

Gender variation in a monoecious woody vine *Schisandra chinensis* (Schisandraceae) in northeast China

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Demographic variation of gender expression among four natural populations and one cultivated in a monoecious species, *Schisandra chinensis* (Schisandraceae), was studied over three consecutive years in a bid to clarify its sexual system and to better understand reproductive strategies in monoecious plants. We found that gender expression was more variable in the natural populations than in the cultivated one. In the natural populations, plant size was positively correlated with flower production (total, male and female) but not with the female ratio, whereas shade intensity was negatively correlated with the female ratio. In the cultivated population, plant age was positively correlated with flower production and the female ratio within an age range. Hence, gender expression and reproductive output in *Schisandra chinensis* was found to be age-dependent. The female ratio varied with age; young and old plants had lower female ratios. Our study confirmed the sexual system in the species to be monoecy as opposed to dioecy, and supported the hypothesis that monoecious plants can regulate gender expression by altering quantities of pistillate and staminate flowers at the individual plant level to maximize fitness.

Introduction

Among all plant sexual systems, monoecy — separation of the genders into distinct flowers in the same individual — has been less studied. Monoecy has evolved in about 7% of flowering plants (Yampolsky & Yampolsky 1922), and many species often have variable gender allocation patterns, e.g. pure female or pure male phenotype individuals making monoecy exclusive

within a population (reviewed in Sakai & Sakai 2003 and Masaka & Takada 2006). Monoecy is usually considered an acquired condition (Mitchell & Diggle 2005) with shifts back and forth between the male and female phenotypes (Lloyd 1980, Weiblen *et al.* 2000). This developmental and spatial segregation of male and female flowers may allow monoecious plants to adjust the male/female ratio more freely. On the other hand, species with bisexual flowers may be more con-

strained in gender allocation (Sutherland & Delph 1984, Condon & Gilbert 1988, Sarkissian *et al.* 2001, Masaka 2007). Therefore, monoecy may have evolved since it increases efficiency of out-cross pollination without any risk to reproductive assurance as a result of relinquishing one gender function (Ågren & Schemske 1995, Harder *et al.* 2000, Aluri & Ezradanam 2002).

Gender variation in monoecious species is often associated with environmental conditions including light intensity, moisture, soil nitrogen status and season of growth, etc. (Kooistra 1967, Williams & Thomas 1970, McArthur 1977, Freeman *et al.* 1980a, 1980b, 1981, Lovett Doust & Cavers 1982, McArthur *et al.* 1992, Irish & Nelson 1989, but *see* Méndez 1998, Bertin & Kerwin 1998, Bertin 2007). Moreover, hypotheses such as height advantage and size-dependent fecundity have been invoked widely in floral gender allocation studies (Traveset 1992, Klinkhamer *et al.* 1997, Sakai & Sakai 2003). It is assumed that larger plants with more resources allocate greater quantities of their resources to female functions. However, in wind-pollinated species, taller individuals may have an advantage if they allocate more resources to male organs as they will be able to fertilize flowers of shorter individuals (Lloyd 1980, Burd & Allen 1988, Murakami & Maki 1992, Bickel & Freeman 1993, Fox 1993, Dajoz & Sandmeier 1997, Klinkhamer *et al.* 1997, Masaka & Takada 2006). It thus follows that the size-related hypotheses do not explain the gender variation in wind-pollinated monoecious species.

Schisandra chinensis (Schisandraceae), a woody vine distributed in northeast China, was traditionally considered both monoecious and dioecious (*see* Li 1985). In natural populations, its gender expression can vary greatly among individuals. However, its reproductive system and the mechanisms that drive gender variation have remained unclear (but *see* Ueda 1988). Consequently, verifying the gender system in this species as well as the relationship between gender variation and certain influential factors may enrich our understanding of the evolution of monoecy.

Since the fruits have medicinal properties, the species is of great economic value. *Schisan-*

dra chinensis, therefore, in recent years has been cultivated as an economic crop. Based on previous studies, we found that gender-ratio variation could influence fruit production in the species in any individual or group. Particularly, the effect of age on gender ratio as well as fruit production cannot be ignored. Studies on gender expression with regard to age in woody monoecious species are very scarce owing to the fact that their development takes a long time. On the other hand, the already established cultivated populations provide good study conditions excluding the influence of genetics and different environmental factors on gender variation, while offering a chance to consider only the effect of age. Therefore, investigating the variation in gender expression with regard to age in cultivated plants is of significance not only for understanding how monoecy develops, but also when evaluating the reproductive status of the plantation.

In this study, we examined gender variation in four natural and one cultivated populations of *Schisandra chinensis*. We particularly address the following questions: (1) What is the variation in gender expression among populations, and between years in natural populations? (2) What are the effects of plant size and shade intensity on gender expression? (3) Are gender expression or reproductive output age-dependent? We further discuss reproductive strategies in the monoecious plant in different stages of its life history and in the period when the plantations were under study.

Material and methods

Study species

Schisandra chinensis is a fairly large, woody vine distributed in northeastern China. It often climbs small and medium-sized broad-leaved trees or shrubs. Its long-oval leaves alternate on the long shoots and cluster on the spur shoots. The ivory-white (or rarely pink) flowers (Fig. 1) are unisexual, and the staminate and pistillate flowers are similar in size. Each flower has six to nine solitary petals, and two to four flowers cluster in leaf axils. The pedicels of male flowers are shorter (1.5–2.0 cm) and mostly concentrated

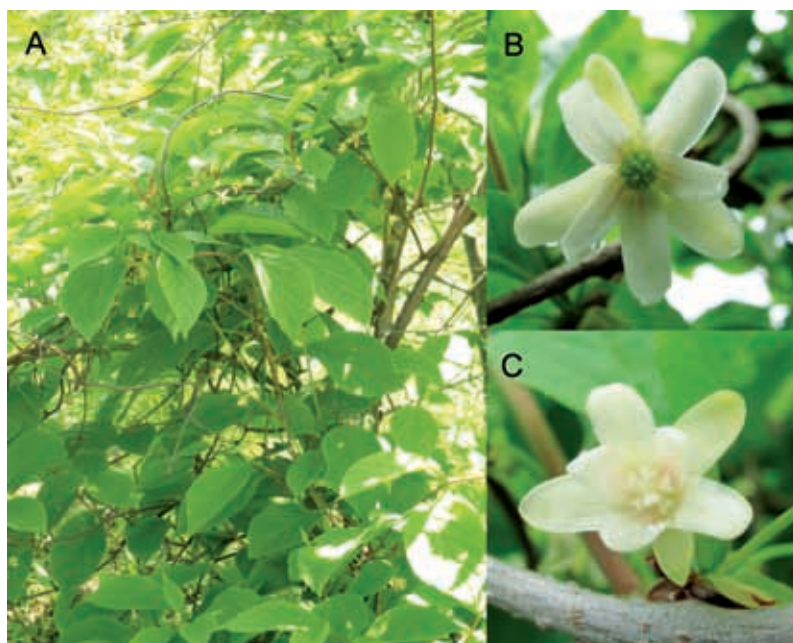


Fig. 1. *Schisandra chinensis*. — **A:** Habit. — **B:** Female flower. — **C:** Male flower.

on the lower parts of the plant and on the spur shoots; the pedicels of female flowers are longer (3.0–4.0 cm) and they mostly grow on the upper parts of the plants and on long shoots. The staminate and pistillate flowers may alternate. There are five stamens in each staminate flower. There are numerous and distinct carpels in a pistillate flower, and the stigma dilates into an undulate crest. None of the staminate or pistillate flowers have nectaries. The flowering period in the study populations (in eastern region of Liaoning Province, China) was from late May to early June every year, lasting up to two weeks, and anthesis took four to five days in individual flowers. In an individual plant, the pistillate flowers could be in blossom three to five days earlier than the staminate flowers. The species is self-compatible; however, the benefits of outcrossing were obvious since fruits from outcrossing pollination were plumper (X. N. Zhao unpubl. data). Although the floral morphology of the species suggests animal pollination, only a few small insects were observed visiting the flowers. Since there were no effective pollinators in the flowering season, it was inferred that the species is mainly pollinated by wind. The receptacle elongated after pollination and each carpel developed into a small berry. The fruits matured

from mid/late August to September. The flesh of the aggregate berries is red, with one to two kidney-shaped seeds in a berry.

Study site

We carried out most of our observations at four principal field sites (Baishilazi Nature Reserve; Fenghuang Mountain Nature Reserve; Long Tan Mountain forest garden; Laotuding Nature Reserve). Quantitative data on gender variation and plant size were collected in four areas within eastern Liaoning Province in China (Table 1). Vegetation in these areas mainly consisted of deciduous broad-leaved forests, among which were a few conifers. Most *S. chinensis* plants climbed low trees and shrubs.

The cultivated population was about ten kilometers away from the FC population (Table 1). Seedlings from one maternal individual were similar genotypically, and this minimized potential influences from genetic factors. The cultivated plants were studied between 1998 and 2010. Two hundred two-year-old seedlings were planted every year, so that there were plants in varying age groups from 2 to 13 years old. However, gender ratios in these plants were

recorded only in 2008, 2009 and 2010. A growth framework was constructed with cement poles and iron wires, on which the woody vine could climb. The frames were 1.8 meters tall. The wire between the rows was 2.0 meters long, and the spacing between the poles was 0.7 meters.

Gender variation in the natural populations

Investigations were carried out from late May to early June in 2008, 2009 and 2010 when *S. chinensis* was in its flowering season. Walking upwards on the mountain, we studied the flowering individuals on both sides of the road. When we found a new plant, we attached a rain-proof label with a unique number to the stem about 1.3 meters from the ground, to avoid repeated counts. We then measured the diameter of the main stem 10 cm from the ground with a caliper (as a parameter of plant size) as well as shade

intensity in the habitat using a portable photometer. The shade intensity = $1 - L_h/L_o$, where L_h = light density (lux) where the main stems were, L_o = light density (lux) in open ground. We also recorded the total number and gender of the flowers on the plants. In addition, we calculated the female ratio (female ratio = number of female flowers/total number of flowers) for each plant.

Standardized phenotypic gender (G_i) of each plant was calculated according to Lloyd (1980) as follows:

$$G_i = O_i / (O_i + p_i E),$$

where O_i is the number of pistillate flowers of plant i , p_i is the number of staminate flowers of plant i , and $E = \sum O_i / \sum p_i$. G_i may thus vary between 0 for plants producing only staminate flowers and 1 for plants producing only pistillate flowers (also see Sarkissian et al. 2001).

Table 1. Location and main accompanying vegetation (broad-leaved trees, conifers and climbers) at the study populations of *Schisandra chinensis*. KD = KuanDian Baishilazi Nature Reserve; FC = FengCheng FengHuang mountain Nature Reserve; XY = XiuYan LongTan mountain forest garden; BX= BenXi Laotuding Nature Reserve.

Populations	Lat. (N), Long. (E)	Alt. (m)	Broad-leaved trees	Conifers	Climbers
KD	40°54', 124°46'	460–860	<i>Quercus mongolica</i> , <i>Juglans mandshurica</i> , <i>Betula chinensis</i> , <i>Fraxinus rhynchophylla</i> , <i>Acer barbinerve</i>	<i>Abies holophylla</i> , <i>Larix olgensis</i> , <i>Pinus koraiensis</i>	<i>Euonymus alatus</i> , <i>Lonicera monantha</i> , <i>Philadelphus schrenkii</i> , <i>Crataegus pinnatifida</i> , <i>Corylus heterophylla</i>
FC	40°18', 130°03'	190–540	<i>Quercus liaotungensis</i> , <i>Tilia amurensis</i> , <i>Acer triflorum</i> , <i>Fraxinus rhynchophylla</i> , <i>Syringa wolffii</i>	<i>Pinus tabulaeformis</i> , <i>Picea koraiensis</i> , <i>Abies nephrolepis</i>	<i>Acer barbinerve</i> , <i>Lathyrus cyrtobotrya</i> , <i>Corylus mandshurica</i> , <i>Acer ginnala</i> , <i>Corylus heterophylla</i>
XY	39°03', 132°56'	220–610	<i>Quercus aliena</i> , <i>Philadelphus schrenkii</i> , <i>Crataegus pinnatifida</i> , <i>Tilia amurensis</i>	<i>Larix kaempferi</i> , <i>Pinus tabulaeformis</i> , <i>Pinus koraiensis</i>	<i>Euonymus macropterus</i> , <i>Acer ginnala</i> , <i>Acer triflorum</i> , <i>Corylus heterophylla</i> , <i>Lespedeza bicolor</i>
BX	41°18', 124°52'	420–890	<i>Quercus mongolica</i> , <i>Betula platyphylla</i> , <i>Syringa velutina</i> , <i>Fraxinus rhynchophylla</i> , <i>Acer barbinerve</i>	<i>Pinus koraiensis</i> , <i>Abies holophylla</i> , <i>Pinus sylvestris</i> var. <i>mongolica</i>	<i>Acer triflorum</i> , <i>Viburnum sargentii</i> , <i>Corylus mandshurica</i> , <i>Philadelphus schrenkii</i> , <i>Lonicera caerulea</i> var. <i>edulis</i>

Gender variation and reproductive output in the cultivated population

In order to exclude the effect of complex environmental factors such as nutrition, moisture, light intensity and height of plants on gender variation while only examining whether gender expression and reproductive output in *S. chinensis* are age-dependent, in 2008 we conducted our experiments in the garden under the same environmental conditions. Thirty cultivated plants were collected at random from the garden during the flowering period for each age group and tagged. Diameters of the main stems were first measured as was done in the natural populations. The number of flowers in each plant was then recorded including their gender, and female ratio was calculated.

For each age group of the marked 30 plants, fruits were collected (aggregate or infructescences fruit) after maturity and counted per plant. Ten more floral fruits were collected randomly and the number of berries (carpel fruit) counted.

We repeated the investigations in the following two years. In consecutive years, same plants belonged to different age groups. For example, seven-year-old plants in 2008 became nine years old in 2010. However, the data for 12-year-old plants came only from 2009 and 2010, while the data for 13-year-old plants only from 2010.

Statistical analyses

Two-way ANOVA was used to compare female ratios among populations, years and shade intensities, with population as the fixed factor and year or shade intensity as the random factor. Pearson's correlation analysis was used to test relationships between female ratio and shade intensity in the habitats, as well as between plant size/age and female flower production, and between male flower production and female ratio. MANOVA followed by a post-hoc LSD test was used to test the differences in shade intensity among the populations' habitats, as well as differences in numbers of fruits per plant and berries per aggregate fruit. Since some individuals were measured repeatedly over the three years, individual plants

were regarded as random factors. The significance level was set at 0.05 and all statistical analyses were carried out in SPSS ver. 16.0.

Results

Gender variation in natural populations

Of the 494 plants in the four populations studied in the three years, 92.8% produced both staminate and pistillate flowers. A few plants produced only staminate flowers in certain years, and these individuals were often young or living in habitats with high shade intensities. We did not find any individuals that produced only female flowers. Notably, 16 marked plants produced only staminate flowers in 2008, and five of them produced pistillate flowers in 2009. An additional seven of them also produced pistillate flowers in 2010.

At the individual level, female ratio varied from 0.2 to 0.6, although several plants had female ratios exceeding 0.8. At the population level, the mean female ratios ranged from 0.27 to 0.46 (Table 2), and the phenotypic gender (G_i) was biased towards male in the four natural populations (Fig. 2A).

The differences in the female ratio among populations and years were significant (two-way ANOVA: $F_{3,12} = 3.972$, $p = 0.028$; and $F_{2,12} = 5.943$, $p = 0.017$, respectively). However, there was no significant effect of population \times year interaction on the female ratio ($F_{6,22} = 1.156$, $p = 0.214$).

Mean female ratio for all populations was significantly lower in 2009 than those in 2008 or 2010 (see Table 2).

Effect of plant size and shade intensity on gender variation in the natural populations

We found that shade intensity and plant size affected gender variation in the species. Linear regression analysis revealed, that in higher shade intensity, the plants produced more male flowers ($r = -0.776$, $p < 0.01$; Fig. 3).

Number of flowers (total, male and female) was positively correlated with plant size (see

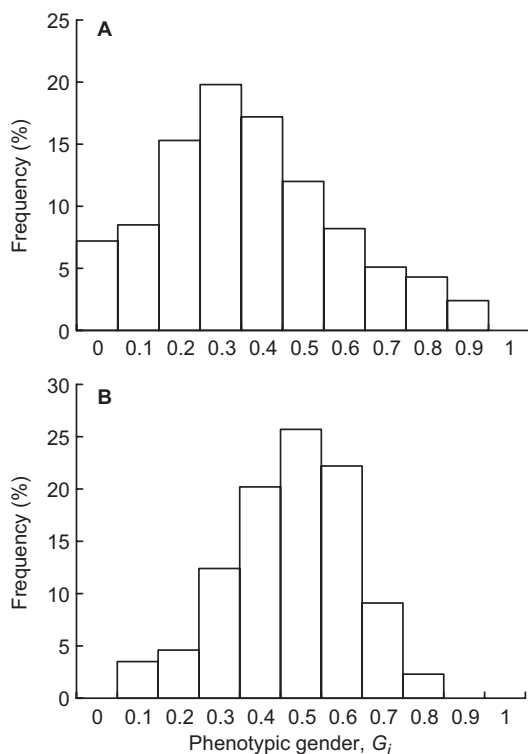


Fig. 2. Frequency distributions of standardized phenotypic gender (G_i) in (A) natural and (B) cultivated populations of *Schisandra chinensis*. $G_i = 0$ means pure male, $G_i = 1$ means pure female.

Table 3). However, in natural populations plant size and female ratio did not correlate (Table 3).

Plant size \times shade intensity interaction had no effect on female ratio (two-way ANOVA: $F_{1,332} = 1.803$, $p = 0.089$); i.e., higher female ratios were not found in smaller plants that grew in bright conditions or in larger plants that grew in shady conditions.

Table 2. Locality, shade intensity and female ratio in four investigated populations of *Schisandra chinensis* in three consecutive years. Values are means \pm SEs, and different letters indicate significant differences (post-hoc LSD, $p > 0.05$) between years or populations.

Population	Shade intensity	Female ratios			
		2008	2009	2010	Mean
KD	0.41 \pm 0.27 ^a ($n = 109$)	0.37 \pm 0.29 ($n = 36$)	0.33 \pm 0.24 ($n = 34$)	0.39 \pm 0.25 ($n = 39$)	0.36 \pm 0.26 ^a
FC	0.44 \pm 0.29 ^a ($n = 118$)	0.39 \pm 0.31 ($n = 55$)	0.31 \pm 0.30 ($n = 32$)	0.36 \pm 0.29 ($n = 31$)	0.35 \pm 0.30 ^a
XY	0.36 \pm 0.21 ^b ($n = 140$)	0.45 \pm 0.21 ($n = 41$)	0.36 \pm 0.23 ($n = 47$)	0.46 \pm 0.24 ($n = 52$)	0.42 \pm 0.23 ^b
BX	0.53 \pm 0.22 ^c ($n = 127$)	0.30 \pm 0.24 ($n = 44$)	0.27 \pm 0.25 ($n = 41$)	0.33 \pm 0.27 ($n = 42$)	0.30 \pm 0.25 ^c
Mean		0.38 \pm 0.26 ^a	0.32 \pm 0.25 ^b	0.39 \pm 0.27 ^a	

Gender variation and reproductive output in the cultivated population

All cultivated plants produced both staminate and pistillate flowers. Female ratio in most individuals (about 80.5%) was between 0.3 and 0.6, with an average of 0.52. Thus, phenotypic gender was female-biased as compared with that in the natural populations, and there was a significant difference between the two (two-way ANOVA: $F_{1,18} = 3.885$, $p < 0.05$; Fig. 2B).

Number of flowers (total, male and female) as well as female ratio all were positively correlated with age of the plant (Table 3). In general, young plants (2–3 years old) had lower female ratios. In middle-aged plants (4–10 years old), flower production increased greatly and the female ratio increased to around 0.6. When the plants got old (> 10 years), both flower production and female ratio decreased considerably (Fig. 4). Therefore, gender variation was age dependent in the species.

Excluding young individuals, middle-aged individuals had higher aggregate-fruit production per individual (mean \pm SE = 126.5 \pm 24.7, $n = 450$) than old individuals (mean \pm SE = 62.1 \pm 14.5, $n = 360$). In addition, we found that in old plants some fertilized carpels aborted and could not develop into berries. Therefore, the number of berries per aggregate fruit in old plants was smaller (mean \pm SE = 16.6 \pm 2.5, $n = 90$) as compared with that in middle-aged plants (mean \pm SE = 33.7 \pm 3.1, $n = 90$) and the difference was significant (MANOVA: $F_{1,180} = 3.261$, $p < 0.05$). Hence, the reproductive output of *S. chinensis* is age-dependent.

Discussion

Gender variation and gender system of *S. chinensis*

Gender variation in the perennial woody vine, *S. chinensis*, is more pronounced in natural populations. Phenotypic gender was more male-biased in the natural populations than in the cultivated one. This may have been a result of disadvantageous habitat conditions in the field (also see Ganeshiah & Uma Shaanker 1991).

Smaller plants, especially those growing in the shade, produced only staminate flowers and were phenotypically male. On the other hand, in cultivated conditions, unisexual plants were not found.

Gender in flowering plants is governed by a complex interplay of genetic and environmental factors (Eckhart 1992, Cipollini & Whigham 1994, Wolfe & Shmida 1996). In some cases, monoecious individuals may represent one of

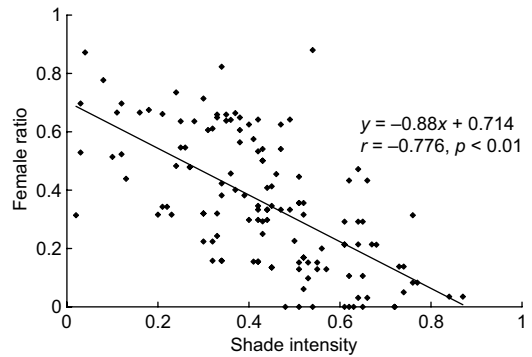


Fig. 3. Relationship between the shade intensity and female ratio in the natural populations of *Schisandra chinensis*. Data from 2010.

several gender morphs in a population, including genetic males and females (Freeman *et al.* 1981, Méndez 1998, Glawe & de Jong 2005). For example, Ueda (1988) described *S. chinensis* as monoecious or dioecious. However, our results seem to support a notion that the male phenotype

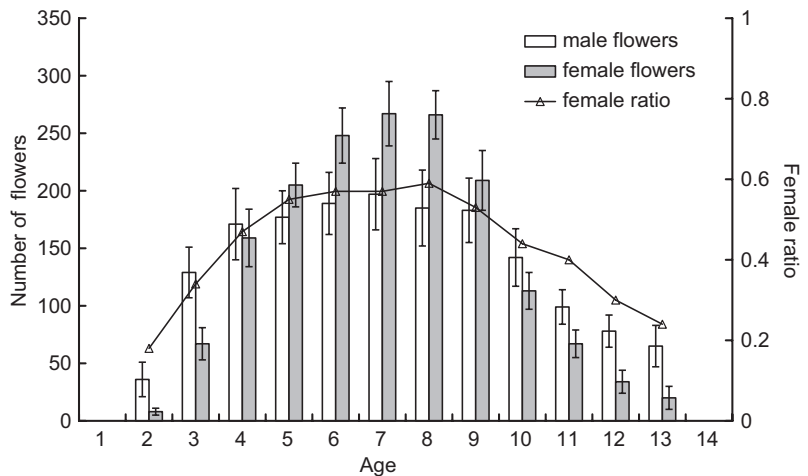


Fig. 4. Flower production and female ratio in the cultivated populations of *Schisandra chinensis*. Values are means \pm SEs.

Table 3. Pearson's correlations between plant size in the natural populations and plant age in the cultivated population, and flower production in *Schisandra chinensis*.

	Number of flowers			Female ratio
	total	male	female	
Plant size	0.865**	0.903***	0.661*	0.354
Plant age	0.982***	0.797*	0.753**	0.722**

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

and some phenotypes with high female ratios (may have been regarded as female phenotype in the past) are environmentally-induced unstable phenotypes. Hence, we conclude that the gender system in this species is explicitly monoecy. Our study on *S. chinensis* might serve as a reference for research on gender systems in similar perennial species with complicated gender expressions. Since previous records of gender systems are largely based on preserved specimens or one-time surveys in the field, gender variation among different habitats or years may have been overlooked.

In natural populations of *S. chinensis*, varying female ratios among individuals might depend on the environmental conditions, particularly shade intensity in the habitat (*see* Table 2). This conclusion is supported by previous studies on monoecious plants, where the influence of light intensity on gender expression was very evident (Poole & Grimball 1939, Dzhaparidze 1967, Freeman *et al.* 1981, Glawe & de Jong 2005).

A puzzling question was why in all four natural populations studied, the female ratios were lower in 2009 than in the other years? We speculate that this could have resulted from differences in precipitation among years. Data from the local weather service showed that a drought persisted in the study area from the autumn of 2008 to the first half of 2009. In particular, precipitation from March to June 2009 was about a quarter of the amount usually recorded for the same period in normal years (77.4 mm *vs.* 317.8 mm). This might have led to the low female ratio in 2009 as compared with that in the other two years. A decrease in female ratio due to drought has also been recorded for other plants (Solomon 1985, Delph & Lloyd 1991). This was, however, not experienced in the cultivated population because of artificial irrigation. In addition, we also consider another factor, namely that reproductive effort of plants in a preceding year could affect gender expression in the following year (*see* Aluri & Ezradanam 2002, Zhang *et al.* 2008). According to the resource-allocation theory, the adjustment of gender expression in harsh conditions could be an advantage in monoecy, leading to greater reproductive efficiency (Harder *et al.* 2000, Kawagoe & Suzuki 2005, Bertin 2007, Pannell *et al.* 2008).

Effects of plant size and age on gender expression

Resource-dependent gender plasticity is frequently observed in natural plant populations. Indeed, unless males and females increase equally in fitness, biasing resource allocation becomes the more successful strategy (Willson 1983, Solomon 1989, Burd & Head 1992). Therefore, reproducing via the female gender function is usually delayed until the plant is larger (Charnov 1982, Bickel & Freeman 1993, Ashman 1994, Zhang 2006). In certain conditions, total flower production correlates positively with plant size and age. In the natural populations studied here, however, production of pistillate flowers correlated positively with plant size while female ratio did not. In the cultivated population, flower production (total, male and female) was clearly age-dependent (Table 3 and Fig. 4). The reason for this is that cultivations are a comparatively homogeneous habitat for plants. Hence, the effect of plant age on gender expression is pronounced, since the effects of environmental conditions can be excluded.

In natural populations, however, the effects of environmental factors on gender expression may mask those of plant size, so that inconsistency in gender expression would show. Theoretically, size-dependent variation in gender should often be part of an adaptive life history when reproductive investment increases with plant size and contributions as female and male parents involve different costs (Lloyd & Bawa 1984, Charnov & Bull 1985, de Jong & Klinkhamer 1994). Since larger plants can afford these costs more readily than smaller plants, relative allocation to female function commonly increases with plant size (Freeman *et al.* 1980a, Bierzychudek 1984, Schlessman 1987, Klinkhamer *et al.* 1997, Kudo 1993, Wright & Barrett 1999). Alternatively, if production of staminate flowers declines with increasing plant size, very large plants may produce no staminate flowers, and thus function exclusively as females (Policansky 1981, Lloyd & Bawa 1984). There is some discrepancy between the experimental results and the above theory: namely in the main stage of the life history of *Schisandra chinensis*, production of the staminate flowers did not decrease. Even the phenotypic gender was female-biased. This result

is, however, consistent with findings for *Arum italicum* (Méndez 1998) and *Sagittaria trifolia* (Sarkissian *et al.* 2001, Huang *et al.* 2002), but not for *Arisaema dracontium* (Clay 1993). In any case, as plants age, their female flower production or ratio would decrease more quickly than production of staminate flowers. The reason may be due to reproductive output in the main stage of the life history affecting gender expression in older plants. Therefore, in cultivated conditions, individual gender variation in *S. chinensis* was a reproductive strategy of monoecious species as proposed by Masaka and Takada (2006).

In the cultivated population, reproductive output was clearly age-dependent. Plants in the main stage of their life history not only have more fruits per plant, but also have more small berries per aggregate fruit. However, in older plants, the internodes of flowers branching from the upper parts of the plant will be longer, the number of the female flowers will reduce correspondingly, and the number of fruits per plant will also decrease. Particularly, since aged plants cannot maintain vigor and resource limitation may be occurring (dense cultivation makes the pollen limitation impossible), some carpels will not develop into berries making quality of aggregate fruits poor. Resource compensation theory assumes trade-offs between male and female functions, and also assumes that reproductive success can be increased by specializing in one sexual function (Charnov 1982, Uma Shaanker & Ganeshiah 1984, Geber 1999). The decrease in frequency of female flowers and fruit production in aged plants shows that they cannot sustain the higher female reproductive output and opt for relatively high male reproductive output. The decline in female investment could be an adaptive strategy to conserve resources (Brunet 1996). Age dependency of gender expression and reproductive output found in the woody monoecious species require more studies to find effects of temporal factors on gender shifting or maintenance of plant sexual systems (Thomson & Barrett 1981, Brunet & Charlesworth 1995).

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