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THE BREEDING SYSTEM AND REPRODUCTIVE ECOLOGY OF THE ENDANGERED PLANT *FAGOPYRUM DIBOTRYS* (D. DON) HARA

MING-LIN CHEN*, YA-LI YOU, HUI-HUI WEN AND YING LI

Provincial Key Laboratory of Biotic Environment and Ecological Safety in Anhui,
Anhui Normal University, Wuhu 241000, Anhui Province, P. R. China

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Abstract

Distyly has been confirmed in *Fagopyrum dibotrys* (D. Don) Hara. The species are dimorphic in style length, anther height, pollen size and number but not in flower diameter, pollen surface ornamentation and stigma papilla cells. In *F. dibotrys* populations, style-morph ratios vary from isoplethy (1L : 1S) to strongly L-biased, or they more often contain only the L-morph. Moreover, it was found that larger isoplethic populations of *F. dibotrys* could produce more seeds than smaller single-morph populations. *F. dibotrys* had a smaller population size, morph-biased populations, and lower seed setting, which could be the reasons for the decrease in its population.

Introduction

Fagopyrum dibotrys (D. Don) Hara, (Polygonaceae), is an important wild plant resource and has long been used as a regular medicinal herb. Contemporary researches have shown that *F. dibotrys* has specific anti-cancer effects (Liu *et al.* 1981). Recently, *F. dibotrys* was listed as an endangered species in China (first batch) by the State Council of China in 1999.

Distyly is a type of heterostyly that is characterized by the presence of two styles, long-styled and short-styled. For a species to be described as distylous, the principal requirement is that stigma and anther heights should differ reciprocally between morphs, i.e., they must show reciprocal herkogamy (Lloyd and Webb 1992). Quantitative morphological data are necessary to compare the positions of stigmas and anthers and recognize morphs in a population.

The distylous breeding system of *F. dibotrys* has never been studied in detail. The aims of the study were to: (1) determine whether the species is typically distylous, (2) identify and understand polymorphism within the species, (3) determine the influence of the breeding systems on reproductive success and adaptation and (4) identify factors that have led to the endangerment of *F. dibotrys*.

Materials and Methods

To confirm distyly in *F. dibotrys*, corolla diameter, stigma and anther height, stigma-anther separation and relative reciprocity of the species were determined. From each of the four studied population (Siheshan = SHS, Tongcheng = TCH, Hongcun = HC, and Datongcun = DTC, Table 1), 30 flowers of each morph long styled (LS) and short styled (SS) were collected and kept in 70% ethanol until measurement. Corolla diameter was measured when the flower was at the full-open stage. Because the five stamens were at about the same height, anther height (AH) was considered as the height of each of the five stamens, up to the midpoint of each anther; the mean height of anthers was then calculated. Stigma height (SH) was measured from just above the ovary to the tip of the stigma. Stigma-anther separation refers to the spatial separation between the anther and

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* Author for correspondence: <chenminglin0553@aliyun.com>.

stigma. Floral morphological parameters of the two species were measured with a caliper to the nearest 1 mm (Fig. 1). Reciprocal herkogamy was determined based on the reciprocity index, which is calculated as (anther height – reciprocal stigma height)/(anther height + reciprocal stigma height) (Hernández and Francisco 2007, Sanchez *et al.* 2008).

To determine the number of pollens produced by *F. dibotrys*, anthers from 20 flowers per morph from the SHS population were placed on individual slides. The number of pollen grains per flower was counted using a light microscope (Chen 2012). The long diameter was selected as the index of pollen size; the long diameter of 100 moderately sized pollen grains from each flower was measured, and the mean was calculated.

Sampled stigma and pollen of LS and SS morphs of *F. dibotrys* were taken from the SHS population (Table 1). The pollen grains were examined using SEM (Hitachi S4800 microscope, Japan) after Chen (2012).

Table 1. Population of *Fagopyrum dibotrys*.

Codes	Sites	Longitude and latitude	Habitat	Experiments	Note
ZY	Anqing Zongyang	117°24′03.59″, 30°54′16.91″	Grassy slopes	MF	●
TCH	Tongcheng	117°00′42.35″, 31°06′32.59″	Uplands	MF, MA	▲
SZS	Tongling Shizishan	117°51′07.08″, 30°57′04.32″	Slope wasteland	MF, SSR	▲
SHS	Wuhu Siheshan	118°21′6.09″, 31°25′55.93″	Hills	MF, MA, PS, PN, SEM, SSR, SE	▲
HT	Wuhu Hantang	118°21′08.28″, 31°26′04.68″	Riverside	MF	●★
XGL	Wuhu Xiaogeli	118°10′15.23″, 30°43′36.06″	Wetlands	MF	●
DT	Maanshan Dangtu	118°29′47.93″; 31°34′18.35″	Slope wastelands	MF	●
GD	Xuancheng Guangde	119°23′54.24″; 30°53′50.27″	Wastelands	MF	●
XK	Chizhou Xiaokeng	117°30′57.92″; 30°20′57.92″	Mountain forest	MF	●
SHT	Chizhou Shitai	117°31′18.72″, 30°11′22.61″	Uplands	MF	●
YX	Huangshan Yixian	117°55′57.31″, 29°55′0.34″	Grassy slopes	MF, SSR	●
HC	Huangshan Hongcun	118°02′50.1″, 29°59′29.92″	Grassy slopes	MA, MF, SSR	▲
DTC	Huangshan datongcun	117°59′9.93″, 30°01′29.57″	Riverside	MA, MF	▲
HCK	Huangshan Hucuankou*	117°59′9.93″, 30°01′39.88″	Riverside	MF	●
WC	Huangshan wancun	117°59′9.35″, 30°00′42.86″	Riverside	MF	●
TC	Huangshan tachuan	117°59′49.67″, 30°00′20.11″	Uplands	MF	●
LC	Huangshan Luocun*	117°58′45.43″, 29°59′11.66″	Fields	MF	
XAG	Xian botanical garden	118°57′25.74″, 34°12′27.75″	Garden	MF	●
HZG	Hangzhou botanical garde	120°7′15.05″, 30°15′21.99″	Garden	MF	*●
ZSH	Nanjing zhongshan	118°49′55.87″, 32°03′2.09″	Hills	MF	*●

MA: Morphometric analysis; PS: Pollen size; PN: Pollen number; MF: Morph frequency; SSR: Seed setting rate; SE: Seeding experiments. * Cultivated populations; ▲ Larger populations (≥100 M^2); • Smaller populations (<100 M^2).

To estimate the relative frequencies of the two style morphs in population of *F. dibotrys*, five 2 × 2 m sampling areas for each morph were selected for the larger populations (≥100 m^2), and all plants were recorded in much smaller population. Morph frequencies in each population were tested against the expected equilibrium (isoplethy: both morphs in equal frequencies) typical for distylous species, using a goodness of fit G test (Haddadchi 2013).

The seed setting rate experiments of *F. dibotrys* were conducted in 2012 in the SHS, HC, SZS and YX field populations (Table 1). Five 2 × 2 m sample plots for each morph were selected for the four populations; in each sample, four inflorescences were selected randomly and observed until they died.

Results and Discussion

The anthers and stigmas of the species were reciprocally positioned in the flowers of the two morphs. Typically, there are eight stamens at the base of tepals in two whorls: five stamens are present in the outer whorl and three, in the inner whorl. In addition, the two morphs have eight nectary glands arranged on the flower receptacle alternately with stamens. The stigma-anther polymorphism in the four study populations demonstrates that *F. dibotrys* possesses a conventional distylous floral morphology (Fig. 1A, B). The suite of floral traits varied across populations (Table 2).

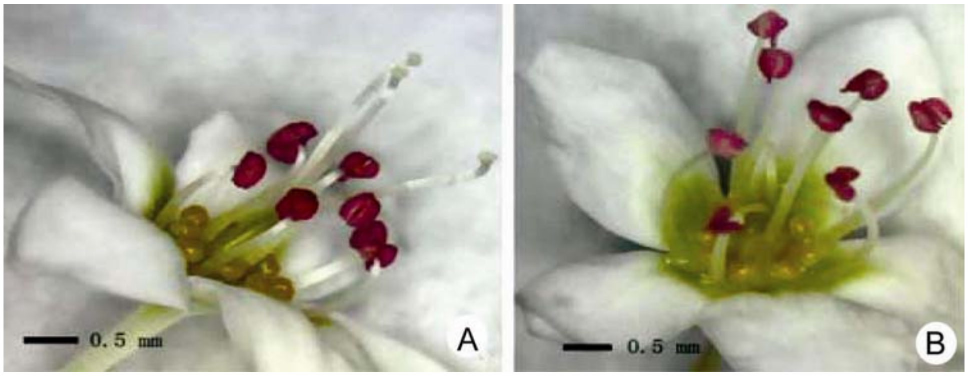

Fig. 1. Flowers of the L- and S- morphs of *Fagopyrum dibotrys* (A: LS; B: SS).

The stigma-anther separation of SS morphs was greater than that of LS morphs in all four populations of *F. dibotrys* (Table 2). Some differences between floral morphs in ancillary traits associated with floral polymorphism were also observed. For example, the corolla diameter of the L- and S-morphs showed no obvious differences within each study population (Table 1), but showed significant differences among some populations: the diameter of both morphs in the DTC population was greater than that in the SHS (LS: $t_{58} = 4.00$, $p < 0.05$; SS: $t_{58} = 3.49$, $p < 0.05$), TCH (LS: $t_{58} = 2.58$, $p < 0.05$; SS: $t_{58} = 2.33$, $p < 0.05$) and HC populations (LS: $t_{58} = 3.42$, $p < 0.05$; SS: $t_{58} = 2.73$, $p < 0.05$). Anthers of the LS and SS flowers were longer in the DTC population and smaller in the HC population, but the differences were not statistically significant between populations (Table 2). Reciprocal herkogamy (represented by the reciprocity index) had values near zero (Fig. 2), and significant separations could be easily observed between style morphs and populations.

The pollen grains of the two morphs of *F. dibotrys* differed in size and number (Table 3; Fig. 3), but were not different in shape. Although the pollen short diameter was not very different between both morphs of the species, the long diameter of SS morphs was longer than that of LS morphs. The flowers of LS morphs produced significantly smaller pollen grains ($t_{198} = 16.64$, $p < 0.01$) in greater numbers ($t_{48} = 17.31$, $p < 0.01$) than flowers of the SS morphs.

Micromorphological characters of pollen and stigmas: The two morphs of the species had tricolpate pollen with reticulate ornamentation and a prolate shape (Fig. 4A, B). The styles of the two species were elongated, ending in a big, capitate stigma, the surface of which was covered with tense cobblestone-like papilla, and no major differences were found between the two morphs of both species (Fig. 4C, D, E, F). The stigma height of the LS morphs was higher than that of the SS morphs in all study populations.

Table 2. Mean value (±SE) of floral traits for LS and SS individuals across four population of *Fagopyrum dibotrys* (n = 30 per morph per population)[1].

Population	Morph	Corolla diameter (mm)	Anther height (mm)	Stigma height (mm)	Stigma-anther separation (mm)
SHS	LS	6.74 ± 0.340^{a}	2.05 ± 0.168^{a}	3.54 ± 0.206^{a}	-1.49 ± 0.184
	SS	6.57 ± 0.467^{A}	3.57 ± 0.208^{A}	1.71 ± 0.193^{A}	1.86 ± 0.154
	t_{58}	1.61	31.14^{*}	35.50^{*}	8.5^{*}
TCH	LS	6.90 ± 0.357^{a}	1.99 ± 0.156^{ab}	3.52 ± 0.197^{ab}	-1.53 ± 0.202
	SS	6.73 ± 0.417^{A}	3.52 ± 0.225^{B}	1.70 ± 0.143^{A}	1.82 ± 0.206
	t_{58}	1.66	30.58^{*}	41.04^{*}	5.51^{*}
HC	LS	6.79 ± 0.372^{a}	1.92 ± 0.158^{bc}	3.41 ± 0.235^{b}	-1.49 ± 0.166
	SS	6.69 ± 0.400^{A}	3.58 ± 0.197^{AC}	1.76 ± 0.159^{A}	1.82 ± 0.163
	t_{58}	1.07	36.21^{*}	31.82^{*}	7.76^{*}
DTC	LS	7.20 ± 0.535^{b}	2.15 ± 0.221^{d}	3.72 ± 0.248^{c}	-1.56 ± 0.187
	SS	7.02 ± 0.529^{B}	3.81 ± 0.183^{D}	1.98 ± 0.182^{B}	1.83 ± 0.166
	t_{58}	1.34	31.66^{*}	30.87^{*}	5.77^{*}

[1] Values within a column followed by the same letter (lowercase letters within a column stand for LS; capital letters within a column stand for SS) are not significantly different at the $p < 0.05$ level. Morph comparisons within populations were done with the t test (df = 58 in all cases). $^{*}p < 0.05$.

Table 3. Pollen grain size and number for *F. dibotrys*[2].

Parameters	LS of *F. dibotrys*	SS of *F. dibotrys*
Pollen number	1251 ± 103^{a}	759 ± 94^{A}
Long diameter (µm)	50.54 ± 4.885^{a}	62.25 ± 5.066^{A}

[2] Values within a line followed by the same letter (lowercase letters within a column stand for LS; capital letters within a column stand for SS) are not significantly different at the $p < 0.05$ level.

The findings for morph frequency in all the study populations are shown in Table 4. The style-morph ratios varied from isoplethy (1L : 1S) to strongly L-biased or, more often, only L-morph. Populations fixed for the S-morph, or with S-biased morph ratios, were occasionally observed. Moreover, style-morph ratios were associated with population size: large continuous populations always exhibited 1 : 1 morph ratios, whereas smaller, fragmented populations were often L-biased.

There was no significant difference between the seed setting rate of LS and SS morphs (Table 5, $p > 0.05$) within populations, but there was a significant difference between LS and SS morphs from different populations (Table 5, $p < 0.05$). Secondly, we found a higher seed setting rate in larger populations; for instance, it was higher in the larger SHS population than in the smaller YX population (LS: $t_{38} = 2.30$, $p < 0.05$; SS: $t_{38} = 3.95$, $p < 0.05$). In addition, SZS populations containing only L-morphs produced less fruits than isoplethic populations (Table 5, $p < 0.05$).

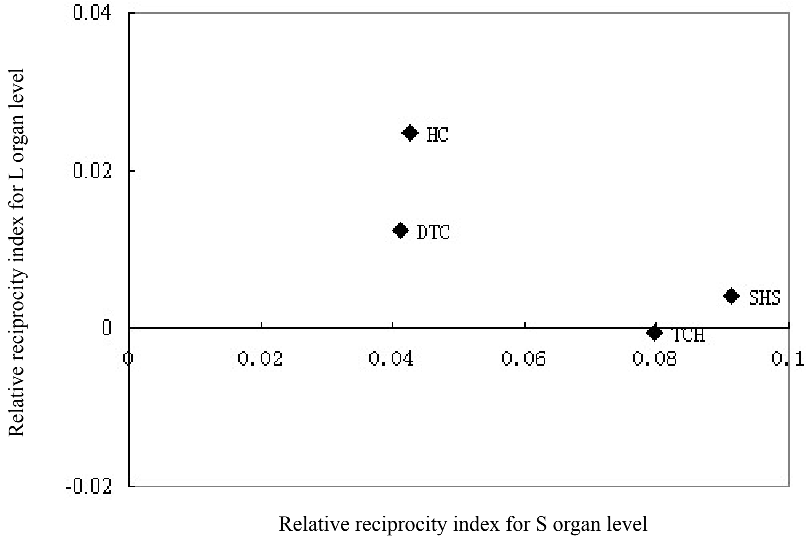

Fig. 2. Relative reciprocity ratio of the long and short organ levers in four populations of *Fagopyrum dibotrys*. Abbreviations for species are adjacent to each point on the graph. The population is denoted with a solid rhombus.

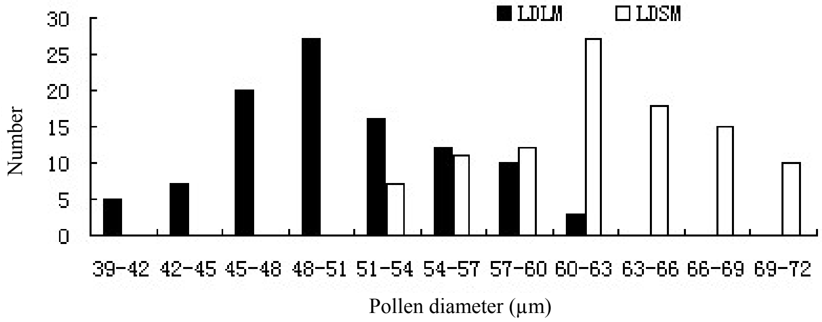

Fig. 3. Distribution of pollen size for plants with the L (N=100) and S-morph (N=100) flowers of *F. dibotrys* from the SHS population (note: LDLM = long diameter of the long morph; LDSM = long diameter of the short morph).

Floral variation and relative reciprocity were studied in detail in different populations of *F. dibotrys*. SS morphs of the species investigated in this study were found to have significantly larger and less pollen grains than LS morphs, but no significant difference was found in flower diameter, pollen and stigma surface ornamentation of the two morphs. Some differences were also found among sections of populations, which are probably associated with habitat differences. Thus, it showed that the species is distylous.

Traditionally, reciprocal herkogamy between different morphs has been considered as a necessary condition to characterize a plant as heterostylous, but many studies also consider the incompatibility system to be quite important (Lloyd and Webb 1992, Barrett 2002). Perfect reciprocal herkogamy in a population is achieved when the anthers of one morph are positioned at the same level as the stigmas of the other. Ideally, this should be true for each anther and stigma of all flowers in the population, but actually, different degrees of reciprocal herkogamy between morphs can be found in natural populations of heterostylous species (Sanchez *et al.* 2008). In this study, the positions of stigmas and reciprocal anthers of the morphs largely coincided, which further indicates that the species is distylous.

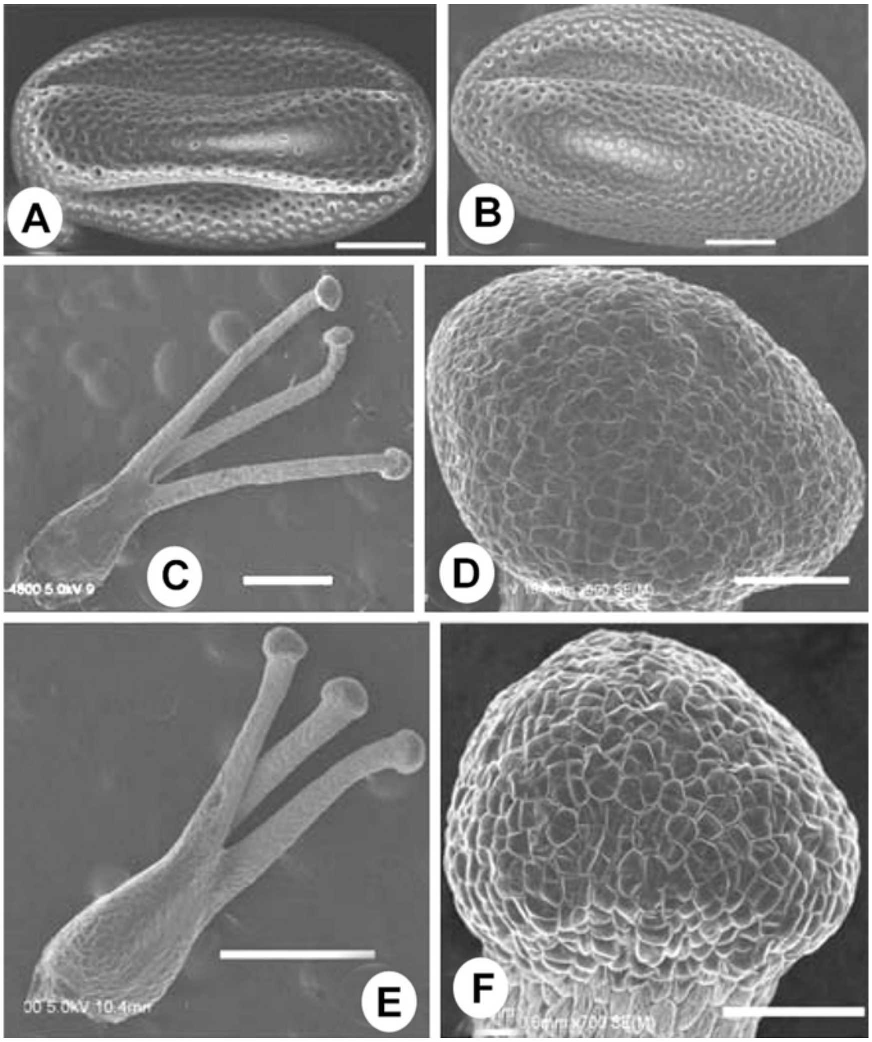

Fig. 4. Micromorphological characteristics of *Fagopyrum dibotrys* under SEM (A: Pollen of LS; B: Pollen of SS; C: Long style; D: Stigma surface of LS; E: Short style; F: Stigma surface of SS. Bars: A, B: 10 µm; C, E: 500 µm; D, F: 50 µm.

Nectar volume is typically different for different distylous species. For example, nectar volume increased in the anthesis period and decreased in wilting flowers of *Gelsemium sempervirens*, and it was positively correlated with corolla width but not length. Even after controlling for differences in flower size, nectar volume did not differ between morphs (Leege and Wolfe 2002). However, Cawoy *et al.* (2008) reported that nectar secretion in *Fagopyrum* spp. was strongly influenced by floral morph type, plant age, and inflorescence position and light; a higher volume of nectar was found in SS morphs. In contrast, in our study, no difference was found in nectary morphology between morphs (Fig. 2); this probably implies a nectar reward to promote differential pollination and improve pollination efficiency.

Table 4. Style-morph ratios for *Fagopyrum dibotrys* in study populations.

Population codes	LS morph	SS morph	Style-morph ratios	df	G test
ZY	562	0	Fixed for the LS morph	1	-
TCH	7000	6873	≈1 : 1	1	1.16*
SZS	821	0	Fixed for the LS morph	1	-
SHS	1732	546	L-biased	1	648.92
HT	657	0	Fixed for the LS morph	1	-
XGL	1089	0	Fixed for the LS morph	1	-
DT	432	0	Fixed for the LS morph	1	-
GD	1762	0	Fixed for the LS morph	1	-
XK	765	0	Fixed for the LS morph	1	-
ST	789	0	Fixed for the LS morph	1	-
YX	2235	1245	L-biased	1	285.57
HC	2219	2095	≈1:1	1	3.56*
DTC	875	798	≈1:1	1	3.54*
HCK	9850	5435	L-biased	1	1293.6
WC	0	1245	Fixed for the SS morph	1	-
TC	324	1085	S-biased	1	433.78
LC	578	560	≈1:1	1	0.28*
XAG	246	0	Fixed for the LS morph	1	-
HZG	186	0	Fixed for the LS morph	1	-
ZSH	78	0	Fixed for the LS morph	1	-

* $p < 0.05$ according to the results of the *G* test, for inequality of frequencies.

Variation between morphs in stigma-anther separation is seen in numerous distylous species, but the functional significance of stigma-anther separation in animal-pollinated hermaphrodite plants is still controversial. In some species, stigmas and anthers are placed much closer to each other in LS morphs than in SS morphs (Webb and Lloyd 1986), while in natural populations of other species, stigma-anther separation is greater in LS morphs, e.g., *Jasminum fruticans* and *Gaertnera vaginata*. Under natural conditions, since high self-pollen deposition can result in physical or physiological blockage of compatible pollen, which is not desirable (Shore and Barrett 1984, Broyles and Wyatt 1993). Parra-Tabla *et al.* (2005) showed that anther-stigma separation was inversely proportional to the number of self-pollen grains deposited in *Ipomoea wolcottiana* flowers. As the anthers are located above the stigmas in SS morphs, self-pollination occurred more easily in SS morphs than in LS morphs. Therefore, the greater stigma-anther separation in SS than

LS morphs may reduce the chance of self pollen grains deposited on its stigmas. This is in agreement with our results: SS morphs of *F. dibotrys* had greater stigma-anther separation than LS morphs and self-pollination occurred more easily in SS morphs. Moreover, the location of anthers above the stigmas in SS morphs also contributes to the ease of self-pollination. We reasoned that greater stigma–anther separation may result in greater interference between pollen removal and deposition, and thus result in avoidance of inbreeding.

Table 5. Seed setting rate for *Fagopyrum dibotrys* populations[3].

Population	LS (%)	SS (%)	n
SHS	8.41±1.68 [a]	8.32±1.71 [a]	20
HC	8.23±1.47 [a]	8.15±1.40 [a]	20
SZS	5.08±1.08 [b]	-*	20
YX	6.55±1.10 [c]	6.49±0.79 [c]	20

[3] Values within a column or a line followed by the same letter are not significantly different at $p < 0.05$. *No data were available because only LS morphs were present in the SZS population.

Frequencies of flower morphs have been studied in great detail (Endels *et al.* 2002, Haddadchi 2013), especially with respect to its influence on pollination (Ågren 1996) and inbreeding (Goodwillie 2000). In most distylous species populations, large populations always exhibit 1 : 1 morph ratios or a slight L-bias (Chen 2012). Female reproductive success has been associated with the breeding system of the species (Kunin 1997). In this study, single-morph populations of *F. dibotrys* produced less fruits than isoplethic populations. This means that in LS morphs, self- and illegitimate cross-pollinations produce less fruit and seed than legitimate cross pollinations, suggesting that self- and intra-morph compatibility is weak in *F. dibotrys* populations. Female reproductive success has also been shown to be positively correlated with population size and species abundance (Kunin 1993). In agreement with this, it was also found that larger populations of *F. dibotrys* can produce more fruit, which indicates that population size can affect the seed setting rate. In addition, there was a significant difference in the seed setting rate between some of the populations (e.g., SZS and HC populations). Based on all these results, the seed setting rate is affected by many factors such as population size, structure, and flower morphs. However, it has also been reported that there is no correlation between female reproductive success and population density (Schmitt 1983), so this points need detailed investigation in the future.

Many studies have reported sporophytic self-incompatibility in certain species (Cawoy *et al.* 2009) caused by isoplethy in the population structure, resulting in legitimate pollination and higher seed setting rates. Although strict self- and intra-morph incompatibility is seen in many distylous species (Liu *et al.* 2012), *F. dibotrys* showed poor self- and intra-morph incompatibility, which may be one of the adaptive characteristics of clonal heterostylous plants. At the same time, it proved that this species is a promising material for studying the evolution of distyly, like the clonal plant *Nymphoides montana*. The isoplethic equilibrium in such species may be maintained by factors such as founder events, the extent of clonal growth, and sexual recruitment, but they need to be studied in more details (Eckert and Barrett 1995).

In the conclusion, *F. dibotrys* is described as distylous, with polymorphism involving variation among populations. These results indicated that smaller population size, morph bias in the population structure, lower fruit setting rate and seed germination rate may be the main reasons endangering *F. dibotrys* populations. Therefore, efforts should be made towards adjusting population structure and increasing population size in order to conserve this species.

Acknowledgments

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