
A few more hypotheses for the evolution of dioecy in figs (Ficus, Moraceae)

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In figs (*Ficus*, Moraceae) there are two breeding systems: monoecy is the ancestral condition but approximately half the 750 odd species are functionally dioecious. Three hypotheses have been proposed for the evolution of dioecy in figs, invoking seasonality (Kjellberg et al. 1987), the reduction of non-pollinating wasp species (Kerdelhue and Rasplus 1996), and the persistence of pollinator populations within small groups of trees (Kameyama et al. 1999). However, there are two major problems with these ideas. Firstly, dioecy has probably evolved only twice (Weiblen 2000), which severely limits our ability to test between alternative hypotheses. Secondly, it is very simple to suggest ways in which dioecy can evolve from monoecy (Charnov 1982). To illustrate this problem, and enlarge on some recent progress in our understanding of functionally dioecious figs, we are proposing a few more hypotheses.

Trade-offs in the fig – fig wasp interaction

The fig is a closed, urn-shaped inflorescence (the syconium) lined with uniovulate female flowers and male flowers. Species-specific fig wasps (Agaonidae: Hymenoptera) carrying pollen from their natal fig enter through the narrow ostiole. Once inside, they pollinate and, simultaneously, lay eggs in some of the female flowers, and then die. Ovules that receive an egg develop into a gall on which the larvae feed. Those missed by the wasps, if pollinated, produce a seed. A few weeks later, the wingless male wasps chew their way out and mate with the gall-encased females. The females then emerge and collect pollen, either passively or by actively filling thoracic pollen pockets. Meanwhile, the male wasps cut a tunnel through the syconium wall, and the females disperse. A few days later, the syconia,

which retain the now mature seeds, ripen and are fed on by a diversity of vertebrates.

Dioecious figs differ in that functionally male trees produce wasps and pollen, and female trees only seed. The syconia on male trees have short-styled female flowers, which are easily probed by the wasps ovipositor (Fig. 1A). Conversely, on female trees the flowers have long styles and the ovules are, therefore, inaccessible (Fig. 1B; Galil 1973, Verkerke 1987, Weiblen 2000). Wasps are deceived into entering female syconia, even though they fail to reproduce, through mimicry of the syconia on male trees. From studies on the cultivated fig (*F. carica* L.), males appear to be the heterozygous sex (Storey 1955) and the adult sex ratio is approximately one-to-one. Divergence from parity or evidence of environmental sex determination have not been reported but studies are still limited.

In monoecious figs, male fitness is equivalent to the number of pollen-carrying female wasps that disperse, while female fitness is of course reflected in the number of seed dispersed. Male investment, however, includes the non-dispersing male wasps reared (Fig. 2), although the proportion of males is normally low as a result of Local Mate Competition. In any particular syconium there is a balance between pollen and egg limitation at lower foundress numbers, and over-exploitation of potential seed and an increased proportion of male wasps when there are more foundresses (Fig. 2; Herre 1989, Anstett et al. 1996, Nefdt and Compton 1996). Overlaying this fundamental trade-off are numerous others reflecting the differing roles of rearing wasps or dispersing seed (Table 1), any one of which could potentially afford a route for dioecy to evolve.

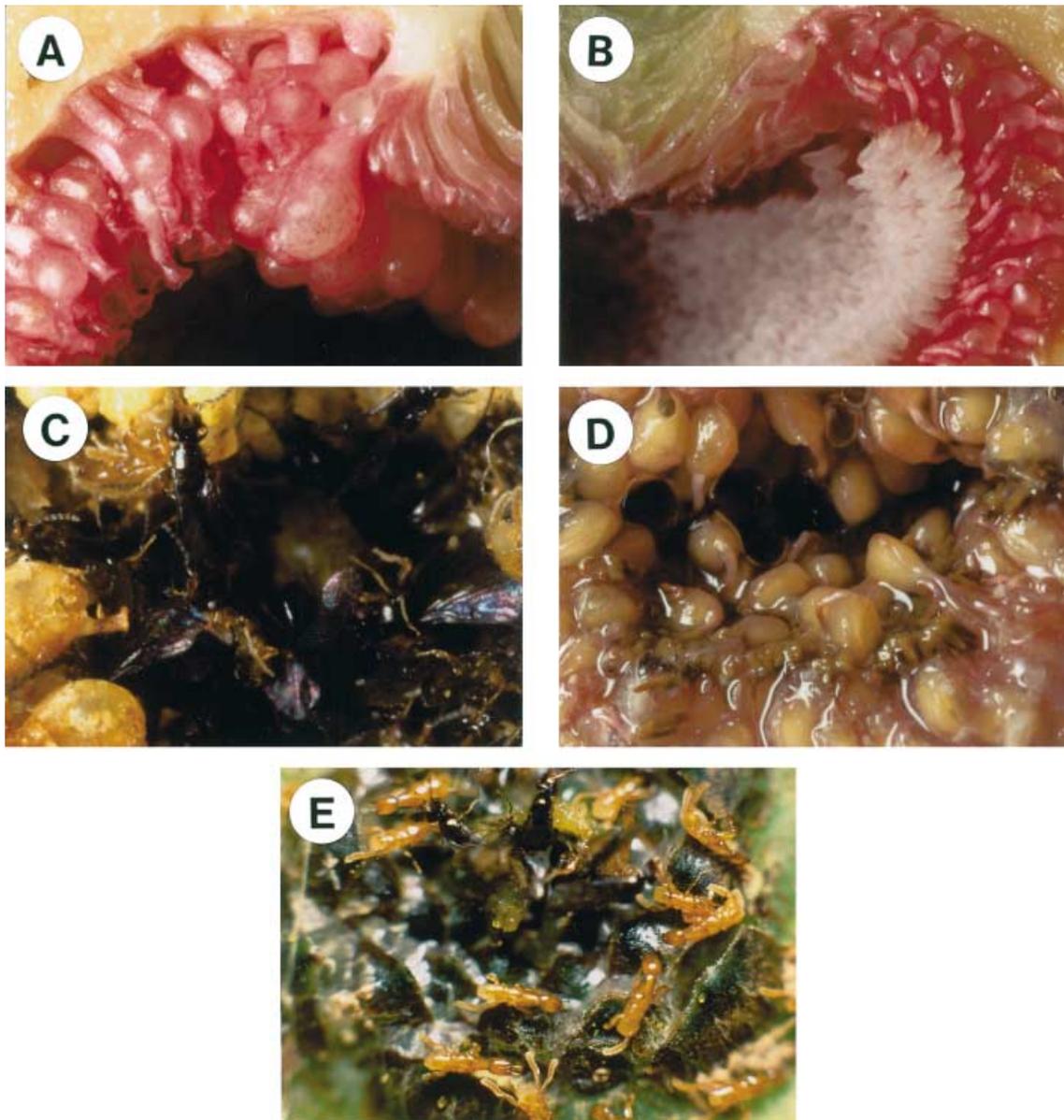


Fig. 1. A–D Cross sections of a dioecious fig, *F. schwarzii* Koord. A: a receptive male syconium showing immature male flowers around the ostiole and the short-styled female flowers with cup shaped stigma, B: a receptive female syconium with long-styled female flowers and flat, white stigma, C: a mature male syconium showing the female pollinators emptying into the wide lumen, D: a mature female syconium with the internal space filled with seed, E: a view of the surface of a mature male syconium of *F. schwarzii*. After cutting a tunnel through the ostiole, male pollinators scatter over the surface distracting the attentions of predatory ants, while the mated female pollinators escape carrying the fig's pollen.

A few possible scenarios for the evolution of dioecy in figs

1) *Disperser driven selection for large, nutritious fruit* – Monoecious figs are inefficient in terms of nutrient investment as roughly 50% of the ovules are destroyed by the pollinators. However, larger fruit tend to be seed rich (Herre 1996), and larger dispersers with potentially longer dispersal distances select bigger figs (Kalko et al.

1996, Shanahan and Compton 2001). But, larger figs also require more foundresses, hence suffer from inefficient male investment (Herre 1989, 1996), and as the variance in foundress numbers also increases, more syconia are either pollen limited or over-exploited by the wasps. Thus, fruit size may be limited by wasp production.

Once past a critical size threshold, positive feed-back to protect more ovules (longer styles), increase pollen

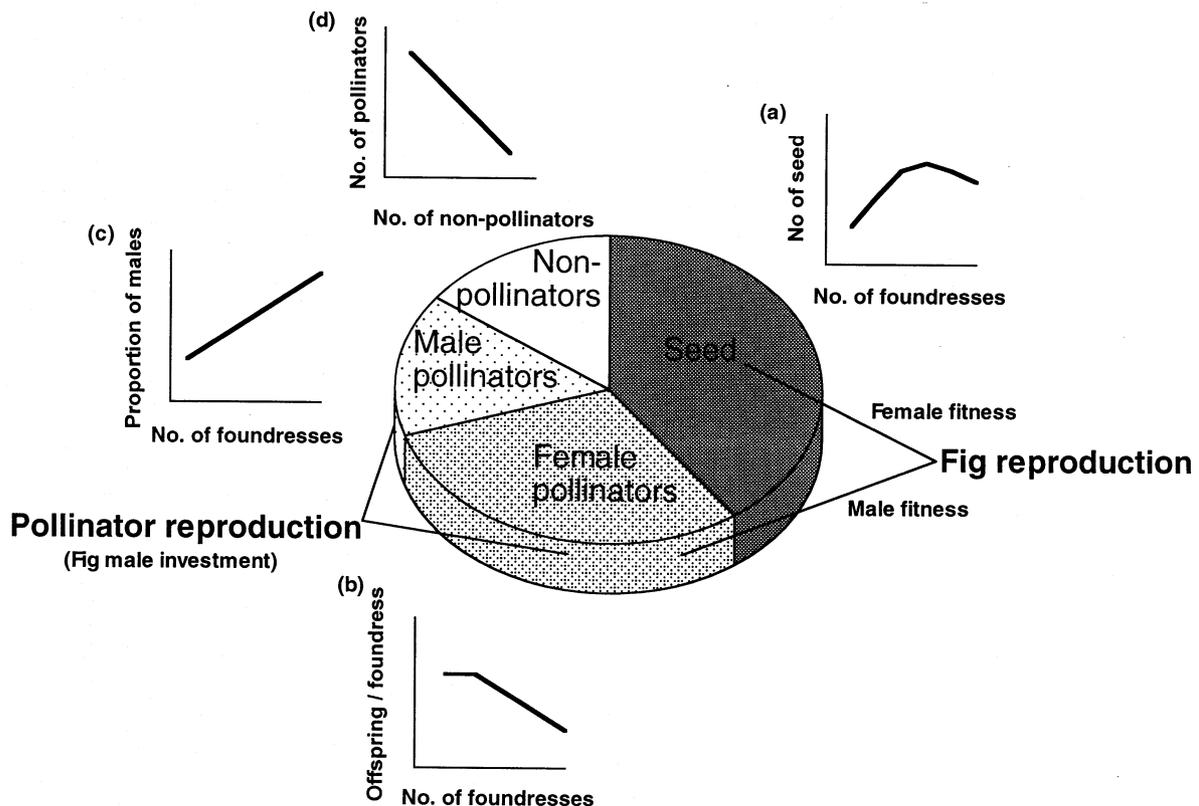


Fig. 2. Schematic representation of the utilisation of fig ovules within the syconium of a monoecious fig. For each pollinator wasp reared a potential seed is eaten. The fig's female fitness and investment is reflected in the number seed dispersed, while male fitness is equivalent to the number of female pollinators that disperse carrying fig's pollen. However, male investment includes the ovules destroyed by the non-dispersing male wasps. (a) At high numbers of foundresses (the parental female wasps that entered the fig to pollinate and oviposit) female fitness may decrease through the over-exploitation of ovules by pollinator larvae, but most syconia are pollen limited (Herre 1989, Anstett et al. 1996, Nefdt and Compton 1996). (b) The reproductive interests of the fig wasp and the fig are in conflict, as the wasp only benefits from laying more eggs. However, the number of offspring per foundress decreases with increasing foundress number (Herre 1989, Kinoshita et al. 2002) indicating a selection pressure on the wasps to avoid syconia entered by too many foundresses. (c) At low foundress numbers the proportion of male wasps is low because of Local Mate Competition, but increases with the number of foundresses (Herre 1985, 1987, Kinoshita et al. 1998). Hence, the fig's male effort becomes progressively more inefficient with increasing foundress number. Moreover, species with high mean foundress numbers suffer from increased virulence of nematode parasites as a result of greater horizontal transmission (Herre 1993) and increased probability of fungal infection (Michalaides and Morgan 1994, Michalaides et al. 1996). (d) Most non-pollinators, galls similar to the pollinator or parasitoids of galls, have a negative impact on pollinator production either through competition for the same ovules or direct predation, but have little effect on seed production (West et al. 1996, Kerdelhue et al. 2000).

saturation (more foundresses), and invest in nutritious pulp would result in proto-female syconia, while proto-male trees would be selected to increase the accessibility of ovules (fewer foundresses) and avoid wasting nutrients in the pulp. Hence, an efficient seed disperser with a preference for large, nutritious fruit could precipitate the evolution of dioecy. The very large size of some dioecious figs (Table 2), the higher foundress numbers in female syconia (Patel and McKey 1998, Weiblen et al. 2001), and indications of better fruit quality (Lambert 1992, Kinnaird et al. 1999), all lend credence to this hypothesis. Cauliflory in some dioecious figs may also be related to the recovery of nutrients from male syconia after the wasps have emerged. In at least one species, *F. benguetensis* Merr., female syconia are borne

amongst the leaves and dispersed by bats, while on male trees they are in tight clusters at the base of the trunk where they rot after emergence of the wasps (R.D. Harrison, unpubl.).

2) *De-coupling of wasp and seed size* – Fig seed are very small reflecting an unpredictable environment and the need to reach rare micro-sites, but larger pollinators carry more pollen, have more eggs, and experience higher survival. Because pollinators utilise the same ovules, wasp size is correlated to seed size in monoecious figs and the syconium has been described as a step-down valve for pollinator size (Herre 1989). However, pollinators have a rather low probability of reaching a receptive syconia which must limit selection for larger wasps and stabilise the interaction.

Table 1. Known and potential (*italic*) trade-offs between female (seed production) and male (pollinator and pollen production) roles in monoecious figs. The sign indicates the direction of the effect, (+) positive, (–) negative, (o) or neutral. Refer to text for sources.

	Seed production	Pollinator + pollen production
<i>Pollination and oviposition</i>		
Ovule		
More foundress pollinators	(+) Each ovule develops into one seed Greater % of flowers pollinated	(–) Or is eaten by one pollinator larvae Higher % of male pollinators, greater virulence of nematodes, higher risk of fungal infection
Smaller ovules	(–) Greater % of ovules eaten (+) <i>More seed per fruit, greater coverage of germination microsites</i>	(–) Smaller wasps carry less pollen (passively pollinated spp.), and have lower fecundity (more foundresses)
More male flowers	(–) <i>Less space for seed</i>	(+) Higher pollen loads, especially in passively pollinated species (–) less space for galls
Variable style length	(+) Protects some seed	(–) <i>Oviposition less efficient, creates niche for non pollinators</i>
<i>Syconia structure</i>		
Larger syconia	(+) More seed per fruit	(–) More foundresses required
Larger lumen	(–) <i>Fewer seed per fruit</i>	(+) <i>Protected environment for grooming, easier emergence from galls (–) less space for galls</i>
Temperature regulation	(o) <i>?Not so strict</i>	(–) Strict, larger syconia require more water for evaporative cooling
<i>Other interactions</i>		
More nutrients in fruit	(+) <i>Better quality seed dispersal</i>	Zero benefit, ovules eaten by pollinator wasted
Non pollinators	Little or no impact	(–) Compete with, or parasitize pollinator larvae
Ant predators	(o) <i>Delay pollination/induce pollen limitation</i> (–)	(+) Protect against non pollinators ((–) some predation of pollinators)
<i>Phenology</i>		
Crop asynchrony	(+) <i>Covers wider seed dispersal/germination environments</i>	(–) Longer window for non pollinators to oviposit
Self pollination	(–) Inbreeding depression	(+) Assured high pollinator production (–) min. reduction of pollen dispersal
Short development time	(?–) Seed development restricted to schedule of wasp development, usually longer in dioecious figs	(+) Shorter generation time, shorter window for parasitoids to attack
Short wasp emergence and fruiting phases (to avoid overlap)	(–) Much seed wasted, shorter germination and seed dispersal window	(–) Restricted to narrow pollination window because of short lifespan of pollinators
Large, infrequent crops	(+) Attracts wide range of seed dispersers	(–) Fewer pollination opportunities
Seasonality	There is a best season for seed dispersal/germination	Best season for male effort is earlier, so wasps pollinate seed of best seed season

Increased selection for larger wasps (e.g. increased density or fruiting frequency of fig trees) could, therefore, exacerbate this trade-off and induce dioecy. The large differences in the numbers (Table 3) and sizes of seed and wasp offspring (*F. stolonifera* King, seed: 0.6 ± 0.03 mm, Galls: 1.3 ± 0.06 mm; *F. cereicarpa* Corner, 0.8 ± 0.04 mm, Galls: 1.4 ± 0.10 mm; R. D. Harrison, unpubl.) especially in species with larger syconia, and the higher fruiting frequency in many dioecious species (Corlett 1987, 1993, Patel 1996, Harrison 2000, Harrison et al. 2000) support this idea. Interestingly, in at least two species (*F. deltoidea* and *F. variolosa*) the seeds are bigger than the wasps suggesting a possibility of the reverse of the mechanism given above.

3) *Ant predation selects for larger lumens* – In many dioecious figs the male syconia swell suddenly just before the emergence of the wasps, creating a large lumen (Fig. 1C; Galil 1973, Verkerke 1987, Patel and Hossaert-McKey 2000). This allows the female wasps to empty out into a protected space, where they can collect pollen and groom. In these species, the male wasps co-operate in cutting a wide tunnel, usually through the ostiole, enabling the female wasps to disperse rapidly and escape ant predators. The males may also spill over the surface of the syconia, which distracts the ants while the female wasps are escaping (Fig. 1E). Male wasps will continue to search for unmated females while the latter remain in their galls, and hence this co-operative male behaviour is probably dependent

Table 2. Comparison of mature female and male syconia sizes (mm) for some functionally dioecious figs.

Ficus section	Species	Female		Male		Source
		Height	Breadth	Height	Breadth	
Ficus	<i>F. fulva</i> Reinw.		16.0 ± 0.2		14.8 ± 0.2	Harrison et al. 2000
	<i>F. grossularioides</i> Burm.		10–20		10–25	Corlett 1993
	<i>F. hirta</i> Vahl.	15–17	15–17	18–28	15–25	Hill 1967
	<i>F. pyriformis</i> Hook.	25–38	17–23	25–35	14–19	Hill 1967
	<i>F. variolosa</i> Lindl.	9–11	9–10	12–20	11–14	Hill 1967
Kalosyce	<i>F. callicarpa</i> Griff var. <i>augustifolia</i>	approx. 50	approx. 70	100	140	Corner 1938
Neomorphe	<i>F. variegata</i> Bl.	20–22	22–26	25–35	25–41	Hill 1967
Rhizocladus	<i>F. pumila</i> L.	60–75	55–65	60–75	55–65	Hill 1967
	<i>F. sarmentosa</i> Buch.	11–12	11–12	11–12	11–12	Hill 1967
Sycidium	<i>F. exasperata</i> Vahl.		17.2 ± 2.3		19.3 ± 3.7	Patel and Hossaert McKey 2000
	<i>F. obscura</i> Bl.	8.03 ± 0.6	8.7 ± 0.6	9.5 ± 0.4	9.3 ± 0.6	Lambert 1992
	<i>F. parietalis</i> Bl.	15.57 ± 1.4	16.6 ± 1.3	23.9 ± 2.1	29.1 ± 1.7	Lambert 1992
	<i>F. asperifolia</i>	20	20	24	32	Verkerke 1987
	<i>F. irisana</i> Elm.		14.1 ± 0.4		13.3 ± 2.3	Chen 2000
Sycocarpus	<i>F. fistulosa</i> Reinw.	14–17	15–18	20	30	Galil 1973
	<i>F. hispida</i> L.		26.6 ± 3.7		26.0 ± 4.6	Patel and Hossaert McKey 2000
	<i>F. hispidioides</i> S. Moore		47 ± -0.1		51 ± 0.1	Weiblen 2001

Table 3. Comparison of ovule, gall and seed numbers in some functionally dioecious figs

Ficus section*	Species	Sex	Ovules	seed/gall	Source
Ficus	<i>F. carica</i> L.	f	1200		Khadari et al. 1995
		m	1200		
	<i>F. erecta</i> Thumb var. <i>beeheyana</i>	f	420	203 ± 90	Tzeng 1997
		m	930	346 ± 215	
	<i>F. hirta</i> Vahl.	f	~500		Hill 1967
		m	~400		
	<i>F. grossularioides</i> Burm.	f	425 ± 82	260 ± 50	Corlett et al. 1990
		m	377 ± 51	184 ± 45	
	<i>F. pyriformis</i> Hook.	f	~500		Hill 1967
		m	~500		
<i>F. variolosa</i> Lindl.	f	40	20–25	Hill 1967	
	m	150–250	?		
Neomorphe	<i>F. variegata</i> Bl.	f	216 ± 46	63 ± 20%	Weiblen et al. 1995
		m	167 ± 37	69 ± 19%	
Rhizocladus	<i>F. pumila</i> L.	f	~5–6000		Hill 1967
		m	~5–6000		
	<i>F. sarmentosa</i> Buch.	f	~200		Hill 1967
		m	~150		
Sycidium	<i>F. asperifolia</i> Miq	f	~1700		Verkerke 1987
		m	~1000		
	<i>F. exasperata</i> Vahl	f	590	566 ± 161	Patel and Hossaert McKey 2000
		m	440	345 ± 138	
<i>F. heteropleura</i> Bl.	f	77 ± 6	66.7 ± 4	Corlett et al. 1990	
	m	125	78 ± 27		
	<i>F. irisana</i> Elm.	f	388 ± 81	209 ± 94	Chen 2000
		m	273 ± 46	115 ± 63	
Sycocarpus	<i>F. fistulosa</i> Reinw.	f	1393 ± 120	1218 ± 49	Corlett et al. 1990
		m	816	208 ± 62	
	<i>F. hispida</i> L.	f	1153	1077 ± 310	Patel and Hossaert McKey 2000
		m	732	597 ± 266	
	<i>F. hispidioides</i> S. Moore	f	4125 ± 625	85.5 ± 3.2%	Weiblen et al. 2001
		m	3749 ± 312	52.3 ± 4.3%	

*sensu Corner 1965.

on the female wasps being able to empty into the lumen (F. Kjellberg, pers. comm.).

However, large lumens restrict the number of seed in a fruit, especially for smaller syconia. In dioecious figs, seeds fill the internal space of mature female syconia (Fig. 1D) in all but the largest diameter species. Hence, it is easy to envisage how an increase in predation by ants could induce dioecy. Larger lumens and protection from ant predation may also be linked to active pollination, as in passively pollinated species the lumen is usually loosely filled with male flowers and pollen dusted interfloral bracts, requiring the wasps to groom after emerging on to the surface of the syconium (Kjellberg et al. 2001).

4) *Non-pollinators and predator satiation* – Non-pollinating wasps are a ubiquitous element of the fig – fig wasp interaction and usually have a negative impact on pollinator production but little effect on seed production (West et al. 1996, Kerdelhue et al. 2000). The time-window during which a given non-pollinator species can oviposit on any particular syconium is quite short (Kerdelhue et al. 2000, Weiblen et al. 2001), so if non-pollinator populations were high, syconia with more usable ovules might raise a greater proportion of pollinators through the effects of predator satiation, especially if combined with a high degree of crop synchrony and modifications to flower structure that enhanced the pollinators ability to monopolise ovules (short styles). Conversely, individuals with fewer usable ovules would have a reproductive output decidedly orientated towards seed production as most wasps would be non-pollinators. These individuals would be selected to invest more in ‘inviolate seed’ (West et al. 1996) and suppress inefficient wasp production. These proto-female figs would also serve as a non-pollinator sink adding to the predator satiation effect (Weiblen et al. 2001). Hence, non-pollinators could quickly drive a population of formerly monoecious figs towards two end points, individuals with non-exploitable seed ovules or usable gall ovules.

This scenario is supported by the fact that non-pollinators are generally unable to occupy the ovules of female syconia, the shorter development time and higher synchrony of crops on male trees compared to female trees in many dioecious figs (Table 4, Corlett 1987, 1993, Patel 1996, Harrison 2000), and from the higher proportions of non-pollinators in crops with higher levels of asynchrony in monoecious figs (Cook and Power 1996, West et al. 1996). Avoidance of non-pollinators through predator satiation is a possible explanation for the high degree of crop synchrony at receptivity observed in most monoecious figs.

5) *Chronic pollinator shortages, crop asynchrony and inbreeding depression* – When monoecious fig trees suffer from low pollination success they develop a more staggered phenology (Bronstein and Patel 1992, Cook and Power 1996). But if asynchrony develops to the

point that receptive and male phase syconia overlap, which rarely happens, self-pollination occurs. This is an efficient mechanism for boosting pollinator numbers, as survival must be high for such short dispersal distances. Hence, if there were a chronic scarcity of pollinators, considerable advantage would accrue to the male effort. The cost of reduced pollinator dispersal would be minimal as most syconia are pollinated on the first day of wasp emergence, and wasps emerging on subsequent days are thus still forced to disperse (as occurs in some dioecious figs; R. D. Harrison, pers. obs.). However, the low value of selfed seed would create a trade-off. Proto-male individuals would be selected to eliminate seed production, while proto-female trees would benefit from avoiding inbreeding by eliminating pollinator production.

This type of completely asynchronous phenology has been reported in two species of dioecious fig, *F. hispida* L. (Patel 1996) and *F. cereicarpa* Corner (Harrison 2000). In *F. cereicarpa* a single male tree maintained a continuous production of pollinators for 18 months. The strongly seasonal phenology of *F. carica* (Kjellberg et al. 1987) and *F. erecta* Thunb. (Tzeng 1997) also involves the production of a special wasp breeding cohort on male trees in the spring. Moreover, in all dioecious figs studied so far the duration of seed development is approximately twice as long as that of wasp development (Table 4, excepting ‘over-wintering’ crops in seasonal species), suggesting selection for the rapid cycling of wasp cohorts might have a negative impact on seed quality (Patel and McKey 1998, Harrison et al. 2000).

Discussion

The diversity of dioecious figs and the plethora of ways in which sexual specialisation has occurred, makes suggesting ways in which dioecy may have evolve quite easy. Unfortunately, however, the value of any of these hypotheses is limited by our inability to test competing ideas, and because similar evidence can be invoked to support different hypotheses. In a more general comparison, embracing a wider range of plants, figs may be interesting but this would require identifying the characters associated with dioecy that are not unique to fig biology.

One important distinction to be drawn is that between factors that may contribute to maintaining dioecy and those that are responsible for its evolution. For example, the bimodal distribution of style length appears to be an essential character of dioecious figs, and in the two independent reversals from dioecy to monoecy style lengths reverted to a unimodal distribution, as found in ancestral monoecious lineages (Weiblen 2000). Also, while studying the evolution of dioecy may be problematic, a better understanding of

Table 4. Duration of developing (C phase) and male/fruit (D/E) phases for several functionally dioecious figs

Ficus section	Species	Sex	Phase (days)		Source
			developing	male/fruit	
Ficus	<i>F. fulva</i> Reinw.	f	55.2 ± 3.21	10.4 ± 1.25	Harrison et al. 2000
		m	29.9 ± 1.76	7.0 ± 0.62	
Kalosyce	<i>F. aurantiacea</i> Griff.	f	total*	> 7months	Chou and Yeh 1995
		m	total*	10–11 weeks	
Syceidium	<i>F. exasperata</i> Vahl.	f	64.4 ± 20.3	7.0 ± 0.0	Patel and McKey 1998
		m	57.4 ± 6.3	7.0 ± 1.5	
	<i>F. grossularioides</i> Burm.	f	total*	70	Corlett 1993
		m	total*	65	
Sycocarpus	<i>F. hispida</i> L.	f	53.9 ± 7.7	7.0 ± 2.8	Patel and McKey 1998
		m	37.1 ± 4.9	7.0 ± 0.0	
	<i>F. fistulosa</i> Reinw.	f	total*	70–100	Corlett 1987
		m	total*	70–100	
	<i>F. schwarzii</i> Koord.	f	85.1 ± 14.7	32.0 ± 12.7	Harrison 2000
		m	39.0 ± 5.2	13.9 ± 3.6	

*Only estimates of the total period of syconia development, from first appearance to removal available.

sexual specialisation in dioecious figs is both attainable and very interesting because it reveals much about the different selection pressures acting on seed and wasp production.

Another interesting question is, why are monoecious figs so successful? If it is so simple to suggest mechanisms for the evolution of dioecy with all its apparent advantages, then why are not all figs dioecious? A curious character of many monoecious figs is that, despite low densities, they produce large, infrequent crops. Hence, the density of trees bearing crops at any moment is phenomenally low, and the pollinators must disperse long distances (Nason et al. 1996). However, low foundress numbers (Herre 1989) may make it advantageous to benefit from both pollen and wasp eggs, and large synchronous crops attract a diverse array of dispersers despite limits to fruit quality. Given the improbability of either wasps or seeds surviving selection will tend to favour large numbers of small seeds and wasps, and a combination of high synchrony and long distances between individuals should limit non-pollinator populations. So large infrequent crops may in fact stabilise monoecy.

Monoecious and dioecious figs thus appear to be associated with divergent suites of characters, which is possibly why switches between them have occurred so infrequently. However, figs are very diverse, and both monoecious and dioecious groups include a wide array of species. Until more species have been studied, and we have a clearer picture of the phylogenetic relationships between them, it is difficult to reliably identify correlated characters.

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