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Resource allocation for coevolved figs and fig wasps in monoecious figs: Where and how are seeds and wasps produced?

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Abstract
In the female flowers of monoecious fig species, styles of various lengths are arranged in three or more layers inside the syconium (Fig. 1). Pollinating fig wasps pollinate the female flowers at the same time as they oviposit in the ovaries of the female flower. One fig ovary can produce either one seed or one wasp. Thus, there is a strong conflict of interest between figs and their pollinating wasps. In this study, four monoecious fig species were sampled to investigate the allocation of fig resources to seed and wasp production. Our observations support the view that seeds and wasps can develop in any layer of ovaries of female flowers, because both were produced in inner and outer layers of ovaries. This finding clearly deleted rejects the 'short-length-ovipositor hypothesis' (under which wasps develop only in short-styled female flowers). In all species studied, the average production of seeds in a fig was usually higher than the production of wasps, although the proportions of flowers yielding seeds and wasps varied between species. There was also a tendency for seed production in the inner layers of ovaries to be higher than wasp production to be higher in the outer layers of ovaries. We interpret the higher levels of seed rather than wasp production as indicating dominance by the fig in this symbiosis. The production of seeds and wasps differed significantly among species. In *Ficus altissima*, production of both seeds and wasps were significantly higher than in any other species, while *F. virens* var *sublanceolata* showed the lowest production of both seeds and wasps. In *F. altissima*, *F. microcarpa*, and *F. benjamina*, some fruits yielded only seeds or only wasps, which might reflect the re-emergence of the pollinators without oviposition and or mortality due to parasitism or competition from non-pollinating wasps.

Keywords: Monoecious figs, resource allocation, seed and wasp production

1. Introduction

Fig trees (Moraceae: *Ficus*) and their pollinators (Chalcidoidae: Agaonidae) provide a classical example of a highly coevolved mutualism (Ramirez, 1974; Galil, 1977; Wiebes, 1979; Berg, 1989). They depend on each other to complete their life cycle and to reproduce. At the receptive female flower phase (B phase) of fig tree, species-specific fig wasps pollinate the female flowers (with the pollen they carry from their natal figs), and lay eggs in the ovaries of some of the flowers. The pollinator's larvae develop at the expense of potentially viable seeds (Wiebes, 1979; Herre, 1989; West and Herre, 1994; Anstett et al., 1997). A few weeks later, the fig inflorescence or syconium, produces both seeds and wasps. When the female wasps disperse to another tree, pollinate and lay eggs, a new reproductive cycle of the two partners will begin. Non-pollinating wasps also oviposit in the syconia of figs and compete in the ovaries with pollinating wasps or parasitize the pollinator's larvae, which constitutes pressure on utilization of female flowers of for seeds and or wasps production.

Previous studies (Kjellberg et al., 1987a; Herre, 1989; West and Herre, 1994) showed that the short-term reproductive benefits of the two partners were not identical with respect to the utilization use of female flowers. There are obvious conflicts of interest between the partners (Herre and West, 1997), but the fig-wasp mutualism is stabilized through the adaptation and co-ordination of morphological, physiological, phenological, and ecological traits (Kjellberg et al., 1987b; Berg, 1990; Ware et al., 1993).

This coevolution resolves or ameliorates the resource conflicts. Monoecious figs have evolved long and short styled female flowers with different pedicel lengths, but they are not perfectly heterostylic (see Fig. 1a). Style length or pedicel length of female flowers can limit the

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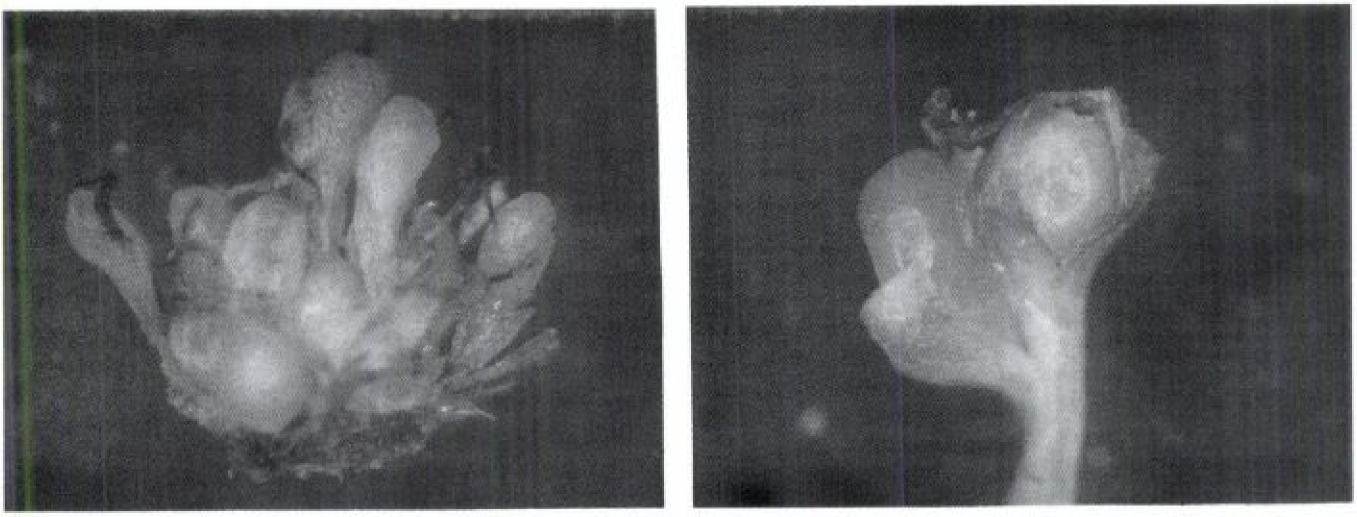

(a) (b)

Figure 1. Stratification of female flowers in the syconium of monoecious figs. (a) Stratification of ovaries in *F. virens* var *sublanceolata* Miq. (b) Seed and wasp were produced in different ovaries in *F. benjamina* L.

inherent conflict between figs and pollinating wasps by affecting the production of seeds and fig wasps (Compton and Nedft, 1990; Nedft and Compton, 1996; Ganeshaiah and Kathuria, 1999; Berg, 1990; Kerdelhué and Rasplus, 1996a,b; Anstett, 2001). Longer-styled flowers (i.e. most flowers without a pedicel beneath the flowers, whose ovaries form the outer layers of ovaries) usually produce seeds while shorter-styled flowers (i.e. having pedicel beneath the flowers, whose ovaries form the inner layers of ovaries), mostly develop into galls containing the wasps (West and Herre, 1994; Kerdelhué and Rasplus, 1996b; Nedft and Compton, 1996).

Moreover, parasitic non-pollinating wasps mostly develop in the inner or interval ovary layers (near the cavity of syconium), in the same ovaries as pollinators (West and Herre, 1994; Kerdelhué and Rasplus, 1996a,b). The 'short-length-ovipositor hypothesis' predicts that the ovipositor length of pollinators is not long enough to reach the ovaries of all long-styled flowers, implying that pollinators should only be able to oviposit successfully in ovaries flowers with shorter styles, but will still pollinate the other flowers.

However, some researchers have suggested that pollinators' ovipositors are in fact long enough to oviposit in most of the female flowers in monoecious figs and pollinating wasps also would pollinate most of the flowers and thereby obtaining better progeny nourishment and a lower mortality for their larvae (Bronstein, 1988; Compton and Nedft, 1990; Jousselin and Kjellberg, 2001).

There is also evidence to support the 'abortion hypothesis', which predicts that syconia with relatively few seeds and many wasp larvae would be aborted by the tree (Murray, 1985). Non-pollinating wasps thus compete for ovaries with pollinators, West and Herre (1994) put forward the 'unbeatable seed hypothesis', which predicts that a proportion of ovaries are protected from oviposition, so that wasps are unable to colonize all the ovaries. Either the 'short-length-ovipositor', or the 'unbeatable-seeds hypothesis' assume that oviposition sites are in short supply (Nedft and Compton, 1996).

The 'insufficient-egg-supply hypothesis' (Murray, 1985; Bronstein, 1988; Herre, 1989; Nedft and Compton, 1996) assumes that egg deposition is limited by the total number of eggs borne by individual female wasps (foundresses), the number of ovaries flowers in each fig and the mean number of foundresses entering the receptive fig.

Recently, it has been proposed that time and efficiency costs of ovipositing into long-styled flowers limits the overexploitation by pollinators (Patel et al., 1995; Nedft and Compton, 1996; Weiblen, 2000). Furthermore, it has been hypothesized that the stratification of female flowers and the number of foundresses entering a receptive syconium determines the production of seeds and wasps (Anstett et al., 1996; Anstett, 2001).

In this study, we studied four monoecious fig species in terms of the production of seeds and wasps in the different ovary layers and the resource allocation of figs for seeds and wasps, both pollinating and non-pollinating wasps.

2. Material and Methods

Species, study sites, and collections

Four monoecious fig species of the subgenus *Urostigma F. virens* Ait, *F. virens* var. *sublanceolata* Miq, *F. altissima* Bl., *F. microcarpa* L., and *F. benjamina* L. were studied (Table 1). Figs (the syconia, or floral heads, of fig

Table 1. Characteristics of the monoecious figs studied.

Species	Sampled crops (figs)	Wasps[1]	Wasps[2]	Seeds[3]	Seeds[4]	Aborted female flowers	Total female flowers
F. virens	3 (70)	113.9±54	26.3±15	141.0±46	40.9±25	97.0±64	354.7±60
F. virens var *sublanceolata*	2 (40)	60.9±20	28.3±11	88.8±38	27.3±14	123.8±39	272.9±50
F. altissima	5 (50)	219.4±119	49.1±47	285.7±111	79.6±58	62.9±77	560.3±102
F. microcarpa	2 (38)	44.9±32	14.3±15	160.2±73	60.4±35	70.4±40	273.6±37
F. benjamina	5 (79)	67.8±64	17.1±20	109.1±132	50.5±70	309.3±130	480.9±128

[1]Average number of wasps in a fig. [2]Average number of wasps in outer ovary layer of female flowers. [3]Average number of seeds in a fig. [4]Average number of seeds in inner and internal ovary layer of female flowers.

Table 2. Resource allocation in the sampled monoecious figs (%).

Species	Wasps	Wasps[1]	Seeds	Seeds[2]	Aborted female flowers[3]
F. virens	32.1±15	7.4±5	39.8±13	11.5±7	27.3±16
F. virens var *sublanceolata*	23.1±9	10.6±5	31.7±10	10.1±5	45.4±13
F. altissima	39.2±21	8.8±8	51.0±18	14.2±10	11.2±13
F. microcarpa	16.4±13	5.2±9	58.5±24	22.1±12	25.7±16
F. benjamina	13.3±14	3.6±5	22.7±23	10.5±12	64.3±28

[1]Wasps in outer ovary layer of female flowers in a fig. [2]Seeds in inner and internal ovary layer of female flowers in a fig. [3]Aborted female flowers in a fig.

Table 3. The number of wasps divided by the number of seeds produced in each fig species studied.

Species	Paired differences					t	df	Sig. (2-tailed)
	Mean	Standard deviation	Standard error mean	95% Confidence interval of the difference Lower	Upper			
F. virens	−26.74	81.66	9.76	−46.21	−7.27	−2.74	69	0.008
F. virens var *sublanceolata*	−27.85	43.91	6.94	−41.89	−13.81	−4.01	39	0.000
F. altissima	−70.58	200.42	28.34	−127.54	−13.62	−2.49	49	0.016
F. microcarpa	−115.24	97.74	15.85	−147.37	−83.11	−7.26	37	0.000
F. benjamina	−41.24	153.90	17.31	−75.71	−6.77	−2.38	78	0.020

Table 4. The number of wasps in longer-styled flowers divided by the number of seeds in shorter-styled flowers.

Species	Paired differences					t	df	Sig. (2-tailed)
	Mean	Standard deviation	Standard error mean	95% Confidence interval of the difference Lower	Upper			
F. virens	−14.76	32.76	3.94	−22.63	−6.89	−3.7	68	0.000
F. virens var *sublanceolata*	0.95	16.89	2.67	−4.45	6.35	0.3	39	0.724
F. altissima	−31.58	90.19	13.29	−58.37	−4.80	−2.37	45	0.022
F. microcarpa	−46.07	45.71	7.41	−61.10	−31.05	−6.21	37	0.000
F. benjamina	−33.63	78.40	8.99	−51.54	−15.71	−3.73	75	0.000

trees) were collected from Guangdong, Guangxi, and Yunnan provinces, and observations and experiments were carried out at the South China Botanical Garden (E113°18', N23°06'), in Guangzhou city of Guangdong province.

The developmental phases of figs, are Phase A (pre-female flower phase), the developmental period of the bracts and female flowers; Phase B (female flower phase), the time when female flowers are mature and ready to accept wasps to pollinate and oviposit; Phase C (interfloral phase), the developmental period of wasp larvae and seeds, which begins after the oviposition and pollination; Phase D (male flower phase), the time when male flowers, wasp offsprings and seeds all reach their maturity; and. Phase E (post floral phase), which begins after the wasps disperse from the syconium with pollen inside their body. Then the figs ripen quickly for frugivorous predators (Galil, 1968).

Individual figs were gathered at their male phase (D Phase), as male wasps emerged from their natal ovaries, or at their post-floral phase (E Phase) when all the female wasps had emerged and left an exit hole on natal figs. The figs were brought to the lab and dissected under a dissecting microscope. We counted all the galls in the figs to determine the resource allocation to all the wasps (once the female wasps dispersed, it is not possible to distinguish galls that produce non-pollinating wasps from those that give rise to pollinating ones). Each fig was cut into either two or four parts, and the number of seeds, wasps (including non-pollinating wasps), aborted flowers (undeveloped flowers), and total number of female flowers were counted from the same randomly-chosen section which represented one half or one quarter of each fig. When counting the contents, e.g. the seeds in the figs, we removed the counted female flowers counted one by one so that we could distinguish and count those that had aborted flowers or had contained wasps.

According to previous studies, most non-pollinators occupy the inner layers of ovaries. Seeds in ovaries, excluding the outermost ones, and wasps in ovaries, excluding the innermost ones, were counted in dissected section of the figs of each species to test the 'short-length-ovipositor hypothesis'.

Production of seeds and wasps

Between 40 and 80 figs each were collected from different crops (Table 1), at different times or from different individual trees. For each fig species, the number of seeds, wasps, aborted flowers, and total female flowers were counted. The proportions of seeds, wasps, and aborted flowers were estimated by dividing their average number per fig by the average number of female flowers per fig.

Figs producing only seeds or only wasps

Figs that contained seeds without any wasps or wasps without any seeds were found in some figs in *F. altissima*, *F. microcarpa*, and *F. benjamina*. The proportions of figs with only seeds and only wasps were calculated from the total amount of figs assembled.

Data analysis

All the observed data were analyzed using SPSS 11.5. The comparisons of wasps versus seeds in each species were analyzed by Paired T-test. The multiple comparisons of wasp and seed production among species were analyzed by proc GLM univariate analysis with *post hoc* tests.

3. Results

Production of seeds and wasps in the sampled species

In our material, wasps generally occupied most of the inner and internal layers of ovaries (i.e. near the cavity of figs) and seeds were mostly produced in outer ovary layers (i.e. near the wall of figs) (see Fig. 1b and Table 2). We observed that both seeds and wasps could be produced in any ovary layers in these fig species. The average production of seeds in a fig was significantly higher than that of wasps (including non-pollinating wasps) in all the species sampled and seed production in the inner and internal layers was also significantly higher than that of wasps in the outer ones except for *F. virens* var. *sublanceolata* (Tables 3 and 4).

Among the species sampled, production of seeds and wasps differed significantly. Both seeds and wasps in *F. altissima* were produced at significantly higher rates than in all the other sampled species, while *F. virens* var *sublanceolata* showed the lowest production of both seeds and wasps (Table 5). *F. microcarpa* and *F. virens* exhibited intermediate seed and wasp production. According to our other observations, there was a larger fig diameter but less fruit tissue in *F. altissima* (per. obs.), so we assume that *F. altissima* utilizes more resources for the production of seeds and wasps. However, whether the proportion of unvisited fruit or aborted fruit of *F. altissima* is smaller than in other species, needs further study.

Figs producing only seeds and only wasps

Production of seeds without the presence of any wasps or production of wasps alone without any seeds was only found in three fig species, *F. altissima*, *F. microcarpa*, and *F. benjamina* (Table 6). The average production of seeds in the figs with "only seeds" was less than the normal production of seed in figs with both seeds and wasps in *F. altissima*. However, in *F. microcarpa* and *F. benjamina*, the average production of seeds in "only seed figs" was much higher than that in normal figs and also much higher than that in *F. altissima*.

The average numbers of wasps in the "only wasp figs" in *F. altissima* and *F. benjamina*, were similar to the normal

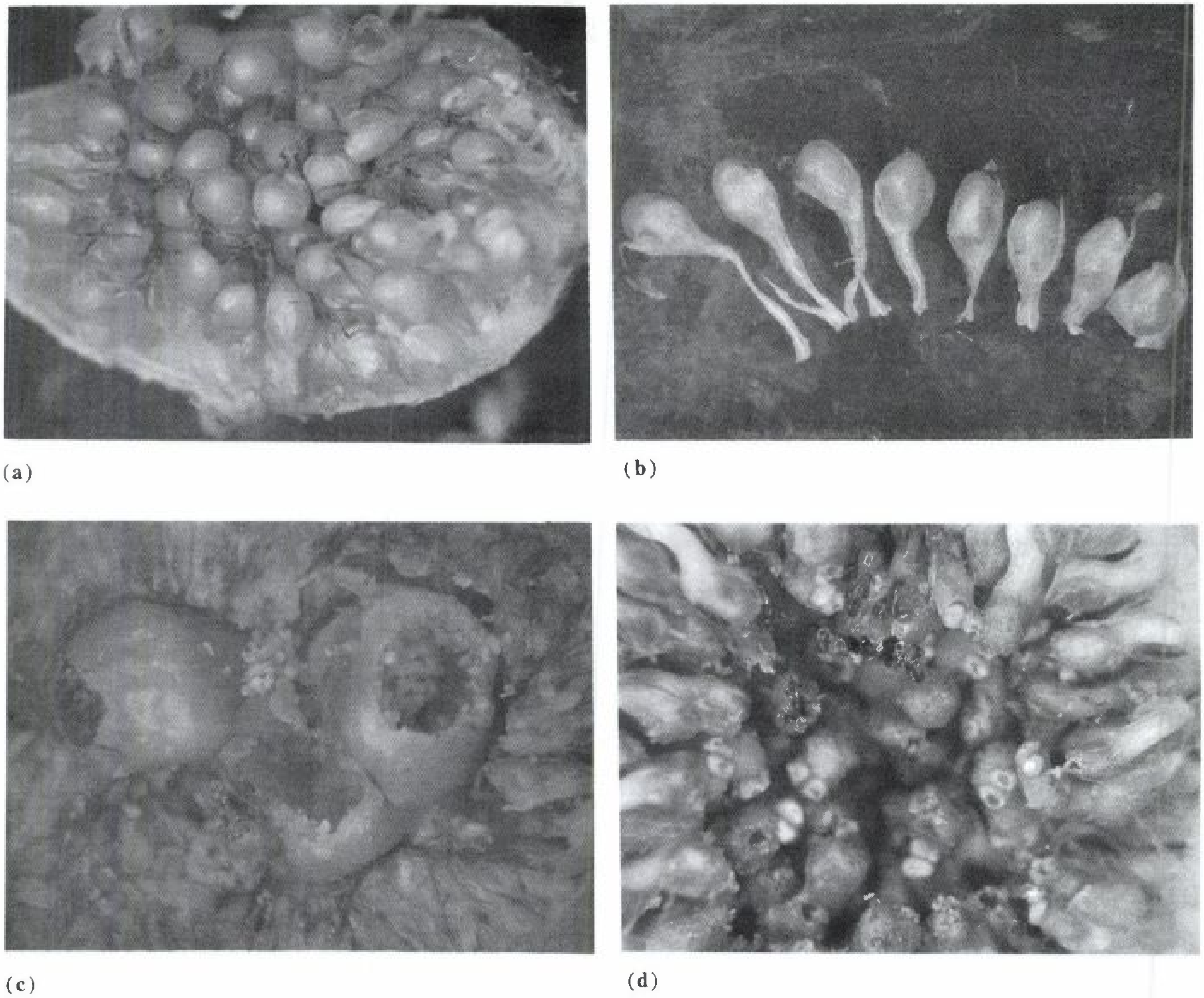

Figure 2. Seed and wasp production in monoecious figs: (a) and (b) seeds produced in female flowers with different pedicel lengths of *F. benjamina*; (c) galls of wasps in only-wasp produced figs in *F. altissima*; and (d) normal galls of pollinators in *F. altissima*.

production of wasps in the figs that produced both seeds and wasps. The average production of seeds in the "only seed figs" in *F. altissima* and *F. benjamina* was much higher than that of wasps in "only wasp figs" though the frequency of "only seed figs" was much lower than that of "only wasp figs" (Table 6). Investigation showed that seeds in the "only seed figs" could be produced in any female flowers with different style or pedicel lengths (Figs. 2a and b). The size of galls in "only wasp figs" was much larger but fewer in number than in normal figs (Figs. 2c and d).

4. Discussion

Several hypotheses have been proposed to explain the allocation of plant resources between figs and fig wasps in an attempt to explain the ratio of seed versus wasp production and why there is no overexploitation between the figs and fig wasps. Comparison of monoecious figs with dioecious figs led previous researchers to believe that the distribution of female flowers in monoecious figs was bimodal and the "short" and "long" style length limited the overexploitation by fig wasps (Ramirez, 1980, 1976; Galil, 1977; Janzen, 1979; Wiebes, 1979). The 'short-length-ovipositor hypothesis' proposed that wasps had ovipositors not long enough to access the long-styled female flowers so the wasps could only oviposit in the short-styled flowers. This would spare the long-styled flowers for seed development. When the unimodal distribution and stratification of female flowers in monoecious figs was tested, results suggested that seeds and pollinator larvae could develop in any layer of ovaries. Style lengths were

Table 5. Mean differences between monoecious fig species for wasp production (above diagonal) and seed production (below diagonal). Mean wasp and seed production by species respectively was: *F. virens*, 113.9 and 141.0; *F. virens* var *sublanceolata*, 60.9 and 88.8; *F. altissima*, 219.4 and 285.7; *F. microcarpa*, 44.9 and 160.2; *F. benjamina*, 67.8 and 109.1. Standard errors of mean differences are presented in brackets. An asterisk (*) denotes mean difference is significant at 0.05 level.

Species	*F. virens*	*F. virens* var *sublanceolata*	*F. altissima*	*F. micorcarpa*	*F. bejamina*
F. virens	–	52.93 (±13.46)*	−103.23 (±12.58)*	68.91 (±13.68)*	45.99 (±11.15)
F. virens var *sublanceolata*	51.82 (±18.46)*	–	−156.16 (±14.41)*	15.98 (±15.39)	−6.94 (±13.18)
F. altissima	−147.07 (±17.25)*	−198.89 (±19.76)*	–	172.14 (±14.62)*	149.22 (±12.27)*
F. micorcarpa	−19.59 (±18.77)	−71.41 (±21.10)*	127.48 (±20.05)*	–	−22.91 (±13.41)
F. bejamina	31.50 (±15.29)	−20.33 (±18.08)	178.56 (±16.83)*	51.08 (±18.39)*	–

Table 6. Only seed or only wasp production in the sampled monoecious figs.

Species		Figs1	Figs2	Figs3	Seeds4	Female flowers5	Wasps6	Female flowers7
F. microcarpa	Number	6.0	–	38	242.7	286.7	–	–
	Percent (%)	15.8	–	–	84.7	–	–	–
F. altissima	Number	2.0	10.0	50	260.0	576.0	184.0	555.3
	Percent (%)	3.3	16.7	–	45.1	–	33.1	–
F. benjamina	Number	5.0	33.0	79	368.8	599.2	52.0	425.6
	Percent (%)	6.3	41.8	–	61.5	–	12.2	–

Note: 1Total figs with only seeds. 2Total figs with only wasps. 3Total sampled figs. 4Average seeds in a fig producing only seeds. 5Average female flowers in a fig with only seeds. 6Average wasps in a fig producing only wasps. 7Average female flowers in a fig with only wasps.

not associated with the probability of maturing seeds or wasps (Anstett et al., 1996; Kerdelhué and Rasplus, 1996; Nedft and Compton, 1996; Otero et al., 1996). The 'unbeatable strategy' was thought of as an alternative mechanism limiting wasp larvae production, because parasites were discovered developing at the expense of pollinator larvae, but not utilizing the free flowers (West and Herre, 1994). In the 'short-length-ovipositor' and 'unbeatable-seeds hypotheses', eggs were thought to be limiting (Nedft and Compton, 1996). However, there was still debate about the 'limited-egg-supply hypothesis' (Bronstein and Hossaert-McKey, 1996).

Recently, Anstett (2001) proposed a new hypothesis to explain the benevolence of wasps in mutualism based on the relationship of seed and wasp production, and the position of flowers in monoecious figs. He suggested that the ratio of seeds to wasps at the syconium level depends on the number of foundresses (female wasps) per fig, and that the selection on ovipositor length may depend on fig style length distribution and total female flowers as well as fig wasp population dynamics. Otero and Ackerman (2002) rejected the 'short-length-ovipositor hypothesis' based on their investigation on female flower style length and seed production in two monoecious figs.

Our results showed that seeds and wasps could both develop in any ovary layers of female flowers, which was is consistent with studies on other monoecious species (West and Herre, 1994; Nedft and Compton, 1996; Ganeshaiah et al., 1999; Otero and Ackerman, 2002). Moreover, some figs in the sampled species produced only seeds in female flowers without any wasps and those seeds could develop in female flowers with any pedicel lengths.

Furthermore, the average production of seeds and wasps was not identical in any species sampled in this study. In each species, the average number of seeds in a fig was always more than that of wasps. This suggested that the short-term reproductive benefits between figs and fig wasps were not identical with respect to the utilization of female flowers (Kjellberg et al., 1987a; Herre, 1989; West and Herre, 1994). The observed "seed-preference of fig production", namely the higher seed production and the production of "only seeds" figs in our study seemed to support the view that figs may dominate the resource allocation in the fig/wasp mutualism (West and Herre, 1994).

According to previous studies, the ratio of seeds versus pollinators depends on the number of foundresses entering a fig at the female phase and increased competition between foundresses decreases the production of wasps (Anstett et al., 1996; Bronstein and Hossaert-McKey, 1996; Joussellin et al., 2001; Nedft and Compton, 1996; Herre and West, 1997; Otero and Ackerman, 2002). The higher seed production in our study may suggest that there were low levels of foundress competitions in the syconia of the sampled species sampled.

The presence of aborted flowers in the figs in our study indicated that wasps – including pollinators and non-pollinators – could not pollinate all the female flowers as effectively and were unable to lay eggs in all the female flowers. Figs producing "only-seeds" or "only-wasps" had less production under natural circumstances than predicted in a previous study (Anstett et al., 1996). The "only-seed" production is very likely related to pollinators or to the re-emergence of fig foundresses (Moore et al., 2003). The "only-wasp" production may be caused by non-pollinating wasps or wasps without pollen (Galil and Eisikowitch, 1971; Bronstein and Hossaert-McKey, 1996; Kerdelhué and Rasplus, 1996; Gu et al., 2003).

Although the mechanism by which figs regulate resource allocation for seeds and wasps needs further work, this study demonstrates that seeds and wasps can develop in female flowers in spite of their positions in figs. Seeds showed an obvious dominance in the production. However, whether the "only-seed" or "only-wasp" production is associated with the evolution of dioecious figs (Kerdelhué and Rasplus, 1996a; Greef, 2002; Dufay and Anstett, 2003) and the mechanism involved are both unclear and deserve attention.

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