

Non-pollinating Afrotropical fig wasps affect the fig-pollinator mutualism in *Ficus* within the subgenus *Sycomorus*

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Ficus are species-specifically pollinated by chalcidoid wasps (Agaonidae), and the fig tree-fig pollinator mutualism has long been studied. A diversity of other chalcids, both gall-makers or parasitoids, co-occur in each monoecious *Ficus* species, and use the fig resource by developing in ovaries that they transform into galls. The oviposition sequence and impact on the mutualism of these non-pollinating fig wasps were studied on two *Ficus* species of the subgenus *Sycomorus* in the Ivory Coast.

Field observations, fig measurements and counts of wasps and seeds from mature figs were conducted. Four groups of fig wasp species oviposit in the ovaries at different stages of syconial development, and were demonstrated to lay eggs in the internal ovary layers; the most external flowers seem to be protected against oviposition and thus develop into seeds. Non-pollinating wasp species, by parasitizing pollinator larvae or by competing for oviposition sites, have a significant negative impact on the pollinator population and dynamics, and thereby on *Ficus* male function (i.e. pollen dispersal). In contrast, but for one species, they do not affect the seed production, that is, the tree female function.

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Almost all of the ca 750 fig species (Berg 1989) with few exceptions (Rasplus in press) are pollinated by a single species of chalcidoid wasp from the family Agaonidae, which entirely relies upon the fig resource for its reproduction. The fig or syconium is an urn-shaped receptacle that contains both female and male flowers. As the female primordia reach maturity and the stigmata become receptive, pollen-loaded female wasps, attracted by host-specific volatiles (Ware et al. 1993), enter the fig cavity through the ostiolar bracts. These foundresses lay eggs through the styles of a certain proportion of the female flowers, passively or actively pollinate the others and die. When their offspring reaches the adult stage, the male flowers mature; the emerging female wasps then escape from the syconium in search of an attractive fig and disseminate pollen. According to Galil and Eisikowitch (1968), the five phases of the syconial growth are designated as follows: Phase A (pre-female): young sy-

conia prior to the receptivity of female flowers. Phase B (female): pollen-loaded females penetrate into the syconial cavity, oviposit in the ovaries and pollinate the female flowers. Phase C (interfloral): wasp larvae develop within the occupied ovaries which are transformed into galls. Phase D (male): male flowers mature, wasps reach the imaginal stage; males fertilize females before they leave the syconium via the tunnel chewed by the pollinator males. Phase E (post-floral): syconia ripen, grow in size and become coloured and soft.

The organization of this obligate mutualism has long been studied. Many authors (Ramirez 1970, Galil 1977, Janzen 1979, Wiebes 1979) have paid attention to this species-specific plant-insect interaction and consider it as a remarkable example of coevolution (Kjellberg et al. 1987; but see Lachaise 1994).

However, such a mutualism should not be artificially isolated from its multi-species community context. A di-

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versity of non-pollinating chalcidoid wasps are also associated with each species of monoecious tropical fig tree (up to thirty species: Compton and Hawkins 1992). Those insects, reclassified by Bouček (1988) as Aganidae, are taxonomically, ecologically and biologically poorly known (Wiebes 1977, Gibson 1993), but their influence on the mutualism can no longer be ignored (Bajinath and Ramcharun 1988, Bronstein 1991, West and Herre 1994). The majority of them are assumed to be species-specific (Ulenberg 1985, van Noort 1993a, b, 1994), but this supposition needs to be confirmed by further taxonomical studies.

Like pollinators, a few non-pollinating fig wasps, considered as true gall-makers, enter the fig receptacle forcing their way between the ostiolar bracts to oviposit through the styles; however, they lack pollen-loading adaptations, and hence are unable to efficiently transport pollen (Galil and Eisikowitch 1969, Galil et al. 1970) but see Newton and Lomo (1979). Unlike pollinators, however, most of the non-pollinating fig wasps oviposit through the fig wall in the ovaries or in previously gall-transformed flowers and do not transfer pollen. They may nonetheless have a potentially great impact on the system by competing for oviposition sites or even killing pollinator larvae, or by using fertilized ovaries and thus eating a certain proportion of seeds. Regardless of the way they oviposit however, all the non-pollinating fig wasps are directly dependent upon the fig tree-fig pollinator relationship for their survival (Bronstein 1991).

Monoecious figs are receptacles in which flowers develop at different heights in a space-stressed environment (Fig. 1), and present imperfect heterostyly (Verkerke 1989). The purpose of the present work was to test whether or not non-pollinating fig wasps directly affect the success of two African fig/pollinator mutualisms. There are two conflicting hypotheses:

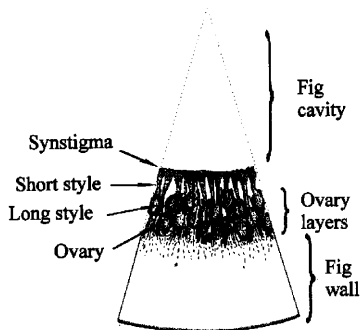


Fig. 1. Schematic representation of female flowers within a fig.

On the one hand, non-pollinating fig wasps may be commensal in relation to the mutualism. Owing to different ovipositor lengths, the various gall-maker species could be expected to reach different ovary layers, thus limiting interspecific competition for oviposition sites and not affecting the pollinator offspring development. If they only oviposit in unpollinated ovaries, the seed production will not be lowered. Consequently, they may have no impact on the pollinator dynamics, or on the *Ficus* male and female functions.

On the other hand, non-pollinating fig wasps may be parasites in relation to the mutualism. Many of them are assumed to be parasitoids or inquilines of the pollinator (Janzen 1979, Ulenberg 1985, Godfray 1988, Compton et al. 1994), and therefore to have a direct influence on the population dynamics of the latter. Some others are gall-makers; these may oviposit in the same ovary layers as the pollinator and act as competitors, or lay eggs in pollinated flowers and thus could be functional seed eaters. Consequently, the non-pollinating fig wasps, either parasites or gall-makers, may have a negative impact on both the female and on the male functions of the tree, and on the pollinator dynamics.

Field observations permitted us to characterize the non-pollinating versus pollinating wasp oviposition sequences in relation to fig growth; counts of seeds and representatives of the various insect species provided data concerning the impact of the non-pollinating insects on each of the two mutualistic systems studied.

We argue here that from both ecological and evolutionary points of view, it is important to take into account the presence of the non-pollinating fig wasps while studying the fig tree-fig pollinator system. Ignoring the non-pollinating fauna's impact in the coevolution model would lead us to underestimate important selective pressures on the mutualist partners.

Study site

The study site is located in the Ivory Coast, 160 km north-west of Abidjan, in the Lamto Ecological Station (5°02'W-6°13'N). The area is situated in the southern part of the arboreal savanna which penetrates the partially destroyed rain forest of the southern Ivory Coast. Every year in January, villagers set fire to the dry savanna. This management practice drives biological cycles of the savanna, favouring geophytic and hemiphytic vegetation, and keeping the savanna from evolving towards a semi-deciduous climax forest.

Study system

We have focused on two *Ficus* of the subgenus *Sycormorus*, *Ficus sur* Forskål and *F. vallis-choudae* Delile, that have distinct, albeit very similar faunas. Only five species of this subgenus can be found in continental Af-

rica (Berg and Wiebes 1992). All species are monoecious, have imperfect heterostyly and a low number of staminate flowers relative to other species (2 to 3% of the total number of flowers in subgenus *Sycomor*, vs 10 to 30% in other *Ficus* sections: see Berg 1989 and Verkerke 1989). The *Ficus* investigated are found at high densities in the Lamto Ecological Station.

Ficus sur is a widely distributed and common species in savannas, secondary forests, woodland and moist forests of Africa, up to 1800 m in altitude (Berg 1990). It is a moderate-sized tree, ranging from 4 to 25 m in height, bearing figs on leafless branchlets hanging down from the trunk and the bigger branches. The mature fig is a subglobose syconium measuring 2–4 cm in diameter and containing about 3000 flowers (Verkerke 1988a).

Ficus vallis-choudae is widely distributed in woodland and often flooded places, and can be found from Guinea to Ethiopia, and south to Zimbabwe and Mozambique. This is the only non-cauliflorous species of the subgenus *Sycomor* in continental Africa (Berg 1990). It is a tree, 10 to 20 m tall, bearing solitary figs in the leaf axils. The mature syconium is a subglobose receptacle of 5–10 cm in diameter containing more than 4000 flowers (Kerdellhué unpubl.).

Both species are favoured in fire-protected savanna and high densities of trees are observed in such areas (Vuattoux 1970).

Like all species of the subgenus *Sycomor*, both *Ficus* studied are pollinated by *Ceratosten* (Agaonidae: Blastophagini) species. *C. megacephalus* pollinates *F. vallis-choudae*, and two species of *Ceratosten*, *C. silvestrianus* Grandi and *C. flabellatus* Grandi, co-occur in *Ficus sur*. *Ceratosten capensis* Grandi is also occasionally reported as a pollinator of *F. sur* in West Africa

(Michaloud et al. 1985, Compton et al. 1994), but this is definitely a misidentification and we are now quite confident that this species uniquely occurs in South and East Africa (Wiebes 1989) and is absent from West Africa (Rasplus in press). In *Ceratosten* species, the females actively fill their thoracic pockets with pollen just before emergence; in spite of the cleansing movements of the insects, the pollen is thus safely carried to an attractive young syconium (Galil and Eisikowitch 1969), where the foundresses actively pollinate, unloading the thoracic pollen pockets by the use of their fore-legs while ovipositing.

The non-pollinating fig wasp faunas of both *Ficus* species are summarized in Table 1. Descriptions of the new species and revision of the non-pollinating wasps occurring in the *Ficus* of the subgenus *Sycomor* are presently in progress (Rasplus and Kerdellhué unpubl.). The fauna of *Ficus sur* is significantly more speciose than that associated with *F. vallis-choudae*. Four genera of chalcidoids are associated with both *Ficus* species. Most of the wasp species associated with members of the subgenus *Sycomor* are species-specific.

Biological data are scarce about non-pollinating fig wasps. *Sycophaga* species (Agaonidae: Sycophaginae), confined to the Afrotropical region, are all believed to be gall-makers, which was confirmed for the species involved in our study. The females penetrate the fig through the ostiole, which is composed of numerous bracts that apically close the fig (Galil and Eisikowitch 1968), and lay eggs directly in the flowers, as the pollinators do. They are able to induce parthenogenetic proliferation of nucellar tissues, which allows the development of the larvae that feed on it, and to inhibit fig abortion (Galil and Eisikowitch 1968). They, however, re-

Table 1. Taxonomy and biology of the non pollinating fig wasp faunas occurring in West Africa in the two species of *Ficus* studied.

FAMILY Sub-family Genus	<i>Ficus sur</i>	<i>Ficus vallis-choudae</i>	Biology
AGAONIDAE			
Agaoninae			
<i>Ceratosten</i>	<i>silvestrianus</i> Grandi <i>flabellatus</i> Grandi	<i>megacephalus</i> Grandi	Pollinators. Enter the fig through the ostiole
Sycophaginae			
<i>Sycophaga</i>	<i>silvestrii</i> Grandi	<i>silvestrii</i> Grandi	Gall-makers. Enter the fig through the ostiole
<i>Apocryptophagus</i>	sp1 sp2 sp3	sp4	Gall-makers. Oviposit through the fig wall
Sycoryctinae			
<i>Apocrypta</i>	<i>guineensis</i> Grandi	<i>robusta</i> Grandi	Parasitoids or inquiline. Oviposit through the fig wall
<i>Sycoscapter</i>	<i>nigrus</i> (Risbec) sp2	<i>nigrus</i> (Risbec) sp2	Parasitoids or inquiline. Oviposit through the fig wall
Epichrysolallinae			
New genus near <i>Acophila</i>	sp1		Gall-maker. Oviposit through the fig wall
EURYTOMIDAE			
<i>Sycophila</i>	n.sp.		Parasitoids or inquiline. Oviposit through the fig wall

main dependent on the mutualists to escape from the fig through the exit tunnel chewed by the pollinator males. Our data show that *S. silvestrii* is found in several *Ficus* species around Lamto (*F. sur*, *F. vallis-choudae*, *F. Sycomorus* and *F. mucuso*: Rasplus and Kerdelhué unpubl.). Species of *Apocryptophagus* (Agaonidae: Sycophaginae), an Old World genus, oviposit from outside the fig (Ansari 1967). Like all Sycophaginae (Bouček 1988, 1993), they are assumed to be gall-forming (Godfray 1988), an observation that is supported here at least for one of the species studied (i.e. *Apocryptophagus sp1*).

The genus *Apocrypta* (Agaonidae: Sycoryctinae) was recently revised (Ulenberg and van Pelt 1985), and all the species known so far appear strictly associated with those *Ficus* pollinated by *Ceratosolen*. *Apocrypta* are therefore believed to be parasitoids or inquilines of the *Ceratosolen* and some other gall-makers (*Apocryptophagus*, *Sycophaga*). We call 'parasitoid' any insect whose larva directly feeds on the developing larva of another species. An 'inquiline' is supposed to be phytophagous but unable to induce gall formation; the adult thus oviposits in a previously gall-transformed ovary occupied by a gall-maker larva. Inquilines may be commensal but can also develop at the expense of the gall-maker whose larva finally starves to death. In that case, they are functionally parasites. It is uncertain whether the death of the gall-maker larva is caused directly or indirectly by the larva of *Apocrypta* (Godfray 1988). *Sycoscapter* species (Agaonidae: Sycoryctinae) are poorly known and thought to be parasitoids or inquilines of pollinator. They seem to be less species-specific than any other fig wasps. The two species observed in Lamto are widespread in Africa and occur on most fig species within the *Sycomorus* subgenus.

All the species of Epichrysomallinae are gall-makers within the syconium; they usually develop galls in the flowers (Galil and Copland 1981), but also in the fig wall (Rasplus unpubl.) or on twigs (Ferrière 1929). In Africa, the subfamily is well represented with nearly 40 species, mostly undescribed. One species occurs in Lamto on *Ficus sur*. The species of *Sycophila* (Eurytomidae) found on *F. sur*, like most of the African species of eurytomid fig wasps, is associated with galls of Epichrysomallinae (Compton 1992). Whether it is a parasitoid, inquiline or entomophytophagous (Zerova and Fursov 1991) is still a matter of debate.

Even though the exact biology of the non-pollinating fig wasps is still questionable, we considered the species of *Apocrypta*, *Sycoscapter* and *Sycophila* as the only true parasitoids and inquilines, assuming that all the others were strictly gall-makers.

Except for the Epichrysomallinae and Eurytomidae species, all the fig wasps involved have wingless males and winged females. Males emerge from the galls into the syconial cavity just before females. Copulation takes place either in the female galls (*Apocryptophagus*, *Apocrypta*, *Sycophaga* and *Ceratosolen* species), in the fig cavity just after the female emergence (*Sycoscapter*), or

outside the syconium (*Sycophila* and *Acophila*) (Rasplus unpubl.). Then, males of the pollinator chew an exit tunnel through the fig wall, and the females of all the species present leave the syconium, while the wingless males invariably die within the cavity. All the non-pollinating fig wasps thus emerge at the same time as the pollinator, and are dependent on the exit tunnel chewed by the *Ceratosolen* males to leave the syconium.

Materials and methods

Our study was conducted from March to July 1994, that is, over late dry and early rainy seasons, on 13 *Ficus sur* and 16 *F. vallis-choudae* trees. They were all found within a ca 2 ha area, located half in fire-protected, half in herbaceous savanna.

Fig growth and wasp oviposition sequence

In situ observations of oviposition by non-pollinating fig wasps were made daily on all accessible figs, and the diameters of the syconia on which the wasps were observed to oviposit were recorded to the nearest 0.1 mm with callipers. 25 figs of each *Ficus* species have also been gathered, measured and opened in order to identify and count wasps ovipositing in the receptacle.

Ten to twenty young figs were labelled every month on two trees of each *Ficus* species and their diameters measured in situ to the nearest 0.1 mm every two to three d until the syconium dropped off.

Syconial wall thickness and diameter were measured on an additional 47 figs of *F. sur* and 40 of *F. vallis-choudae* at different growth stages.

Impact of non-pollinating wasps on the mutualism

To determine whether non-pollinating fig wasps affect the mutualism, it was relevant to get quantitative data about the numbers of fig wasps and seeds that mature in one single fig. During our four-month study, 91 syconia of *F. sur* and 108 of *F. vallis-choudae* were collected at maturity, a few hours before the escape of the insects, i.e. when figs were soft but before any exit hole was observed. They were placed in emergence boxes closed by a very thin piece of tulle. After the exit of the winged wasps was completed, the insects were removed from the box, the figs sliced open to collect the entrapped males, and all wasps killed in 70% ethanol. Afterwards, the wasps were sorted by species and sex, and then identified and counted. In the subfamilies Sycophaginae and Agaoninae, males from the different species are undistinguishable; we assigned the males to the same species as the females present within the syconium.

Once all wasps were removed from the fig, the syconium was cut in four equal parts. One quarter was then air dried, and 24 h later the seeds were scraped free and counted. The total number of seeds produced by each sampled fig was obtained by multiplying that result by

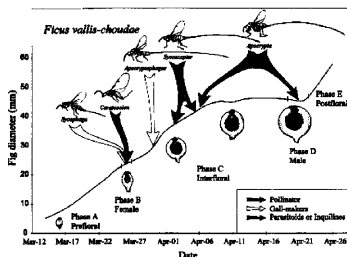


Fig. 2. Growth curve of a *Ficus vallis-choudae* fig observed from 12 March to 26 April. The arrows show the extreme diameters on which the fig wasps oviposit.

four. This approximation seems valid: in ten syconia, we also counted the seeds from the other quarters to estimate the error linked to the method, and the difference between the actual and the estimate total of seeds never exceeded 8%.

Statistical treatments

We mostly used ANOVA and General Linear Model analyses on raw data with STATISTICA software. Whenever necessary, logarithmic transformations were performed.

Results

Fig growth and wasp oviposition sequence

Growth of 109 figs of *F. sur* and 75 figs of *F. vallis-choudae*, observed during the four months of the study on 6 and 5 trees, respectively, was highly variable but consistent in shape (Fig. 2). In *F. vallis-choudae*, maximal growth rate occurs in phases A and B; growth slows down during the 2–3 week-long phase C (see also Bronstein 1988a), at which point the diameter stabilizes. Just before insect emergence, the fig suddenly grows in size

again until full maturation. By the end of phase E, the syconia reach 40 to 70 mm in diameter. Full development of *F. vallis-choudae* figs takes six weeks. The variation in growth among figs is even more significant in *F. sur*. The time of syconial development varies from 18 to 45 d; the curve may show no growth stabilization at the end of the phase C, but when such a plateau exists, it lasts up to 20 d. When mature, the figs measure 22 to 50 mm. Variation in curve shape is predominantly among trees and seasons, whereas figs observed on one particular tree during the same month vary little in their growth pattern.

The fig wall thickness was significantly and positively correlated with the syconial diameter in both *Ficus* species (*F. sur*: $N=47$, $R^2=0.65$, $p<0.05$; *F. vallis-choudae*: $N=40$, $R^2=0.71$, $p<0.05$; Fig. 3).

Four guilds of non-pollinating sycophilous insects were observed, following one another to oviposit in the growing fig. We are quite confident about the diets of those wasps: 1. Gall-makers and their parasites that oviposit through the fig wall of *F. sur* before the pollinators arrive. 2. Gall-makers that enter the syconium at the same time as the pollinator. 3. Gall-makers that oviposit through the fig wall a few days after pollination. 4. Parasitoids and inquilines that arrive last and oviposit through the fig wall. The non-pollinating fig wasps lay eggs in figs of more or less variable diameters and clearly show different average syconial sizes for ovipositing (Figs 4 and 5). The species of *Apocrypta* and *Sycoscapter*, which arrive mostly after the fig diameter stabilizes, show large ranges of larval development time, as the offspring has to emerge at the same time as the pollinator, regardless of the timing of oviposition.

Impact of non-pollinating wasps on the mutualism

We first measured the average numbers of individuals of each insect species and the average number of seeds contained in a mature syconium of both *Ficus* species. Then, in order to study the non-pollinating wasp effect on the mutualism, we precisely looked for any impact of each group of wasps, parasitoids and gall-makers, on either pollinator or seed production.

Guild composition. On average, a mature syconium of *F. vallis-choudae* measures 50.2 ± 0.6 mm (mean \pm SE,

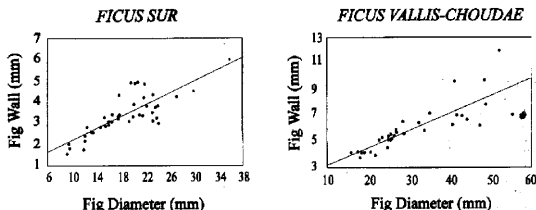


Fig. 3. Relationship between fig wall and fig diameter for 47 figs of *Ficus sur* and 40 of *F. vallis-choudae* of any phase. The lines result from Linear Model Analyses.

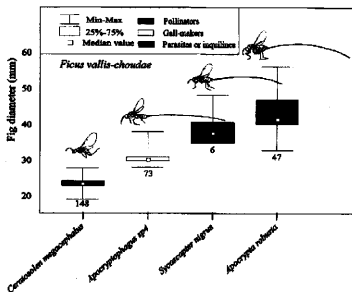


Fig. 4. Fig wasp oviposition sequence on *Ficus vallis-choudae*. The 25%–75% limits correspond to the fig diameters below and above which 25% of the ovipositing individuals were sampled.

$N=105$) in diameter. It contains 1769.0 ± 71.3 seeds ($N=106$) and 767.5 ± 52.1 ($N=106$) fig wasps, including 631.2 ± 50.2 ($N=106$) pollinators, 66.6 ± 8.1 ($N=106$) parasitoids and inquilines, and 69.6 ± 11.8 ($N=106$) gall-makers.

On average, a fig of *F. sur* is 33.7 ± 0.5 mm in diameter, (mean SE, $N=91$) and contains when mature 922.4 ± 52.3 ($N=91$) seeds and 483.5 ± 34.5 ($N=91$) insects, including 264.8 ± 30 ($N=91$) pollinators. Non-pollinating wasps are thus quantitatively important, as the number of parasitoids and inquilines averages 69.8 ± 8.3 ($N=91$), and the number of gall-makers reaches 149.7 ± 16.0 ($N=91$).

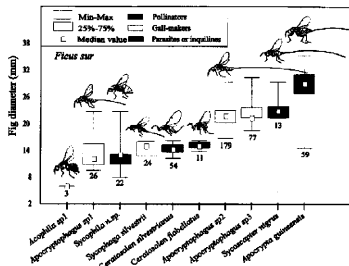


Fig. 5. Fig wasp oviposition sequence on *Ficus sur*. The 25%–75% limits correspond to the fig diameters below and above which 25% of the ovipositing individuals were sampled.

In both *Ficus*, the numbers of insects (*F. sur*: $N=90$ $R^2=0.35$ $p<0.05$; *F. vallis-choudae*: $N=106$ $R^2=0.42$ $p<0.05$) and seeds (*F. sur*: $N=90$ $R^2=0.19$ $p<0.05$; *F. vallis-choudae*: $N=106$ $R^2=0.21$ $p<0.05$) are positively correlated with the syconial diameter (Fig. 6). Given these results, we used the syconial diameter as first independent variable in our linear regressions to correct for fig size effect in correlations between a factor and the number of seeds or of any species of insects.

Parasitism. Parasitism rate was calculated as the proportion of parasitoid individuals among all fig inhabitants. We found a negative impact of the parasitism rate on the number of maturing pollinators (*F. sur*: $N=90$ $R^2=0.12$

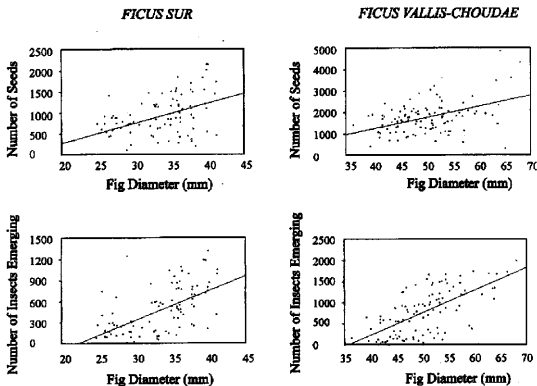


Fig. 6. Number of seeds and number of insects emerging as functions of fig diameter at maturity. Counts were made on 91 syconia of *Ficus sur* sampled from 10 trees and on 108 of *F. vallis-choudae* sampled on 12 trees. The lines result from Linear Model Analyses.

Table 2. Multiple regression model explaining the number of seeds by the fig diameter and the number of pollinators in *F. sur*.

N=91	R ² = 0.21	R ² = 0.19	F _{1,88} = 11.56	p<0.0000	SE Estim. = 449.02	
	Beta	SE (Beta)	B	SE (B)	t	p
Intercept			-502.11	371.05	-1.35	0.18
Diameter	0.37	0.10	40.21	11.48	3.50	<0.05
Pollinators	0.15	0.10	0.26	0.18	1.43	>0.05 N.S.

Table 3. Multiple regression model explaining the number of seeds by the fig diameter and the number of pollinators in *F. vallis-choudae*.

N=105	R ² = 0.23	R ² = 0.21	F _{2,10} = 11.94	p<0.0001	SE Estim. = 649.52	
	Beta	SE (Beta)	B	SE (B)	t	p
Intercept			-569.32	549.85	-1.03	0.30
Diameter	0.39	0.10	44.52	11.81	3.76	<0.05
Pollinators	0.12	0.10	0.18	0.15	1.20	>0.05 N.S.

Table 4. Multiple regression model explaining the number of seeds by the fig diameter and the number of gall-makers in *F. sur*.

N=91	R ² = 0.22	R ² = 0.20	F _{2,88} = 12.56	p<0.0001	SE Estim. = 445.03	
	Beta	SE (Beta)	B	SE (B)	t	p
Intercept			-820.21	356.08	-2.30	0.023
Diameter	0.50	0.10	54.50	10.88	5.00	<0.05
Gall-makers	-0.19	0.10	-0.62	0.32	-1.91	<0.1

Table 5. Multiple regression model explaining the number of seeds by the fig diameter and the number of gall-makers in *F. vallis-choudae*.

N=105	R ² = 0.23	R ² = 0.22	F _{2,102} = 15.62	p<0.0001	SE Estim. = 646.21	
	Beta	SE (Beta)	B	SE (B)	t	p
Intercept			-1065.85	512.90	-2.07	0.04
Diameter	0.51	0.09	57.90	10.37	5.58	<0.05
Gall-makers	-0.14	0.09	-0.87	0.55	-1.58	>0.1 N.S.

p<0.05; *F. vallis-choudae*: N=106 R²=0.28 p<0.05). In contrast, no significant effect of the parasitism was found on either of the two gall-maker genera, *Sycophaga* or *Apocryptophagus* (p>0.05).

Parasitism rate is negatively correlated with the overall number of insects (*F. sur*: N=90 R²=0.05 p<0.05; *F. vallis-choudae*: N=106 R²=0.23 p<0.05), whereas the number of parasitoids and inquilines increases with the number of insects emerging from the figs (*F. sur*: N=90 R²=0.22 p<0.05; *F. vallis-choudae*: N=106; R²=0.07 p<0.05). However, a low percentage of the variation of both the parasitism rate and the number of parasitoids and inquilines is explained by the overall number of insects, which is due to the high number of factors actually affecting the insect communities.

Non-pollinating fig wasps and seed production. In both *Ficus*, the number of seeds is significantly positively correlated with the syconial diameter. In contrast, the number of pollinator offspring emerging has no significant impact on seed production (Tables 2 and 3).

Non-pollinating gall-makers have a significant negative impact on seed production in *F. sur* (N=91 R²=0.22

p<0.05; Table 4), but not in *F. vallis-choudae* (Table 5). A separate analysis showed that emerging *Sycophaga* alone has a negative impact on seed number (N=91 R²=0.22 p<0.05), whereas the number of *Apocryptophagus* has no significant effect. This corroborates our previous results on non-pollinating fig wasps of *Ficus sur* (Compton et al. 1994), and those of West and Herre (1994) showing that *Idarnes* wasps do not develop at the expense of viable seeds in six species of monoecious New World figs (subgenus *Urostigma*, section *Americana*).

Correlations among pollinating and non-pollinating gall-maker abundances. We found a negative impact of the non-pollinating gall-makers of the genus *Sycophaga* on the number of emerging *Ceratostolen* (N=91 R²=0.25 p<0.05) in *F. sur*. A one-way analysis of variance showed that *Ceratostolen* emerging from figs containing *Sycophaga* average 143, whereas their number reaches a mean of 316 when *Sycophaga* are absent (F_{1,89}=7.50 p<0.05; see Fig. 7).

Among gall-makers, *Apocryptophagus* sp. are the last to oviposit in the syconium. The number of their off-

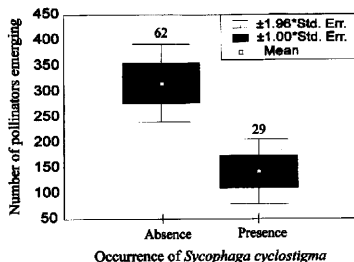


Fig. 7. Mean number of *Ceratosolen* emerging from *Ficus sur* syconia depending on whether or not *Sycophaga silvestrii* occurs (One-way ANOVA results). 62 and 29 are the numbers of figs sampled.

spring in *F. sur* is significantly lowered by the emerging *Ceratosolen* and *Sycophaga*, that is, by the offspring of the gall-makers that oviposit first ($N=86$ $R^2=0.2$ $p<0.05$).

We finally performed stepwise multiple regressions to explain pollinator abundances in both *Ficus* species. In *F. vallis-choudae*, the fig diameter and the number of *Apocryptophagus* only have been retained in the model with positive and negative slope respectively (Table 6). In *F. sur* (Table 7), the factors actually accounting for the number of *Ceratosolen* emerging are the fig diameter (with positive slope), the number of *Sycophaga* (with negative slope), the number of *Apocryptophagus* (with negative slope) and the number of *Apocrypta* (with positive slope).

Discussion

Fig growth and wasp oviposition sequence

Since the fig wall thickens while the syconial diameter increases, access to the ovaries from the outside requires longer and longer ovipositors. During fig development, four well-defined groups of wasps followed one another in ovipositing into the syconium. This can be seen as exemplifying four strategies developed to exploit the same resource.

In *Ficus sur*, some gall-makers, closely followed by a parasite, oviposit into very young figs long before pollination occurs. These insects, namely *Apocryptophagus spl*, *Acophila spl* and *Sycophila n.sp.*, are all much larger than those appearing later (pers. obs.). These pioneer species induce large galls that protrude into the fig cavity. As they arrive first, they avoid most interspecific competition for oviposition sites, but they deposit eggs in unpollinated syconia, which may have two negative consequences. First, the larvae have to feed on non-developing nucelli, which may result in lower benefit. Previous studies show that wasps developing in unpollinated flowers suffer high female mortality rates (Galil and Eisikowitch 1971), or can be of smaller adult size (Compton et al. 1991), which is probably due to resource limitation. Parthenogenetic proliferation of the vegetable tissues has to be induced. During oviposition, epichryso-malline females inject the contents of their acid gland reservoirs in the ovaries, which stimulates parthenogenetic nucellar development (Galil and Copland 1981). Furthermore, there is a risk that no pollinator will enter the fig; if so, abortion is likely to occur (Bronstein 1988a), resulting in the death of the developing larvae. Possibly for these reasons, females tend to visit many syconia and to lay few eggs in each; this behaviour probably reduces the risk that all their offspring may die in

Table 6. Stepwise multiple regression model explaining the number of pollinators by the fig diameter and the numbers of *Apocryptophagus* in *F. vallis-choudae*. The number of *Apocrypta* has not been kept in the model.

N=105	$R^2 = 0.41$	$R^2 = 0.40$	$F_{2,102} = 35.71$	$p < 0.0001$	SE Estim. = 399.61	
	Beta	SE (Beta)	B	SE (B)	t	p
Intercept			-1961.67	318.69	-6.15	<0.05
Diameter	0.67	0.08	53.78	6.45	8.33	<0.05
<i>Apocryptophagus</i>	-0.34	0.08	-1.57	0.37	-4.23	<0.05

Table 7. Stepwise multiple regression model explaining the number of pollinators by the fig diameter and the numbers of *Sycophaga*, *Apocryptophagus* and *Apocrypta* in *F. sur*.

N=86	$R^2 = 0.34$	$R^2 = 0.31$	$F_{4,81} = 10.68$	$p < 0.0001$	SE Estim. = 230.26	
	Beta	SE (Beta)	B	SE (B)	t	p
Intercept			-782.30	193.60	-4.04	<0.05
Diameter	0.53	0.1	32.54	6.02	5.40	<0.05
<i>Sycophaga</i>	-0.34	0.09	-0.65	0.18	-3.57	<0.05
<i>Apocryptophagus</i>	-0.25	0.1	-0.77	0.30	-2.55	<0.05
<i>Apocrypta</i>	0.21	0.09	0.83	0.35	2.35	<0.05

aborted syconia (see Addicot *et al.* 1990). The number of their offspring is in any case space-limited because the bulk of the galls protrude into the fig cavity. In West Africa, such insects are not found in *Ficus vallis-choudae*; in this species, the thick walls of young figs may act as a natural barrier to oviposition.

Sycophaga species are the sole non-pollinating fig wasps in *F. sur* and *F. vallis-choudae* that enter the receptacle through the ostiolar bracts to oviposit in the flowers at the same time as the pollinator. Consequently, the ovipositing *Sycophaga* females gain protection against predation, which allows them to lay many eggs. They oviposit in pollinated as well as in unpollinated syconia (Galil and Eisikowitch 1968), and have developed abilities to induce nucellar development and avoid syconial abortion (Galil *et al.* 1970).

Other species of *Apocryptophagus* are the last gall-makers to lay eggs in the growing fig. They oviposit through the fig wall, and the females are subject to high predation by ants (pers. obs.). Nevertheless, by lying down flat on the fig wall, they are able to limit their detection by predators. Arriving last, they oviposit in figs that are very unlikely to abort, but undergo severe interspecific competition because of a lack of potential oviposition sites.

The wasps that arrive last, *Apocrypta* and *Sycocapter* species, are parasitoids or inquilines of the previous fig dwellers, but they apparently are able to parasitize a few different species of fig wasps (Kerdelhué unpubl., but see below). After dissection of a female flower in which an *Apocrypta* was ovipositing, we once observed the deposited egg on a larva; this would suggest that this species is a true parasitoid. Both *Apocrypta* and *Sycocapter* are able to oviposit in figs of a large range of diameters, and hence have access to a greater number of attractive figs at a given time than any other fig wasp. They oviposit from the outside and thus face significant predation pressures by ants while their ovipositor is stuck in the fig wall (pers. obs.). By reducing the time of oviposition, predators presumably prevent the females from laying a large number of eggs in the same syconium (Compton and Robertson 1988; Kerdelhué and Rasplus pers. obs.).

Interestingly, all these fig wasps emerge during the fig's male phase, and escape from the receptacle through the exit tunnel digged by the pollinator males. Regardless of their strategy and biology, they have to adjust their larval development time to the total duration of the fig growth, which is highly variable. If their development were too short, the adults, unable to chew an exit hole, would die entrapped within the fig; in contrast, if it were too long, the insects would inevitably die in the galls as the fig ripened, and hence be consumed by frugivores (Leighton and Leighton 1983; Thomas 1984; Lambert and Marshall 1991). We assume that the synchronous emergence of all the wasps is due to varying larval growth rate between species, and adaptive variability within species, or to pauses during insect development.

Impact of non-pollinating wasps on the mutualism

Guild composition

The total numbers of non-pollinating species co-occurring within *Ficus sur* and within *F. vallis-choudae* in Lamto are 11 and 6 respectively. Assuming that there is an upper limit to ovipositor length, the fig diameter and the thick syconial wall of *Ficus vallis-choudae* may explain why its fauna is more depauperate than that of *F. sur*. The number of species found in one receptacle averages 3 in *F. vallis-choudae* and 4 in *F. sur*.

In both *Ficus*, the average total of insects emerging from a mature syconium is far below the average number of seeds produced. Hence, the number of oviposition sites does not seem to be limiting (also see Bronstein 1988b), as a majority of ovaries remain larva-free and produce seeds. If the fig wasps have access to all the flowers to oviposit, interspecific competition will then be reduced.

In *F. vallis-choudae*, an overwhelming majority (82%) of the emerging fig wasps are pollinators, whereas 45% of the individuals found in *F. sur* are non-pollinating insects. In view of these data, we argue that the non-pollinating fauna of *F. sur* may represent a considerable pressure on the mutualists. Its actual impact on the fig tree-fig pollinator relationship is discussed below.

Parasitism

Sycophila were absent from the figs we sampled and *Sycocapter* scarce; most of the parasitoids and inquilines we found during our study were species of *Apocrypta*. We showed that the number of emerging parasitoids is negatively correlated with the number of pollinator offspring. This suggests that *Apocrypta* species parasitize *Ceratosolen* larvae, and reduce the total number of pollinator offspring, significantly altering the *Ficus* male function. Worth stressing is that *Apocrypta* only occurs in those *Ficus* that are pollinated by *Ceratosolen* species (Ulenberg 1985). However, there is some evidence suggesting that *Apocrypta* may occasionally parasitize *Sycophaga* and *Apocryptophagus* species, as we observed *Apocrypta* individuals escaping from unpollinated figs. Accordingly, *Apocrypta* can be assumed to parasitize mostly pollinator larvae, and occasionally other gall-makers.

In both *Ficus*, the parasitism rate varies as a negative function of the total number of fig wasps emerging, whereas the number of parasitoid and inquiline individuals is a positive function of the total number of insects; however, this factor only explains little variation in both 'parasitism rate' and 'number of parasites', and one ought to be cautious while interpreting these results. Yet, in the closed fig system, parasitism would thus be a host density-dependent phenomenon, and a dilution effect would occur: the more numerous the gall-makers are within a fig, the less likely they are to get parasitized.

Non-pollinating fig wasps and seed production

The number of seeds produced by either *F. sur* or *F. vallis-choudae* is positively correlated with the syconial diameter. Larger figs contain relatively more flowers, and hence produce more seeds (Bronstein 1986) and shelter more insect larvae. This may be due to lower space pressure within the receptacle, that enables more flowers to mature into seeds or galls.

Acophila sp1 as well as *Apocryptophagus sp1*, which oviposit before pollination occurs, can limit seed production when they are numerous. By inducing large galls that protrude into the receptacle cavity before the pollinator entry, they alter the synstigma (Verkerke 1989), thereby reducing *Ceratosolen* pollination and oviposition activities (pers. obs.).

A high number of emerging *Sycophaga silvestrii* is positively correlated with a lowered number of seeds in *F. sur*. We can thus assume that, although ovipositing through the styles, *S. silvestrii* is able to reach the deepest ovary layers, that is, those flowers that are generally assumed to be primarily devoted to seed production. Consistent with this, deep galls were observed in figs containing very large numbers of insects. In most cases, *Sycophaga silvestrii* lay eggs in the most internal ovaries, that is, in short-styled flowers (pers. obs.). Unlike the pollinators and owing to a longer ovipositor than that of *Ceratosolen* species, they can oviposit in long-styled flowers when many foundresses compete for oviposition sites. However, ovipositing in the external ovary layer is presumably limited because of the particular shape of these thin-styled flowers (Verkerke 1986, 1988b, Kjellberg et al. 1987), and because pollinators usually chew the stigmas of the flowers in which they cannot oviposit (Galil and Eisikowitch 1969).

In contrast, there is no clear evidence of any effect of *Apocryptophagus* on the number of seeds, even though individuals of these species were often found in large numbers within the sampled figs. This is a striking result, since the species that oviposit through the fig wall could be expected to lay eggs in the most external ovaries, and hence to have a negative impact on seed production. Considering that deep galls have not been observed in *F. vallis-choudae*, and the deepest galls in *F. sur* mostly contained *Sycophaga* individuals, we assume that the external ovary layers could be protected against insects that oviposit through the fig wall. It could thus be considered as being primarily a seed-producing layer; even though all the flowers are physiologically identical (Verkerke 1988a, b).

Correlations among pollinating and non-pollinating gall-maker abundances

Evidence suggests that *Sycophaga silvestrii* significantly lowers the numbers of pollinator offspring. It enters the fig concomitantly with *Ceratosolen*, and oviposits preferentially in the more accessible short-styled flowers. Up to 19 *Sycophaga* foundresses may compete for oviposition sites with *Ceratosolen* females (pers. obs.),

which are less efficient at laying eggs because of a shorter ovipositor, and probably because of their active pollination behaviour. Competitors like *Sycophaga* species, by drastically reducing pollinator oviposition, have thus a significant negative impact on the fig male function.

Apocryptophagus sp2, *sp3* and *sp4* are the last gall-makers to oviposit in the growing fig. We showed that their offspring are significantly limited by the number of previous gall-makers, namely *Ceratosolen* and *Sycophaga*, which both oviposit from the inner side of the fig. This is evidence that *Apocryptophagus* species lay eggs in the internal ovaries, which are mostly already occupied, and may be subject to a lack of oviposition sites. Thus, in spite of a diversity of ovipositor lengths and oviposition strategies, all the gall-makers studied that are involved in the mutualism use the same resource and consistently lay eggs in the internal ovary layers.

Our results support the assumption that all the gall-makers infrequently develop within the external ovary layer, which therefore turns into a seed layer. Although the species that lay eggs from the outside have ovipositors of varying lengths, they actually all reach flowers located at the same depth (see also Compton et al. 1994) because they oviposit at successive stages of fig growth, as the syconial wall thickens. Temporal partitioning prevails over concomitant resource partitioning.

The fig tree-fig pollinator mutualism provides the guild of non-pollinating fig wasps, either gall-makers, parasitoids or inquilines, a unique resource. On the one hand, the system seems to have evolved towards a high protection of the seed production against gall-makers that oviposit either from inside the fig cavity or from the outside, as shown by our results and those of West and Herre (1994). This results in the existence of a so-called external seed-layer. The style shape of the deepest flowers may limit oviposition through the styles. How oviposition in long-styled flowers through the fig wall is prevented needs to be elucidated, and remains conjectural (see below).

On the other hand, the *Ficus* male function suffers from the non-pollinating fig wasps. By parasitizing *Ceratosolen* larvae, or competing for the same oviposition sites, they alter the pollinator population growth and dynamics, and thus reduce pollen dissemination. Active pollination occurs in a majority of monoecious fig trees; this behaviour limits the waste of pollen grains, and could be seen as partly compensating for the negative impact of the non-pollinating fig wasps on the fig male function.

Finally, the occurrence of numerous non-pollinating fig wasps may imply energetical costs to the plant, but we could not quantify these. For instance, pollinator larval mortality may be increased in case of resource limitation during fig growth.

The occurrence and success of a more or less numerous guild of non-pollinating wasps exploiting the fig tree-fig pollinator mutualism, as well as the evolution of

the system towards the protection of an external seed layer raise new evolutionary questions. The 'commensalism hypothesis' (Bronstein 1991), assuming that non-pollinators may be tolerated because they inflict no costs on the fig, would explain the success of most of the gall-makers. *Acophila spl* and *Apocryptophagus spl* seem to be of quantitatively little importance to the mutualists; the other species of *Apocryptophagus* neither use ovaries that were to produce seeds, nor compete with the pollinator for oviposition sites, and so actually do not affect *Ficus* fitness; it is thus not puzzling that they have not been excluded from the mutualistic system. The main question is: why do the *Apocryptophagus* species that oviposit last not lay eggs in the most external ovary layer? Most of these flowers are pollinated several days before these species oviposit. It can then be hypothesized that the early development of a seed provides a physical protection to the ovary against oviposition. This may be the reason why gall-makers that lay eggs from the outside in pollinated figs have been strongly selected to have extra-long ovipositors and to lay eggs in the internal ovary layers. The wasps that have a considerable impact on the pollinator population and hence on pollen dissemination, namely the *Apocrypta* and *Sycophaga* species, are supposedly tolerated because the fig tree cannot distinguish between their larvae and those of the *Ceratosolen* species, which all breed in galls induced by ovipositing through the styles (mimicry hypothesis: see Bronstein 1991).

Our work shows that the influence of the non-pollinating fig wasps on the mutualists should not be ignored. It is important to study their biology, as gall-makers and parasites do not affect the system in the same way. The latter are very likely to influence the pollinator population dynamics by increasing its mortality, whereas the former can limit the number of oviposition sites and the overall resource availability. All the non-pollinating fig wasps, however, are restricted to the internal ovary layers and hardly affect seed production. Trying to understand the evolution and maintenance of *Ficus*/pollinator mutualisms without taking into account the occurrence of the whole guild of insects would probably lead to a deadlock. The fig tree/fig pollinator system is, in addition, a good material for understanding community structures.

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