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Floral Biology of *Tricyrtis setouchiensis* Hr. Takahashi (Liliaceae)

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Tricyrtis setouchiensis has some floral-biological features distinct from other species of *Tricyrtis*. The flower of *T. setouchiensis* opens for three days, which is longer than the lifespan of two days in the closely related species, *T. affinis* and *T. macropoda*. The male phase of *T. setouchiensis* is in the first day and the female phase is in the last two days. This relatively long female phase is also distinct from the other xenogamous species of *Tricyrtis* with long-life flowers, because their male phase is in the first half of their flower-lives and their female phase is in the latter half. Perianth of *T. setouchiensis* is patent at a position of one third of the way up from the base just like *T. affinis*. However, *T. setouchiensis* has orange-yellow spots in the basal part of perianth. The spots seem to function as nector guides. Whereas *T. affinis* has large purple spots in the same position. Therefore there is a difference in the spot coloration between *T. setouchiensis* and *T. affinis*. *Tricyrtis setouchiensis* may preserve the nectar guide common to most *Tricyrtis* species with upright flower unlike and *T. macropoda*, which appears to have no nectar guides, and *T. affinis*.

Introduction

Pollination and/or breeding systems are more or less different even among closely related species in the genus *Tricyrtis*. *Tricyrtis nana* is an autogamous species unlike *T. flava* and *T. ohsumiensis* which are outbreeders, and the latter two are different from each other in their blooming (Takahashi 1987a). Pollination of *T. affinis* is characterized by the refined system through the patent tepals (Takahashi 1989). On the other hand pollination of *T. macropoda* with recurved perianth, which is closely related to *T. affinis*, is fairly different from the pollination system of *T. affinis* (Takahashi unpublished). *Tricyrtis setouchiensis* is morphologically closely related to *T. affinis*, *T. macropoda* and *T. pilosa* (Takahashi 1974, 1980). The flower shape of *T. setouchiensis* is very similar to that of *T. affinis*. The preliminary observations of *T. setouchiensis*, however, showed that the flowers bloomed for more than two days, though the flowers of *T. affinis* as well as *T. macropoda* live for two days.

The aim of this paper is to describe the pollination system of *T. setouchiensis* and to compare especially with that of *T. affinis*.

Materials and Methods

Field investigations were carried out at Mt. Koutsu-san, Yamakawa-cho, Mao-gun, Tokushima Prefecture, and at Inohana, Sumoto City, (Isl. Awaji-shima), Hyogo Prefecture, Japan.

Blooming sequence was observed for 50 flowers at Inohana in early October 1992. Insects foraging on the flowers were observed and collected at both sites. UV absorption in the flower was examined with the same methods used by Takahashi (1987a).

Artificial breeding experiments were performed with the plants obtained from the Koutsu-san population and transplanted in pots at Gifu University, Gifu (central Japan). Cross-pollination was made in the first-, second- and third-day flowers and self-pollination in the second-day flowers. The anthers of the flowers for cross-pollination and apogamy testing were removed before flower opening. All the experiments were carried out in an insect-free greenhouse. Hand pollination was done during 0900–1200 hr.

Germinability of the seeds obtained by the breeding experiments was tested with almost the same methods used by Takahashi (in preparation). However, the stratification period was 60 days, and the germinating seeds were counted for 60 days after incubation at 20°C, because seeds of *T. setouchiensis* germinate very well under these conditions (Takahashi 1986).

Fruit and seed set in the Koutsu-san population were examined in 1993.

Numbers of ovules and pollen grains in the flowers from the Inohana population were counted with the same methods used by Takahashi (in preparation) and the pollen/ovule ratio was calculated. Only the ovule number was counted in the Koutsu-san population.

Results

Blooming sequence Although most flowers split the perianth tip in the evening (around 1800 hr), their perianth opening takes place obviously at midnight and they fully open by dawn of the next day (the first day of flowering). The opening of some flowers is delayed a few hours. Most anthers dehisce at 0700–0800 hr, but the style-branches are horizontally spreading out and the stigmata are not mature yet. The style-branches begin to bend down the following midnight and the stigmata are receptive and situated lower than the anther level by dawn of the second day. The flower begins to close in the evening of the third day and wilts by dawn of the fourth day.

Table 1. Insects collected on the flowers of *Tricyrtis setouchiensis* and their foraging objects

Insect	Foraging object
Apidae	
Bombus diversus diversus	nectar (and pollen[1)])
Anthopholidae	
Amegilla sp.	nectar (and pollen[1)])
Halictidae	
Lasioglossum sp.	pollen
Syrphidae	
4 species	pollen
Sphingidae	
1 species	nectar

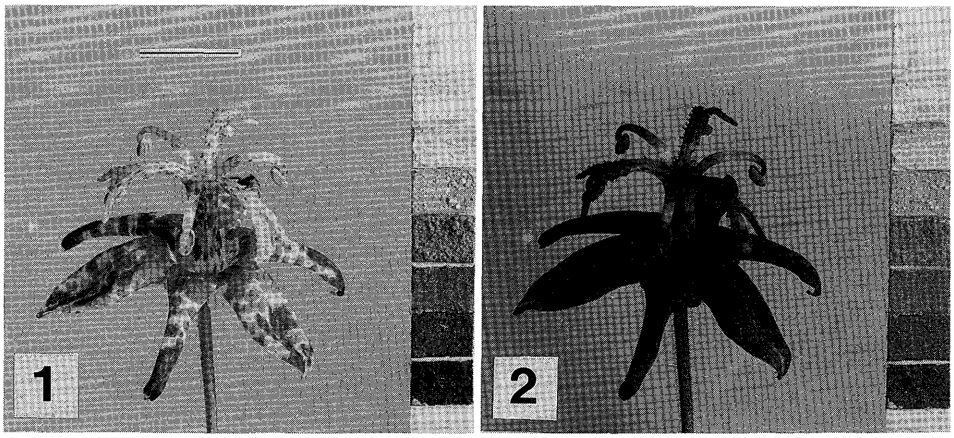
[1)]Pollen grains were deposited on the bees only while they foraged for nectar in the morning of the first day.

Pollinators and their behavior The insects collected on the flowers of *T. macropoda* are listed in Table 1. The most abundant foragers were *Bombus diversus diversus* and *Amegilla* sp., the main pollinators of this plant. Both bee species alight on the patent perianth and suck nectar. Their back touches the anthers and the stigmata on the second- and third-day flowers. However, autogamy seems hardly to occur because most pollen grains are removed by the bees usually on the first day. Small bees of *Lasioglossum* and *Ceratina* and some species of flies forage for pollen usually without touching stigmata. Howkmothes suck nectar while hovering without touching the anthers and the stigmata.

Flower color and UV absorption The perianth is white and has small purple spots on the adaxial side. Large orange-yellow spots, which seem to be nectar guides, are found on the adaxial side in the basal part of the perianth. Purple spots are also noted on the filaments and the style.

The purple and orange-yellow spots absorb almost completely UV light and the other parts show fairly strong UV absorption (Figs. 1 and 2). The UV absorption pattern is similar to that of other species of the section *Tricyrtis* (Takahashi 1984, 1989).

Breeding experiments The results of breeding



Figs. 1–2. Flowers of *Tricyrtis setouchiensis*. 1, under visible light; 2, under UV light. Bar = 1 cm.

experiments are shown in Table 2. About 90 percent of the flowers cross-pollinated on the second or the third day fruited, while about 60 percent of the flowers cross-pollinated on the first day. The flowers which were self-pollinated on the second day produced fruits at a rate of about 84 percent. About 25 percent of the flowers fruited autogamously. The seed numbers per fruit averaged about 45 to 50 in the flowers cross-pollinated on the second or third day and in the self-pollinated flowers, against about 30 and 25 in the flowers cross-pollinated in the first day and in the intact flowers, respectively.

Some 86 out of 114 flowers examined in the Koutsu-san population produced fruits (75.4 percent). Since 29 out of the 86 fruits had already been dehisced and some seeds appeared to have been dispersed, the seeds were counted in 57 capsules. The mean seed number per fruit was 70.8 (Table 2).

The results of this experiment show that the first-day flowers of *T. setouchiensis*, whose stigmata appear to be immature, produce many fruits in the first-day flowers when pollen grains are deposited on the stigmata and that the flowers have a potential to set some fruits through autonomous self-pollination. However, autogamy hardly occurs in natural populations because the pollinators rarely touch the

Table 2. Results of breeding experiments in *Tricyrtis setouchiensis*. The experiments were carried out with the plants cultivated in insect-free greenhouse. The control was examined in the Koutsu-san population. Seed set in the control was examined in 57 fruits (see text)

	No. of samples	No. of flowers fruited	Fruitage rate (percent)	No. of viable seeds in a fruit	
				range	mean±SD
Cross-pollination in first-day flowers	57	34	59.6	0–80	31.6±23.4
Cross-pollination in second-day flowers	53	48	90.6	0–98	49.1±31.0
Cross-pollination in third-day flowers	48	42	87.5	5–80	44.4±23.2
Self-pollination in second-day flowers	62	52	83.9	1–85	47.9±21.4
Leaving emasculated flowers	51	0	0	–	–
Leaving untreated flowers	83	21	25.3	0–80	24.9±21.2
Control	114	86	75.4	11–140	70.8±30.1

stigmata of the first-day flowers and most pollen grains are removed on the first day by pollen foragers.

Pollen/ovule ratio The number of ovule and pollen grains and the pollen/ovule ratio are shown in Table 3. The mean ovule number was 90.2 and 93.7 in the populations of Inohana and Koutsu-san, respectively. The pollen/ovule ratio in the Inohana population was 1237.

Discussion

Although the floral morphology of *T. setouchiensis* is very similar to that of *T. affinis*, the former species has some distinct pollination system features. The flower-life of three days in *T. setouchiensis* is longer than in *T. affinis* as well as *T. macropoda* which is also closely related to the former species; both the latter species have two-day flowers (Takahashi 1987a and unpublished data). The different length of the male and female phase (one and two days, respectively) is another characteristic feature because the female phase of most species with long-lived flowers in the genus *Tricyrtis* is the latter half of their life (Takahashi 1994 and unpublished data). The third-day flowers were frequently visited by pollinators which did not appear to discriminate them from the younger flowers, and this suggests that the third-day flowers also secrete much nectar. Much cost should be required in the long-lived flowers which secrete nectar throughout their lives (Southwick 1984, Primack 1985), though they may be favorable for total display to attract pollinators (Weiss 1991).

The long lifespan of the flowers may not only contribute to total display to pollinators but also offer an opportunity for receiving many pollen grains on the stigmata in *T. setouchiensis*, because the female phase is longer than the male one. The ovule number in the flowers of *T. setouchiensis* is higher than in *T. affinis* (about 70–75; unpublished data by Takahashi). The open-pollinated flowers of the latter species produced about 55 seeds on the average: about 74 percent of the ovules became seeds (Takahashi 1989). The flowers of the former species produced about 71 seeds and about 76 percent of the ovules developed to seeds. On the other hand, in the flowers of *T. macropoda*, which contain a few more ovules (about 110) than *T. setouchiensis*, about 50 percent of ovules matured to seeds (Takahashi unpublished). Therefore, the long female phase may account for setting much seeds in the fruits. Seed-set rates, however, may vary under different conditions such as visitation frequency of pollinators, weather, flower density (e.g., Dieringer 1992). Pollination efficiency of pollinators, cost to produce new flowers, nectar volume and the like should also be compared among these species to elucidate the adaptive meanings of the long-lived flower in *T. setouchiensis*.

The orange-yellow spots in the basal part of the perianth of *T. setouchiensis* are remarkable in evolutionary implication. They are probably the nectar guide and found in most species with upright flowers in all sections of the genus *Tricyrtis* except for the section Brachycyrtis which produces pendulous flowers (Takahashi 1984, 1987a, and unpublished). Although the main pollinators are almost the same, the

Table 3. Numbers of ovules and pollen grains and pollen/ovule ratio in *Tricyrtis setouchiensis* in the Inohana population and number of ovules in the Koutsu-san population

Population	Sample no.	Ovule no.		Pollen grain no. ($\times 10^2$)		Pollen/ovule	
		range	mean±SD	range	mean±SD	range	mean±SD
Inohana	30	66–110	90.2±12.1	696–1386	1106±170	882–1617	1237±197
Koutsu-san	10	71–105	93.7±10.2	–	–	–	–

large purple-spots are in the same part in *T. affinis* whose pollination system appears to be refined; its pollinators can much easily take rewards owing to the perinath morphology (Takahashi, 1989). *Tricyrtis macropoda*, whose pollinators are also almost the same, has none of the spots in that part and the probable nectar guide has possibly degenerated with relation to its recurved perianth (Takahashi unpublished data). Phytogeographical data also suggest that *T. affinis, T. macropoda* and *T. setouchiensis* have appeared relatively recently (Takahashi 1987b). Therefore, it seems to be reasonable that the orange-yellow nectar guide is an ancestral character among the species with upright flowers in *Tricyrtis*, and *T. setouchiensis* may preserve it unlike the other closely related species.

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高橋　弘：**セトウチホトトギスの花部生態学**

セトウチホトトギスの花部生態学的研究を行い，ホトトギス属の他の種，特にこの種に近縁なヤマジノホトトギスおよびヤマホトトギスと比較した．セトウチホトトギスの花は3日間咲いていて，2日間しか咲いていないヤマジノホトトギスやヤマホトトギスより花の寿命が長い．セトウチホトトギスは1日目が雄性期で，残りの2日間が雌性期である．花の寿命が長いものも含めて，これまでにわかっている他殖型の他の種は，雄性期と雌性期はほぼ半分ずつであるので，この種はそれらと異なる．セトウチホトトギスの花は，花被が下から約1／3のところで水平に開き，ヤマジノホトトギスとよく似ている．しかし，ヤマジノホトトギスは花被の基部にある蜜標と考えられる斑紋は紫色であるのに対して，セトウチホトトギスは直立型の花を着ける多くの種と同様に，黄橙色である．また，ヤマホトトギスは同じ位置にはそのような斑紋認められない．蜜標と考えられる斑紋に関しては，これら近縁3種の中で，セトウチホトトギスのみが祖先形質を保持しているのかも知れない．主要なポリネーターがトラマルハナバチとコシブトハナバチの一種であること，花全体が紫外線をよく吸収すること，高い自家和合性を示すことなどはヤマジノホトトギスと同様である．