

クロユリの開花フェノロジーと自家不和合性

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Takeshi Yashima^{*,***} Eiichiro Kinoshita^{**,****} and
Tatemi Shimizu^{*} : **Flowering Phenology and
Self-incompatibility in *Fritillaria camtschaticensis*
(L.) Ker-Gawl.**

八島武志^{*,***}・木下栄一郎^{**,****}・清水建美^{*} : クロユリの開花
フェノロジーと自家不和合性

Gene flow influences genetic structure of plant populations, and pollen and seed dispersal are major factors associated with gene flow (Levin and Kerster 1974). Pollen flow and subsequent pollination success largely depend on breeding system and inflorescence architecture as well as behavior of pollinators (Wyatt 1982).

Fritillaria camtschaticensis exhibits variability in breeding system. The plant inhabiting central Honshu is diploid (Shimizu 1983), and most plants bear one male or cosexual flower (Shimizu *et al.* in press). Thus this species can be classified as an androdioecism (Yampolsky and Yampolsky 1922; Lloyd and Bawa 1984). However, this species sometimes bears two flowers, and a variety of combinations of flower types were found; male and male, female and female, or male and cosexual. In addition, *F. camtschaticensis* can reproduce by means of clonal growth as well as seeds (Shimizu and Umebayashi 1995). It was shown by demographic studies that *F. camtschaticensis* in Mt. Hakusan produced a lot of mature seeds, but seedling emergence rarely took place, and thus it was assumed that natural populations of *F. camtschaticensis* in Mt. Hakusan could be maintained mainly by clonal multiplication (Shimizu *et al.* in press).

Variability in breeding system as well as clonal multiplication in *F. camtschaticensis* may have had profound influence on genetic structure of natural population. Thus we studied

breeding system, flowering phenology and pollinators behavior, and report that (1) *F. camtschaticensis* is self-incompatible, (2) flowering phenology synchronizes among individuals, and (3) dye particle movements by pollinators are limited within dozens of meters from donors.

Study Site

This study was conducted in Mt. Hakusan in the central Honshu. Self- or cross-pollination experiments, observations of flowering phenology and measurements of pollen movement were carried out in some sites. All sites are located between 2400–2450 m above sea level, where a lot of dense patches of *F. camtschaticensis* scattered, and demographic and genetic studies were simultaneously conducted nearby.

Methods

Pollination experiment

In mid-July, 1994, 115 cosexual flowers were bagged by fine-mesh cloth before anthesis, and the bags were removed after flowering period. Stamina of 71 flowers were removed before anthesis, and artificial pollinations were conducted after flowers opened. Out of 99 flowers, 43 flowers were self-pollinated; 28 flowers were used for transferring pollen to stigma of the same flower (autogamous selfing) and 15 for transferring pollen to stigma of different flower on the same plant (geitonogamous selfing). Fifty-six

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Table 1. Pollination experiments and fruit production

Mode of crossing		Combination of flower type (Maternity × Paternity)	No. of flowers manipulated	No. of fruit produced	Fruit / Flower Ratio
Self-Pollination	in the same flower		28	1	0.04
	between flowers	C × C	12	0	0.00
	between flowers	C × M	3	1	0.33
Cross-Pollination		C × C	31	26	0.84
		C × M	25	21	0.84
Control			16	2	0.13

C, Cosexual flower; M, Male flower.

Table 2. Fruit production under natural conditions

Site	No. of cosexual flowers observed	No. of mature fruit	Fruit / Flower Ratio
Mizuyajiri	53	45	0.85
Nanryu	20	15	0.75

flowers were cross-pollinated. Pollen donors were chosen from plants growing at least 10 m apart from recipients. The rests of them, 16 flowers, were controls, and they were not emasculated and bugged during flowering season. Fruits were collected in late September, and the number of fertile seed were counted. When a fruit contains more than ten fertile seeds, the fruit is regarded as mature one. In addition to these experiments, cosexual flowers were tagged in the experimental quadrats for demographic study and they were exposed to natural pollinators to measure seed set (for details see Shimizu *et al.* in press).

Flowering phenology

Plants with flower buds were tagged and flowering periods were recorded at four sites near Murodo-Daira. First days of flowering were determined by the following criterion that insects were freely accessible to stamens or pistil of the flower. End of flowering period of each flower was determined when all the following floral traits were not displayed: pollen release from anthers, stigmatic receptivity, scent and nectar secretion.

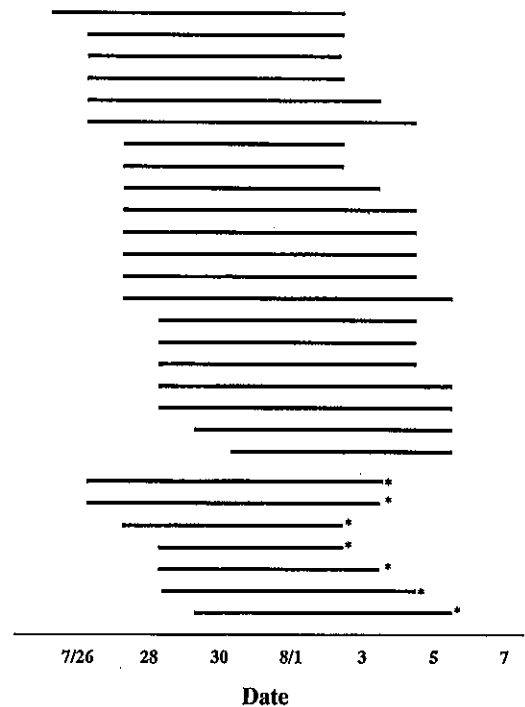


Fig. 1. Range of blooming time of male and cosexual plants in Site 1. Asterisks indicate cosexual plants.

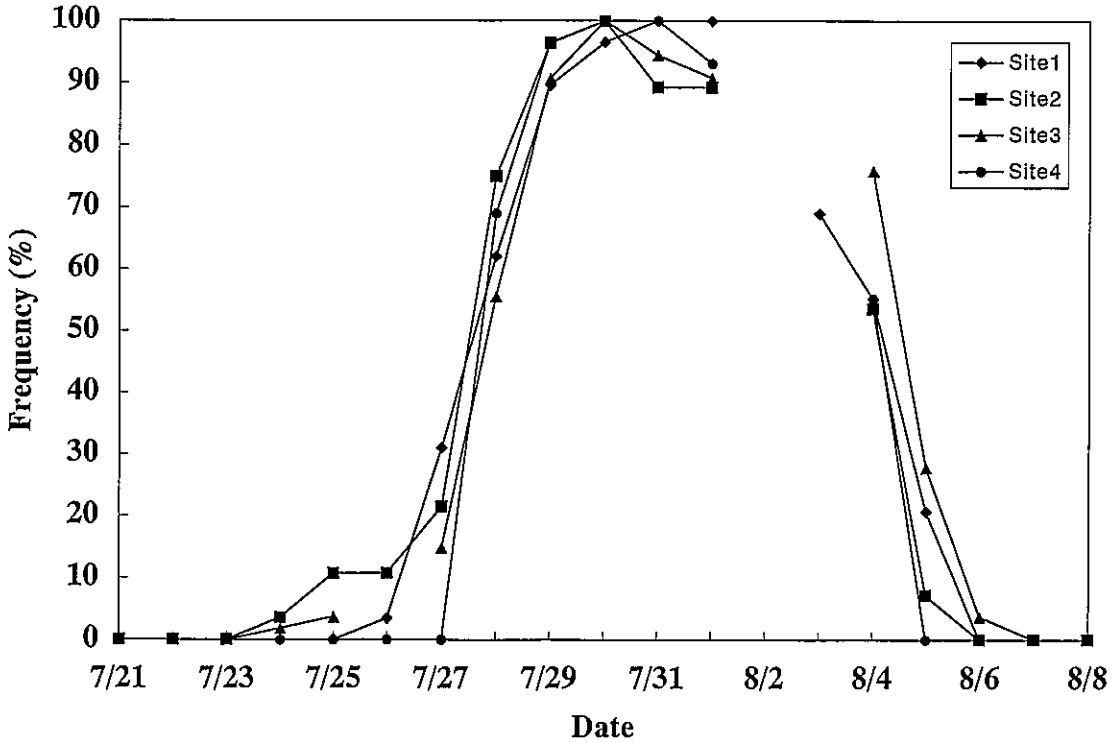


Fig. 2. Daily change of percentages of blooming plants at four sites in 1994. On August 2 and 3 the number of flowering plants were not counted because of heavy rain. Site 1, $N = 29$; Site 2, $N = 28$; Site 3, $N = 54$; Site 4, $N = 29$.

Measurement of pollen movement

Study sites were carefully chosen where *F. camtschaticensis* grew as dense as possible over wide area. Four plants growing in the center of study sites were chosen for dye donors. Fluorescent dye powders, which is usually used for painting, were used as a pollen analogue (cf. Waser and Price 1982). In this study four colors, yellow, red, green and blue, were used. Dye powders were applied to anthers of newly-opened flowers at dawn. In the daytime behaviors of insects visiting *F. camtschaticensis* flowers were observed, and the number of visitors and the time spent at the flower by each visitor were recorded. In the night, to investigate presence or absence of fluorescent powders on stigma, each of the surrounding plants were irradiated by ultra-violet light.

Results and Discussion

Pollination experiments

While few mature fruits were produced by self-

pollinations, a number of fruits were produced by cross-pollination (Table 1). Fruit/flower ratio is 0.04 in autogamy. In geitonogamy fruit/flower ratios were 0.0 in $C \times C$ experiment and 0.33 in $C \times M$ experiment, but the latter may be invalid because of too small number of experiments. Since plants bearing both cosexual and male flower were very rare in natural habitats, self-pollinations between them were difficult. In cross-pollination, 47 of 56 flowers produced mature fruits and fruit/flower ratio is 0.84. In the control fruit/flower ratio is 0.13. In experimental quadrats for demographic study fruit/flower ratio is 0.85 at Mizuyajiri population and 0.75 at Nanryu population, respectively (Table 2).

These results clearly show that *F. camtschaticensis* is self-incompatible. Cross-pollination exhibited high fecundity regardless of the combinations of parents. This result also demonstrates that pollen grains from cosexual flowers are as fertile as those from male flowers, and morphologically cosexual flowers are functionary cosex-

ual.

Flowering phenology

Figure 1 shows flowering period of each of 28 plants in Site 1. Flowering period, on the whole, ranged from July 26 to August 5 in this site. The days when more than 80 % of flowers were in bloom ranged from July 29 to August 2. Flowering phenology synchronized among plants. Figure 2 shows relative frequencies of flowering plants at four sites. Flowering started on July 24 at both Site 2 and Site 3 and on July 28 at Site 4. Peak of flowering was July 30, in which all plants in the four sites were blooming. Mass-flowering may allow this species to attract dipterous pollinators (see below) effectively by offering visual signals or giving off floral scent.

Pollinator and pollen movement

A few insect species were observed to visit *F. camtschaticensis* flowers. Out of them, dipterous species *Aldrichina grahami* is the most probable candidate for a pollinator, since this species visited *F. camtschaticensis* flowers most frequently; this species occupied about 75 % of visitors in number, and spent more than 75 % of the total foraging time. In addition, almost all of *A. grahami* captured were covered with large amount of pollen of *F. camtschaticensis*.

Figure 3 shows flight distance of fluorescent dye particle. Dye particles were deposited on 110 flowers at Manzaidani and on 27 flowers at Tenbou-Hodou. At Manzaidani more than 90 % of dye particles were deposited within 10 m from donors (Fig. 3 A) and most of dye particles were deposited within 20 m at Tenbou-Hodou (Fig. 3 B).

If dye powder is a good indication of pollen movement in *F. camtschaticensis*, pollen can be carried away by pollinators as far as 20 m in natural populations of Mt. Hakusan, and occasional long distance breedings may be also possible. Close correlations between dye powder movements and pollen movements were shown (Waser and Price 1982; Murawski 1987), although there are opposite results that the dye movement may not reflect pollen flow (Handel 1983; Thomson *et al.* 1986).

In conclusion, self-incompatibility, synchronized flowering and active pollinator movements show that outcrossing occurs in natural popula-

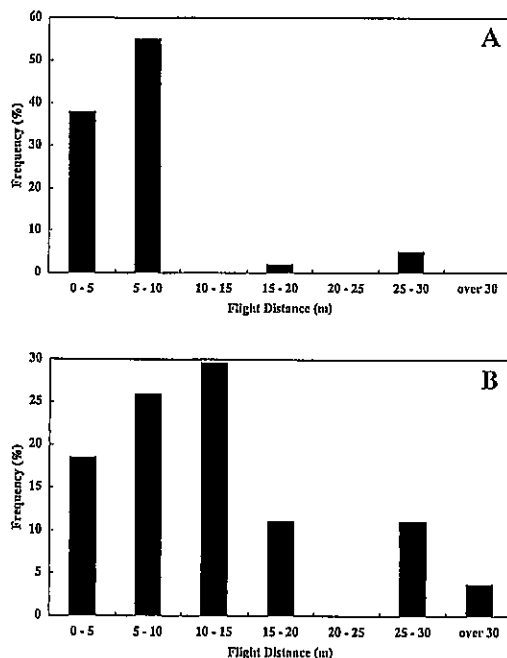


Fig. 3. Flight distance of fluorescent dye particles from the donors. A, Manzaidani, $N = 110$; B, Tenbou-Hodou, $N = 27$.

tions of *F. camtschaticensis* in Mt. Hakusan.

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摘 要

本州の高山帯に生育するクロユリは2倍体で多くの個体は1個の花をつける。花は形態的に雄性あるいは両性で、性表現はいわゆる雄性両性花異株(Androdioecy)である。しかし、2個以上の花をつける場合さまざまな性型の花の組み合わせがみられるため、単純な雄性両性花異株ではない。これら交配様式の複雑さは盛んな栄養繁殖とともにクロユリ集団の構造を複雑にしている一要因であると考えられる。そこでクロユリの集団構造を解析する一環としてクロユリの交配実験や訪花昆虫などの観察を行った。その結果、クロユリは自家不和合性であり、一方、両性花の花粉は雄花の花粉と同等の稔性を示し、両性花は形態的ばかりではなく機能的にも両性であることが判明した。開花は標高が同じくらいの地点ではほとんど同調し開花時期の差は認められなかった。花粉媒介者はケバクロバエ (*Aldrichina grahami*) で、蛍光パウダーによって推定した送粉に有効な飛行距離は約20mであった。これらの結果から白山のクロユリ集団は外交配を専ら行っていると結論できる。(received September 12, 1997; accepted December 1, 1997)