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Active Pollination of *Ficus sur* by Two Sympatric Fig Wasp Species in West Africa[1]

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ABSTRACT

Ceratosolen silvestrianus and *C. arabicus* are two species of agaonine fig wasps that co-occur in the figs of *Ficus sur* in West Africa. Our work in the Ivory Coast shows that both are active pollinators, and that they may be found together in the same syconia. In our study area, *C. silvestrianus* is much more abundant than *C. flabellatus.* We found no competitive effect for oviposition sites on *C. silvestrianus,* and hypothesize that habitat preferences allow the coexistence of two sympatric active pollinators in the same *Ficus* host in the Ivory Coast.

RESUME

En Afrique de l'Ouest, deux espèces d'hyménoptères Agaoninae, *Ceratosolen silvestrianus* et *C. flabellatus,* sont associées à *Ficus sur.* Notre étude en Côte d'Ivoire a montré que toutes deux pollinisent activement, et peuvent se développer ensemble au sein d'une même figue. Dans notre lieu de récolte, *C. silvestrianus* est bien plus abondant que *C. flabellatus.* Nous n'avons pas mis en évidence pour *C. silvestrianus* de coût lié à la compétition avec *C. flabellatus.* La présence de deux pollinisateurs actifs sur un même site pourrait être due à l'existence d'une mosaïque d'habitats différents, abritant chacun préférentiellement une des deux espèces.

Key words: *active pollination; competition;* Ficus; *fig; fig wasp; Ivory Coast; mutualism.*

Almost all of the *ca.* 750 *Ficus* species (Berg 1989) are pollinated by single species of agaonine wasps (Chalcidoidea: Agaonidae: Agaoninae), which rely entirely upon a single fig species for nutrition during development. The fig, or syconium, is an urn-shaped receptacle that contains hundreds or thousands of flowers. When the female primordia reach maturity and the stigmas become receptive, pollen-loaded female wasps, attracted by specific volatiles (Ware *et al.* 1993), crawl through the ostiolar bracts and enter the fig cavity. These foundresses lay eggs through the styles of a certain proportion of the female flowers, pollinate some others and then die. The male flowers mature in synchrony with the emergence of the foundresses' offspring; the female wasps mate and then leave the syconium in search of an attractive fig, thereby disseminating pollen among the *Ficus* population.

Although the vast majority of interactions reported involve one fig-one fig wasp specificity, some exceptions have been reported (Wiebes 1979). For example, two species of agaonine wasps, *Ceratosolen arabicus* Mayr and *C. galili* Wiebes, co-occur in *Ficus sycomorus* L. and in *F. mucuso* Ficalho in Africa (Wiebes 1964). However, in *F. sycomorus, Ceratosolen galili* was shown to never bring pollen into the syconia (Galil & Eisikowitch 1968, 1969, Compton *et al.* 1991). A second example involves *Courtella gabonensis* Wiebes and *C. camerunensis* (Wiebes), which are both known to pollinate *Ficus ottoniifolia* Miquel (Michaloud *et al.* 1985). To our knowledge, these are the only studied cases of co-occurrence of two pollinators on a single host *Ficus.*

Recently, Rasplus (1996) reviewed the cases in which more than one species of pollinator occur in a single host *Ficus,* or where one species of wasp pollinates at least two species of *Ficus.* The pollinators of 80 out of the 105 African *Ficus* species

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are known; 12 are found in at least two fig species, and 14 *Ficus* are inhabited by at least two species of Agaoninae.

In West Africa, *Ceratosolen silvestrianus* Grandi and *C. flabellatus* Grandi (Agaonidae: Agaoninae) can be found in *Ficus sur* Forsskål. Previous observations showed that although both species are able to pollinate (Michaloud *et al.* 1985; Compton *et al.* 1994), they never do so in the same syconium, suggesting either that interspecific recognition and avoidance occurs, or that each species has evolved a preference for receptive figs of different diameters. The present study examines the pollination of *Ficus sur* in the Ivory Coast. The questions we address are:

—Are both *Ceratosolen silvestrianus* and *C. flabellatus* active and effective pollinators?
—Are they always found in figs of different trees within a population of *Ficus sur,* or in different figs of the same tree, or can they co-occur in the same syconium?

We discuss what mechanisms, if any, enable resource partitioning between these pollinator species.

STUDY SITE

The study site is located in the Ivory Coast, 160 km north west of Abidjan, at the Lamto Ecological Station (5°02′W, 6°13′N). The area is situated in the southern part of the arboreous 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 various biological cycles, favoring geophytic and hemiphytic vegetation, and keeping the savanna from developing towards a semi-deciduous climax forest (Devineau *et al.* 1984). The *Ficus* we studied are favored in the fire-protected savanna, characterized by high tree densities (Vuattoux 1970).

MATERIALS AND METHODS

FICUS AND CHALCID SPECIES.—*Ficus sur* is a continental Afrotropical fig species from the subgenus *Sycomorus.* It is widely distributed and common in savannas, secondary forests, woodland and moist forests, up to 1800 m in altitude (Berg 1990). It is a moderate-sized tree (*ca.* 4 to 25 m in height), bearing figs on leafless branchlets that hang down from the trunk and the larger branches. The mature fig measures 2–4 cm in diameter and contains about 3000 flowers (Verkerke 1988a).

Like all species of the subgenus *Sycomorus* and of the sections *Sycocarpus* and *Neomorphe, Ficus sur* is invariably pollinated by *Ceratosolen* species (Agaoninae: Blastophagini; Wiebes 1994). In West Africa, *C. silvestrianus* and *C. flabellatus* co-occur, whereas a third species, *Ceratosolen capensis* Grandi which is absent from West Africa (Rasplus 1996; see Fig. 1), is the only pollinator of *F. sur* in South Africa, and may co-occur with *C. flabellatus* in East Africa (Wiebes 1989). In *Ceratosolen* species, the ovipositing foundresses actively pollinate, unloading their thoracic pollen pockets by the use of their forelegs, and then chewing the stigmatas, possibly involved in activating pollen germination (Galil & Eisikowitch 1969). Just prior to emergence, female offspring actively fill their pollen pockets, and later remove them within a receptive young syconium.

Our study was conducted on 13 *Ficus sur* trees from March to July 1994 and from April to June 1995, that is, over late dry and early rainy seasons. They were all found within a *ca.* 2 ha area, mostly located in fire-protected savanna.

OBSERVATIONS AND COUNTS.—The syconial diameter was measured to the nearest 0.1 mm with a calliper for 127 receptive figs, which were opened in order to identify and count foundress wasps. We used these data to determine either the number of foundresses from each species (when the wasps were found dead, *i.e.,* in 27 of the 127 figs) or the diameter of the figs attracting each *Ceratosolen* species (when the wasps were found while ovipositing and pollinating, *i.e.,* in 100 figs). To determine whether *Ceratosolen silvestrianus* and *C. flabellatus* foundresses actively pollinate, the behavior of the ovipositing females in receptive figs was observed with an inverted pair of binoculars. In addition, some females of both species were caught while flying near attractive figs and dissected; their pollen pockets were then observed under a microscope to determine whether pollen grains were being transported.

The number of pollinator progeny for each fig was recorded. One hundred thirty-eight mature syconia of *Ficus sur* (91 in 1994 and 47 in 1995) were collected from the 13 trees a few hours prior to the escape of the insects, measured, and placed in emergence boxes closed by a very thin piece of tulle. After the exit of all female wasps, the insects were removed from the boxes; the figs were then sliced open in order to collect the entrapped wingless males. All the insects were killed in a dish con-

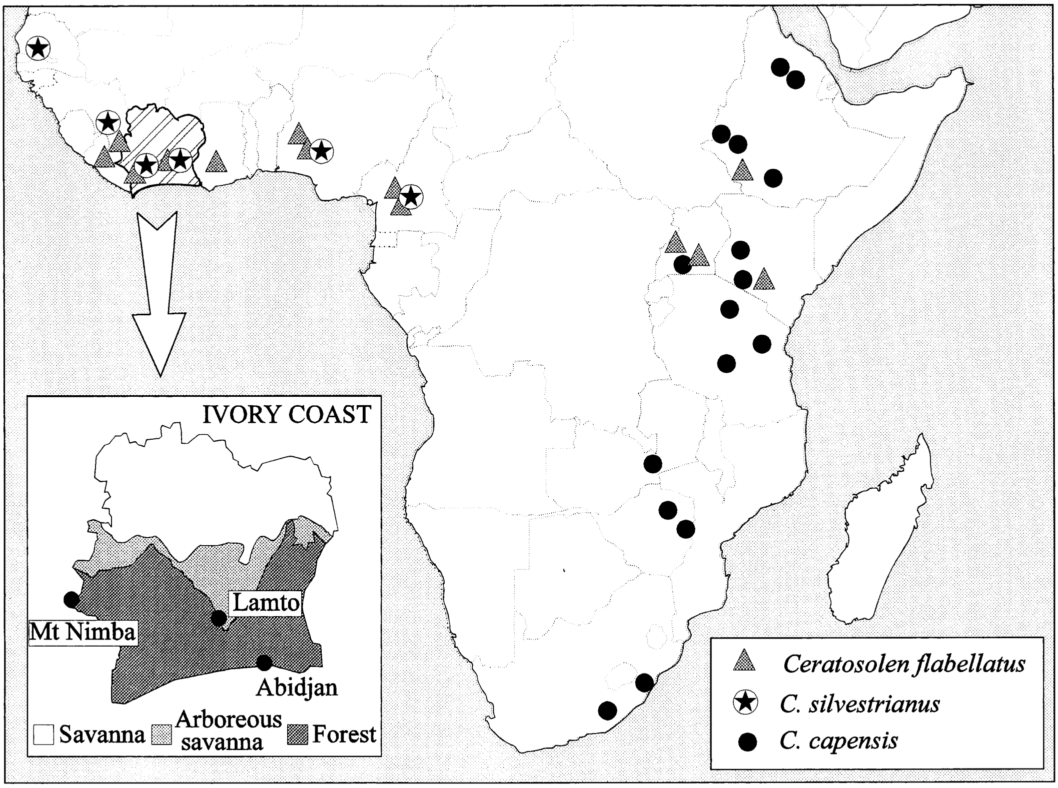

FIGURE 1. Distribution of *Ceratosolen flabellatus, C. silvestrianus* and *C. capensis* in Africa (after Wiebes, 1981, modified). The enlargement of the Ivory Coast shows the locations of the Lamto Ecological Station and of Mount Nimba.

taining 70 percent ethanol. All the wasps (*i.e.*, pollinators, gall-makers and parasites) were sorted by species and sex, and then identified and counted; the data presented here, however, only concern pollinating wasps. We were unable to distinguish males of the two *Ceratosolen* species. Thus, whenever all females belonged to a single species, we considered the males in that syconium as conspecific to the females. When figs contained both species, only the number of females was recorded.

To determine the number of seeds produced, the syconium was cut in four equal parts once all wasps were removed from the fig. One quarter was placed in a drying oven at 50°C for 24 hours. The seeds were then scraped free and counted. The estimated total number of seeds produced by each sampled fig was obtained by multiplying that result by four. In several 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 estimate total of seeds did not exceed six percent on average.

STATISTICAL TREATMENTS.—We performed General Linear Model Regressions and, whenever possible, one way ANOVAs. In cases where the model hypotheses did not hold for these parametric tests, we used either Student *t* tests or non-parametric statistics (Mann-Whitney *U*-test).

RESULTS

ACTIVE POLLINATION OF *FICUS SUR* FIGS BY THE TWO SYMPATRIC *CERATOSOLEN* SPECIES.—Both *Ceratosolen silvestrianus* and *C. flabellatus* are effective pollinators of *Ficus sur* at the Lamto Ecological Station. All the wasp-occupied syconia sampled produced seeds, regardless of whether they contained only *C. silvestrianus* or only *C. flabellatus*. Consistent with this, all the female wasps we dissected of both species had pollen grains in their thoracic pockets. Moreover, we observed the active pollination behavior described by Galil and Eisikowitch (1969) for the foundresses of both *Ceratosolen* species.

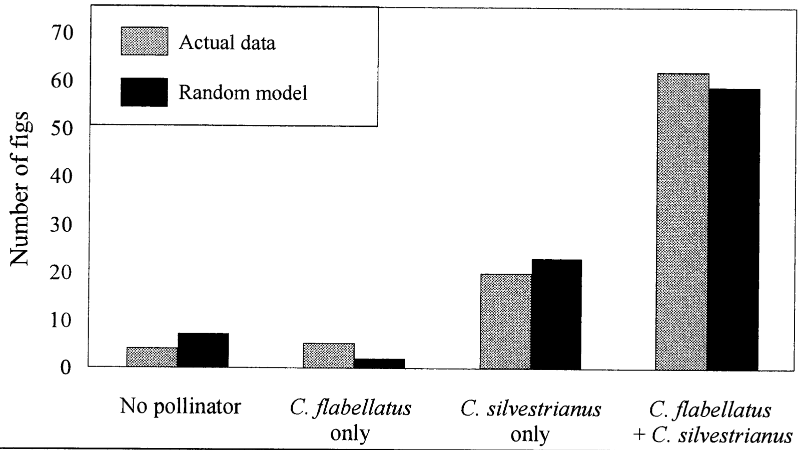

FIGURE 2. Distribution of 91 figs depending on the emerging *Ceratosolen* species. The actual data represent the figs sampled in 1994; the model predictions represent a random distribution calculated from the observed probabilities that a fig has been pollinated by *C. silvestrianus* (82/91) or by *C. flabellatus* (25/91). The two distributions are not significantly different.

FIG ATTRACTIVENESS TO *CERATOSOLEN SILVESTRIANUS* AND *C. FLABELLATUS*.—The 27 young figs in which we counted dead foundresses all contained *Ceratosolen silvestrianus* females. We thus only determined the mean number of foundresses for this species. On average, we found 2.66 ± 0.43 females (Mean ± SE, $N = 27$ figs, range 1–10) ovipositing in the same fig.

The mean diameter of the syconia in which we found ovipositing wasps was 14.69 ± 0.11 mm (Mean ± SE, $N = 217$ observed wasps) for *C. silvestrianus*, and 14.73 ± 0.13 mm ($N = 46$) for *C. flabellatus*. The difference between the means is non-significant ($t = -0.16$, $P > 0.1$). Among the 127 collected figs, 107 had been entered only by *C. silvestrianus* females, 9 by *C. flabellatus* foundresses, and 11 by both species.

POLLINATOR AND SEED PRODUCTION IN MATURE FIGS.—In 1994, the numbers of pollinators emerging and seeds produced were determined for 91 mature figs, randomly sampled on 13 trees. Out of these, four syconia were unpollinated, five contained *C. flabellatus* alone, 62 *C. silvestrianus* alone, and 20 were inhabited by both *Ceratosolen* species. This distribution is not significantly different from random ($\chi^2_{(1)} = 0.28$, $P > 0.05$; see Fig. 2 for explanations). The remaining analyses were conducted on the 134 pollinated mature figs we collected in 1994 and 1995.

A mature *Ficus sur* fig contains 902.4 ± 42.4 seeds and 260.9 ± 24.0 pollinators (Mean ± SE; $N = 134$ for both). Seeds are significantly more numerous than pollinator offspring in all figs, containing *C. silvestrianus* only, *C. flabellatus* only, or both *Ceratosolen* species (Table 1). The numbers of seeds and pollinators are each significantly positively correlated with the diameter of the mature fig (Tables 2 and 3). It is worth stressing that the number of pollinators does not appear as a significant factor in a stepwise regression model explaining the number of seeds. However, less than 25 percent of the variation in the numbers of seeds and pollinators is explained by fig diameter, which is due to the large number of factors actually affecting the fig tree-fig pollinator mutualism (for in-

TABLE 1. *Comparison of mean pollinator numbers and mean seed numbers for the three possible combinations of pollinating species.*

Pollinator	Pollinator number	Seed number	t-value	df	P
C. silvestrianus only, $N = 84$ figs	204.30	900.42	−11.68	166	<0.05
C. flabellatus only, $N = 17$ figs	321.70	817.00	−3.32	31	<0.05
Both *Ceratosolen* species, $N = 33$ figs	381.60	948.85	−5.71	64	<0.05

TABLE 2. *Regression model of seed number as a function of fig diameter in* F. sur.

$N = 132$	$r^2 = 0.23$	adj $r^2 = 0.23$	$F_{1,130} = 40.05$	$P < 0.0001$		SE Estim. = 430.25
	Beta	SE (Beta)	B	SE (B)	t	P
Intercept			−829.50	276.52	−3.00	<0.05
Diameter	0.48	0.08	51.83	8.19	6.32	<0.05

stance, parasitoids and gall-makers: Kerdelhué & Rasplus 1996; predators: Compton & Robertson 1988).

Seed production of the figs pollinated by *Ceratosolen silvestrianus* only, *C. flabellatus* only, or by both species were not significantly different from one another (Table 4).

The mean number of emerging females of *Ceratosolen silvestrianus* or *C. flabellatus* does not depend on the occurrence of the congeneric species (Mann-Whitney U-test: $P > 0.05$). In addition, the numbers of *C. silvestrianus* and of *C. flabellatus* females emerging from the same syconia are not significantly different (Mann-Whitney U-test: $P > 0.05$).

DISCUSSION

We did not detect direct competition between *C. silvestrianus* and *C. flabellatus*. Both are active, specific pollinators of *F. sur*, exploit fruits of approximately the same size, and, in contrast to previous observations (Michaloud *et al.* 1985; Rasplus, pers. comm.), show no avoidance of fruits pollinated by the congener; the two *Ceratosolen* species can be found in the same fruits, and hence are not completely exclusive. Yet, they produce the same number of offspring regardless of the presence of the other species in a given syconium. The breakdown of the 'one-to-one' rule (*i.e.*, one fig tree-one fig pollinator) thus does not seem to have a negative impact on either of the two pollinator species.

Given the theory that competitive coexistence of two species in the same habitat requires some form of ecological difference, or social factors by which individuals of a species discriminate between heterospecifics and conspecifics (Chesson 1991), how can the coexistence of these two pollinators be explained?

Despite the large number of flowers which develop per fig (see Verkerke 1988a, b) competition could occur if the two wasps were to preferentially attack a limited supply of the same, specific types of flowers. Our emergence data suggest that such competition does not occur, since the same number of offspring of each species are produced regardless of the presence of the competitor. This may be due to niche partioning, that is either because each species indeed exploits different flower types, or because each exploits only a fraction of the available flowers regardless of the presence of the competitor.

Another possibility is that there is a large-scale spatial component to the coexistence of the two species. *C. silvestrianus* is more numerous than *C. flabellatus* at Lamto, while the reverse is true at near-by Mount Nimba (see Fig. 1). A hypothesis explaining the local and continental distributions of both pollinators could be that that of *C. silvestrianus* is biased towards humid savannas and associated forest edges, whereas *C. flabellatus* is mostly found in rain forests. Lamto is within the 'V-Baoulé', an indentation of Guinean savannas into the rain forest zone. We do not know if the present zone of overlap between the two species' distributions represents an overlap in habitat types, or if one or both species is, in fact, invading the home range of its competitor. This mechanism of allopatric adaptation has been used to explain the coexistence of two pollinators (*Courtella gabonensis* and *C. camerunensis*) of *Ficus ottoniifolia* in Gabon (Michaloud *et al.* 1985).

Our results are consistent with the hypothesis that *F. sur* has a tightly evolved mutualism with each of its two pollinators (Pellmyr & Huth 1994).

TABLE 3. *Regression model of the number of pollinators as a function of fig diameter in* F. sur.

$N = 133$	$r^2 = 0.12$	adj $r^2 = 0.12$	$F_{1,131} = 18.73$	$P < 0.0001$		SE Estim. = 262.01
	Beta	SE (Beta)	B	SE (B)	t	P
Intercept			−453.85	167.54	−2.71	<0.05
Diameter	0.35	0.08	21.50	4.97	4.33	<0.05

TABLE 4. *One-way ANOVA with seed production as the dependent variable.*

$F_{1,47} = 0.79$ $P > 0.1$ NS		$F_{1,115} = 0.24$ $P > 0.1$ NS		$F_{1,98} = 0.38$ $P > 0.1$ NS	
Treatment	Seeds	Treatment	Seeds	Treatment	Seeds
C. flabellatus only $N = 17$ figs	817.00	*C. silvestrianus* only $N = 84$ figs	900.42	*C. flabellatus* only $N = 17$ figs	817.00
Both *Ceratosolen* sp. $N = 33$ figs	948.85	Both *Ceratosolen* sp. $N = 33$ figs	948.85	*C. silvestrianus* only $N = 84$ figs	900.42

The majority of female flowers produce seeds apparently because the pollinators lay their eggs mostly in the short-styled flowers, and because the numerous female flowers of *Ficus sur* are seldom saturated with insects. The wasps pollinate figs at a very specific growth stage.

Concerning *Ficus* sex allocation, seeds invariably outnumber pollinator offspring, even when both species co-occur in the same fig. A majority of female flowers are thus destined to seed production, and a smaller number are transformed into galls to produce pollinators (*Ficus* male function). Verkerke (1988b) also found that *Ficus sur* figs contain considerably fewer male than female flowers.

Whether or not having two pollinators in the zone of sympatry presents a cost to *Ficus sur* could not be determined from our study. Ignoring gene flow from habitats containing only one of the pollinators, one potential cost to the fig in the zone of overlap would be decreases in overall seed production due to the competitive displacement of one of the pollinators to exploiting flowers ordinarily destined to produce seeds. This prediction could be evaluated by comparing flower exploitation patterns within and outside of the zone of sympatry; if the zone of sympatry has arisen recently, and/or there is sufficient gene flow, then there should be little difference in the flower exploitation patterns between populations. Habitat preferences on the part of the pollinators could mean more efficient pollination and can aid in the colonization of favorable new environments.

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