultural crops. In *Lilium* breeding, early flowering cultivars have been developed by the crosses of *L. formosanum* with *L. longiflorum* (= *L. × formolongi*).

In this study, inheritance of dormancy and early flowering traits of F<sub>1</sub> progenies of intraspecific hybrids between dormant and non-dormant types of *L. longiflorum* and interspecific hybrids between *L. formosanum* and *L. longiflorum* populations were investigated.

### MATERIALS AND METHODS

#### Plant materials and culture

Three populations of *L. longiflorum*, Yakushima (LYA) and Kikai Jima (LKI) in the Ryukyu Archipelago, Japan and Pitouchiao (LPI), Taiwan and two populations of *L. formosanum*, a Wulai (FWU) population in Taiwan and a domesticated population in Fukuoka (FFU), Japan were used.

All the seeds were sown in November 2009 or 2010 in cell trays containing the mixture of sphagnum peat moss: vermiculite (Redi-Earth Sun Gro Horticulture Distribution Inc., U.S.A.), and grown in incubators (16/8 h photoperiod, 70% humidity, 15°C) for 5 months. They were transplanted in the following May to the plastic pots containing red loam: commercial soil (4:1) to grow in an open field. Nitrogen was used as a fertilizer in the soil mixture with the ratio of (15 g/10000 cm<sup>2</sup>) and leaf mold was used after transplantation to prevent the soil evaporation.

#### Hybridization method and culture of F<sub>1</sub> progenies

The inter- and intra-specific cross hybridization started immediately after flowering. Flowers of female plants (FFU, FWU, LPI and LKI) were emasculated 2

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days before anthesis. Anthers were kept in dry condition at room temperature to produce mature pollen grains after harvest and used during 7 days after emasculation to conduct intraspecific cross hybridization from end of May to end of June. Mature pollen grains were kept in  $-20^{\circ}\text{C}$  to carry out interspecific cross hybridization from middle of July to mid-October. Pollination was carried out 2 days after anthesis and mature capsules were harvested 2 months after pollination. Seeds were dried for one month at  $25^{\circ}\text{C}$ .

The seeds of the  $F_1$  progenies were cultured in November 2010 and 2011 using the same mentioned methods. Scaly leaf morphology was checked to confirm seedlings hybridity. Weekly leaf number and early flowering ability in the first year of at least 10 individuals were measured for all populations.

## RESULTS AND DISCUSSION

Total leaf numbers of the parents were larger in FFW, FFU and LPI (non-dormant populations) than in

LKI and LYA (dormant populations), and the former three populations showed an early flowering ability (Table 1) in accordance with our previous reports (Mojtahedi *et al.*, 2011, 2012). Hybrids of FFU  $\times$  FWU, FFU  $\times$  LPI and FWU  $\times$  LPI continued leaf development in the summer, while the other hybrids did not (Fig. 1). FFU  $\times$  FWU, FFU  $\times$  LPI and FWU  $\times$  LPI developed 24–25 leaves and some of them flowered in less than 300 days after seed sowing, while the other hybrids produced only 3–5 leaves and did not flower in a year (Table 2). It is clearly shown that the  $F_1$  progenies of dormant  $\times$  non-dormant type and its reciprocal non-dormant  $\times$  dormant type populations are dormant type. It can be concluded that dormancy is dominant over non-dormancy in *L. longiflorum* and *L. formosanum*.

*Allium*  $\times$  *wakegi*, a natural interspecific hybrid between Welsh onion (*A. fistulosum*, non-bulbous species) as a maternal plant and shallot (*A. cepa* aggregatum group, bulbous species) as a paternal plant, forms bulbs and has dormancy (Tashiro, 1984; Hizume, 1994; Tashiro *et al.*, 1995). The hybrids of the reciprocal

**Table 1.** Total leaf number and flowering performance of *L. formosanum* and *L. longiflorum* in different populations in the first year growth

Population <sup>z</sup>	Total leaf number <sup>y</sup>	% of first year flowering <sup>x</sup>	Days to first flowering after	
			seed sowing (min–max)	transplantation (min–max)
FFW	$37.6 \pm 4.0$	65	280 (265–295)	110 (95–125)
FFU	$54.1 \pm 2.4$	90	332 (300–365)	162 (130–195)
LPI	$24.5 \pm 3.3$	19.7	260 (240–280)	90 (70–110)
LKI	$5.5 \pm 0.3$	0	452 (445–460)	282 (275–290)
LYA	$4.1 \pm 0.1$	0	450 (440–460)	282 (270–295)

<sup>z</sup> FFW, FFU, LPI, LKI and LYA; see text

<sup>y</sup> Total leaf number in the first year growth  $\pm$  SE

<sup>x</sup> (Number of flowered plants/Number of total plants)  $\times$  100

**Table 2.** Total leaf number and flowering performance of  $F_1$  progenies in the first year growth

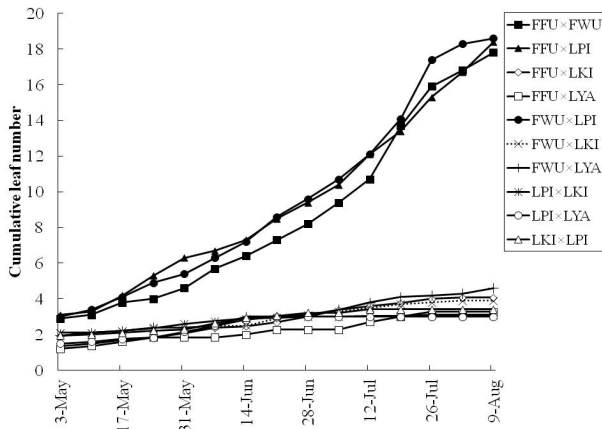
Cross combination <sup>z</sup>	Total leaf number <sup>y</sup>	% of first year flowering <sup>x</sup>	Days to first flowering after	
			seed sowing (min–max)	transplantation (min–max)
FFU $\times$ FWU	$25.2 \pm 3.5$	20	292 (285–300)	122 (115–130)
FFU $\times$ LPI	$25.3 \pm 3.4$	14	297 (285–310)	162 (150–175)
FFU $\times$ LKI	$4.1 \pm 0.1$	0	– <sup>w</sup>	–
FFU $\times$ LYA	$3.3 \pm 0.1$	0	–	–
FWU $\times$ LPI	$24.0 \pm 2.4$	55	282 (255–310)	147 (120–175)
FWU $\times$ LKI	$3.9 \pm 0.2$	0	–	–
FWU $\times$ LYA	$4.6 \pm 0.1$	0	–	–
LPI $\times$ LKI	$3.1 \pm 0.1$	0	–	–
LPI $\times$ LYA	$3.0 \pm 0.0$	0	–	–
LKI $\times$ LPI	$3.4 \pm 0.1$	0	–	–

<sup>z</sup> FFW, FFU, LPI, LKI and LYA; see text

<sup>y</sup> Total leaf number in the first year growth  $\pm$  SE

<sup>x</sup> (Number of flowered plants/Number of total plants)  $\times$  100

<sup>w</sup> Not flowered until now



**Fig. 1.** Growth patterns of F<sub>1</sub> hybrids of interspecific cross hybridization between *L. formosanum* (FFU, FWU) and *L. longiflorum* or intraspecific cross hybridization between dormant (LKI, LYA) and non-dormant (LPI) type of *L. longiflorum* populations. FFU, FWU, LPI, LKI and LYA; see text.

crossings also form bulbs (Arifin *et al.*, 2000) in agreement with our results. On the other hand, bulb formation in the F<sub>1</sub> progenies of non-dormant type chives (*Allium schoenoprasum*) × dormant type *A. schoenoprasum* var. *foliosum* was not observed, indicating the trait is recessive (Xiao *et al.*, 2010). Dormancy trait in bulbous plants may be species dependent.

Early flowering ability was not inherited in the progenies when at least one parent is a dormant type in our study. It is in contradiction to the fact that the cultivars of *Lilium* × *formolongi* with early flowering ability were developed by the crosses of *L. formosanum* × *L. longiflorum* (Beattie and White, 1993; Shimizu, 1971), although it is unknown whether *L. longiflorum* with early flowering ability was used in their breeding. It was also reported that the early flowering ability of *L. formosanum* as female parent in its hybrids with *L. auratum*, *L. speciosum*, *L. regale* as male parents is dominant (Saruwatari, 2009). Hai *et al.* (2012) introduced the hybrids of *L. formolongi* with *L. brownii* var. *colchesteri* that flowered within their first year growth.

It is reported that threshold plant size (Hiramatsu *et al.*, 2012) and development of adequate scaly leaves during the first six months of their vegetative growth is one of the obligatory requirements to move into reproductive phase in *L. longiflorum* and *L. formosanum* (Mojtahedi *et al.*, 2012). The leaf number of all the F<sub>1</sub> progenies did not reach to the minimum threshold number of leaves to start the reproductive phase. Low degrees of flowering rate and little net production during spring to summer in the first year in northern *L. longiflorum* populations (Hiramatsu *et al.*, 2002) associated with quiescence in leaf development during summer set off the theory that the early flowering ability is adaptive strategy to grow without dormancy throughout the year (Mojtahedi *et al.*, 2012). Whenever the dormancy trait is expressed, it causes less leaf develop-

ment that makes little net production and the early flowering ability would be suppressed. Our results proved this theory in the F<sub>1</sub> progenies. In conclusion, deep bulb dormancy in the F<sub>1</sub> progenies of the *Lilium* populations studied is dominant, while early flowering ability is recessive.

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