TR93-2

INTERACTIONS BETWEEN FIGS
(*FICUS* SPP., MORACEAE)
AND FIG WASPS
(CHALCIDOIDEA, AGAONIDAE)

THESIS

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by

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PREFACE

Natura nusquam magis quam in minimis tota est

(Nature is nowhere more perfect than in the minutest of her works)

Pliny: Roman naturalist and philosopher 1 A.D.

Most research cannot be done in isolation and these studies are no exception. Although the contribution of colleagues is acknowledged in each section, I would like to make special mention of of the following people: my senior supervisor, Dr Steve Compton, for providing me the opportunity to investigate fig/fig wasp biology and for his considerable input in the investigations; Prof. Perry Kaye provided much needed assistance in the chemical aspects of the study; Profs M. Brown and V. Moran for having enough faith in my ability to give me a second chance at Rhodes University; the 'fig team', in particular Sally Ross, Simon van Noort and Costas Zachariades, provided many hours of field assistance and company. Finally I would like to thank my wife, Kathy Holton, for her support and encouragement during my studies.

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ABSTRACT

Fig trees (*Ficus* spp., Moraceae) and fig wasps (Chalcidoidea, Agaonidae) are uniquely associated. In one fig wasp group, the pollinators (Agaoninae), each species is generally host species-specific. The relationship is one of obligate mutualism where the wasps provide pollination services and in return utilises some of the ovules for larval development. Non-pollinating fig wasps (generally belonging to subfamilies other than the Agaoninae) may be gallers or parasitoids, and can also be host species-specific. In the accompanying studies we examined the factors governing the interactions between fig wasps and their host trees.

Surveys of fig trees and their associated pollinating fig wasps conducted in southern Africa, Madagascar and The Comores generally confirmed their specific relationships. An examination of *F. sycomorus* in Madagascar resulted in the reclassification of *F. sakalavarum* as a distinct species with its own specific pollinator species. Biological and chemical evidence is presented demonstrating that the pollinators were able to distinguish their hosts through volatiles which emanated from the figs when they were ready to be pollinated. Environmental factors were found to influence wasp behaviour. Ambient temperature governed the timing of wasp emergence from their natal figs. When dispersing from their natal figs, the fig wasps flew upwards and then were blown downwind. Once nearing trees bearing figs ready to be pollinated, the wasps lost height and flew upwind towards the trees. *E. baijnathi* females apparently avoided figs which already contained a conspecific foundress. Scanning electron microscope studies of pollinating female fig wasp antennae showed that while all the species possessed multiporous plate sensilla, in only a few species were these sensilla elongated. Multiporous plate sensilla elongation is rare or absent among other female chalcids and may have evolved within the Agaoninae in order to facilitate their location on receptive host figs. Pollinator choice specificity appears to break down in a number of cases. In the first case examined, two pollinator species were recorded from the figs of African *F. sycomorus*. One, *C. arabicus*, pollinates the figs while the other, *C. galili*, acts as a 'cuckoo' by utilising some of ovules for oviposition without providing pollen. In the second case three pollinating fig wasp species were recorded from the figs of *F. lutea*. Two were found to be incidental visitors and were not specifically attracted to the tree. The hybrid seeds from these crosses were successfully germinated but the seedlings did not grow passed the cotyledon stage of their development. In the concluding study the consequences of *Ficus* phenology and the structure of the fig's unusual inflorescence on the non-pollinating fig wasp community were examined. Various factors affecting the population levels and species richness were also examined. Future possible research directions were discussed.

CHAPTER 1

GENERAL INTRODUCTION

The impact fig trees (*Ficus* spp. Moraceae) have made on man is reflected in the numerous references made to them in folklore, religion, agriculture and health. They feature in both Greek and Roman mythology (Condit, 1947 and references therein) but it is in religion where their significance is most noticeable. *Ficus religiosa* L. (the pipal or bo tree) was accredited with its scientific name because of its religious significance in India and was the sacred tree under which Buddha was reputed to have meditated in order to obtain perfect knowledge and enlightenment (Corner, 1985a). Furthermore, it is also the tree of fertility and propagation not only to the Indians, but also to the Hellenes and the Italians (Condit, 1947). A further species, *F. sycomorus* L., besides being sacred to the Egyptians, was also prized for its wood and fruit (Galil, 1967). Although not of particular religious significance to the Jews and the Christians, the Bible makes 58 references to fig trees and their fruit (Cruden, 1955), thereby demonstrating their importance to those communities. The Moslems, on the other hand, had a high regard for *Ficus* calling it the Tree of Heaven as it was considered the most intelligent plant, being only one step removed from animals. Even today in some Central African tribes the trees are held in sacred respect as their ancestors are believed to dwell in them (Abbiw, 1990). Numerous references have been made to their healing properties where they are reputed to cure anything from epilepsy to infertility (Abbiw, 1990; Ake Assi, 1990).

It is believed that figs were first cultivated in southern Arabia *ca.* 2900 B.C. and were later grown in Asia Minor and along the Mediterranean (Storey, 1975). Archimedes (700 B.C.) wrote of figs being cultivated on the Greek Island of Paros (Condit, 1947) although trees were grown in Crete as early as 1600 B.C. (Storey, 1975). Only *F. sycomorus* and *F. carica* L. have been cultivated for food.

Fig trees

Ficus is one of 50 genera of Moraceae (Berg, 1989a) and dates from at least the Cretaceous (> 100 million years) (Galil, 1977; Murray, 1985). Figs are assumed to have evolved from a discoid or a cup-shaped inflorescence similar to that seen in the other genera of Moraceae. The closing of the inflorescence has been considered a 'self-defense' adaptation against generalist seed predators (Berg, 1989a).

The classification of *Ficus* is based on the work of Corner (1965) as modified by Berg (1986). There are some 750 described *Ficus* worldwide of which about 500 species occur in Asia and Australasia, some 150 in the Neotropics and 105 in Africa (includes Madagascar and the Mascerene Islands)(Berg, 1989a). Although approximately 50% of *Ficus* are gynodiecious having so called both male and female plants (Berg, 1989b) only 10 species occur in Africa, all of which are in the subgenus *Ficus* (Berg, 1989b). Two of these occur in the southern African subregion (van Greuning, 1990) and four in Madagascar (Berg, 1986). On mainland Africa the subgenus *Sycomorus* is represented by five species, two of which are in southern Africa while seven are found in Madagascar and the Comores (Berg, 1986, 1989b). The subgenus *Urostigma* has 79 described species of which 72 are placed within the section *Galoglychia* which is limited to Africa. The subgenus *Pharmacosycea* is poorly represented in Africa with four described species, two of which occur in Madagascar (Berg, 1986) while none are found in southern Africa.

Figure 1. An electron micrograph of the interior of a fig showing the ostiole (O) with accompanying protective bracts (B) and the ovules (F) lining the inside of the syconium (S.G. Compton and L. Vincent are acknowledged for the use of the photograph).

Ficus is characterised by its specialized inflorescences (Figure 1). The flowers of the fig or syconium (= sykon (fig) Greek) line the inside wall of an urn-shaped receptacle and are only accessible through a bract-lined entrance or ostiole (Boucek, 1988). Fig trees may be either monoecious (figs having both male and female flowers) or gynodiecious (some figs produce both pollen and gall flowers while others seed flowers but no staminite flowers). They are predominantly tropical or sub-tropical, growing in a diversity of habitats that range from desert to rain forest. They may grow as trees, shrubs or lianas and be terrestrial or hemi-epiphytic. Many of the latter growth form kill their hosts through strangulation or by tree splitting.

Fig Wasps

Far less well known are the small Hymenoptera (Chalcidoidea, Agaonidae) which are always found in association with the figs. Although Aristotle and his pupil, Theophrastus, (*ca.* 340 B.C.) appeared to appreciate that these small 'psen' played a role in caprification (pollination) of the cultivated fig (*F. carica*) the mechanism remained a mystery. Two thousand years later Ramirez (1969) and Galil and Eisikowitch (1969) independently and simultaneously established the mechanism fig wasps (Agaoninae *sensu* Boucek, 1988) used to pollinate the figs. Pre-agaonid wasps are thought to have been associated with the early *Ficus* forms as seed predators, gall makers or parasitoids (Ramirez, 1976).

The females of many pollinating wasp species possess pollen baskets (corbiculae) which are filled before they leave their natal fig. Arriving their new host figs, the females deliberately unload the pollen with their front legs and place it on the flower stigma (ethodynamic pollination) (Galil, 1973; Ramirez, 1969). Where the pollinating wasps do not possess corbicula the pollen is incidently carried on their bodies from the natal to the host tree (topocentric pollination) (Galil, 1973; Okamato and Tashito, 1981) although a genus of South American pollinating wasp is said to eat pollen in the natal fig and later regurgitate once finding fig flowers ready to pollinate (Ramirez, 1969).

The fig wasps have evolved anatomically in order to overcome the barriers presented by the syconium in order to gain access to the flowers within the fig lumen. Their flattened heads, mandibles modified with lamellae or teeth, and strong fore legs assisting them in their journey through the ostiole (Figure 2).

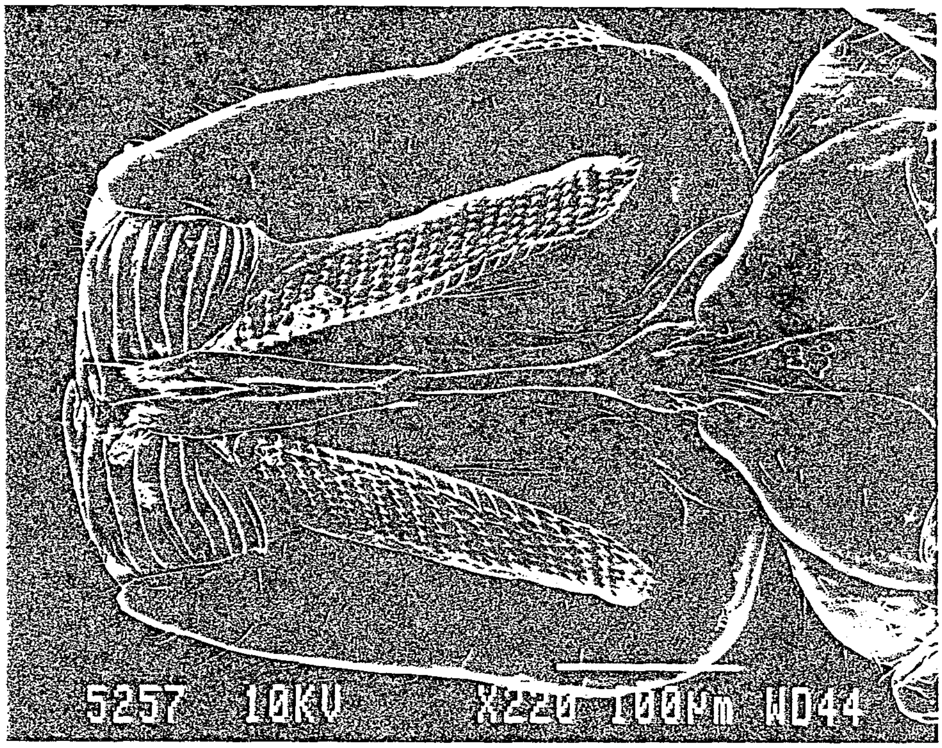

Figure 2. Electron micrograph of the mandibles used by the pollinating fig wasp to force its way through the ostiole in order to gain access to the flowers within the fig.

However, the agaonines are not the only chalcid wasps associated with figs. The non-pollinating fig wasps belong to the Torymidae, Orymidae, Pteromalidae and Eurytomidae (Joseph, 1954, 1955, 1956, 1958, 1959, 1964, 1965; Abdurahiman and Joseph, 1978a, 1978b, 1978c, 1979; Boucek, 1988). There have been referred to as *secondary sycophiles* (Galil and Eisikowitch, 1974), *mess mates* (Wiebes, 1977) or *interlopers* (Bronstein, 1988) and may be phytophages, inquilines or parasitoids. Most of these non-pollinating wasps oviposit from outside the fig (Ansiri, 1967; Joseph, 1954; Ulenberg, 1985). The exceptions are the sycoecines (Galil *et al.*, 1970; Newton and Lomo, 1979; Baijnath and Ramcharun, 1983; van Noort, 1992) which, like the pollinators, have to penetrate the fig lumen in order to oviposit. A single species of fig tree may support more than 20 species of fig wasp (Boucek *et al.*, 1981; Hawkins and Compton, 1992; Hill, 1992).

Among fig wasps there is a marked sexual dimorphism. The males of all the pollinating fig wasps are wingless with large mandibles and, while most non-pollinating fig wasps males are flightless, some species have fully developed wings. Fighting and non-fighting flightless male morphs have been reported in some non-pollinating wasp species (Vincent 1991).

Fig - Fig Wasp Developmental Cycles

Fig crop development on any one tree is usually synchronized. However, trees tend to develop out of phase with each other at all times of the year (Janzen, 1979a; Wharton *et al.*, 1980; Milton *et al.*, 1982; Baijnath and Ramcharun, 1983; Newton and Lomo, 1983; Corlett, 1984; Windsor *et al.*, 1989; Bronstein, 1990). The development cycle of the fig has been conveniently divided into five phases (Galil and Eisikowitch, 1968a) (Figure 3). Sequentially they are:

Phase A (Pre-female stage): Both male and female flowers are undeveloped and the ostiole opening is closed.

Phase B (Female stage): The female flowers have matured and the ostiole opens allowing the pollinating female wasps to penetrate the fig lumen. Making their way through the bracts many fig wasps lose their wings and parts of their antennae and cannot leave the fig. The female pollinates the flowers while ovipositing down some of the ovules. The female wasps are thought to secrete from the acid gland while laying. This secretion is thought to stimulate the pathenogenetic development and consequent galling of the endosperm which in turns provides food for the developing wasp larvae (Hill, 1976b; Joseph and Abdurahiman, 1981; Joseph, 1984; Verkerke, 1986, 1989). Gall forming Eurytomidae wasps are thought to adopt a similar strategy (Copland and King, 1972).

Pollination is not a prerequisite for fruit development although fig that have not been serviced usually abscise and abort. The act of oviposition and/or the action of the secretions of the wasp gallers' acid glands probably prevent the abortion of the figs (Berg, 1983; Verkerke, 1988a, 1988b, 1988c, 1989).

The experimental introduction of female wasps without pollen results in a high wasp progeny mortality indicating that pollination is beneficial to both the fig and the wasp progeny (Galil and Eisikowitch, 1971).

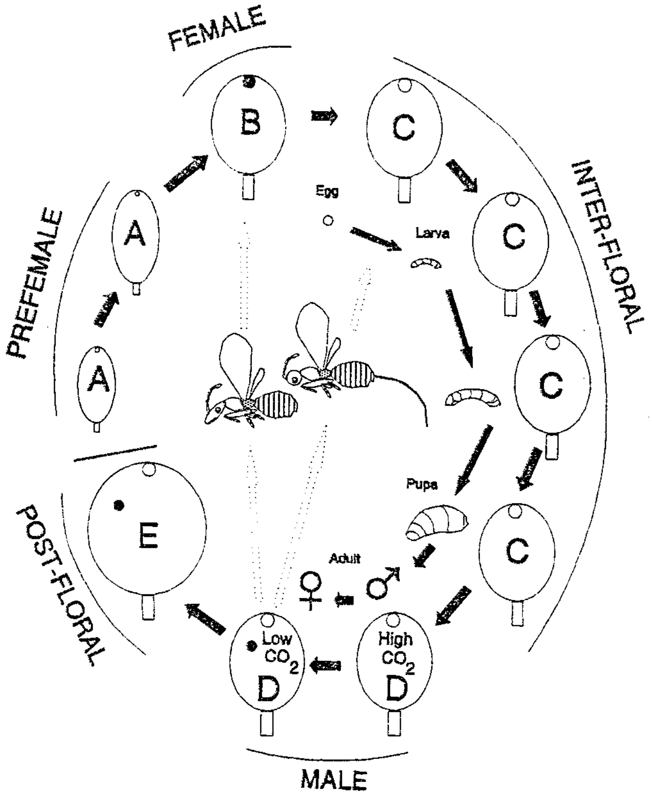

Figure 3. Fig-fig wasp development cycles. Parasitoids will arrive later than the seed predators and oviposit from outside the fig after probing with their long ovipositors. See text for general description. (Modified from Galil and Eisikowitch, 1968).

Phase C (Interfloral Stage): Agaonine larvae and seeds develop simultaneously. Only the sclerotised pericarp encasing the pupae is left at pupation. Usually a single larva develops in each seed gall (Galil and Eisikowitch, 1971). Bladders or empty galls are thought to be galled ovules where the larvae have died.

Phase D (Male stage): Immediately prior to the males emerging from the fig the internal atmosphere of *F. religiosa* figs are rich in carbon dioxide. This is thought to inhibit both the ripening of the fig and the emergence of the female wasps from their galls (Galil *et al.*, 1973). After a male has located a gall containing a female, it makes a small incision through which it inserts its telescopic (solenogastric) abdomens and copulates with the inhabitant. Some figs, especially those of the subgenus *Sycomorus*, have their lumen filled with liquid. The emerging males are probably able cope with this environment because of their large water-repellant spiracle peritrema (Compton and McClaren, 1989).

The agaonine males use their well-developed mandibles to make an exit hole through the fig wall; the carbon dioxide escapes and the females are stimulated to emerge from their galls. The ethodynamic females then seek out the male flower anthers and load pollen before leaving their natal fig in order to find another host fig with receptive figs (Phase B).

Phase E (Postfloral stage): The figs ripen and become attractive to various birds (Breitwisch, 1983; Jordano, 1983; Wheelwright, 1985; Bronstein and Hoffman, 1987; Lambert, 1989a, 1989b; Lambert and Marshall, 1991; Midya and Brahmachary, 1991; Waters, pers. comm.), bats (August, 1981; Morrison, 1978; Phua and Corlett, 1989; Ulzurrum and Heideman, 1991) and mammals (Lambert, 1990; Hemingway, pers. comm.) which act as the primary dispersers of the seeds (Janzen, 1979b; Bronstein, 1988). Ants may act as secondary dispersers (Roberts and Heithaus, 1986; Kauffmann *et al.*, 1991).

Early researchers suggested that figs had both 'long' and 'short' styled flowers and because of their limited ovipositor length, fig wasps were only able to deposit their eggs in the 'short' styled flowers. This was seen to be the main factor controlling the proportion of flowers producing seed and that producing wasps (Galil and Eisikowitch, 1968a, 1968b, 1974; Ramirez, 1970, 1976; Wiebes, 1977, 1979a, 1982, 1984, 1986; Faegri and van der Pijl, 1979; Janzen, 1979a, 1979b; Berg, 1983, 1989a; Murray, 1985; Kjellberg *et al.*, 1987a) and was thought to be critical to the evolutionary stability of the fig-pollinating fig wasp mutualism (Kjellberg *et al.*, 1987a, 1987b).

However, more recent work on monoecious figs (Newton and Lomo (1979) on *F. lutea* Vahl, Galil and

Eisikowitch (1968b) on *F. sycomorus*, Bronstein (1988, 1992) on *F. pertusa*, Nefdt (1989) on *F. cordata* subspecies *salicifolia* (Warb.) C.C. Berg, *F. burtt-davyi* Hutch., *F. verruculosa* Warb, *F. lutea*, *F. thonningii* Bl., *F. sycomorus*, *F. abutilifolia*(Miq.) Miq., *F. ottoniifolia* (Miq.) Miq., *F. sur* Forssk., *F. sansibarica* Warb. and *F. capreifolia* Delile and Baijnath and Ramcharun (1983) on *F. sur*) indicates that fig flower style length is unimodal. These observations have placed some doubt on the evolutionary significance of monoecious 'short' and 'long' styled flowers. Bronstein (1992) discusses the evolutionary aspects of the consequences of the 'conflict' between the fig and its fig wasps in maximising their individual 'fitness'.

Objectives

The objective of these studies was to investigate the interactions between figs and their fig wasps.

1. Host specificity. This section examined the host specificity between African fig wasps and their host trees. Reason for the breakdown in host specificity are discussed and one case was resolved through the resurrection of a fig tree taxon to species level.

2. Biological evidence for volatile attractants. Evidence is presented for the presence of *Ficus* volatiles. These volatiles were shown to be species specific and emanate from the fig only when the fruit was ready to be pollinated.

3. Chemical evidence for volatile attractants. Gas chromatograms of fig volatiles showed that not only was the composition of the volatile profile different for each species but that it changed when the figs were ready to be pollinated.

4. Fig wasp behaviour. The emergence of pollinators from their natal figs, their subsequent dispersal and finally their arrival at their new hosts was examined.

5. Perception of volatiles. The antennal sensilla were examined and related to their role in perceiving the species-specific volatiles.

6. Breakdown of host specificity. Two case studies were undertaken in an attempt to explain the presence of more than one species of pollinating fig wasp penetrating the figs of a particular *Ficus* host.

7. Fig wasp parasitoids. The consequences of the phenologies of fig trees as well as the structure of their inflorescences on the biology of the non-pollinating fig wasps are discussed. The effect of homopterans and their accompanying ants on the wasp communities was described. Factors influencing species composition of African fig wasp communities are discussed.

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CHAPTER 2

HOST SPECIFICITY

Paper 1: African figs and fig wasps: The wasp's eye view of *Ficus* species. *Mitteilungen aus dem Institut fur Allgemeine Botanik Hamburg* 24 (S.G. Compton, A. B. Ware and S. van Noort - 1991).

Paper 2: Does pollinator specificity of *Ficus* species break down in southern Africa, Madagascar and The Comores. Submitted to *Annals of the Missouri Botanical Garden*. (A.B. Ware, S.G. Compton and P.B. Phillipson)

AFRICAN FIGS AND FIG WASPS:

THE WASP'S EYE VIEW OF *FICUS* SPECIES

S. G. Compton, A.B. Ware and S. van Noort

ABSTRACT

Fig trees (*Ficus* species, Moraceae) are pollinated by agaonine fig wasps (Hymenoptera, Agaonidae, Agaoninae). We describe the plant characteristics that determine the host specificity of the wasps and assess the role of fig wasps in the reproductive isolation of *Ficus* species. The practicalities of using the pollinators to identify and delimit *Ficus* species are examined and cases where the classifications of the trees and wasps do not correspond are reviewed. We conclude that fig wasp host relationships provide useful pointers to where future taxonomic studies should be directed.

INTRODUCTION

Our understanding of the systematics of African fig trees (*Ficus* spp., Moraceae) has improved greatly over the last few years, thanks mainly to the work of C.C. Berg (for example Berg, 1986, 1988; Berg and Hijman, 1989). Through the production of identification keys and adequate descriptions, Berg's revisions have made African *Ficus* accessible to biologists interested in this taxonomically 'difficult' genus. They have also resulted in the detection of large numbers of synonymies, and only 105 African and Malagasy species are currently recognised.

Fig trees are of particular interest to ecologists and evolutionary biologists because of their unique pollination system. All fig trees depend entirely on fig wasps (Hymenoptera: Agaonidae, subfamily Agaoninae) for pollination (Boucek, 1988). There are numerous other groups of fig wasps, for example the Sycoecinae, but these do not act as pollinators. The structure of the figs, together with the trees' unusual asynchronous flowering phenology, are adaptations that facilitate pollination by the wasps, but exclude other potential pollinators (Verkerke, 1989; Berg, 1990; Janzen, 1979). The tiny flowers of *Ficus* are positioned on the inside of the fig, where they can only be reached by crawling through the narrow bract-lined ostiole. Once inside, the wasps pollinate the flowers and gall a proportion of the ovules, inside which the wasp larvae develop. Agaonines are only found in association with fig trees, and can breed nowhere else. As the trees provide sites for the development of wasp larvae, while the wasps transfer pollen for the trees, the interaction is mutualistic.

The relationship between *Ficus* species and Agaonine species is believed to be usually highly specific, with each tree species pollinated by only one wasp species, which does not breed in the figs of any other *Ficus*. The host relationships of the fig wasp genera broadly correspond with the subdivisions of *Ficus* recognised by Berg. Thus, trees belonging to subgenus *Sycomorus*, are pollinated by *Ceratosolen* species, trees in subgenus *Urostigma*, section *Urostigma* are pollinated by *Platyscapa* species, and so on. An exception to this correspondence between trees and wasps is found in *Urostigma*, section *Galoglychia*, the most species rich Section in Africa. Even here, however, the disparity in classifications is only present in three of the six subsections (Wiebes, 1990).

The generally parallel phylogenies of the fig trees and their wasps has led to the suggestion that speciation in the trees and the wasps may be linked and Thompson (1989) has concluded that figs and fig wasps represent one of the strongest cases for such co-speciation having taken place. This is because gene flow in both groups is intimately linked with that of their partners. In this paper we examine those physical and chemical features of the plants which influence host specificity in fig wasps and examine the role of the wasps in the reproductive isolation of *Ficus* species. We then review cases where the classifications of the trees and wasps do not correspond and examine possible reasons for the disparities.

Reproductive isolation in African *Ficus*

Agaonines are effectively the sole pollinators of fig trees, although rare instances of pollen grains being transported by other fig wasps have been reported (Newton and Lomo, 1979; Compton, Holton, Rashbrook, van Noort, Vincent and Ware, 1991). Agaonine host choice therefore controls the limits of gene flow in *Ficus* species.

The pollination syndrome in *Ficus* has some similarities with that of the bee orchids (*Ophrys* spp., Orchidaceae). In bee orchids it is host-specific aculeate bees and wasps, fooled into pseudocopulating with the flowers, which typically act as prepollination isolating factors. Paulus and Gack (1990a, 1990b) argue that speciation in *Ophrys* has resulted from a change in pollinators and that many of the morphologically distinct variants and subspecies of *Ophrys* species should be regarded as good species because they each have their own specific pollinators. However, species need not have detectably different morphologies, as it is only necessary that their pollinators should be able to distinguish between them.

Figs are only attractive to their specific pollinators during a short period of their development, when large numbers of agaonines can be collected at the trees (Bronstein, 1987). The wasps are attracted to the trees by volatile compounds released from the figs (van Noort, Ware and Compton, 1989). The blend of these chemicals does not remain constant and attractiveness corresponds with a short period when the ostiole opens and there is a detectable change in the smell of the figs (Ware, Kaye, Compton and van Noort, in prep.). The *Ficus* species we have tested have elements of their volatile profile that are consistent and differ from those of other species (Ware, Kaye, Compton and van Noort, in prep.). These differences appear to form the basis of the specificity of their attraction.

Most plant species are not isolated by single barriers, but by combinations of different factors (Stebbins, 1950; Levin, 1978). In *Ficus* species the ostiole provides a physical filter that limits entry to the fig (Janzen, 1979). This supplements the isolation generated by the specificity of the volatile attractants. Fig wasps have anatomical modifications that facilitate entry through the ostiole. These include a flattened head, the presence of teeth or ridges on the mandibles and short, heavy fore-legs with strong tibial spines. Ostiole shape and size varies greatly between *Ficus* species (Ramirez, 1974) and fig wasp head shapes appear to be adapted to the ostiole characteristics of their associated tree. This is reflected in the parallel development of head shape in agaonine and sycoecine fig wasps that share the same hosts, such that when the agaonid has a long thin head, so does the sycoecine (van Noort and Compton, in prep.). Despite these adaptations, successful entry into the figs is not assured and, for example, around one per cent of the *Elisabethiella baijnathi* females entering the figs of *F. burtt-davyi* become trapped in the ostiole (Compton and Robertson, in prep.). Failure rates are likely to be much higher when wasps attempt to enter figs for which they are not adapted.

Despite the physical barrier posed by the ostiole, fig wasps do occasionally succeed in entering the 'wrong' figs, and may even succeed in reproducing (Compton, 1990). The colonisation of non-host trees seems to result from the accidental arrival of a few wasps at trees with unpollinated figs, rather than from a breakdown in the specificity of the volatile attractants (Ware and Compton, in prep.). Once on a tree bearing figs, a proportion of the fig wasps appear to be drawn inside them, irrespective of the *Ficus* species.

The occasional 'mistakes' made by agaonines result in the transfer of pollen between fig species, with the possibility of hybrids being produced. In the case of a *F. lutea* tree growing in Grahamstown that was pollinated by wasps from *F. thonningii* and *F. sur*, viable hybrid seeds were produced from both crosses (Compton, 1990). This was despite *F. sur* and *F. lutea* being in separate subgenera. Hybrids have also been produced from crosses involving the edible fig *F. carica* (Condit, 1950), suggesting that cross-incompatability may be poorly developed throughout the genus. However, we have not been able to grow successfully any *F. lutea* hybrids, and such hybrid weakness/inviability may also result in reproductive isolation in *Ficus* .

Exceptions to the one fig: one agaonine relationship

Agaonines have been collected from about 70% of the African *Ficus* species (Wiebes and Compton, 1990; Compton, unpublished), a higher proportion than that known from other *Ficus*-rich continents. Africa is therefore particularly suitable for using fig wasps to assess the status of *Ficus* species.

Table 1. African *Ficus* species with different agaonines associated with their subspecies or synonyms[1]

Berg code	*Ficus* taxa	Agaonines
5	*F. asperifolia*	*Kradibia gestroi afrum*
	F. ureolaris[1]	*Kradibia hilli*
11	*F. sycomorus*	*Ceratosolen arabicus* & *Ceratosolen galili*
	F. sakalavarum[1]	*Ceratosolen namorakensis*
28	*F. c. cordata*	*Platyscapa desertorum*
	F. c. salicifolia	*Platyscapa awekei*
60	*F. n. natalensis*	*Elisabethiella socotrensis* & *Alfonsiella longiscapa*
	F. n. lepieurii	*Alfonsiella fimbriata*
82	*F. c. cyathistipula*	*Agaon fasciatum*
	F. c. pringsheimiana	*Agaon kiellandi*
95	*F. o. ottoniifolia*	*Courtella camerunensis* & *Courtella gabonensis*
	F. o. lucanda	*Courtella scobinifera*

Tables 1-3 are based on host records summarised by Wiebes in Wiebes and Compton (1990), supplemented by a small number of more recent records. Table 1 lists four examples where pairs of *Ficus* subspecies are pollinated by different agaonids and two where different pollinators are associated with previously recognised tree species that, while morphologically distinct, are now regarded as synonyms. These taxa appear to be candidates for recognition as separate species. However, the examples in Table 1 represent only a few of the 27 African *Ficus* that do not display a one:one relationship with the agaonines. These additional cases where trees have two or more associated agaonines may indicate the presence of cryptic *Ficus* species (Table 2). Conversely, there are also numerous examples of the same agaonine being collected from more than one *Ficus* (Table 3). This brings into question the status of these *Ficus* species, although several are so different in appearance that their specific status seems beyond doubt.

Table 2. African *Ficus* species with more than one associated agaonine (excluding cases listed in Table 1).

Berg code	*Ficus* species	Agaonines
1	*F. palmata*	*Blastophaga psenes* & *Blastophaga vaidi*
11	*F. sycomorus*	*Ceratosolen arabicus* & *Ceratosolen galili*
12	*F. mucoso*	*Ceratosolen arabicus* & *Ceratosolen galili*
13	*F. sur*	*Ceratosolen capensis* & *Ceratosolen flabellatus* & *Ceratosolen ? silvestrianus*
15	*F. vallis-choudae*	*Ceratosolen megacephalus* & *Ceratosolen ? silvestrianus*
36	*F. lutea*	*Allotriozoon heterandromorphum* & *Elisabethiella stuckenbergi* & *Ceratosolen capensis*
47	*F. abutilifolia*	*Nigeriella fusciceps* & *Elisabethiella comptoni*
58	*F. craterostoma*	*Alfonsiella michloudi* & *Alfonsiella* sp. indesc.
60	*F. n. natalensis*	*Elisabethiella socotrensis* & *Alfonsiella longiscapa*
66	*F. thonningii*	*Elisabethiella stuckenbergi* & *Alfonsiella brongersmai* & *Alfonsiella longiscapa*
95	*F. ottoniifolia*	*Courtella camerunensis* & *Courtella gabonensis*
97	*F. artcarpoides*	*Courtella penicula* & *Courtella hladikae*

Numerous non-pollinating fig wasps share the figs with the agaonines. The host relationships of these species can provide additional evidence on the status of their hosts, although these wasps have no influence on gene flow in the plants. Sycoecine fig wasps are ovule-gallers associated with *Ficus* section *Galoglychia*, and like agaonines must enter the figs to oviposit. Their larvae do not need the figs to be pollinated and therefore can develop independently of the agaonines.

Table 3. African *Ficus* species which share agaonines with congeners.

Berg code	*Ficus* species	Shared agaonines
1	*F. palmata*	*Blastophaga psenes*
-	*F. carica*	*Blastophaga psenes*
2	*F. exasperata*	*Kradibia gestroi afrum*
5	*F. asperifolia*	*Kradibia gestroi afrum*
6	*F. capreifolia*	*Kradibia gestroi afrum*
11	*F. sycomorus*	*Ceratosolen arabicus* & *Ceratosolen galili*
12	*F. mucosa*	*Ceratosolen arabicus* & *Ceratosolen galili*
13	*F. sur*	*Ceratosolen capensis*
36	*F. lutea*	*Ceratosolen capensis*
13	*F. sur*	*Ceratosolen ? silvestrianus*
15	*F. vallis-choudae*	*Ceratosolen ? silvestrianus*
23	*F. variifolia*	*Dolichoris flabellata*
24	*F. dicranostyla*	*Dolichoris flabellata*
36	*F. lutea*	*Elisabethiella stuckenbergi*
66	*F. thonningii*	*Elisabethiella stuckenbergi*
40	*F. vasta*	*Elisabethiella socotrensis*
41	*F. wakefieldii*	*Elisabethiella socotrensis*
60	*F. n. natalensis*	*Elisabethiella socotrensis*
58	*F. craterostoma*	*Alfonsiella michaloudi*
59	*F. lingua*	*Alfonsiella michaloudi*
60	*F. n. natalensis*	*Alfonsiella longiscapa*
66	*F. thonningii*	*Alfonsiella longiscapa*
60	*F. n. leprieurii*	*Alfonsiella fimbriata*
67	*F. kamerunensis*	*Alfonsiella fimbriata*
76	*F. conraui*	*Agaon kiellandi*
82	*F. cyathistipula pringsheimiana*	*Agaon kiellandi*
86	*F. densistipulata*	*Agaon kiellandi*
90	*F. sagittifolia*	*Agaon c. cicatriferens*
91	*F. subsagittifolia*	*Agaon c. multum*

Table 4. Host relationships of selected sycoecine fig wasps.

Berg code	*Ficus* species	Agaonines	Associated sycoecines
40	*F. vasta*	*Elisabethiella socotrensis*	*Crossogaster triformis*
60	*F. n. natalensis*	*Eliseabethiella socotrensis*	*Phagoblastus barbarus*
60	*F. n. natalensis*	*Alfonsiella longiscapa*	*Crossogaster* A *Philocaenus* A
60	*F. leprieurii*	*Alfonsiella fimbriata*	*Phagoblastus liodontus*
67	*F. kamerunensis*	*Alfonsiella fimbriata*	*Phagoblastus* D
58	*F. craterostoma*	*Alfonsiella michaloudi*	*Phagoblastus* A *Phagoblastus* B *Phagoblastus liodontus*
59	*F. lingua*	*Alfonsiella michaloudi*	*Phagoblastus* B
58	*F. craterostoma*	*Alfonsiella* sp. indescr.	Phagoblastus C *Crossogaster oderans*
66	*F. thonningii*	*Elisabethiella stuckenbergi*	*Phagoblastus barbarus* *Crossogaster oderans*
66	*F. thonningii*	*Alfonsiella brongersmai*	*Phagoblastus barbarus* *Phagoblastus* E *Philocaenus* A *Crossogaster oderans*
82	*F. c. cyathistipula*	*Agaon fasciatum*	*Sycoecus thaumostocnema*
82	*F. c. pringsheimiana*	*Agaon kiellandi*	*Sycoecus* A
90	*F. sagittifolia*	*Agaon c. cicatriferens*	*Sycoecus* B
91	*F. subsagittifolia*	*Agaon c. multum*	*Sycoecus* C
95	*F. o. ottoniifolia*	*Courtella camerunensis* & *Courtella gabonensis*	*Seres* A
95	*F. o. ulugurensis*	*Courtella camerunensis*	*Seres* B
95	*F. o. lucanda*	*Courtella scobinifera*	*Seres levis*
97	*F. artocarpoides*	*Courtella pendicula* & *Courtella hladikae*	*Seres* C

Sycoecines collected from trees where there is not a one agaonine: one *Ficus* relationship are listed in Table 4. There are often several sycoecines associated with a particular *Ficus*, but host specificity can be well developed. Although host records of sycoecines are not as numerous as those of the pollinators, some interesting patterns do emerge. *Phagoblastus* D and *Philocaenus* A occur in *F. thonningii* pollinated by *Alfonsiella brongersmai*, but have never been found in numerous samples from *F. thonningii* pollinated by *Elisabethiella stuckenbergi*. Similarly, *Phagoblastus barbarus* occurs in *F. n.*

natalensis when pollinated by *Elisabethiella socotrensis*, but not when pollinated by *Alfonsiella longiscapa*. In both examples the sycoecines suggest that the trees with two pollinators may actually be closely related species.

DISCUSSION

The large number of differences between the currently recognised *Ficus* species and the host records of the agaonines may have a variety of causes. Table 5 summarises various factors which could result in apparent or real breakdowns in the one:one relationship between *Ficus* species and agaonine species. Some of the explanations are well documented, while others are hypothetical.

Incorrect assignments of species-pairs can result from misidentifications of either the trees or the wasps, contamination of collections and mislabelling of specimens. Such errors should be detected eventually, as subsequent samples indicate anomalies, but at present a large proportion of the data is still based on single collections. Delimitation of species also remains a problem in certain groups of both trees and wasps. The *F. thonningii* species group is especially problematic, while the separation of closely related wasps such as *Elisabethiella stuckenbergi* and *E. socotrensis* also leads to uncertainties. Closely related species may be indistinguishable using classical taxonomic methods and alternative approaches may be required to differentiate them.

Well documented case studies have shown that there are genuine exceptions to the one agaonine: one *Ficus* species pattern. In West Africa, the nominate subspecies of *F. ottoniifolia* is pollinated by two different agaonines. These show habitat preferences, with trees in the forest pollinated mainly by one species, those in savannah by another (Michaloud, Michaloud-Pelletier, Wiebes and Berg, 1985). *F. sycomorus* also has two associated agaonines, but here only one wasp species pollinates the tree (Galil and Eisikowitch, 1968). The same two wasps are associated with *F. mucoso*, where it is again the same wasp species that pollinates the tree (Wiebes, 1989). Mistakes by the wasps may also be responsible for two or more agaonines entering figs on the same tree, as was described above with *F. lutea*. Another example may include the two *Alfonsiella* species recorded in small numbers from

F. thonningii (Boucek, Watsham and Wiebes, 1981) that appear to be the legitimate pollinators of other tree species. Another explanation for different *Ficus* species sharing pollinators may be that they have alternative forms of reproductive isolation which have superseded the wasps. This would be analogous to the situation with some atypical bee orchids, which remain distinct species despite sharing the same pollinators (Paulus and Gade, 1990b).

Table 5. Possible causes of exceptions to the one agaonine: one *Ficus* species relationship.

TAXONOMIC

1. Misidentifications of the trees or wasps will lead to incorrect assignments of species-pairs.
2. Natural variation in trees or wasps can result in uncertainties about the delimitation of species.
3. Agaonine species from different hosts may be anatomically the same, but have different host preferences.
4. *Ficus* species with different pollinators may be morphologically similar, but have cryptic differences that allow them to be distinguished by the wasps.

BIOLOGICAL

5. Trees may have two or more sympatric pollinators or may have different pollinators in different habitats or in different parts of their range.
6. One or more of the associated agaonids may no longer act as a pollinator.
7. Wasps can make 'mistakes', occasionally pollinating and even reproducing inside the 'wrong' figs.
8. Some *Ficus* species may rely on post-fertilization isolating mechanisms, rather than pollinator specificity.

The numerous examples of mis-matches between the wasps and the trees suggest that we have much to learn about both the biology and taxonomy of African figs and fig wasps. In particular, with our present state of knowledge it is often impossible to distinguish the factors that are responsible for apparent breakdowns in the one:one relationship. Data on fig wasp host relationships are nonetheless of immediate value to both *Ficus* and agaonine taxonomists, because they point to areas where future studies should be directed.

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DOES POLLINATORSPECIFICITY OF *FICUS* SPECIES BREAKDOWN IN SOUTHERN AFRICA,MADAGASCARAND THE COMORES?

A. B. Ware, S. G. Compton and P. B. Phillipson

ABSTRACT

Fig trees (*Ficus* spp.) are only pollinated by fig wasps (Hymenoptera, Agaonidae, Agaoninae) and each *Ficus* species is usually pollinated by its own specific species of fig wasp. This one-to-one relationship has led biologists to view figs and fig wasps as one of the classic examples of coevolution between plants and animals. In this paper we summarise the host relationships of the pollinating fig wasps recorded from South Africa, Namibia, Madagascar and The Comores and examine those cases where the one-to-one relationship appears to break down. We discuss possible reasons for such apparent breakdowns in specificity and how these anomolies relate to the hypothesis of coevolution between the trees and their pollinators. A consideration of one such case leads us to propose that *Ficus sakalavarum* Baker from Madagascar is a distinct species from the related *F. sycomorus* L.

INTRODUCTION

The *Ficus*-fig wasp pollinator relationship is one of obligate mutualism. Fig trees (*Ficus* spp., Moraceae) are dependent upon female fig wasps (Hymenoptera, Chalcidoidea, Agaonidae, Agaoninae *sensu* Boucek, 1988) for pollination and in return the wasps use some of the ovules for oviposition and subsequent larval development (Galil, 1977). Baker (1961), Hill (1967), Ramirez (1970), Galil (1977), Wiebes (1979), Janzen (1979) and Michaloud *et al.* (1983), among others, have remarked on the specificity of the relationship between each species of fig tree and their pollinating wasps and the fig-fig wasp relationship has been viewed as one of the best documented examples of plant-insect co-evolution (Janzen, 1979; Thompson 1982, 1989; Bronstein and McKey, 1989). Furthermore, because Agaoninae are host specific and usually the trees' sole pollinators (for exceptions see Newton and Lomo, 1979; Compton *et al.*,

1991) the wasps control the limits of gene flow in *Ficus* species. This, together with the similarities between the phylogenies of the Agaoninae and *Ficus* (Wiebes, 1982), has led to the suggestion that speciation of the two groups is linked (Thompson, 1989).

The present classification of *Ficus* is based on the 'rather weak differentiating morphological and anatomical "key" characters' of Corner (1965)(Berg, 1990). Even so there is broad agreement between these subdivisions and the phylogeny of the Agaoninae as proposed by Wiebes (1982). For example, trees belonging to the subgenus *Sycomorus* are pollinated only by wasps of the genus *Ceratosolen*, and those of the subgenus *Urostigma* section *Urostigma* by *Platyscapa* wasps and so on. However, within the subgenus *Urostigma* section *Galoglychia* this correspondence breaks down (Berg, 1989; Wiebes, 1990). The host specificity of certain fig wasp species is not always absolute and several cases of two or more Agaoninae species found in association with one species of African *Ficus* have been documented (Galil and Eisikowitch, 1968; Boucek *et al.*, 1981; Michaloud *et al.*, 1985; Compton, 1990; Compton *et al.*, 1991; Wiebes and Compton, 1990; Ware and Compton, in press).

In this study we record the host specificity of fig tree pollinators from South Africa, Namibia, The Comores and Madagascar. We discuss possible reasons for exceptions to the one *Ficus* species - one pollinator species pattern, and the implications of this on the taxonomy of the fig tree species.

NATURAL HISTORY AND THE BASIS OF FIG WASP SPECIFICITY

The *Ficus* inflorescence (the fig or syconium) is unusual in that the flowers are contained within a globular receptacle and access to them is through a narrow bract-lined entrance - the ostiole. Fig structure prevents incidental pollination (Verkerke, 1989; Berg, 1990; Janzen, 1979) and the anatomy and behaviour of the pollinating fig wasps have evolved to overcome these barriers (Ramirez, 1974). For example, the head shapes of pollinating females are related to the ostiole structure of their host figs (van Noort, 1992). During the passage through the ostiole to the lumen of the fig the female wasps typically lose their wings and part of their antennae, and cannot leave. Their decision to attempt entry into a fig is therefore essential to their future reproductive success.

Fig pollination and development has been divided into five phases (Galil and Eisikowitch, 1968):

1. the prefemale phase - when the female flowers are undeveloped and the ostiole is closed;
2. the female phase - when the ostiole opens allowing the pollinating wasps access to the mature female flowers;
3. the interfloral phase - once pollination has taken place the seeds and the fig wasp larvae develop simultaneously;
4. the male phase - when the male flowers, wasps and the seeds have reached maturity, the flightless male wasps chew their way out of their galls and seek flower galls containing conspecific females, they chew through the galls and copulate with the trapped females; the females then, actively or passively collect pollen and leave their natal fig through exit holes chewed through the wall of the fig by the males;
5. the postfloral phase - the figs ripen and are eaten by frugivores which disperse the seeds.

Fig crop development is usually synchronous on each tree (for an exception see Baijnath and Ramcharun, 1983), but not between trees (Bronstein, 1987; Wharton *et al.*, 1980; Windsor *et al.*, 1989). This means that female fig wasps must leave their natal trees in order to find suitable figs in which to oviposit. Fig wasps are only attracted to trees bearing figs that are ready to be pollinated (Bronstein, 1987; Ware and Compton, in prep A.). Volatiles emanating from the figs were shown to be the source of the attraction (van Noort *et al.*, 1989; Ware *et al.* in press, Ware and Compton, in prep. B). Therefore, host plant specificity, at least in part, seems to result from the flying wasps being attracted to specific volatile components released by their host figs.

Pollinator fig wasps are not the only wasps which are uniquely associated with figs (Boucek, 1988). Some wasp species belonging to other subfamilies of Agaonidae also feed on the developing figs, while others parasitise the wasp larvae. Many of these non-pollinating wasps are also apparently host specific (Ulenberg, 1985; van Noort, 1992) and can provide additional evidence on the species status of their hosts, but as none of these species pollinate the figs they have no effect on fig gene flow.

Table 1. A list of southern African *Ficus* species (numbers from Berg (1989)) together with their associated agaonines (numbers from Wiebes and Compton (1990)) together with the number of trees sampled.

Ficus species	Agaonine species	Number of trees sampled
- *F. carica* L.	1 *Blastophaga psenes* L.	3
6 *F. capreifolia* Delile	2 *Kradibia gestroi* (Wiebes)	2
7 *F. pygmaea* Hiern	?	0
11 *F. sycomorus* L.	7 *Ceratosolen arabicus* Mayr	27
	14 *Ceratosolen galili* Wiebes	
13 *F. sur* Forssk.	11 *Ceratosolen capensis* Grandi	30
27 *F. ingens* (Miq.) Miq.	24 *Platyscapa soraria* Wiebes	16
28a *F. cordata* subsp. *cordata* Thunb.	25 *Platyscapa desertorum* Compton	17
28b *F. cordata* subsp. *salicifolia* (Vahl) Berg	20 *Platyscapa awekei* Wiebes	11
29 *F. verruculosa* Warb.	21 *Platyscapa binghami* Wiebes	8
36 *F. lutea* Vahl	28 *Allotriozoon heterandromorphum* Grandi	4
	38 *Elisabethiella stuckenbergi* Grandi	
	11 *Ceratosolen capensis* Grandi	
42 *F. glumosa* Delile	39 *Elisabethiella glumosae* Wiebes	23
43 *F. stuhlmannii* Warb.	48 *Alfonsiella binghami* Wiebes	10
45 *F. tettensis* Hutch.	44 *Nigeriella excavata* Compton	6
47 *F. abutilifolia* (Miq.) Miq.	40 *Elisabethiella comptoni* Wiebes	17
50 *F. trichopoda* Baker	32a *Elisabethiella bergi bergi* Wiebes	13
58 *F. craterostoma* Mildbr. & Burr.	- *Alfonsiella* sp. indet.	2
60a *F. natalensis* subsp. *natalensis* Hochst.	38 *Elisabethiella stuckenbergi* Grandi	17
	42 *Elisabethiella socotrensis* Mayr	
	53 *Alfonsiella longiscapa* Joseph	
62 *F. burtt-davyi* Hutch.	36 *Elisabethiella baijnathi* Wiebes	18
63 *F. ilicina* (Sonder) Miq.	37 *Elisabethiella enriquesi* (Grandi)	11
66 *F. thonningii* Bl.	38 *Elisabethiella stuckenbergi* Grandi	31
96a *F. tremula* subsp. *tremula* Warb.	75 *Courtella wardi* Compton	5
98a *F. polita* subsp. *polita* Vahl	70 *Courtella bekiliensis* (Risbec)	3
99 *F. bizanae* Hutch. & Burtt-Davy	- *Courtella* sp. indet.	3
101 *F. sansibarica* subsp. *sansibarica* Warb.	72 *Courtella armata* (Wiebes)	5
104 *F. bubu* Warb.	80 *Courtella michaloudi* (Wiebes)	2

Table 2. A list of *Ficus* species from Madagascar and The Comores (numbers from Berg (1989)) and their associated agaonines (numbers from Wiebes and Compton (1990)) together with the number of trees sample for their pollinators.

Ficus species	Agaonine species	Number of trees sampled
3 *F. pachyclada* subsp. *arborea* (Perrier) C.C. Berg	- *Kradibia* sp. indet.	2
8 *F. bojeri* Baker	- ?	0
9 *F. brachyclada* Baker	4 *Kradibia cowani* Saunders	1
10 *F. politoria* Lam.	5 *Kradibia saundersi* Wiebes	1
11 *F. sycomorus* L.	7 *Ceratosolen arabicus* Mayr	11
	14 *Ceratosolen galili* Wiebes	
- *F. sakalavarum* Baker	9 *Ceratosolen namorakensis* (Risbec)	13
17 *F. tiliifolia* Baker	8 *Ceratosolen stupefactus* Wiebes	2
18 *F. torrentium* Perrier	- ?	0
19 *F. polyphlebia* Baker	17 *Ceratosolen longimucro* Wiebes	3
20 *F. botryoides* Baker	16 *Ceratosolen blommersi* Wiebes	5
21 *F. trichoclada* Baker	- ?	0
22 *F. karthalensis* C.C.Berg	- ?	0
25 *F. assimilis* Baker	- ?	0
26 *F. ampana* C.C.Berg	- ?	0
30 *F. madagascariensis* C.C.Berg	- ?	0
32 *F. menabeensis* Perrier	23 *Platyscapa bergi* Wiebes	6
33 *F. humbertii* C.C.Berg	- sp. indet.	2
36 *F. lutea* Vahl	28 *Allotriozoon heterandromorphum* Grandi	3
50 *F. trichopoda Baker*	32 *Elisabethiella bergi* Wiebes	3
51 *F. grevei* Baill.	- sp. indet.	11
52 *F. rubra* Vahl	46 *Nigeriella avicola* Wiebes	0
53 *F. marmorata* Baker	- *Nigeriella* sp. indet.	4
54 *F. bivalvata* Perrier	- ?	0
64 *F. antandronarum* subsp. *bernardii* C.C.Berg	- *Elisabethiella* sp. indet.	3
65 *F. reflexa* subsp. *reflexa* Thunb.	41 *Elisabethiella reflexa* Wiebes	2
98 *F. polita* Vahl	70 *Courtella bekiliensis* (Risbec)	0

MATERIALS AND METHODS

Male phase figs were collected from trees belonging to 22 of the 23 *Ficus* species recorded in the southern Africa floristic region (van Greuning, 1990), and 15 of the 26 species recorded for Madagascar and The Comores (Berg, 1986). The figs were placed in plastic containers closed with fine netting and, once they had emerged, the wasps were either stored dry with silica gel or in alcohol. Voucher specimens of representative trees are lodged at the following herbaria: BG, GRA, K, MO, P, RUH, TAN. In general, the taxonomy of the figs follows Berg (1989) and that of the wasps Wiebes and Compton (1990) and Boucek (1988).

RESULTS AND DISCUSSION

Agaoninae were collected from all of the *Ficus* species sampled (Table 1 and Table 2). When these results are added to previously published records, pollinators have now been collected from more than 70% of 105 *Ficus* species known from Africa, Madagascar and The Comores (Berg, 1989).

Typically, each *Ficus* species is associated with a single species of Agaoninae. However, of the *Ficus* collections we have examined, four species from southern Africa (*F. sycomorus* L., *F. cordata* Thunb., *F. lutea* Vahl, *F. natalensis* Hochst.), and *F. sycomorus* from Madagascar and The Comores were found to host more than one pollinator species (Table 1 and Table 2).

These examples of *Ficus* species where host/pollinator specificity appears to break down are discussed individually below.

F. sycomorus

The distribution of *F. sycomorus* and its pollinator *Ceratosolen arabicus* Mayr within southern Africa are shown in Figure 1. Except in the western part of the sub-continent, trees of southern African *F. sycomorus*, in common with their East African counterparts (Galil and Eisikowitch, 1968), were also host to *C. galili* Wiebes. This species acts as a 'cuckoo', which, although having fully-formed pollen carrying apparatus and utilising the ovules for larval development, does not pollinate the figs and hence has no influence on its host's gene flow (Galil and Eisikowitch, 1968; Compton *et al.*, 1991). *Ceratosolen galili* is not a sister species to *C. arabicus* (Wiebes, 1989), suggesting that it or its ancestors colonised *F. sycomorus* from another *Ficus* species, rather than having evolved *in situ* from *C. arabicus*.

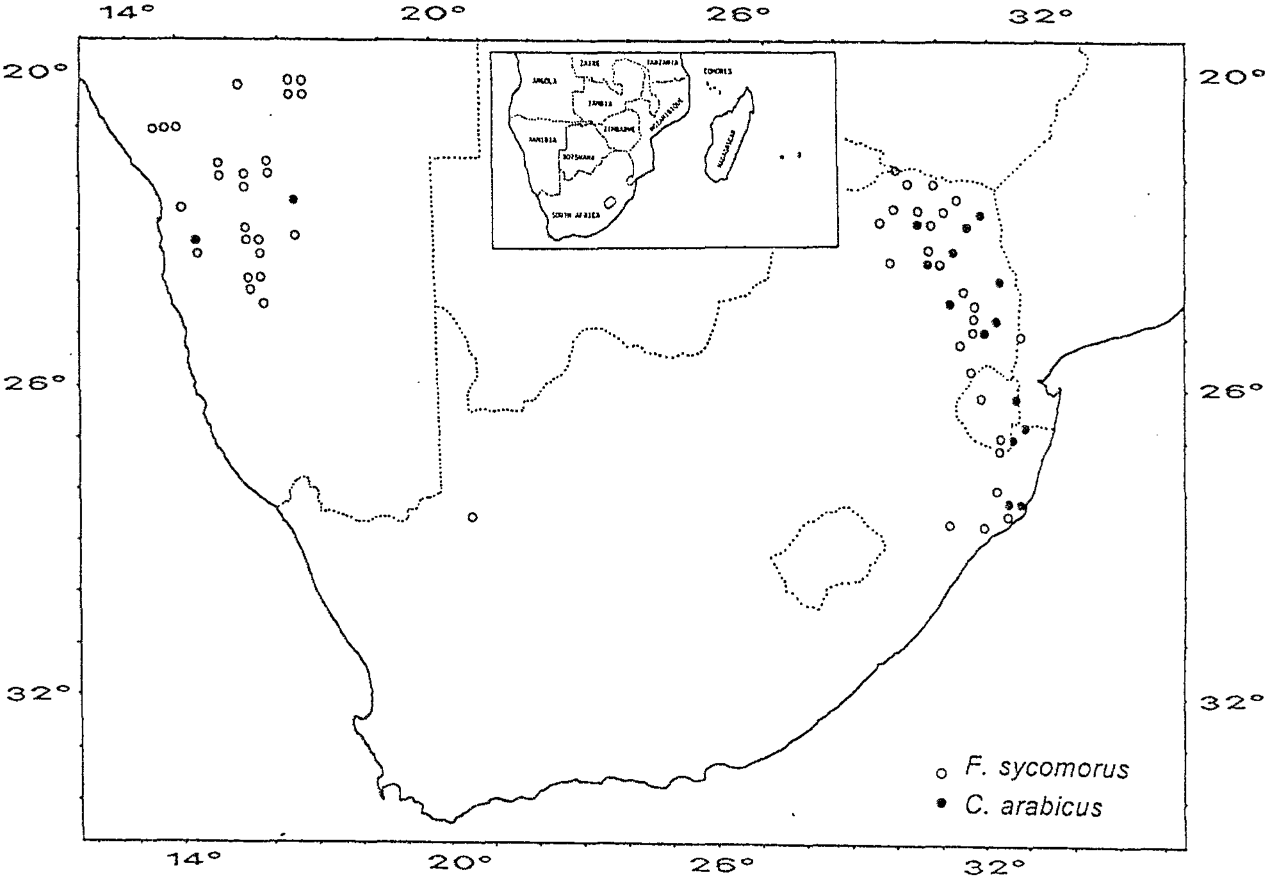

Figure 1. Our distribution records of southern African *F. sycormus* and associated pollinator, *C. arabicus* (●); other southern African distribution records of *F. sycomorus* (○) are from van Greuning (1990) and von Breitenbach (1986) and are without pollinator records.

Ficus sycomorus also occurs in Madagascar and The Comores. Two forms of *F. sycomorus* have been recognised in Madagascar, both originally described as distinct species; namely the small-fruited *F. cocculifolia* Baker (1886) and the large-fruited *F. sakalavarum* Baker (1886). *Ficus sakalavarum* was later reduced to a variety (Perrier de la Bâthie, 1928) and then to a subspecies (Perrier de la Bâthie, 1952) of *F. cocculifolia*. It was only much later that Berg (1986) equated both taxa with the African *F. sycomorus*, and included them both in his concept of this species. Berg (1986), however, suggests that the "sakalavarum" form may represent a distinct subspecies within *F. sycomorus*. The taxonomy of *F. sycomorus* in Madagascar therefore remains problematic.

Three species of Agaoninae, namely *C. arabicus, C. galili* and *C. namorakensis* (Risbec), were found associated with the figs of *F. sycomorus sensu* Berg (1986) in Madagascar (Figure 2 & 3). However, the latter wasp species was only found in the "sakalavarum" form and only *C. arabicus* and/or *C. galili* were found in the "cocculifolia" form. The distribution of the two forms overlap in Madagascar (Figure 2 & 3) indicating that geographic factors alone are not responsible for the restriction of *C. namorakensis* to the figs of "sakalavarum". The non-pollinating fig wasp faunas of the two forms are also distinct (Ulenberg, 1985; Compton, unpublished), suggesting that fig wasps as a whole distinguish between the two forms of *F. sycomorus*. The differing preferences shown by the two pollinators, *C. namorakensis* and *C. arabicus*, are even more significant, because they indicate that the two forms are reproductively isolated, even in areas where they are sympatric.

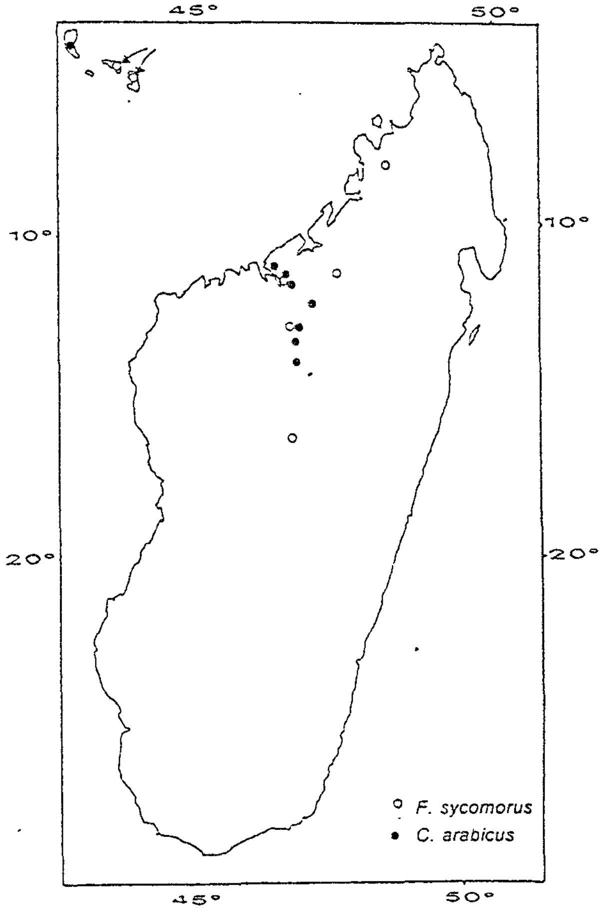

Figure 2. Our distribution records of Malagasy and Comoran *F. sycomorus* (⊙) together with their associated pollinators; other Malagasy and Comoran *F. sycomorus* records (○) are from Perrier de la Bathie (1928, 1952) and are without pollinator records.

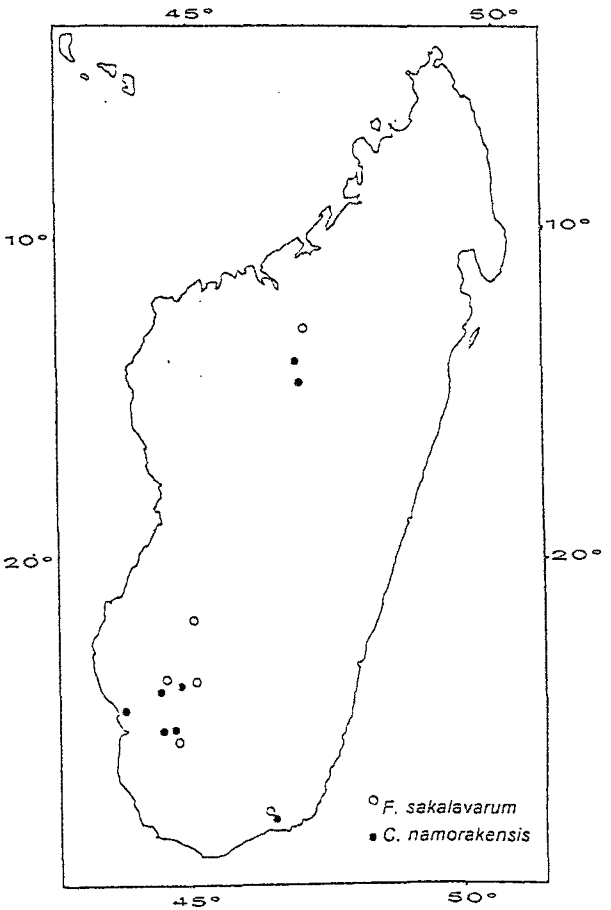

Figure 3. Our distribution records of *F. sakalavarum* (⊙) together with their associated pollinators; other *F. sakalavarum* records (○) are from Perrier de la Bathie (1928, 1952) and are without pollinator records.

In the field we had no difficulty in differentiating between the "cocculifolia" and "sakalavarum" forms of *F. sycomorus*, provided they were bearing male phase or postfloral phase figs. The male phase figs of *F. sycomorus* measured up to about 20 mm in diameter, while the "sakalavarum" form were considerably larger (100-150 mm in diameter) with a much thicker syconium wall. A single "sakalavarum" fig measuring only 40 mm was sampled, which produced a solitary female pollinator (whereas hundreds are usually present). This fig was clearly abnormal. A more distinctive difference between the two forms concerned the postfloral phase figs (when they are ready for dispersal). During this development phase the figs of "sakalavarum" change colour only slightly, changing from green to a somewhat yellowish green, they are glabrous and slightly soft, but they never become juicy. In contrast, like African *F. sycomorus*, the figs of the "cocculifolia" form change from green to yellow or red, they usually remain somewhat pubescent and they become soft and juicy. There also appears to be differences in the fruiting phenologies of the two forms. On individual trees of the "sakalavarum" form few figs matured at any one time, while figs of the "cocculifolia" form developed synchronously, like those of African *F. sycomorus*.

The morphological and developmental differences between the two forms may reflect different dispersal systems. Several putative avian dispersers were recorded eating postfloral phase "cocculifolia" figs in Madagascar, while no birds were observed eating "sakalavarum" figs (Ross pers. comm.), nor did we record any avian-associated fruit damage. The ripe figs of *F. sycomorus* in Africa and the "cocculifolia" form in Madagascar are reported by Perrier de la Bâthie (1952) and Palmer & Pitman (1972) as favourite food of the closely related African and Madagascar Green Pigeons (*Treron calva* (Temminck) and *T. australis* (L.)). In mainland Africa and in Madagascar the fruit of these plants has also been recorded as being eaten by humans and other mammals (Perrier de la Bâthie, 1952; Palmer & Pitman, 1972), while the "sakalavarum" form is reported to be inedible or even poisonous to humans (Perrier de la Bâthie, 1952). Zebu cattle, which readily feed on fallen figs, appear to be the main potential dispersers of "sakalavarum" figs at the present time. Since zebu cattle are not indigenous in Madagascar, the figs may originally have been dispersed by the giant lemurs or the ostrich-like *Aepyornis* that occurred on the island, all of which are now extinct.

Unfortunately the two forms are not always easy to distinquish in the herbarium (Berg, 1986). Vegetative differences have not been detected and collections of "sakalavarum" may have immature fruits approximately the same size as more mature fruits of *F. sycomorus*. Unless the developmental phase of these specimens has been determined or other relevant information is known, positive identification may not be possible.

On The Comores, only the "cocculifolia" form of *F. sycomorus* has been recorded, and this occurs on the islands of Anjouan, Mayotte and Grande Comore (Table 2; Perrier de la Bâthie, 1952; Compton, 1992). Only *C. arabicus* and *C. galili* were found associated with these plants, and these plants appear to be morphologically indistinguishable from African *F. sycomorus*.

It seems clear that the small-fruited plants in Madagascar and The Comores are conspecific with African *F. sycomorus*. The large-fruited plants represent a related, but distinct, species, endemic to Madagascar, to which the name *F. sakalavarum* should be applied. This species is pollinated by the Malagasy-endemic wasp *C. namorakensis*. Differences between the two species are summarised in Table 3.

Table 3. Distinguishing characters between *F. sycomorus* and *F. sakalavarum*.

	F. sycomorus	*F. sakalavarum*
1. Ripe fig diameter (mm)	15-20	(40)-100-150
2. Ripe fig wall thickness (mm)	1-2	>5
3. Ripe fig colour	yellow or red	yellow-green
4. Ripe fig texture	juicy	dry
5. Fig maturation	synchronous	asynchronous
6. Pollinator wasp	*C. arabicus*	*C. namorakensis*
7. "Cuckoo" wasp	*C. galili*	none recorded
8. Possible seed dispersers	birds, man and various other mammals	cattle
9. Natural distribution	Africa (widespread), The Comores, western Madagascar	western and southern Madagascar

F. cordata

Two subspecies of *F. cordata* (subsp. *cordata* and subsp. *salicifolia* (Vahl) C.C. Berg) are recorded from the South African/Namibian region (Berg, 1989; van Greuning, 1990), and a third (subsp. *lecardii* (Warb.) C.C. Berg) is known from West Africa (Berg, 1989). From the distribution maps produced by van Greuning (1990) and von Breitenbach (1986) and our own records it is evident that the two southern African subspecies are allopatric (Figure 4). The two subspecies are morphologically distinguishable (Berg & Wiebes, 1992) and they are consistently pollinated by different species of fig wasps (*Platyscapa desertorum* Compton and *P. awekei* Wiebes, see Table 1). They also have distinct non-pollinator fig wasp faunas (Compton, unpublished).

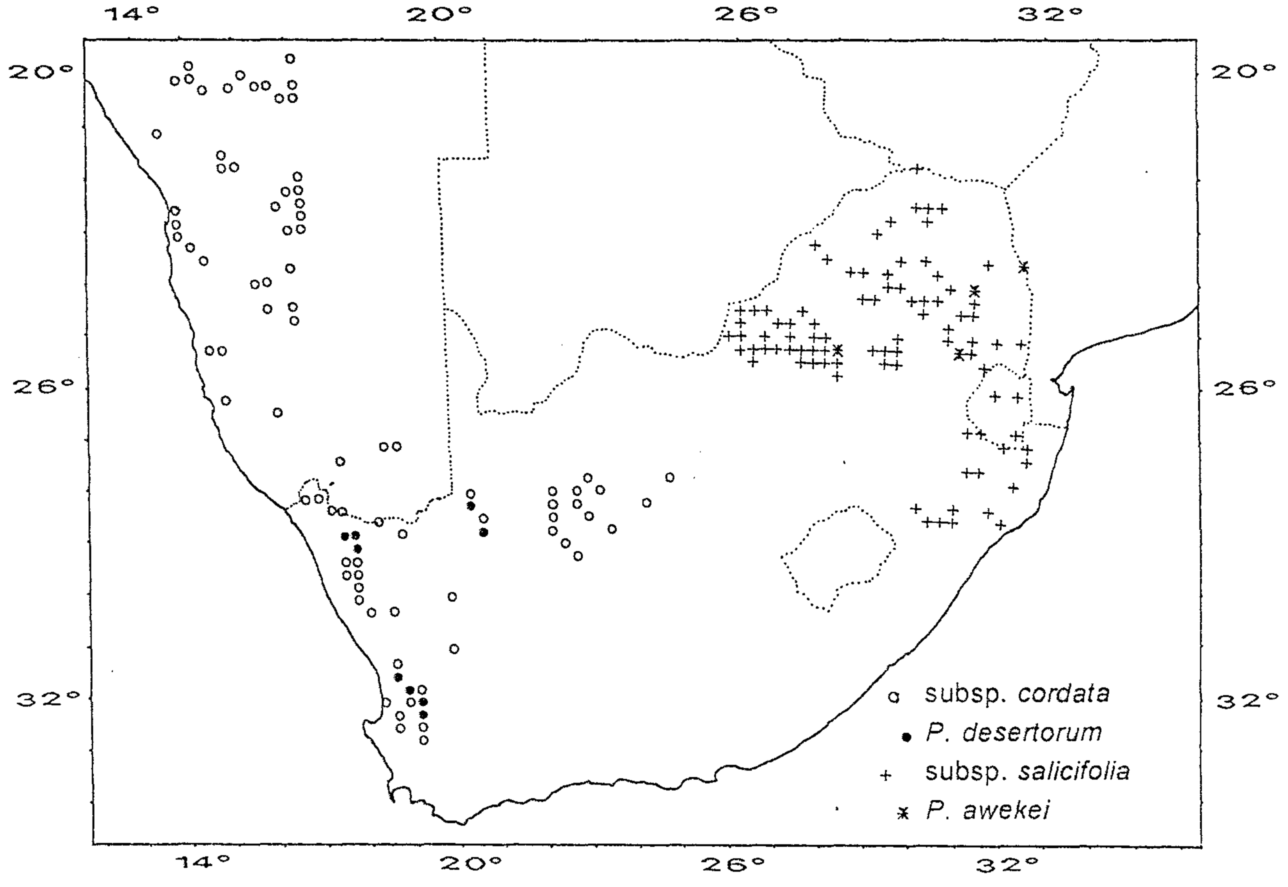

Figure 4. Our distribution records of southern African *F. cordata* subsp. *cordata* together with their associated pollinators (●) and *F. cordata* subsp. *salicifolia* (✱); other *F. cordata* subsp. *cordata* (o) and *F. cordata* subsp. *salicifolia* records (+) are from van Greuning (1990) and von Breitenbach (1986) and are without pollinator records.

Since they have different pollinators and are geographically separated, *F. cordata* subsp. *cordata* and *F. cordata* subsp. *salicifolia* are likely to be genetically isolated. A strong case could therefore be made for the reinstatement of *F. salicifolia* at the species level (see Paulus and Gack, 1990 for the treatment of a similar situation in the Orchidaceae). However, there is theoretically no reason why a *Ficus* species should not attract different pollinators in different parts of its range (Compton *et al.*, in press). Therefore, in order to assess their taxonomic status, it would be important to know whether the attractant chemicals produced by the figs of two forms differ. The third subspecies creates a further complication. *Ficus cordata* subsp. *lecardii* is somewhat intermediate between the two southern African forms of *F. cordata*, and its pollinator is unknown (C.C. Berg, pers. comm.). Clearly more work is required on this species before the significance of its two pollinators can be assessed fully.

F. natalensis

Species within the widespread African *Ficus* "thonningii / natalensis" complex are taxonomically problematic throughout their range (Berg, 1989; Dowsett-Lemaire and White, 1990). *Ficus thonningii* is highly variable in appearance, and Berg and Wiebes (1992) have informally recognised 10 different forms. *Ficus natalensis* is more homogeneous, the typical subspecies occurs in southern Africa and further north, while a second (subsp. *leprieurii* (Miq.) C.C. Berg) occurs only in tropical Africa. *Ficus thonningii* and *F. natalensis* are closely related and frequently confused (Berg & Wiebes, 1992).

On the basis of their pollinators three partially sympatric southern African forms within the "thonningii / natalensis" complex can be recognised (Figure 5). In South Africa *Ficus thonningii* is consistantly pollinated by a single pollinating species, *Elisabethiella stuckenbergi* (Grandi), although further north (i.e. in Zimbabwe) it has been recorded as host to *Alfonsiella longiscapa* Joseph and *A. brongersmai* Wiebes (Boucek *et al.*, 1981). Southern African *F. natalensis* subsp. *natalensis* has been recorded as the host of three pollinating species, namely *E. stuckenbergi*, *E. socotrensis* Mayr and *A. longiscapa*.

The species of non-pollinating fig wasps reared from *F. natalensis* subsp. *natalensis* trees pollinated by *E. socotrensis* appear to be the same as those from figs pollinated by *E. stuckenbergi*, while those associated with *F. natalensis* subsp. *natalensis* figs pollinated by *A. longiscapa* are distinct (S. Compton, unpublished). For example, *Phagoblastus barbarus* (Grandi) (Agaonidae, Sycoecinae) is found in figs pollinated by both *Elisabethiella* species, but not those pollinated by *A. longiscapa* (van Noort, 1992). The host preferences of the wasps therefore suggest there may be a 'cryptic' form of *F. natalensis* pollinated only by *A. longiscapa* and distinct from both *F. thonningii* and the *F. natalensis* subsp. *natalensis* pollinated by species of *Elisabethiella*. Although we have only recorded it from a small number of trees in Natal (Figure 5), *A. longiscapa* appears to be the normal pollinator of *F. natalensis* subsp. *natalensis* elsewhere in Africa (Wiebes, 1988; Compton, unpublished). Yet another pollinator, *Alfonsiella fimbriata* Waterston appears to be associated with *F. natalensis* subsp. *leprieurii* (Berg & Wiebes, 1992).

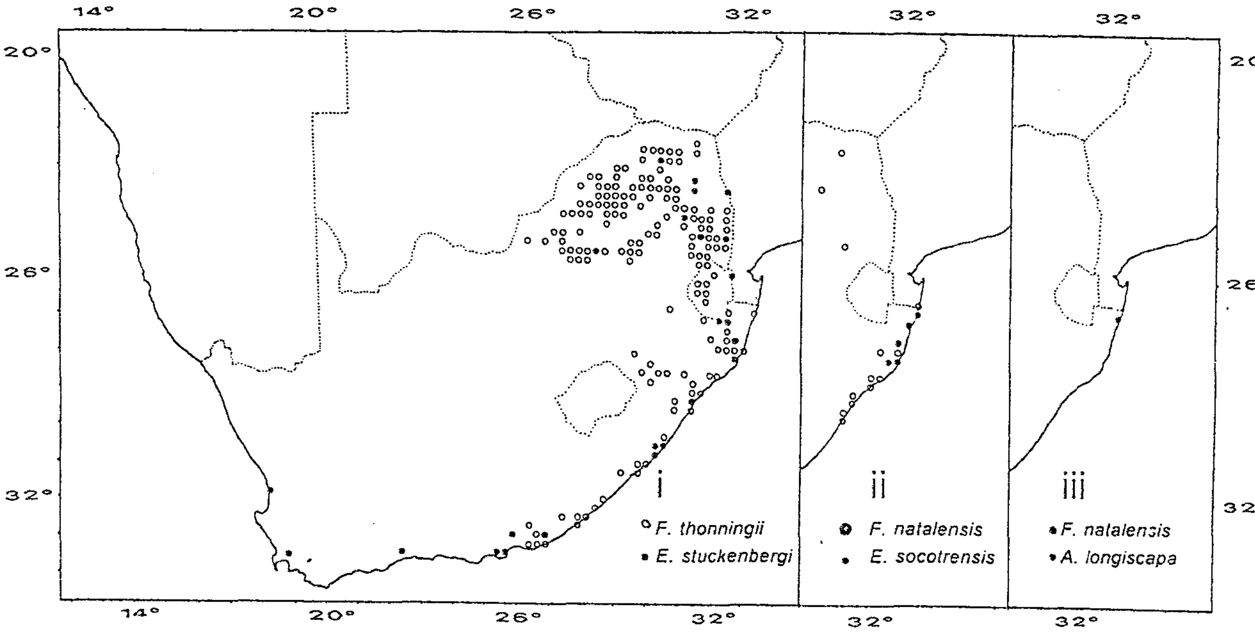

Figure 5. Our distribution records of southern African *Ficus* "thonningii / natalensis" together with their associated pollinators (●); other *Ficus* "thonningii / natalensis" records (○) are from van Greuning (1990) and von Breitenbach (1986) and are without pollinator records. *F. thonningii* (i) is only associated with one pollinator species while *F. natalensis* (ii and iii) is associated with two different agaonines.

An additional complicating factor surrounds the taxonomic status of the *Elisabethiella* pollinators. Differentiation between *E. socotrensis* and *E. stuckenbergi* is difficult and some South African specimens are morphologically intermediate between the two species (Wiebes, pers. comm.). The problem is further aggravated in that *E. socotrensis* is associated with two completely distinct *Ficus* species, *F. wakefieldii* Hutch., in Zambia and North-east African *F. vasta* Forssk. (Wiebes & Compton, 1990; Compton, unpublished).

The pollination of some *F. natalensis* subsp. *natalensis* by *A. longiscapa* in southern Africa suggests that these trees may be closely allied to components of the "thonningii / natalensis" complex from tropical Africa which share the same pollinator. Although these trees are sympatric with *E. socotrensis* pollinated *F. natalensis* subsp. *natalensis*, if pollinator choice is consistent they must be reproductively isolated.

Given the close relationship or possibly conspecificity of southern African *E. socotrensis* and *E. stuckenbergi*, together with identical non-pollinating fig wasp faunas, it seems reasonable to conclude that the *Elisabethiella* pollinated trees of the "thonningii / natalensis" complex in southern Africa represent components of a single variable species. Alternatively, if *E. socotrensis* is a good species, distinct from *E. stuckenbergi*, this would suggest that in southern Africa *E. socotrensis* pollinated trees of *F. natalensis* subsp. *natalensis* are reproductively isolated from *F. thonningii*. Both these hypotheses are consistent with a species specific pollinator / host relationship.

Hybridization is a possible source of some of the observed morphological variability. Chromosome counts of *Ficus* spp. are mostly diploid (2n = 26) (Condit, 1933, 1964; Ohri and Khoshoo, 1987), including counts of some *F. thonningii* (Condit, 1964). However *F. burkei* (Miq.) Miq. and *F. hochsetteri* (Miq.) A. Rich. which are now regarded as varieties of *F. thonningii* (Berg, 1989), have been recorded as being tetraploid (2n = 56) (Condit, 1964). These tetraploids may be a result of interspecific hybridization and this hypothesis may account for the diversity of "thonningii / natalensis" forms and the resultant species delimitation difficulties experienced by taxonomists (Berg, 1990; Ramcharun *et al.*, 1990). Further progress in delimitating species within the "thonningii / natalensis" complex may require a combination of karyological and modern molecular approaches such as DNA restriction techniques.

F. lutea

F. lutea is widely distributed in Africa, Madagascar and The Comores (Berg, 1990; Compton, 1992). In South Africa its natural distribution is restricted to the more humid forests of Natal (van Greuning, 1990), but it is planted as an ornamental tree elsewhere. Within its natural range, *F. lutea* appears to be pollinated exclusively by *Allotriozoon heterandromorphum* Grandi (Compton, unpublished). A tree planted in Grahamstown, some 500 km outside the tree's normal distribution range was pollinated by *A. heterandromorphum* and by small numbers of both *Elisabethiella stuckenbergi* and *Ceratosolen capensis* Grandi (species that normally pollinate *F. thonningii* and *F. sur* respectfully). As reported elsewhere (Ramirez, 1988), this suggests that the normal host tree specificity exhibited by Agaoninae can breakdown under conditions where a tree's pollinator is rare or absent.

Hybrid plants involving the edible fig *F. carica* have been artificially produced (Condit, 1950) and naturally occurring hybridization has been reported (Ramirez, 1988). We have successfully germinated seed from *F. lutea* which was naturally pollinated by *E. stuckenbergi* and *C. capensis*, but have not been able to coax these hybrids past the cotyledon stage of their development (Ware and Compton, 1992). The hybrid weakness/inviability shown by these crosses may be widespread and effectively act as post germination isolating mechanisms within *Ficus*.

CONCLUSIONS

An examination of cases of *Ficus* species for which more than one pollinating wasp species has been recorded has served to highlight numerous gaps in our understanding and knowledge of fig and fig wasp biology. In the case of *F. sycomorus*, work on the wasps combined with field work on the trees has helped to redefine species limits. In the other cases further work needs to be done. The situation in the *Ficus* "thonningii / natalensis" complex is of particular interest with respect to the role that hybridisation and polyploidy may play in *Ficus* evolution.

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CHAPTER 3

BIOLOGICAL EVIDENCE FOR VOLATILE ATTRACTANTS

Paper 3: Pollinator-specific volatile attractants released from the figs of *Ficus burtt-davyi*. *South African Journal of Science* **85**; 323-324. (S. van Noort, A.B. Ware and S.G. Compton - 1989).

Paper 4: Fig wasp responses to host plant volatiles. Submitted to *Journal of Insect Behaviour*. (A.B. Ware and S.G. Compton).

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Research Letters/Navorsingsberigte

Pollinator-specific volatile attractants released from the figs of *Ficus burtt-davyi*

There are about 750 species of fig trees (*Ficus* spp., Moraceae), all of which are pollinated by tiny fig wasps of the family Agaonidae.[1] With rare exceptions, each species of fig tree is pollinated by a single species of fig wasp, which is only found in association with that one kind of tree.[2] After completing their development inside mature figs, adult female wasps fly off in search of 'receptive' immature figs. These are normally on other trees because the figs on any one tree are typically all at the same stage of development.[3,4] Once the female finds a receptive fig she enters it via the ostiole, pollinates the flowers, lays her eggs and dies. It has generally been assumed,[5-7] supported by some circumstantial evidence,[8] that trees bearing receptive figs release chemicals which attract fig wasps to them. Here we provide experimental confirmation of the release of pollinator-specific attractant volatiles from the figs of *F. burtt-davyi* Hutch. and show that the volatiles emanate from the ostioles of the figs.

Materials and methods

Unpollinated figs were collected from *F. burtt-davyi, F. thonningii* Bl. and *F. sur* Forsk. trees growing in Grahamstown. To ensure that the figs were receptive, they had been sealed inside cotton bags until the time when the other figs on the trees had been pollinated. The attractiveness of the figs was tested in July 1988 using *Elisabethiella baijnathi* Wiebes wasps emerging from a single *F. burtt-davyi* growing in the 1820 Settlers Gardens in Grahamstown. During the experiments the figs were kept in white cotton bags which prevented visual attraction but allowed the diffusion of volatiles. The bags were suspended as 1.2 m above the ground on 18 black wooden poles placed in a circle about 5 m away from the tree. The attractiveness of each bag was monitored using an adjacent sticky trap, which consisted of a clear plastic cylinder (diameter 5 cm, surface area 200 cm^2) sprayed with pruning sealant. Empty bags and their associated sticky traps acted as controls.

In the first experiment (days 1 – 3), the bags contained either 10 unpollinated *F. burtt-davyi* figs (A), 10 unpollinated *F. thonningii* figs (B), or were empty (C). The bags and associated traps were alternated around the tree (ABCABC etc.) and replaced every 24 hours. The experiment was then repeated on days 4 – 6, using unpollinated *F. sur* figs in place of those of *F. thonningii*.

A third experiment determined the site where attractants were released from the figs of *F. burtt-davyi*. Thirty bags and their associated sticky traps were placed in a 10-m radius around the tree and left for four hours. Ten bags were empty, a further 10 bags each contained 50 unpollinated figs with their ostioles sealed by painting beeswax over the opening, and the remaining bags contained 50 unpollinated figs that had been painted basally with beeswax. The last acted as controls for any possible attractive properties of the beeswax.

Table 1. Mean (± s.e.) numbers of *Elisabethiella baijnathi* collected on sticky traps placed next to cotton bags containing 'receptive' figs or control (empty) bags.

Day	*F. burtt-davyi*	*F. thonningii*	*F. sur*	Controls
1	83.5 ± 17.7	46.7 ± 15.0	–	29.8 ± 5.5
2	50.2 ± 15.3	29.0 ± 3.9	–	31.0 ± 5.0
3	600.5 ± 178.5	71.8 ± 37.8	–	60.3 ± 15.1
4	53.0 ± 11.8	–	15.7 ± 2.8	14.2 ± 2.7
5	92.7 ± 21.0	–	17.7 ± 2.4	19.5 ± 3.4
6	845.9 ± 258.5	–	56.8 ± 28.7	56.7 ± 18.0

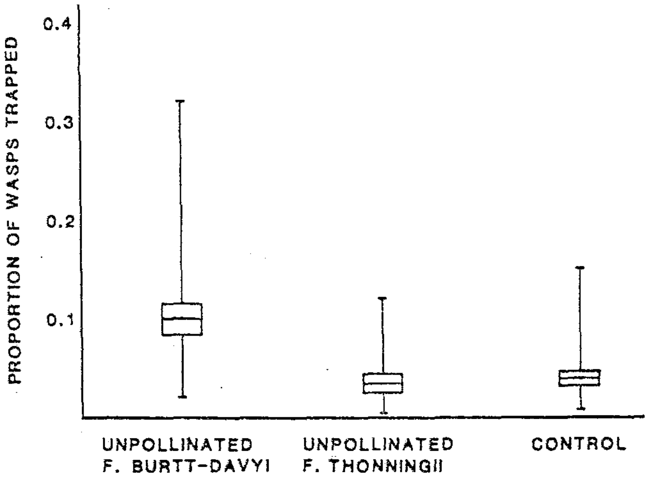

Fig. 1. *Elisabethiella baijnathi* trapped next to control (empty) cotton bags and bags containing receptive figs of *F. burtt-davyi* or *F. thonningii*. More wasps were attracted to the figs of *F. burtt-davyi* than to those of *F. thonningii* or controls ($t_{[34]} = 3.96$, $P<0.001$ and $t_{[34]} = 3.65$, $P<0.01$, respectively). Equal numbers of wasps were trapped near control bags and those containing *F. thonningii* figs ($t_{[34]} = 0.41$, $P>0.5$).

Results

There was considerable variation in the quantity of fig wasps trapped on different days, reflecting differences in the numbers of wasps emerging from the tree (Table 1). Because of this, the data from experiments 1 and 2 were standardised by converting the number of wasps on each trap to a proportion of the total wasps collected that day and arc sine transformed for statistical analysis. Significantly more fig wasps were attracted to the figs of *F. burtt-davyi* than those of *F. thonningii* or to control bags, but there was no difference in the numbers of wasps at the control and *F. thonningii* bags (Fig. 1). *E. baijnathi* females were therefore attracted to the figs of the tree they pollinate, but not to the figs of *F. thonningii*. Similar results were obtained in experiment 2, where significantly more wasps were attracted to the figs of *F. burtt-davyi* than to those of *F. sur* or controls (Fig. 2). This showed again that *E. baijnathi* was only attracted to the figs of its host tree.

F. burtt-davyi figs with their ostioles covered with wax were no more attractive than control bags (mean wasps per trap = 27.3 and 12.3, Fig. 3). In contrast, figs with basal wax remained highly attractive (mean wasps per trap = 148.4).

Discussion

Jermy *et al.*[9] have emphasized the advantages of field studies of olfaction over those which are carried out in the laboratory. Here we have shown that under natural conditions the pollinator of *F. burtt-davyi* is attracted to the smell of its receptive unpollinated figs, but is not attracted to the unpollinated figs of two other species. The wasps were not attracted if the ostioles of the figs were covered, showing that the source of attraction came from within the figs.

Further experiments have shown that pollinated *F. burtt-davyi* cease to be attractive to the pollinator, and preliminary GC-MS analysis has revealed at least one volatile compound which is released prior to pollination, but not subsequently.[10] Identifica-

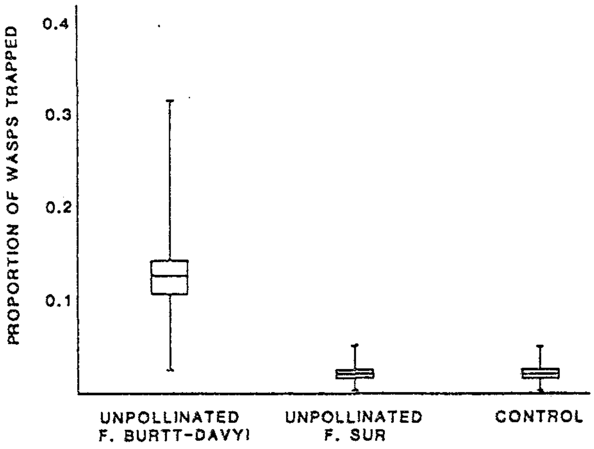

Fig. 2. *Elisabethiella baijnathi* trapped next to control (empty) cotton bags and bags containing receptive figs of *F. burtt-davyi* or *F. sur*. More wasps were trapped near *F. burtt-davyi* than *F. sur* ($t_{[34]}$ = 6.89, $P<0.001$) or controls ($t_{[34]}$ = 6.97, $P<0.001$). There was no difference in the numbers of wasps trapped at *F. sur* figs and controls ($t_{[34]}$ = 0.054, $P>0.5$).

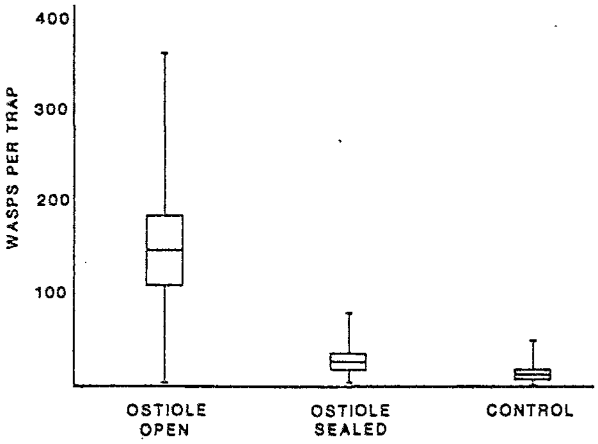

Fig. 3. *Elisabethiella baijnathi* trapped next to control (empty) cotton bags and bags containing receptive figs of *F. burtt-davyi* with beeswax sealing their ostioles or applied at their bases. Figs with their ostioles covered did not attract wasps and when compared with controls ($t_{[18]}$ = 1.17, $P>0.1$). In contrast, figs with basal wax remained highly attractive ($t_{[18]}$ = 3.37, $P<0.01$).

tion and synthesis of this compound is proceeding, in preparation for its bioassay.

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FIG WASP RESPONSES TO HOST PLANT VOLATILES

A. B. Ware and S. G. Compton

ABSTRACT

Fig trees (*Ficus* spp. Moraceae) are pollinated by fig wasps belonging to the family Agaonidae. Each tree species is usually pollinated by a single species of wasp. Previous experiments have shown that the wasps are attracted to the trees by volatiles emanating from the figs. Using fig-bearing trees and arrays of sticky traps baited with figs, we investigated the specificity of wasp attraction and its timing. The pollinators of two closely related *Ficus* species are specifically attracted to figs of their host at the time when figs are ready to be pollinated. Some non-pollinating fig wasps appear to use the same cues.

INTRODUCTION

Fig wasps (Chalcidoidea, Agaonidae) are intimately associated with fig trees (*Ficus* spp., Moraceae)(Boucek, 1988). Each of the 750 or so *Ficus* species (Berg, 1988) is generally pollinated by a specific species of pollinating wasp belonging to the subfamily Agaoninae (Wiebes, 1979; Wiebes and Compton, 1990). The fig trees are totally dependent on the wasps for pollination and in return provide sites for their larval development inside the fruits - the figs.

In addition to the pollinators there are also many species of non-pollinating fig wasps with larvae that also develop inside the figs. These belong mainly to subfamilies of the Agaonidae other than Agaoninae, but include representatives of other chalcid families (Boucek, 1988). Some of the species gall the fig ovules while others parasitise the gall formers. A few non-pollinating wasp species are like the pollinators and enter the lumen of the fig prior to oviposition (van Noort, 1992), but the majority reach the ovules from the outside, penetrating the wall of the figs with their long ovipositors. Although the host relationships of most non-pollinating species are unknown, some of them are like the pollinating wasps and are exclusively associated with a single *Ficus* species (Ulenberg, 1985; van Noort, 1992).

In most *Ficus* species the development of fig crops tends to be synchronised within any one tree, but is not synchronised between trees (Wharton *et al.*, 1980; Bronstein and Patel, 1992; Bronstein, 1988, 1992; Bronstein *et al.*, 1990). Adult females of pollinating fig wasps are short-lived, surviving at most a few days (Kjellberg *et al.*, 1988), while the longevity of some female non-pollinating wasps can extend to one or two months (Joseph, 1958; Compton *et al.*, in prep). The gaps between fig crops on each tree may be months or even years (Bronstein, 1987; Windsor *et al.*, 1989). The combination of the within-tree fruiting synchrony and the short life-spans of the wasps means that both the pollinating and the non-pollinating female wasps must usually leave their natal trees in order to find figs that are suitable for oviposition (Bronstein, 1987, 1992).

Van Noort *et al.* (1989) showed that the pollinating wasp *Elisabethiella baijnathi* Wiebes located the figs of its host tree, *Ficus burtt-davyi* Hutch., using volatiles released by the figs when they were ready to be pollinated ('receptive' or 'female phase' figs: Galil, 1977). Figs at other stages of development were not attractive to the pollinators, nor were figs which had their ostioles covered, suggesting that the attractants emanated from within the figs during this short period of their development (van Noort *et al.*, 1989). The responses of non-pollinators were not investigated, but those species which oviposit at the same stage of fig development as the pollinators could potentially make use of the same volatiles, whereas wasps which oviposit into figs at a later stage of development might be expected to utilise alternate cues.

Here we examine aspects of the specificity of the volatiles used by fig wasps to find their host trees. Using arrays of sticky traps baited with figs of different developmental stages, we determined when wasps are attracted to the figs of *F. thonningii* Bl. and compared the specificity of the volatile attractants produced by this tree and *F. burtt-davyi*. We also experimentally prolonged the period when figs remained attractive to their pollinators, in order to determine the length of time figs would 'wait' for their pollinators.

MATERIALS AND METHODS

The study was conducted in the 1820 Settlers Botanical Gardens situated at Grahamstown, in the eastern Cape Province of South Africa. Three local eastern Cape *Ficus* species grow in the gardens. Two, *F. burtt-davyi* (some 110 individuals), *F. thonningii* (57 trees, some of which have been planted), are closely related and are placed in the section Galoglychia of the subgenus Urostigma, while the third, *F. sur* Forssk. (10 trees), belongs to the subgenus Sycomorus. The locations of most of the trees in the gardens are indicated in Figure 1 and the fig wasps associated with these species locally are listed in Table 1.

Table 1. Indigenous *Ficus* spp. present in the Grahamstown Botanical Garden, together with the wasps normally found associated with the trees in Grahamstown.

Ficus spp.	Pollinator	Non-pollinators
F. thonningii Bl.	*Elisabethiella stuckenbergi* Grandi	*Otitesella tsamvi* Wiebes
		Phagoblastus barbarus Grandi
		Sycoryctes sp.*
		Philotrypesis sp.*
F. burtt-davyi Hutch.	*Elisabethiella baijnathi* Wiebes	*Otitesella uluzi* Compton
		Otitesella sesquianellata van Noort
		Sycoryctes sp.*
		Philotrypesis sp.*
F. sur Forssk.	*Ceratosolen capensis* Grandi	*Sycophaga cyclostigma* Waterston
		Apocrypta guineensis Grandi
		Apocrytophagus spp.

*The *Philotrypesis* and *Sycoryctes* species recorded from *F. thonningii* and *F. burtt-davyi* cannot be distinguished at present, and may not be host tree specific.

Sticky traps, each consisting of a cylinder (10 cm radius; 30 cm length) covered with cellulose and sprayed with pruning sealant (Frank Fehr, Durban), were used to investigate the attraction of fig wasps to figs at different stages of fig development. Poles, bearing the sticky traps placed at a height of 1.2 m, were placed in a 3 X 3 array about 40 m from the nearest fig tree. Each pole was positioned 5 m from its nearest neighbour. Twenty-five receptive phase *F. thonningii* figs were placed in each of three cotton bags (treatment A) and 25 post pollinated figs in each of a further three bags (treatment B). The final three empty bags acted as controls (treatment C). The bags were attached to the poles immediately above the sticky traps and placed in position (orientated ABC:BCA:CAB) at 07hr00. The sticky traps were removed for analysis 6 hours later. The experiment was conducted twice in December 1989.

We then investigated how long unpollinated figs could potentially remain attractive to fig wasps. *F. burtt-davyi* was chosen for these experiments because it is a smaller species than *F. thonningii* and all its figs are within reach from the ground. We selected two *F. burtt-davyi* trees growing about 100 m apart that were of comparable size and had produced approximately 5000 figs at the same stage of development. Approximately half of the figs on one of the trees were surrounded by cotton bags during their early pre-female phase. This prevented any pollination or oviposition by fig wasps. Single sticky traps were then placed in each tree to monitor arrivals of fig wasps and were replaced weekly.

The specificity of the volatile attractants emanating from the figs of *F. thonningii* and *F. burtt-davyi* figs was investigated in two field choice experiments. In the first experiment a 3 X 3 array of sticky traps was used as before, but with the cotton bags containing either 25 receptive phase figs of *F. thonningii* (three bags) or 25 receptive phase figs of *F. burtt-davyi* (three bags). The last three empty bags again acted as controls. Two replicate trials were conducted in December 1989 and January 1990.

In a long term experiment monitoring the specificity of wasp attraction, the arrivals of wasps at *F. thonningii* and *F. burtt-davyi* trees in the Botanical Gardens were monitored over a two year period. Single sticky traps were placed in five trees of each species. In *F. burtt-davyi* the traps were positioned between 0.5 and 1.5 m above ground level, while in the taller *F. thonningii* they were placed at a height of approximately 2 m. The traps were replaced weekly and the numbers and identity of the trapped fig wasps were recorded. The relative positions of the trees that contained traps are indicated in Figure 1.

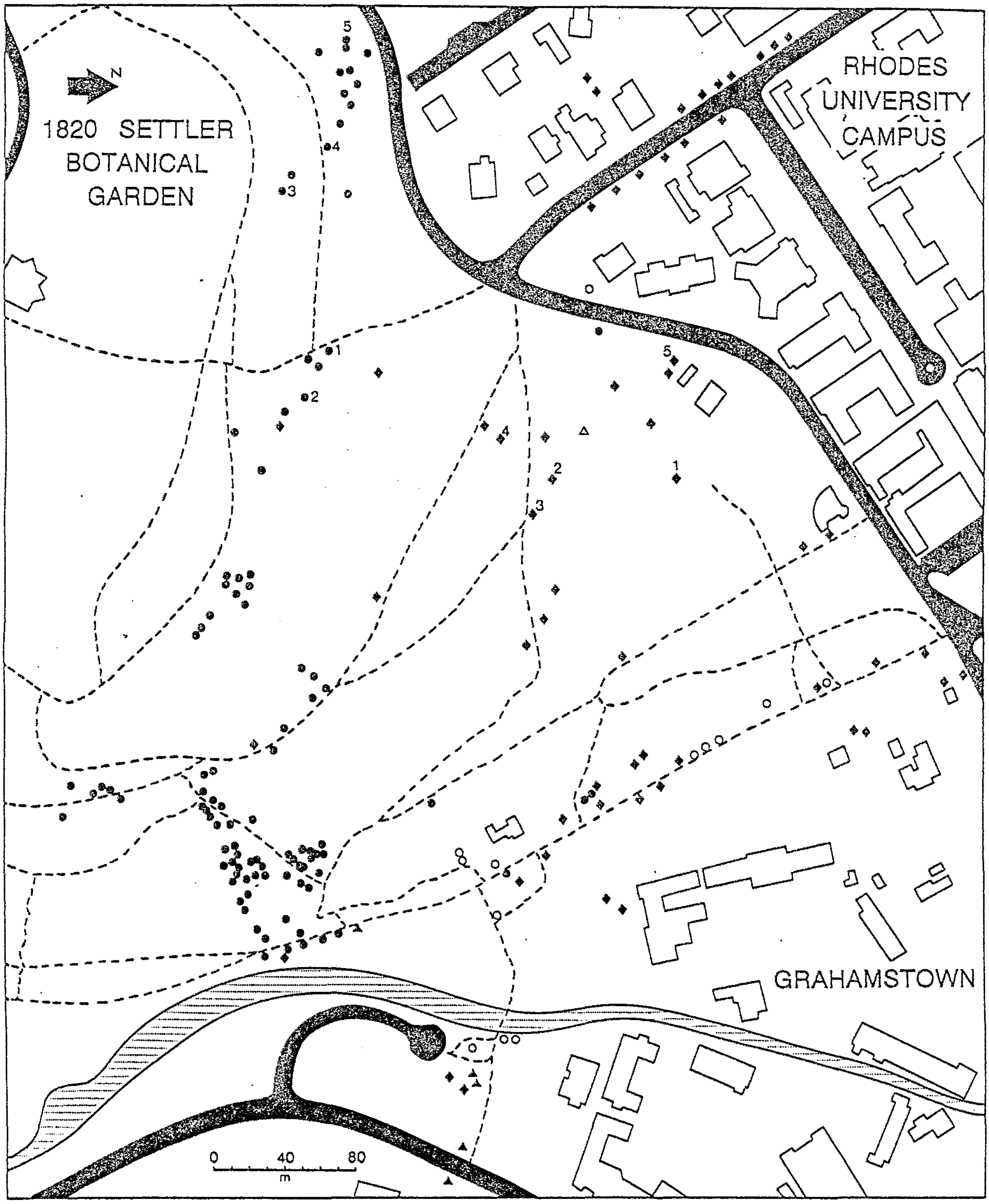

Figure 1. Portion of the 1820 Settlers Botanical Garden (Grahamstown, South Africa) showing the relative positions of *F. thonningii* (◈), *F. burtt-davyi* (●) and *F. sur* (▲) trees. Additional exotic fig trees are represented by the open symbol (○). The numbers indicate those trees used to monitor the arrivals and departures of the fig wasps.

RESULTS

F. thonningii is pollinated by *E. stuckenbergi*, and significantly more females of this species were recorded from sticky traps placed near receptive phase *F. thonningii* figs than on traps near pollinated figs or the control bags (Table 2). There was no difference between the number of *E. stuckenbergi* trapped on the control sticky traps and those near the pollinated figs (Table 2). A similar preference for unpollinated figs of *F. thonningii* was shown by the non-pollinating species, *Phagoblastus barbarus*, *Philotrypesis* sp. and *Otitesella* spp. although too few examples of the latter species were trapped for statistical significance to be recorded.

In the experiment that examined the duration of fig attractiveness, figs on the control *F. burtt-davyi* tree were rapidly pollinated by their pollinating wasp (*E. baijnathi*) and within about two weeks the wasps ceased to be attracted to the tree (Figure 2). In contrast, large numbers of wasps continued to arrive at the *F. burtt-davyi* tree with bagged figs for a period of five weeks (Figure 2). The figs therefore remained attractive to their pollinating wasps for an extended period when pollination was prevented. Far fewer wasps were collected on the control tree, presumably because they avoided the traps by entering the figs.

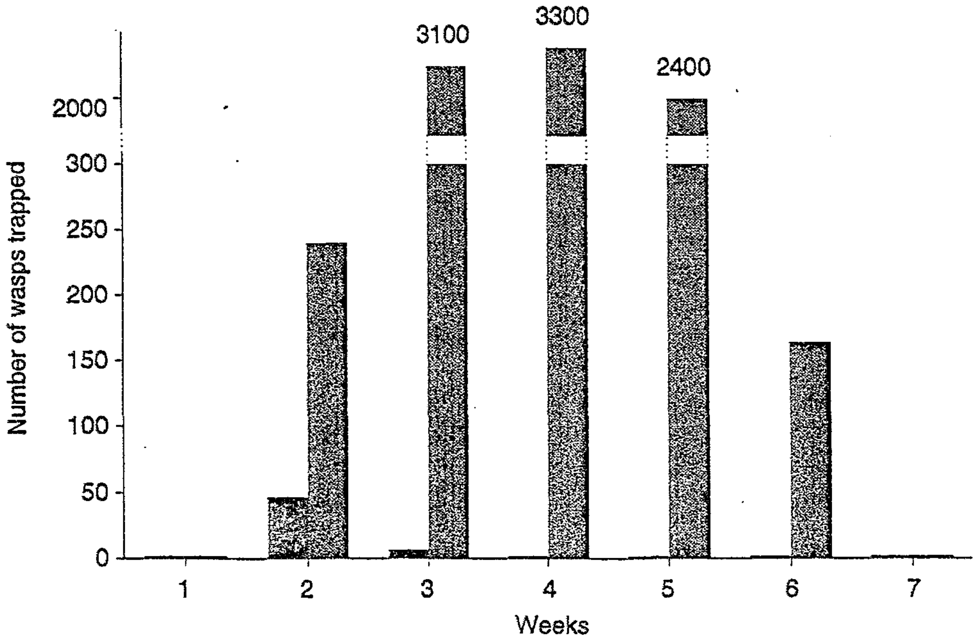

Figure 2. The effect of bagging pre-receptive (= pre-female) figs (hatched bar) of *F. burtt-davyi* on the numbers of pollinating wasps, *E. baijnathi*, trapped. The solid bars indicate the number of wasps trapped on a similar tree which remained unbagged.

Table 2. The fig wasps trapped near cotton bags containing either pollinated or unpollinated (receptive) *F. thonningii* figs. The control bags were empty. Combined results from two trials.

Wasp species trapped	Number of wasps trapped									Mann-Whitney U comparisons			
	Receptive figs			Post-pollinated figs			Control			Control / receptive figs		Control / post-pollinated figs	
	n traps	Mean/ trap	Range	n traps	Mean/ trap	Range	n traps	Mean/ trap	Range	U	P	U	P
E. stuckenbergi	6	162.6	5-638	6	4.8	1-14	6	1.8	0-4	36.0	**	27.0	ns
P. barbarus	6	3.3	0-7	6	0.3	0-1	6	0	-	32.5	*	21.0	ns
Philotrypesis sp.	6	4.3	0-8	6	0.7	0-1	6	0	-	33.0	*	21.0	ns
Otitesella spp.	6	2.5	0-11	6	0	-	6	0	-	25.5	ns	21.0	ns

ns = not significant; * = $P < 0.5$; ** = $P < 0.01$

Table 3. The fig wasps trapped near cotton bags containing either unpollinated (receptive) figs of *F. thonningii* or *F. burtt-davyi*. Control bags were empty.

Wasp species	Number of wasps trapped									Mann-Whitney U comparisons					
	Receptive figs *F. burtt-davyi*			Receptive figs *F. thonningii*			Control			Control / *F. thonningii*		Control /*F. burtt-davyi*		*F. thonningii* / *F. burtt-davyi*	
	n traps	Mean/ trap	Range	n traps	Mean/ trap	Range	n traps	Mean/ trap	Range	U	P	U	P	U	P
E. stuckenbergi	6	3.2	0-6	6	53.8	31-66	6	2.5	0-4	36	***	21	ns	36	***
E. baijnathi	6	10.0	4-17	6	1.5	0-3	6	1.2	1-2	23.5	ns	36	***	36	***
P. barbarus	6	0.2	0-1	6	10.8	2-18	6	0.3	0-1	36	***	25	ns	36	***
Philotrypesis sp.	6	0.5	0-3	6	1.3	0-5	6	0	-	27	ns	21	ns	23.5	ns

ns = not significant; *** = $P < 0.001$.

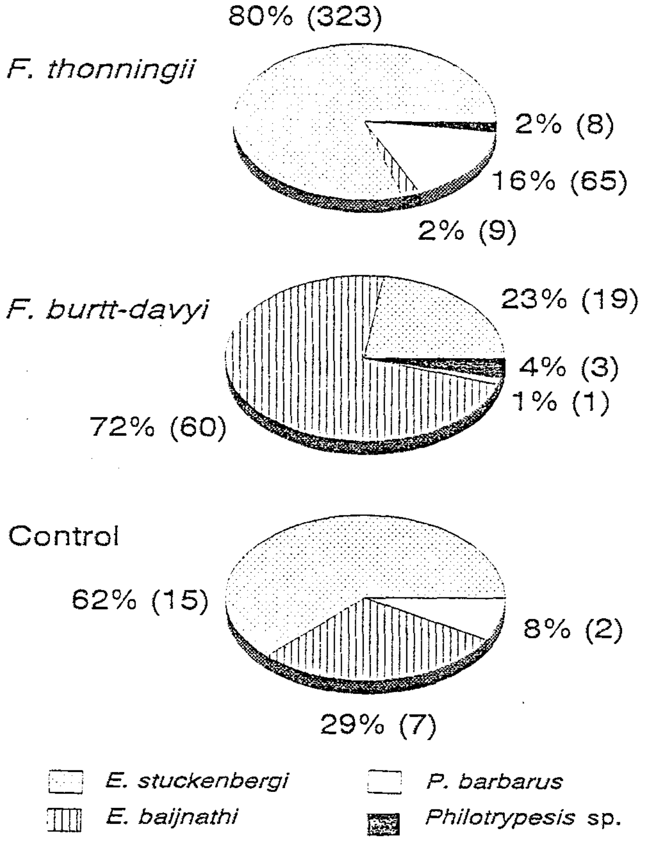

Figure 3. The numbers of wasps, together with with their relative percentages, simultaneously trapped near bags containing receptive figs of *F. thonningii* or *F. burtt-davyi*. Empty bags acted as controls.

The specificity of wasp attraction was confirmed when individuals were provided with a choice between the receptive figs of two closely related *Ficus* species. The ratios of wasps on different treatments were similar during the two trapping periods and the data have therefore been combined for analysis. Significantly more *E. stuckenbergi* and *P. barbarus* (wasps associated with *F. thonningii*) were trapped near receptive *F. thonningii* figs than on traps near *F. burtt-davyi* figs or the controls (Table 3; Figure 3). Likewise, significantly more *E. baijnathi* were trapped near figs of its host species, *F. burtt-davyi*. No preferences were shown by the *Philotrypesis* sp., which may be associated with both *F. thonningii* and *F. burtt-davyi*.

The fruiting phenologies of the five *F. burtt-davyi* and five *F. thonningii* trees that were monitored for two years are shown in Figure 4. On the four trees of each species that produced figs the crops varied in duration from as little as 8 weeks in summer to over 20 weeks during winter. The development of the figs on any one tree was generally well synchronised, but the trees fruited at different times of the year. Most of the wasps trapped on the trees belonged to species known to be specifically associated with that *Ficus* species (Table 4). *F. sur* is the third indigenous fig species growing in the botanical gardens. Only very small numbers of the wasps associated with this species were recorded from traps placed in *F. thonningii* and none in *F. burtt-davyi* trees (Table 4).

Table 4. The wasps caught in sticky traps on *F. thonningii* and *F. burtt-davyi* trees and their normal host *Ficus*.

Trap location	Origins of wasps on traps			
	F. thonningii	*F. burtt-davyi*	*F.sur*	Host tree Indeterminate
F.thonningii	2120	13	22	696
F. burtt-davyi	1	1204	0	120

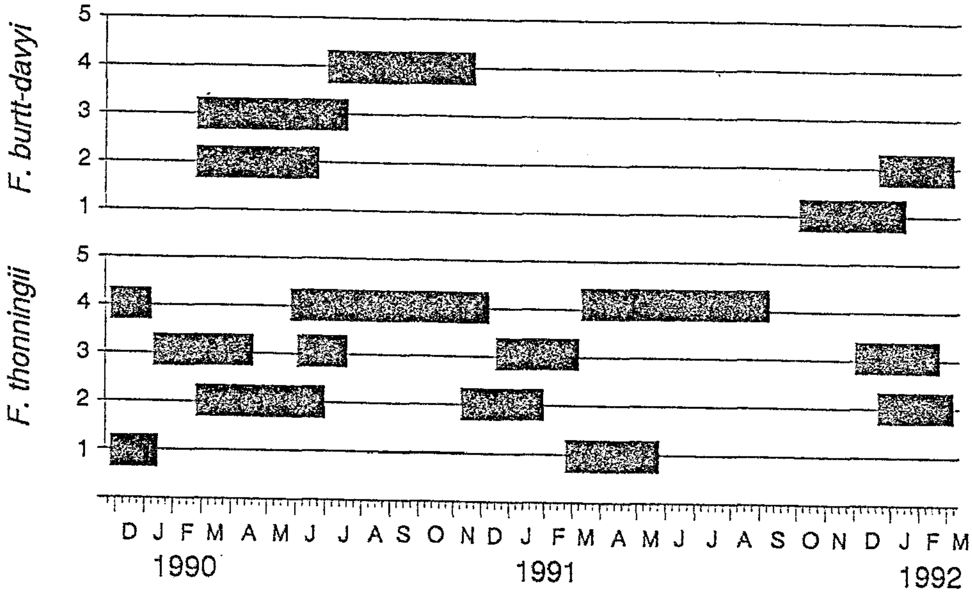

Figure 4. The fruiting phenologies of 10 fig trees used in the long term monitoring of fig wasp arrivals and departures. Intercrop periods are shown with thin solid lines while the period when the trees were bearing fruit are denoted by solid blocks.

Few wasps were present in the 10 trees when they were not bearing fruit (Table 5). During each fruit crop, the trapped wasps initially comprised those adult female wasps which had been attracted to the tree to oviposit. After a few weeks these were then followed during the second half of the crop period by their progeny as they emerged from the mature figs (Table 5, Figures 5 and 6). Only the wasps trapped during the first half of each crop period had therefore flown to the trees from elsewhere, and only the trapping results during this period have been included in the following analyses.

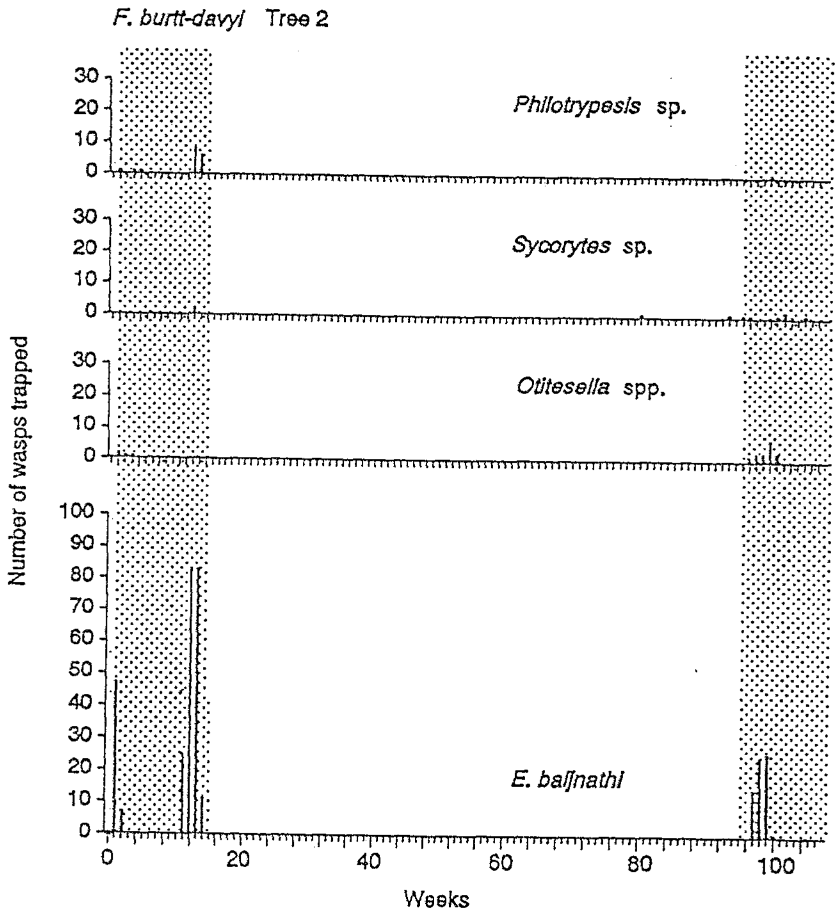

Figure 5. Identity and numbers of fig wasps trapped at a *F. burtt-davyi* tree. The shaded areas represent those periods when figs were present on the tree.

On *F. thonningii* trees the numbers of *E. stuckenbergi* and *P. barbarus* were significantly higher during the first half of the crop periods than during the intercrop periods (Table 6). In contrast there were no such differences in the trapping rates of *E. baijnathi*, the species that pollinates *F. burtt-davyi*. The reverse situation was present on the *F. burtt-davyi* trees, where there were no increases in the numbers of *E.*

Table 5. The fig wasps (all species) trapped at *F. thonningii* and *F. burtt-davyi* trees during their intercrop, receptive (first half of crop period) and producer (latter half of crop period) stages.

Tree #	Number of crops	Total crop period (Wks)	Intercrop period (Wks)	Number of wasps trapped (mean / week)		
				Intercrop period	Receptive period	Producer period
F. thonningii						
1	1	21	98	2.37	18.66	13.29
2	2	42	77	1.35	14.29	25.74
3	1	38	81	2.10	15.32	8.35
4	1	63	56	0.91	8.32	22.10
5	0	0	119	0.75	-	-
Total	5	164	431	1.25	12.79	15.39
F. burtt-davyi						
1	2	15	90	0.12	0.40	2.80
2	3	28	77	0.04	7.29	15.79
3	4	21	84	0.02	39.91	0.76
4	3	19	86	0.26	50.42	3.16
5	0	0	105	0.04	-	-
Total	12	83	442	0.10	24.35	6.75

stuckenbergi and *P. barbarus* trapped on the trees during receptive periods, but numbers of *E. baijnathi* did increase (Table 6). Thus, during periods of fig receptivity the three species were only preferentially attracted to their own host trees (Table 6).

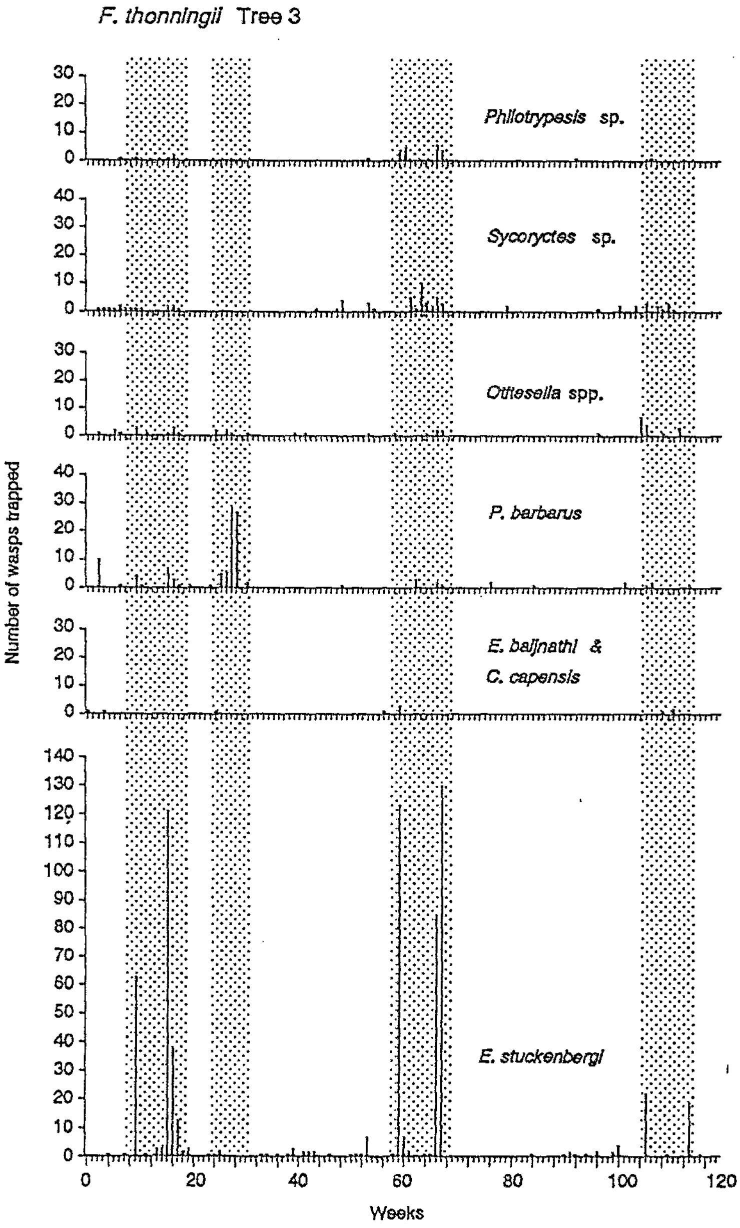

Figure 6. Identity and numbers of fig wasps trapped in a *F. thonningii* tree. The shaded areas indicate those periods figs were present on the tree.

Table 6. Comparisons of the numbers of wasps trapped during intercrop periods with the numbers trapped during the first half of each crop period (which includes the receptive female phase of fig development).

Tree #	Number of wasps trapped (mean/week)											
	E. stuckenbergi				*P. barbarus*				*E. baijnathi*			
	Receptive period	Inter-crop period	Mann-Whitney *Z*	*P*	Receptive period	Inter-crop period	Mann-Whitney *Z*	*P*	Receptive period	Inter-crop period	Mann-Whitney *Z*	*P*
F. thonningii												
1	29.29	0.5	-2.899	***	0.14	0.25	-2.787	**	0	0.01	0.227	ns
2	6.85	0.42	-3.436	***	3.15	0.49	-3.676	***	0	0.05	0.969	ns
3	11.00	0.54	-1.019	ns	0.60	1.05	-1.719	ns	0.05	0.03	-0.711	ns
4	9.71	0.36	-3.903	***	1.93	0.13	-3.295	***	0	0	1.000	ns
5	-	0.37	-	-	-	0.20	-	-	-	0.09	-	-
TOTAL	11.40	0.44	-5.905	***	2.03	0.41	-6.291	***	0.02	0.20	0.413	ns
F. burtt-davyi												
1	0	0	1.000	ns	0	0	1.000	ns	0.13	0.06	-1.103	ns
2	0.07	0	0.260	ns	0	0	1.000	ns	5.29	0	-5.586	***
3	0	0	1.000	ns	0	0	1.000	ns	38.00	0.02	-5.548	***
4	0	0	1.000	ns	0	0	1.000	ns	51.00	0.17	-4.486	***
5	-	0	-	-	-	0	-	-	-	0.03	-	-
TOTAL	0.02	0	0.311	ns	0	0	1.000	ns	22.67	0.06	-9.473	***

ns = not significant; ** = $P < 0.01$; *** = $P < 0.001$

DISCUSSION

In the Grahamstown Botanical Gardens the overlap in the fruiting periods of *F. burtt-davyi* and *F. thonningii* and the close proximity of the trees meant that adult wasps associated with the two species could potentially colonise the trees of either species. However, long term monitoring of wasp arrivals at *F. thonningii* and *F. burtt-davyi* trees showed that the trees' pollinators were only attracted to their respective host trees. The two wasp species were thus able to distinguish their own host figs in the presence of receptive figs of the other species. This was confirmed in the experiments using figs placed in cotton bags, which also showed that, as in the case of *F. burtt-davyi* (van Noort *et al.*, 1989), the pollinators of *F. thonningii* were not attracted to their host figs unless they were at the receptive stage.

P. barbarus was the only non-pollinating wasp recorded on the traps in large numbers. This species was also found to be attracted to receptive phase figs of only its host tree (*F. thonningii*). *P. barbarus* enters the figs to oviposit at the same time as the pollinators, and like them may be attracted by the changes in the volatiles that are released during the receptive period (Ware *et al.*, in press).

These experiments have confirmed the specificity of wasp responses to the volatile attractants released by two closely related *Ficus* species, and have shown that figs normally remain attractive for a short period, unless pollination is prevented. Gas chromatograph analysis of volatiles produced by the figs of these species has shown that additional compounds are released during their receptive phase of development and these are likely to be the basis for the observed specificity of attraction (Ware *et al.*, in press). Only isolation and bioassay of the attractant volatiles will confirm this link.

Bronstein (1992), in discussing the proximate factors that determine whether or not a fig tree will be pollinated, suggested that localised wasp extinction could be a major factor limiting fig production. This is because in small tree populations there may be no receptive figs for the short-lived pollinating wasps to colonise. However, if they remain unpollinated, the figs of *F.burtt-davyi* were able to maintain their attractiveness to pollinators for extended periods. This could potentially overcome local shortages of extended receptive period in *F. burtt-davyi* is that a smaller number of fig trees can maintain the wasp populations in each local area (Bronstein *et al.*, 1990). This is in contrast to another African species, *F. sycomorus*, where unpollinated figs abscise only about a week after the start of the female phase (Galil and Eisikowitch, 1969).

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CHAPTER 4

CHEMICAL EVIDENCE FOR VOLATILE ATTRACTANTS

Paper 5: Fig volatiles: their role in attracting pollinators and maintaining pollinator specificity. In press *Plant Systematics and Evolution* (A.B. Ware, P.T. Kaye, S.G. Compton and S. van Noort).

FIG VOLATILES:
THEIR ROLE IN ATTRACTING POLLINATORS AND MAINTAINING POLLINATOR SPECIFICITY

A. B. Ware, P. T. Kaye, S. G. Compton and S. van Noort

ABSTRACT

Each fig tree species (*Ficus*) is totally dependent on a specific species of wasp for pollination and the larvae of these wasps only develop in the ovules of their specific *Ficus* host. Because the fig crop on any particular tree is generally highly synchronised, the short lived female wasps must leave their natal tree in order to find figs which are suitable for oviposition. Chemical volatiles produced by figs when they are ready for pollination are thought to be the means by which the wasps detect a suitable host. Gas chromatograms of the fig volatiles of 7 species of *Ficus* showed them to be species specific. Age related changes in the volatile profiles were noted as extra volatiles are produced when the figs were ready for pollination.

INTRODUCTION

The relationship between fig trees (*Ficus* spp., Moraceae) and their pollinating wasps (Chalcidoidea, Agaonidae, Agaoninae; *sensu* Boucek (1988)) is often considered to be the extreme example of plant-animal coevolution (Janzen, 1979). There are some 750 *Ficus* species worldwide (Berg, 1988), each of which is generally pollinated by females of its own specific species of wasp (Wiebes, 1979; Michaloud *et al.*, 1985; Wiebes and Compton, 1990). The trees are totally dependent on the wasps for pollination, while the wasp larvae develop only in the ovules of their *Ficus* hosts.

Figs (also called syconia) are hollow, roughly spherical inflorescences, lined on their inner surface with hundreds of unisexual flowers. The pollinating female wasps enter the fig through the bract-lined entrance (the ostiole) and pollinate the flowers, some of which are also used for oviposition. These foundress wasps usually lose their wings during the passage through the ostiole and are unable to leave.

Fig development can be divided into five distinct phases (Galil and Eisikowitch, 1968). In the prefemale phase, the ostioles of the young developing figs have not yet opened. This stage is followed by the female phase where the female flowers mature and the ostiole opens to allow the pollinators to enter the fig. Once pollination has taken place the figs enter the inter-floral phase where both seeds and wasp larvae are developing. The male phase commences with the maturing of the male flowers and the emergence of the wingless males of the pollinator wasp which seek out and mate with the female wasps while they are still in their natal galls. After emerging from their galls the pollinator females acquire a load of pollen either actively or passively (Galil and Eisikowitch, 1973). They then leave their natal fig through a hole chewed through the fig wall by the males. Finally the fig ripens (post-floral phase) and attracts various avian or mammalian frugivores which disperse the seeds (Janzen, 1979).

Fig development on individual trees is normally highly synchronised, forcing the short-lived adult females (Kjellberg *et al.*, 1988) to leave their natal trees and search elsewhere for figs containing flowers that are ready to be pollinated. Factors involved in host finding and host specificity are only partially understood. A potential attractant is chemicals released from the figs (Janzen, 1979; Ramirez, 1970). Bronstein, (1987) provided indirect evidence for chemical attraction when she showed that large numbers of pollinators of the neotropical *F. pertusa* L. arrived at their host tree only when the figs were ready to be pollinated. Confirmation of long distance chemical attraction was provided by van Noort *et al.* (1989) who showed that the pollinators of *F. burtt-davyi* Hutch. were attracted only to the figs of their host *Ficus* and this only occurred when the figs were at the appropriate stage of development.

There have been few previous studies of the volatiles released by fig trees. Jennings (1977) found that the differences between the steam distillate volatiles of ripe figs from 4 cultivars (some are gynocarpic and do not require the services of the pollinating wasps to set fruit) of *F. carica* L. were only quantitative.

Other studies have concentrated on either the leaf volatiles (Buttery *et al.*, 1986) or the composition of volatiles from stem exudates (Warthen and McInnes, 1989), but neither leaves nor stems play a role in attracting fig wasps (van Noort *et al.*, 1989). Barker (1985) provided gas chromatograph evidence of the existence of fig volatiles.

Host specificity of Ficus species is likely to be achieved through a combination of these long distance volatile attractants, short range, contact stimuli provided by the fig surface and other physical characteristics of the fig. These may include the chemical properties of the fig surface (Ware and Compton, 1992) and the physical characteristics of the fig ostiole (Ramirez, 1974; Janzen, 1979) through which the wasps must crawl in order to reach the fig flowers and oviposit (Galil, 1977).

In this paper we address questions related to the chemical nature of the long distance attractants produced by figs. Initially we determined whether the figs of each *Ficus* species has a characteristic bouquet, a possible means by which the wasps could distinguish their host tree species from other *Ficus*. Changes in the composition of the bouquet of the figs of several species were then examined in relation to their developmental cycle. Changes observed in the volatile profile of the figs during the period when the fig flowers are ready for pollination could account for the observation that wasps are attracted only to the trees at this stage of fig development.

MATERIALS AND METHODS

The volatiles of seven *Ficus* species were investigated: *F.sur* Forssk., *F. burtt-davyi*, *F. thonningii* Bl., *F. lutea* Vahl, *F. ingens* (Miq.) Miq., *F. macrophylla* Desf. from the Grahamstown area, eastern Cape Province, South Africa, and three cultivars of *F. carica* (Calimyrna, Kardota and White Genoa) from the Citrusdal area of the western Cape Province, South Africa. *F. macrophylla* is native to Australia while *F. carica* is of Mediterranean origin. The other species are native to South Africa.

Cotton bags were used to enclose prefemale stage figs in order to prevent wasps from pollinating the figs. Once the figs had reached the attractive female phase, determined by confirming that wasps had entered other figs on the same tree, they were harvested and within 10 minutes were placed in a glass tube (internal diameter 30mm, length 300mm). Air cleaned with activated charcoal was directed over the figs at approximately 1*l*/minute for 5 hours and the volatiles, chemicals in the vapour phase, that were released trapped on activated charcoal (Orbo 32, Supelco, Bellefonte, PA). The volatiles of unpollinated prefemale and pollinated inter-floral stage figs were processed in a similar way. With the exception of the locally scarce *F. lutea* and *F. macrophylla*, prefemale, female and inter-floral stage figs from at least three trees of each species were analyzed independently. The number of figs processed depended on their size. For large figs such as *F. carica* as few as 8 figs were used, while for *F. burtt-davyi*, the species with the smallest figs, at least 20 figs were used during each volatile trapping experiment.

Volatiles were eluted from the charcoal traps with 1ml dichloromethane (Merck Cat No 6048). The eluant was then sealed in glass ampoules and stored at 4°C. When required, the contents of each ampoule were concentrated to approximately 10ul by evaporation with a stream of nitrogen, and 1ul of the resultant concentrate was chromatographed on a fused silica capillary column (SGE; 25m with an internal diameter of 0.22mm) on a Hewlett Packard (HP) 5890 gas chromatograph (GC) fitted with a flame ionisation detector and using nitrogen as a carrier gas. The instrumental parameters were: injection port temperature 210°C, flame ionization detector temperature 210°C, nitrogen carrier gas 20ml/minute. The initial oven temperature of 40°C was maintained for 1 minute and then was increased at a gradient of 5°C/min to a maximum temperature of 180°C, which was then maintained for 5 minutes. The temperature was then increased at a rate of 10°C/min until the oven temperature reached 250°C which was maintained for 10 minutes before the run was terminated. Purge time for the injection port was set at 0.5 minutes. The results were analyzed on an HP 3393A integrator, the attenuation being set to zero.

RESULTS

Differences in volatile profiles

The volatiles released from the female phase figs of the seven *Ficus* species each resulted in a unique gas chromatogram (Fig. 1; Fig. 6). All the chromatograms were complex, containing many peaks each of which represented an individual volatile compound. Most of the volatiles were present in trace quantities (a full scale deflection at an attenuation of zero represented approximately 5ng of material), some of which may be caused through the degradation of the figs, insect damage or even directly from small insects such as scale insects. The profiles from different individual trees of the same species were generally similar (see below for an exception) showing that each tree species has its own characteristic bouquet. For example the volatile profiles of the three cultivars of *F. carica* were found to be essentially similar, differing quantitatively rather than qualitatively (Fig. 2). The general uniformity within species was observed in the prefemale phase chromatograms of some ten *F. burtt-davyi* (Fig. 3). However, the female phase figs of a further 2 trees were found to contain an additional major peak, which eluted at *ca.* 12 minutes.

Age related changes in volatile profiles

The chromatograms of *F. burtt-davyi* figs at the female stage of development showed an additional volatile eluting at *ca.* 12 minutes (Fig. 3 and Fig. 4). As mentioned above, some trees produced a further additional peak with a slightly reduced retention time at this stage of their development (Fig. 3). The volatile profiles of prefemale and inter-floral phase figs of *F. burtt-davyi* were similar (Fig. 4). Similarly, in *F. ingens* the female phase figs produced extra volatiles that were not recorded before or after this stage of development. In this case there were consistently two additional peaks, with retention times of *ca.* 24 and 25 minutes (Fig. 5). One additional peak was present in the female phase chromatogram of *F. lutea* with a retention time of *ca.* 12 minutes (Fig. 6). Unfortunately, no inter-floral fruit was available for comparison because most of the figs of *F. lutea* figs were not pollinated.

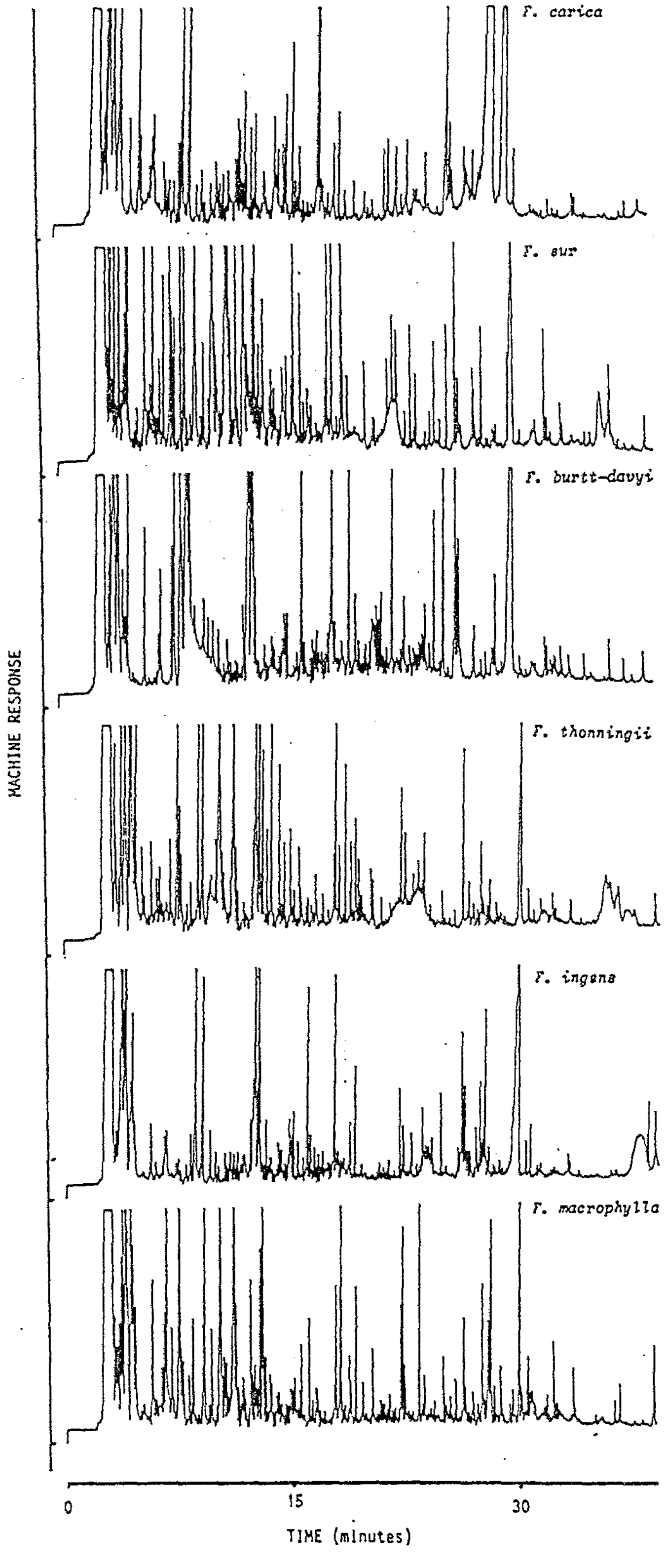

Figure 1. Chromatograms of volatiles from female phase figs from six individual trees of six *Ficus* species. A full amplitude response at the detector represents at least 5 ng of material while the retention time indicates how long the volatiles remained on the column before reaching the detector. The smaller more volatile compounds generally elute first while the oven temperature is still low. See text for instrumental parameters.

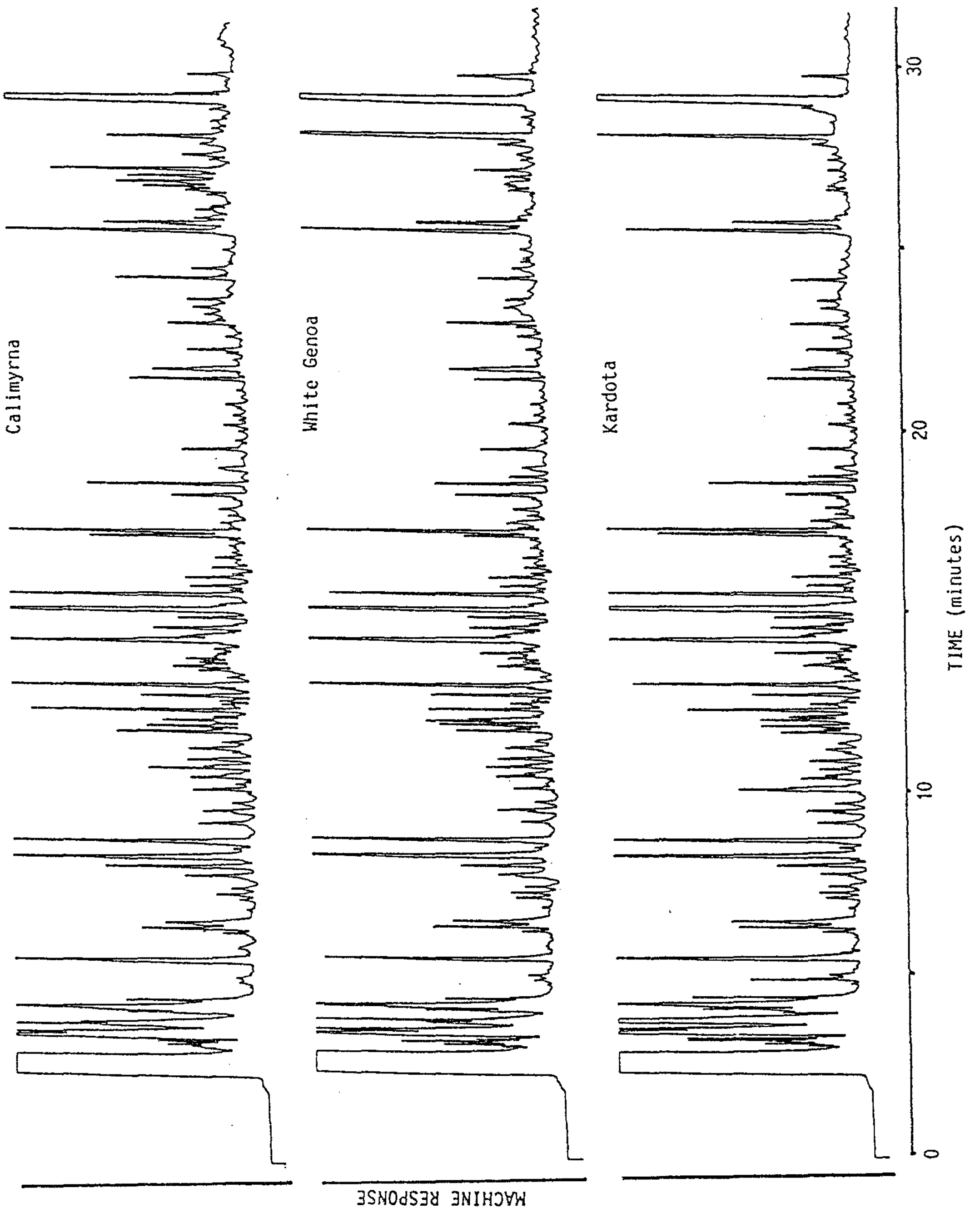

Figure 2. The volatile profiles of female phase figs from three cultivars of *F. carica*.

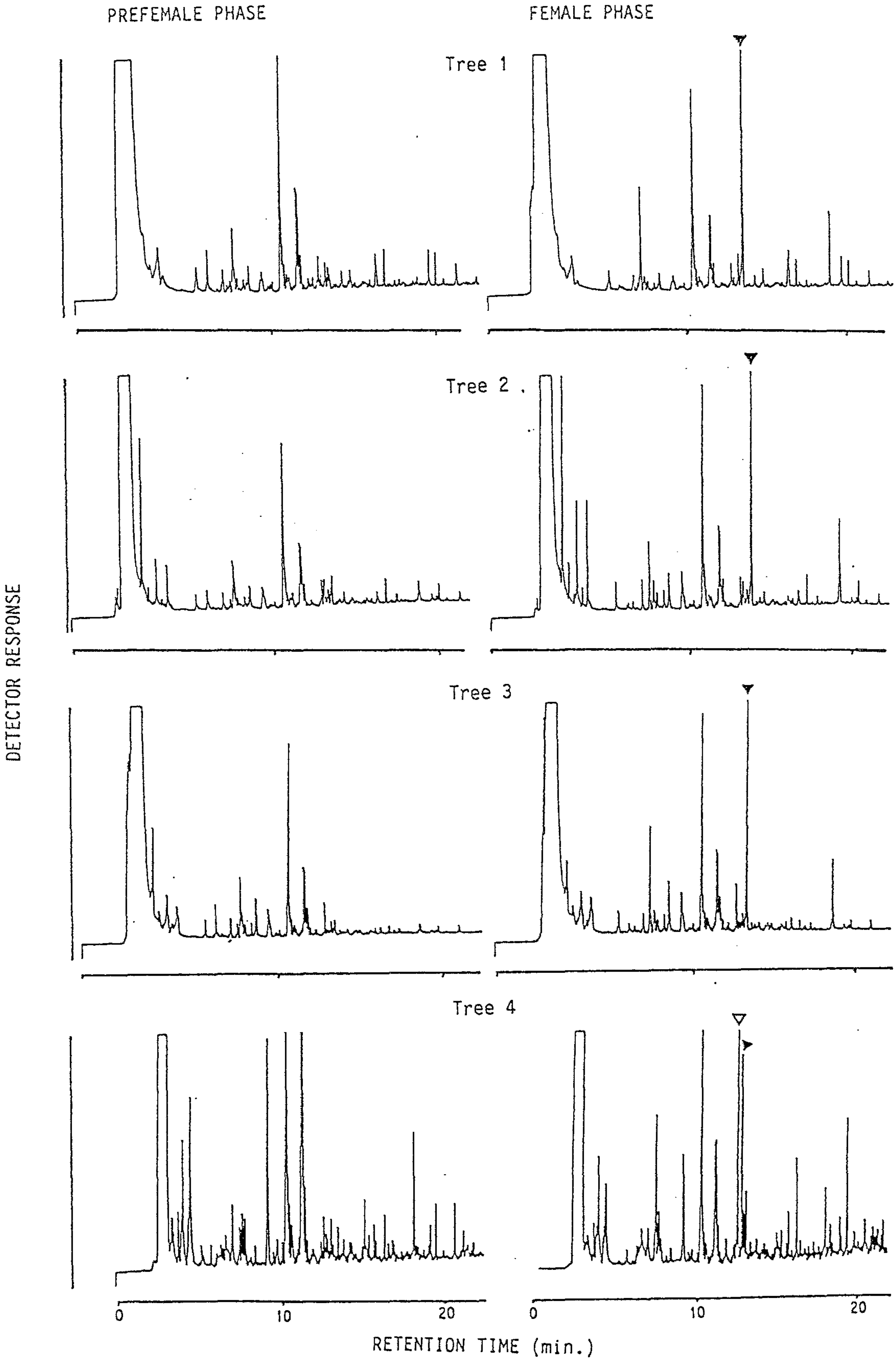

Figure 3. The volatile profile of prefemale and female phase figs of four individual trees of *F. burtt-davyi*. The closed symbol highlights the additional volatile recorded from figs in the female phase. The open symbol indicates that volatile which was released from female phase figs of two individual trees.

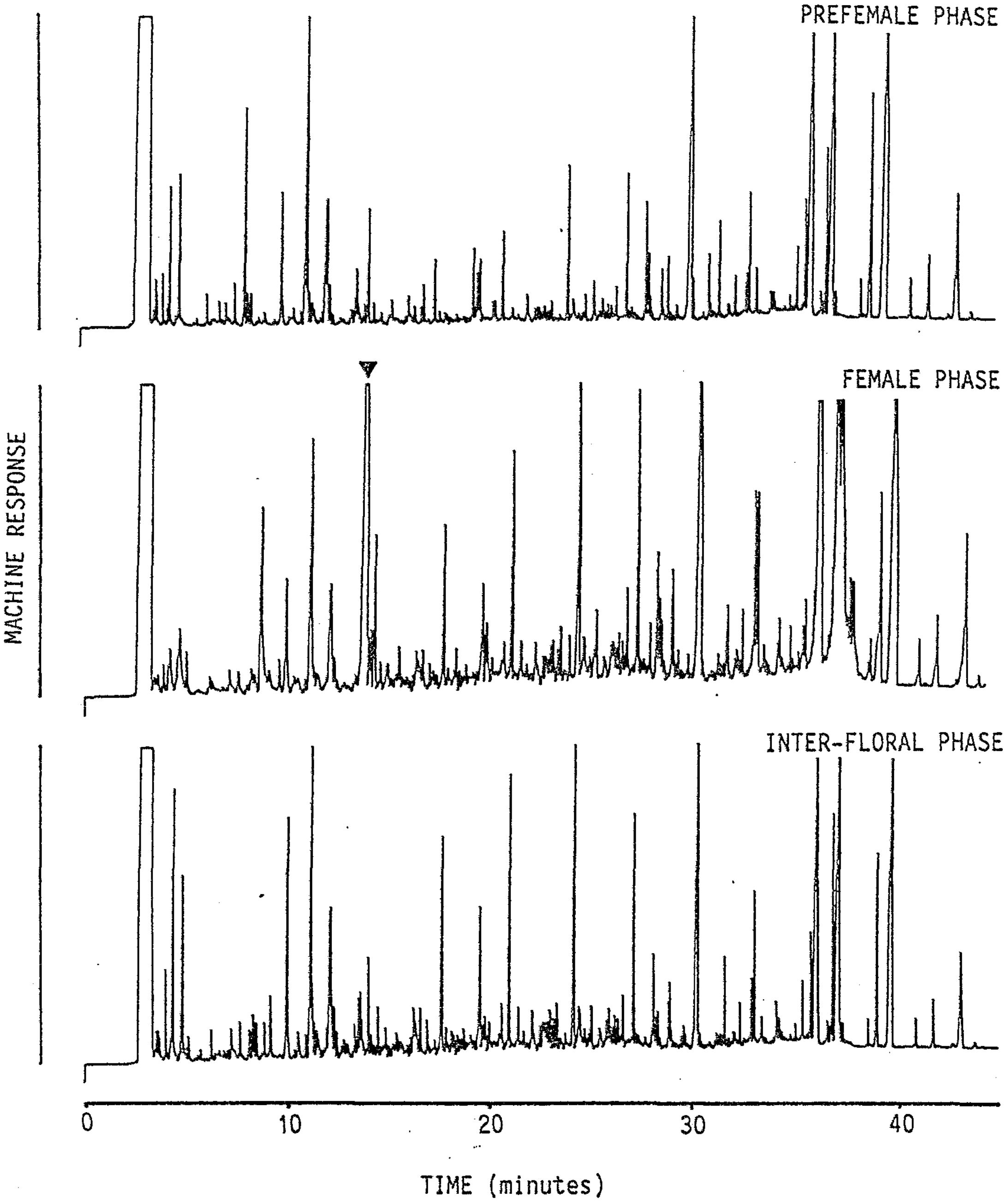

Figure 4. The gas chromatograms of prefemale, female and inter-floral phase figs from *F. burtt-davyi.* The closed symbol indicates the additional volatile peak occurring in the volatile profile of female phase figs.

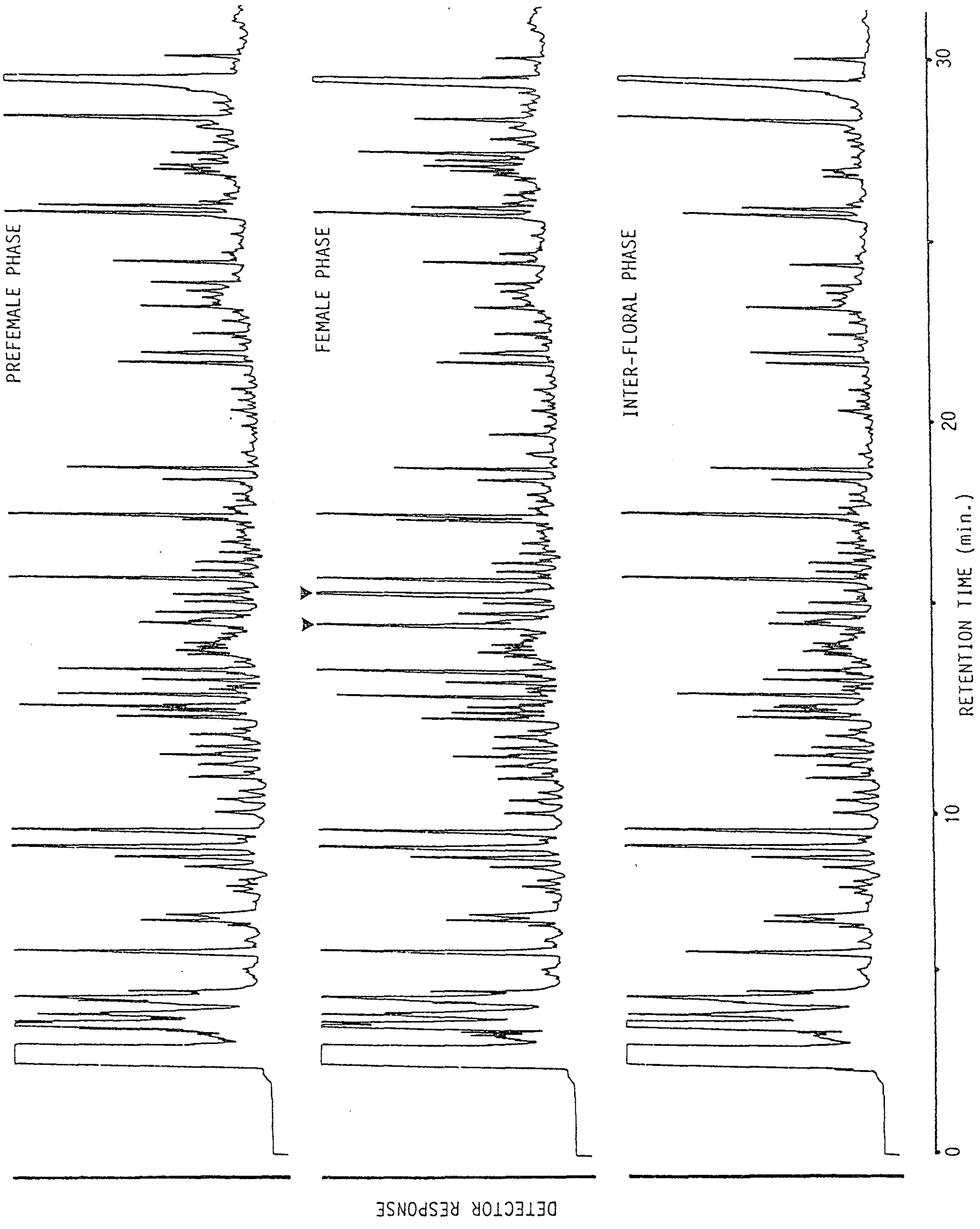

Figure 5. Gas chromatograms of the volatiles from prefemale, female and interfloral stage figs of *F. ingens*. The symbols indicate additional volatile components produced by female phase figs.

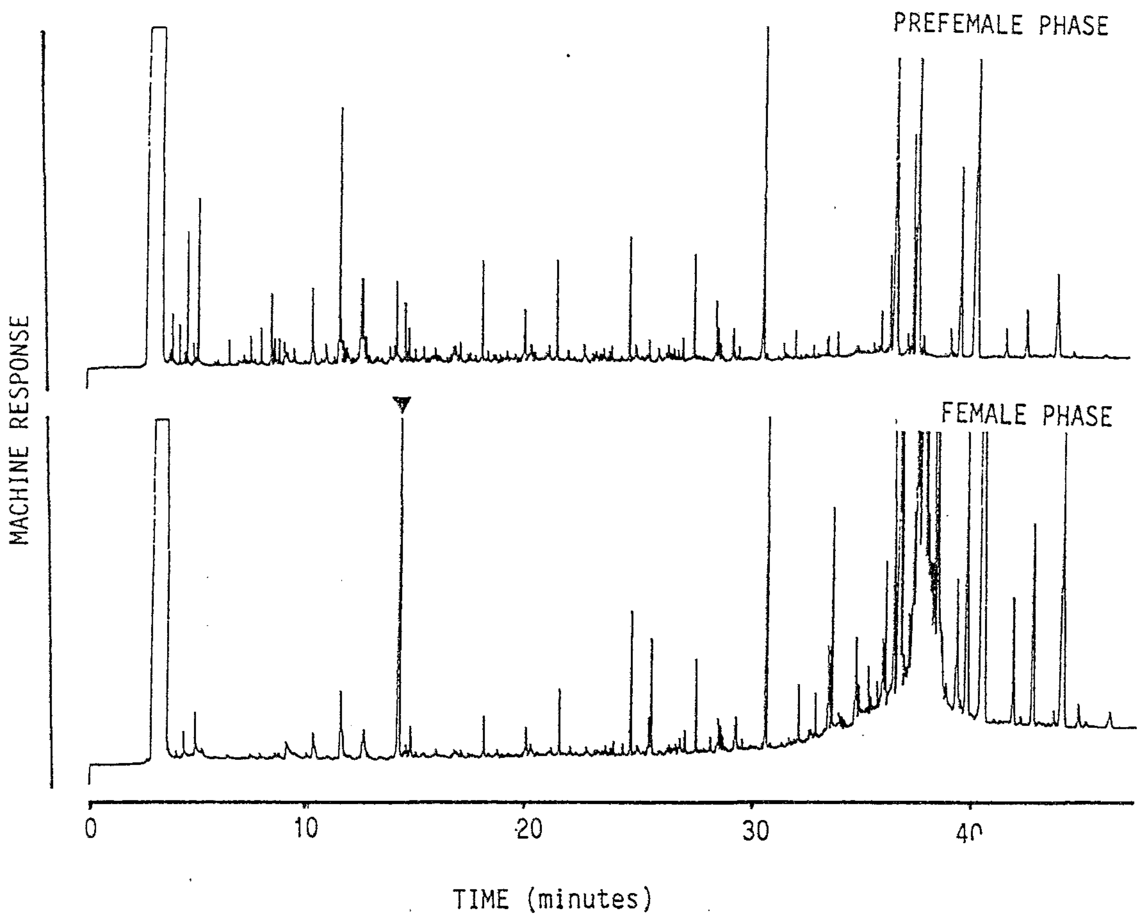

Figure 6. The volatile profiles of the prefemale and female stage figs of *F. lutea*. The symbol indicates the additional volatile produced by female phase figs.

DISCUSSION

Flower volatiles play a vital role as olfactory cues in attracting pollinating insects (Pellmyr and Thien, 1986). Figs are no exception in attracting their pollinators, even though their flowers are contained within a syconium. Many insect use these olfactory cues together with visual stimuli such as colour (Tabashnik, 1985; Owens and Prokopy, 1986) and shape (Rausher, 1978; MacKay and Jones, 1989) to find their host plant. Van Noort *et al.*, (1989) have shown that the wasp pollinators of *F. burtt-davyi* do not require these additional visual aids to find receptive figs of their host.

The movement of volatile molecules in the atmosphere is complex (Murlis *et al.*, 1992). To be effective and reliable sources of information, volatile attractants have to be consistently emitted and easily distinguished from the background of naturally occurring odours. Electrophysiological studies have shown that cues resulting from single volatile compound are probably the exception rather than the rule (Visser, 1986). This implies that the fig volatiles are probably an uncommon mixture of compounds of the immediate environment and present themselves in reasonable amounts only when the figs are ready to be pollinated.

In pollinating systems such as those between some orchids (*Ophrys*) and male bees, the partnership can also be highly specific (Hills *et al.*, 1972; Borg-Karlson *et al.*, 1985). Here each orchid species possesses a unique blend of volatiles, components of which may mimic the pheromones of attractive female bees. The plants deceive the male bees which, while attempting to copulate with them, pollinate the flowers. Among such orchids, speciation potentially results from mutations which lead to changes in the plants' attractive volatiles (Hills *et al.*, 1972).

Similarly, the volatiles produced by figs may facilitate the obligate relationship between fig trees and their pollinators. The figs of each Ficus species produce a different bouquet of volatiles, which is largely consistent within species, allowing host specific pollinators to differentiate between them. Furthermore, additional volatile(s) are released at the time the pollinators are attracted. Presumably it is these additional compounds, either alone or in combination with the 'normal' volatile bouquet which form the basis of attraction. Female phase volatiles could therefore be of biological significance because this is the period when pollinators are attracted to their respective host trees. Identification, synthesis and bioassay of the compounds are now required in order to confirm these findings.

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CHAPTER 5

STUDIES OF FIG WASP BEHAVIOUR

Paper 6: Dispersal of adult female fig wasps I. Arrivals and departures. Submitted to *Entomologia expermenatalis et applicatus* (A.B. Ware and S.G. Compton).

Paper 7: Dispersal of adult female fig wasps II. Movements between trees. Submitted to *Entomologia expermenatalis et applicatus* (A.B. Ware and S.G. Compton).

DISPERSAL OF ADULT FEMALE FIG WASPS.

I: ARRIVALS AND DEPARTURES

A.B. Ware and S.G. Compton

ABSTRACT

Ficus burtt-davyi, like most other fig trees (*Ficus* spp., Moraceae) is pollinated by its own unique species of fig wasp, in this case *Elisabethiella baijnathi* (Chalcidoidea, Agaonidae). Because fig crop development on any one tree is synchronised the small, short-lived female wasps have to fly to other trees in order to find figs which are at a suitable stage of development for oviposition. This paper examines the effects of temperature on the timing of emergence of the wasps from their natal figs, their dispersal from the surface of the figs and their subsequent behaviour on arrival at new host trees.

INTRODUCTION

Fig trees (*Ficus* spp. Moraceae) and fig wasps (Chalcidoidea, Agaonidae) are intimately associated (Boucek, 1988). Each *Ficus* species is usually pollinated by just one species of pollinating fig wasp (Agaonidae, Agaoninae) (Wiebes 1979; Wiebes and Compton, 1990). The fig trees are totally dependent on the females of their specific pollinating wasp for pollination and the fig wasps can only develop inside the fruits of their host *Ficus*. Non-pollinating fig wasps (belonging to other subfamilies of Agaonidae) can be equally host plant specific (Ulenberg, 1985; van Noort, 1992).

Floral structure in *Ficus* is unusual in that the inflorescences (the figs, also called syconia) are hollow, roughly spherical and lined on the inside with hundreds or thousands of unisexual flowers. Entrance to the centre of the fig (the lumen) is through a narrow bract-lined passage, the ostiole. Fig development can be divided into five distinct phases (Galil and Eisikowitch, 1968). During the prefemale stage the female flowers develop within the lumen of the fig and the ostiole is closed. In the next development stage, the female stage, the female flowers are mature and are receptive to pollination. The ostiole opens allowing the pollen-laden female fig wasps to penetrate the lumen of the fig in order to lay their eggs. While passing through the ostiole the wasps lose their wings and parts of their antennae and they are unable to leave the fig. The interfloral phase follows during which the flowers and wasp larvae develop simultaneously. The male phase commences with the maturing of the pollen bearing male flowers. The female flowers at that time contain fully developed seeds. The flightless male wasps have also reached maturity and chew their way out of their ovules and seek out ovules containing conspecific females for mating. The females leave their galls and after loading pollen leave the fig through an exit hole chewed by the males. Finally the figs ripen (postfloral phase), ready to be eaten by birds and mammals which subsequently disperse the seeds (Janzen, 1979).

Fig crop development tends to be synchronised within each tree with gaps of months or even years between crops (Bronstein, 1987; Windsor *et al.*, 1989). This means that the wasps cannot oviposit in figs on their natal trees and the newly emerged wasps are forced to fly to other trees in order to find suitable figs for oviposition. Adult life spans of the pollinators are short (Kjellberg *et al.*, 1988; Compton *et al.*, in prep.) and the wasps locate suitable figs for oviposition using volatile attractants which emanate from the figs when they are ready to be pollinated (= female phase)(Bronstein, 1987; van Noort *et al.*, 1989; Ware *et al.*, in press). Some non-pollinating fig wasps may utilize the same attractants as the pollinators to find their hosts (Compton, submitted).

The biology of fig wasps when they are within the figs has been comparatively well documented (Galil, 1977; Janzen, 1979) but little is known about free-living adult female fig wasps (Bronstein, 1992). This study examines factors that influence the emergence and departure of female wasps from their natal figs and their arrival at receptive trees. Observations were also made on their behaviour when leaving their natal trees and after finding a suitable host tree.

MATERIALS AND METHODS

Ficus burtt-davyi Hutch. is the most common of the indigenous *Ficus* species occurring in the eastern Cape Province of South Africa. At our field site in the 1820 Settlers Botanical Garden, Grahamstown, the trees grow as rock-climbing shrubs against small cliffs and are pollinated by the fig wasp *Elisabethiella baijnathi* Wiebes. Crop development in this species is highly synchronised (Compton *et al.*, in press). Non-pollinating fig wasps associated with this species include *Otitesella sesquianellata* van Noort, *O. uluzi* Compton, *Philotrypesis* sp. and *Sycoryctes* (= *Sycoscaperidea sensu* Boucek) sp. Most of these wasps breed only on *F. burtt-davyi* in the area, although the latter two species cannot presently be distinguished from those that utilise *F. thonningii* Bl. and may not be host tree specific.

Emergence of Fig Wasps and Departure from Their Natal Figs.

In order to determine the time of day when female fig wasps emerged from their natal figs, five wasp producing trees (male phase) were visited regularly during the daylight hours in summer while five further crops were monitored in winter. Selected branches were marked and on each visit any figs with wasp exit holes were counted and removed. Ambient temperatures were also recorded during visits to two winter and two summer crops. Observations of the pollinators' preflight behaviour on the surface of the figs were also recorded.

In a laboratory experiment, the critical take-off temperature for pollinator females was investigated. Groups of forty wasps were initially subjected to 30 minutes pre-conditioning at each temperature in a dark controlled-environment room before being released at the base of a box (115 cm high, 20 cm deep and 20 cm wide, with the top and one side constructed of clear plastic sheets) placed under a fluorescent light. A record was made of how many wasps took flight during the following 30 minute period.

In the field, the diel patterns of flight activity of *E. baijnathi* were determined using five sticky traps placed 1.5 m above the ground in the centre of the area where the fig trees were growing. Each trap consisted of a clear cellulose acetate sheet measuring 60 cm x 20 cm and sprayed with pruning sealant (Frank Fehr, Durban). The traps were replaced daily at 06h00 and 18h00 and all fig wasps trapped were identified and counted. Trapping was carried out during three, one week long, periods both in summer and winter.

Arrivals at Receptive Trees

The timing of wasp arrivals at a tree with receptive figs was studied by bagging pre-receptive *F. burtt-davyi* figs. Once the figs had become receptive, the surrounding cotton bags prevented the wasps from entering the figs and the wasps moved around on the bag surface trying to gain entry. Bags were visited every three hours during the daylight hours over three day periods. All *E. baijnathi* females around the bagged figs were counted and removed.

In a further investigation, previously bagged branches of two trees bearing pre-receptive figs were exposed to the wasps once they had matured and were ready to be pollinated. The behaviour of individual pollinators as they landed and explored the branches was then recorded using a dictaphone. Similarly, patterns of entry into individual figs was examined by exposing branches of unpollinated, previously bagged receptive figs to the wasps for 15 minutes. The figs were then re-bagged and taken to the laboratory where the number of foundresses in each was determined.

RESULTS

The Timing of Fig Wasp Emergence, Departure and Arrivals

Table 1. The timing of fig wasp emergence as indicated by the number of *F. burtt-davyi* figs with exit holes.

	Number of trees	Morning	Afternoon	Night
		06h00-12h00	12h00-18h00	18h00-06h00
Summer	5	636	154	129
Winter	5	1159	265	0

The fig wasps associated with *F. burtt-davyi* usually emerged from their natal figs between 06h00 and 12h00 (Table 1). No wasps emerged before 06h00 during the winter sample periods. However, in mid-summer some wasps had emerged from their natal fig prior to the first sample of the day, possibly in the period when most of the wasps emerged from the figs (Figure 2).

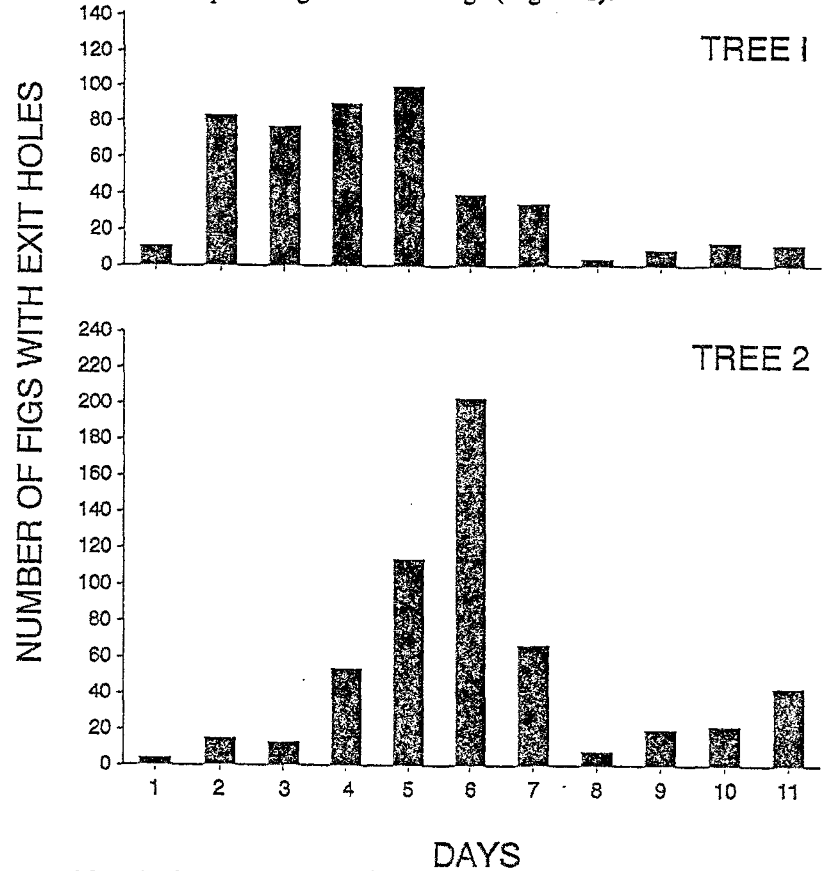

Figure 1. The number of figs with fig wasp exit holes during the 11 day dispersal phases of two synchronously fruiting *F. burtt-davyi* trees (winter 1990).

Fig crops, together with their associated fig wasps, develop more quickly during summer than winter and subsequent wasp emergence dates are also more closely synchronised. During the summer months, the ambient temperatures remained between 16°C and 30°C and the wasps from each of the five trees completed their emergence in 2-3 days. Because wasp emergence was synchronised in summer and they emerged over a short period, the effect of day to day temperature variation on the emergence rates could not be adequately assessed. This was not the case in winter where the emergence periods were of longer duration and ranged between 7 and 20 days (Figure 1). Figure 2 shows the variation in emergence rates from the two winter crops where temperature data was also collected. Early in the mornings of days 5-7 a disproportionately large numbers of figs were found with exit holes (Figure 2). Prior to these observations (days 4-6) being made, berg wind conditions (offshore winds with accompanying high temperatures) were prevalent (Figure 3) and this appears to have led to the timing of the wasp emergence being brought forward.

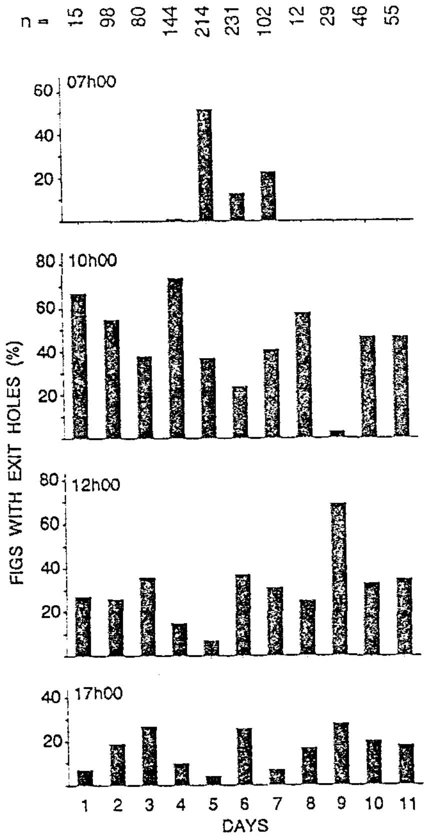

Figure 2. Exit holes produced at different times of the day in two synchronously fruiting *F. burtt-davyi* trees (winter 1990).

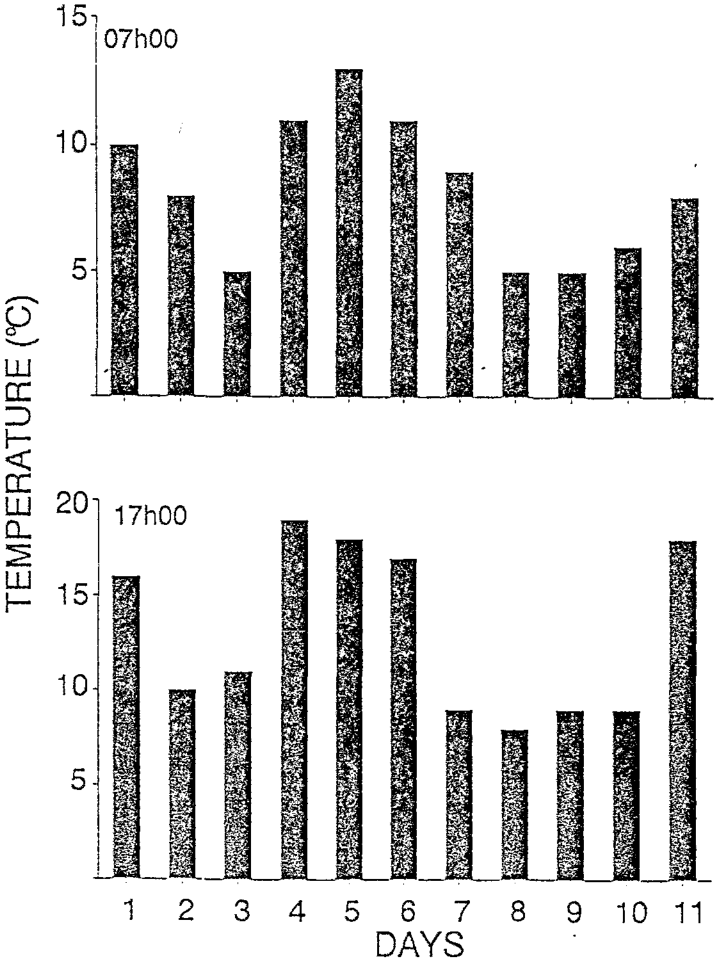

Figure 3. The morning and evening ambient temperatures in the 1820 Settlers Botanical Garden during the 11 day wasp dispersal phase from two *F. burtt-davyi* trees.

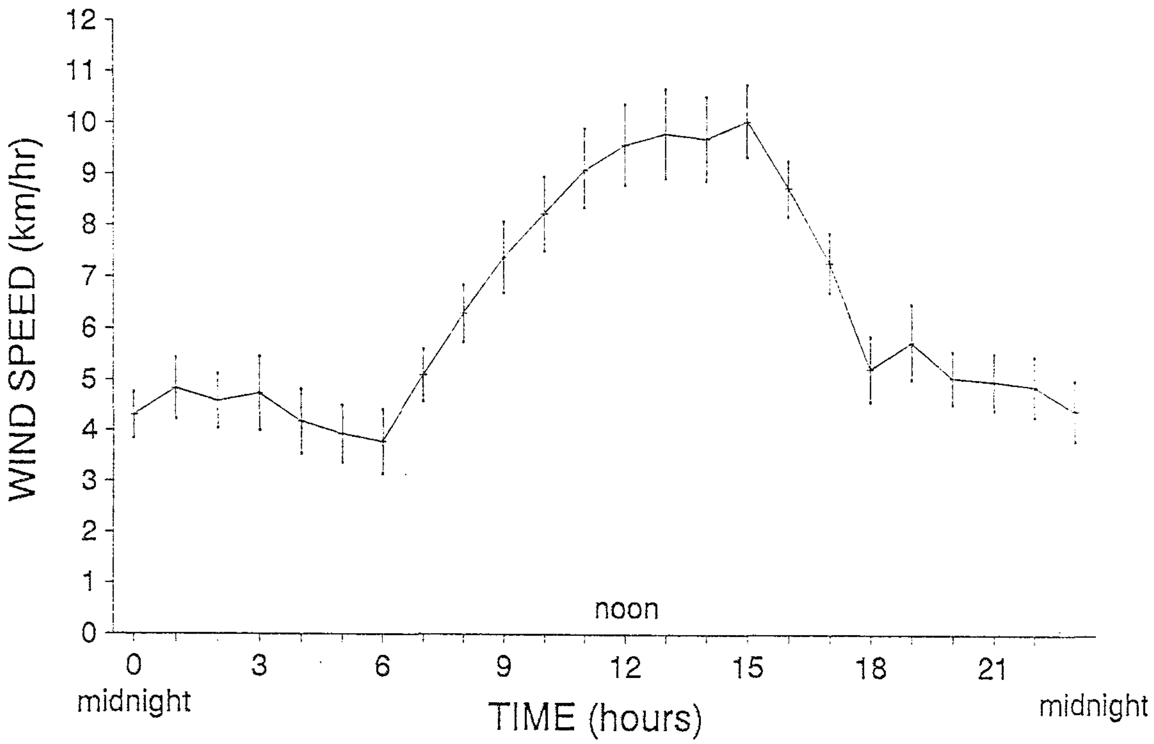

Figure 4. The average hourly windspeeds (+/- standard error) experienced in Grahamstown during March 1989.

Support for temperature playing a role in the timing of emergence comes from regression analysis of temperature and the number of wasps emerging from the figs over the day. The daily early morning temperatures (07h00) were significantly correlated with temperature at 17h00 the previous day (Spearman Rank: $r = 0.724$; $P < 0.05$). It was therefore not surprising to find that the proportion of figs with exit holes produced early in the morning (before 07h00) was positively correlated not only with the 07h00 temperature on the morning of emergence (Spearman Rank: $r = 0.724$; $P < 0.05$) but also the temperature experienced the previous day at 17h00 (Spearman Rank: $r = 0.799$; $P < 0.001$). Thus, the delay in wasp emergence on day 9 (when the majority of wasps only emerged between 10h00 and 12h00) (Figure 2) can be related to the low temperatures experienced both that morning and the previous day (Figure 3). Wasps therefore emerged later in the day when the mornings are cold although the previous day's temperature may also be important in influencing the emergence pattern.

In the laboratory the critical takeoff temperature for *E. baijnathi* was found to be between 15 and 16°C. Below this temperature no wasps were active in the air while at 20°C almost all the wasps were observed to fly (Figure 5). The critical takeoff temperature was also the temperature at which fig wasps began to exit from their natal figs. Thus it appears that the wasps responded to the ambient temperatures and only emerged from their natal figs when the temperatures were likely to be high enough to allow flight to take place.

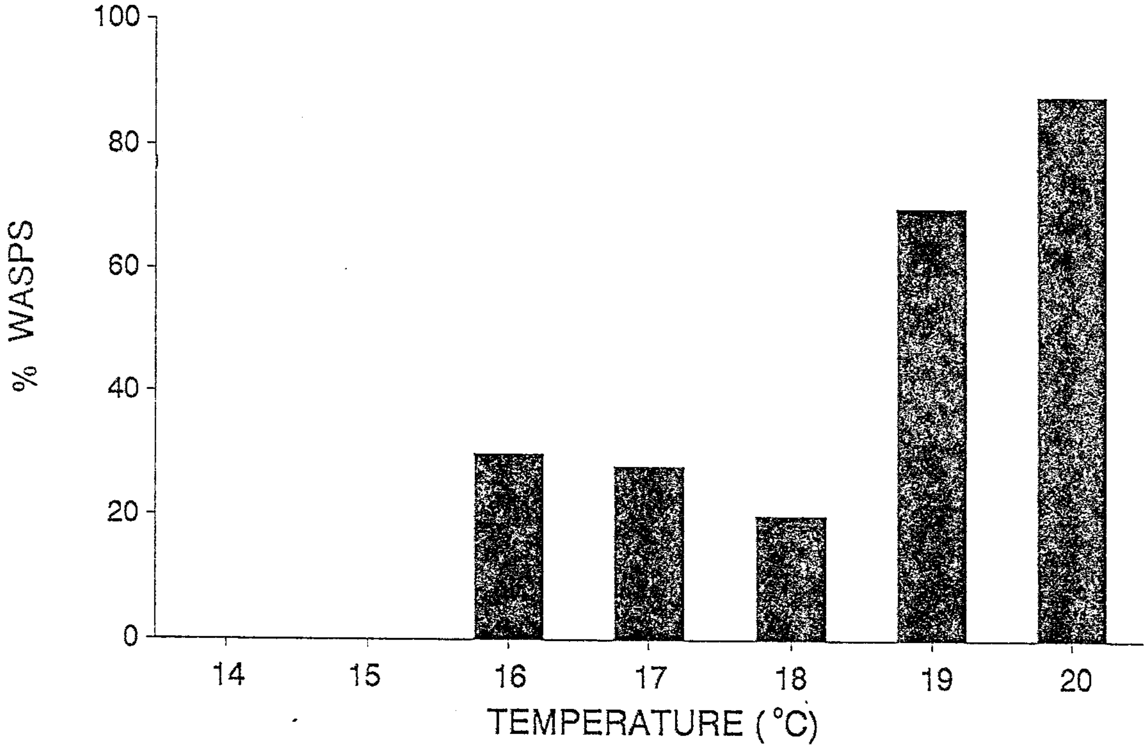

Figure 5. The flight take-off frequencies of *E. baijnathi* females at varying laboratory temperatures.

The wasps trapped on the sticky traps indicated that all the fig wasps associated with the locally occurring *Ficus* species were essentially day flying (see Table 2). In summertime a few wasps were captured on the sticky traps before 06h00. These wasps may have been trapped in those few hours after sunrise before the traps had been replaced.

Table 2. The number of fig wasps trapped on sticky traps positioned in an area where fig trees were growing. The traps were replaced every morning at 06h00 and again in the evenings at 18h00. Monitoring was over three, one week periods in both winter and summer.

Species*	Number of wasps trapped					
	Summer		Winter		Total	
	Day	Night	Day	Night	Day	Night
E. stuckenbergi[1]	20	7	49	0	69	7
P. barbarus[1]	3	0	37	0	40	0
E. baijnathi[2]	11	8	16	0	27	8
C. capensis[3]	1	0	1	0	2	0
A. guieneensis[3]	2	0	3	0	5	0
S. cyclostigma[3]	1	0	2	0	3	0
Otitesella spp.[1,2]	2	0	23	0	25	0
Sycoryctes sp.[1,2,3]	2	3	16	0	18	3
Philotrypesis sp.[1,2]	3	0	8	0	11	0
Total	45	18	155	0	200	18

* The fig wasps species are normally associated with the following *Ficus* [1]*F. thonningii* Bl. [2]*F. burtt-davyi* Hutch. and [3]*F. sur* Forssk.

Few *E. baijnathi* were recorded arriving at the receptive figs after midday and the majority of the wasps (84%) arrived at the receptive trees between 06h00 and 12h00 (Table 3). These arrivals corresponded with the times when the wasps left their natal figs (Table 1).

Table 3. The number of pollinating fig wasps (*E. baijnathi*) on bagged receptive figs of a single *F. burtt-davyi* tree. The wasps were removed after being counted.

Date	Percentage of wasps caught					Number caught
	06h00	09h00	12h00	15h00	18h00	
24/12/89	1	42	37	17	3	267
26/12/89	6	79	12	3	0	180
28/12/89	6	61	20	10	4	71
Total	3	58	26	11	2	518

Fig Wasp Behaviour

Shortly after the female *E. baijnathi* emerged from the figs, they positioned their wings above their body and, after flaring their antennae, took off near vertically. They were then carried away from the trees by the wind and were lost from sight. Fig wasps arriving at branches bearing receptive figs did not necessarily land on the figs themselves (Table 4). Those not landing on the figs walked along the branches, presumably searching for a suitable fig or flew away. The patrolling appeared to be more directed than their choice of landing site as more visits were made to figs than to leaves (Table 4). Wasps were observed to visit a total of 96 figs but only successfully entered the figs on 17 occasions (Tables 4 and 5).

Table 4. The arrival of the pollinating fig wasp *E. baijnathi* at branches of two receptive *F. burtt-davyi* trees.

Date	Number of wasps	Landing site		Number of times visiting	
		Leaf	Fig	Leaf	Fig
28/12/89	18	9	9	25	58
6/ 1/92	15	11	4	15	38
Total	33	20	13	30	96

E. baijnathi females seldom antennated leaves and this activity was usually reserved for figs (Table 5). Once on a fig, just over 50% of the wasps (17) eventually successfully penetrated an ostiole while some 25% flew off without attempting entry. The remaining individuals attempted to enter a fig but aborted their efforts and either continued searching on the same tree or flew away. For those wasps that were observed to enter the figs the time taken from landing (n = 32) to entry averaged 115.6 seconds (s.d. = 73.0, n = 17; Table 5). Because of difficulties following flying insects it is not clear how many such searching periods individual females had to make. The time taken for the wasps to disappear into a fig once they had started entry averaged 84.12 seconds; s. d. = 36.09, n = 17; Table 5).

Table 5. Pollinator fig wasp (*E. baijnathi*) searching behaviour for suitable figs of *F. burtt-davyi* in which to oviposit.

Date	Number of wasps	Antennate			Penetrate ostiole[1]		
		None made	Leaf	Fig	None made	Successful	Failed
28/12/89	18	4	1	13	7	7	5
6/ 1/92	15	4	1	10	2	10	4
Total	33	8	2	23	9	17	9

[1] May abort attempt to enter the ostiole of one fig and successfully penetrate another.

Whether wasps discriminate against receptive figs that have already been entered by others was also examined. The number of foundresses entering figs was found to be more regular than expected from a random (Poisson) distribution with more figs having a single foundress then expected ($\text{Chi}^2_{[3]} = 67.67$; $P < 0.001$) (Figure 6).

Figure 6. The numbers of *E. baijnathi* foundresses that entered figs of *F. burtt-davyi*. The circles represent a Poisson (random) distribution.

DISCUSSION

The timing of emergence of adult fig wasps from their figs is initially determined by the males, which chew the exit holes that allow the females to escape. In the case of *E. baijnathi*, exit holes were mainly produced during the mornings, with temperature apparently influencing the precise timing of their production. Fig wasps are typically less than 2 mm in length, and with their slow flight have no directional control above wind speeds of around 30 cm/sec (Ware and Compton, submitted). Wind speeds are relatively low during the mornings and the timing of wasp emergence coincides with a time when conditions for flight by the females are improved and may be an adaptation to avoid the increasingly high windspeeds that develop as the day progresses.

Under laboratory conditions the females will only fly at ambient temperatures above 15°C. This compares with recorded threshold temperatures for aphid flight of between 12.8 and 15.5°C (Robert, 1987). Fig wasps in the field were nonetheless recorded flying below 15°C, probably due to the influence of solar radiation, which would heat the small black bodies of the females by a few degrees during the short pre-flight period when they are on the surface of the figs (Lewis and Taylor, 1964).

Given that *E. baijnathi* generally leave their natal figs during the morning, and that arrivals at receptive trees also occur at this time, it appears that most of the wasps arriving at receptive trees had emerged locally. Alternatively, conditions may inhibit the wasps from flying in the afternoons. Their dispersal ability is, however, limited by their short life span of some 2-3 days (Compton *et al.*, in press) and such deliberate prolongation of exposure to the elements seems unlikely.

Most southern African fig wasps, like *E. baijnathi*, are dark and are likely to be diurnally active. Others, such as *Allotriozoon heterandromorphum* Grandi, from *F. lutea* Vahl (Newton and Lomo, 1979; Ware and Compton, 1992a), *Alfonsiella* species (Compton, unpublished) and *Ceratosolen arabicus* Mayr, from *F. sycomorus* L. (Galil and Eisikowitch, 1968; Compton *et al.*, 1991), fly at night and have been collected at light traps (Ware and Compton, unpublished; H.G. Robertson, pers. comm.). These wasps all display 'ophionid' features such as yellow coloration and large eyes, that are typical of many night-flying insects (Huddleston and Gould, 1988).

The maximum extent to which *E. baijnathi*, or any other fig wasps, can migrate is unknown, but fig wasps recorded on Anak Krakatoa in 1984 must have flown from neighbouring islands more than 2 km away (Compton *et al.*, 1988). Even more impressive are the records of *Allotriozoon heterandromorphum* Grandi in figs of an isolated *F. lutea* Vahl tree whose nearest known conspecific was 80 km away (Compton, 1989; Ware and Compton, 1992a).

The observed flaring of the antennal sensilla when *E. baijnathi* females are about to takeoff from their natal figs appears to be an ability that is limited to the few species of Agaoninae that have Type IV sensilla arrangements (Ware and Compton, 1992b). Host finding may be aided if the multiporous plate sensilla on the antennae remained flared in flight because this results in a greater volume of air being sampled (Kaissling, 1971).

Once receptive trees had been detected, and females had landed, they generally antennated the figs and not the leaves. Similarly *E. baijnathi* is not stimulated into antennating figs of other species (Ware and Compton, 1992a), which suggests that recognition of the substrate occurs before antennal contact chemoreceptors are employed. This initial recognition of receptive figs could involve non-contact chemoreceptors on their antennae or tarsal contact chemoreceptors. Alternatively, *E. baijnathi* may react to the shape of *F. burtt-davyi* figs and begin antennating once the correct curvature has been detected. Visual cues have also been shown to be important in habitat location by some hymenopteran parasitoids (McAuslane *et al.*, 1991; Drost and Carde, 1992).

Ramirez (1986) found that the number of foundress pollinators in the figs of *F. citrifolia* did not differ from a random (Poisson) distribution. However, the figs he used were saturated (all figs contained foundresses) and fig wasps may be 'forced' to enter figs already containing foundresses if they cannot find any uninhabited figs. This lack of a choice of foundress free figs was avoided in our studies, which found that the distribution of foundress females inside the figs of *E. baijnathi* was overdispersed. This could imply that the wasps are able to determine whether figs have been previously entered and avoid them. Collections of naturally pollinated figs have often shown that the majority of figs receive only one pollinator (Compton and Nefdt, 1990; Ramirez, 1986) suggesting that this result was not a consequence of high densities of wasps vieing for entry in our experiment. Such avoidance of figs which already contain foundresses would improve the reproductive success of *E. baijnathi* females, through the avoidance of competition for oviposition sites, and would also influence their progeny sex ratios, which become less female biased when two or more females share a fig (Nefdt, 1989).

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DISPERSAL OF ADULT FEMALE FIG WASPS.

II. MOVEMENTS BETWEEN TREES

A.B. Ware and S.G. Compton

ABSTRACT

Fig wasps (Chalcidoidea, Agaonidae, Agaoninae) are the exclusive pollinators of fig trees (*Ficus* spp., Moraceae). Fig development on the African fig tree, *F. burtt-davyi*, is normally synchronised on individual trees, but not between trees. Consequently the females of each generation of the pollinating species (*Elisabethiella baijnathi*) have to disperse to other trees to find 'receptive' figs which are suitable for oviposition. This paper examines this aspect of fig - fig wasp biology. The flight speed of insects is closely linked to their size and directional flight is difficult for small insects, such as fig wasps, in all but the lightest of wind. We investigated the movements of fig wasps between trees using sticky traps placed around fig trees or near cotton bags containing figs. Away from the trees, the densities of flying wasps at different heights was also determined. When the wasps disperse from their natal figs they take-off near-vertically and they are unable to exert directional control once they enter the air column and are subsequently blown downwind. Near receptive host trees the wasps lose height and then fly upwind at speeds of around 25 cm/sec.

INTRODUCTION

Flight speed in insects is closely linked to their size with smaller insects flying more slowly than larger insects (Lewis and Taylor, 1974). Directional flight for small insects will usually be problematic in all but the lightest of winds, as they have no control over where they are carried. Small species can nonetheless achieve directional control by flying close to vegetation or to the ground, where there is a 'boundary zone' of relatively slow moving air produced by frictional drag (Taylor, 1958).

Pollinating fig wasps (Hymenoptera, Chalcidoidea, Agaonidae, Agaoninae *sensu* Boucek, 1988) are small insects, usually between 1 and 3 mm in length, that are intimately associated with fig trees (*Ficus* spp., Moraceae). Each *Ficus* species is generally pollinated by one particular wasp species, which occurs on no other Ficus species (Wiebes, 1979; Wiebes and Compton, 1990). Fig trees are unusual in that their flowers are contained within an urn-shaped inflorescence - the fig. Pollinator access to the flowers is limited to the 'female' phase of fig development, which is also the period when the flowers are receptive to pollination (Galil, 1977). The female pollinating wasps penetrate the fig through a narrow bract-lined entrance, the ostiole, and in the process usually lose their wings and part of their antennae. Once having entered the fig, they are unable to leave. After pollination the ostiole closes (Verkerke, 1989) and the larvae develop inside ovules galled by the females.

In most *Ficus* species, fig development on any one tree is synchronised, which forces the female fig wasps to leave their natal trees in order to find figs at the correct stage of development for oviposition (Bronstein, 1989). As a consequence of the asynchronous fruiting, the often low densities of conspecifics (Wharton *et al.*, 1980; Gautier-Hion and Michaloud, 1989) and the small proportion of figs which are suitable, the short-lived wasps (Kjellberg *et al.*, 1988; Compton *et al.*, in press.) often have to fly long distances to find them. The pollinating fig wasps detect figs that are suitable for oviposition using species-specific volatile attractants that are released from receptive figs when they are ready for pollination (van Noort *et al.*, 1989; Ware *et al.*, in press; Ware and Compton, in prep).

The ability of the pollinators to find their hosts is impressive. Even when fig trees are isolated from their conspecifics, such as those planted outside their natural distribution range (Compton, 1990; Ware and Compton, 1992) or on islands previously sterilised by volcanic activity and now separated by expanses of water (Compton *et al.*, 1988), at least small numbers of pollinating wasps find them.

Non-pollinating fig wasps (belonging mainly to the Agaonidae, but in subfamilies other than the Agaoninae) may either gall the ovules like the pollinators or may parasitise the gall formers. Some of these wasp species are also *Ficus* species-specific (Ulenberg, 1985; van Noort, 1992). Those non-pollinating wasps that enter the figs to lay their eggs at the same time as the pollinators may utilise the same volatile cues as the pollinators to find the figs while those ovipositing from the outside at a later stage probably use other cues (Compton, in press).

In a previous paper (Ware and Compton, submitted) we investigated the effects of ambient temperature on the timing of wasp emergence from their natal figs, as well as their behaviour when the pollinators leave their natal figs and arrive at a suitable host tree. Here we describe the patterns of dispersal of certain African fig wasps from their natal trees, within the general air column and as they approach trees with receptive figs. Their flight speeds and the effects of wind direction on their movements is also described.

MATERIALS AND METHODS

The Study Site

Field studies were undertaken in the 1820 Settlers Botanical Garden, Grahamstown, South Africa during 1989. A large number of shrub-like *F. burtt-davyi* Hutch. grow there as rock climbers on the steeper N-E facing slopes of Gun Fire Hill. Two other indigenous *Ficus* species, *F. thonningii* Bl. and *F. sur* Forssk., also grow in the gardens. The pollinators of these three Ficus species are *Elisabethiella baijnathi* Wiebes, *E. stuckenbergi* Grandi and *Ceratosolen capensis* Grandi respectively. The development of figs in both *F. burtt-davyi* and *F. thonningii* crops are well synchronised on individual trees but not between the trees, and this prevents the wasp populations from cycling on the same trees (Compton *et al.*, in press). This is not the case with *F. sur*, whose crops often contain figs at all stages of development (Baijnathi and Ramcharun, 1983; Compton *et al.*, in press).

Wasp Aerial Densities

A single vertical black pole, 20 cm in diameter and 460 cm in length, was placed vertically amongst the *F. burtt-davyi* trees about 20 m from the nearest fig tree. A continuous series of sticky traps, consisting of nine cellulose transparencies sprayed with pruning sealant (Frank Fehr, Durban) were placed along the length of the pole. The traps were 60 cm in length except for those at the bottom and top of the pole, which were 20 cm long. The traps were exposed over six non-consecutive weekly periods in February, March, July and August.

A "snap-shot" of wind speed variation with height at the site of the pole was obtained by measuring wind speeds at nine different heights (between 0.1 and 4.5 m above ground level), using a hand-held Casella low speed air meter. Wind speed estimates were obtained on 10 different days between 12h00 and 15h00. Based on these results the average wind profile for the site was produced. This information, together with the numbers of wasps trapped at the site, was used to estimate the relative aerial densities of fig wasps in the area.

Fig Wasp Flight Speeds

We estimated the flight speeds of three wasp species reared from *F. burtt-davyi*. These were *E. baijnathi* and two non-pollinating species, *Philotrypesis* sp. and *Sycoryctes* (= *Sycoscapter sensu* Boucek, 1988) sp. In preliminary experiments it was established that the wasps preferred to fly upwards rather than horizontally on take-off, and flight speed estimates were for near-vertical flight. Newly emerged individuals were placed into a box (115 cm high X 22 cm long X 22 cm deep) with the top and one length composed of transparent sheets. The box was placed under an incandescent lamp in a room maintained at 25°C. Using a stop watch, the flight speeds of ten individuals of each species were measured over a distance of 1 m from take off from the base of the box.

Flight Direction

The direction from which fig wasps flew to traps baited with receptive figs was examined using single sticky traps place on poles at a height of 1.2 m, below to cotton bags containing receptive figs. As insufficient pollinators of *F. burtt-davyi* were available we used figs of *F. thonningii*. The trial, with three replicate traps, was initiated at 07h00 and terminated 5 hours later. After noting the general wind direction, the sticky traps were removed, divided into 10 equal vertical sections and the number of wasps trapped in each section was recorded. Wind speeds were also monitored at irregular intervals during this period.

Dispersal from Natal Trees and Arrival at Trees Bearing Figs Ready for Pollination

The movements of fig wasps leaving their natal trees and arriving at receptive trees were investigated using arrays of sticky traps. Poles (each supporting three sticky traps (30 X 21 cm) placed at 0.5, 1 and 2 m above ground level) were placed approximately 4 m from the *F. burtt-davyi* trees. When the topography allowed, eight poles were placed equidistantly about the tree, but where this was not possible certain poles were omitted. The traps were replaced daily, when the numbers and identities of the wasps trapped were recorded. Prevailing daily wind directions were also noted. The temperature during the observation periods ranged between 25 and 27°C.

RESULTS

Wasp Aerial Densities

Although there was considerable variation in wind speeds between days, the pattern of increasing wind speed with height was consistent and ranged from near zero velocity at 0.1 m from the ground up to an average of nearly 10 km/hr at a height of 4.5 meters (Figure 1). This information, together with the numbers of wasps trapped at each height on the vertical pole, allowed wasp density profiles to be estimated. No fig wasps were trapped below 0.1 m. Between this level and 1.7 m, the average density of fig wasps (all species) increased. Wasp densities then plateaued out until 4.5 m, after which they increased markedly (Figure 2). Among the three commonly trapped wasp species, the same trend was evident for the two species of pollinating wasp. However, the density of the non-pollinating wasp, *Phagoblastus barbarus* Grandi (which is associated with *F. thonningii*), remained relatively constant over the range of heights examined (Figure 3). Based on the average wind speeds experienced in the area, the wasp densities (all species) varied in the ratio of approximately 1: 2: 4 at heights of 0.5, 1, and 2 m respectfully.

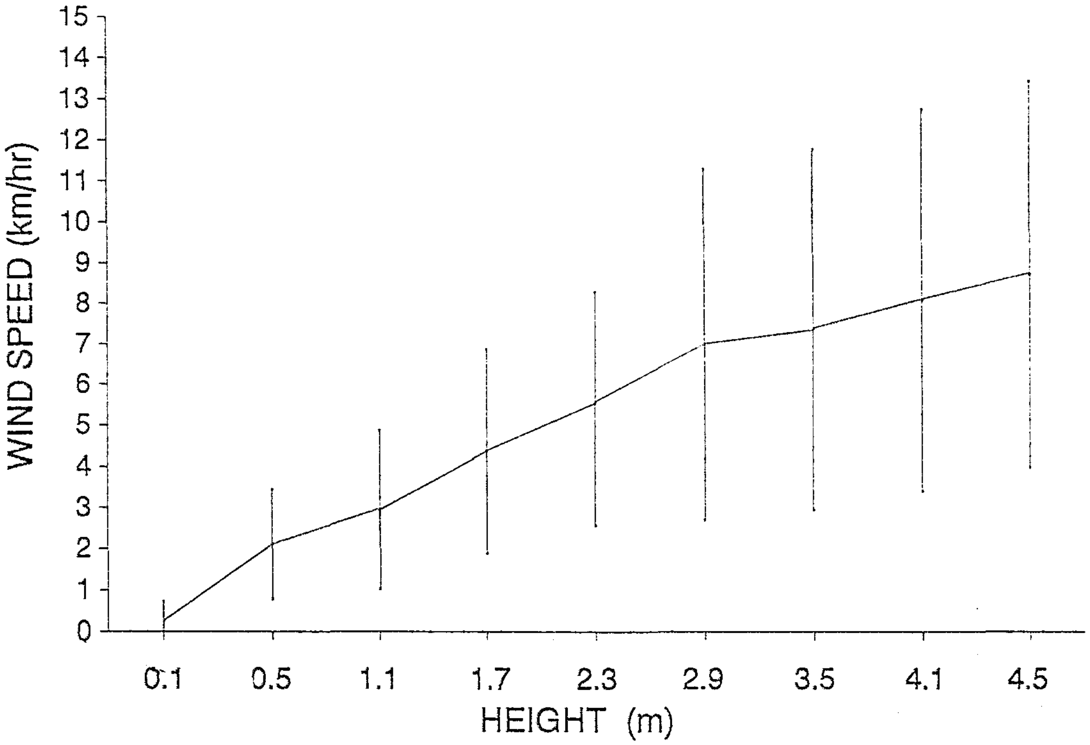

Figure 1. The wind profile at various heights above ground at a site in the 1820 Settlers Botanical Gardens, Grahamstown, South Africa averaged from 10 occasions throughout the year (1 km/hr = 27.8 cm/sec). The large standard deviations are indicative of the large variation in wind speeds experienced in the area.

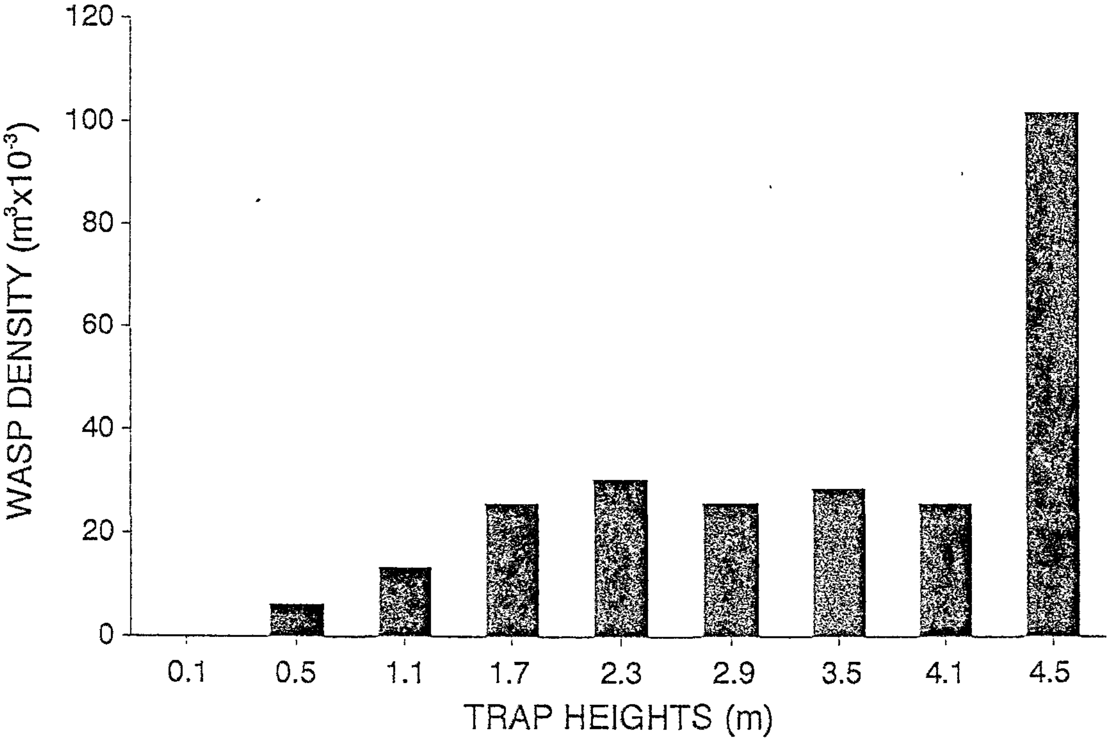

Figure 2. Densities of total fig wasps at different heights in the 1820 Settlers Botanical Gardens.

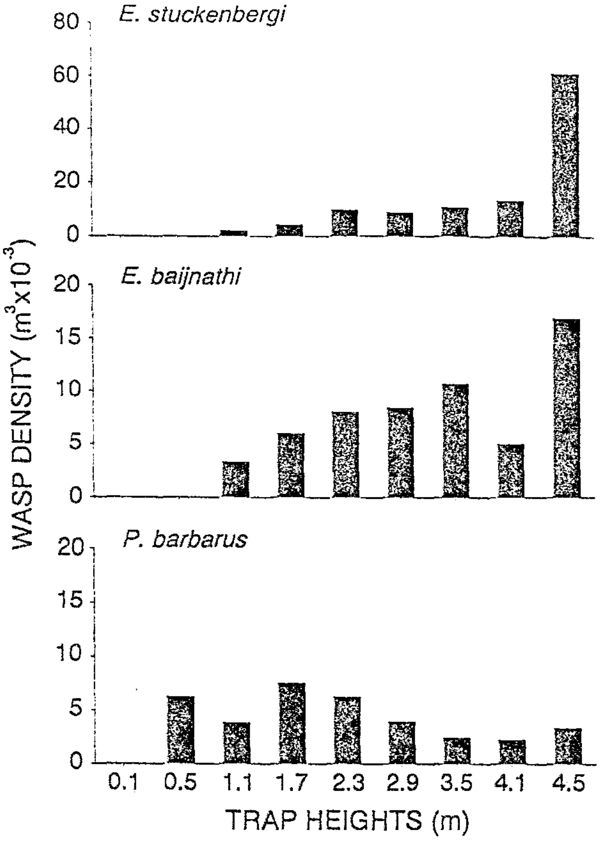

Figure 3. Densities of three fig wasp species at different heights in the 1820 Settlers Botanical Garden in Grahamstown.

Flights Speeds

In the laboratory the estimated flight speeds of the three wasp species ranged between 11 and 37 cm/sec (equivalent to 0.4 and 1.3 km/hr respectfully) (Table 1). This means that, based on the average wind speeds (Figure 1), the wasps would have to fly at heights of less than 0.3 m above ground level if they were to be able to maintain directional control (Figure 1). Under the windiest conditions recorded they would have to fly at less than 0.15 m above the ground.

Table 1. Fig wasp flight speeds measured at 25°C over a distance of 1 m.

SPECIES	n	FLIGHT SPEEDS (cm/sec) MEAN	FLIGHT SPEEDS (cm/sec) RANGE
Elisabethiella baijnathi	10	27.06	19.86 - 37.04
Philotrypesis sp.	10	20.67	11.00 - 34.38
Sycoryctes sp.	10	21.30	16.57 - 27.78

Wasp Dispersal from Natal Trees

Wasps leaving their natal trees flew mainly downwind (Table 2). Because of the rocky terrain and cliff faces in the 1820 Settlers Botanical Garden, it was rarely possible to place a full complement of traps around each tree. However, all eight trap poles were positioned around one tree, allowing the movements of the wasps to be assessed in detail (Figure 4). Only 2% of the wasps recorded at this tree were trapped upwind. Using the Rayleigh Test (Baschelet, 1981), which determines whether there is evidence for bias in any given direction, it was found that the wasps moved in a mean preferred direction of 11° from the recorded direction of the wind (mean angular deviation = 21°; $Z = 1438$; $P < 0.001$).

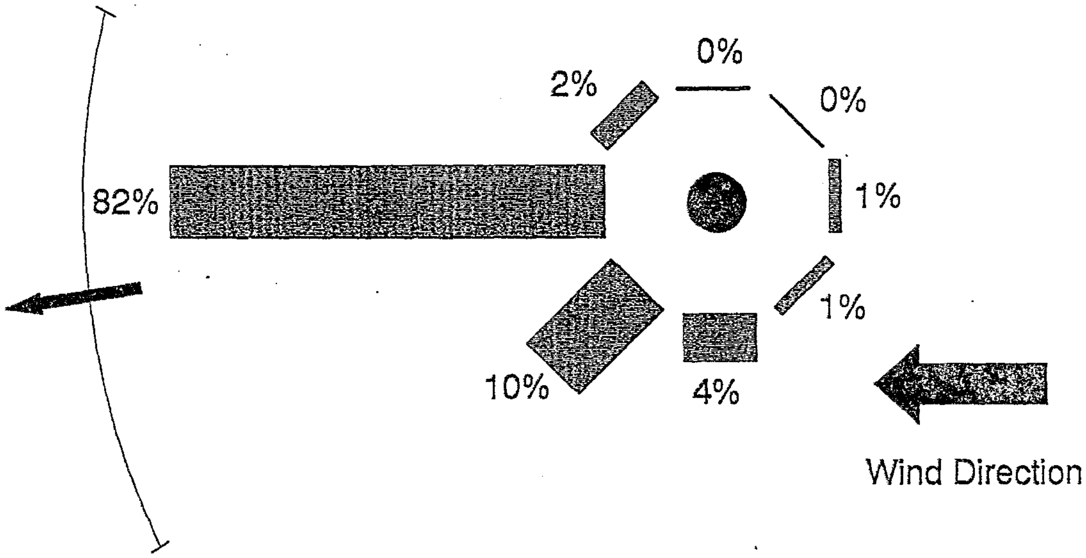

Figure 4. The relative percentages of emigrating *E. baijnathi* trapped around a wasp producing *F. burtt-davyi* tree relative to the prevailing wind direction. The small arrow indicates the mean preferred angle of wasp distribution and is flanked by an arc indicating the mean angular variation (21°).

Wasp Arrivals at Receptive Trees

E. stuckenbergi females were observed to retain directed flight when flying near bagged figs provided wind speeds were low. No wasps were observed flying once wind speeds had increased to beyond 100 cm/sec. Unfortunately their small size did not permit behavioural observations if the wasps were further than about 50 cm from the bags. *E. stuckenbergi* flying near the receptive figs displayed a casting behaviour (a swaying flight 10 -20 cm from the bags) before flying towards the bagged figs.

Significantly more wasps were trapped on the leeward side of the traps (Table 3) indicating the upwind movement of the wasps towards the bagged receptive figs. In the more natural situation, wasps were again trapped downwind of *F. burtt-davyi* trees bearing receptive figs (Figure 6).

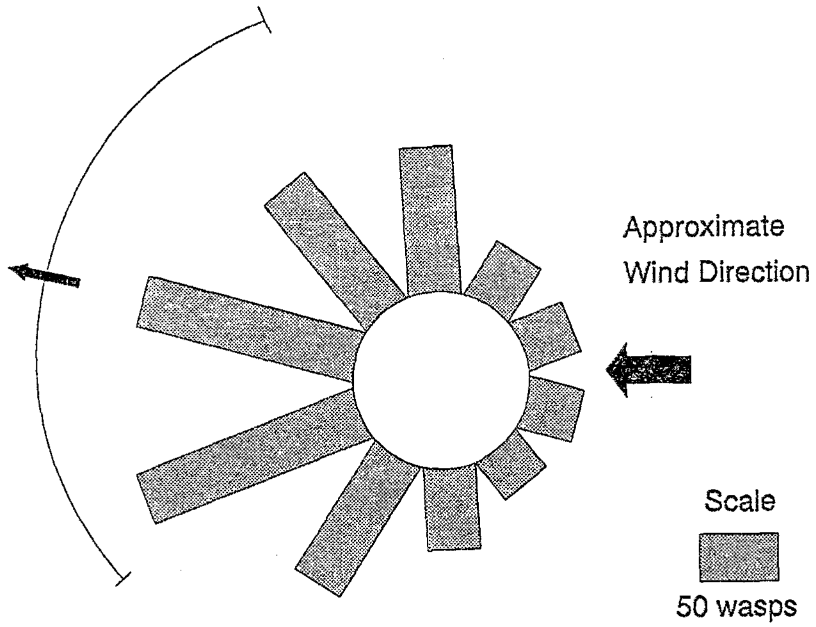

Figure 5. Numbers of *E. stuckenbergi* recorded at sticky traps baited with receptive *F. thonningii* figs. The mean preferred direction is indicated with a small arrow which is flanked by an arc representing the mean angular variation.

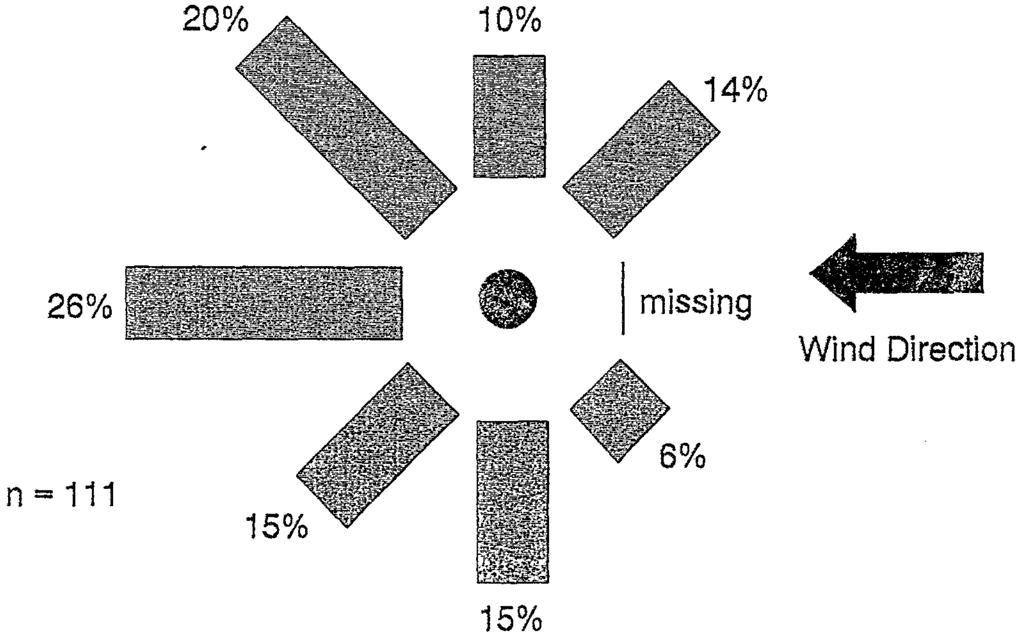

Figure 6. The percentages of *E. baijnathi* trapped around a receptive *F. burtt-davyi* tree relative to the prevailing wind direction.

Table 2. Comparisons between the numbers of wasps caught at different heights upwind and downwind on *F. burtt-davyi* trees producing fig wasps and those receptive trees attracting fig wasps. Producer trees have wasps emerging from the figs. Receptive trees have figs that are ready to be pollinated.

TREE #	HEIGHT	TRAP DAYS	TRAPS PLACED		WASPS TRAPPED AT DIFFERENT HEIGHTS UPWIND			DOWNWIND			$\text{CHI}^2_{(2)}$	*P*
			UPWIND	DOWNWIND	0.5m	1m	2m	0.5 m	1m	2m		
PRODUCER TREES												
13	0.7	6	15	17	0	1	5	71	205	182	24.78	***
23	2.0	2	4	6	0	1	1	0	5	9	13.87	***
27	1.0	3	8	7	3	4	3	13	18	9	3.87	ns
TOTAL		11	12	27	3	6	9	85	228	200	253.62	***
RECEPTIVE TREES												
34	2.5	7	15	15	28	55	33	58	121	50	32.93	***
12	0.5	4	10	12	5	3	12	29	9	26	21.01	***
13	0.7	3	9	6	1	9	10	4	6	7	4.74	ns
99	1.8	2	6	4	5	12	16	2	32	18	31.10	***
36	2.3	2	5	5	2	5	2	15	8	4	0.09	ns
TOTAL		17	45	43	41	84	73	108	176	105	45.03	***

ns = not significant; *** = $P < 0.001$

Wasp Densities in Relation to Trap Heights

More wasps were caught downwind than upwind, although the proportion caught downwind were much higher around producer trees (30:1) than receptive tree (3:1) (Table 2; Figure 7). The high densities of wasps trapped around wasp producing trees were a result of the synchrony of tree fruiting which resulted in large numbers of wasps being trapped over short periods. Wasps leaving their natal figs were blown downwind and most impacted on the nearby traps before gaining height (Table 2; Figure 6).

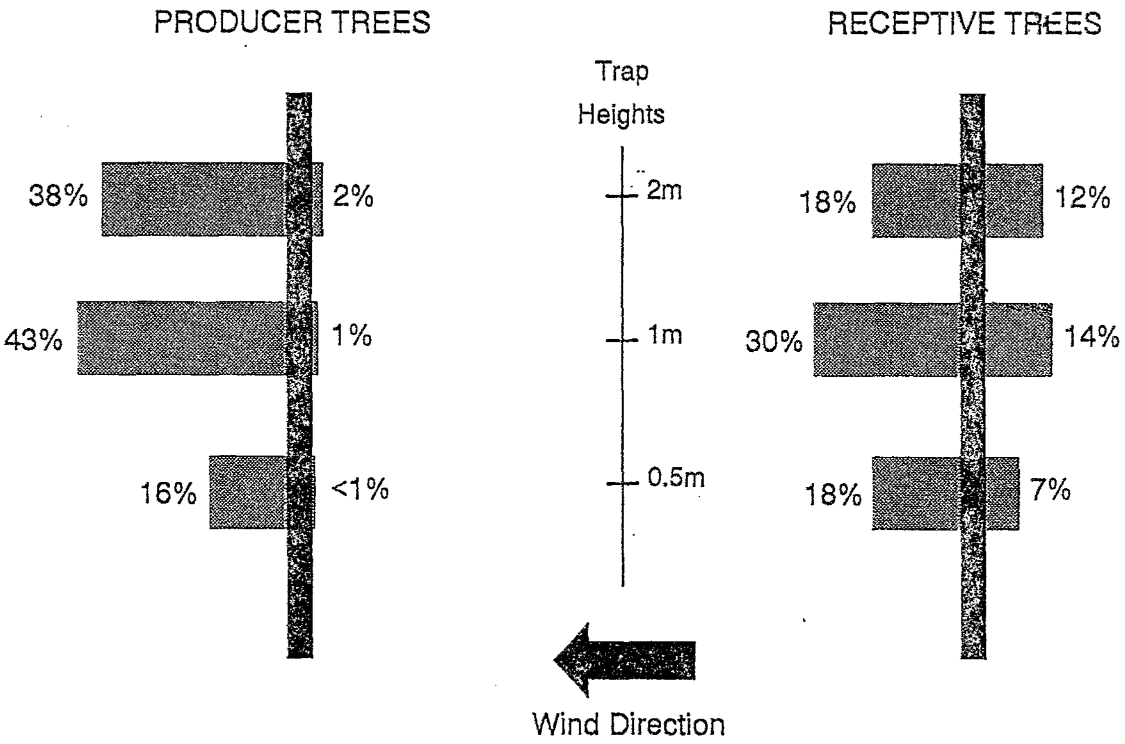

Figure 7. The percentages of *E. baijnathi* trapped on all sticky traps positioned at 0.5, 1 and 2 m above ground level surrounding producer and receptive *F. burtt-davyi* trees relative to the prevailing wind directions.

The densities of wasps at different heights around the trees was expected to be similar to those recorded away from the trees, unless the wasps had modified their behaviour. Upwind, wasp densities were generally as predicted with most wasps collected on the more elevated traps (no significant deviations were recorded around four of the five traps (Table 3; $P > 0.05$). Therefore, when upwind of the trees, the wasps did not modify their flying heights. In contrast, far more wasps than expected were captured

Table 3. Pollinating fig wasps (*E. stuckenbergi*) trapped at sticky traps near cotton bags containing receptive figs of *F. thonningii*. The direction from where the wind was blowing was used as the reference point (0°) for the circular statistical analysis.

TRAP #	NUMBER OF WASPS TRAPPED	WASPS TRAPPED (%)		MEAN PREFERRED DIRECTION	MEAN ANGULAR DEVIATION	RAYLEIGH TEST	
		UPWIND	DOWNWIND			Z	P
1	151	34	66	174°37′	65°41′	17.76	***
2	176	30	70	165°01′	59°32′	37.07	***
3	675	22	78	174°38′	55°39′	182.52	***

*** = $P < 0.001$

downwind of receptive trees on traps that were closest to the ground. The total number of pollinators trapped at sticky traps placed at 0.5 m was equal to those trapped at the 2 m traps; some 4 times higher than would have been expected. Similarly, the 1 m trap had more than 1.5 times a many wasps as the 2 m trap whereas the density of wasps expected at this height should have been half as many as the number trapped at 2 m (Table 3; Figure 7). These findings were significantly different from the generally expected wasp densities of the area (Chi$^2_2$ = 149.2; $P < 0.001$). Together with the increased number of wasps trapped downwind these results suggest that wasps downwind of receptive trees alter their general flight behaviour by losing height and flying upwind.

Relatively large numbers of *E. stuckenbergi* were trapped along with *E. baijnathi* at two of the receptive *F. burtt-davyi* trees. This allowed us to examine whether there was some inherent component of the trees which resulted in the large numbers of *E. baijnathi* trapped low down on the leeward side of trees bearing receptive figs independent of specific fig wasp behaviour. There were no differences in the heights that the two species of wasps were trapped upwind. However, there were significant differences in the heights that *E. baijnathi* were trapped downwind and those of *E. stuckenbergi* trapped either upwind or downwind (Table 4). This was because the number of *E. stuckenbergi* trapped at 0.5, 1 and 2 m did not differ significantly from the expected wasp densities for the area (ratio 1:2:4) (Chi$^2_{[2]}$: upwind = 3.46; $P > 0.5$; downwind = 0.138; $P > 0.05$). More *E. stuckenbergi* were trapped upwind (30 wasps) than downwind (24 wasps) of the two experimental trees.

Table 4. Comparison of numbers of two species of wasp trapped upwind and downwind of two receptive trees of *F. burtt-davyi*. The respective numbers of wasps trapped at 2m, 1m and 0.5m are given in parenthesis.

		E. baijnathi			
		UPWIND (22:12:6)		DOWNWIND (33:15:33)	
		Chi$^2_{[2]}$	*P*	Chi$^2_{[2]}$	*P*
E. stuckenbergi	UPWIND (22:18:1)	4.79	ns	21.65	***
	DOWNWIND (13:7:4)	0.92	ns	18.02	***

ns = not significant; *** = $P < 0.001$

DISCUSSION

Wind, Wasp Densities and Flight Speeds

As expected (Taylor, 1960), wind speeds at the study site were consistently lowest near ground level and increased with height. In unobstructed sites, Taylor (1960) showed that densities of small flying insect decreased with height. This was not the case at our botanical gardens site, where the wasp densities were relatively stable in the air column up to 4.5 m. This may reflect the vegetation and topography of the site, as bushes in the vicinity of our trapping pole were approximately 2 m high.

Flight speeds in insects are closely related to their body size (Lewis and Taylor, 1974) with smaller insects flying more slowly. Previous studies have shown that the vertical flight speed for the greenbug, *Schizaphis graminum* (Rondani), ranges from 22-67 cm/sec (Halgren, 1970) while that of another aphid, *Aphis fabrae* Scopoli is between 20 and 30 cm/sec (Kennedy and Booth, 1963). These species are of comparable size to the fig wasps studied here, and their flight speeds are similar.

When the wasp's flight speeds are related to the wind speeds recorded at the study site, it is apparent that the boundary layer for fig wasps, where controlled flight is possible, is normally less than 0.5 m above ground level. The wasps therefore, have to fly close to vegetation or the ground if they are to actively reach a host tree.

Dispersal from Natal Trees

Wasps leaving their natal trees initially fly upwards and are then taken downwind by the prevailing air currents. In the laboratory, fig wasps are strongly attracted to light and, as with nitidulids (Blackmer and Phelan, 1991) and migrating aphids (Kennedy and Booth, 1963; Kennedy and Ludlow; 1974, Robert, 1987), their initial vertical flight behaviour in the field may be phototactic. After this initial upward movement, directional control would be lost once the insect entered the air column if the air was not too unstable the wasps could, nonetheless to some extent, control their flight height. As wind speeds normally increase with height above ground level, the higher the wasps fly at this time the further they are likely to disperse within any given time period. Given that the pollinating wasps are short-lived and that receptive trees may be some distance away, this rapid dispersal from their natal trees may be necessary in order to allow a chance for subsequent location of a suitable host plant.

Arrivals at Receptive Trees

Figs that are ready to be pollinated release volatiles that are attractive to flying wasps (van Noort *et al.*, 1989; Ware *et al.*, in press; Ware and Compton, in prep.). Wasps utilising these volatiles will necessarily detect them downwind of the trees and then need to fly towards the source of emission. The nature of odour plumes and how insects use them to find their source has recently been reviewed by Murlis *et al.* (1992). The observed casting (or zigzagging) anemotactic response of fig wasps when close to receptive figs is similar to that of other insects tracking upwind in search of their hosts (Willis *et al.*, 1991; Nottingham and Croaker, 1987; Charlton and Carde, 1990). The increased numbers of *E. baijnathi* trapped close to the ground when downwind of the receptive *F. burtt-davyi* trees and the different heights that *E. stuckenbergi* and *E. baijnathi* were trapped as they arrived implies that *E. baijnathi* alone was responding to the volatile attractants by dropping out of the air column and then moving at low heights upwind.

Compton and Robertson (in prep.) estimated that 95% of adult female *E. baijnathi* produced in the 1820 Settlers Botanical Garden failed to find a receptive fig in which to oviposit. The short adult life span of the adult fig wasps, predation and environmental effects such as dehydration, will ultimately limit the distance that they can travel. Nevertheless, despite their small size, fig wasps are remarkedly efficient colonisers of their host trees. Given the mutualistic relationship between the fig trees and their pollinating wasps, it is reasonable to speculate that evolutionary pressures have maximised the effectiveness of the volatile attractants emanating from the figs. These studies described here suggest how fig wasps utilise these cues to find their host figs.

These results allow us to produce an hypothesis that describes the way in which *E. baijnathi, in* particular, and perhaps fig wasps in general, manage to travel from fig tree to fig tree. An initial vertical flight ensures that the wasps rapidly enter the air column where they are blown downwind. On perception of host tree volatile attractants the wasps lose height. Once in the boundary layer the wasps use controlled upwind flight to search for the receptive figs releasing the volatiles.

This study complements a previous investigation (Ware and Compton, submitted) where the role temperature played on fig wasp emergence and pre-dispersal fig wasp behaviour were examined. These studies have highlighted the roles that environmental factors play in the dispersal and host finding behaviour of fig wasps.

ACKNOWLEDGEMENTS

We are grateful to Mr J. Cameron for permission to work in the 1820 Settlers Botanical Gardens. John MacLaughlan and Mike Way are thanked for their field assistance. The financial support of Rhodes University and the FRD to ABW is gratefully acknowledged.

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CHAPTER 6

PERCEPTION OF VOLATILES

Paper 8: Preparation of small, delicate insects for scanning electron microscopy. *Proceedings of the Electron Microscopy Society of southern Africa* **19**; 39-40 (A.B. Ware and R.H.M. Cross - 1989).

Paper 9: Repeated evolution of elongate multiporous plate sensilla in female fig wasps (Hyemoptera: Agaonidae: Agaoninae). *Proceedings of the Koninlijke Nederlandse Akademie van Wetenschappen* **95**; 275-292 (A.B. Ware and S.G. Compton - 1992).

Elektronmikroskopievereniging van Suidelike Afrika ONDERSTEPOORT (1989)

PREPARATION OF SMALL, DELICATE INSECTS FOR SCANNING ELECTRON MICROSCOPY

A.B. Ware and R.H.M. Cross

Rhodes University, Grahamstown, South Africa

- Problems likely to be encountered in the preparation of most biological specimens for electron microscopy are minimised by having access to living material at the outset, proceeding to one of a variety of "approved" preparative procedures[1]. Unfortunately this ideal scenario does not always present itself and researchers are often required to make the best of what they have - sometimes material collected decades previously and presented in a variety of "preservatives" of dubious nature and questionable efficiency.

Fig wasps are small (length 3 mm), delicate insects which have presented difficulties in preparation by conventional methods, with collapse of eyes and antennae being commonly encountered problems. Although most conventional solvent-dependent preparative procedures have relied upon aldehyde fixation with ethanol as the principal dehydrating agent, the use of rapid heat-assisted air drying from acetone has been reported[2,3] to be successful in the preparation of fresh and long-term preserved material. Twelve different procedures were used to investigate the effectiveness of the acetone treatments:

A. Cryo treatment of (1) fresh material quench-frozen in sub-cooled nitrogen, gold-coated and viewed on the SEM cryo stage.
B. Critical-point drying from liquid carbon dioxide after glutaraldehyde fixation, ethanol dehydration, amyl acetate transition and gold coating of (2) 20 year-old alcohol-preserved material and (3) fresh material.
C. Acetone treatment followed by accelerated hot air drying and gold coating on: (4) fresh, (5) 48 hour frozen, (6) 48 hour alcohol-preserved, and (7) 20 year old alcohol-preserved wasps.
D. Air-dried (4 days), gold-coated (8) 48 hour frozen and (9) 48 hour alcohol-preserved wasps.
E. Gold coating alone of (10) 48 hour alcohol-preserved, (11) 48 hour frozen and (12) freshly-collected wasps.

Although several of these treatments appear to be quite contrary to the well-established norms of specimen preparation for electron microscopy, they were included for evaluation as they represent some of the common means by which specimens are "preserved" in the field.

CryoSEM gave good preservation of insect form; the major disadvantage of this method being the physical damage caused during the freezing process where appendages were easily lost or broken (fig 1). The other conventional treatment, critical-point drying, was less successful in preventing collapse of eyes and abdominal segments (fig 2). All other treatments showed some collapse of eyes, abdomen and/or antennae with the worst case being (fig 3) when the heat-accelerated acetone vapourization was terminated too early.

Acetone treatments appear to be as effective as critical-point drying in attempting to preserve the natural appearance of long-term alcohol-stored specimens where artefacts arise in all cases during the preparative process. The results of other treatments, while showing some promise for the preparation of long-term preserved material, have been inconsistent and are therefore inconclusive at this stage.

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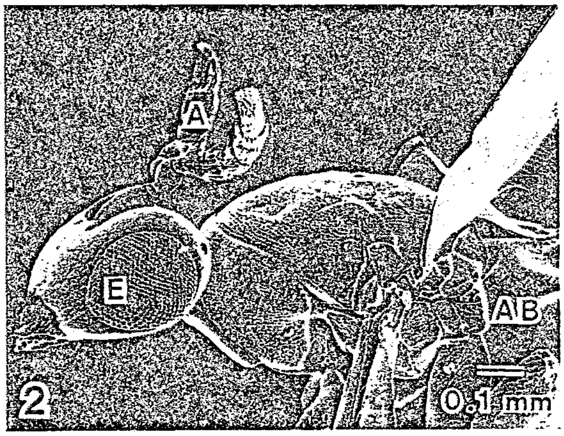

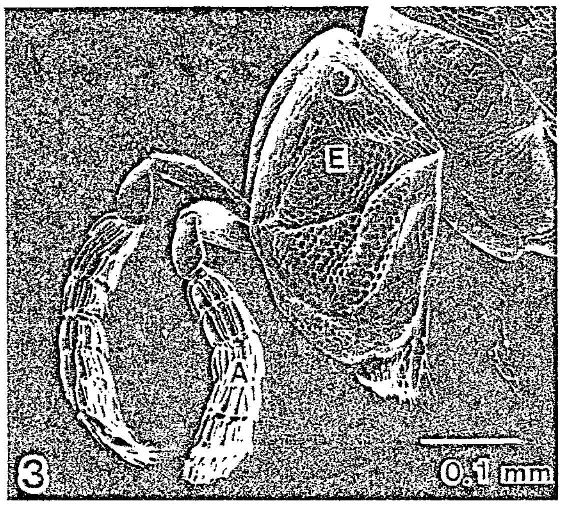

Fig. 1. Fig wasp - cryo (treatment 1) showing loss of appendages (arrowed). x 60

Fig. 2. Fig wasp - critical-point dried (treatment 3) showing some collapse of eye (E), antennae (A) and abdomen (AB). x 66

Fig. 3. Fig wasp - abbreviated acetone treatment of fresh material (treatment 4) showing extensive collapse of eye and antennae. x 125

Proc. Kon. Ned. Akad. v. Wetensch. 95 (2), 275–292 June 22, 1992

Repeated evolution of elongate multiporous plate sensilla in female fig wasps (Hymenoptera: Agaonidae: Agaoninae)

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Communicated by Prof. J.T. Wiebes at the meeting of September 30, 1991

ABSTRACT

Multiporous plate sensilla (MPS) are a characteristic feature of the antennae of chalcids (Hymenoptera, Chalcidoidea). The elongate *sensilla chaetica* form of MPS occurs in the males of many chalcid species, but is rare amongst females other than in fig wasps. Female fig wasps (Agaonidae, Agaoninae) were classified according to the position, shape and size of their MPS. In this group MPS elongation, with its concomitant increased surface area, has apparently evolved independently on at least nine occasions. This repeated evolution may be related to the life history of fig wasps and their mutualism with figs.

INTRODUCTION

Multiporous plate sensilla (MPS), also known as multiporous pitted sensilla (Zacharuk, 1980), thin walled sensilla (Slifer, 1970) or longitudinal sensilla (Bouček, 1988), are a characteristic feature of chalcid (Hymenoptera, Chalcidoidea) antennae (Bouček, 1988). Snodgrass (1925) distinguished two forms of MPS: *sensilla linearia* (= *sensilla placodea*) are plate-like structures attached to the antennal segments over most of their length, while *sensilla chaetica* are hair-like and detached from the antennal segments except at their base. *Sensilla linearia* are almost ubiquitous among female chalcids (Miller, 1972; Weseloh, 1972; Voegelé et al., 1975; Barlin and Vinson, 1981; Dahms, 1984; Wibel et al., 1984) and their possession can be considered as the plesiomorphic condition. *Sensilla chaetica* have a more restricted distribution, but are a feature of many male chalcids and some female fig wasps (Agaonidae).

MPS are considered to have an olfactory function (Zacharuk, 1985) and chalcids are assumed to use them to detect their hosts (Vinson, 1985). *Sensilla chaetica* are typically more elongate than *sensilla linearia.* The functional significance of sensilla elongation and its associated detachment from the antennal surface may be related to an increase in receptor surface area, which in turn should result in improved sensitivity. However, sensilla elongation is not the only way in which increased receptor surface area can be achieved. An alternative is for the number of sensilla to be increased. This requires that the size of the antennae be enlarged through the lengthening, branching or thickening of some of the antennal segments.

The Agaonidae comprises wasps which have an intimate association with fig trees (*Ficus* spp., Moraceae) (Bouček, 1988). The pollinating fig wasps belong to the subfamily Agaoninae and are highly host specific (Michaloud et al., 1985; Wiebes and Compton, 1990). The relationship between trees and agaonines is mutualistic, with the wasps both pollinating the trees and utilising some of the ovules for egg laying (Galil, 1977; Janzen, 1979).

Fruit production on each fig tree is typically highly synchronized. This ensures cross-pollination, but means that females of each wasp generation must seek out new trees before they can oviposit. Because the female wasps are short-lived (Kjellberg et al., 1988) they must locate a suitable tree quickly. The trees are identified through species-specific volatile chemicals released from the figs (Ware and Compton, in prep.). The wasps are only attracted by the volatiles when the figs are 'receptive' and ready to be pollinated (Bronstein, 1987; van Noort et al., 1989). Microscopic examination of fig wasp MPS has confirmed that they are covered in the pores that are typical of olfactory receptors (Ware and Compton, in prep.) and they are likely to be the organs by which female fig wasps perceive their host figs.

This paper examines the MPS of female agaonine fig wasps and has two objectives: to record the presence and arrangement of the *sensilla chaetica* and *sensilla linearia*, and to determine how often elongation of sensilla has evolved within the subfamily. The functional significance of sensilla elongation is discussed in relation to the life history of the wasps.

MATERIALS AND METHODS

Antennae from the females of 25 agaonid species were examined with a dissecting stereomicroscope and a scanning electron microscope (JEOL JSM 84). The presence of either *sensilla linearia* or *sensilla chaetica* was noted, together with their position on the antennal segments. A literature survey was also undertaken to extend these observations to cover all but one of the described genera of Agaoninae.

Preliminary observations showed that, because there was a continuum of sensilla forms, the distinction between *sensilla linearia* and *sensilla chaetica* was not clear-cut. The following criteria were nonetheless adequate to distinguish between them: *sensilla linearia* were plate-like and were usually attached to the antennae over all or most of their length. Where these sensilla extended beyond the apical aspect of the antennal segment they were finger-like. In contrast, *sensilla chaetica* were attached to the antennae at their origins only, with the rest of the structure free and ending in a distinct point. The lengths of both *sensilla linearia* and *sensilla chaetica* were highly variable. For our analysis we defined elongation as having occured if the detached portions of the sensilla were at least 1.5 times the length of the antennal segment to which they were attached.

Sensilla elongation was expected to result in an increase in the total surface area of the MPS. To confirm this we examined the antennae of two congeneric species, one with *sensilla chaetica* and the other with *sensilla linearia*. Based on scanning electron micrographs, estimates of the numbers and average lengths of their sensilla were produced. The exposed surface areas of individual sensilla were then calculated.

Sensilla linearia approximate to cylinders, and we estimated that one third of their surface area was attached to the antennae. Their surface area was therefore calculated as $2/3(2\pi rh + \pi r)$. *Sensilla chaetica* are cone-like with their bases attached to the antennae. Their surface area was therefore calculated using $\pi r \sqrt{r^2 + h^2}$.

RESULTS

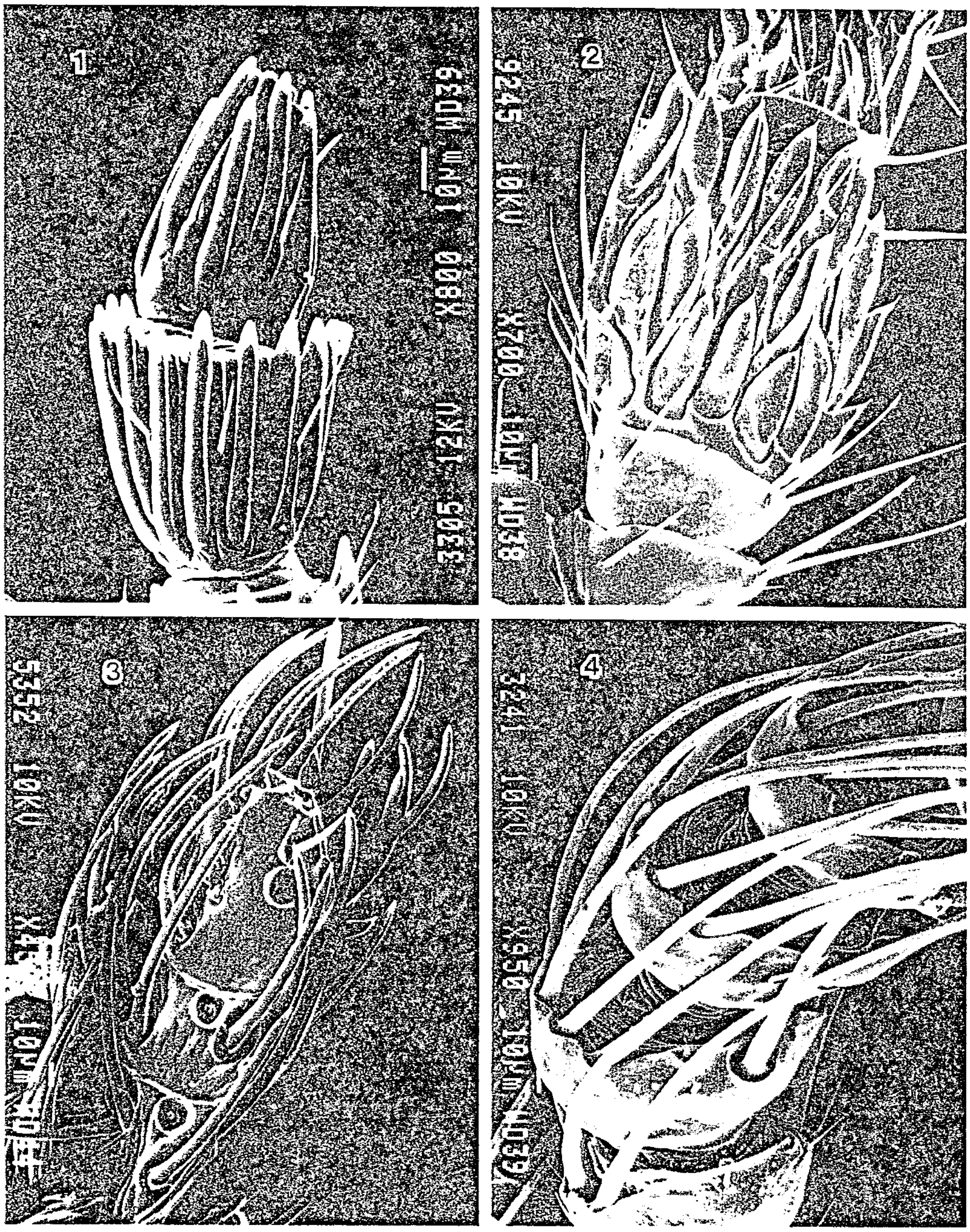
Arrangements of sensilla

MPS were found on the club and funicle segments but never on the anelli, pedicel or scape. The simplest form of MPS arrangement (designated Type I) consisted of a single, although sometimes irregular, whorl of *sensilla linearia* (Figure 1). In a modification of this arrangement, at least one antennal segment had two or more whorls of *sensilla linearia* (Type II; Figure 2). *Sensilla chaetica* also occured in two distinct arrangements. They either originated from the sides of their antennal segment, sometimes from sockets (Type III, Figure 3), or from sockets situated axially (Type IV; Figure 4).

Descriptions obtained from the taxonomic literature were adequate to assign the antennae of 218 agaonine species to one of the four groups outlined above (Table 1). *Sensilla chaetica* were recorded in 22.5% of the species while *sensilla linearia* were found in 76.6%. The remaining two species possessed antennae with both *sensilla linearia* and *sensilla chaetica*. Sensilla elongation was present in 45 species, all of which had *sensilla chaetica* (Appendix 1a).

The Type I arrangement of *sensilla linearia* was recorded in 95 species and Type II in 76 species. In the latter group there was considerable variation in the number of MPS per whorl and the number of whorls per antennal segment. The first funicle segment nonetheless consistently had only a single whorl of MPS, even when the remaining segments had two or more.

A degree of sensilla detachment was noted among some of the species with *sensilla linearia*. This was most pronounced in *Elisabethiella pectinata* (Joseph) (Figure 5), *Platyscapa bergi* Wiebes, *Pegoscapus tomentellae* Wiebes and *Pegoscapus tonduzi* (Grandi). In *Platyscapa quadraticeps* (Mayr) the MPS on



Figs. 1-4. Scanning electron micrographs of agaonid antennal segments illustrating the four types of MPS arrangements. 1. *Elisabethiella stuckenbergi* (Type I), 2. *Allotriozoon heterandromorphum* (Type II), 3. *Courtella armata* (Type III) and 4. *Elisabethiella baijnathi* (Type IV).

Table 1. The distribution of the major antennal sensilla arrangements within the genera of Agaoninae. See the text for description of the types of MPS arrangements.

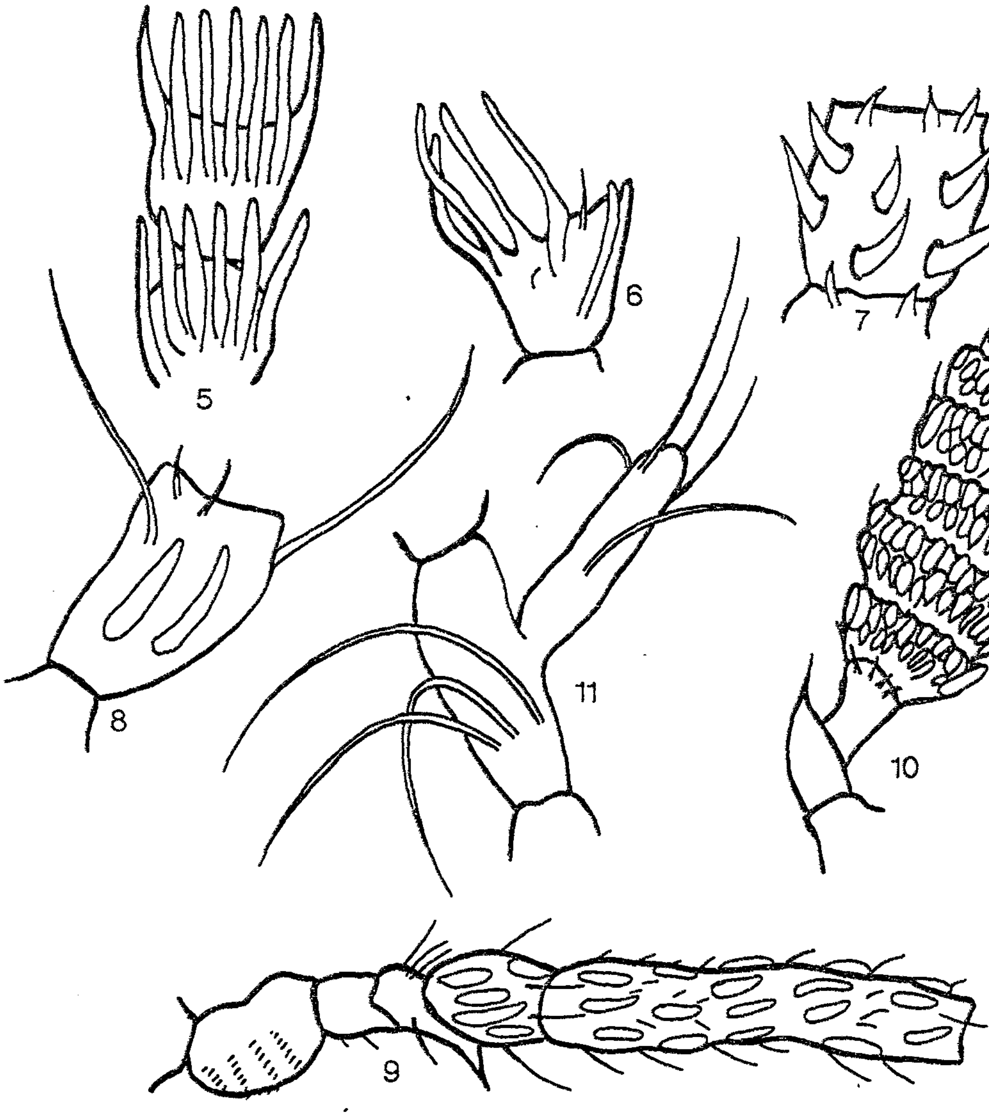
Tribes	Genus	Number of species examined	Antennal sensilla arrangement types			
			I	II	III	IV
Agaonini	*Elisabethiella*	15	+	+	+	+
	Nigeriella	4	+	−	+	−
	Courtella	13	−	−	+	−
	Agaon	12	−	−	+	−
	Allotriozoon	3	−	+	−	−
	Paragaon	2	−	−	+	−
	Alfonsiella	7	−	−	−	+
	Pleistodontes	9	+	+	−	−
	Tetrapus	3	+	−	−	−
Blastophagini	*Dolichoris*	8	+	+	+	−
	Blastophaga	11	+	+	+	−
	Wiebesia	1	−	−	+	−
	Liporrhopalum	9	−	+	+	−
	Platyscapa	13	+	+	−	−
	Maniella	0	?	?	?	?
	Deilagaon	3	−	+	−	−
	Waterstoniella	8	+	+	−	−
	Eupristina	6	+	+	−	+
	Pegoscapus	20	+	−	+	−
	Kradibia	10	+	+	−	−
	Ceratosolen	63	+	+	−	−
Total Agaoninae		220	95	76	39	10

funicle segments 5–7 were typical *sensilla linearia* attached over their entire length, whereas some of those on segment 8 arose apically and were attached only at their origins (Figure 6).

The Type III arrangement of *sensilla chaetica* was recorded in 39 species. They ranged from the short stocky sensilla of *Blastophaga silvestriana* Grandi (Figure 7) to the long slender hair-like MPS of *Blastophaga clavigera* (Mayr) (Figure 8). The Type IV sensilla arrangement was found in 11 species. The two species with both *sensilla linearia* and *sensilla chaetica* (*Nigeriella fusciceps* Wiebes and *B. clavigera*) had a combination of Type I and Type III MPS arrangements (Figure 8).

Distribution of Sensilla Arrangements

The Agaoninae can be divided into two tribes, the Agaonini and the Blastophagini (Bouček, 1988). *Sensilla linearia* were recorded in five and *sensilla chaetica* in six of the nine genera of the Agaonini (Table 1). *Elisabethiella* was the only genus in which all four sensilla types were found, although combinations were also recorded in two other genera.



Figs. 5-11. Agaonine antennal MPS arrangements 5. Fifth antennal segment of *Elisabethiella pectinata* (redrawn from Joseph, 1959). 6. Eighth segment of *Platyscapa quadraticeps* (redrawn from Grandi, 1923). 7. Sixth segment of *Blastophaga silvestriana* (redrawn from Hill, 1967). 8. Tenth antennal segment of *Blastophaga clavigera* (redrawn from Grandi, 1928). 9. Elongation of antennal segments as seen in the second funicle segment of *Ceratosolen tentacularis* (redrawn from Grandi, 1928). 10. thickening of antennal segments as in *Deilagaon chrysolepidis* (redrawn from Bouček, 1988). 11. branching of the seventh antennal segment of *Dolichoris flabellata* (redrawn from Wiebes, 1978).

Sensilla linearia were recorded from almost all the Blastophagini, while *sensilla chaetica* were more restricted in distribution. When the two forms are compared at species level, *sensilla chaetica* are clearly rarer in the Blastophagini (in 12 out of the 152 species surveyed compared with 38 of 68 species).

Elongation of sensilla

Elisabethiella stuckenbergi (Grandi), a species with the Type 1 arrangement of *sensilla linearia* (Figure 1), had an estimated total MPS surface area only half that of *Elisabethiella baijnathi* Wiebes, a species with the Type IV arrangement of *sensilla chaetica* (Figure 4; Table 2). This was despite *E. stuckenbergi* being the larger of the two species and having more individual sensilla.

MPS elongation was recorded in 11 of the 21 genera. Seven of these also include species with sensilla that are not elongate, showing that elongation has occured independently in each genus (Figure 12). Using the phenogram modified from Wiebes (1982) and assuming an absence of reversals, it appears that elongation of the MPS has arisen at least four times in the Agaonini (i.e. in *Elisabethiella*, *Nigeriella*, *Alfonsiella/Paragaon* and *Courtella/Agaon*) and five times in the Blastophagini (in *Dolichoris*, *Blastophaga* G, *Liporrhopalum*, *Eupristina* and *Pegoscapus*). In total, sensilla elongation may therefore have evolved on at least nine occasions within the Agaoninae. If elongation also evolved independently within congeners then this figure will be an underestimate.

Antennal modifications

We recorded only isolated examples of structural modifications to the antennae that would allow an increased number of sensilla to be carried. Antennal segment elongation is present in *Ceratosolen tentacularis* (Grandi) (Figure 9) and *Liporrhopalum longicornis* (Grandi); there is antennal thickening in all *Deilagaon* spp. (Figure 10), and the antennae of *Ceratosolen flabellatus* Grandi and *Dolichoris flabellata* Wiebes are branched (Figure 11).

DISCUSSION

Sensilla elongation and detachment has evolved repeatedly in the females of agaonines, but not in the females of other chalcids, where elongation has occured mainly in males. This suggests that female fig wasps and the males of other chalcids share common advantages in possessing elongate sensilla with their correspondingly greater surface area. Alternate ways that surface area can be increased include the elongation, thickening or branching of antennal

Table 2. A comparison of the exposed surface areas of the MPS on the antennae of fig wasps with *sensilla linearia* and *sensilla chaetica*. Numbers of sensilla and their total surface area refer to pairs of antennae.

Species	MPS		Total number of sensilla	Area per sensilla (mm^2)	Total surface area of sensilla (mm^2)
	Form	Type			
Elisabethiella stuckenbergi	*Sensilla linearia*	I	146	0.55	80
Elisabethiella baijnathi	*Sensilla chaetica*	IV	106	1.56	166

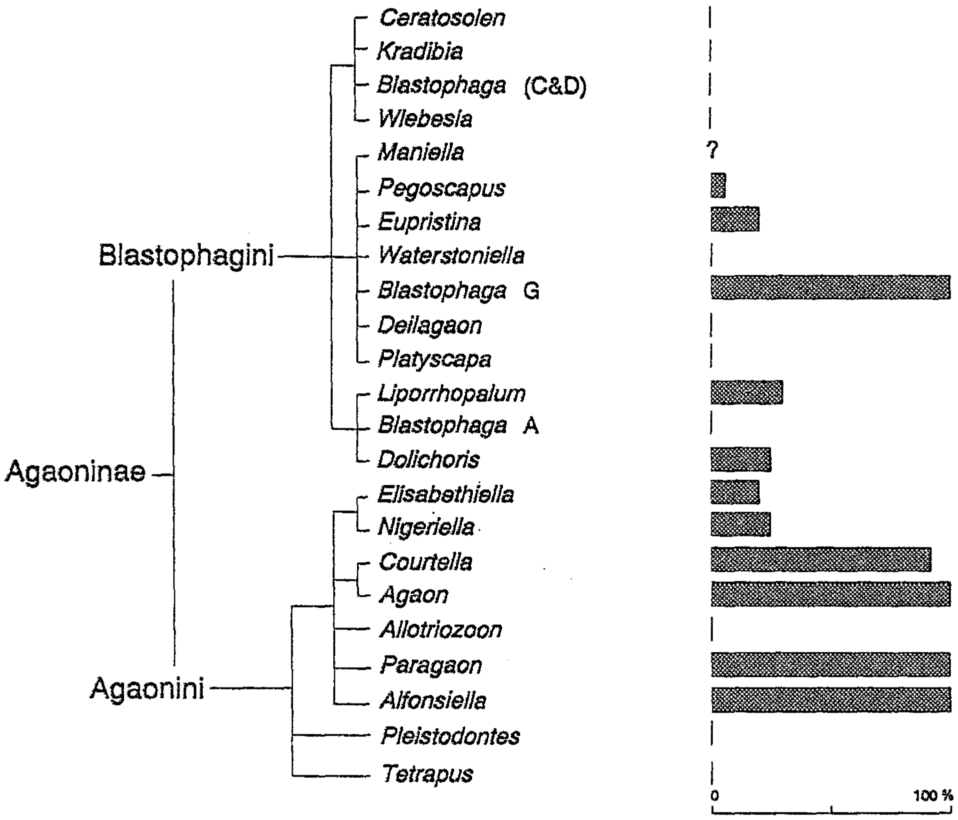


Fig. 12. The phylogeny of Agaonine genera (modified from Wiebes, 1982) and evolution of elongate MPS.

segments, all of which are found in male chalcids in the families Pteromalidae, Eulophidae and Encyrtidae. Such antennal modifications are comparatively rare among female chalcids, however, including agaonids. Why the antennal enlargement is uncommon amongst female fig wasps is uncertain, but could be related to the narrow confines of the figs through which the wasps must crawl after emerging from their natal galls.

Antennae with large surface areas are likely to have developed among male chalcid wasps to improve their efficiency at finding mates. In fig wasps, males seek out females and mate with them before the latter leave their natal galls, so any modifications of the female antennae are unlikely to be related to mate detection or recognition. We therefore suggest that the repeated evolution of elongate and detached sensilla in female agaonids has resulted from their need to detect trace quantities of volatiles in order to find suitable oviposition sites (van Noort et al., 1989). As MPS elongation is evident within several different lineages of agaonines, such selection pressures acting on host finding ability have clearly been important during the evolution of fig wasps. In addition to the elongation of *sensilla chaetica* there has also been a trend towards the placement of the sensilla into sockets on the surface of the antennal segment. In at least one agaonid species these allow the sensilla to be flared, which may further increase their sensitivity (Nijhout and Sheffield, 1979; Ware and Compton, in prep.).

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Appendix 1a. The structure and position of the multiporous plate sensilla (MPS) of female agaonines. Data were derived from the literature and/or from examining dry-mounted specimens (*). A + indicates those species which possess elongated sensilla. See text for a description of the types of MPS arrangements.

	Antennae Type	References (Appendix 1b)
AGAONINI		
ELISABETHIELLA Grandi		
allotriozoonoides (Grandi) 1916	I	7,61
articulata (Joseph) 1959	III +	23,61
bergi Wiebes 1989	I	61*
baijnathi Wiebes 1989	IV +	61*
comptoni Wiebes 1989	I	61*
dyscritus (Waterston) 1920	I	30
enriquesi (Grandi) 1916	I	5,61*
glumosae Wiebes 1989	I	61*
hilli Wiebes 1989	IV +	61
longiscapa Wiebes 1986	I	59,61
pectinata (Joseph) 1959	I	23,61
platyscapa Wiebes	II	61
reflexa Wiebes 1975	I	48,61
socotrensis (Mayr) 1885	I	16,61*
stuckenbergi (Grandi) 1955	I	18,61*
NIGERIELLA Wiebes		
avicola Wiebes 1975	I	48,65
excavata Compton 1990	I	65*
fusciceps Wiebes 1974	III & I +	47,65
letouzeyi Wiebes 1974	I	47,65

Appendix 1*a*. (Contd.)

	Antennae Type	References (Appendix 1b)
COURTELLA Kieffer		
armata (Wiebes) 1974	III +	46,59*
bekiliensis (Risbec) 1956	III +	43*
bispinosa (Wiebes) 1969	III +	42
camerunensis (Wiebes) 1974	III +	24,46
gabonensis Wiebes 1985	III +	63
hladikae (Wiebes) 1979	III +	54
malawi Wiebes 1990	III +	63
medleri (Wiebes) 1972	III +	45
michaloudi (Wiebes) 1979	III +	54*
penicula (Wiebes) 1974	III	24,46
scobiniferum (Waterston) 1920	III +	27,46
sylviae Wiebes 1986	III +	56,59
wardi Compton 1990	III +	65*
AGAON Dalmon		
acutatum Wiebes 1989	III +	63
baliolum Wiebes 1974	III +	46,63
cicatriferens Wiebes 1989	III +	63
fasciatum Waterston 1914	III +	27,63
gabonese Wiebes 1989	III +	63
kiellandi (Wiebes) 1974	III +	46,63
megalopon Wiebes 1976	III +	49,63
obtusum Wiebes 1989	III +	63
paradoxum (Dal) 1818	III +	5,32,41,63
spatulatum Wiebes 1968	III +	41,63
taiense Wiebes 1989	III +	63
tridentatum Joseph 1959	III +	23
ALLOTRIOZOON Grandi		
heterandromorphum Grandi 1916	II	5*
prodigiosum Grandi 1916	II	5*
nigeriense Wiebes 1974	II	46
PARAGAON Joseph		
perplexum Joseph 1959	III +	23,49
josephi Wiebes 1986	III +	59
ALFONSIELLA Waterston		
bergi Wiebes 1988	IV +	60
binghami Wiebes 1988	IV +	60
brongersmai Wiebes 1972	IV +	4,44
fimbriata Waterston 1920	IV +	29
longiscapa Joseph 1959	IV +	4,23,44
michaloudi Wiebes 1988	IV +	60*
natalensis Wiebes 1972	IV +	44
PLEISTODONTES Saunders		
blandus Wiebes 1963	I	33,40
froggatti Mayr 1906	I	6

Appendix 1a. (Contd.)

	Antennae Type	References (Appendix 1b)
greenwoodi (Grandi) 1928	I	15
immaturus Wiebes 1963	II	33
imperialis Saunders 1883	I	16
nitens (Girault) 1915	I	17
plebejus Wiebes 1963	II	33
rennellensis Wiebes 1968	I	40
rieki Wiebes 1963	I	33
TETRAPUS Mayr		
americanus Mayr 1885	I	16
costaricanus Grandi 1925	I	11
mexicanus Grandi 1952	I	17
BLASTOPHAGINI		
DOLICHORIS Hill		
boschmai (Wiebes) 1964	II	56
cristata (Grandi) 1928	III +	14,53
flabellata Wiebes 1978	III +	53
inornata Wiebes 1979	I	53
nervosae (Hill) 1967	I	20,53
umbilicata Wiebes 1979	II	53
valentinae (Grandi) 1916	I	53
vasculosae Hill 1967	II	20
BLASTOPHAGA Gravenhorst		
clavigera Mayr 1885	III & I +	16
errata Wiebes 1966	II	39
gomberti Grandi 1928	II	13
inopinata Grandi 1926	II	16
intermedia Grandi 1926	I	16
javana Mayr 1885	II	16,20
psenes (Linnaeus) 1758	I	*
puncticeps Mayr 1906	II	16
pumilae Hill 1967	II	20
quadrupes Mayr 1885	II	16
silvestriana Grandi 1929	II	20
WIEBESIA Bouček		
contubernalis (Grandi) 1927	II	12
LIPORRHOPALUM Waterston		
cuspidatae Hill 1969	II	21
dubium (Grandi) 1926	II	16
giacominii (Grandi) 1926	II	16
gibbosae Hill 1967	III +	20,21
longicornis (Grandi) 1926	II	16
midotis Hill 1969	II	21
phillippinensis Hill 1969	III +	21
rutherfordi Waterston 1920	III +	21,27

Appendix 1a. (Contd.)

	Antennae Type	References (Appendix 1b)
subulatae Hill 1969	II	21
uniglandulosae Hill 1969	III	21
PLATYSCAPA Motschoulsky		
arnottiana Abdurahiman 1980	I	64
awekei Wiebes 1977	I	51*
bergi Wiebes 1986	I	59
binghami Wiebes 1980	I	64*
coronata (Grandi) 1928	I	14,20,51
corneri Wiebes 1980	II	64
desertorum Compton 1990	I	65*
etiennei Wiebes 1977	I	51
fisheri Wiebes 1977	I	51
ishiiana (Grandi) 1923	III	10,20,51
quadraticeps (Mayr) 1985	I	9,51
soraria Wiebes 1980	II	64*
tjahela (Abd & Joseph) 1975	I	1,51
DEILAGAON Wiebes		
annulatae Wiebes 1977	II	50
chrysolepidis Wiebes 1977	II	3,50
megarhopalum (Grandi) 1924	II	7,10,50
WATERSTONIELLA Grandi		
borneana Wiebes 1982	II	57
fiorii Grandi 1924	II	10
javana Wiebes 1982	II	57
malayana Wiebes 1982	II	57
masii (Grandi) 1921	II	10
solomonensis Wiebes 1980	I	55
sumatrana Wiebes 1982	I	57
williamsi Wiebes 1982	I	57
EUPRISTINA Saunders		
altissima Bal. & Abd. 1981	I	2
aurivillii Mayr 1906	I	16
bakeri Grandi 1927	II	12
belgaumensis Joseph 1954	II	3,22
masoni Saunders 1883	I	26
verticillata (Waterston) 1921	IV +	20,31
PEGOSCAPUS Cameron		
aguilari (Grandi) 1919	I	8
baschieri (Grandi) 1952	I	17
bifossulatus Mayr 1885	I	16
brasiliensis Mayr 1928	I	16
carlosi (Ramirez) 1970	I	25
cumanensis (Ramirez) 1970	I	25
estherae (Grandi) 1919	I	8
flagellatus Wiebes 1983	III +	58

Appendix 1a. (Contd.)

	Antennae Type	References (Appendix 1b)
ileanae (Ramirez) 1970	I	25
jimenezi (Grandi) 1932	I	8
kraussii (Grandi) 1952	I	17
mariae (Ramirez) 1970	I	25
oroczoi (Ramirez) 1970	I	25
silvestrii (Grandi) 1919	I	8
standleyi (Ramirez) 1970	I	25
tomentellae Wiebes 1983	I	58
tonduzi (Grandi) 1919	I	8
tristani (Grandi) 1919	I	8
urbanae (Ramirez) 1970	I	25
williamsi (Grandi) 1923	I	9
KRADIBIA Saunders		
brownii Ashmead 1904	II	52
copiosae (Wiebes) 1980	II	55
cowani Saunders 1883	II	26,52
gestroi (Grandi) 1916	II	52*
hilli Wiebes 1978	II	52,65*
jacobsi (Wiebes) 1964	II	37
nigricorpus (Girault) 1915	I	3
setigera Wiebes 1978	II	52
sumatrana (Grandi) 1926	I	16,52
wassae (Wiebes) 1980	II	55
CERATOSOLEN Mayr		
abnormis Wiebes 1963	II	34,56
acutatus Mayr 1906	I	5,62
adenospermae Wiebes 1965	I	38,56
albulus Wiebes 1963	II	34
appendiculatus (Mayr) 1885	II	20
arabicus Mayr 1906	II	7*
armipes Wiebes 1963	I	34,56
bakeri Grandi 1927	I	12,56
bianchii Wiebes 1963	I	34,56
bimerus Wiebes 1965	I	38,56
bisulcatus (Mayr) 1885	I	16
blommersi Wiebes 1989	II	62
boschmai Wiebes 1963	I	34
brongersmai Wiebes 1963	II	34
calopilinae Wiebes 1963	II	34
capensis Grandi 1955	I	18,36,62*
carayoni Grandi 1963	I	18
coecus (Coquerel) 1855	I	62
constrictus (Mayr) 1882	II	16,20
corneri Wiebes 1963	II	34
dentifer Wiebes 1963	I	34
elisabethae Grandi 1923	II	10
emarginatus Mayr 1906	I	16
feae Grandi 1916	I	5

Appendix 1a. (Contd.)

	Antennae Type	References (Appendix 1b)
flabelatus Grandi 1916	II	5*
fusciceps Mayr 1906	I	62
galili Wiebes 1964	I	36,62*
grandii Wiebes 1963	I	34
gressitti Wiebes 1980	I	55
hewitti Waterston 1920	II	31
hooglandi Wiebes 1963	II	34
humatus Wiebes 1963	II	34
imbecilis Grandi 1927	II	12
immanis Wiebes 1981	I	56
indigenus Wiebes 1981	I	56
internatus Wiebes 1978	II	52
iodotrichae Wiebes 1963	II	34
josephi Wiebes 1963	II	34
jucundus Grandi 1927	I	12
julianae Grandi 1916	I	5
longicornis Joseph 1959	II	23
longimucro Wiebes 1989	II	62
medlerianus Wiebes 1980	I	55
moderatus Wiebes 1963	II	34
namorokensis Risbec 1956	I	43,47
nanus Wiebes 1963	I	34
nexilis Wiebes 1979	II	55,62
notus (Baker) 1913	II	35
nugatorius Grandi 1952	II	17
orientalis Wiebes 1963	II	34
pilipes Wiebes 1963	II	34
praestans Wiebes 1963	II	34
pygmaeus Grandi 1927	I	12
silvestrianus Grandi 1916	I	5
solitarius Wiebes 1980	II	55
solmsi complex Mayr 1885	II	20
sordidus Wiebes 1963	I	34
stupefactus Wiebes 1989	II	62
tentacularis (Grandi) 1926	II	16
vechti Wiebes 1963	II	34
vissali Wiebes 1981	II	56

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CHAPTER 7

BREAKDOWN OF HOST SPECIFICITY

Paper 10: Studies of *Ceratosolen galili*, a non-pollinating agaonid fig wasp. *Biotropica* **23**; 188-194 (S.G. Compton, K.C. Holton, V.K. Rashbrook, S. van Noort, S.L. Vincent and A.B. Ware - 1991).

Paper 11: Breakdown of pollinator specificity in an African fig tree. *Biotropica* **24**; in press. (A.B.Ware and S.G. Compton - 1992).

BIOTROPICA 23(2): 188–194 1991

Studies of *Ceratosolen galili,* a Non-Pollinating Agaonid Fig Wasp[1]

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ABSTRACT

The African fig tree *Ficus sycomorus* is host to two species of agaonid fig wasps, *Ceratosolen arabicus* and *C. galili.* Our studies of *C. galili* in southern Africa confirm that it does not actively pollinate the figs of *F. sycomorus,* although some accidental pollination takes place. The absence of pollination behavior in *C. galili* raises questions about the reasons why other agaonids pollinate the figs and thereby maintain the fig–fig wasp mutualism. *C. galili* larvae did not suffer elevated mortality rates when developing in unpollinated flowers and the only potential "cost" of not pollinating that we detected was that adult female *C. galili* were smaller than those of *C. arabicus* that developed on the same tree.

UMCABANGO-NJE

Umkhiiwane wase Afrika, i *Ficus sycomorus,* ungosokhaya wohlobo olubili lweminyouu, okuyi- *Ceratosolen arabicus* ne *C. galili.* Ucwaningo lwethu lwe *C. galili* yase Afrika yase-Ningizimu luginisekisile ukuthi ayiyiqholi neze imikhiwane ye *F. sycomorus,* nakuba kwenzeka ngengozi iqholeke lemi khiwane. Ukungaqholi kwe *C. galili* kususa imibuzo ngeziza thu ezenza ukuba eminye iminyouu eyi agaonids iziqhole izimbali zomkhiwane ngaleyondlela igcine ubudlelwano phakathi kwayo iminyouu nemikhiwane. Izibungu ze *C. galili* azange zitshengise izinga eliphakeme lokufa ngenkathi zikhula ezi mbalini ezingaqholiwe. Ukukhubazeka, nokho, esakubona wukuthi iminyouu yesifazane endala yayiyimincane ngemizimba kunaleyo yeminyouu eqhololayo, i *C. arabicus* eyayikhula kanye nayo esihlahlemi esisodwa.

EACH OF THE 750 OR SO SPECIES OF FIG TREES (*Ficus* spp., Moraceae) is, with a few exceptions, pollinated by a single species of host specific fig wasp (Hymenoptera, Agaonidae). In Africa, the exceptions to this general pattern include *F. ottoniifolia* (Miq.) Miq. and *F. sur* Forssk., where two species of agaonids are known to pollinate each of the trees (Michaloud *et al.* 1985). *F. sycomorus* L. is also associated with two agaonids, but may be unique in that only one of them pollinates the figs. Working in East Africa, Galil and Eisikowitch (1968, 1969) showed that *Ceratosolen arabicus* Mayr was a legitimate pollinator of *F. sycomorus.* The second species, *C. galili* Wiebes colonized the figs, but had pollen pockets that were never used. *C. galili* was therefore a "cuckoo" that exploited the mutualism. Recently Wiebes (1989) recorded both wasps from *F. mucoso* Ficalho, a fig tree closely related to *F. sycomorus,* and again found that only the females of *C. arabicus* carried pollen.

The absence of active pollination by *C. galili* raises questions about how the behavior evolved in agaonids and why they should continue to carry out this behavior, which forms the basis of the fig–fig wasp mutualism. Kjellberg *et al.* (1987) considered that maintenance of the wasps' elaborate pollination behavior indicated that there was consistent selection favoring its retention. A direct advantage of pollination was shown for *Blastophaga quadraticeps* Mayr, because its larvae suffered increased mortality rates if they developed in unpollinated flowers (Galil & Eisikowitch 1971). Increased larval mortalities also occur in *Elisabethiella baijnathi* Wiebes and *C. capensis* Grandi when they develop in unpollinated flowers (Nefdt & Compton, pers. comm.). Pollination benefits to wasp larvae may therefore be a general phenomenon, perhaps due to improved larval nutrition (Verkerke 1989). *C. galili* nonetheless appears to have circumvented the problems of developing in unpollinated flowers, and it is unclear why a similar abandonment of pollination behavior has not been observed in other species.

This paper describes studies of *C. galili* and some other fig wasps associated with *F. sycomorus* in southern Africa. These studies aimed to answer the following questions: Does *C. galili* fail to pollinate the figs of *F. sycomorus* also in southern Africa? If so, then does *C. galili* "pay a price" for not pollinating the figs? Do *C. galili* females seek out

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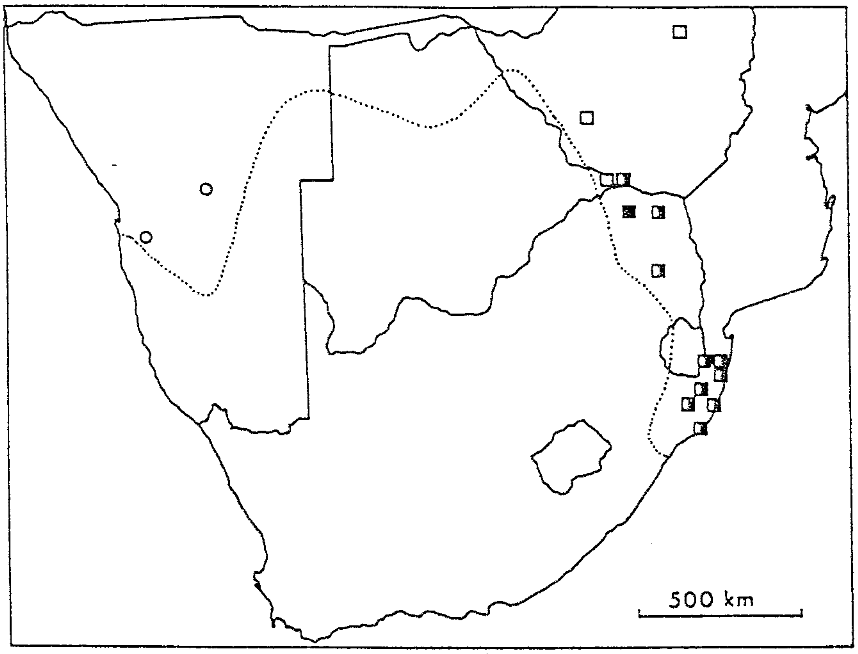

FIGURE 1. Records of *Ceratosolen* species in collections of *F. sycomorus* figs. The dotted line indicates the approximate southern limit of the distribution of the fig species. Squares are *F. s. sycomorus,* circles *F. s. gnaphalocarpa.* Open squares/circles indicate the presence of *C. arabicus,* closed squares *C. galili.* Mixed squares indicate that both wasp species were present.

figs which contain flowers already pollinated by *C. arabicus*? Are the two agaonids equally successful at entering the figs? Do the two species compete for oviposition sites? Do any of the other fig wasps associated with *F. sycomorus* require fertile seeds for their larvae and consequently fail to develop in figs which lack *C. arabicus*?

F. sycomorus is distributed throughout most of tropical and subtropical Africa. Two subspecies are generally recognized, *F. s. sycomorus;* which in southern Africa is found in the east, and *F. s. gnaphalocarpa* in the west. The two subspecies (or forms) are distinguished only by the placement of the figs, which occur on modified leafless branches in *F. s. sycomorus,* but are borne among the leaves by *F. s. gnaphalocarpa* (Berg, in press).

Figure 1 is based on collections of mature *F. sycomorus* figs (Compton, pers. comm.) and summarizes our distribution records for the two *Ceratosolen* species in southern Africa. *C. galili* was at least as common as *C. arabicus* in the more humid east of the subcontinent, but was not recorded from *F. s. gnaphalocarpa* growing in Namibia. In a two year study Wharton *et al.* (1980) similarly failed to detect *C. galili* in Namibia.

In southern Africa *F. sycomorus* also supports numerous species from the family Torymidae. One of the torymids (the seed predator *Sycophaga sycomori* L.) behaves like an agaonid in that females enter the figs through the ostiole to oviposit. The remaining species have long ovipositors and oviposit into the fig flowers from the outside of the figs. The biology of these wasps is largely unknown, but some are seed gallers, while others may be parasitoids or inquilines.

METHODS

Haphazardly sampled figs were obtained from thirteen *F. sycomorus* trees growing at various localities in northern Natal, South Africa (Table 1). "Immature" crops were at the early inter-floral stage (*sensu* Galil 1977). At this time the figs contained remains of the female wasps which had entered to lay their eggs. Counts of wasps which had successfully entered the cavities of the figs were obtained by cutting the figs in half through the ostiole and searching for the wasps' remains under a dissecting microscope. Subsamples were examined for the presence of wasps which had failed in their attempts to enter the lumens of the figs and had become trapped in the ostiolar bracts.

"Mature" crops consisted of figs containing wasps that had completed their larval development

TABLE 1. *Descriptions of* F. sycomorus *collections in Natal.*

Tree	Collection date	Locality	Degree square	Figs sampled	Sample size (figs)
1	6.12.88	Rd. south of Ndumu Game Park	2632CC	Immature	50
2	6.12.88	Rd. south of Ndumu Game Park	2632CC	Immature	50
3	9.12.88	Mkuzi Game Park	2732CA	Immature	50
4	8.12.88	Mkuzi Game Park	2732CA	Immature	50
5	10.12.88	Outside entrance to Mkuzi Game Park	2732CA	Immature	50
6	8.12.88	Rd. south of Ndumu Game Park	2632CC	Immature	10
7	7.12.88	Ndumu Game Park	2632CD	Immature	10
8	5.12.88	Tar road bridge over Pongola River	2732AB	Mature	25
9	6.12.88	Rd. south of Ndumu Game Park	2632CC	Mature	25
10	7.12.88	Ndumu Game Park	2632CD	Mature	25
11	8.12.88	Ndumu Game Park	2732CA	Mature	25
12	10.12.88	Outside entrance to Mkuzi Game Park	2732CA	Mature	25
13	10.12.88	Outside entrance to Mkuzi Game Park	2732CA	Mature	24

and were ready to emerge. Here, figs collected haphazardly from the trees were placed individually in netting-covered jars. After the wasps had emerged they were killed and then recorded, together with any wasps remaining inside the figs.

Figs from three of the mature crops were grouped according to the species of *Ceratosolen* which had emerged from them. These were used to determine whether seeds were only produced in figs containing *C. arabicus.* Flowers which had not produced wasps were scored as being either seeds, "unpollinated," or bladders. "Unpollinated" flowers were those which showed no evidence of their ovules having expanded due to pollination or galling. Bladders (*sensu* Galil & Eisikowitch 1971) superficially resemble seeds, but are hollow. They may represent flowers where wasp larvae died at an early stage of development (Galil & Eisikowitch 1971).

Samples of 20 recently emerged *C. galili* females were collected from each of seven figs, together with one control sample of 20 *C. arabicus* females. The wasps were crushed under glass cover slips and examined under a compound microscope for the presence of pollen in their pollen baskets and superficially on their body surfaces.

The dry weights of adult females of the two *Ceratosolen* species were compared. The wasps were dried at 40°C in an oven and then weighed individually on a kahn Microbalance.

RESULTS

CAN *C. GALILI* POLLINATE THE FIGS OF *F. SYCOMORUS*?—Comparisons of the figs colonized by *C. arabicus* and *C. galili* confirmed that, as in East Africa, the former species routinely pollinated the flowers, while the latter did not (Table 2). However, two healthy seeds were detected in figs which only produced *C. galili,* showing that occasionally this species can pollinate a few flowers. None of 140 females of *C. galili* investigated, and all of 20 *C. arabicus,* had pollen in their pollen baskets. Three *C. galili* did

TABLE 2. *The contents of figs colonized by* C. arabicus *and/or* C. galili. *Flowers which produced wasps are not included.*

Tree	Agaonid(s)	No. figs	Totals		
			Seeds	Bladders	Unpollinated
8	*C. arabicus*	4	200	23	0
	C. galili	5	0	59	250
9	*C. arabicus* + *C. galili*	5	78	57	123
	C. galili	5	0	54	223
10	*C. arabicus* + *C. galili*	3	98	8	81
	C. galili	5	2	30	250
Combined	*C. arabicus*	4	200	23	0
	C. arabicus + *C. galili*	8	176	65	204
	C. galili	15	2	143	723

TABLE 3. *Comparison of the dry weights of* C. arabicus *and* C. galili *at three locations in southern Africa.*

		C. arabicus			*C. galili*				
Locality	Sex	*N*	Mean (mg)	SD	*N*	Mean (mg)	SD	*F*	*P*
Pongola River, Natal 1	F	20	0.097	0.015	20	0.079	0.012	18.68	<0.001
Pongola River, Natal 2	F	20	0.131	0.022	21	0.104	0.012	23.68	<0.001
Limpopo River, Botswana	F	16	0.082	0.009	16	0.063	0.009	33.38	<0.001
Pongola River, Natal 1	M	19	0.117	0.183	18	0.061	0.008	6.21	<0.001

Between localities (females): *C. arabicus* $F_{(2\&53)} = 40.58$, $P < 0.001$; *C. galili* $F_{(2\&54)} = 59.26$, $P < 0.001$.

have some pollen attached superficially to their bodies (one, one, and six pollen grains, respectively), which suggests how "accidental" pollination can take place.

Does *C. galili* "pay a price" for not pollinating the figs?—The numbers of bladders in the figs provide a relative estimate of the larval mortalities of *C. arabicus* and *C. galili* (Table 2). More bladders were present in figs containing *C. galili* only (16% of the flowers, compared with 10% for *C. arabicus* only), but the difference was not significant ($Z = 0.705$, $P > 0.05$). Galil and Eisikowitch (1971) found that differential mortalities of female agaonid larvae occurred in figs which had not been pollinated, resulting in a collapse of the normally female-biased sex ratios. This was not true of *C. galili*. A count of 4991 individuals from 12 figs containing only *C. galili* revealed that 73.9 percent were female, a sex ratio similar to that of *C. arabicus*.

The body weights of adult *C. arabicus* and *C. galili* are compared in Table 3. Wasps from different trees varied significantly in body size; but from any one crop, *C. galili* were consistently smaller. The difference in weights between the females (around 0.02–0.03 mg) was not due to the pollen load of *C. arabicus*. Pollen of this weight (extracted from a honey bee pollen basket) had a volume almost equal to that of the gaster of the wasps.

Do *C. galili* females prefer figs containing *C. arabicus*?—Adult female *C. galili* might be expected to preferentially colonize figs that already contain *C. arabicus* if their larvae gain any benefit from developing in figs containing pollinated flowers. However, *C. galili* females were the most abundant wasps in the immature fig samples and were the only occupants of about half the figs (Table 4). Combinations of species did occur and occasionally females of *C. galili*, *C. arabicus* and *S. sycomori* were all present in a single fig. Nonetheless, figs containing females of both agaonids were consistently underrepresented in the samples, compared with figs containing only one species (for combined totals $\chi^2_{(1)} = 160.39$, $P < 0.001$).

As with the immature fig samples, *C. galili* was the more numerous agaonid in the mature figs (Table 5). Figs containing combinations of the two species were again underrepresented, confirming that *C. galili* females do not actively seek out figs pollinated by *C. arabicus*.

Are the two agaonids equally successful at entering the figs?—In figs which contained only

TABLE 4. *The combinations of wasps entering the figs of* F. sycomorus.

		Figs containing single species			Figs containing combinations of species		
Tree	No. of figs	*C. arabicus*	*C. galili*	*S. sycomori*	*C. arabicus* + *C. galili*	*S. sycomori* + *C. galili*	*C. arabicus* + *C. galili* + *S. sycomori*
1	50	20	20	1	7	1	1
2	50	23	14	0	10	1	2
3	50	12	28	0	6	4	0
4	50	2	42	1	1	4	0
5	50	13	30	0	7	0	0
Total	250	70	134	2	31	10	3

TABLE 5. *The frequencies of* C. arabicus, C. galili *and* S. sycomori *females reared from figs of* F. sycomorus.

		Numbers of figs where wasps were present as				
		Single species			Combinations of species	
Tree	No. of figs	*C. arabicus*	*C. galili*	*S. sycomori*	*C. arabicus* + *C. galili*	*S. sycomori* + *C. galili*
8	25	5	19	0	1	0
9	25	1	13	2	8	1
10	25	2	21	0	2	0
11	25	3	15	0	4	3
12	25	1	15	0	3	6
13	24	0	23	1	0	0
Total	149	12	106	3	18	10

C. galili the number of females which successfully entered the figs varied between 1 and 55, with an overall mean of 5.66 females per fig (Table 6). *C. arabicus* was never recorded at such high densities, and neither was *C. galili* in figs which it was sharing with the other species.

A proportion of the females that had attempted to enter the figs failed to do so and became trapped in the ostiolar bracts. *C. galili* had a particularly high failure rate and on trees 1–5, 77.2 percent of all the females that had attempted entry were found dead part way through the ostioles (Table 7). These were all facing inward and were not females which were attempting to exit the figs. *C. arabicus* females were significantly more successful at gaining entry, with only 13.6 percent failing to do so ($\chi^2_{[1]} = 68.12$, $P < 0.001$).

DO THE TWO SPECIES COMPETE FOR OVIPOSITION SITES IN SHARED FIGS?—Competition between the agaonids was examined using data from tree 9, where the two species shared a relatively high proportion of the figs. As males of the two species are difficult to separate, the comparisons were based on females only. When alone, a mean of 146.3 *C. galili* females were reared from each fig, compared with a mean of 92.9 females per fig when sharing with *C. arabicus*. Although suggestive of competition for oviposition sites, this difference was not significant ($Z = 1.47$, $P > 0.05$).

DO THE TORYMID FIG WASPS REQUIRE FERTILE SEEDS FOR THEIR LARVAE?—Nine species of torymid fig wasps were reared from the mature figs (Table 8, counts of the two rare *Watshamiella* spp. are combined). All of the torymids were recorded from figs where *C. arabicus* was absent, showing that none of them are conventional seed predators requiring fertile seeds for their larval development.

DISCUSSION

These studies in the southern part of the range of *F. sycomorus* confirm that *C. arabicus* is its only active pollinator. *C. galili* accidentally pollinated a few flowers by carrying pollen on its body surface, but the number of seeds produced in this way was negligible. Newton and Lomo (1979) recorded similar accidental pollination by a sycoecine fig wasp which enters the figs of *F. lutea* Vahl. *C. galili*

TABLE 6. *The numbers of wasps successfully entering the figs of* F. sycomorus. *Sample sizes were 50 figs per tree. The ranges are given in parentheses.*

	Mean wasps per fig			
	Single species present		Both species present	
Tree	*C. arabicus*	*C. galili*	*C. arabicus*	*C. galili*
1	1.30 (1–2)	2.30 (1–18)	1.43 (1–3)	1.71 (1–4)
2	1.74 (1–4)	2.86 (1–6)	2.30 (1–10)	2.00 (1–4)
3	1.50 (1–3)	3.46 (1–25)	1.33 (1–2)	2.00 (1–6)
4	1.00 (1)	12.74 (2–55)	1.00 (1)	1.00 (1)
5	1.23 (1–2)	1.33 (1–3)	1.29 (1–2)	1.43 (1–4)
Total	1.46	5.66	1.64	1.68

TABLE 7. *The numbers of wasps that failed to gain entry into figs and were trapped in the ostiolar bracts.*

Tree	No. of figs	Mean plus range per fig		
		C. arabicus	*C. galili*	*S. sycomori*
1	10	0.5 (0–3)	9.8 (0–33)	0.5 (0–4)
2	10	0	1.4 (0–4)	0
3	10	0	3.9 (2–7)	0
4	10	0	9.8 (1–24)	0
5	10	0	2.7 (0–6)	0
6	10	0	0.3 (0–2)	0
7	10	0.1 (0–1)	0.5 (0–2)	0.4 (0–2)
Total	70	0.09	4.06	0.13

females were less successful than those of *C. arabicus* at getting through the ostioles of the figs. This may have been due to interference resulting from the very high densities of *C. galili* trying to enter the figs. A similarly high proportion of wasps become trapped when large numbers of female *Elisabethiella baijnathi* Wiebes attempt to enter the figs of *F. burtt–davyi* Hutch. (Nefdt & Compton, pers. comm.).

C. galili larvae commonly developed in figs lacking any pollinated flowers, and there was no evidence that this resulted in elevated mortality rates. However, the adult females they produced were consistently smaller than those of *C. arabicus*. This could reflect differences in the quantity or quality of the food available to *C. galili* larvae developing in unpollinated flowers. Smaller species of agaonids contain fewer eggs, and within a species, egg loads are correlated with body size (Nefdt & Compton, pers. comm.). *C. galili* females are, therefore, likely to carry fewer eggs than those of *C. arabicus* emerging from the same tree. This appears to be the only potential "cost" to *C. galili* of not pollinating the flowers, although other explanations for the size difference, such as phylogenetic constraints, are equally plausible. If other agaonids which have for-

TABLE 8. *The composition of fig wasp assemblages reared from figs of* F. sycomorus. *Counts are of females only.*

	Tree 8 (15 figs)			Tree 9 (15 figs)			Tree 10 (15 figs)		
	N (figs)	Total wasps	Range per fig	*N* (figs)	Total wasps	Range per fig	*N* (figs)	Total wasps	Range per fig
Ceratosolen galili	10	686	(0–201)	13	1368	(0–234)	13	3660	(0–411)
Ceratosolen arabicus	6	585	(0–129)	6	368	(0–109)	3	39	(0–145)
Sycoscapteridea (pale) sp. indet.	15	321	(3–46)	15	731	(0–110)	9	118	(0–26)
Sycoscapteridea (dark) sp. indet.	13	257	(0–52)	6	72	(0–24)	5	40	(0–14)
Sycoscapter sp. indet.	13	227	(0–52)	0	0	0	2	2	(0–1)
Apocryptophagus gigas Mayr	11	93	(0–17)	3	18	(0–10)	10	98	(0–23)
Apocrypta longitarsus Mayr	5	29	(0–11)	12	183	(0–28)	10	52	(0–12)
Eukoebelia sycomori Wiebes	5	14	(0–9)	4	9	(0–4)	0	0	0
Watshamiella spp. indet.	1	1	(0–1)	8	6	(0–2)	1	1	(0–1)
Sycophaga sycomori	0	0	0	4	436	(0–152)	0	0	0

saken pollination are detected, then it will be interesting to see if they also are smaller than their associated pollinator.

C. arabicus and *C. galili* differ in both appearance and behavior. *C. arabicus* flies at night and is often collected at light traps (Wharton *et al.* 1980, Compton & Robertson, pers. comm.). Associated with this are its "Ophionoid" features, such as yellow coloration and enlarged eyes (Huddleston & Gauld 1988). In contrast, *C. galili* is a black, day flying species, which usually emerges from the figs in the early afternoon (S. G. Compton, pers. obs.). This may be the reason for the apparent rarity of *C. galili* in dry habitats, because its diurnal flight period should make it more prone to dehydration. The rarity of figs containing both *Ceratosolen* species may also be related to their different flight preferences. Figs cease to be attractive to agaonids after they have been pollinated. If the attraction wanes within hours of pollination, then figs entered at night may already be unsuitable by the following day. Alternatively, females may distinguish and avoid figs that have already been entered by the other species.

The evolution of agaonids with the biology of *C. galili* requires the following: there must be two agaonids sharing the same host *Ficus* (otherwise the tree will not be pollinated and will go extinct); and a mutation for the loss of pollination behavior must occur and be sufficiently advantageous to become "fixed" throughout the species. The nature of these hypothetical advantages is uncertain. Morphological evidence suggests that *C. arabicus* and *C. galili* are not "sister species" (Wiebes 1989) and therefore *C. galili* cannot be derived from *C. arabicus*. Presumably the ancestors of *C. galili* originally pollinated some other fig species, and subsequently colonized *F. sycomorus* while it was already being pollinated by *C. arabicus*. Given that there do not seem to be major hurdles associated with forsaking pollination, the apparent rarity of species such as *C. galili* may be due to the infrequency of such colonization events in the history of *Ficus*–agaonid coevolution.

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Breakdown of Pollinator Specificity in an African Fig Tree[1]

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ABSTRACT

A single giant-leafed fig tree (*Ficus lutea*) is planted on the Rhodes University campus in Grahamstown, South Africa, some 500 km outside its normal distribution range. Small numbers of fig wasps (Hymenoptera, Agaonidae) which normally pollinate two other *Ficus* species entered and successfully pollinated the figs of this tree. One of the wasp species reproduced successfully. Monitoring of adult fig wasps arriving at the tree established that these alien species were not attracted to *F. lutea.* However, from laboratory studies it appears that once having landed on *F. lutea* figs, these wasps were stimulated to search for the ostiole, through which they gained entrance to the fig cavity. Females of a third pollinator species were also present on the tree, but they failed to initiate ostiole searching behavior when on the figs. Hybrid seeds resulting from the entry of the alien wasps germinated successfully, but did not progress past the cotyledon stage, indicating postgermination deficiencies in the hybrids.

Key words: *Agaonidae; coevolution; Ficus; host specificity; Hymenoptera; mutualism; pollination specificity; South Africa.*

FIG TREES (*Ficus* spp.; Moraceae) and their pollinating wasps (Chalcidoidea, Agaonidae, Agaoninae, *sensu* Bouček 1988) have an obligatory mutualistic relationship. Each of the 750 or so species of fig tree (Berg 1988) is generally pollinated by a single species of fig wasp, which is uniquely associated with that tree (Wiebes 1979, Michaloud *et al.* 1985). The maintenance of the specificity of the relationship between fig tree species and their particular agaonine pollinators has long been held as the extreme example of coevolution (Janzen 1979). However, the mechanisms determining this specificity are not clearly understood.

Crop development on individual fig trees is often synchronized, forcing adult female pollinating wasps (foundresses) to leave their natal trees in order to find trees with figs suitable for oviposition. They appear to recognize suitable host trees through *Ficus*-specific volatiles released from the figs when they are ready for pollination (= female phase; Galil 1977) (van Noort *et al.* 1989). On finding receptive figs, the pollinators must then negotiate a bract-lined pore (the ostiole) in order to gain access to the female flowers lining the inside of the fig (the lumen). The flowers are pollinated while the wasps oviposit down some of the styles (Galil 1977, Janzen 1979). Ovipositor lengths of fig wasp species are highly correlated with the mean style lengths of the *Ficus* species they utilize (Nefdt 1989). Host specificity in fig wasps may therefore be determined by a combination of long range attraction, short range stimuli on the fig surface, the physical barrier imposed by the ostiole, and the suitable lengths of the styles. Fig trees are also hosts to numerous species of nonpollinating fig wasps, mainly belonging to other subfamilies of Agaonidae (Bouček 1988). These either have larvae that develop inside ovules they have galled, like those of the pollinators, or are parasitoids of other fig wasps. Many nonpollinating fig wasps may also be host tree specific (Bouček *et al.* 1981, Ulenberg 1985, van Noort, pers. comm).

Newton and Lomo (1979) studied the pollination biology of the giant-leafed fig tree, *Ficus lutea* Vahl (= *F. vogelii* (Miq.) Miq.), in its natural habitat in tropical Africa. Although the southernmost limit of its distribution is Natal, South Africa (van Greuning 1990), *F. lutea* is planted further south as an ornamental tree. One such tree is present in Grahamstown, some 500 km outside its normal range. Compton (1990) recorded that females of two species of agaonines not normally associated with *F. lutea* had entered and pollinated the figs of this tree, and that one of the wasp species reproduced successfully. Furthermore, he noted that individuals of three nonpollinating fig wasp species normally associated with other *Ficus* spp. also reproduced successfully. The objectives of this paper are to address questions raised by these initial observations. Are the volatiles released from the figs of *F. lutea* attractive to a range of pollinator species and therefore not as species specific as supposed? How important are short-range stimuli on the fig surface in determining host specificity? Does ostiole structure play a role in preventing alien wasps from entering

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the "wrong" figs? Does the oviposition and pollination behavior of alien wasps change when they enter the "wrong" figs? If fig wasps can pollinate the "wrong" tree, do the hybrid seeds grow successfully?

MATERIALS AND METHODS

A 10 m high (220 cm DBH) *F. lutea* tree growing on the Rhodes University campus in Grahamstown (eastern Cape Province of South Africa) was the object of this investigation. As far as could be ascertained, its nearest known conspecific is another planted specimen at the Addo Elephant National Park some 80 km to the west (Compton 1990). A 6 m high *Liqustrum lucidum* Ait. (Oleaceae) planted some 20 m away from the Grahamstown *F. lutea* was used as a control tree.

The first *F. lutea* figs appeared in March 1990 and at its peak in May the crop size was estimated to be 250,000. At this time many of the figs were aborting as they had not been pollinated (no foundresses were recorded from samples of fallen figs). The flowering/fruiting cycle of *L. lucidum* was December–January.

MONITORING OF FIG WASPS ARRIVING AT THE TREES.—Wasps visiting the trees were detected using sticky traps made from cellulose sheets (21 × 30 cm) secured to white cylinders (10 cm radius). The sheets were made sticky by spraying with pruning sealant (Frank Fehr Ltd., Durban). Three traps were hung in each of the *F. lutea* and *L. lucidum* trees at heights of 1.5, 2, and 4 m. The traps were replaced weekly and any fig wasps caught were counted and identified. Monitoring of fig wasp arrivals began in November 1989, three months after the previous *F. lutea* crop had finished, and at about the time when the new crop was initiated. Trapping continued for 35 weeks.

FOUNDRESSES AND THEIR PROGENY.—Approximately nine weeks after the initiation of the *F. lutea* crop most of the figs had not been pollinated and began to abort. The remaining fruit were harvested once the figs had ripened (= male phase; Galil 1977). Any figs that already had exit holes produced by wasp progeny were ignored. Each fig was bisected and, where possible, the identity of the foundresses was established. Some nonpollinating fig wasps oviposit through the fig wall from the outside and the progeny of these develop without evidence of a foundress.

We examined the germination and postgermination success of seeds from crosses with *F. lutea*, *F. sur* Forssk and *F. thonningii* Bl. (maternal parent always *F. lutea*). The seeds were germinated on moistened filter paper in Petri dishes at room temperatures (20–28°C). After germination, the seeds were transferred to pots containing a 25:75 mixture of vermiculite and sterilized potting soil, and grown indoors.

SHORT-RANGE RESPONSES OF FIG WASPS.—Branches of *F. lutea* bearing female phase figs were placed in glass containers (50 × 50 × 30 cm). Into each container a different pollinator species was released; approximately 500 *Ceratosolen capensis* Grandi from *F. sur* were placed with 16 figs, 500 *Elisabethiella stuckenbergi* Grandi from *F. thonningii* with 58 figs, and 700 *Elisabethiella baijnathi* Wiebes from *F. burtt-davyi* Hutch. with 32 figs. To ascertain whether the surface hairs on the figs of *F. lutea* were important in preventing *E. baijnathi* from penetrating the lumen of the fig (the figs of *F. burtt-davyi* are glabrous), 200 *E. baijnathi* females were released onto 10 *F. lutea* figs that had their surface hairs removed. At the end of each observation period of approximately 6 hr, the total numbers of wasps that successfully penetrated the fig lumens were recorded. *C. capensis*, which was found to readily enter *F. lutea* figs in the female phase, was used as a control to test that the figs provided to the other wasps were suitable for entry.

WASP BEHAVIOR WITHIN THE FIGS OF *F. LUTEA*.—Figs were transversely bisected while wasps were passing through the ostioles. The cut edge of the half fig containing the wasp was placed onto a glass slide, where it became firmly attached by the exuding latex. The behavior of the wasp within the lumen could be observed through the microscope slide using a dissecting microscope. Oviposition and pollination by *E. baijnathi*, *E. stuckenbergi*, and *C. capensis* was observed both in their usual host figs and in those of *F. lutea*.

RESULTS

MONITORING OF FIG WASP ARRIVALS.—Species composing the wasp fauna normally associated with *F. lutea* in its native range were never recorded from the sticky traps on the tree. Only small numbers of other fig wasps were collected ($N = 51$ representing 0.49 wasps/trap/week; Table 1). The two most frequently trapped fig wasps were *C. capensis* and *Sycophaga cyclostigma* Waterston, both normally as-

TABLE 1. *Fig wasps collected over a 35 week period on sticky traps placed in* Liqustrum lucidum *and* Ficus lutea *trees. The receptive period when the figs were potentially attractive to pollinators was approximately 7 weeks.*

Species	*L. lucidum* Total period	*L. lucidum* Receptive period	*F. lutea* Total period	*F. lutea* Receptive period	Mann Whitney *U* Statistic (wasps on *L. lucidum* and *F. lutea*) Total sample period	Mann Whitney *U* Statistic (wasps on *L. lucidum* and *F. lutea*) Receptive period only
Pollinators						
C. capensis	10	6	21	19	0.65	0.22
E. baijnathi	0	0	2	0	0.37	1.00
E. stuckenbergi	3	2	4	4	0.68	0.78
Nonpollinators						
A. guineensis	0	0	9	3	0.03[a]	0.37
S. cyclostigma	2	0	13	0	0.37	1.00
P. barbarus	1	0	2	1	0.78	0.79
Total	16	8	51	27		

[a] $P < 0.05$.

sociated with *F. sur*. Lower densities of the pollinators normally associated with *F. thonningii* and *F. burtt-davyi* were also recorded.

Counts from the sticky traps in the control *L. lucidum* tree were equally low and there was no indication that any of the pollinating wasp species were significantly more abundant in the *F. lutea* than the control tree (Table 1) ($P > 0.05$ for all pollinating species; Mann Whitney *U* statistic). Only the parasitoid *Apocrypta guineensis* Grandi normally associated with *F. sur* (Compton & Robertson 1988, Ulenberg 1985), was collected significantly more often from the *F. lutea* tree than the control tree ($P = 0.03$; Mann Whitney *U* statistic). When counts for all the pollinating wasps were combined, there was again no significant difference in the number of wasps trapped on *F. lutea* and *L. lucidum* over the whole period ($P = 0.811$; Mann Whitney *U* statistic), nor during the period when the fig tree was potentially attractive ($P = 0.474$; Mann Whitney *U* statistic). Furthermore, if the wasps were being attracted differentially to the fig tree during the period when the figs were receptive, then the number of wasps trapped on the *F. lutea* should have increased relative to those on *L. lucidum*. This was not the case (χ^2 with Yates' correction = 1.62; $P > 0.05$).

FOUNDRESSES AND THEIR PROGENY.—By the end of July the figs had matured to the male phase, 97 of which were sampled (of these, 8 figs had wasp exit holes and were excluded from the following counts). Foundresses of *Allotriozoon heterandromorphum* Grandi, the pollinator normally associated with *F. lutea* (Newton & Lomo 1979, Wiebes & Compton 1990), were recorded from 61.8 percent of the figs (Table 2). These wasps reproduced successfully in all the figs in which foundresses were found, as well as in an additional 8 figs from which the wasps are assumed to have escaped after laying their eggs (Table 2). A single female *Sycoryctes* sp. was reared from a fig containing *A. heterandromorphum*. Some other species of this genus are known to be parasitoids (*e.g.*, Compton & Nefdt 1990) and *A. heterandromorphum* is likely to have been its host. Neither *C. capensis* nor *S. cyclostigma*, the two wasps usually associated with *F. sur*, succeeded in reproducing in the figs of *F. lutea*, despite foundresses being found in 29 percent of the figs (Table 2). In contrast, *E. stuckenbergi*, the pollinator normally associated with *F. thonningii*, produced progeny in all the figs in which foundresses were recorded (Table 2). *E. baijnathi*, the pollinator of the most common *Ficus* in the area, *F. burtt-davyi*, were never recorded as foundresses in the lumen of *F. lutea* figs, nor were its progeny recorded.

GERMINATION STUDIES.—In three series of germination trials, the seeds from *F. lutea/F. thonningii* and *F. lutea/F. sur* hybrid crosses took 8 to 13 days to germinate while the pure *F. lutea* seeds took from 34 to 38 days. However, despite their rapid germination times, the hybrid seedlings were unsuccessful and, under our growing conditions, post-germination survival was zero with no hybrids progressing beyond the cotyledon stage. In contrast, over 90 percent of the pure *F. lutea* seedlings grew successfully to at least the first true leaf stage.

TABLE 2. *Fig wasps found in the figs of a* F. lutea *tree growing out of its natural range in Grahamstown, South Africa.*

		Wasp progeny	
Foundress(es)	Number of figs	Species	Frequency (figs)
A. heterandromorphum	40	*A. heterandromorphum*	40
		Sycoryctes sp.	1
A. heterandromorphum +*S. cyclostigma*	12	*A. heterandromorphum*	12
A. heterandromorphum +*Crossogaster silvestrii*	3	*A. heterandromorphum*	3
		C. silvestrii	3
C. capensis	9	None present	9
C. capensis +*S. cyclostigma*	3	None present	3
E. stuckenbergi	3	*E. stuckenbergi*	3
S. cyclostigma	5	*A. heterandromorphum*	1
		None present	4
None present	14	*A. heterandromorphum*	7
		None present	7

Laboratory studies.—A total of 303 female *C. capensis* entered the lumens of 13 *F. lutea* figs, while 29 female *E. stuckenbergi* entered 21 figs.

Their behavior appeared to be identical to that when they searched for the ostiolar openings on their usual host figs. In contrast, no *E. baijnathi* females entered the syconia of the *F. lutea* figs. Females of this species antennated the surface of their host figs, but this behavior was not evident when they were in contact with the figs of *F. lutea,* even when the covering of surface hairs had been removed.

Once inside the *F. lutea* figs, the ovipositor-probing behavior of both *E. stuckenbergi* and *C. capensis* appeared no different from that observed in their own host figs. Once probing had commenced, the wasps removed pollen from their pollen baskets with their front legs and proceeded to deposit it into the nearby stigmas.

DISCUSSION

In natural situations, receptive figs can attract large numbers of their associated pollinators over relatively short periods (Bronstein 1987). No *A. heterandromorphum* (the normal pollinator of *F. lutea*) were recorded from sticky traps placed in the *F. lutea* tree, showing that this wasp species was uncommon in our study area. Nevertheless, despite the tree's isolated location, 55 of the figs were found by these pollinators (an estimated 0.022% of the total crop). That *A. heterandromorphum* females were able to locate and pollinate the figs of such an isolated host is indicative of the effectiveness of the tree's volatile attractants and the host-finding ability of the wasps. This is even more impressive when one considers the small size of the pollinating wasps and that they are probably short-lived (Kjellberg *et al.* 1988). In contrast, the low numbers of alien fig wasps trapped on the *F. lutea* during its receptive female phase can be considered as background noise resulting from chance arrivals at the tree, rather than a breakdown in the specificity of attraction.

Once agaonines land on a fig it appears that short-range stimuli, probably including the surface chemistry of the fig, stimulate them to search for the ostiolar opening. Our laboratory investigations indicated that the surfaces of receptive *F. lutea* figs are recognized by females of both *C. capensis* and *E. stuckenbergi.* These stimuli are thus not species specific. Nevertheless, the failure of *E. baijnathi* to antennate the surface of *F. lutea* figs shows that the surface stimuli they present are not the same as those of its normal host.

The ostiole is generally considered to act as a filter which prevents nonadapted fig wasps from entering the "wrong" figs (Janzen 1979). That the ostiole acts as a barrier is demonstrated by the anatomy of the heads and bodies of agaonids, which show numerous adaptations to facilitate entry into the figs (Ramirez 1974). There is also evidence of convergence in head shape between agaonines and sycoecines, another group of fig wasps that penetrates the fig via the ostiole (van Noort and Compton, pers. obs.). However, despite the evidence for adaptations related to the penetration of ostioles of specific fig species, the ostiole of *F. lutea* figs did not act as a barrier to females of *E. stuckenbergi, C. capensis, P. barbarus* and *S. cyclostigma,* all of which successfully penetrated the figs.

In other studies, Michaloud (1988) used a light to attract several species of nocturnal agaonines, and induced *Agaon paradoxum* Dalman to enter figs of *F. natalensis leprieurii* (Miq.) Berg, a tree which is normally pollinated by *Alfonsiella fimbriata* Waterston. "Mistakes" made by agaonines entering the wrong figs were also reported by Ramirez (1970). Clearly, wasps adapted to enter the figs of one host *Ficus* are not precluded from entering the figs of other species and the filtering effect of the ostiole may not be as effective as previously imagined. From our observations of the fig wasps that colonize *F. lutea,* it appears that the long range, *Ficus*-specific, attractants released by the figs (van Noort *et al.* 1989, Ware *et al.*, pers. comm.) form the basis of host specificity in agaonines and that features of the figs themselves have, at most, a secondary role in determining pollinator specificity.

During 1989 and 1990, six species of fig wasp (two pollinators, three other gall formers and one putative parasitoid) successfully reproduced in the Grahamstown *F. lutea.* Two of these are normally associated with *F. lutea,* three with *F. thonningii* and the host of one is indeterminate (this study; Compton 1990). However, although they frequently entered the figs, the two species normally associated with *F. sur* failed to reproduce. Thus, wasps from *F. thonningii* (subgenus Urostigma, section Galoglychia) were able to reproduce successfully in the closely related *F. lutea* (subgenus Urostigma, section Urostigma); whereas, those from the more distantly related *F. sur* (subgenus Sycomorus) could not.

Because of its isolated location, the figs of the Grahamstown *F. lutea* remained unpollinated, and therefore receptive, for an extended period. This seems to have facilitated the incidental colonization of its figs by alien pollinators. While this increased the likelihood of fig hybrid production, other natural barriers preventing hybridization had not been altered. However, few naturally occurring fig hybrids have been recorded and in these cases at least one parent tree was an introduced species (Ramirez 1988). Why have natural *Ficus* crosses been so rarely recorded? One possibility is that hybrids are relatively common, but difficult to identify in the field (Ramcharun *et al.* 1990). Alternatively, the weakness of the hybrid seedlings recorded in this study could be a general reason why *Ficus* hybrids fail to reach maturity.

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CHAPTER 8

NON-POLLINATING FIG WASP

Paper 12: African fig wasp parsitoid communities. In *Parasitoid Community Ecology* (Eds Hawkins, B.A. and Sheenan, W.). In press (S.G. Compton, J.-Y. Rasplus and A.B. Ware)

AFRICAN FIG WASP PARASITOID COMMUNITIES

S.G. Compton, J.-Y. Rasplus and A.B. Ware

WHAT ARE FIG TREES AND FIG WASPS?

Fig trees are a group of approximately 750 species placed in the genus *Ficus* (Moraceae), and characterised by their unique inflorescence - the fig. Around 105 *Ficus* species are found in Africa, where they range in size from small shrubs to huge rainforest emergents (Berg, 1990). The term 'fig wasps' is sometimes applied to all the hymenopterans that develop inside figs, but more often is restricted to certain chalcid wasps (Hymenoptera, Chalcidoidea), belonging mainly to a single family, the Agaonidae (Boucek, 1988). All agaonid species are associated exclusively with fig trees. The few detailed studies of parasitoid fig wasps have found that they are actually 'entomophytophagous' (Zerova and Fulsov, 1991) inside galls produced by other species, feeding initially on plant tissue and only later destroying the larvae of their hosts (Abdurahiman and Joseph, 1978a,b).

Most of the interest shown in *Ficus* biology has centred on the mutualistic interaction between the trees and the pollinating fig wasps (Agaonidae, subfamily Agaoninae). Fig wasp parasitoid communities nonetheless also offer many interesting avenues for research, due to such features as their complexity, the replication provided by the communities centred around each of the hundreds of *Ficus* species, and their predominantly tropical distribution, which sets them apart from the better-known temperate parasitoid communities.

Here we first describe the fig wasp communities associated with two African fig trees, emphasising the consequences of the trees' unusual phenological characteristics and the unique structure of their inflorescences on host accessibility to parasitoids. We then describe how homopterans can adversely effect the fig wasp parasitoids, through their attraction of predatory ants. Finally, we expand our perspective and discuss geographical influences on the composition of the local parasitoid communities found on the two trees and then review what is known of the factors influencing species richness among African fig wasp communities in general.

THE FIG ENVIRONMENT

Interactions between fig wasp parasitoids and their hosts are greatly influenced by the morphology of figs, because their structure governs host accessibility. Usually spherical in shape, fully developed figs of Afrotropical species vary in size from only about 8 mm diameter in *F. antandronarum bernardii* to larger than a cricket ball in *F. sycomorus* form sakalavarum. Each fig is lined on its inner surface by hundreds or thousands of unisexual flowers. Agaonines transport the pollen into the fig via the ostiole, a bract-lined tunnel. Pollination occurs while the agaonines are galling some of the female flowers and ovipositing down their styles. In monoecious *Ficus* species the majority of the flowers have ovules that are accessible for oviposition (Bronstein, 1988; Nefdt, 1989), whereas in dioecious species the flowers in figs of 'female' trees have very long styles that prevent successful oviposition (Verkerke, 1987). Consequently the pollinators fail to reproduce and these figs produce only seeds.

Oviposition by a few non-pollinating fig wasps also takes place after entry through the ostiole, but most species, including all the putative parasitoids, use their long ovipositors to reach the ovules from the outside, through the walls of the figs. Not surprisingly, parasitoids associated with trees that produce smaller figs also have shorter ovipositors than species attacking hosts that develop in larger figs (Compton, unpublished). The latter have some of the longest ovipositors, relative to their body size, of any hymenopterans (Compton and Nefdt, 1988).

Fig wasp life cycles are closely integrated with the developmental cycle of the figs. The first potential colonisers of a new fig crop are certain species belonging to the subfamily Epichrysomallinae which gall fig primordia during the 'pre-floral' stage (Galil, 1977), before individual flowers have differentiated. These galled figs develop into grossly distorted structures incapable of supporting most other fig wasps, apart from some parasitoids specifically associated with the epichrysomalids (Compton and van Noort, in press).

Most galling fig wasps only utilise figs that are at the next stage of development, the 'female' stage. At this time the figs are 'receptive' and draw their specific species of pollinator to the trees through the release of volatile chemicals, which are not attractive to other agaonines (van Noort *et al.* 1989; Ware and Compton, in press; Ware *et al.*, in press). Parasitoids probably use other cues to find the trees, because they tend to arrive at the trees during the following 'interfloral' stage, when the pollinator larvae are present (Compton and Dallas, unpublished). After the progeny of the various wasp species complete their development within the figs they emerge together during the 'male' phase, when the female pollinating wasps of the next generation collect the pollen prior to dispersing. After mating is completed the male agaonines chew a communal exit hole, through which the female wasps escape. The males of many non-pollinating species are also capable of producing exit holes, but this does not appear to be the case with at least one parasitoid, *Apocrypta guineensis*, and this can lead to mass mortalities of adult females in heavily-parasitised figs where few if any male pollinators were present (C. Zachariades, pers. comm.).

Figs vacated by pollinators become attractive to fruit eating vertebrates and any wasps that have not completed their development by this time risk being eaten by birds, fruit bats etc. In strongly seasonal climates, such as those experienced in the Cape province of South Africa, fig development times are extended during the winter period and can last several months, whereas in the summer wasp generations cycle within a few weeks.

TWO EXAMPLE COMMUNITIES

The Trees

Among African fig trees, *F. burtt-davyi* and *F. sur* are the two species with distributions that extend the furthest south. *F. burtt-davyi* (subgenus *Urostigma*, section *Galoglychia*) is a monoecious species with an exclusively southern African distribution extending from Mozambique to the southern Cape Province (van Greuning, 1990). It can grow as a strangler of other trees (Compton and Musgrave, submitted), as a shrub on coastal sand dunes, or as a rock-splitter growing out from bare rock faces. The figs of

F. burtt-davyi are small, reaching a maximum diameter of about 15 mm at maturity and are produced in the leaf axils.

F. sur is also a monoecious species, but belongs to subgenus *Sycomorus*. It has a much wider distribution than *F. burtt-davyi*, extending from the Cape northwards throughout the less arid regions of the continent (Berg, 1990). *F. sur* is often found in riverside vegetation, where it can reach a far larger size than *F. burtt-davyi*. The figs are also larger, reaching over 30 mm at maturity, and containing around 3000 flowers. They are typically borne on leafless branches growing out from the old wood. On certain trees a few of the fig-bearing branches are produced below ground level, resulting in 'geocarp' figs projecting from the soil surface.

The wasps

The fig wasp community associated with *F. burtt-davyi* around Grahamstown (eastern Cape Province, South Africa) consists of the pollinator (*Elisabethiella baijnathi*), three other ovule-gallers (*Phagoblastus* sp., *Otitesella uluzi* and *O. sesquianellata*) and two parasitoids, *Sycoscapter* sp. (= *Sycoryctes* sp.) and *Philotrypesis* sp. *E. baijnathi* and *Phagoblastus* females lay their eggs from the interior of the fig, while the other species oviposit from the outside. Both parasitoids will attack all the galler species, although the pollinator may be the preferred host. The four phytophagous fig wasps do not reproduce on any other tree species in the Grahamstown area, whereas the parasitoids cannot at present be distinguished from congeners which develop in the figs of *F. thonningii*, and may turn out to be associated with both trees.

In the Grahamstown area the species which form the *F. sur* fig wasp community are all specifically associated with this tree. The pollinator of *F. sur* in Grahamstown is always *Ceratosolen capensis*, while the non-pollinating fig wasps comprise the parasitoid *Apocrypta guineensis* together with the gall-forming *Sycophaga cyclostigma* (which enters the figs to oviposit, like the pollinator) and three *Apocryptophagus* spp.

A. guineensis is catholic in terms of its host insect requirements, and individuals have been reared from all the potential host species. Uniquely among the species in either of the two Grahamstown communities, more than a single individual of *A. guineensis* sometimes emerges from the very large galled ovules produced by one of the *Apocryptophagus* species. The fig wasp community associated with *F. sur* in West Africa is more complex. At the Ecological Station at Lamto, in Ivory Coast, where this is by far the most common *Ficus* species, 11 fig wasps species have been recorded. These comprise two species of pollinators (*C. capensis* and *C. flabellatus*), five gall formers (*Sycophaga cyclostigma*, three *Apocryptophagus* species and an epichrysomalline, *Acophila* sp.) and four parasitoids (*A. guineensis*, two *Sycoscapter* spp. and a eurytomid, *Sycophila* sp.). A survey of the other 15 *Ficus* species in the Lamto area (Rasplus, unpublished) found that these wasps were generally associated only with *F. sur*. The two *Sycoscapter* spp. parasitoids were exceptional in that were also reared from related *Ficus* species (*F. sycomorus* and *F. vallis-choudae*).

C. flabellatus appears to be a genuine second pollinator of *F. sur*, a situation which has also been recorded from other African fig trees (Michaloud *et al.*, 1985). *Apocryptophagus* sp.1 (a species close to *A. gigas*) forms large galls that protrude into the central cavity of the figs and can completely occlude it. Oviposition by this species, and *Acophila* sp., occurs before pollinator entry (Figure 1). *Apocryptophagus* sp. 2 oviposits at about the same time that pollination is occurring, while the third species in the genus oviposits at a later stage (Figure 1).

Among the parasitoids, oviposition by *Sycophila* occurs slightly later than that of the *Acophila* sp. (Figure 2). Like *Apocrypta* species, it is probably entomophytophagous, exploiting the gall tissue made available by *Acophila*. Oviposition by the *Sycoscapter* species occurs somewhat later. The oviposition period of *A. guineensis* is unusually broad, and consequently this species must be exploiting galls containing host larvae of greatly varying sizes.

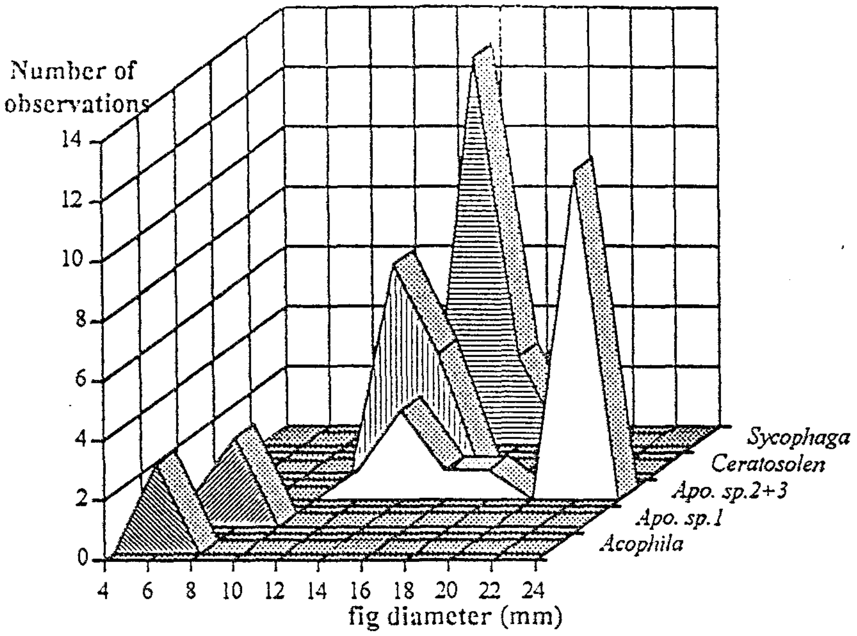

Figure 1. A comparison of the sizes of *F. sur* figs probed by gall-making fig wasps.

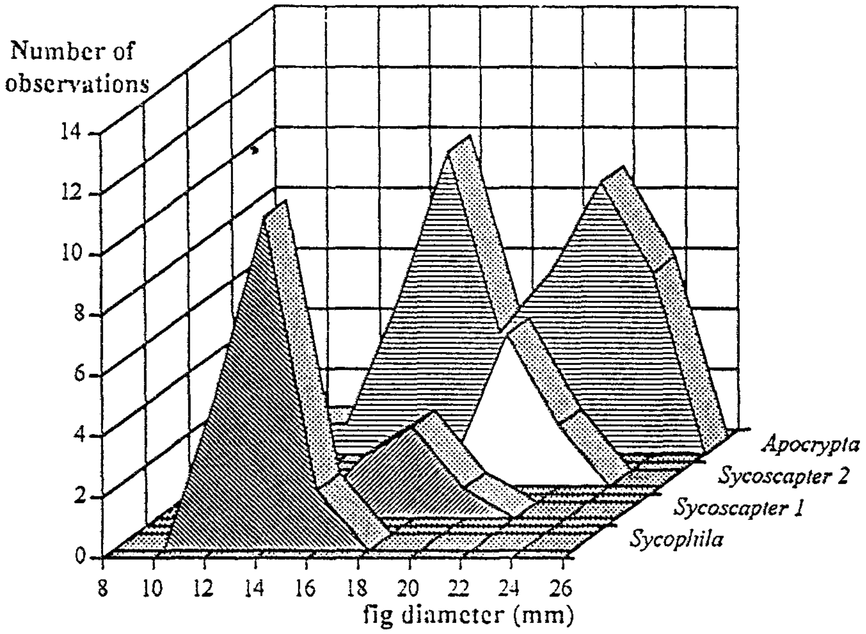

Figure 2. A comparison of the sizes of *F. sur* figs probed by parasitoid fig wasps.

Spatial structuring of resources within figs

The figs of *F. burtt-davyi* and *F. sur* enlarge considerably after pollination (Baijnath and Ramcharun, 1983; Baijnath and Ramcharun, 1988), and ovules become progressively more distant from the periphery of the figs (Nefdt, 1989). Variation in the ovipositor lengths of those fig wasps that oviposit from the outside of the figs might therefore be expected to reflect the timing of their oviposition, with those species with longer ovipositors utilising hosts in older figs. Alternatively, variation in ovipositor lengths might also reflect differential exploitation of hosts at varying depths in the figs (Bronstein, 1991).

In the *F. burtt-davyi* community the ovipositors of the species that oviposit from the outside of the figs show a progressive increase in length that corresponds to the periods when they oviposit (Compton and Nefdt, 1990; Compton, in prep.). Individual ovipositor lengths among the parasitoids associated with *F. sur* are highly variable (Figure 3). Ovipositor lengths again reflect the timing of oviposition by the two *Sycoscapter* species, but the ovipositors of *A. guineensis* are shorter than would have been predicted (Figures 2 and 3).

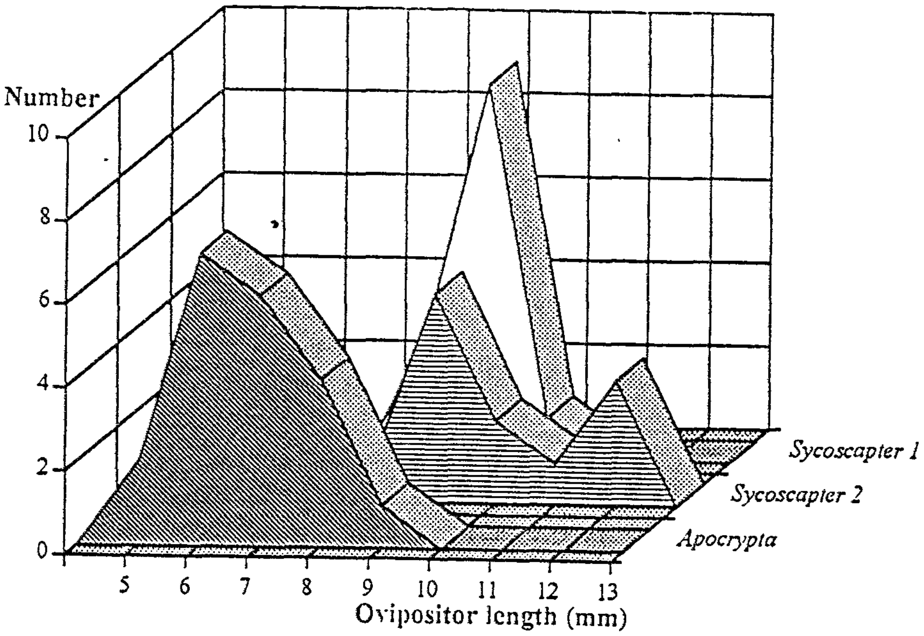

Figure 3. Variation in the ovipositor lengths of parasitoids associated with *F. sur*. Mean ovipositor lengths (+ S.D.) were: *Sycoscapter* sp. 1, 9.2 + 0.4, n = 13; *Sycoscapter* sp.2, 10.3 + 1.3, n = 12; *Apocrypta guineensis* 7.1 + 1.1, n = 20.

Contrary to earlier ideas (Janzen, 1979), style length variation within the figs of African *Ficus* species is unimodal (Nefdt and Compton, in preparation), with no separation into discrete long- and short-styled flowers. The ovipositors of the *E. baijnathi* females that pollinate *F. burtt-davyi* are longer than the majority of the styles and most ovules are therefore available for oviposition (Compton and Nefdt, 1990). In contrast, the *C. capensis* females that pollinate *F. sur* have relatively shorter ovipositors, and the longer-styled flowers are consequently unavailable (Nefdt, 1989).

Flowers with longer styles have ovules closer to the outer surface of the figs, and therefore any larvae they contain are potentially easier to reach by parasitoids probing from the outside of the figs. Conversely, if the parasitoids' ovipositors cannot reach them, larvae developing in the shortest-styled flowers may occupy 'enemy-free space' (Jeffries and Lawton, 1984) and be immune from attack (G. Michaloud, in Kjellberg and Valdeyron, 1984). Interestingly, *E. baijnathi* females preferentially oviposit into the shorter-styled flowers in *F. burtt-davyi* figs, but as the density of wasp foundresses increases, so progressively longer styled flowers are used (Figure 4). Consequently, when they are at higher densities the pollinator larvae may be more accessible to probing parasitoids.

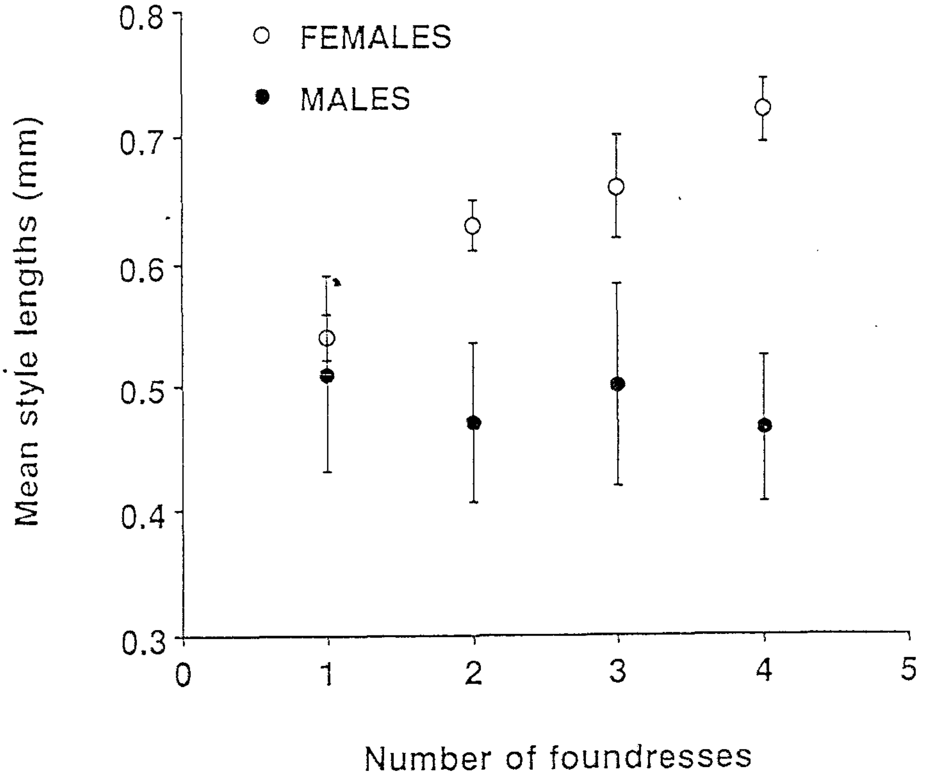

Figure 4. Variation in the mean style lengths of flowers occupied by *Elisabethiella baijnathi* progeny in relation to the number of foundress females entering the figs. The distribution of female progeny changes with increasing density, with more wasps closer to the periphery of the figs, where they are potentially easier to reach by parasitoids ovipositing from the outside of the figs.

The parasitoids associated with *F. burtt-davyi* have ovipositors of sufficient length to reach all the ovules in the figs (Figure 5) and utilization of hosts within the whole range of style lengths has been confirmed (Nefdt, 1989). This is despite the often tortuous routes taken by the ovipositors en route to the ovules (Compton and Nefdt, 1988) and shows that host larvae in the shortest-styled flowers do not occupy 'enemy-free space' in the sense that they are immune from attack from parasitoids. A lack of immunity is also evident when rates of parasitism in *F. burtt-davyi* flowers with different style lengths are considered, as larvae in the shorter-styled flowers are just as likely to be attacked as those at the periphery of the figs (Figure 6; Nefdt, 1989).

Within *F. sur* figs, the depth of the fig wall and the thickness of the zone containing the ovules are highly correlated with overall fig diameter (Figure 7). These changes in the depths that the parasitoids have to probe is reflected in the lengths of their ovipositors, which correspond closely to the depths they have to penetrate (Figure 7). This suggests that spatial partitioning of host utilisation by the parasitoid species is likely to be absent, as is the case with the wasps in *F. burtt-davyi* figs (Nefdt, 1989).

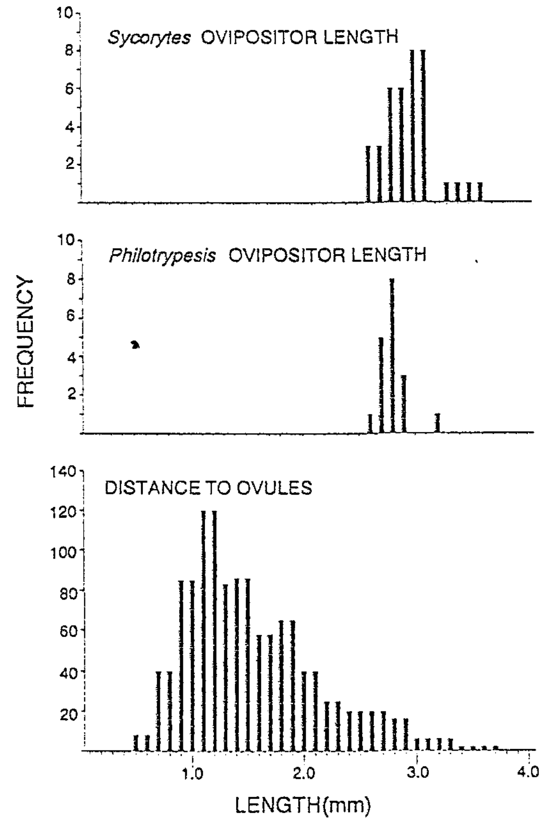

Figure 5. Frequency histograms indicating the lengths of *Sycoscapter* (top) and *Philotrypesis* (middle) ovipositors in relation to the distance they must travel from the outside of the figs to reach the ovules of *F. burtt-davyi* (bottom). The distance from the ovules was measured using figs at the 'inter-floral' phase. *Philotrypesis* oviposits slightly earlier than *Sycoscapter* during this period.

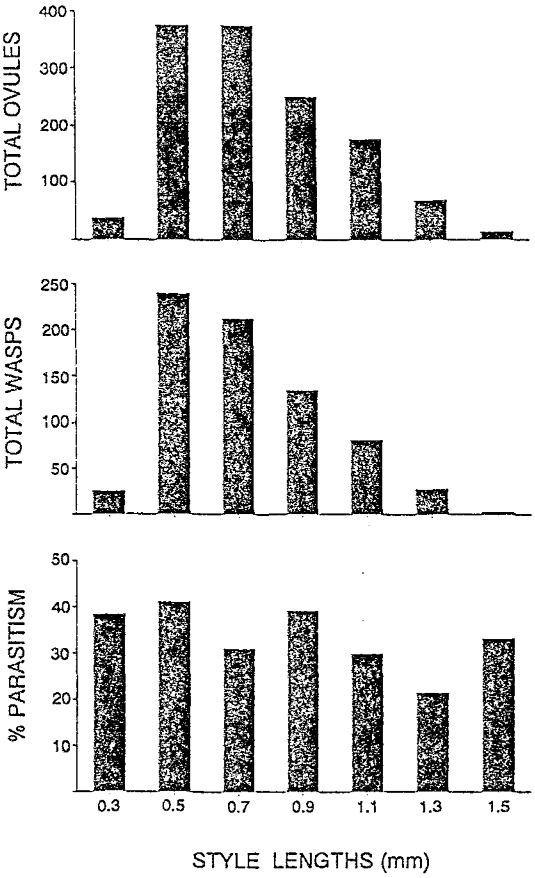

Figure 6. Frequency histograms showing the distribution of flowers of varying style lengths within the figs of *F. burtt-davyi* (top), the numbers of those flowers containing fig wasps (centre) and the relative numbers of parasitoids (bottom). The fig wasps present were *Elisabethiella baijnathi, Otitesella sesquianellata* and *Otitesella uluzi* (gallers), together with *Sycoryctes* sp. and *Philotrypesis* sp. (parasitoids).

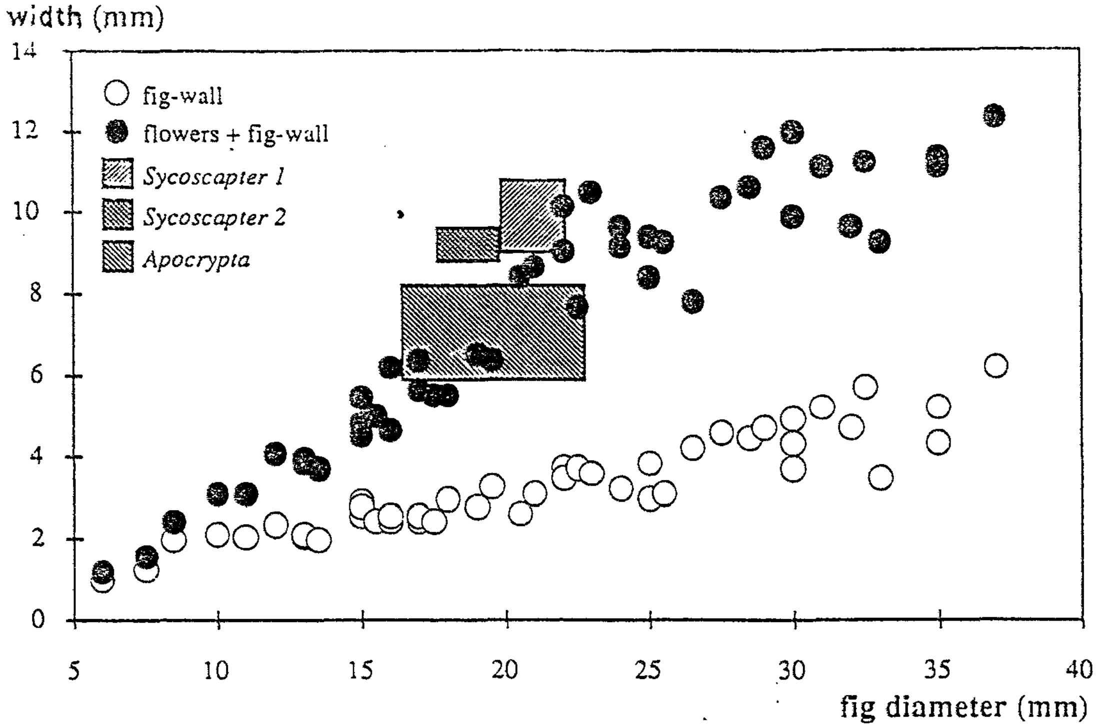

Figure 7. Changes in the distance that parasitoids must probe with increasing diameter of *F. sur* figs. Also indicated are the potential distances that the parasitoids can probe, in relation to the size of the figs at the times when they oviposit. Each block defines one standard deviation from the mean ovipositor length and the mean diameter of figs that were probed by each species.

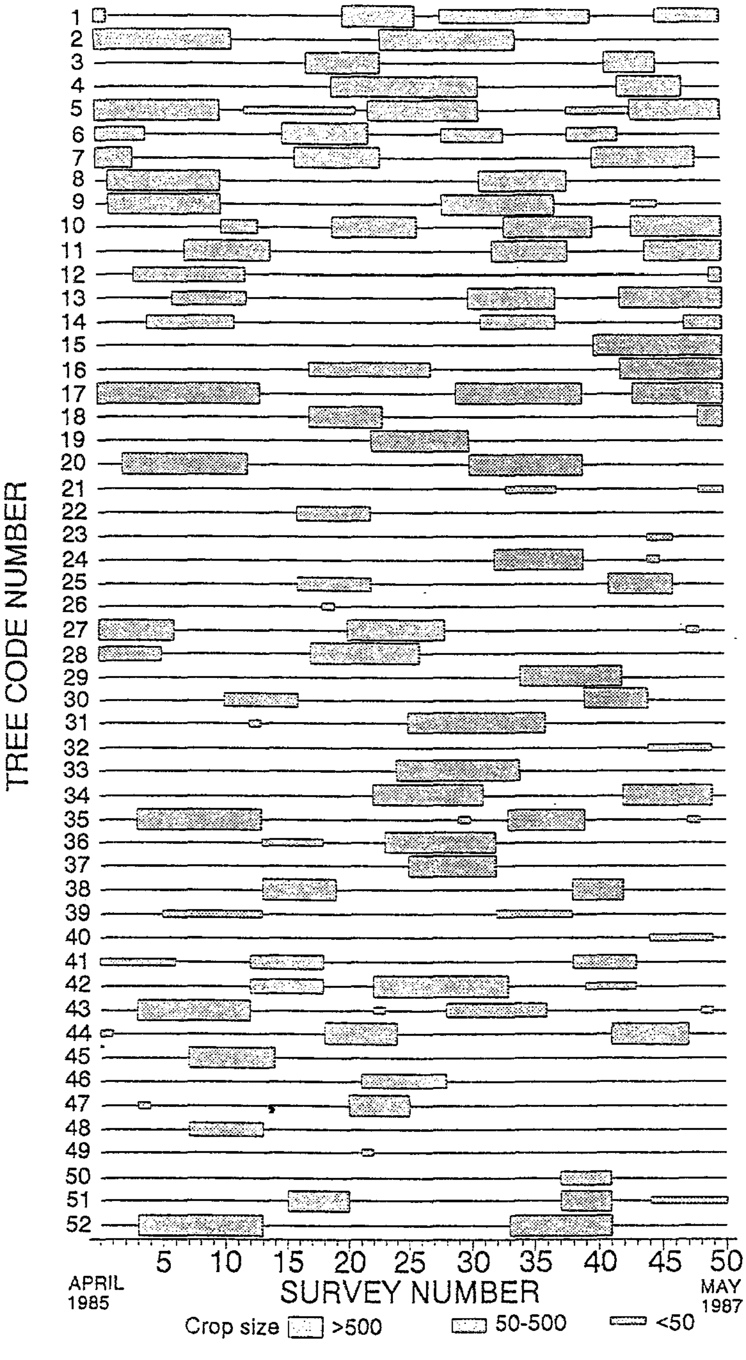

Figure 8. The fruiting patterns of 52 *F. burtt-davyi* trees growing in Grahamstown. The small crops of very short duration (for example on trees 26 and 49) aborted at an early stage of development.

The fruiting phenologies of 52 *F. burtt-davyi* trees growing as rock-splitters in Grahamstown are summarised in Figure 8. Figs were present on a proportion of the trees throughout the two year sampling period, with an overall average of 14.02 (27.0%) bearing figs at any one time. Thus, although there was some seasonal variation in the numbers of crops, with peaks during spring and autumn (Figure 9), figs were available continuously for colonisation. Crop sizes ranged from just a single fig to several tens of thousands. On each tree fig production was synchronised and only two of the crops (<2%) were sufficiently asynchronous for wasps to be able to immediately oviposit on the same tree that they had emerged from.

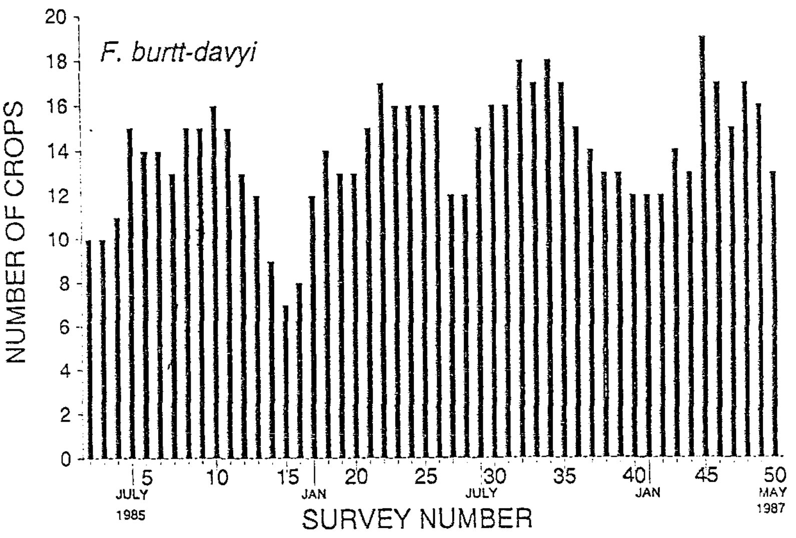

Figure 9. The numbers of *F. burtt-davyi* trees bearing figs in Grahamstown over a two year period. Some figs are present in the area throughout the year, but the abundance of fruiting trees tends to decline during mid-summer and mid-winter.

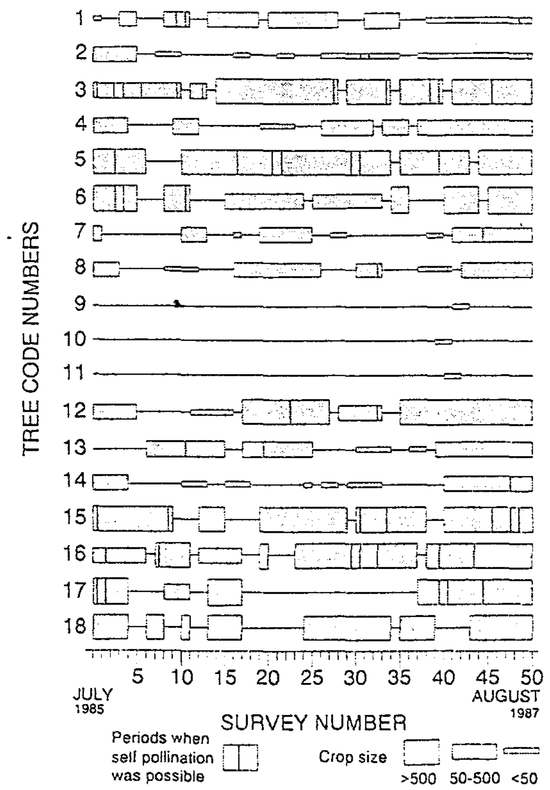

Figure 10. The fruiting patterns of 18 *F. sur* trees growing around Grahamstown. Vertical lines within the bars indicate periods when wasps were emerging while unpollinated figs were present on the same tree.

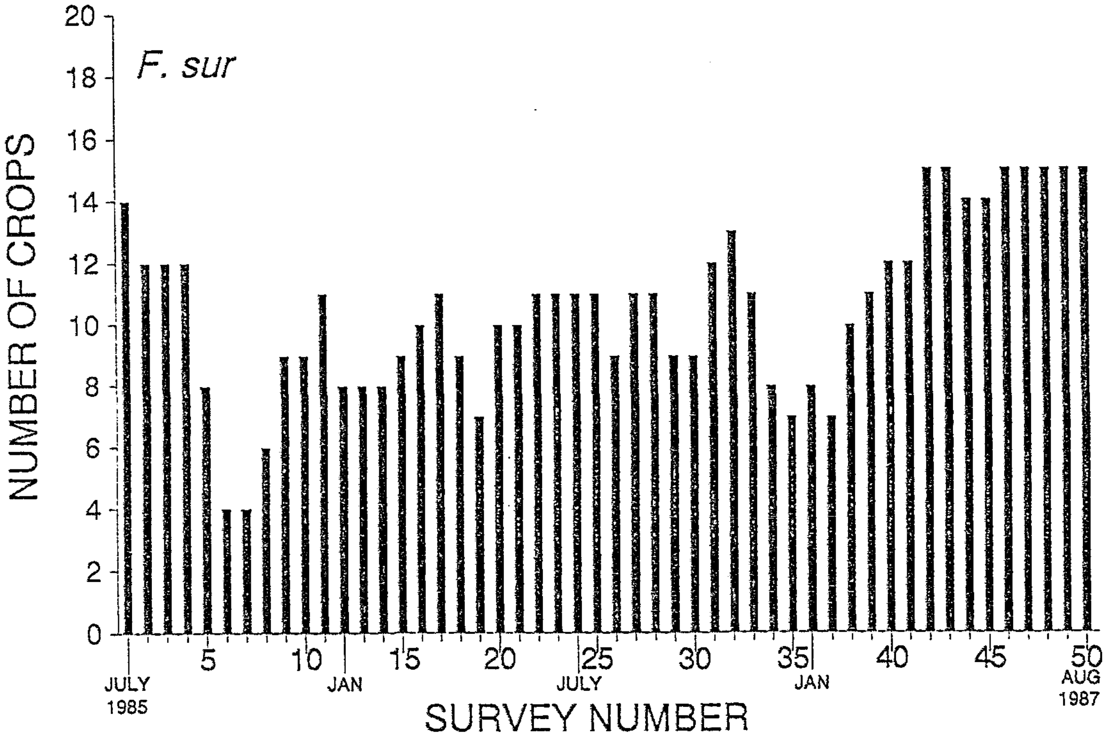

Figure 11. The numbers of *F.sur* trees bearing figs around Grahamstown over a two year period. Figs are present in the area throughout the year, with no clear seasonal trends in abundance. Count numbers 8 and 9 are slight under-estimates, resulting from certain trees being inaccessible due to flooding.

Fruit production among 18 *F. sur* trees in the same area showed a rather different pattern (Figure 10). On most trees the figs were present for a much greater proportion of each year (mean crops per sampling period was 10.6,= 58.9% of the trees) and there were no obvious seasonal patterns in fruiting frequencies (Figure 11). Fruit production within crops was also highly asynchronous on many trees, providing frequent opportunities for self pollination (Figure 9).

The distance that female fig wasps can disperse between trees, and their chances of successfully doing so, will depend on their longevity. In the laboratory, when kept at moderate temperatures and high humidities, adult females of pollinating fig wasps survived at most three days (Table 1). The availability of sugar solution did not increase longevity, suggesting that adults do not feed. Adult females of the other galling species survived rather longer, but sugar only extended the lifespan of *O. uluzi* (*S. cyclostigma* inexplicably survived longer if only water was present). Survivorship patterns were different among the parasitoids, all of which lived for extended periods only if sugar was available (Table 1).

Table 1. The longevities of adult female fig wasps maintained at 20°C and 75-80% relative humidity on diets of either distilled water or a 10% sucrose solution. Mean longevities for *Philotrypesis* sp. and *Apocrypta guineensis* with sugar are underestimates as the trial were terminated after 40 and 60 days respectfully.

Species	Water			Sugar			*Z*	*P*
	N	Mean (days)	Range	N	Mean (days)	Range		
Gallers								
Elisabethiella baijnathi	24	1.25	1-2	25	1.40	1-2	1.10	ns
Ceratosolen capensis	20	2.15	1-3	20	2.15	1-3	-0.03	ns
Phagoblastus sp.	16	3.44	2-5	17	4.06	2-8	0.68	ns
Sycophaga cyclostigma	20	8.40	4-10	20	5.75	2-10	-3.85	***
Otitesella uluzi	26	3.88	2-6	30	14.9	2-34	5.43	***
Apocryptophagus sp. 1	10	9.90	7-12	15	8.27	2-15	-1.21	ns
Parasitoids								
Philotrypesis sp.	18	1.5	1-5	22	24.86	1-40	5.02	***
Sycoscapter sp.	15	4.73	1-9	25	20.64	1-30	4.06	***
Apocrypta guineensis	20	3.35	2-6	14	39.57	3-60	4.54	***

ns = $P > 0.05$; *** = $P < 0.001$

The longevities of adult fig wasps appear to correspond with different oviposition strategies. Those species which enter the figs to oviposit must lay all their eggs within a day or so after entry, as the flowers soon begin to deteriorate (Greef and Compton, personal observations). They are pro-ovigenic (Table 2), with short adult life spans and do not feed. *Apocryptophagous* sp. 1, despite ovipositing from the outside of the figs, appears to have a similar strategy, and seems to be adapted for rapid oviposition. In contrast, the three parasitoids (and the galler, *O. uluzi*) are syn-ovigenic (developing their eggs progressively), with extended life spans, feed on sugar sources and appear adapted for slower rates of oviposition. This is presumably a reflection of the greater difficulties they experience in host finding.

As the gaps between *F. burtt-davyi* crops on a single tree typically extend for several months, the adult wasps cannot normally colonise figs on their natal trees, but have to fly off in search of other fig-bearing trees in the area. The situation is different with *F. sur*, where wasp populations can often cycle on individual trees, without any repeated need for dispersal.

Table 2. Egg loads of galler and parasitoid fig wasps associated with *F. burtt-davyi* and *F. sur*. 'Internal' ovipositing species lay their eggs after entering the figs, while 'external' species lay their eggs from the outside of the figs. Females of syn-ovigenic species contained both mature and developing eggs, whereas pro-ovigenic females contained only mature eggs.

Species	Oviposition	N	Number of eggs		Syn/Pro-ovigenic
			Mean	Range	
Gallers					
Elisabethiella baijnathi	Internal	20	79	67- 94	Pro-ovigenic
Ceratosolen capensis	Internal	20	238	180-370	Pro-ovigenic
Phagoblastus sp.	Internal	20	88	59-121	Pro-ovigenic
Sycophaga cyclostigma	Internal	20	124	96-158	Pro-ovigenic
Otitesella uluzi	External	9	91	65-119	Syn-ovigenic
Apocryptophagus sp.1	External	20	310	210-360	Pro-ovigenic
Parasitoids					
Philotrypesis sp.	External	10	25	15- 36	Syn-ovigenic
Sycoscapter sp.	External	10	41	34- 51	Syn-ovigenic
Apocrypta guineensis	External	10	20	8- 40	Syn-ovigenic

Interactions with ants

A complex mutualism involving ants and *Hilda patruelis* (Tettigometridae), a honeydew-producing homopteran, develops on trees belonging to several African *Ficus* species, including *F. sur* (Compton and Robertson, 1988, 1990). Ants are attracted on to the figs by the honeydew, where they then disturb wasps that are trying to oviposit through the fig wall, capturing some of them. This results in lower rates of parasitism by *A. guineensis*, which can be more or less excluded from individual figs or even whole trees where ant densities are highest. External-ovipositing ovule-gallers like *Apocryptophagus* spp. are also affected, but fig wasps that oviposit from the inside of the figs, such as the pollinators, are relatively immune from the ants, because they spend little time on the fig surface. Consequently, the presence of *H. patruelis* leads to reduced levels of parasitism of the tree's pollinators, together with reduced ovule-destruction, and an indirect mutualism between the tree and the ants is established.

In contrast to *F. sur*, *F. burtt-davyi* is rarely colonised by *H. patruelis*. As alternative attractants for ants are also uncommon, the parasitoids can probe the figs with much reduced risks of predation. The *H.*

patruelis - ant combination occurs on a large proportion of *F. sur* trees and others in *Ficus* subgenus Sycomorus throughout Africa (Cushman *et al.*, in prep.). The frequent presence of ants on trees belonging to this subgenus has not influenced fig wasp species richness- they have just as many associated wasps as other monoecious fig trees (Compton and Hawkins, 1992). However, among the drosophilid flies that also breed in the figs, it has resulted in changes in courtship behaviour that improve the chances of escaping from the ants (Lachaise and McEvey, 1990). Similar selection pressures for ant avoidance are likely to be operating on the parasitoids which utilise species such as *F. sur*, but comparisons of features such as probing times or mobility between species such as *A. guineensis* and the parasitoids from *F. burtt-davyi* have not been made.

Regional scale influences on community richness

Table 3. Species richness of local and sub-regional fig wasp communities associated with *F. sur* in southern Africa. 'North' includes Zimbabwe, Zambia and Malawi. Local parasitoid richness is significantly lower in the Cape than in Natal (Mann-Whitney, $Z = 2.88$, $P < 0.01$) and the Transvaal (Mann-Whitney, $Z = 1.98$, $P < 0.05$), but not elsewhere. Local galler richness in the Cape was not significantly different from the three other subregions.

Subregions	Number of Samples	Regional Pools		Mean Local Richness	
		Gallers	Parasitoids	Gallers	Parasitoids
North	10	6	3	2.80	1.10
Transvaal	14	7	5	3.36	1.57
Natal	8	6	4	3.75	1.88
Cape	15	5	1	3.00	1.00

Grahamstown is situated close to the southern edge of the range of *F. sur*, and several species found further north are absent from this sub-region. A total of twelve fig wasp species have been recorded from *F. sur* in southern Africa, of which 11 were collected in Transvaal, 10 in Natal and just six in the Cape Province (Table 3). Of the six species which fail to reach the far south of the continent, five are putative parasitoids. This is not due to undersampling in the Cape, as sample-recruitment curves (Figure 12) suggest that no new species are likely to be collected there. Within South Africa there is thus a north to south decline in the species richness of the communities in the different sub-regions, but this simple latitudinal pattern does not appear to extend further north into the tropics, where sub- regional richness may even decline (Figure 12).

The variation in the sizes of the sub-regional communities is reflected in the species richness of local fig wasp communities found on individual trees (Table 3). Local communities in the Cape are significantly depauperate in parasitoid species compared with the other regions of South Africa, but are not depauperate in gallers.

F. burtt-davyi has a much smaller distribution than *F. sur*, but habitat-related differences in fig wasp community composition can be detected even within a localised area of the eastern Cape. In the coastal forests around Alexandria the ovule-galling *Phagoblastus* is far more common than around Grahamstown, and an additional *Sycoscapter* parasitoid is also present. This increased sub-regional species pool has a corresponding influence on average local community richness (the wasps colonising individual trees), which is significantly higher in the forests (Table 4). The rarity / absence of certain species around Grahamstown may reflect its more extreme climate, with hotter summers and colder winters than the coastal areas, although they are only about 80 km apart.

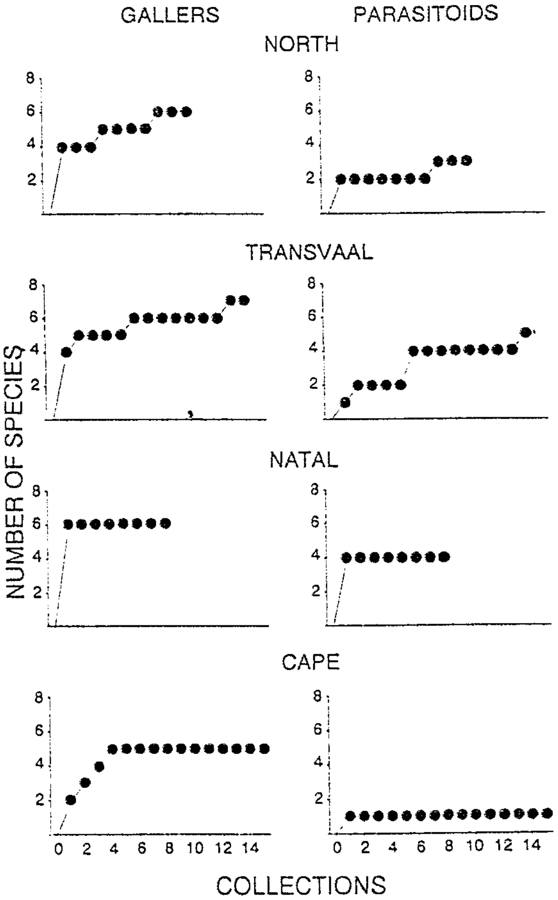

Figure 12. Sample recruitment curves for collections of wasps from figs of *F. sur* in four sub-regions of southern Africa. 'North' includes Zimbabwe, Zambia and Malawi. Transvaal, Natal and Cape are provinces of South Africa. The flattening of the curves suggests that all the species associated with *F. sur* in the Cape have been collected.

Table 4. A comparison of the species richness of local fig wasp communities associated with *F. burtt-davyi* in forest and inland areas of the eastern Cape (South Africa).

	Alexandria Forest			Grahamstown			Mann-Whitney Z	*P*
	N	Mean	Range	N	Mean	Range		
Gallers	10	3.40	2-4	30	2.50	1-4	-2.84	**
Parasitoids	10	2.30	1-3	30	1.53	0-2	-2.81	**

** = $P < 0.01$

AFRICAN FIG WASP COMMUNITIES IN GENERAL

As with *F. sur* and *F. burtt-davyi* , African fig wasp communities are typically composed of a single species of pollinating wasp, with larvae that develop inside galled ovules (Verkerke, 1989), together with other wasp species that gall the ovules, and their parasitoids. In rare instances the communities may also include a second species of pollinator, as in *F. sur*, (Michaloud *et al.*, 1985) or wasps that gall the vegetative parts of the figs (Compton and van Noort, in press; Rasplus, unpublished).

Table 5. The distribution of parasitoid genera within the southern African subgenera and subsections of *Ficus*.

Subgenera	Sycidium	Sycomorus	Urostigma				
Subsections			*Urostigma*	*Galoglychia*	*Platyphyllae*	*Chlamydodorae*	*Caulocarpae*
Wasp genera							
Apocrypta		+					
Watshamiella		+	+	+	+	+	+
Sycoscapter	+	+	+	+	+	+	+
Philotrypesis	+		+	+	+	+	+
Ormyrus						+	+
Eurytomidae (various)		+	+	+	+	+	+

So far as is known, there is a general consistency in trophic relationships within the various taxonomic groups of fig wasps (Compton and van Noort, in press), but this may partly reflect the small number of species that have had their biology investigated. In southern Africa, gallers are found in Agaoninae, Sycoecinae, Epichrysomallinae, Sycophaginae and Otitesellinae (all Agaonidae), while parasitoids are found within the Sycoryctinae (Agaonidae), the Eurytomidae and Ormyridae. The mix of putative parasitoids potentially associated with each fig species is largely independent of a tree's taxonomic affiliations because most of the genera that contain parasitoids are widely distributed among the taxonomic subdivisions of *Ficus* (Table 5). *Apocrypta* is an exception as it is restricted to subgenus Sycomorus (Ulenberg, 1985), where it 'replaces' *Philotrypesis*.

Host tree specificity is well developed among the pollinating fig wasps, with each *Ficus* species generally having its own unique species of agaonine (Wiebes and Compton, 1990). Tree specificity is also well developed among the gall-forming sycoecine wasps (van Noort, 1991), epichrysomalline wasps (Rasplus, unpublished) and in the parasitoid genus *Apocrypta* (Ulenberg, 1985). Equivalent data for other parasitoid groups is not available. Similarly, the extent of host insect specificity among parasitoid fig wasps is largely unknown, although an association between epichrysomalline and eurytomid fig wasps is evident (Compton, in press). Eurytomids have not been recorded from *Ficus* species that do not also support epichrysomalline fig wasps, and this relationship also extends to individual crops or figs.

In the southern African fig wasp communities analyzed by Compton and Hawkins (1992) and Hawkins and Compton (1992) the total fig wasp faunas associated with different *Ficus* ranged from about 3-30 species, with the numbers of putative parasitoid species varying between 1 and 18. Parasitoid: galler ratios varied from about 3:1 to 1:3, with phytophagous species outnumbered parasitoids in many of the communities. Factors influencing the species richness of the gallers in the communities included ecological factors such as the size of the trees and the habitats where they occur, but species-area effects were not significant (Compton and Hawkins, 1992). The numbers of parasitoid species were strongly correlated with the number of gallers in each community, and thus presumably the diversity of potential hosts. Dioecious fig species also supported fewer wasps than monoecious species.

Only sub-sets of the total fig wasp faunas associated with each Ficus species form the local communities found on any individual crop. Nonetheless, as many as 18 species, 11 of them putative parasitoids, have been reared from one *F. thonningii* crop, with up to nine species (five parasitoids) occupying a single fig

(Compton, unpublished). The major factor determining parasitoid community richness at the level of individual crops was the size of the regional pool associated with that particular tree species (Hawkins and Compton, 1992). Local and regional diversities were linearly related, with no evidence of saturation of local communities. Latitudinal gradients in local community species richness were also present among the parasitoids, with marginally fewer species present at more tropical latitudes. No equivalent gradient was detected among the gall-forming groups.

DISCUSSION

How do fig wasp parasitoid communities compare with the better-known north temperate systems that are also based around endophytic hosts? One noticeable feature is that fig wasp parasitoid: host ratios are markedly lower than in parasitoid communities centred on hosts that gall or mine trees (Askew, 1975; Askew and Shaw, 1986) and they are more typical of those found in early successional communities centred on 'unapparent' herbs (Askew, 1980; Hawkins, 1988; Hawkins *et al.*, 1990; Tscharntke, 1992). Another 'early-successional' feature of fig wasp parasitoids may be their high host plant specificity, at least in the best-studied genus, *Apocrypta*. This is against the general pattern, where parasitoid communities on trees are dominated by generalists (Askew, 1980; Hawkins *et al.*, 1990; Rasplus, this volume) and could explain the lack of saturation in fig wasp communities (Hawkins and Compton, 1992). The parasitoid faunas associated with *F. burtt-davyi* and *F. sur* nonetheless show that not all fig wasp parasitoids are necessarily tree specific.

Early successional communities contain host plants with low apparency, that are relatively difficult to detect by parasitoids (Askew and Shaw, 1986). Despite their often large stature, fig trees may also be exceptionally unapparent to searching parasitoids. This is because the trees can be at low densities, especially in tropical forests (Gautier-Hion and Michaloud, 1989), and at any one time only a fraction of them are bearing figs, and hence offer potential hosts. The problem of host finding is especially acute for parasitoids associated with dioecious *Ficus* species, where at times of the year figs on most of the trees may contain no hosts at all (Kjellberg *et al.*, 1987; Nair and Abdurahiman, 1984). Furthermore, on trees with phenologies like that of *F. burtt-davyi*, only one parasitoid generation can be produced before dispersal is required again.

There is a second, and quite different, possible explanation for the low parasitoid:galler ratios in fig wasp communities, which would also explain the apparent prevalence of entomophytophagous parasitoids. Seeds of most plants are rich in 'secondary compounds', many of which are toxic and may have a defensive function (Janzen, 1969). Fig seeds, however, are unlikely to contain any such defensive compounds, because the trees are totally reliant on pollinating fig wasps, the larvae of which also feed on the seeds. Consequently, fig seeds may be unusually easy to eat.

Price (1991) has suggested that parasitoids are less likely to be regulating their host populations in communities like those of fig wasps where ratios of parasitoid species to host species are low. The results of a life table study of the wasps from *F. burtt-davyi* agree with this prediction (Compton and Robertson, in prep.). Average rates of parasitism of *E. baijnathi* in Grahamstown tend to be less than 10% and key factor analysis suggests that parasitoids are a minor factor in comparison with the mortalities that occur during the movement of adults between trees. Pollinator parasitism rates were perhaps slightly higher at Lamto, where about 25% of the emerging adults were *A. guineensis*.

In concluding a review of fig wasp parasitoids it is perhaps prudent to emphasise just how little is known about them. In particular we lack such basic information as whether they are all genuinely parasitoids, how host specific they are or even how many species we are dealing with. Abdurahiman and Joseph (1978b) and Joseph (1984) have shown that phytophagous fig wasps have enlarged acid glands, the contents of which are presumably used to gall the ovaries, whereas in parasitoid species these glands are reduced. Direct observations on the biology of even a majority of the species in a continent as under-studied as Africa is unlikely ever to happen, and this anatomical difference may provide the 'short-cut' that is required, once the species have been clearly delimited. Systematic treatments of three African phytophagous groups are available or in preparation, covering the Agaoninae, Sycoecinae and Epichrysomallinae (by J. T. Wiebes, S. van Noort and J.-Y. Rasplus respectively), but Ulenberg's (1985) revision of *Apocrypta* remains the only detailed coverage of any of the parasitoid groups. This lack of basic taxonomic information remains the major obstacle impeding community level studies of these fascinating insects.

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CHAPTER 9

SYNOPSIS

These studies encompassed many aspects which govern the interactions between figs and their fig wasps. In this section the individual research projects making up the thesis are placed in perspective and avenues for future research are explored.

Survey results of figs and their associated pollinators showed that each *Ficus* species was generally associated with a single pollinating wasp species (Papers 1 and 2). Exceptions where more than one species of pollinator was associated with a 'single' fig species are discussed in Paper 1. The situation was resolved for one of these discrepencies when *F. sakalavarum* was reclassified as a distinct species with its own specific pollinator wasp species (Paper 2).

In order to maintain this specificity, fig wasps must be able to differentiate between their host *Ficus* and congeneric species. Biological evidence for such recognition of *Ficus* by their pollinators is presented in Papers 3 and 4. *Elisabethiella baijnathi* was attracted to receptive figs of its host tree, *F. burtt-davyi*, even when visual contact was excluded by surrounding the figs with cotton bags. These experiments confirmed the volatile nature of the attractants and showed that they were only present when the figs were ready to be pollinated. Other parts of the host plant, pollinated figs and figs of other species did not attract *E. baijnathi*. The arrivals of fig wasps at the trees of two conspecific *Ficus* species over a two year period confirmed that these wasp species were only attracted to their host trees when they were bearing figs that were ready to be pollinated. The two species of pollinating fig wasps were only trapped at bagged figs of their respective host trees confirming both the volatile nature of the attractants and their specificity in attracting only their specific pollinator.

The chemical basis for such species-specific volatile attractants was examined in Paper 5 where charcoal-trapped fig volatiles were analyzed by gas chromatography. Not only did the figs of each *Ficus* species examined present a unique volatile profile, but additional components were recorded only at the time when figs became attractive to their pollinators. These additional compounds, alone or in combination with the other volatile components, probably form the basis of the fig wasp attraction.

Perception of the volatiles emanating from the figs which are ready to be pollinated will be influenced by environmental conditions and the pollinators will have to adopt appropriate behaviours in order to find the volatile source. In the first of the two papers examining fig wasp dispersal behaviour (Paper 6), fig wasp departures from their natal tree and their arrivals at trees bearing receptive figs was examined. Ambient temperatures were found to influence the timing of fig wasp emergence from their natal figs. The lowest temperature at which the pollinating fig wasps began to emerge from their natal figs was found to be related to the critical take-off temperature of the wasps. *E. baijnathi* females arriving at a new host fig avoided figs that already contained a conspecific foundress. In Paper 7 the dispersal of the wasps was examined. Air movement influenced both the fig wasps departing from their natal trees and those arriving at trees bearing receptive figs. On departure from their natal trees, the wasps flew upward and were then carried with the wind. On arrival at a host tree bearing figs ready to be pollinated, the wasps approach the tree from downwind and close to the ground.

Chemosensory receptors of insects are generally found on the antennae. Paper 8 examines some techniques for preparing fig wasp for examination under scanning electron microscopy. In Paper 9 the occurrence of elongated multiporous plate sensilla was examined. Although elongation of the mutiporous sensilla is common among male chalcids, among female chalcids it may uniquely occur among some species of pollinating fig wasp. Elongation results in increased sensilla surface area and may have evolved in order to detect the minute quantities of volatiles emanating from figs ready to be pollinated.

Two cases where more than one pollinator species was recorded from a single *Ficus* species was investigated. In Paper 10 we examined the biology of the 'cuckoo' of *F. sycomorus*, *C. galili*, which exploited the mutualism between *F. sycomorus* and its pollinator *C. arabicus* by utilising the ovules without pollinating the figs. In the second case examined, three pollinator wasp species were found to simultaneously pollinate the figs of a single *F. lutea* (Paper 11). The small number of its normally associated pollinator that were present are thought to have travelled long distances to find this host tree and as a result a large proportion of the crop remained unpollinated. The two other pollinating fig wasp species were shown to have been "incidental" arrivals and had not been attracted to the tree. Although hybrid seeds from the two fig crosses did germinate, the seedlings did not grow beyond the cotyledon stage of development and this may indicate post germination weakness / inviability.

Pollinator fig wasps represent only one species member of the fig wasp community associated with each *Ficus* species. In Paper 12 the consequences of the structure of the fig and the trees' phenologies on the biology of these non-pollinating fig wasps were examined. The influence of ants and homopterans on the populations was discussed as was community species composition.

Future Research

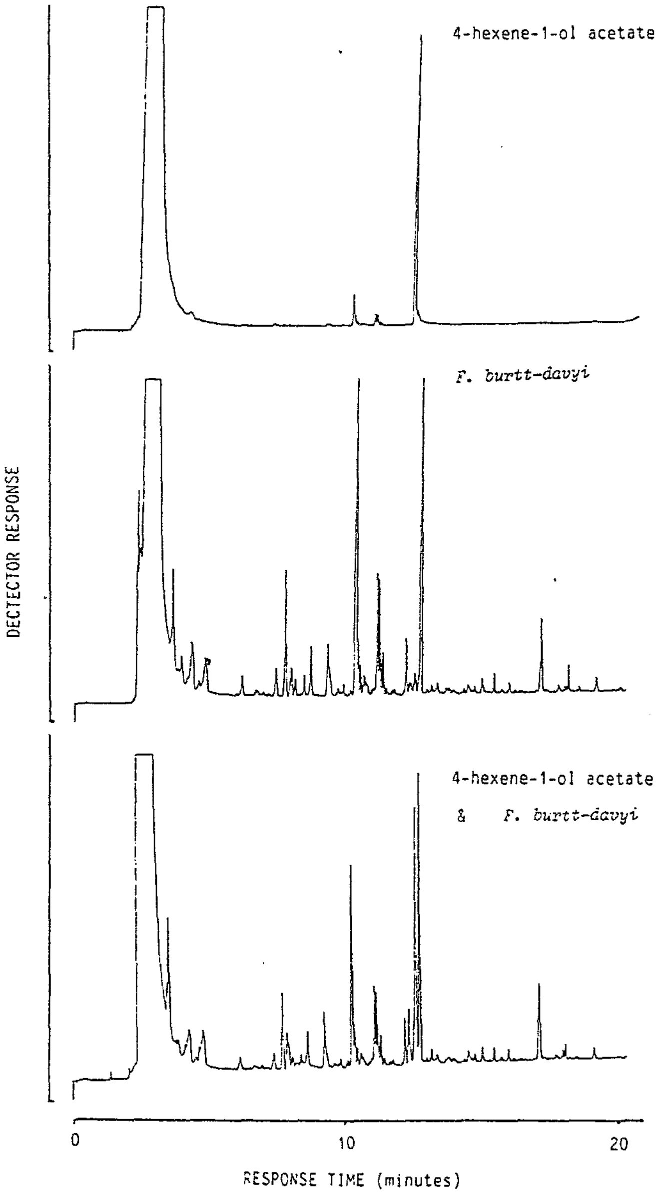

Figure 1. Gas chromatogram of 4-hexene-1-ol acetate and its coelution with the volatiles from receptive *F. burtt-davyi* figs.

Both the biological and the chromatographic evidence showed that volatiles emanating from the figs when they are ready to be pollinated are responsible for attracting the pollinators. The next logical phase of research should be to isolate, identify and synthesise the compound(s) concerned. An attempt was made to identify the additional volatile compound present in the chromatograph of receptive figs of *F. burtt-davyi*. High resolution GC-MS analysis (done at Oxford University) identified the volatile in question as 4-hexene-1-ol acetate. The compound was synthesised, but unfortunately did not coelute when rerun with the original sample (Figure 1). As the equipment available at Rhodes University was not suitable for this type of analysis this avenue of research was abandoned.

Although aspects of fig wasp biology outside the figs were investigated, little is known about how far the wasps can travel when in search of receptive figs. Indications are that they do not usually venture far (Paper 7) although small numbers may travel long distances (Paper 11). A mark - release - recapture program, perhaps using fluorescent dyes or powders, should be able to determine at what distance volatiles are perceived.

The volatile(s) attracting the wasps to their hosts are thought to be detected by the multiporous plate sensilla positioned on the antennae of the wasps. Once the volatile attractants have been synthesised, electroantennogram studies would be able to confirm that the function of these sensilla is the perception of these volatiles.

The apparent breakdowns of wasp host choice may be an indication that cryptic tree species and/or wasp species are involved. For example, morphological variation within species may account for the differences between *Elisabethiella stuckenbergi* and *E. socotrensis*, both of which are found in figs of southern African *F. natalensis* subspecies *natalensis*. If the wasps prove to be distinct species then there may be two cryptic *Ficus* species. Analysis of the wasp mitochondrial DNA could determine their species status. Similarly, using chloroplast DNA, fig trees of the difficult "thonningii / natalensis" complex could potentially be assigned to definite species.

Perhaps the central question of fig biology is: Have figs and fig wasps co-evolved? The generally observed one *Ficus* species / one agaonine species relationship is certainly highly suggestive the two groups have coevolved but conclusive proof is still needed. By determining the phylogenies of both figs and their pollinating fig wasps independently, possibly using DNA restriction fragment polymorphism techniques they could be compared. If the phylogenies produced in this manner could be shown to mirror one another, then figs and their associated fig wasps could be said to have co-evolved.