

## FLOWER SPECIALIZATION IN A PASSIVELY POLLINATED MONOECIOUS FIG: A QUESTION OF STYLE AND STIGMA?

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The stability of the mutualism between figs and their pollinator wasps depends on the patterns of seed and wasp production. In *Ficus maxima*, a passively pollinated monoecious fig, we estimated the correlations among different flower characteristics and determined their relationships with pollination success and pollinator oviposition. Across flowers, stigma length shows an allometric relationship with style length, and style length correlates negatively with style width. Longer-styled flowers are more likely to be pollinated and receive higher pollen loads. This is probably explained by their larger stigmatic surface that increases their chance of receiving the passively dispersed pollen. Consistent with findings in other species, flowers with longer styles are less likely to receive a pollinator's egg. This oviposition pattern is probably explained by a combination of factors: (1) wasps ovipositor are too short to reach flowers with extremely long styles, and 17% of flowers are inaccessible; (2) sometimes, there are too few pollinators to use all accessible flowers; (3) oviposition is more difficult through the long stigmas and thin styles associated with long-styled flowers. Given the patterns of pollinator egg distribution, the style/stigma size relationship in *F. maxima* appears advantageous for the fig since it leads to preferential pollination of flowers that are not used by wasps. It might reflect flower functional specialization and contribute to the mutualism stability.

**Keywords:** allometry, coevolution, mutualism, pollination, style/stigma relationship.

### Introduction

It is widely accepted that natural selection acts on flowering plants to improve pollination performance. Many flower traits are thought to have evolved to promote pollinator contact with floral organs during their visit and increase the quantity of pollen deposited as well as the precision of its placement (Cresswell 2000). In tightly coevolved pollination interactions, one might expect flowers to be finely tuned to maximize pollination efficiency of their visitors. The fig/fig wasp pollination mutualism represents an ancient (ca. 90 million years) and highly diverse model system to investigate plant-pollinator coadaptations (Berg 1989; Herre 1989; Kjellberg et al. 2001; Machado et al. 2001; Weiblen 2001; Joussetin et al. 2003b). However, little is known about how the differences in flower morphology observed both within and among fig species affect pollen deposition by wasps.

There are more than 700 species of figs (*Ficus*, Moraceae); each of them is pollinated by one or more species of Agaonid wasps (Corner 1985; Berg 1989; Rasplus 1994; Molbo et al. 2003). The enclosed fig inflorescence is lined by uniovulate

female flowers with their bases on the outer fig wall and their stigmatic surfaces pointed inward. This specialized inflorescence is known as a syconium, and it defines the genus *Ficus*. When a fig's syconia are receptive, they emit scents that attract the pollinator wasps (Ware and Compton 1994; Gibernau et al. 1998; Grison-Pigé et al. 2002). Pollen-bearing female wasps (foundresses) enter the syconium by the ostiole, which is the bract-lined opening situated at the apex of the syconium. On entering the fig cavity, wasps pollinate the flowers.

*Ficus* species exhibit two modes of pollination on the basis of whether wasps pollinate passively or actively. In all passively pollinated figs (one-third of all fig species; Kjellberg et al. 2001), the numerous stamens dehisce at wasp emergence so that pollen gets trapped on various parts of the wasps' bodies when they leave their natal fig (Ramirez 1969; Galil and Neeman 1977; Galil and Meiri 1981; Ramirez and Malavasi 1997; Kjellberg et al. 2001). The pollen trapped on the wasps' bodies is then passively released in the fig cavity when wasps lay their eggs. In the remaining two-thirds of *Ficus* species, wasps locate the stamens of their natal fig and load pollen into thoracic structures known as pollen pockets with their forelegs. When laying eggs in receptive figs, these wasps actively unload pollen (Galil and Eisikowitch 1969; Ramirez 1969; Frank 1984). Therefore, active pollination relies not only on floral traits but also on the directed behavioral traits of the pollinators.

In addition to pollinating fig flowers, female wasps also lay eggs into some of them. The flowers within a monoecious fig

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vary continuously from longer-styled flowers that have short pedicels with ovules close to the fig wall to shorter-styled flowers that have long pedicels with ovules close to the fig cavity (fig. 1) (Bronstein 1988; Nefdt and Compton 1996). To lay their eggs, pollinating wasps probe their ovipositor down the style to reach the ovule of individual flowers. Ovules that have been fertilized and did not receive a wasp egg can produce a seed, while ovules that have received a pollinator egg can produce a wasp if they are transformed successfully into galls (Verkerke 1989).

Figs benefit both from seed production and from wasp production that comes at the expense of some would-be seeds. The foundresses' female offspring are the only vectors that disperse pollen from their natal figs. However, the reproductive success of wasps depends only on the number of flowers hosting their offspring (Janzen 1979; Herre 1989; Herre and West 1997). Why fig wasps do not oviposit into all the flowers and destroy all ovules presents an intriguing but still incompletely resolved question (Herre 1999; Yu et al. 2004).

Several hypotheses have been proposed to explain egg deposition patterns of pollinating fig wasps in monoecious figs and why there are always some flowers left for seed production. The wasps' ovipositors may generally be too short to reach all the flowers, since pollinating wasps preferentially lay their eggs in shorter-styled flowers of several fig species (Nefdt and Compton 1996; Jusselin et al. 2001) (fig. 1). However, in many fig species, wasp ovipositors can reach most if not all ovules (Bronstein 1988; Nefdt and Compton 1996; Otero and Ackerman 2002). Other hypotheses include insufficient egg supply relative to the number of flowers in figs (Nefdt and Compton 1996), differential quality of oviposition sites (Anstett et al. 1996; Herre 1999; Anstett 2001), and the existence of structural or chemical floral constraints that preclude wasp oviposition (West and Herre 1994). The insufficient eggs hypothesis is clearly true in some fig species (Nefdt and Compton 1996): wasps oviposit first in the more

accessible short-styled flowers, and because too few foundresses enter the fig cavity, the long-styled flowers are left for seed production. However, it cannot be a general explanation. In several *Ficus* species, many figs are visited by sufficient foundresses to saturate all flowers with their eggs, but seeds are still produced (Herre 1989, 1999; Anstett et al. 1996). The existence of a structural floral constraint is supported by the observation that parasitic wasps that lay their eggs from the outside of the fig through the fig wall also use short-styled flowers (West and Herre 1994). However, no biological traits preventing wasp oviposition or larval development have been identified.

Although patterns of oviposition have received much attention, relatively little is known about the patterns of pollen deposition within the inflorescence. However, pollen distribution should strongly affect the outcome of the interaction for the fig, since only flowers that received pollen and no pollinator egg can develop into seeds. A previous study on three actively pollinated monoecious figs showed that the presence of pollen on a flower's stigma does not depend on whether the flower received a pollinator egg (Jusselin et al. 2003a). Since short-styled flowers are more likely to receive a wasp egg, this independence implies that in these species style length did not influence a flower's probability of receiving pollen. However, in a passively pollinated monoecious fig, *Ficus maxima*, flowers that were less likely to receive an egg showed a greater tendency to be pollinated (Jusselin et al. 2003a).

In this study, we tested whether pistil traits affect the probabilities of pollination and oviposition by investigating the relationship between style length, style width, and stigma length and the distribution of pollen and eggs among flowers in *F. maxima*. In addition, to clarify the factors that are responsible for the oviposition pattern in this species, we tested whether wasps' ovipositors were long enough to reach the ovule of all flowers within the syconium.

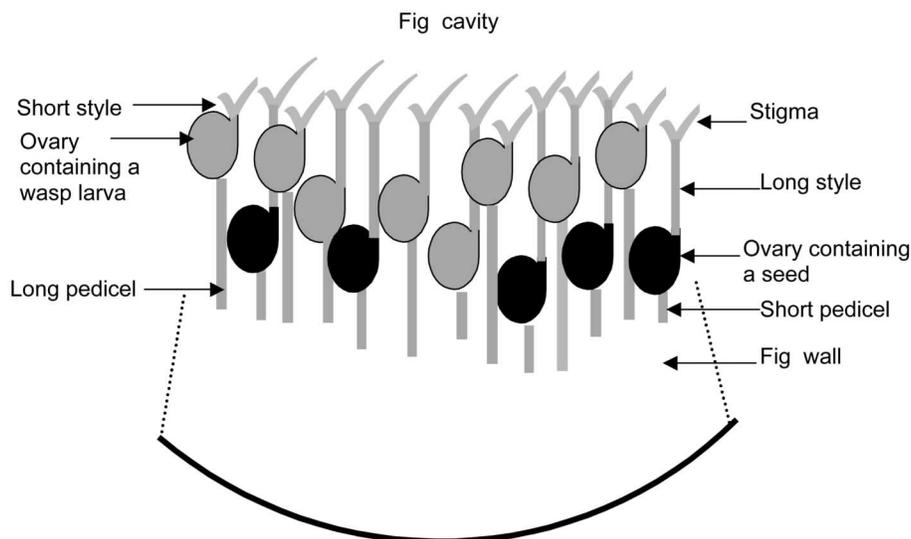


Fig. 1 Schematic drawing of the fig cavity after pollination and oviposition

## Material and Methods

### Background Biology

*Ficus maxima* belongs to the New World subgenus *Pharmacosycea*, section *Pharmacosycea* (Berg 1989), and is pollinated by *Tetrapus americanus* (Wiebes 1995; Molbo et al. 2003). These species are representatives of the basal lineages of *Ficus* and the agaonid pollinators for figs, respectively (Herre et al. 1996; Machado et al. 2001; Weiblen 2001). *Ficus maxima* inflorescences are spherical and ca. 2 cm in diameter. Each fig inflorescence possesses 500–600 uniovulate female flowers and more than 100 male flowers. Adult female pollinator wasps are ca. 2 mm long and can produce ca. 190 offspring (E. A. Herre, unpublished data).

### Flower Observation

We collected freshly pollinated *F. maxima* syconia in Gamboa (near the Panama Canal, Republic of Panama) in May 2001. Twenty-two fruits were collected from one tree on the day that pollinators were seen entering through the ostiole. Each fig was kept for 24 h in individual plastic vials to ensure that foundresses had time to deposit the pollen they transported. Picking up the figs from the tree does not seem to affect pollen deposition and oviposition behavior (Greef and Compton 1996). Then, we cut each fig open and counted the number of foundresses. For each fig, 20–25 flowers were randomly chosen and removed with fine forceps. The flowers were soaked for 48 h in a solution of aniline blue (0.01%) in 0.1 M  $K_3PO_4$  and NaOH (20%) to soften the tissues (Kearns and Inouye 1993). They were then placed on a microscope slide. Each flower was squashed gently under a coverslip and observed under a compound microscope. We counted the pollen grains on the stained stigmas and noted the presence or absence of a pollinator egg within the ovule.

For all flowers, we measured style and stigma lengths to the nearest 0.01 mm under a dissecting microscope. The style was defined as the strictly nonreceptive area between ovary and stigma: it was measured from its insertion on the ovary to the start of the stigmatic surface. The stigmatic area was defined as the region that presents receptive surfaces: it is covered with papillae. We distinguished two parts in the stigmatic area: (1) the lower unitary stigmatic base and (2) the two upper stigmatic branches. Stigma length was the combined length of the stigmatic base and each upper branch.

### Style Length, Style Width, and Stigma Length Relationship

We examined the relative size relationship of style and stigma length using allometric analyses (Niklas 1994). Both measurements were log transformed, and linear regressions were performed. The relation between stigma length ( $Y$ ) and style length ( $X$ ) was described by the equation  $Y = bX^a$ , linearized under the form  $\log(Y) = \log b + a \log(X)$ . The value of the slope establishes whether the relation between style length and stigma length is isometric ( $a = 1$ , the form of the flower stays the same when style length increases) or allometric ( $a \neq 1$ , as style length increases, stigma length does not

increase at the same rate). We used SAS (PROG REG; SAS Institute 1996) to estimate the parameters of the allometric equation. The slopes were tested for departure from 0 and 1.

We further tested whether flowers switch to producing really long stigmas beyond some critical style length. We used the method of Eberhard and Gutierrez (1991) to test for nonlinearity, and we fitted the partial regression equation  $\log Y = b + a \log X + c \log X^2$  to our data. If  $c$  differs significantly from 0, it suggests the existence of a switch point. The significance of  $c$  is tested with a  $t$ -test.

In addition, because style thickness could influence wasp oviposition (Verkerke 1989), we measured style width for a subset of 50 flowers. The relation between style length and style width was examined using linear regressions.

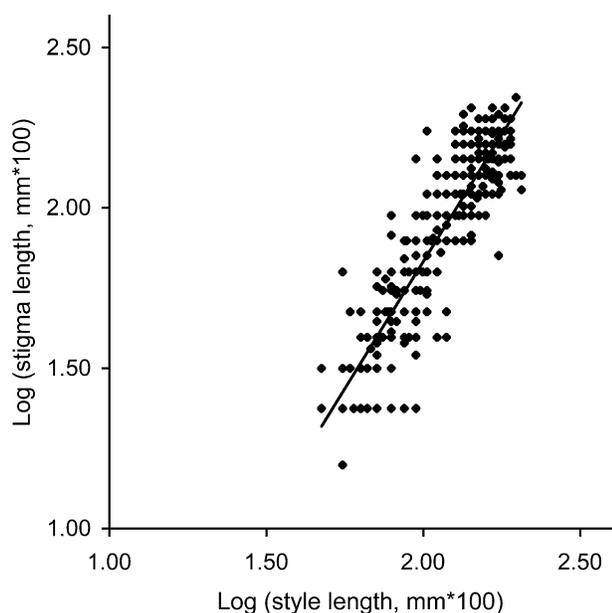
### Distribution of Pollen Grains and Pollinator Eggs among Flowers

The distribution of pollen grains among flowers was analyzed with generalized linear models (GLIM 1985). The probability of a flower receiving pollen was analyzed with a binomial error and a logit function. A full model was fitted to the data with number of foundresses and style length (or stigma length) as covariates and fig as a random factor. We also examined whether the number of foundresses and style length or stigma length affected the number of pollen grains found on stigmas. We assumed that pollen loads had a Poisson-distributed error variance, and a log link was used. Because of overdispersion, we used Pearson's  $\chi^2$  to adjust the scale parameters (Crawley 1993). Style length and number of foundresses were treated as covariates and fig as a random factor.

We also analyzed whether number of foundresses and style length affected the probability of a flower receiving a pollinator egg. Number of foundresses and style length (or stigma length) were again treated as covariates and fig as a random factor. In addition, to determine whether there was a negative association between being pollinated and receiving a pollinator egg, we treated the presence of pollen on stigmas as a fixed factor with two levels (0, pollinated; 1, not pollinated).

### Ovipositor Length, Style Length, and Flower Accessibility

To determine whether all flowers were accessible to oviposition, wasp ovipositor length was compared with style length. The ovipositors of 20 foundresses chosen at random were measured. Following Nefdt and Compton's (1996) procedure, each wasp was dissected to reveal the entire length of the ovipositor (from the basal plates to the tip), placed in a drop of water between a slide and a cover slip, and measured to the nearest 0.01 mm. To compare ovipositor length with the actual distance that wasps had to probe with their ovipositor, we measured style length from the point where it enters the ovary to the top of the stigma for 40 flowers selected randomly from three receptive figs. Comparisons between style length and ovipositor length gave an estimate of the proportion of flowers that would be accessible to the wasps, assuming that the whole ovipositor can be inserted.



**Fig. 2** Relation between style length and stigma length of *Ficus maxima* flowers.

## Results

### Style Length, Style Width, and Stigma Length Relationship

Stigma length ( $Y$ ) varied positively with style length ( $X$ ) (fig. 2;  $r^2 = 0.8488$ ,  $\log Y = 1.57\log X - 1.3$ ,  $t = 54.57$ ,  $P < 0.001$ ). The slope of the regression significantly exceeded 1 ( $F = 399$ ,  $P < 0.0001$ ), indicating that stigma length increases relatively faster than style length. When we fitted the partial regression equation  $\log Y = b + a\log X + c\log X^2$  to our data, we could not reject the linearity of the relationship ( $t_1 = 2$ ,  $P = 0.29$ ), which implies that there is no bimodality in the relationship between style and stigma length in *Ficus maxima*. Style width ( $W$ ) varied negatively with style length ( $L$ ) ( $\log W = -0.77\log(L) + 2.6$ ,  $R^2 = 0.60$ ).

### Distribution of Pollen Grains and Pollinator Eggs among Flowers

The number of foundresses found inside the fig cavity varied from one to seven. The presence of pollen grains on the stigma of a flower was significantly affected by the style length of the flower and the number of foundresses found in the fig: the probability of receiving pollen for a flower increased with style length and foundress number (fig. 3). Style length and foundress number had interacting effects: when the number of foundresses increased, the probability of receiving pollen increased for all flowers but increased disproportionately for long-styled flowers (table 1). Replacing style length by stigma length in the model did not significantly change the percentage of variance explained by the model (35.2% for stigma length compared with 35.1% for style length).

Pollen loads on stigmas varied from 0 to 21 pollen grains (mean = 1.8). It increased with number of foundresses

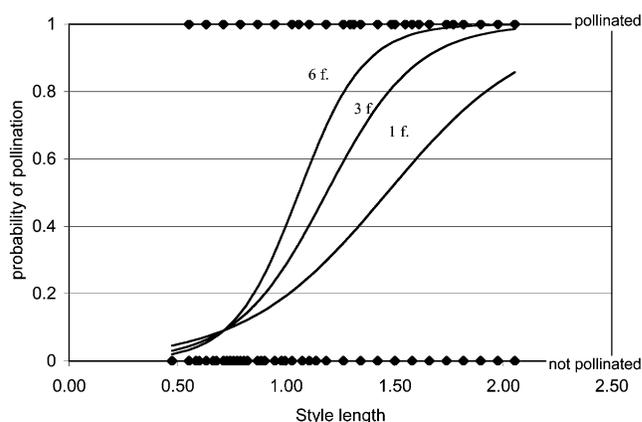
( $\chi^2 = 23.9$ ,  $df = 1$ ,  $P < 0.001$ ) and style length ( $\chi^2 = 134$ ,  $df = 1$ ,  $P < 0.001$ ).

The presence of a pollinator egg within the ovule of a flower was significantly influenced by the style length of the flower and the number of foundresses found in a fig. The probability of receiving a pollinator egg for a flower increased with foundress number but decreased with style length (fig. 4). Style length and foundress number had interacting effects (table 2): although more flowers were occupied when number of foundresses increased, the increase in oviposition primarily affected shorter-styled flowers (fig. 4). Similar to the previous analysis, replacing style length with stigma length in the model did not significantly change the percentage of deviance explained (15.5% for stigma length compared with 14.5% for style length).

The presence of pollen on the stigma of a flower was negatively correlated to the presence of an egg in the ovule (table 1). A log-linear model analysis conducted on the same species but on a smaller data set (only 15 figs) had given similar results (Jousselin et al. 2003a). The same analysis conducted on the data presented here confirmed this result ( $\chi^2 = 9.2$ ,  $df = 1$ ,  $P < 0.01$ ).

### Ovipositor Length, Style Length, and Flower Occupancy

Ovipositor length varied from 1.35 to 1.93 mm (average =  $1.59 \pm 0.15$  mm). Total style length (including the stigmatic base) varied from 0.59 to 2.05 mm (average =  $1.16 \pm 0.11$  mm). On the basis of the proportion of styles longer than the mean ovipositor length of their pollinators, 83% of flowers were accessible to the wasps in this *F. maxima* tree. This exceeded the average proportion of flowers occupied per fig (mean =  $32\% \pm 24\%$ ). Although the proportion of flowers occupied increased with number of foundresses, it was always less than 80% in all the figs examined (range = 4%–74% of flowers occupied by a wasp egg per fig).



**Fig. 3** Black diamonds show the observed incidence of pollination in relation to style length. Curves show the probability  $P$  of a flower being pollinated for one, three, and six foundresses as estimated from logistic regressions ( $P = 1/1 + \exp(4.05 - 0.43 \times F) + (2.47 \times X) + (0.60 \times F \times X)$ ,  $F$  = number of foundresses,  $X$  = style length) using a logit link.

**Table 1**  
**Factors Influencing the Probability of Receiving Pollen for a Flower**

Explanatory variables	$\chi^2$ (df = 1)	P
Number of foundresses	23	<0.001
Style length	254	<0.001
Presence of wasp egg	5	0.03
Number of foundresses × style length	8	0.01

Note. Data collected on 22 inflorescences (535 flowers).

Then, we examined the style length of flowers actually occupied by pollinator eggs. Since the style measurements of flowers for which we had determined ovule content did not include the stigmatic base, we approximated inaccessible flowers in this set of flowers as flowers with a style >1.50 mm (stigmatic bases measure roughly 0.1 mm). Very few flowers with styles longer than 1.50 mm had received a pollinator egg (only 5%), whereas 40% of flowers with styles <1.50 mm have received a wasp egg. We observed only one fig, with six foundresses, where 100% of examined flowers with styles >1.5 mm were used by pollinators.

**Discussion**

*Pollen Deposition, Pollinator Egg Distribution, and Pistil Morphology*

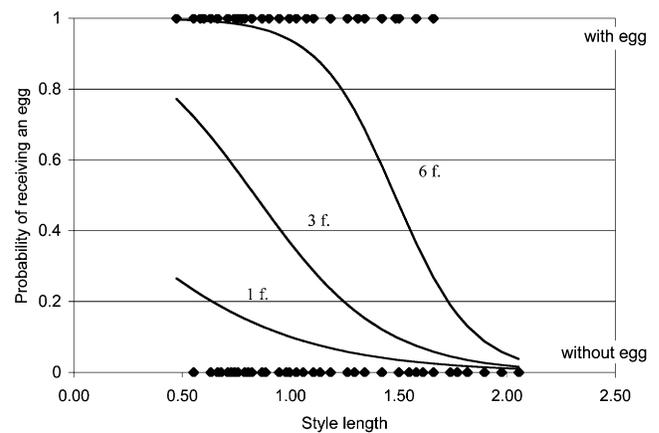
This study is the first to document pollen distribution within *Ficus* inflorescences in relation to flower characteristics as well as egg distribution. Our observations of 535 flowers in a *Ficus maxima* tree show that long-styled flowers are more likely to receive pollen than short-styled ones and also receive more pollen grains per pollinated flower. This is probably the result of the allometric relationship between style length and stigma length. Longer-styled flowers present a much larger receptive surface, which increases their chance of receiving pollen. In *F. maxima*, the long branches of the bifid stigmas project into the fig cavity so that they touch the pollinators' bodies as they search for oviposition sites: the longer the branches, the larger the contact area between the stigmas and the wasps' bodies and the more efficient they will be at brushing off the pollen.

As previously shown in other monoecious fig species (Nefdt and Compton 1996; Jousselin et al. 2001; but Otero and Ackerman 2002), in *F. maxima*, shorter-styled flowers are more likely to receive wasp eggs. Many hypotheses have been proposed to explain wasps' oviposition pattern. Our goal is not to discuss these hypotheses, since this has been done in recent studies and reviews (Herre 1999; Anstett 2001; Jousselin et al. 2001; Cook and Rasplus 2003; Yu et al. 2004), but to determine whether some of them can be rejected in the case of *F. maxima*. Measurements of ovipositor and style length and observations of the range of flowers occupied by wasp eggs indicate that the flowers with the longest styles are protected from oviposition (17% of flowers are inaccessible). The utilization of accessible (short-styled)

flowers increases with foundress number, which is in agreement with the egg limitation hypothesis, but it rarely reaches 100%. Further, given that a single foundress can on average produce 190 offspring, then three foundresses should be enough to fill all ovules. Hence, egg limitation and ovipositor/style length relation certainly play a role in limiting over-exploitation of *F. maxima* figs, but they are probably not the only factors. As suggested in other studies, pollinators' oviposition may be influenced by other aspects of pistil morphology (Verkerke 1989; West and Herre 1994; Jousselin et al. 2001). To lay an egg, wasps must insert their ovipositor in the stylar canal. In *F. maxima*, style length is negatively correlated with style width. This had also been observed in *Ficus tonifolia* and *Ficus sur* (Verkerke 1989). The insertion and guidance of the ovipositor of pollinators might be difficult in the narrow stylar canal of long-styled flowers (Verkerke 1989). The very long stigmas associated with long-styled flowers might also limit the accessibility of the ovule. These characteristics might render some of the flowers unsuitable for oviposition.

*Does Flower Morphology Reflect Adaptation to Wasp Behavior?*

Given the wasps' oviposition behavior, the observed pattern of pollen receipt seems to be advantageous for the fig since it leads to preferential fertilization of flowers that do not receive an egg. Hence, in terms of selection acting on the fig tree, pollen is not "wasted" on a flower that might be transformed into a gall. This indicates that the relationship between stigma length and style length might have been favored by selection for increasing seed production. An allometric relationship between style length and stigma length implies that as style length increases, the appropriate size ratio is modified: the flower changes form. A change of form in an organ often reflects a change of function. The elongate bifid stigmas characterizing long-styled flowers could thus



**Fig. 4** Black diamonds show the observed incidence of a pollinator egg in a flower in relation to style length. Curves show the probability *P* of a flower receiving a pollinator egg for one, three, and six foundresses as estimated from logistic regressions ( $P = 1/1 + \exp(0.88) + (0.92 \times F) - 1.85 \times X + (-0.38 \times F \times X)$ , *F* = number of foundresses, *X* = style length) using a logit link.

**Table 2**  
**Factors Influencing the Probability of Receiving a Pollinator Egg for a Flower**

Explanatory variables	$\chi^2$ (df = 1)	P
Number of foundresses	9.6	0.01
Style length	104	<0.001
Number of foundresses $\times$ style length	6.4	0.0011

Note. Data collected on 22 inflorescences (535 flowers).

increase pollen receipt on these flowers and represent a functional specialization. However, there are no flowers reserved for seed production or wasp production, since when we tested for flower dimorphism, we found no clear distinction between longer-styled flowers and shorter-styled flowers. More data on other trees and other species will be necessary to validate our interpretation that the style/stigma allometric relationship might represent an adaptation to pollinators' oviposition behavior. Visual inspections show that the patterns measured in several inflorescences of this *F. maxima* tree are repeated in other *F. maxima* trees and in other *Pharmacosycea* fig species. Alternatively, the style/stigma relationship we observed is merely the result of developmental constraints.

It would not be surprising if pistil morphology exhibited adaptation to pollinators' oviposition pattern. Comparative analyses across species showed that stigma arrangement is certainly adapted to pollination behavior (Jousselin et al. 2003b). In actively pollinated figs, stigmas all reach the same height in the fig cavity, and their receptive surfaces are in contact with each other (Verkerke 1989). Active pollination is supposed to have evolved in fig wasps as a way to increase the fertilization of flowers in which their larvae develop. The fused stigmas that equalize the chance of fertilization of all flowers is probably an adaptation to the directed behavioral

traits of the pollinators (Jousselin and Kjellberg 2001). In contrast, in passively pollinated figs such as *F. maxima*, in which wasps carry the pollen on various parts of their body and cannot have control of which flowers receive pollen, stigmas are elongate and project into the fig cavity. Consequently, pollination occurs thanks to the stigmas touching the pollinators' bodies. Hence, in the fig/fig wasp association, as in other specialized pollination mutualisms, flower morphology seems to be finely tuned to optimize pollinator efficiency.

### Conclusions

We suggest that the stigma/style size relation observed in *F. maxima* could be an adaptation to increase the pollination of flowers not used by wasps. In addition, the analysis of pollinators' oviposition patterns indicates that a combination of factors might act simultaneously in *F. maxima* to prevent the overexploitation of flowers by wasps. Comparisons of our results with other studies (Bronstein 1988; West and Herre 1994; Nefdt and Compton 1996; Herre 1999; Anstett 2001; Weiblen 2001; Otero and Ackerman 2002) indicate that different host-pollinator species combinations achieve mutualism stability through different mechanisms. This situation is similar to the one observed in another very specialized pollination mutualism: the yucca/yucca moth system. As the number of studies increase, it seems also that the factors regulating the mutualism differ according to species (Addicott and Bao 1999; Pellmyr 2003).

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