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Seedling Growth Response to Biotic and Abiotic Stresses in *Lilium longiflorum* and *L. formosanum* in Relation to Their Life History Strategies

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According to Grime's C–S–R concept for plant life history strategies, habitat differentiation between genetically highly related bulbous species, *Lilium formosanum* and *L. longiflorum*, were discussed from the reproductive performance of two–year–old seedlings experimentally exposed soil nutrient and light stresses. Reduction of individual flower number was significant and larger in *L. formosanum* than in *L. longiflorum* when fertilizer was not applied under sufficient light intensity. The result strongly supports the prediction that rapid growth and early onset of sexual reproduction specific to *L. formosanum* is reasonably demonstrated only in the highly disturbed vegetation without any stress. *Lilium formosanum* produced approximately 60% of malformed, unfunctional flowers in the second year of normal cultivation, but *L. longiflorum* did not. It is highly likely that the malformed flowers are caused by virus infection. It can be concluded that *L. formosanum* is so susceptible to viruses as to seriously reduce reproductive success, and thus, the species is kept out from the nutritionally less productive seaside vegetation often established on limestone soils, where *L. longiflorum* and calcicole species are preferably grown.

INTRODUCTION

Ability of early reproduction in perennial crops is a very attractive characteristic in agriculture for getting flowers and fruits in a short cultivation period and for rotating the breeding cycle rapidly. Regrettably, however, the ability has been found to be rather rare in perennial plants since photosynthetic resources captured within perennial plant individual are restricted to dominantly allocate into storage organs until they reach the threshold size for the reproductive stage.

Lilium formosanum has been recognized as the outstanding bulbous species with the early reproductive ability (Wilson, 1925; McRae, 1998). We previously exhibited in the field experiment under a cultivated condition in the temperate zone that 89 to 100% of *L. formosanum* seedlings originated from three natural low land populations reached the first flowering in as little as eight to ten months after seed sowing (Hiramatsu *et al.*, 2002). In the same experiment, the rate of seedlings with such early reproductive ability were not more than 26% among four natural insular populations of *L. longiflorum*, the most genetically related species to *L. formosanum* (Hiramatsu *et al.*, 2001a). Thus, the extreme high potential of early reproduction seems specific to *L. formosanum*, so far.

According to the Grime's C–S–R concept (Grime, 1977; Grime *et al.*, 1996), in which plant life history strategies were categorized into three types ('competitors', 'stress–tolerators', and 'ruderals') by combination of intensities of the two external factors such as 'stress' and 'disturbance', the ability of rapid growth and consequent early onset of sexual reproduction were considered as the major life–history strategy specifically evolved under the environment where disturbance often operates as natural selection. This strategy concept is well concordant with the fact that natural populations of *L. formosanum* are favored in the inland vegetation often affected by human and natural disturbance such as in the margins of arable lands and forests, and on the mountain slopes and cliffs (Hiramatsu *et al.*, 2001b).

It is also significant for understanding evolutionary history of *L. formosanum* to recognize the fact that in the mainland of Taiwan, where *L. formosanum* is natively distributed, its natural population was never found in the habitats of *L. longiflorum* (Hiramatsu *et al.*, 2001b). *Lilium longiflorum* is preferably grown well–lit grassy fields often established on the limestone by the seacoast (Wilson, 1925; Hiramatsu *et al.*, 2001b). The limestone soils are generally characterized by high pH, soil solution HCO_3^-, and low solubility and availability of minerals, in particular P and Fe (Tyler, 1992, 1996). Grime *et al.* (1996) stated that the ruderal strategy with early diversion of captured resources into sexual reproductive organs is not compatible with undisturbed, highly–stressed habitats, where the stress–tolerators are often growing. The evidence accumulated may lead us to the prediction that *L. fromosanum* reduces fitness under stressful environments where mineral nutrients are severely restricted.

In addition to the lack of information on growth response to abiotic stresses, little has been known how biotic stresses affect the growth of *L. formosanum*. Many kinds of viruses have been known to cause serious damage on growth and flowering of *Lilium* species and cultivars, to which *L. formosanum* is believed to be very susceptible (McRae. 1998). Suppose that virus

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infection causes deterioration in sexual reproduction of *L. formosanum*, individuals infected with virus may gradually reduce their fitness beyond one–year growth.

The present study, first, demonstrated difference in effects of a macronutrient stress on fitness between *L. formosanum* and *L. longiflorum*, in combination of a light intensity stress. Second, variation in reproductive success during two–years field cultivation of the seedlings was compared between the two species. Distinct primary strategies considered to have operated the speciation between the species were then discussed.

MATERIALS AND METHODS

Light intensity and soil nutrient stresses

The experiment was carried out in the experimental field inside of an unheated greenhouse of the University Farm located in northern Kyushu, Japan. One–year–old seedlings were established from the seeds of natural populations in Kikai Jima (LKI) and Pitouchiao (LPI) in the mainland of Taiwan for *L. longiflorum*, and of naturalized population in Fukuoka prefecture, northern Kyushu, Japan (FFU) for *L. formosanum*. In November, bulbs were once dug up and disinfected. Forty bulbs of each population with approximately same size variation were transplanted into each of four experimental blocks in the same experimental field with 15× 15 cm spaces. Four experimental blocks were designed by a combination of treatments with or without fertilizer application (+F, –F) and shading treatments (+S, –S). In fertilized blocks, a slow–release fertilizer comprising 10% of N, P and K was supplemented twice with amount of 100 gm^{-2} and 50 gm^{-2} in April and July, respectively. Shading blocks were covered with double cheese clothes, which reduce light intensity to approximately 12% of unshaded blocks. Systemic insecticide was applied every two months during two–years cultivation to avoid aphids, which are major vectors of virus disease. The sum totals of bolting stem length and flower numbers produced from one bulb were recorded after about 10 months from culture initiation.

The data were statistically analyzed by a three–way analysis of variance (ANOVA) to test for the effects of fertilizer, shading and the population source (genotype) on total shoot length and number of flowers per individual plant.

Flowering during two–years cultivation

To estimate the changes of individual fitness during two years of plant growth, seedlings established from a population of Kume Shima Island (LKU), LPI for *L. longiflorum*, and FFU for *L. formosanum* were cultivated with 15× 15 cm density for two years in the experimental field inside of the unheated greenhouse. One hundred and fifty gm^{-2} of the slow–release fertilizer was supplemented every year. Any pesticide and fungicide was not applied except for the once application during vegetative growth in the first year. The number of bolting stems and flowers with normal and abnormal appearance was recorded in the first and second year of cultivation.

RESULTS AND DISCUSSION

Growth responses under light intensity and soil nutrient stresses

The sum totals of bolting stem length were chiefly dependent on population though they also significantly decreased with reducing soil nutrient; i.e., the values of *L. formosanum* were always more than twice as large as those of *L. longiflorum* (Table 1, Fig. 1). This result indicates that plant height is determined rather geneti-

Table 1. *F* values by three–way ANOVA for total stem length and flower number per plant in one experimental population of *Lilium formosanum* and two of *L. longiflorum* cultivated in combination of with or without fertilizer application and shading treatment.

Effect	*df*	*F* value	
		Total stem length	No. of flowers
Population (P)	2	157.61 ***	4.69 **
Fertilizer (F)	1	15.45 ***	15.21 ***
Shading (S)	1	0.04	72.38 ***
P×F	2	7.48 ***	2.19
P×S	2	0.48	4.08 *
F×S	1	4.85 *	11.57 ***

* $P<0.05$; ** $P<0.01$; *** $P<0.001$

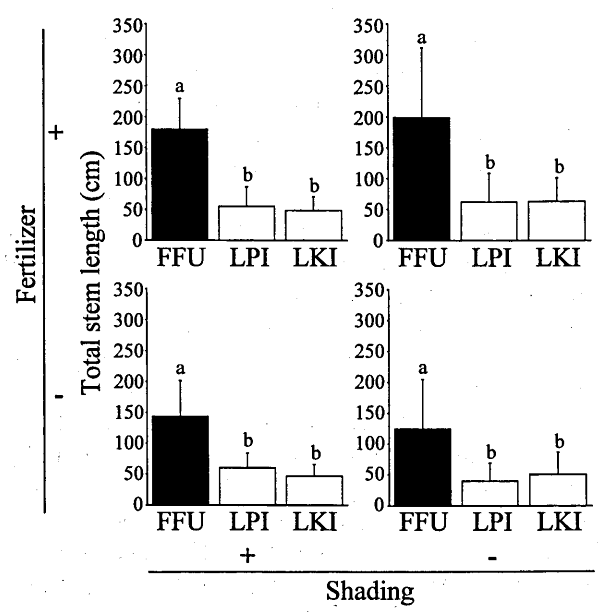

Fig. 1. Total stem length per seedling cultivated in combination with or without fertilizer application and shading treatment for one experimental population of *Lilium formosanum* (shaded bar) and two of *L. longiflorum* (open bar). FFU, LPI, and LKI, respectively, indicates the seed source from a naturalized *L. formosanum* population of Fukuoka in northern Kyushu, and a natural *L. longiflorum* population of Pitouchiao in the mainland of Taiwan and of Kikai Jima Island in the Ryukyu Archipelago. Vertical bars of each histogram are standard deviations. Different letters in each experimental block indicate statistical difference among populations at $P<0.05$ by Games–Howell test.

cally than environmentally.

The flower number per plant was, however, affected significantly by light intensity and soil nutrient rather than population (Table 1). Decreased degrees of the individual flower number with reducing light intensity and soil nutrient were larger in *L. formosanum* than in *L. longiflorum* (Fig. 2). Thus, *L. formosanum* produced more flowers than *L. longiflorum* under the condition without nutrient and shading stresses, while under light and/or soil nutrient stresses the flower number was not different between the species.

This fact suggests that rapid growth and early reproductive ability of *L. formosanum* cannot be demonstrated sufficiently under environments with light and/or soil nutrient stresses. It is highly probable that only in the disturbed, productive vegetation without dense shading by creeper and pioneer tree species, rapid growth and tall stature specific to *L. formosnum* are the most advantageous to resource capture and consequent early onset of sexual reproduction.

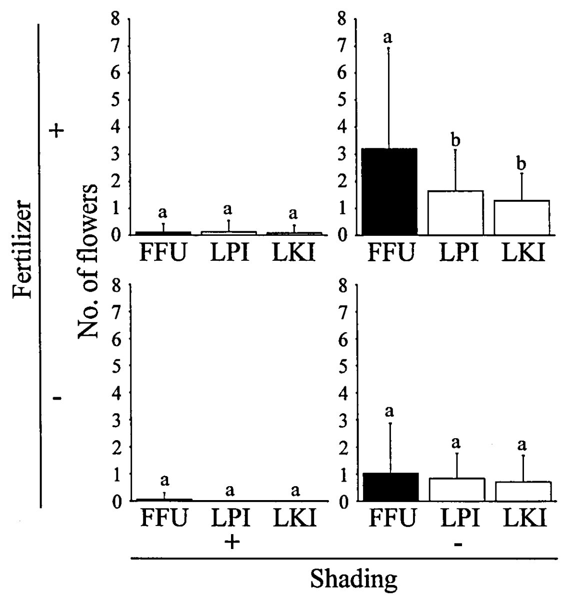

Fig. 2. Flower number per seedling cultivated in the combination with or without fertilizer application and shading treatment in one experimental population of *Lilium formosanum* (shaded bar) and two of *L. longiflorum* (open bar). Vertical bars of each histogram, abbreviations of population names and different letters in each experimental block are the same as in Fig. 1.

The result that reproductive success for *L. longiflorum* is not so much influenced by the nutrient stress indicates that the species is relatively tolerant to the soil nutrient stress. The species is often grown in well–lit grassy field established on limestone, whose soils are difficult to dissolve P and Fe, and are only acceptable for the plant species with specialized ability that transform minerals from unavailable to available for uptake, i.e., calcicole plants (Zohlen and Tyler, 2000). Thus, distinct habitat differentiation recognized between *L. longiflorum* and *L. formsanum* may be partly attributed to the difference in nutrient uptake abilities as seen between calcicole and culcifuge plants.

Variation in flowering during two–years cultivation

All flowers were morphologically normal and functional to set capsules in the first year (Table 2). Number of flowers per bolting stem in *L. formorsanum* was significantly lower than that in both the populations of *L. longiflorum*. However, bolting stems per plant in *L. formosanum* were more than ten times as many as those in *L. longiflorum*, and consequently, estimated number of flowers produced per plant was more than five times.

It was very noteworthy that quite large number of *L. formosanum* plants in the second year produced stems with malformed narrow, twisted leaves without flowers or with malformed flowers possessing the distorted pistil, stamens and perianths (Fig. 3). The malformed flowers of *L. formosanum* hardly set any capsules after flowering.

The reproductive success in the second year was inconsistent with that in the first year. *Lilium formosanum* in the second year produced only as equal number of 'normal' flowers as that in the first year because 60.4% of flowers were morphologically abnormal (Table 2). *Lilium longiflorum* produced

Table 2. Variation in number of bolting stems (mean ± SD), rate of morphologically normal flower, number of morphologically normal flowers per bolting stem (mean ± SD) and estimated number of normal flowers per plant in one experimental population of *Lilium formsanum* and *L. longiflorum*. FFU, LPI and LKU, respectively , indicates the seed source from a naturalized *L. formsanum* population of Fukuoka in northern Kyushu, and natural *L. longiflorum* population of Pitouchiao in the mainland of Taiwan and of Kume Shima Island in the Ryukyu Archipelago. Different letters in each row indicates statistical difference at $P < 0.05$ by Games–Howell test.

Cultivated year	Population	*N*	No. of bolting stems	% of morphologically normal flowers	No. of normal flowers per stem	No. of normal flowers per plant
1st	FFU	58	4.3 ± 1.50^a	100	1.2 ± 0.73^a	5.0
	LPI	56	0.4 ± 0.53^b	100	1.9 ± 1.38^b	0.8
	LKU	60	0.2 ± 0.39^b	100	2.6 ± 1.55^b	0.5
2nd	FFU	50	5.2 ± 1.66^a	39.6	0.9 ± 1.42^a	4.6
	LPI	50	2.2 ± 1.38^b	100	3.4 ± 3.52^b	7.5
	LKU	50	1.8 ± 1.08^b	100	5.3 ± 4.46^c	9.6

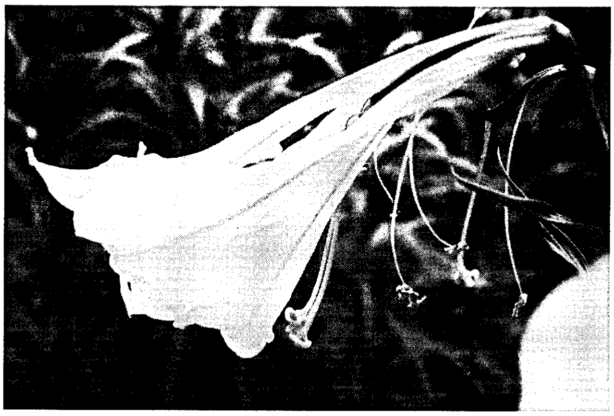

Fig. 3. Morphological abnormality of a flower with split perianths, a distorted stigma and anthers observed in a two–years–old seedling of *Lilium formosanum*.

about two times as many normal flowers as compared to that in the first year. The pattern of changing was similar in the number of bolting stems for each species. Thus, two populations of *L. longiflorum* exceeded *L. formosanum* by 2.9 to 5.0 in estimated number of normal flowers produced per plant, and consequently, the total number of normal flowers per plant across two–years cultivation was equivalent among the three populations.

There are several different viruses that infect lilies. Three of them have been known to cause serious problems; they are lily symptomless virus, tulip–breaking virus and cucumber mosaic virus (McRae, 1998). Vectors of these viruses are several species of aphids. Virus–infected lilies produce distinctive, damaging symptoms, including irregular mottling and flecking of the leaves; reduced plant size; torted and twisted growth; color–breaking in the flowers and leaves. It seems that malformed morphology observed in the stems, leaves and flowers of *L. foromsanum* plants in our experiment is one of the critical virus symptoms reported, and the virus susceptibility of the species is so critical that the species fall into reproductive malfunction.

If once plants are infected with virus, the propagated viruses will be permanently carried in almost whole the tissues of the plants as long as they live. In virus–susceptible *L. formosanum*, therefore, plant will hardly reach or recover its sexual reproduction after virus infection, falling in serious depression of individual fitness, particularly in less productive environments. It can be thus concluded that the ability by which seedlings of *L. formosanum* grow faster to reproductive phase allows the species not only to grow in highly disturbed, productive habitats but also to escape from the risk of fitness reduction by virus infection in the same environment. By contrast, *L. longiflorum* seems to be highly tolerant to viruses so that the species could grow slowly and perennially under less productive conditions.

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