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Variation in floral organ size depends on function: a test with *Commelina communis*, an andromonoecious species

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ABSTRACT

We measured the size of floral organs in andromonoecious *Commelina communis* to test the hypothesis that pollinator-mediated selection might regulate variation in the size of floral organs. We compared variation in floral organ size between *C. communis* perfect flowers, with fertile pistils, and *C. communis* staminate flowers, with sterile pistils. We hypothesized that variation in size of the sexually functionless pistil would be large. We found supporting evidence from eight *C. communis* populations. These results suggest that pollinator-mediated selection may have stabilized variation in the style length of perfect flowers. We also found differences in variation in length among three different types of anthers in both perfect and staminate flowers, only two of which produce fertile pollen. This is consistent with our prediction that mating-related organs should vary less in size than attraction-related organs.

Keywords: andromonoecy, *Commelina*, phenotypic size variation, pollinator-mediated stabilizing selection.

INTRODUCTION

In plants pollinated by animals, flower size and shape should have evolved to maximize pollen transfer given the morphological and behavioural traits of the pollinators (e.g. Grant and Grant, 1965; Stebbins, 1970; Galen *et al.*, 1987). Flowers usually consist of several organs that often differ in function. For example, petals and sepals usually function to attract pollinators, allow for pollinator specialization and protect reproductive structures. Stamens and pistils are involved in dispersing and receiving pollen.

Floral organ size is usually more stable than the size of vegetative organs (Stebbins, 1950; Conner and Via, 1993; Matsui *et al.*, 2001). Since the physical fit between a flower and its animal pollinator determines the success of pollination (Schemske and Horvitz, 1989;

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Robertson and Wyatt, 1990; Harder and Barrett, 1993), flowers that deviate in size from the population mean are likely to disperse and receive less pollen (Berg, 1960; Fenster, 1991). The results of Wolfe and Krstolic (1999) support the hypothesis that pollinator-mediated selection stabilizes flower (petal) size. A physical match between pollinator size and the size of flower parts is more important for organs involved in mating than for organs involved in pollinator attraction; mating-related organs should, therefore, vary less in size than attraction-related organs. For example, gynostemia vary less in length than petals and sepals in an orchid species (Ushimaru and Nakata, 2001), and corolla tube length is more stable than flower size in some species (Conner and Via, 1993; Mazer and Hultgård, 1993; Worley *et al.*, 2000). These findings suggest that organs involved in pollen removal and deposition should have an optimal size, which will be dependent on the pollinators present in any given population. Thus, pollinator-mediated stabilizing selection should regulate phenotypic floral variation within a population depending on organ function.

Many plant species have unisexual flowers that have lost either male or female function. In staminate flowers, pistils are typically reduced in size and lack ovules; in pistillate flowers, stamens are often atrophied. These sexually functionless organs are not involved in pollination in most cases, although some pistillate flowers have stamens that produce sterile pollen to reward pollinators (Haber and Bawa, 1984; Kevan and Lack, 1985; Kawakubo, 1990; Mayer and Charlesworth, 1991). If pollinator-mediated selection controls variation in floral organ size, we predicted that variation in size of sexually functionless organs in unisexual flowers should be large, because pollinator-mediated stabilizing selection would not regulate the size of these organs. Testing this prediction would be one step in understanding the importance of pollinator-meditated selection for the evolution of size variation in floral organs in angiosperms.

Here, we briefly report the results of a test of this hypothesis in an andromonoecious annual herb, *Commelina communis*. We measured the length of petals and sepals and the length of anthers and styles in both perfect and staminate flowers. We then compared the variation in size of six floral organs between these two types of flowers. We also compared size variation among three types of anthers with different functions to test the hypothesis that mating-related organs vary less in size than do attraction-related organs.

MATERIALS AND METHODS

Study species

Commelina communis L. (Commelinaceae) is an annual, andromonoecious weed that is widely distributed in temperate northeast Asia, often growing around rice fields and along roads. A single plant usually has many inflorescences in which perfect flowers bloom before staminate flowers (Fig. 1). Flowers in the A and B3 positions tend to be staminate, with reduced pistils; B1 flowers are perfect in most cases (Morita and Nigorikawa, 1999). The sex of B2 flowers is flexible; perfect and staminate flowers are equally likely (Morita and Nigorikawa, 1999). The flowers of both types open at sunrise each day and they last until noon.

This species has three types of anthers that differ in function: two long, one middle and three short anthers (Fig. 2). Long and medium anthers produce fertile pollen, whereas short anthers produce only a small amount of sterile pollen and thus advertise to pollinators

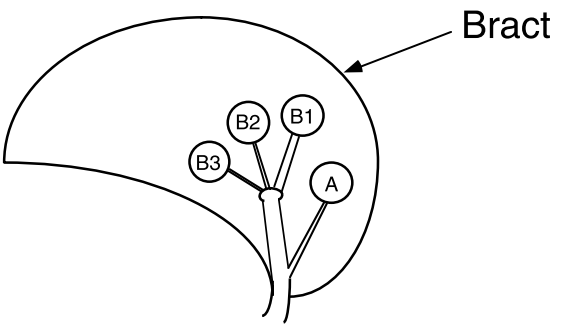

Fig. 1. Inflorescence structure in *Commelina communis* (redrawn from Morita and Nigorikawa, 1999). Flowers bloom sequentially from B1 to B3. A-positioned flowers are often aborted in the field.

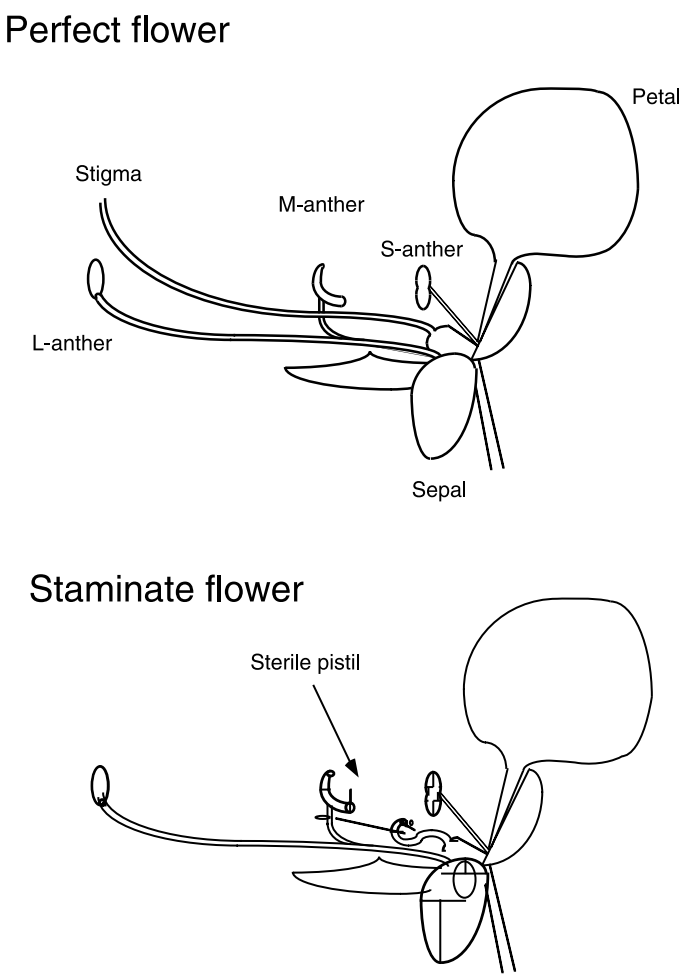

Fig. 2. Side views of perfect and staminate flowers of *Commelina communis*. The length of each floral organ was measured from the base of the flower. L-, M- and S-anthers = long, medium and short anthers, respectively.

(Morita and Nigorikawa, 1999; A. Ushimaru *et al.*, unpublished data). Long anthers produce more pollen grains on average ($n = 3500$) than do medium anthers ($n = 2000$) (Morita and Nigorikawa, 1999), although these figures do not differ between perfect and staminate flowers (Morita and Nigorikawa, 1999). Pollen from long anthers contributes mainly to outcrossing, whereas pollen from medium anthers rewards pollinators of this nectarless species (Morita and Nigorikawa, 1999). We have often observed syrphid flies eating pollen from medium anthers in *Commelina* flowers in the field.

Commelina communis is self-compatible and can experience delayed autogamy and bud pollination (Morita and Nigorikawa, 1999). However, pollen:ovule ratios (2100:2500) for perfect flowers are in line with those for species with facilitated outcrossing (reported by Cruden, 1977, in Morita and Nigorikawa, 1999). Small, generalist pollinators, such as solitary bees and syrphid flies, are the main pollinators of *C. communis* (Tanaka, 1978). We have also frequently seen a bumblebee species, *Bombus diversus* Smith, pollinating *C. communis* at one study site (Ohara, OH).

Variation in size of floral organs

We studied one population of *C. communis* in Otsu City, Kamitanokami (KA, 34°58′N, 135°58′E); five in Kyoto City, Kyoto University campus (KU, 35°01′N, 135°47′E), Syugakuin (SY, 35°02′N, 135°48′E), Yamanaka (YA, 35°02′N, 135°49′E), Iwakura (IW, 35°05′N, 135°47′E) and Ohara (OH, 35°08′N, 135°50′E); and two in Sendai City, Tsunogoro (TS, 38°15′N, 140°50′E) and Tohoku University campus (TU, 38°15′N, 140°51′E). We collected both perfect and staminate flowers from 27 to 65 individuals at each site (Table 1). We measured the length of the stigma and long, medium and short anthers using digital calipers (Fig. 2). We then removed one large petal and one lateral sepal from each flower, flattened them under microscope slides, and measured their lengths (Fig. 2). When possible, we measured the right-hand long anther, petal and sepal and the central short anther of each flower. The mean size of each organ is shown in Table 1. We calculated the coefficient of variation of each floral organ per site by dividing the mean by the standard deviation. We then compared the mean coefficient of variation of each organ between perfect and staminate flowers using a paired *t*-test. We also compared the coefficients of variation of the three types of anther in both perfect and staminate flowers using a two-way analysis of variance.

RESULTS

Across all sites and floral organs, the style length of staminate flowers always had the highest coefficient of variation (Table 1). Moreover, the mean coefficient of variation for style length was significantly higher for staminate flowers than for perfect flowers ($t_7 = 4.51$, $P < 0.01$; Fig. 3). A-positioned staminate flowers tended to have shorter styles (< 2.0 mm in most cases) than staminate flowers in other positions. When we excluded A-positioned staminate flowers from the calculation, the coefficients of variation for all sites decreased to 11.8–29.0, with a mean of 19.1. However, the coefficients of variation for style length still differed significantly between the two types of flowers ($t_7 = 5.6$, $P < 0.001$). Staminate flowers also had significantly larger mean coefficients of variation for medium and short anther heights than did perfect flowers ($t_7 = 2.53$, $P < 0.05$ and $t_7 = 4.36$, $P < 0.01$, respectively). The coefficients of variation for petal and sepal lengths and long anther length did

Table 1. Mean size and coefficient of variation (CV) for six floral organs in eight populations of *Commelina communis*

		Mean size (mm)		CV (%)			Mean size (mm)		CV (%)	
Organ	Site (*n*)	P	S	P	S	Site (*n*)	P	S	P	S
	KA (30)					IW (35)				
Petal		13.48	12.23	7.5	7.6		13.91	13.03	10.0	9.6
Sepal		5.09	4.85	8.3	8.7		5.54	5.25	9.4	9.5
Stigma		12.75	3.29	6.0	32.4		11.86	3.16	10.5	43.4
Long anther		12.02	11.97	6.2	4.7		10.78	10.88	11.0	10.8
Medium anther		6.85	5.97	7.1	13.6		6.35	5.71	12.9	17.4
Short anther		4.23	3.42	6.8	10.6		3.99	3.18	12.9	17.6
	KU (30)					OH (30)				
Petal		13.62	12.63	8.8	12.1		12.36	11.47	4.3	6.7
Sepal		4.97	4.91	9.4	8.7		5.46	5.33	8.6	7.0
Stigma		13.41	3.68	7.6	20.6		11.40	3.30	6.3	34.3
Long anther		11.78	12.11	4.3	5.2		10.82	10.98	3.8	3.3
Medium anther		6.46	6.02	7.3	7.3		5.74	5.17	6.5	6.7
Short anther		4.19	3.23	10.2	11.9		3.83	3.01	8.5	8.6
	SY (31)					TS (29)				
Petal		13.52	12.99	6.8	5.2		11.81	10.60	13.0	14.9
Sepal		5.22	5.07	8.2	9.3		5.35	4.89	9.4	8.8
Stigma		12.91	3.71	6.2	29.8		11.60	3.20	10.7	31.9
Long anther		11.90	12.17	5.2	4.3		10.87	10.79	10.1	9.8
Medium anther		7.20	6.86	7.0	7.3		6.11	5.53	11.1	11.8
Short anther		4.48	3.51	6.9	11.9		3.80	2.90	10.2	11.7
	YA (65)					TU (27)				
Petal		13.92	12.79	12.9	11.9		12.07	10.60	10.8	7.9
Sepal		5.52	5.24	10.9	11.9		5.71	5.13	6.2	9.6
Stigma		12.48	3.65	10.7	31.2		11.49	2.30	9.4	83.5
Long anther		11.34	11.69	11.2	9.4		11.31	11.18	5.6	6.2
Medium anther		6.50	5.84	12.9	14.5		6.79	6.16	6.7	13.1
Short anther		4.33	3.35	12.9	15.8		4.06	3.10	9.7	16.2

Note: P = perfect flowers; S = staminate flowers.

not differ significantly between perfect and staminate flowers ($t_7 = -0.30$, $P = 0.77$; $t_7 = -0.72$, $P = 0.49$; and $t_7 = -1.40$, $P = 0.21$, respectively).

The ranking for coefficient of variation of height was small anther > medium anther > long anther. The differences in coefficients of variation were statistically significant for both perfect (mean square = 14.0, $F_{2,21} = 11.5$, $P < 0.01$) and staminate flowers (mean square = 86.7, $F_{2,21} = 28.5$, $P < 0.001$). The coefficients of variation for the anthers also differed significantly among the sites (perfect flowers: mean square = 20.6, $F_{7,16} = 17.0$, $P < 0.001$; staminate flowers: mean square = 38.3, $F_{7,16} = 28.54$, $P < 0.001$).

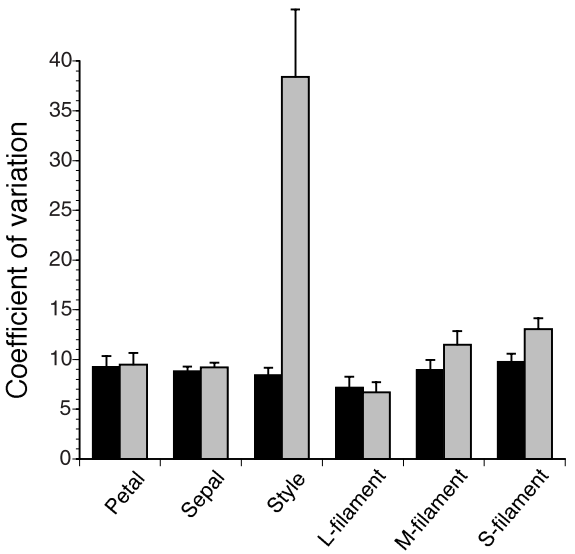

Fig. 3. The coefficient of variation for each floral organ averaged across all eight populations (mean ± standard error). ■, perfect flowers; ■, staminate flowers. L-, M- and S-anthers = long, medium and short anthers, respectively.

DISCUSSION

There was greater variation in style length for staminate than for perfect flowers, whereas variation in petal and sepal lengths and long anther height did not differ between flower types. These results are consistent with our prediction that functionless pistils would exhibit more phenotypic variation in size than fertile pistils, and is concordant with the hypothesis that natural selection can stabilize the size of floral organs (Fenster, 1991; Conner and Via, 1993; Wolfe and Krstolic, 1999; Worley *et al.*, 2000; Ushimaru and Nakata, 2001). Since the expression of flower type is plastic in this species, intra-individual variation might affect variation in the total size of sterile pistils. In related *Murdannia keisak* (Commelinaceae), which has both fertile and sterile anthers in perfect flowers, the length of sterile anthers (coefficient of variation = 9.6) varied more than the length of fertile anthers (coefficient of variation = 5.2, $n = 50$; A. Ushimaru, unpublished data). This difference between fertile and sterile anthers also suggests that stabilizing selection is stronger on the size of fertile organs.

We also found less variation in long anther length than in medium and short anther length in both perfect and staminate flowers (Fig. 3), supporting the hypothesis that organs related to pollen dispersal and receipt are more stable than attraction-related organs (Worley *et al.*, 2000; Ushimaru and Nakata, 2001; but see Ushimaru and Imamura, 2002). Since long anther length is thought to affect the deposition of pollen on an insect's body, anthers whose lengths differ greatly from the population mean might transfer less pollen to pollinators. As we have shown that long anther length varies less than that of anthers that do not donate pollen, it would be worth testing whether long anther length affects pollen donation and is, therefore, under stabilizing selection. The height of medium and short authers varied more in staminate flowers than in perfect flowers. Since the functions of these organs are considered to be the same in both types of flower (Morita and Nigorikawa,

1999), our hypothesis does not explain the difference in size variation. This variation may be related to the developmental processes that reduce the functionality of the pistil in staminate flowers.

In summary, our results are concordant with the idea that pollinator-mediated selection can stabilize the length of styles and anthers that influence pollen deposition and removal in eight populations of *C. communis*. However, the absolute coefficients of variation for stigma and anther heights varied among the eight populations. Floral variation might also be affected by variation in resource availability to individual flowers (Diggle, 1995) and selection on optimal investment per flower (see Worley *et al.*, 2000, and references therein). A comparison of pollinator species and behaviour among populations and resource conditions of each population might help elucidate which selective forces act on phenotypic variation in floral organs in *C. communis*.

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