

キブシ(キブシ科)の性表現と繁殖特性

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論文 (Original Article)

Sex expression and reproductive biology of *Stachyurus praecox* (Stachyuraceae)

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Abstract

Sex expression, sexual differences, flower visitors, and fruit set of *Stachyurus praecox* were examined in forest edges of Mt. Tsukuba for two years. Floral morphology, sexual organs (ovule and pollen), and fruit set suggested that *S. praecox* was gynodioecious. Sex change was not observed for two years. Significant sexual differences were observed in the number of flowers per inflorescences and fruit set. Despite the existence of ovules, fruit set of hermaphrodite flowers was very rare (nearly 0.0%) and was not increased by hand-pollination. Thus, the hermaphroditic flowers seemed to contribute mostly as male and this species is considered to be functionally dioecious. In addition, the rare existence of intermediate inflorescence containing hermaphroditic flowers and female flowers implied that the sex expression of *S. praecox* was instable. About 35% of female flowers set fruit in both years, and hand-pollination did not increase the amount of fruit set. Frequent flower visitors such as hover flies and small solitary bees were likely to be effective pollinators for *S. praecox* flowering in early spring in sunny forest edges.

Key words : fruit set, pollinator, sex expression, sexual difference, *Stachyurus praecox*

Introduction

About 80% of angiosperm species produce hermaphrodite flowers (Proctor *et al.*, 1996). Therefore, the existence of other minor sex expressions has attracted researchers since ancient times (Darwin, 1877), and various hypotheses for the evolution of dioecy have been proposed (Charlesworth & Charlesworth, 1978; Charnov, 1979; Bawa, 1980). As a means to test these evolutionary hypotheses toward dioecy, flowers with intermediate sexual systems such as gynodioecy have been investigated to determine the relative contribution of sexual functions to fitness components (Wolfe & Shmida, 1997; Ashman, 2002; Dorken *et al.*, 2002; Collin & Shykoff, 2003; Glaetli & Goudet, 2006).

Stachyurus praecox Sieb. et Zucc. is an endemic pioneer shrub common in forest edges of warm temperate Japan, and the congeners are distributed in temperate eastern Asia (Li, 1943; Ohba, 1999). The blooming season is early spring when the activity of dominant social pollinators such as bumblebees is not so high. The sex expression of *S. praecox* is known as “perfect or functionally dioecious” (Li, 1943) or “usually dioecious” (Ohba, 1989, 1999), implying that the sex expression of this shrub may include variation. However, the sex expression and related characteristics of *S. praecox* have not been studied in the field. So, I examined the reproductive characteristics of *S. praecox* including sex expression, flower visitors, and fruit set.

Methods

Two populations (2 km apart) of *S. praecox* were investigated on the northern slope of Mt. Tsukuba, Ibaraki, Japan. Reproductive individuals found in two 150 m line transects along a mountain road were measured for size (height and diameter at 10 cm height) and flowering. The flowers that had pistils that were equal in length to stamens were defined as hermaphrodite while the flowers that had stamens shorter than pistils were defined as female. Individual sexuality was determined by observing several inflorescences. The investigation of flowering was conducted in March 2005 and 2006, and fruit set was investigated in May of the same years. The number of individuals investigated was 11 hermaphrodites (356 inflorescences) and 8 females (286 inflorescences) in 2005, and 10 hermaphrodites (470 inflorescences) and 11 females (400 inflorescences) in 2006. The total number of individuals surveyed for reproduction during the two years was 12 hermaphrodites and 13 females.

To check the sexual function, one flower was sampled from 10 hermaphrodites and 10 females, and cross section of a flower was observed using microscope (Nikon SMZ-1500) whether ovule was presence. An anther was sampled from all flowers to count the number of pollen per anther. An anther was broken using tweezers in a petri dish filled with ethanol. Then, all pollen grains in an anther were counted

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using microscope ($\times 60$).

To estimate the light conditions, hemispheric photographs at 1 m height were taken on September 2006 using a fisheye lens (Nikon, FC-E9) within 2 m from each reproductive individual along the forest edge. Then, crown openness of all individuals was measured using the CanopOn 2 free software (<http://takenaka-akio.cool.ne.jp/etc/canopon2/>).

Fruit set was calculated at the inflorescence level and averaged at the individual level and by sex. To detect the pollen limitation for fruit set, outcrossing hand-pollination was conducted on all individuals (female: 1657 flowers of 108 inflorescences, hermaphrodite: 2689 flowers of 150 inflorescences) in 2006. Pollen samples for hand-pollination were corrected from hermaphrodite flowers. The control was naturally-pollinated inflorescences in the same individuals. Flower visitors were observed directly (for 3 times, 1 hr 30 min) and also using digital video cameras

(Sony DCR-TRV50, for 5 times, 5 hr 00 min). This observation was conducted for 3 females and 3 hermaphrodites. In a trial, flower visitors were observed within 20 inflorescences in direct observation and within 3 inflorescences in video camera recording. After the observation, flower visitors were captured and identified in the laboratory.

The effects of crown openness and sex on size on the number of inflorescences per individual were analyzed by two-way ANOVA. The effect of hand-pollination on fruit setting was analyzed by one-way ANOVA. Percentage of crown openness and fruit set were arcsin transformed prior to statistical analysis. All statistical analyses were performed using JMP software (Sall *et al.*, 2004).

Results

Floral morphology of *S. praecox* exhibited female and hermaphrodite characteristics (Photos 1a-c). Ovules were



Photo 1. Flowers and visitors of *S. praecox*. (a) Hermaphrodite inflorescences, (b) female inflorescences, (c) a hermaphroditic flower (middle left) and female flowers (middle right and upper) within an inflorescence of a hermaphroditic individual, (d) ovule (white arrow) of a hermaphrodite flower, (e) visitation by Halictidae sp. Yellow pollen are deposited on the stigma, (f) visitation by *Bombylus major*. Yellow pollen are attached to the proboscis.

Table 1. Sexual differences of *S. praecox*. Values are mean \pm SD.

Traits	Year	Hermaphrodite	Female
D10 (mm)		67.6 \pm 30.4	66.4 \pm 40.5
Height (cm)		324.2 \pm 94.0	290.0 \pm 122.8
Number of individuals surveyed	2005	11	10
	2006	8	11
Number of inflorescences per individual	2005	561.5 \pm 483.4	463.1 \pm 483.9
	2006	444.2 \pm 338.2	321.4 \pm 399.6
Number of flowers per inflorescence	2005*	19.1 \pm 7.2	17.5 \pm 8.4
	2006*	17.7 \pm 7.4	15.1 \pm 6.6
Fruit set (% , natural)	2005*	0.0 \pm 0.0	36.2 \pm 28.1
	2006*	0.0 \pm 0.0	35.6 \pm 35.1
Fruit set (% , hand-pollination)	2006*	0.0 \pm 0.0	35.0 \pm 33.9

* significant difference between sexes (one-way ANOVA, $P < 0.01$)

Table 2. The effects of sex and openness on the number of inflorescences per individual.

Effects	<i>F</i>	<i>df</i>	<i>SS</i>	<i>P</i>
2005				
Sex	0.2	1	33047	0.677
Openness	0.8	1	141146	0.394
Sex \times openness	3.9	1	721411	0.066
2006				
Sex	0.5	1	74336	0.483
Openness	0.0	1	1056	0.933
Sex \times openness	1.2	1	174682	0.286

Table 3. The effects of sex and openness on individual sizes.

Effects	<i>F</i>	<i>df</i>	<i>SS</i>	<i>P</i>
D10				
Sex	0.0	1	5	0.947
Openness	1.0	1	1079	0.327
Sex \times openness	6.6	1	7103	0.018
H				
Sex	0.8	1	6648	0.392
Openness	3.1	1	26963	0.093
Sex \times openness	9.6	1	83440	0.006

recognized in all hermaphroditic flowers (Photo 1d). The number of pollen grains in female flowers was 0.0 ± 0.0 (SD, $n = 10$), while an anther of hermaphrodite flowers contained 3474 ± 1106 ($n = 10$) pollen grains. Since the all flowers contained 8 anthers ($n = 20$), a hermaphrodite flower produces 27792 pollen grains on average. Sex change was not observed during the two years. Mean openness of 25 individuals was $37.5 \pm 5.7\%$. The number of flowers per inflorescences exhibited the sexual difference on both years (ANOVA, $F_{1, 640} = 6.8$, $P = 0.0096$ for 2005; $F_{1, 868} = 27.5$, $P < 0.0001$ for 2006; Table 1). But for the number of inflorescences per individual, there was no significant effect both on 2005 and 2006 (Table 2 and Fig. 1). Individual sizes (D10 and height) were affected only by the interactions between sex and openness (Table 3).

Mean fruit set of hermaphrodites was $0.0 \pm 0.0\%$ in 2005 (only one fruit produced from 356 inflorescences) and $0.0 \pm 0.0\%$ in 2006 (completely zero) while female fruit set was $36.2 \pm 28.1\%$ in 2005 and $35.6 \pm 35.1\%$ in 2006. Hand-pollination was not significantly increase the fruit set of

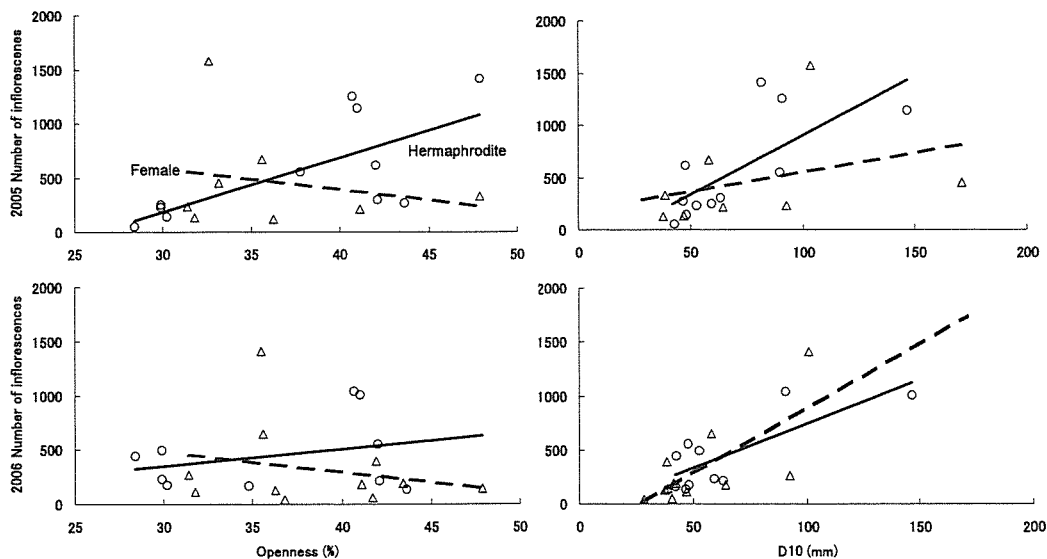


Fig. 1. Relationships of openness (left) and D10 (right) with the number of inflorescences per individual on 2005 (upper) and 2006 (lower). Circles and solid lines were hermaphrodites; triangles and dashed lines were females.

either hermaphrodites ($0.0 \pm 0.0\%$) or females ($35.0 \pm 33.9\%$, ANOVA, $F_{1, 398} = 0.02$, $P = 0.8746$).

Frequent flower visitors were flies and bees (Table 4, Photo 1e, f). Social bees such as bumblebee and honeybee were not observed.

Discussion

Despite no pollen limitation for fruit set, hermaphroditic flowers produced almost no fruits. So, hermaphroditic flowers of *S. praecox* are likely to be on the way of losing female functions rather than becoming completely male. As the germinability of seeds produced by the hermaphroditic flowers was not tested in this study, it is unclear that the hermaphroditic flowers can contribute to the next generation through female functions. However, ovules in hermaphroditic flowers suggest that *S. praecox* is gynodioecy. In addition, the rare existence of polymorphic flowers within an inflorescence (Photo 1c, this plant is out of surveyed population) suggests that the separation of sexes has not been complete yet in *S. praecox*. Evolutionary pathway to dioecy generally goes through gynodioecy or androdioecy from ancestral hermaphrodite (Charlesworth and Charlesworth, 1978). As a result, floral organ of non-functional sex is remaining in some plants of cryptic dioecy (Mayer and Charlesworth, 1991). Even if all seeds from hermaphroditic flowers have already lost germinability (if so, *S. praecox* would be cryptic dioecy), the characteristics of remaining ovules and fruit production imply that it is not long since their sexual function was separate.

In dioecious and subdioecious plants, there are many sexual differences derived from sexual allocation strategy (Geber *et al.*, 1999). Smaller inflorescence size in female *S. praecox* may be a trade-off of female reproductive cost of fruit production (Bell, 1985). On the other hand, sexual difference in individual size and the number of inflorescences per individual was not so clear probably

because the bush including *S. praecox* in forest edges along the road was cut down at some intervals. The relationships of size and the number of inflorescences with openness seemed to be differed between sexes; females did not change or decreased the size and the number of inflorescences with openness while hermaphrodite increased them. This could be growth handicap in females after cutting because of high cost of fruit production. However, further study on *S. praecox* population is needed to clarify the sexual difference in individual size and the number of inflorescences per individual.

Flower visitors of *S. praecox* were predominantly hoverflies and small solitary bees. The bell shape of the flowers suggests that small sized bees that could enter the flower (Photo 1e) or long-proboscis insects such as *Bombylus major* (Diptera) (Photo 1f) and *Polygonia c-aureum* (Lepidoptera) would be effective pollinators. Diurnal visitation rate seems adequate and pollen limitation for fruit set could not be detected in the surveyed populations. Thus, these diverse generalist visitors probably contribute to the effective pollination of *S. praecox*. Pollination by opportunistic generalist insects is a syndrome of dioecious shrubs (Thomson & Brunet, 1990). Since these visitors found in early spring tend to assemble in open sunny sites, forest edges seem to be reasonable as a habitat of *S. praecox*. Another reasonable trait for this habitat is also known in the germination characteristics (Abe & Matsunaga, 2007).

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Table 4. Flower visitors of *S. praecox*.

Species	Order	N	Handling time per flower (sec.)	Percentage of visited flowers within an inflorescenes (%)
Chrysomelidae sp.	Coleoptera	1	115	6.3
<i>Bombylus major</i>	Diptera	8	13	19.4
<i>Eristalis cerealis</i>	Diptera	1	1	10.0
<i>Eupeodes ferquens</i>	Diptera	2	74	8.3
<i>Sphaerophoria macrogaster</i>	Diptera	4	14	13.4
<i>Syrphus ribesii</i>	Diptera	6	31	9.7
Muscidae sp. 1	Diptera	18	7	17.4
Muscidae sp. 2	Diptera	4	13	23.1
Tipulidae sp.	Diptera	2	70	10.1
Halictidae sp.	Hymenoptera	3	25	13.0
Megachilidae sp.	Hymenoptera	1	12	10.0
<i>Polygonia c-aureum</i>	Lepidoptera	1	132	5.9

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キブシ (キブシ科) の性表現と繁殖特性

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要旨

既存の文献から、キブシの性表現には曖昧な点があることが示唆されているが、野外でキブシの性表現を含む繁殖状況について研究された例はみられない。そこで、キブシの花の性表現、性差、訪花昆虫、結果率を筑波山の林縁個体群で2年間調査した。花の形態や性器官(花粉と胚珠)の有無、結実状況よりキブシは雌性両全性異株であることが示唆された。性差は花序当りの花数が雌で有意に少なく、結果率が雌で有意に高かったが、それ以外には有意差がなかった。両性花には胚珠があるものの、結実は非常に稀(ほぼ0.0%)であり、強制受粉を施しても結実しなかった。このため、キブシの両性花はほとんど雄として機能しており、本種は機能的にはほぼ雌雄異株であると考えられた。また、一つの花序内に両性花と雌花が混在する花序が調査個体群外で1個体発見されたことから、キブシの性表現は安定していないものと思われる。一方、雌花は両年とも35%前後の結果率であり、強制受粉でも結果率が増えなかったことから花粉制限は起こっていないと考えられた。訪花昆虫はハエ類や単独性ハナバチが中心であり、春先の林縁環境でこれらの送粉昆虫が有効に機能していた。

キーワード：キブシ、結果率、性差、性表現、ポリネーター

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