

Distyly in *Forsythia suspensa* (Oleaceae)

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Abstract: Distyly provides precise pollen transfer without the costs that are associated with sexual interference and self-pollination. In thirty populations of distylous *Forsythia suspensa*, style-morph ratios varied from isoplethy (1.00 long-morph:1.00 short-morph, n=17 populations) to L-biased (1.14 long-morph:1.00 short-morph, n=13 populations). Under open pollination condition, there was no significant difference in fruit set between long-(9.11% ± 0.01%) and short-(8.93% ± 0.06%) styled morphs ($F_{(1,39)} = 2.47, P = 0.25$). The lower fertilizations of controlled intramorph pollinations (2.71% ± 0.02% in long-long and 2.58% ± 0.01% in short-short combinations) indicated that *F. suspensa* is intramorph-incompatible. There was no significant difference in fruit set of cross-pollination between long-short-(36.41% ± 0.07%) and short-long-(36.27% ± 0.03%) styled morphs combinations ($F_{(1,39)} = 1.38, P = 0.14$). The results of artificial outcrossing indicated that pollinator limitation may occur in the artificial populations of *F. suspensa* in northeast of China, this may be because that the low temperature and much windy in the early spring influence pollinators' kinds and activities.

Key words: distyly; *Forsythia suspensa*; floral trait

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Heterostyly is usually composed of a syndrome of traits including differences in style length and anther height, a suite of ancillary pollen and stigma polymorphisms (Barrett *et al.*, 2000). This sexual polymorphism has evolved independently in at least 28 animal-pollinated angiosperm families (Webb & Lloyd, 1986; Guitián *et al.*, 1998; Han & Kim, 1999; Barrett *et al.*, 2000; Arroyo & Barrett, 2000; Pérez *et al.*, 2004; Massinga *et al.*, 2005). In heterostylous species, populations are composed of two (distyly) or three (tristyly) floral morphs (Barrett *et al.*, 2002). Most heterostylous species have strict intramorph-incompatibility system (Massinga *et al.*, 2005), or some have strong but not strict intramorph-incompatibility system (Jacquemyn *et al.*, 2002). Xue *et al.* (2000) studied that the time and space relations on the glycoprotein forming

from self-incompatibility style of *Shatinyu* (*Citrus grandis* var. *shatinyu*). Distylous flowers differ reciprocally in stigma and anther position, the long- and short-styled morphs (hereafter L- and S-morphs) are similar in morphology to the approach and reverse herkogamous conditions (Barrett *et al.*, 2000). Distyly provides precise pollen transfer without the costs that are associated with sexual interference and self-pollination (Charlesworth D & Charlesworth B, 1979; Kohn & Barrett, 1992; Paillet *et al.*, 2002; Barrett *et al.*, 2002). The persistence of distyly depends on tight linkage of the genes affecting anther height and stigma height, and a single diallelic Mendelian locus with dominance controls distyly (Ganders, 1979).

Distyly has been reported in some species of Oleaceae, such as *Forsythia* (Darwin, 1877; Samp-

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son, 1971; Han & Kim, 1999), *Abeliophyllum distichum* (Kang *et al.*, 2000), *Jasminum* (Verdoorn, 1963; Ornduff, 1974), and *Schrebera* (Verdoorn, 1963). Darwin (1877) reported that thrum (short-styled morph) anthers were smaller than pin (long-styled morph) anthers in *Forsythia suspensa*. The allele determining thrum form is dominant in *Forsythia* (Sampson, 1971). Flower color of short-styled flower was more yellow than long-styled flower in *Forsythia koreana* Nakai, and the flowering of short-styled flower was earlier than long-styled flower (Han & Kim, 1999). However, there is no report on the style-morph (L- and S-morphs) ratios in the *F. suspensa* populations, floral trait difference between two morphs, and fertilization of intramorph and intermorph pollination. The purposes of the present contribution are to supply some of the missing information on style-morph ratios and floral traits of *F. suspensa* in the population of *F. suspensa* in Northeast China, investigating fruit set under open pollination condition, and examining the consequences of intramorph-pollination between intramorph and cross-pollination between intermorph. This data may provide scientific basis for further understanding the distyly of *F. suspensa*.

1 Materials and Methods

Forsythia suspensa, a perennially deciduous shrub, is native to the north and central of China. It is cultivated broadly in China as an ornamental. The capsule is tip and egg-shaped, the number of ventricles is two, with 4–10 ovules in every ventricle. *Forsythia suspensa* flowers during spring (from March to May), and each flower lasts 5–15 days. Two stamens with equal height (occasionally appears three stamens) attaches to the base of the flower tube fused by the base of quatrefoil corolla. Style with the bilobed stigma is united.

We conducted an extensive survey to measure the relative frequencies of the two style morphs in thirty populations of *F. suspensa* (over 400 individuals per population) growing in Dalian City of Liaoning Prov-

ince of China in 2005, and 20 populations (over 500 individuals per population) in Xinyang City of Henan Province of China in 2006. In the Paotai population, the following treatments were carried out; (1) 50 flowers of each of morphs were selected from 50 different individuals to measure seven floral traits, including flower length and width, petal lobe width and length, corolla tube length, stigma and anther heights; (2) Fruit sets of each of two styled morphs were investigated ($n=50$ individuals per morph, and 100 flowers per individual were selected, tagged and harvested after 60 days); (3) Artificial pollination treatments were designed; one is intramorph-pollination, including L-L (pollen from the other flowers of the same individual, $n=20$ individuals) and S-S (pollen from the other flowers of the same individual, $n=20$ individuals) combinations; another is cross-pollination, including L-S (pollen from the S-morph flowers) ($n=20$ individuals) and S-L (pollen from the L-morph flowers) ($n=20$ individuals) combinations. Emasculation was done before the flowers fully open; then the treated flowers were bagged using nylon bags. Hand-pollination was conducted 6–7 days after the flowers fully open. In each treatment, 100 flowers per individual were selected, tagged, treated, and harvested after 60 days.

2 Results

The flowers of *F. suspensa* have four yellow petals, each anther has two anther-petals, and each anther-petal has two clinandria. Dehiscent mode of clinandrium is longitudinal dehiscence. Dehiscent orientation of anther is toward to petals, which may avoid pollen dispersing its own stigma to prevent self-pollination. L-morph flowers are protogyny, and S-morph flowers are protandry.

All fifty populations of *F. suspensa* sampled are dimorphic for style length. In Dalian City, style-morph ratios varied from isoplethy (1.00 L; 1.00 S) ($n=17$ populations) to L-biased (1.14 L; 1.00 S) ($n=13$ populations); and in Xinyang City, style-morph ratio was 1.00 L; 1.00 S. In the L-morph (Fig. 1; A), stigma height was 6.12 ± 0.05 mm ($n=50$), with the anther

height of 2.35 ± 0.04 mm ($n=50$) (Fig. 2); whereas anther height in the S-morph (Fig. 1; B) was 6.02 ± 0.06 mm ($n=50$), with the stigma height of 2.23 ± 0.04 mm ($n=50$) (Fig. 2). The S-morph flower sig-

nificantly exceeded the L-morph flower in size of most corolla dimensions, including flower length ($S/L=1.34$) and width ($S/L=1.25$), petal lobe width ($S/L=1.17$) and length ($S/L=1.11$), and corolla tube

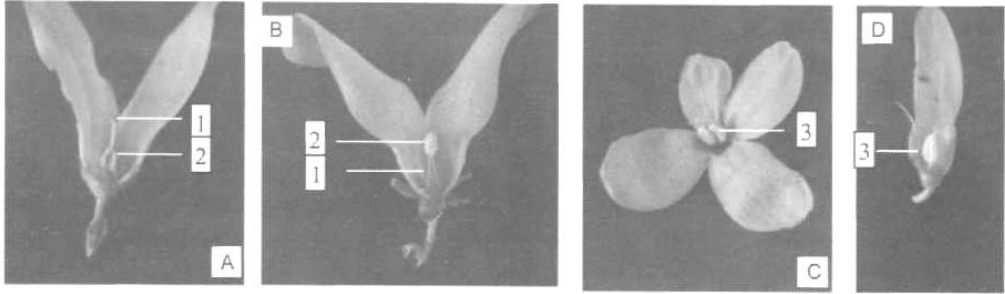


Fig. 1 Distyly in *Forsythia suspensa*

A, long-styled morph; B, short-styled morph; C, short-styled morph with inflated anthers; D, long-styled morph with inflated anthers; 1, stigma; 2, anther; 3, inflated anthers

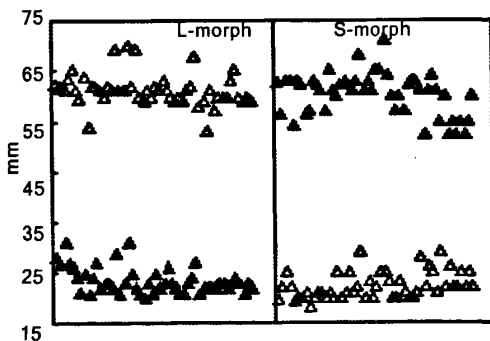


Fig. 2 The range of variation in stigma (\triangle) and anther (\blacktriangle) heights in the long- and short-styled morphs among individuals from the Paotai population growing in the northeast of China

length ($S/L=1.08$). Under open pollination condition, fruit set of L-morph was $9.11\% \pm 0.01\%$ ($n=50$), ranging from 2.33% to 11.24%, while showed $8.93\% \pm 0.06\%$ ($n=50$), ranging from 1.90% to 11.69% in the S-morph. There is no significant difference in fruit set between two floral morphs ($F_{(1,39)}=2.47, P=0.25$). Controlled pollination treatments indicated that fruit sets in the L-L and S-S combinations are $2.71\% \pm 0.02\%$ ($n=20$) and $2.58\% \pm 0.01\%$ ($n=20$), respectively, while showed $36.41\% \pm 0.07\%$ ($n=20$) and $36.27\% \pm 0.03\%$ ($n=20$) in the L-S and S-L combinations, respectively, and there was no significant

difference in fruit sets between the L-S and S-L combinations ($F_{(1,39)}=1.38, P=0.14$).

3 Discussion

Forsythia suspensa exhibits the typical floral morphological syndrome of distylous species, the L-morph flower has a relatively high stigma and low anthers, while the S-morph flower has high anthers and a low stigma. The floral trait differences between the S- and L-morphs in the *F. suspensa* is in agreement with what has been observed in the other distylous species (Ganders, 1979; Riveros *et al.*, 1995; Li & Johnston, 2001).

The lower fruit set under open pollination in the natural populations may be from the lack of pollen availability and viability, pollinator activity, and ecological and physiological factors related to pollination mechanism (Kang *et al.*, 2000). Pollinators visit flowers to collect pollen or nectar, at the same time playing an important role as pollen-vectors, and they influence fruit set rates. The fruit set of artificial cross-pollination (36.34% of the average of the L-S and S-L combinations) in *F. suspensa* is greater than that of open pollination (9.02%), which indicates that pollinator limitation

potentially occurs in the Paotai population. In the Paotai population of *F. suspensa*, pollination appears to be affected primarily by climate factors during the blooming time, such as temperature and wind. If climate conditions are windy and cloudy with low temperature, large size pollinators' activities reduce and their visitation rate are also low. During over 5 days observations, only four species of insects are founded near or on *F. suspensa*, including two species of bee, one species of beetle, and one species of spider.

Heterostyly has evolved to prevent self-pollination and entrust pollination between individuals of different types, and there is an effective incompatibility system in the distylous species (Barrett *et al.*, 2000). Ornduff (1966) suggested that heterostylous species are intramorph-incompatible originally, but the dioecous evolution may be from the selection to promote outcrossing because of the breakdown of incompatibility. The occurrence of unusual incompatibility systems in distylous *Villarsia* (Ornduff, 1988) and tristylous *Narcissus* (Sage *et al.*, 1999) indicate that the morphological components of heterostyly are not always associated with intramorph mating barriers typical of species with diallelic incompatibility (Barrett *et al.*, 2000). Indeed, as more heterostylous species are studied experimentally it is evident that many are self-compatible (Barrett *et al.*, 2000). The lower intramorph fertilization of controlled intramorph pollinations in *F. suspensa* indicated that this species is intramorph-incompatible, and the result is similar with the result by Ryu *et al.* (1976) on heterostyly-incompatibility of *A. distichum* (1.3% fruit set).

Kohn & Barrett (1992) reported that in the heterostylous species, individuals of long-styled morph act as female and short-styled type as male. The fruit set of the S-morph flower in the distylous *Sarcotheca celebica* is lower than that of the L-morph flower (Lack & Kevan, 1987). In some flowers of *F. suspensa*, anthers of L- (Fig. 1; D) and S- (Fig. 1; C)-morphs both appear inflated and persistently un-dehiscent during the flowering, but the frequency of flowers with inflated anther in S-morph ($2.84\% \pm 0.01\%$, $n=1000$) is more than that of L-mor-

ph ($0.12\% \pm 0.01\%$, $n=1000$) in the Paotai population ($U=0.000$, $W=237$, $P<0.01$). This phenomenon may be relation with the natural conditions of the Paotai population, but it is necessary to further study the evolution and adaptive significance of inflated anther occurring in *F. suspensa*.

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连翘的二型花柱

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摘要: 报道了连翘中的二型花柱(长花柱和短花柱)。长花柱的柱头和雄蕊高度分别为 6.12 ± 0.05 mm 和 2.35 ± 0.04 mm, 短花柱则为 2.23 ± 0.04 mm 和 6.02 ± 0.06 mm。短花柱花的花冠大小明显超过长花柱。开放授粉条件下, 长短花柱花的座果率分别为 $9.11\% \pm 0.04\%$ 和 $8.93\% \pm 0.07\%$ 。人工异交的座果率在长-短 ($36.8\% \pm 0.04\%$) 与短-长 ($36.2\% \pm 0.07\%$) 组间无明显差异 ($F_{(1,39)} = 1.38, P = 0.14$)。人工异交实验表明, 传粉者限制可能发生在生长于中国东北部的人工连翘种群中, 这可能是因为该地区早春的低温和多风气候条件影响传粉者的种类和活动。

关键词: 二型花柱; 连翘; 花性状

(上接第 272 页 Continue from page 272)

需要进一步通过拟南芥 β 亚基和 γ 亚基缺失突变体细胞中提取蛋白质试验进行确证。

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