

Agaonid-*Ficus* interactions with special reference to pollination ethology

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Abstract. That certain species of wasps developing inside the wild variety of figs are responsible for the setting and ripening of the fruits (caprification) of the cultivated variety of figs of the same species (*Ficus carica* L) is well known. Besides each species of *Ficus* having its specific agaonid pollinator and a close mutualistic symbiosis, several adaptive modifications in the agaonids and *Ficus* species appear significant in the course of evolution of this relationship. Recent studies on the pollination ethology of the agaonids have shown that besides the passive mode of pollen transfer (topocentric pollination) an active and deliberate type of pollen transfer (ethodynamic pollination) exists, which is associated with the development of specialised structures like the mesothoracic pollen pockets and the fore coxal corbiculae. The ecophysiological changes in the interior of the ripening fig syconia also play an important role in pollination during the post-emergence behaviour of the males and females in some agaonids. Further lines of work in the fascinating area of fig-wasp research are indicated.

Keywords. Agaonidae; *Ficus*; interactions; pollination ethology.

1. Introduction

Since pre-historic times the cultivation of the edible fig (*Ficus carica* L.) has been an important industry in the countries around the Mediterranean Sea. Even then, it was known that the setting and ripening of the cultivated figs were dependent on the local presence of the wild fig (caprifig) tree of the same species. The first report about the strange association between the cultivated fig trees and the chalcidoid wasps (*Blastophaga*) developing inside the caprifigs was probably those of Aristotle and Theophrastus (about 340 B.C.). They knew that these wasps were in some way responsible for the setting and maturation of the fruit. It became the practice to either plant a few caprifig trees among the cultivated fig trees in orchards, or to cut the branches of the caprifig trees bearing ripe figs and hang these branches from the cultivated fig trees at the appropriate phases of the crop development to enable the *Blastophaga* emerge and enter the tender edible figs to effect the setting and ripening of the figs, a procedure known as caprification.

2. *Ficus* species and their specific agaonid pollinators

Studies on the fig wasps during the later period of the last century and the early period of the present century revealed the identity of these wasps as the insects involved in caprification. The works of Saunders (1878), Westwood (1882), Mayer (1882), Mayr (1885), Muller (1856), Cunningham (1889), Eisen (1891), Baker (1913), Condit (1918, 1947, 1963), Grandi (1920), Joseph (1958, 1966), Hill (1967a, b), Wiebes (1973, 1976, 1981), and Abdurahiman and Joseph (1976, 1978) showed that the plants of the genus

Ficus exist in a state of close mutualistic symbiosis with the various chalcidoid wasps belonging to the family Agaonidae and that each species of the plant has its specific agaonid pollinator.

3. The mutualistic symbiosis of *Ficus* and their agaonid wasps and its interaction

Fig-agaonid symbiosis is a complex interrelationship in which morphological, behavioural and physiological effects of the partners are interpreted into a functional whole reminiscent of a unique superorganism (Galil and Eisikowitch 1971). Natural selection has moulded the reciprocal evolution of both symbionts and the adjustment between the two organisms is very finely balanced. Consequently, the characteristics of one partner can be properly evaluated only when considered together with their second partner. The moulding effect of natural selection expresses itself in many minute structural details and correspondingly in behavioural patterns, which are of vital importance for the coexistence of both organisms, the *Ficus* species and the symbiotic wasps. Such instances of mutualistic interaction and adjustments are seen in the following cases (Galil and Eisikowitch, 1971):

3.1. Style length ratios

In monoecious figs (eg. *F. religiosa* L; *F. sycomorus* L; etc.), where two types of female flowers and the male flowers occur in the same syconium (and in the dioecious figs (eg. *F. carica* L; *F. hispida* L; *F. exasperata* Vahl; etc.) where the short-styled and long-styled flowers occur in separate syconia, the differentiation of the female flowers into short-styled flowers in which the wasps are able to oviposit and undergo development, and the long-styled flowers wherein the ovaries are beyond the reach of the wasps' ovipositor, appears vital for the survival of the host plant species and its wasp symbiont. The evolution of long-styled flowers can thus be regarded as a 'self defence' adaptation, preventing the figs against the attack of the agaonid wasps. This also offers clear proof as to the importance of the ovipositor length in the maintenance of an equilibrium in the symbiosis where the plant is able to produce seeds in the long-styled flowers by preventing the oviposition of the wasps with abbreviated ovipositor and at the same time these wasps are able to breed in short-styled flowers.

3.2 Sex ratios

It is well known that the sex ratios in plants and animals are not accidental, but are due to complex characteristics associated with reproduction, for example, with the sexual act and various subsidiary activities of males and females. Since only the females are involved in the production of the eggs which give rise to the new organisms, the fitness of the species as a whole may depend on fixed proportions between males and females, in which the number of males does not exceed certain limits of the minimum required for the fulfilment of their various functions. This holds good for the sex ratio proper in dioecious organisms as well as for the separate male and female organs in monoecious ones. In the syconia of *Ficus*, the significance of sex ratio for the survival potential of both organisms is especially clear. Within the restricted and enclosed living space of the syconium, increase in one of the constituents may occur only at the expense of others.

Thus the development of a large number of male flowers leaves only little room for the female flowers which are intended to give rise to the new generation of seeds and wasps. The same applies to the wasp sex ratio: development of many males results in fewer females, since both compete for the same gall flowers.

Undoubtedly, the wide fluctuations in the number of anthers in the syconia of the different *Ficus* spp. reflect on the efficiency of pollination. In the figs of *Ficus religiosa* and *F. sycomorus*, there are comparatively very few anthers (9–19 and 60–80 respectively). This characteristic is correlated with a highly evolved and efficient pollination process which is accomplished with utmost precision and with great economy of pollen (Galil and Eisikowitch 1969; Galil and Snitzer-Pasternak 1970). On the other hand, the vernal male syconia of the common fig (the profichi of *F. carica*) produces abundant pollen from approximately 200 male flowers, containing several stamens each and the male flowers occupy a considerable part of the fig. *Blastophaga psenes* L., the pollinator of the common fig, lacks pollen pockets so that pollen loading is achieved passively by dusting the wasp's body as it passes between the open anthers on the way out. The large number of anthers and the profusion of pollen is most likely indicative of the absence of highly evolved pollen collecting organs and instincts in the pollinating wasps, such as are found in the pollinators of *F. religiosa* and *F. sycomorus*.

The sex ratio of the fig-inhabiting wasps reflects on several characteristics associated with the copulation act and other duties of the male. When the female wasps are easily accessible and the copulation act is thus assured and brief, polygamous males may fertilise a large number of females. Joseph (1958) compared the sex ratio of *Blastophaga psenes* L. with that of its parasite, *Philotrypesis caricae* L. In the former, the males perform the copulation act while the females are still confined in their respective galls. The sex ratio is, therefore, comparatively low (10–15 males for 100 females according to Grandi 1930; 6–7 males for 100 females according to Condit 1947). In *Philotrypesis*, the more complex sexual act is accomplished in the syconial cavity and the male must accost the female as she leaves her gall. Here the male is much more skilful and the sex ratio is higher (55–60 males for 100 females, according to Joseph (1958).

3.3 Coordination of development spans

In fig symbiosis, coordination of the duration of development of the participating organisms—the syconia and the agaonid wasps—is of vital importance. Were the syconia to drop too early, when the wasps were still at the larval stage, the insects would not reach maturity. Conversely, were the syconia still green and hard upon the maturation of the wasps, the fauna of the fig would be imprisoned and doomed to extinction.

Such coordination in the fig, is particularly complicated because the participating organisms belong to different kingdoms (the plant and the animal). Their responses to changes in climatic conditions, especially to temperatures, may differ. Under these circumstances extreme flexibility of the adapting mechanism is indispensable for ensuring the survival of both the participants. The success of the symbiosis can be ensured by the imposition of the developmental rhythm of the most sensitive component, namely that of the wasps, upon that of the other components. For instance, at the early stages of development, oviposition by the wasps prevents dropping of the figs and ensures development of the figs to final ripening, even in the

absence of flower pollination and embryo formation. The viability and maturation of the unpollinated syconia, due to occupation by the wasps is, therefore, of vital importance to the annual life cycle of the insects. The effect of the secretion of the acid gland of the wasp injected into the fig ovaries during oviposition, is physiologically comparable to that of normal fertilisation in flowers. This is very clearly evident in *F. sycomorus* where no pollination takes place (Galil *et al* 1970). As long as the fig wasp larvae are found within it, the fig shows great resistance to ripening. The situation changes entirely when the wasps reach maturity and the males perforate their galls and issue forth into the syconial cavity. The receptacle then softens and ripening ensues regardless of whether or not these syconia contain seeds. It would seem, therefore, that the wasps accelerate fig ripening, thus adjusting the developmental rhythm of the receptacles to their own.

3.4 Provisioning of food by the agaonid wasp for its developing stages

Blastophaga psenes lays the egg in the short-styled *Ficus* ovaries between the internal integument and nucellus (Longo 1909). This observation was later confirmed by Grandi (1920) and Joseph (1958) in the same species, and also in another agaonid species, viz *Ceratosolen marchali* Mayr, by Abdurahiman and Joseph (1976). Along with each act of oviposition, *B. psenes* injects a little of the secretion of its poison gland which inducts gall formation by the division of the secondary nucellus of the embryonic sac leading to the parthenogenetic development of the endosperm which serves as a provision of food for the developing stages of the insect. The effect of this secretion is physiologically comparable to that of normal fertilization in flowers as already stated above.

3.5 Pollination benefits for the wasps

Perhaps the most intriguing question in connection with the pollination act of *Ficus* spp. (*F. religiosa* and *F. sycomorus*) is how all the structural and behavioural characteristics of the pollinating wasps (Galil and Eisikowitch 1969; Galil and Snitzer-Pasternak 1970) could have arisen, in the absence of any immediate benefit of the process to the wasp itself. What could have been the selective advantage which promoted the development in them of unique pollen pockets and of appropriate instincts to load these pockets inside old figs and empty them inside young receptive figs, during the act of oviposition?

In *Yucca* sp. by the *Yucca* moth (*Tegeticula*) also the pollination act consists of pollen loading and unloading which appears to be without any direct benefit to the insect (Riley 1891). But in *Yucca* the selective advantages which could have promoted development of the necessary structures and instincts in the moth are clearly evident, in as much as unpollinated flowers drop very soon and pollination is thus indispensable for the survival of the larvae which develop within the ovaries.

But in the unpollinated figs of *F. religiosa* in which the wasps had oviposited, an unbalanced development takes place where the nucellar tissue and the parthenogenetic endosperm may be a poor food source for the wasp larvae and insufficient for most females which undergo a differential mortality with regard to the males (Galil and Eisikowitch 1971). In any case, the unbalanced development of the unpollinated figs and especially the scarcity of the female wasps in them, must constitute serious

drawbacks to the perpetuation of the wasps. This might have been, as in *Yucca*, the selective disadvantage which stimulated the evolution of the particular wasp structures and instincts associated with pollination.

4. Pollination ethology

Though the fig wasps were known to be the sole agents of pollination in all *Ficus* species, the manner in which these minute and glabrous bodied wasps effect the transfer of pollen was not well understood till somewhat recently. Galil and Eisikowitch (1969) and Ramirez (1969) discovered the presence in various species of female wasps of unique organs which serve as containers for the transportation of pollen. It is now known that some species of the wasp genera like *Blastophaga*, *Ceratosolen*, *Maniella*, *Liporrhopalum*, *Agaon*, *Allotriozone*, *Elizabethiella* and *Pleistodontes* possess these specialised structures like 'pollen pockets' and 'corbiculae'. (Galil 1973; Galil and Eisikowitch 1968, 1969, 1971, 1974; Ramirez 1974; Galil *et al* 1973a; Galil and Neeman 1977; Mathew Joseph and Abdurahiman 1981). However, it has been found that there is considerable variation in the structure and behaviour of the pollinators of the different species of *Ficus*. In *Blastophaga psenes*, the pollinator of *F. carica*, no such cavities have been located and the pollen is passively carried on the body surface of the female wasp. Galil (1973) termed this type of pollen transfer as "topocentric pollination", in contrast to the "ethodynamic pollination" which occurs in quite a number of fig wasp species wherein the specific structures and behaviour concerned with pollination are involved.

Ramirez (1969) reported the presence of pollen grains in the digestive tracts of twelve species of *Tetrapus*. It is assumed that while these wasps crawl among the masses of stigmas of the *Ficus* flowers in their attempt to oviposit, they also regurgitate the pollen on them.

In *Ceratosolen arabicus*, the pollinator of *F. sycomorus*, Galil and Eisikowitch (1968, 1969, 1971, 1974) described the behaviour of the wasp during different phases of the fig. Before the exit of the fertilised females from the almost ripe figs, the males assemble at the upper part of the syconium. As the amount of the liquid in the syconium decreases, the stamens gradually protrude from their perianths at the male zone of the fig around the ostiole. The males clasp and cut off the anthers and tumble down into the cavity of the fig while still holding the anthers between the legs. Simultaneously the female wasps that emerge out from their galls, approach the cut anthers and grasp them. Using their mandibles and the scapes of the antennae, they widen the narrow dehiscence slit of the anther and with the arolia of the fore legs lift pollen on to the ventral surface of the body. The thorax is curved so that the covering membranes of the mesothoracic pollen pockets stand out along their inner suture leaving a wide opening for the pocket. With the help of the coxal combs of the fore legs, the pollen grains are now shovelled into the pocket. Such females loaded with pollen grains emerge out of the syconium and enter the young syconium to lay eggs in pistils and performs the 'pollination act'. Toward the end of oviposition, the forelegs of the wasp fold back until the arolia reach the lower margin of the pockets and then lower to touch the stigmas bringing the pollen grains on them. In *Ceratosolen hewitti*, the pollination of the dioecious *Ficus fistulosa*, Galil (1973) studied the presence of closed thoracic pockets and coxal combs and showed an identical type of behaviour in pollen loading and unloading. Mathew and

Abdurahiman (1981) discussed the mechanism of pollination in *Ficus racemosa*. In this fig, the pollinator *Ceratosolen fusciceps* Mäyr lacks 'coxal corbiculae' as described by Ramirz (1969). They observed that the female, before the termination of oviposition, folds up her fore legs and scratches the pockets 3–5 times with her arolia and claws. These to and fro movements of the forelegs shovel some pollen grains to the stigmas. This was followed by striking the tarsi against each other and rubbing the arolia and claws on the stigmal surface effecting the transference of pollen.

The pollination ethology of the agaonids breeding in the receptacles of *Ficus religiosa*, *F. costaricana* and *F. hemslyana* has also been studied by various authors and almost identical behaviour patterns reported (Galil and Eisikowitch 1968, 1969, 1971, 1974; Galil and Snitzer-Pasternak 1970; Galil *et al* 1973a). In *Blastophaga quadraticeps* Mayr of *Ficus religiosa* the behaviour of the wasps is somewhat different from that in *Ceratosolen* spp., in that the males do not cut the anthers. The fertilized females remain in their galls while the males bore exit holes. Galil *et al* (1973b) showed that the changes in the internal gas composition of the ripening fig have a decisive role on the differential activities of the males and females of the agaonid wasps. The analysis of the gas inside the syconia before the exit holes are bored by the males showed about 10% CO₂, 10% O₂ and some ethylene and as such the males are active and carry out their usual activities. Once the syconial wall is perforated and as the gaseous composition parallels to that of the atmospheric air, the males get inhibited while the females become active, load pollen in their pockets and leave the receptacles.

The traditional belief that *Blastophaga psenes*, the pollinator in the common fig *F. carica*, effects pollination by carrying pollen stuck to its body surface, is no longer tenable, as the very narrow entrance slits of the ostiole render it very difficult for them to introduce pollen into the female receptive fig. Galil and Neeman (1977) showed that the process of pollination in this case involve: (i) loading of pollen from the ripe fig into the thoracic intersegmental and pleural invaginations that occur in the shrunken body of the insect due to water loss; and (ii) unloading of pollen in the receptive fig, as a result of partial swelling and contortion of the wasps body during oviposition attempts. Nevertheless the process is typically topocentric. The females get passively dusted with pollen and similarly are brushed onto the stigmas of young female flowers by accidental contact.

In fig species where topocentric pollination is reported, the syconium is usually characterised by the presence of innumerable stamens that can yield pollen grains abundantly. The pollinators in such figs do not possess specialised organs for handling pollen and for carrying it from fig to fig (Galil 1973). The cases where ethodynamic type of pollination is reported, is essentially different and invariably such figs possess a comparatively lesser number of anthers per syconium. This reduction in number reflects the precision and economy of the pollination act in such *Ficus* plants.

5. Conclusions

Although there are about 900 species of *Ficus* of which the majority are tropical in distribution, each *Ficus* species having its own specific wasp pollinator, the taxonomy of only about 100 species of wasps have been worked out. The biology of not more than half-a-dozen species has been studied in detail. Similarly the pollination ethology of only about 10 species has been understood so far. Thus these various aspects of the

study of the fig wasps form a very promising area of research which will be highly rewarding. Very little studies have been made to elucidate the morphological aspects of the fig wasps using scanning electron microscope. Such studies, apart from their taxonomic value, are certain to reveal the structural details of the pollen carrying organs developed by the various genera of fig pollinators in response to the necessity for mutualistic symbiosis with the *Ficus* species.

The study of agaonid – fig symbiosis should receive the attention of combined teams of botanists and entomologists. Such combined studies can ultimately lead to an understanding of the phylogeny of the various species of *Ficus* and of the different genera and species of the agaonid pollinators. This, in turn, will enable us to interpret the co-evolution of *Ficus* species and of their specific pollinator wasps.

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