Dynamics of *Blastophaga psenes* Populations, Availability of Caprifigs, and Fig Endosepsis Caused by *Fusarium moniliforme*

T. J. Michailides and D. P. Morgan

Associate plant pathologist and staff research associate, respectively, Department of Plant Pathology, University of California, Davis, Kearney Agricultural Center, 9240 S. Riverbend Ave., Parlier 93648.

We thank M. A. Doster and J. Rasmussen for their help with the statistics and graphics, K. Herman, W. Butler, M. Dibenedetto, and P. Meslé for providing sites and donating caprifigs and Calimyrna figs for these experiments. Research support provided by the California Fig Institute and the California Dried Fig Board (Fresno, California).

Accepted for publication 17 August 1994.

ABSTRACT

Michailides, T. J., and Morgan, D. P. 1994. Dynamics of *Blastophaga psenes* populations, availability of caprifigs, and fig endosepsis caused by *Fusarium moniliforme*. Phytopathology 84:1254-1263.

Propagules of *Fusarium moniliforme*, which causes endosepsis of Calimyrna figs, were vectored on the body of the fig wasp pollinators, *Blastophaga psenes*. Scanning electron microscopy indicated that microconidia and mycelial fragments of *F. moniliforme* were attached to the wasps' bodies along with grains of pollen. Contamination of adult fig wasps occurred after they emerged from the flower galls, the specialized flowers within a fig syconium in which the wasp eggs hatch and develop. No adult wasps artificially removed from the flower galls were infested with propagules of *F. moniliforme* but 91–100% of those that emerged from infected syconia of pollinator cultivars (caprifigs) became contaminated. On bagged branches, more than twice as many spring crop caprifigs were infested with *F. moniliforme* after pollination with five or 10 winter crop caprifigs than when only a single winter crop caprifig was used. Similarly, more than twice as many wasps emerging from spring crop caprifigs that had been pollinated with five or 10 winter crop caprifigs were infested with *F. moniliforme* than were wasps from spring crop caprifigs pollinated with only one winter crop caprifig. Furthermore, pollination of Calimyrna figs with spring crop caprifigs that had been pollinated with five or 10 winter crop caprifigs resulted in higher incidence of endosepsis than when only one winter crop caprifig was used. The use of more spring crop caprifigs than necessary for pollination of Calimyrna fig increased the number of wasps entering the cavities of Calimyrna syconia. The relationship between the number of wasps in the syconium cavity and incidence of endosepsis in the cavity or ostiole of Calimyrna syconia was described with a second degree polynomial equation ($R^2 = 0.94 - 0.98$; $P < 0.01$). The presence of three or more wasps in the fruit cavity resulted in 100% incidence of *F. moniliforme* on the ostioles while the presence of five or more wasps resulted in 100% incidence of contamination within the cavity. In the field, incidence of fig endosepsis increased when high populations of wasps coincided with limited availability of receptive fruit crop.

Additional keywords: caprification, eye-end rot, internal rot, pink rot, symbiosis, vector.

The edible Calimyrna fig (*Ficus carica* L.) and the inedible, pollinating caprifig (*F. carica* L.) are gynodioecious plant species linked by the pollinator fig wasp (*Blastophaga psenes* L.) (34). For reproduction, fig wasps depend on the ovaries of figs in which their larvae develop (34). The fruit of both edible and inedible figs contains numerous ovaries and is called a syconium (Fig. 1). In an immature syconium, tightly packed florets line the inner wall of a fleshy, hollow receptacle. The wasp gains to access the interior florets via an apical ostiole, which is lined with overlapping scales (Fig. 1).

Syconia of the inedible caprifigs bear both female and male flowers in each syconium (hermaphrodites) (Fig. 1) while the syconium of the Calimyrna fig bears only female flowers (3). Caprifig trees produce three to four crops of syconia annually (Fig. 2) (5). The winter crop (mamme) is initiated in the fall and matures in late winter (mid- to late March). The spring crop (profichi) is initiated in late winter and matures in mid-spring (beginning of June). The scant summer crop (mammoni) develops either single or double fruits during summer and autumn. The spring crop of caprifig syconia (profichi) contain the most pollen and are used directly for the pollination of the Calimyrna edible figs (Fig. 2).

Fig fruits of the edible Calimyrna cultivar are susceptible to several diseases among which smut (caused by *Aspergillus niger* Tiegh. [9,30] and other *Aspergillus* spp.) and endosepsis (caused mainly by *Fusarium moniliforme* J. Sheld.) are the most damaging. Figs are also afflicted by a complex of diseases causing mold (*Alternaria, Penicillium, Eurotium,* and *Cladosporium* spp.) or souring (caused by various species of yeasts [9,32]). Smut and mold have been very damaging to the fig industry in some years. For instance, during 1979 to 1990, smut and mold ranged from 4.5 to 17.3% and sour rot from 2.1 to 6.1% of merchantable Calimyrna figs (California Fig Institute, *unpublished data*). Although smut disease is the subject of a separate investigation, in this study we do report whether overpollination had any effects on these diseases; this research, however, emphasized the effects of overpollination on fig endosepsis.

F. moniliforme infects both caprifigs and edible figs, causing fig endosepsis. The first detailed description of fig endosepsis and its transmission by the fig wasp pollinators concluded that the wasps carried *F. moniliforme* propagules on their wings (6). However, the wings and the greater part of the antennae detach as she enters a syconium (2,10,17). Thus, it is not known if the wasp carries conidia of *F. moniliforme* directly into the cavity on her body, or if the fungus grows through the ostiole (Fig. 1).

The discovery that the fig wasp causes endosepsis by vectoring spores of *F. moniliforme* from the caprifig (in which the disease is endemic) to the edible Calimyrna fig, led to legislation to culture caprifig trees and the Calimyrna trees in separate locations (33). Typically, growers of Calimyrna fig either maintain separate isolated caprifig orchards or purchase spring crop caprifig figs that have been managed to reduce incidence of endosepsis (12,20, 21,27). This management involves collecting the winter crop in mid-March, splitting each fig in half, and then either dipping (26,27) or spraying the fig halves with fungicides (20). The treated winter crop caprifig halves are placed in small paper bags and hung back on the caprifig trees to pollinate the young spring crop caprifigs (Fig. 2).

Pollination of Calimyrna fig flowers occurs when the young figs are 9.5–13 mm in diameter. Four to five pollen-loaded, spring crop caprifigs are hung in Calimyrna orchards at 3- to 5-day intervals over a 2- to 3-wk period. The efficiency of pollination is monitored by splitting fruit and checking the presence or absence of wasps in the fruit cavity. Growers, however, occasionally overpollinate the Calimyrna crop. Overpollination can cause excessive fig splitting, but in some years also can increase yields. There are no experimental data concerning the effects of overpollination on fig endosepsis or on the relationship of the wasps' population dynamics. Consequently, we undertook this study 1) to explain how fig wasps become contaminated with propagules of *F. moniliforme*, 2) to evaluate the effects of overpollination on the incidence of endosepsis and other diseases in both caprifigs and Calimyrna figs, and 3) to ascertain the relationships among the population dynamics of fig wasps, caprifig crop availability, and the incidence of endosepsis. Parts of this study have been reported previously (17,18).

MATERIALS AND METHODS

Contamination of fig wasp with *F. moniliforme*. To determine when wasps become contaminated with propagules of *F. moniliforme*, adult wasps were sampled from spring crop caprifig orchards in June and July in 1989, with four sampling methods. First, wasps were collected by placing a sterile glass tube (18 × 2 cm) secured with sticky tape to the ostiolar end of fruit during morning (9:00 A.M.). Fruit chosen for sampling showed signs of loosening of the ostiolar scales, which is when mature fig wasps usually begin to emerge. The test tubes remained attached to the fig fruit for 2 h, which was sufficient to collect at least 50 wasps per test tube. Second, five samples each of 50 emerged wasps were collected arbitrarily from trees in a commercial caprifig orchard in sterile paper bags. Third, mature caprifigs were collected, surface disinfected in 0.08% NaOCl, and placed individually in a sterile glass beaker (250 cm^3) covered with sterile mesh to prevent wasp escape. Fourth, in the laboratory, near-to-mature female and male wasps were dissected directly from the inflorescence galls (flower galls) of mature spring crop caprifigs with the aid of a dissecting microscope (10–20×), and sterile transfer needle and tweezers. Upon removal from the galls, each wasp was squeezed (killed) with the tweezers and five replicates of 35–50 female wasps were selected arbitrarily and placed in petri dishes (9 cm diameter, 7–10 insects per dish) that contained acidified (2.5 ml of a 25%, v/v, lactic acid per liter of medium) potato-dextrose agar (APDA). The dishes were incubated at 23–25 C and the fungi developed from the wasps were recorded 5 days later. Most of the above experiments were repeated on several dates. The means and their standard deviations of the incidences of *F. moniliforme* and *Alternaria* spp. were calculated and presented for each collection method on each sampling date.

Male and female wasps obtained from caprifigs also were prepared for scanning electron microscopy. Insects were fixed in 1% glutaraldehyde in a 0.01 M phosphate buffer (pH = 7.2) for 24 h, rinsed in three half-hour changes of distilled water, dehydrated in ethanol (stepwise in 30, 60, 80, 95, 95, and 95% for 1 h in each step), then stored in 100% ethanol (200 proof) until used. Prior to observation, the insects were critical point dried with carbon dioxide, glued on small aluminum strips, and mounted on SEM stubs. The samples were coated with 60% palladium-40% gold, observed with a scanning electron microscope (International Scientific Instruments DS-130, Santa Clara, CA [dual stage, 10kV, 1.2 A]), and photographed. The spores of *F. moniliforme* were identified based on their characteristic shape and dimensions, using the illustrated manual for identification of *Fusarium* spp. by Nelson et al (25) and those of *Alternaria* and *Cladosporium* spp. based on their shape, dimensions, and characteristic ornamentation (7,11).

Effects of number of winter crop caprifigs on contamination of fig wasps, incidence of *F. moniliforme* in spring crop caprifigs, and endosepsis in Calimyrna figs. Winter crop caprifigs were collected from a commercial orchard, surface disinfected in 0.08% NaOCl for 2 min, sprayed with 95% ethanol, allowed to dry, and then split in halves with a sterile knife. Figs with golden yellow to rusty brown internal color, a symptom associated with the early stages of infections by *F. moniliforme*, were separated for use in a second experiment. The symptomless caprifig halves were arranged in one layer over clean paper towels and one, five, or 10 halves taken arbitrarily were each placed in a sterile brown paper bag (12.5 × 25.0 cm). Ten bags were prepared for each number of fig halves. The bags were closed, arranged in randomized complete block design, and incubated at 25 C for 9 days. After 24–48 h, 35 dead wasps were selected from each replicated bag and placed in five 60-mm petri dishes that contained APDA (seven wasps per dish). The incidence of *F. moniliforme* and other fungi growing on the medium was recorded after 5

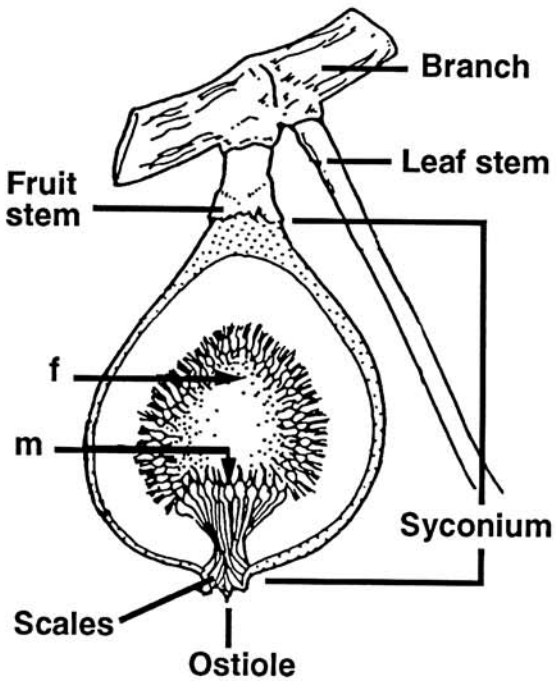

Fig. 1. The fig syconium, depicting the various parts of female (f) and male (m) inflorescences.

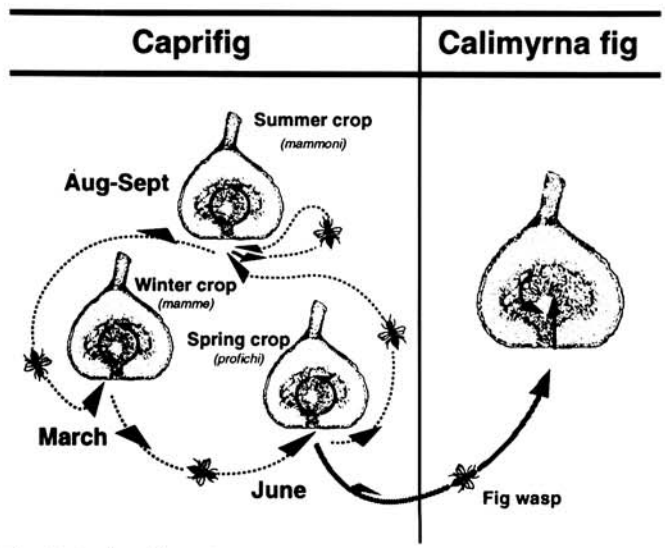

Fig. 2. A simplified diagram of pollination in nonedible caprifigs and edible Calimyrna figs (*Ficus carica* L.). Caprifig trees produce three major crops per year: winter crop (mamme), spring crop (profichi), and summer crop (mammoni). The spring crop caprifigs are collected by the growers, and hung in the orchards of Calimyrna trees so fig wasps (*Blastophaga psenes* L.) can deposit pollen grains in the fruits of Calimyrna fig trees.

days incubation at 25 C. This experiment was repeated twice with other batches of symptomless figs and two additional experiments were done, with figs showing the discoloration symptoms of endosepsis. Analysis of variance was used with the least significant difference (LSD) for mean separation. Incidences of fungi were transformed with the standard arcsine square root transformation only when the variances failed the *F*-max test for homogeneity of variances (8).

Field experiments were established in early March 1987 in an orchard of caprifig trees of cv. Roeding 3 in Madera County. Winter crop caprifigs were removed from 28 shoots bearing 15–25 spring crop syconia and the shoots were covered individually with bags (100 × 50 cm) made from 100% cotton organdy. On 31 March, when spring crop syconia were receptive to the wasps, one, five, or 10 halves of winter crop caprifigs (in 12.5 × 7.0 cm paper bags) were placed in four sets of seven cotton bags. The process was repeated 5 days later so that each treatment had 0, 1 + 1, 5 + 5, or 10 + 10 halves of winter crop caprifigs per bag. Treatment-replications were arranged in a randomized complete block design. Spring crop caprifigs collected from each shoot were evaluated macroscopically as healthy or diseased (obvious external decay). Figs were then split in half and placed in plastic containers with the inflorescences facing up. Three to four drops of melted APDA (45 C) were placed in each cavity of the split figs (19). Incidence of *F. moniliforme* and other fungi growing on the APDA was recorded after 4–5 days of incubation at 23–25 C.

The above experiment was repeated in 1992 and 1993. Spring crop caprifigs were bagged and incubated with one, five, or 10 halves of winter crop caprifigs on 26 and 31 March 1992 and on 23 and 29 March 1993. On 19 May 1992 and 24 May 1993, 28 shoots bearing 10–19 fruit on 15 different Calimyrna trees were covered with cotton bags that had been washed previously in chlorinated water. Two spring crop caprifigs from each treatment were transferred to bagged shoots on Calimyrna trees on 21 May 1992 or 7 June 1993. One or two additional caprifigs were added to each bag on 1 June 1992 or 11 June 1993. Treatments were replicated seven times. Other spring crop caprifigs were collected on 1 June 1992 and 11 June 1993 and sealed in paper bags. After 5 days emerged wasps were counted, and 100 wasps per replication were placed on APDA (10 wasps/dish). Calimyrna figs were harvested on 3 September 1992 and 10 September 1993. Each time, Calimyrna syconia figs were examined for obvious fungal decay, and the incidence of *F. moniliforme* and other filamentous fungi was determined with the agar-drop technique as described above (19). In both years, fruit from nonpollinated controls (bagged shoots to which no wasps were introduced) was evaluated for the incidence of *F. moniliforme* and other fungi, as above (19). The relationships between the number (0, 1, 5, and 10) of winter crop caprifigs bagged with spring crop caprifigs that were used for pollinating the Calimyrna figs and the incidences of *F. moniliforme* in spring crop caprifigs (cavity or ostiole), in wasps emerged from spring crop caprifigs, and of endosepsis disease in Calimyrna figs, were determined with regression procedures (SAS Institute Inc., Cary, NC, release 6.04).

Relationship of flying adult female wasps, availability of caprifig syconia, and fig endosepsis. Flying fig wasp populations were monitored at three locations: 1) from 20 April until 10 November 1989 in a commercial caprifig orchard in Madera County (containing trees of cvs. Roeding 3 and Stanford); 2) in a row of 15 caprifig trees at the Kearney Agricultural Center in Parlier, California, from 13 April until 25 July 1989, and 3) from 23 March through 15 October 1993 in a commercial caprifig orchard in Tulare County (also containing Roeding 3 and Stanford trees). Three to four yellow sticky traps (Pherocon A.M. Trap, Trécé, Inc., Salinas, CA) were hung in trees at each location, and were replaced every 2 wk except for the last set of traps, which was allowed to stay in the field for approximately 50 days.

At the same locations, incidence of endosepsis in caprifigs was determined by periodically collecting six samples of 20 syconia from six trees in the proximity of the sticky traps (for sampling dates see Fig. 3). For all samples, the agar-drop technique (19) was used to determine incidence of *F. moniliforme* and other fungi. In addition, the number of caprifig syconia available for pollination as wasp emerged from the previous crop was determined periodically on 10 random shoots on each of three Roeding 3 and three Stanford caprifig trees in the commercial orchards.

The incidence of *F. moniliforme* on summer crop caprifigs was also determined in 1990 in the orchard in Tulare County and three other caprifig orchards, one each in Fresno, Madera, and Merced counties. Eighty to 120 summer crop caprifigs were collected on each sampling date (sampling from 23 June to 20 October) and processed with the agar-drop technique (19) as described previously. In addition, to determine the levels of contamination of wasps emerging from summer crop caprifigs, on 22 September and 18 October 300 wasps were collected arbitrarily from mature caprifigs in the orchard in Tulare County and placed on dishes containing APDA (10 per dish) as described

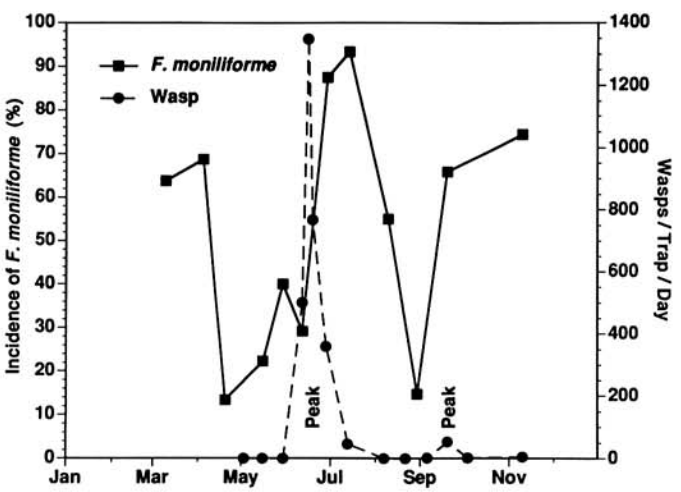

Fig. 3. Flights of fig wasps (*Blastophaga psenes*) in a caprifig orchard in Merced County in 1989 and incidence of *Fusarium moniliforme* in winter, spring, and summer crop caprifigs. Points represent the average number of wasps on four yellow sticky traps and mean incidence of *F. moniliforme* in seven 20-fruit samples.

TABLE 1. Incidence of *Fusarium moniliforme* and *Alternaria* spp. on fig wasps (*Blastophaga psenes*) that matured in spring crop caprifigs (*Ficus carica*)

Date	Wasp collection method	Incidence (%)[a,b]	
		F. moniliforme	*Alternaria* spp.[c]
5 May	From flower galls	0.0 ± 0.0	0.0 ± 0.0
17 June	From plant surfaces	42.0 ± 5.4	53.2 ± 7.3
	At emergence from syconium[d]	2.0 ± 0.9	0.0 ± 0.0
	From flower galls	0.0 ± 0.0	0.0 ± 0.0
23 June	From plant surfaces	78.5 ± 10.2	34.1 ± 9.4
	At emergence from syconium[e]	33.5 ± 7.1	2.0 ± 0.5
	From flower galls	0.0 ± 0.0	0.0 ± 0.0
1 July	From plant surfaces	54.0 ± 8.1	70.4 ± 11.6
	At emergence from syconium[d]	7.6 ± 2.7	0.0 ± 0.0
	At emergence from syconium[e]	4.4 ± 0.9	0.0 ± 0.0
	From flower galls	0.0 ± 0.0	0.0 ± 0.0
1 July	At emergence from diseased syconium	91.0 ± 4.2 – 100.0[f]	...

[a] Incidence was based on five replications of 35–50 wasps incubated on acidified potato-dextrose agar.
[b] Values are means ± standard deviations.
[c] *Alternaria alternata* comprised more than 95% of isolates recovered.
[d] In 250-ml sterile beakers covered with a nylon mesh (0.5 mm opening).
[e] In sterile glass tube secured with a tape to the ostiolar end of the syconium.
[f] In two experiments, respectively.

previously. Data were summarized by calculating the mean and standard deviation for numbers of caprifigs per 10 shoots of each cultivar, fig wasps captured per trap, and incidence of *F. moniliforme* on summer crop caprifigs and of wasps that had emerged from these caprifigs on each sampling date.

Effects of numbers of wasps in fruit syconia on disease incidence. To determine how numbers of wasps affect incidence of endosepsis in Calimyrna figs, a Calimyrna orchard that contained a Roeding 3 caprifig tree located on the west border of the orchard was selected and sampled in 1992 and 1993. In June, 2–3 wk after pollination, 40 Calimyrna fruits were arbitrarily collected from each of 12–25 trees located 3–16 m away from the caprifig tree. Sampling dates were 5 June 1992 and 17 June 1993. All the figs were surface sterilized, allowed to dry, and split in half aseptically; the numbers of wasps in their cavities were counted with the aid of a dissecting microscope (10–20×). Subsequently, fig halves were divided into three groups: halves with zero; halves with one, two, three, four and five wasps; and halves with 6–25 wasps per cavity. Halves were placed in plastic containers with the cut surface facing up. Four drops of melted APDA were placed in each cavity as

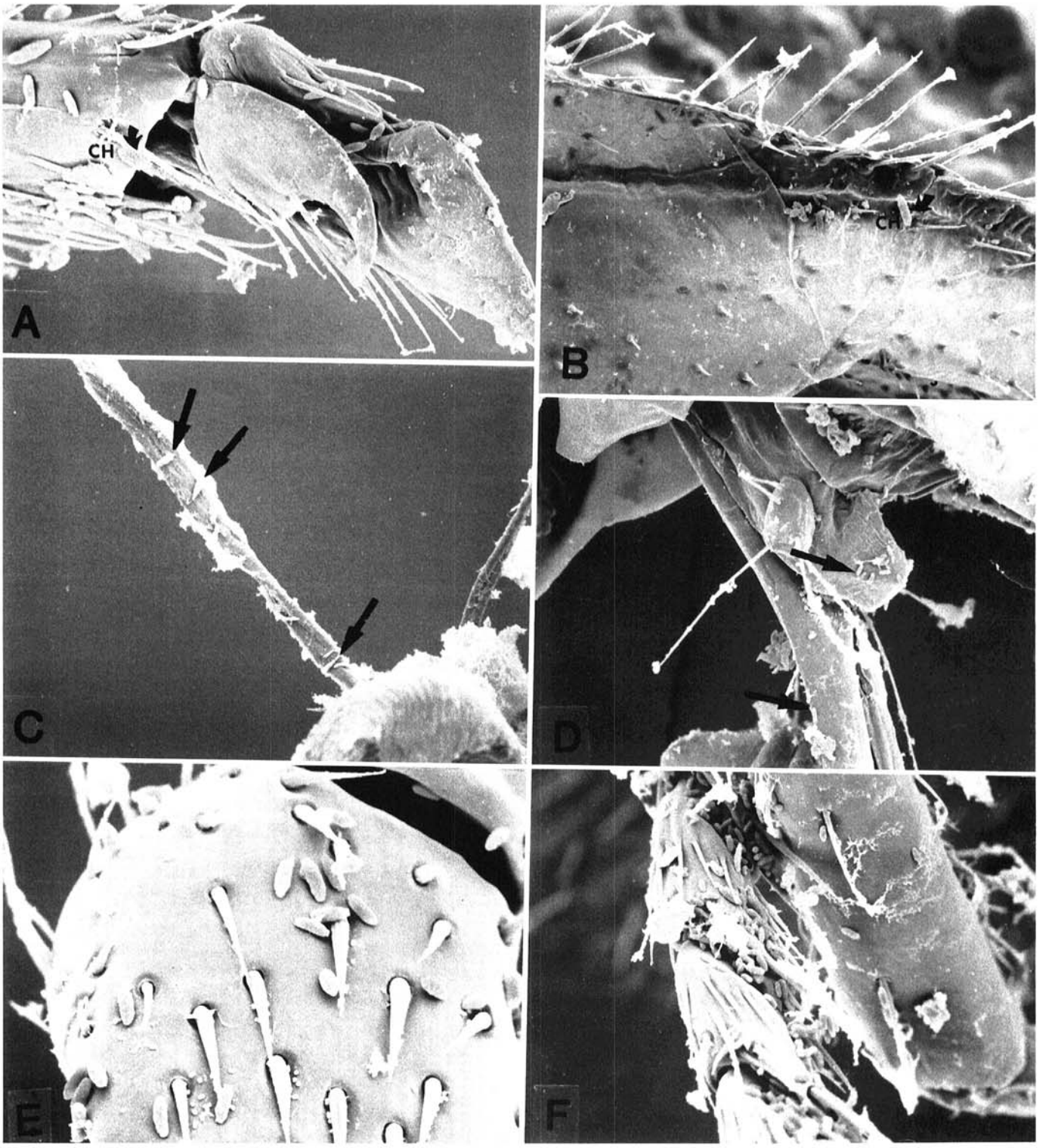

Fig. 4. Scanning electron micrographs of body parts of fig wasp (*Blastophaga psenes*) emerged from winter crop (mamme) caprifigs showing attached propagules of *Fusarium moniliforme*. Spores (microconidia) on **A,** leg (1,030×), **B,** wing (520×), **C,** antennae (235×), **D,** ovipositor (515×), and **E and F,** on different leg parts of fig wasps (1,550x [**E**] & 820x [**F**]). CH (in **A** and **B**) indicates spores of a *Cladosporium* sp.

previously described (19). *F. moniliforme* and other molds were recorded after 4–6 days incubation at 23 C. The relationship between the numbers (0–6) of wasps in a syconium of a Calimyrna fruit and the incidence of *F. moniliforme* in the ostiole or cavity was determined with a regression procedure (SAS Institute Inc., Cary, NC, release 6.04). For this analysis, figs containing 6–25 wasps were considered as having six wasps since 100% of these figs were infested with *F. moniliforme*.

RESULTS

Contamination of fig wasps with *F. moniliforme* and other fungi. *F. moniliforme* was not detected on any female wasps dissected from flower galls of caprifigs (Table 1). In the field emerged wasps collected from plant surfaces had a significantly higher incidence of both *F. moniliforme* and *Alternaria* spp. than those captured in sterile test tubes or beakers as they emerged from syconia, regardless of the collection date (Table 1). Ninety-one to 100% of the wasps emerged from diseased spring crop caprifigs were contaminated with *F. moniliforme* (Table 1). *Alternaria* spp. were recovered consistently only on wasps collected from plant surface. Incidence of *F. moniliforme* on wasps at emergence from syconia was similar among sampling dates except for 23 June, on which incidence of *F. moniliforme* was significantly higher (Table 1).

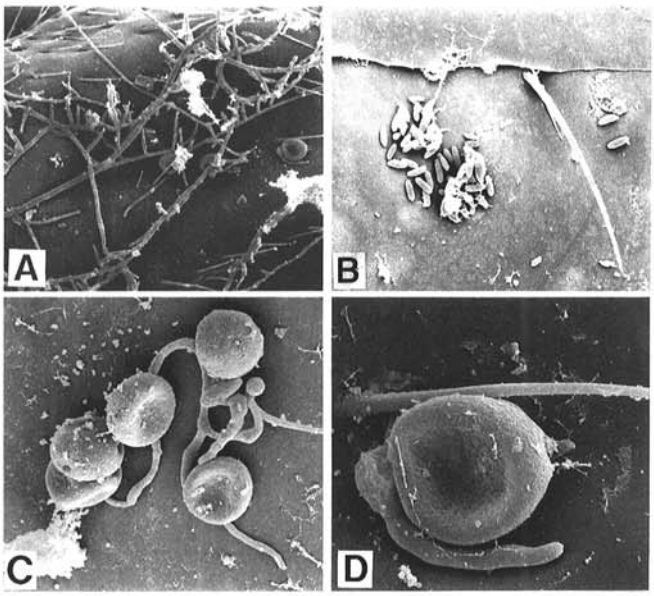

Fig. 5. Scanning electron micrographs of body parts of female fig wasps (*Blastophaga psenes*). **A,** Mycelium, conidiophores (phialides), microconidia of *Fusarium moniliforme,* and pollen grains on the leg of a fig wasp (240×); **B,** a group of microconidia of *F. moniliforme* on a segment of the abdomen of a female wasp (550×); **C,** germinated pollen grains and microconidia of *F. moniliforme* on the body of wasp (775×); and **D,** a germinated fig pollen grain held by a hair on the leg of a female wasp (1,610×).

Scanning electron microscopy. Microconidia of *F. moniliforme*, measuring (3.5)–4.5–(6.5) mm in length, were abundant on almost all insect parts as well as on the bodies of male and female wasps emerged from winter crop caprifigs (Fig. 4A–F). Legs of female wasps (Fig. 4A), wings (Fig. 4B), antennae (Fig. 4C), ovipositor (Fig. 4D), and legs of male wasps (Fig. 4E & F) had numerous microconidia of *F. moniliforme*. In some cases, spores of *A. alternata* and *Cladosporium* spp. were also observed on the wasps (Fig. 4A-B [ch]).

Both female and male wasps obtained from spring crop caprifigs had abundant fig pollen grains, which averaged 12.3 μm in diameter. In addition, microconidia of *F. moniliforme*, mycelia, and phialides were observed on both female and male wasps (Fig. 5). Mycelial fragments with phialides (Fig. 5A), groups of microconidia (Fig. 5B), germinated microconidia of *F. moniliforme* among pollen grains (Fig. 5C), and germinated pollen grains (Fig. 5D) were also present on the body of female wasps emerged from spring crop caprifigs.

Effects of number of winter crop caprifigs on contamination of fig wasps. In two of the three experiments, the incidence of contamination of *F. moniliforme* on wasps that had emerged from five or 10 winter crop caprifigs enclosed in the paper bags was significantly higher than the contamination of wasps that had emerged from one winter crop caprifig (Table 2). Similarly, in all experiments, the incidence of wasps contaminated with *Cladosporium* spp. was greater for the 10 caprifig treatment than for the five or one caprifigs; differences in incidences of wasps contaminated with *Alternaria* spp. or yeasts were noted in only one experiment (Table 2).

Regardless of the number of winter crop caprifigs enclosed in the bags, the incidence of *F. moniliforme* on wasps that had emerged from caprifigs with symptoms of endosepsis ranged from 38–89% (Table 3) compared with 2–58% for symptomless syconia (Table 2). There were no significant differences among the treatments for the incidence of *F. moniliforme* and the other filamentous fungi and yeasts recovered from these wasps. Other fungi recovered occasionally from wasps placed on APDA were *A.*

TABLE 2. Effects of number of symptomless winter crop caprifigs (*Ficus carica*) enclosed in paper bags on contamination of fig wasps[a] with *Fusarium moniliforme* and other fungi and yeasts

Exp.[b]	Number of winter crop caprifigs	Incidence (%)[c]			
		F. moniliforme	*Alternaria* spp.	*Cladosporium* spp.	Yeasts
1	1	7.4	1.0	8.5	14.0
	5	10.7	0.0	3.2	21.0
	10	27.6	1.0	15.8	22.6
	$LSD_{0.05}$	17.1	1.1	10.4	28.1
2	1	10.2	0.5	0.7	21.4
	5	13.0	0.6	1.6	12.4
	10	17.0	0.6	12.4	14.4
	$LSD_{0.05}$	22.3	1.1	6.6	19.7
3	1	0.4 (3.7)[d]	0.1 (1.5)	3.5 (10.8)	4.5 (13.7)
	5	61.8 (57.6)	0.1 (1.5)	2.4 (9.0)	0.1 (1.1)
	10	36.6 (37.3)	3.0 (9.9)	22.1 (28.0)	11.5 (19.8)
	$LSD_{0.05}$	... (19.7)	... (4.8)	... (10.5)	... (11.6)

[a] Fig wasps matured and emerged from the caprifigs while in the paper bag.
[b] Experiments 1 and 2 had ten and experiment 3 had five replications in which one, five, or ten halves of winter crop caprifigs were enclosed in paper bags.
[c] Averages from ten (exp. 1 and 2) or five (exp. 3) replications of five petri dishes that contained acidified potato-dextrose agar and ten wasps per dish; the dishes were incubated at 23 C for 5–7 days.
[d] Values in parentheses are the means of the transformed data, using the standard arcsine transformation; the statistical analysis was performed on the transformed data.

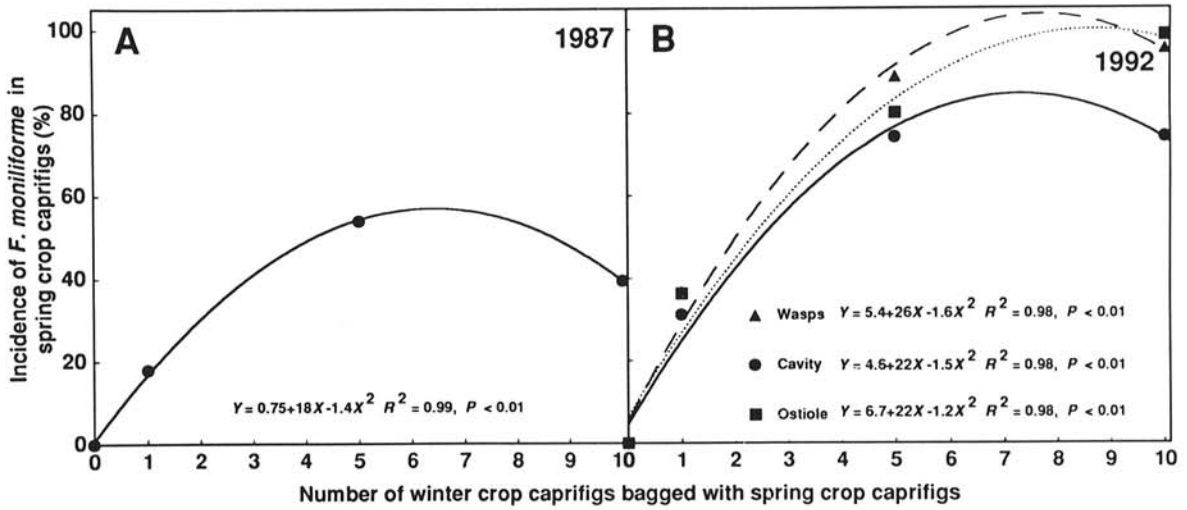

Fig. 6. Effects of number of winter crop (mamme) caprifigs used for pollination of spring crop (profichi) caprifigs on incidence of *Fusarium moniliforme*: **A,** in the cavity of spring crop caprifigs (in 1987); **B,** in the cavity and ostiole of spring crop caprifigs, and on wasps emerged from these fruits (in 1992). Data points represent the average of seven replications of 10–15 fruits and 50 wasps per replication.

niger, Botrytis cinerea Pers.:Fr., *Paecilomyces lilacinus* (Thom) R. A. Samson, and *Penicillium* spp.

Effects of number of winter crop caprifigs on incidence of *F. moniliforme* on spring crop caprifigs and endosepsis in Calimyrna figs. In 1987 and 1992, more than twice as many spring crop caprifigs were infested in the cavity by *F. moniliforme* after pollination with five or 10 winter crop caprifigs than with one (Fig. 6A and B). Contamination of ostioles with *F. moniliforme* followed the same pattern as cavity contamination (Fig. 6B). In contrast, 35% of spring crop caprifigs pollinated with one winter crop caprifig were contaminated by *Cladosporium* spp. but only 12 and 8% of spring crop caprifigs pollinated with five and 10 winter crop caprifigs, respectively. Other fungi most frequently recovered with the agar-drop technique from these figs were *Alternaria* and *Penicillium* spp., *P. lilacinus,* and various yeasts.

In both 1992 and 1993, the fewest wasps (227 and 304, respectively) hatched from spring crop caprifigs pollinated with 10 winter crop caprifigs and the most (364 and 470, respectively) from those pollinated with one winter crop caprifig; the mean numbers (310 in 1992 and 449 in 1993) of wasps hatched from spring crop pollinated with five winter crop caprifigs ranged between those of wasps emerged from caprifigs of the two other treatments. More than twice as many wasps that emerged from spring crop caprifigs pollinated with five or 10 winter crop syconia were contaminated with *F. moniliforme* than wasps that emerged from spring crop caprifigs pollinated with only one winter crop caprifig (Fig. 6B).

The relationships of the number of winter crop caprifigs bagged with spring crop caprifigs and the incidence of *F. moniliforme* in the cavity, the ostiole, and the plated wasps were quadratic ($P < 0.01$) with a maximum level of contamination occurring with six to eight winter crop caprifigs. *Cladosporium* and *B. cinerea* were associated with 52 and 25%, respectively, of wasps that had emerged from spring crop caprifigs pollinated with only one winter crop syconium. The incidence of *Penicillium* spp., however, was significantly ($P < 0.05$) higher on wasps emerged from spring crop caprifigs pollinated with five or 10 than with one winter crop caprifig (data are not shown). Nonpollinated controls enlarged to 25–35 mm, turned yellow within 2 wk after bagging, and dehisced from the shoot; no fungi developed on the solidified agar drops placed in the cavity of these nonpollinated syconia.

In 1992, Calimyrna syconia pollinated with spring crop caprifigs that had been pollinated with five or 10 winter crop caprifigs averaged 88–92% incidence of endosepsis but only 60% were infected when the caprifig used was pollinated with a single syconium from the winter crop (Fig. 7). In 1993, 38 and 63% of the Calimyrna figs pollinated with spring crop caprifigs that had been with five and 10 winter crop syconia, respectively, were infested by *F. moniliforme* (endosepsis disease) but only 14% of those pollinated with caprifigs that had been pollinated with a single syconium (Fig. 7). The relationship between the number of winter crop caprifigs bagged with spring crop caprifigs and incidence of endosepsis of Calimyrna was quadratic ($R^2 = 0.86 - 0.99$; $P < 0.05$). The number of winter crop caprifigs used to pollinate spring crop caprifigs did not affect the levels of smut (6–8% in 1992 and 0–7% in 1993) or Alternaria mold (0–5% in 1992 and 19-44% in 1993; caused by *A. alternata* (Fr.:Fr.) Keissl.) in Calimyrna figs (9). In both years, when caprifigs were not added to bagged Calimyrna shoots, the syconia enlarged up to 25 mm, turned yellow, and dehisced from the shoot into the bag. No fungi developed on the solidified agar drops placed in the cavity of non-pollinated Calimyrna figs.

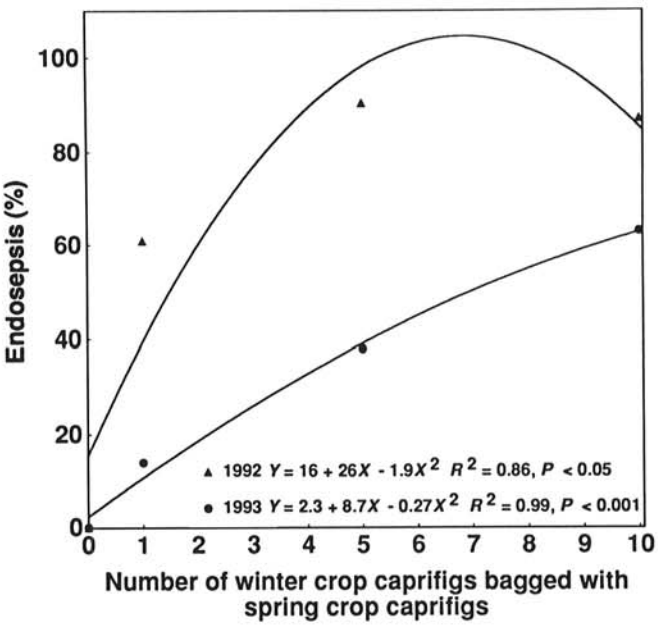

Fig. 7. Effect of number of winter crop (mamme) caprifigs used for pollinating spring crop (profichi) caprifigs, which were then used to pollinate Calimyrna figs, on the incidence of endosepsis of dry Calimyrna fruit. Data are the average of seven replications of 10–15 fruits collected on 4 September 1992 and 10 September 1993.

Relationship of flying adult female wasps, availability of caprifig syconia, and fig endosepsis. In the orchards in Merced and Tulare

counties, the number of wasps captured on sticky traps peaked in mid-June in both 1989 (Fig. 3) and 1993. Wasp populations decreased significantly in late July 1989 and in early July 1993. In each year, a second peak in the wasp population occurred during late September to early October (Table 4). In the orchard at Kearney Agricultural Center, the first peak in flying wasps occurred during the first week of June, with 240 wasps captured per trap per day from late May to early June. By the end of June, an average of only 1.3 wasps were captured per trap per day. A small peak (10 wasps/trap/day) was detected near the end of March 1993 in the orchard in Tulare County.

The availability of summer crop caprifigs present during the season in the orchard in Merced County increased with time for both Stanford and Roeding 3 cultivars (Table 4). The lowest number of syconia available for pollination occurred at the end of June, following the peak of flying wasps in mid-June (Table 4 and Fig. 3). Up to 21 wasps were observed in some of the summer crop caprifigs in July 1988 and June 1993. An average of eight wasp females was recorded for caprifigs collected on 3 July 1989. In this orchard, the incidence of *F. moniliforme* from the end of June to the beginning of July ranged from 80–90% (Fig. 3). In contrast, in the experimental orchard at Kearney Agriculture Center, six to seven summer crop caprifigs were recorded per shoot in June 1989 with one to three wasps per syconium, and the incidence of *F. moniliforme* was only 23.3%. In 1993, in the orchard in Tulare County, 0.2–1.0 summer crop caprifigs were recorded per shoot 1 July but the number of fruit increased to 3.3–5.7 per shoot by 15 October. In this orchard, 86% of the caprifigs had propagules of *F. moniliforme* in July but only 16% in October.

The highest incidence of endosepsis occurred approximately 1 mo after the highest peak of flying wasps. Levels of endosepsis of winter crop caprifigs reached 60–65% from the middle to the end of March and declined in the spring crop caprifigs during April, May, and June (Fig. 3). Disease increased to 90–95% by mid-July in the scarce summer crop caprifigs but decreased during August and September as the availability of caprifig syconia increased. A second but smaller peak in disease and flying wasps occurred from late September to October (Table 4 and Fig. 3). Levels of disease recorded in early November were similar to those determined from the middle to the end of March. Wasp flights did not occur after 10 November.

The incidence of *F. moniliforme* ranged from 82 to 99% in samples of summer crop caprifigs collected during June and July in the four caprifig orchards (Table 5). But in caprifigs sampled in autumn, the incidence of *F. moniliforme* ranged from 43–87%. In addition, 83 and 78% of the wasps that had emerged from caprifigs collected on 22 September and 18 October, respectively, showed contamination with *F. moniliforme*.

Effects of numbers of wasps in fruit syconia on disease incidence. In both experiments, 10–25% of pollinated Calimyrna syconia were infested with *F. moniliforme* when no wasps were detected

TABLE 3. Effect of number of symptomatic winter crop caprifigs (*Ficus carica*) enclosed in paper bags on contamination of fig wasps[a] with *Fusarium moniliforme* and other fungi and yeasts

Exp.[b]	Number of winter crop caprifigs	Incidence (%)[c]			
		F. moniliforme	*Alternaria* spp.	*Cladosporium* spp.	Yeasts
1	1	67.2	0.0	0.7	5.3
	5	37.6	0.8	6.2	13.8
	10	88.8	9.0	0.8	2.6
	$LSD_{0.05}$	17.0	8.4	4.4	8.7
2	1	53.2	10.3	8.3	8.8
	5	58.7	6.9	5.9	9.4
	10	49.5	15.2	10.8	5.4
	$LSD_{0.05}$	29.5	19.3	11.4	14.6

[a] Fig wasps matured and emerged from the caprifigs while in the paper bag.
[b] Both experiments had ten replications in which one, five, or ten halves of winter crop caprifigs were enclosed in paper bags.
[c] Averages from ten replications of five petri dishes that contained acidified potato-dextrose agar and ten wasps per dish; the dishes were incubated at 23 C for 5–7 days.

TABLE 4. Numbers of caprifig fruit developing during summer and fall, and number of fig wasps (*Blastophaga psenes*) trapped on yellow sticky traps in a commercial caprifig orchard in Merced County in 1989[a]

Date[b]	Number of caprifigs per 10 shoots[c]		Fig wasps per trap[d]
	cv. Stanford	cv. Roeding 3	
3 May	...	...	0.3 ± 0.5[e]
16 May	...	...	0.0 ± 0.0
30 May	...	...	0.0 ± 0.0
12 June	...	...	6,510 ± 520.4
16 June	...	...	5,391 ± 268.6
19 June	...	...	2,302 ± 398.3
28 June	1.0 ± 0.9	0.3 ± 0.5	3,241 ± 582.6
13 July	...	...	700 ± 198.7
7 August	30.7 ± 7.6	4.3 ± 0.9	0.3 ± 0.5
29 August	23.0 ± 7.9	8.7 ± 1.0	0.3 ± 0.5
6 September	...	...	32.3 ± 11.9
20 September	26.7 ± 4.0	18.3 ± 4.9	74.3 ± 14.1
10 November	49.3 ± 6.1	21.3 ± 5.0	203.3 ± 109.4

[a] Results in 1993 showed similar trends to those of 1989.
[b] Yellow sticky traps were changed every 2–3 wk except during the period 12–19 June and 20 September to 10 November 1989.
[c] Ten shoots on each of three trees of cv. Roeding 3 and three trees of cv. Stanford were observed.
[d] Fig wasps were counted with the aid of a dissecting microscope (10×).
[e] ± values represent standard deviations.

TABLE 5. Incidence of *Fusarium moniliforme* on summer crop caprifigs collected from four commercial orchards and on wasps (*Blastophaga psenes*) that had emerged from these figs in 1990

Orchard	Site or source	Collection date	*F. moniliforme* (%)[a]
A		23 June	95.8 ± 5.0
		28 June	87.9 ± 4.6
B		6 July	81.7 ± 11.9
C	1	6 July	93.8 ± 4.2
	2	6 July	92.8 ± 7.0
	3	6 July	96.2 ± 3.4
	4	6 July	94.0 ± 3.5
	5	6 July	98.8 ± 1.2
A		13 July	85.8 ± 5.6
D		20 July	98.8 ± 1.2
A	1	22 September	86.3 ± 8.3
	2	22 September	85.9 ± 5.6
	Wasps[b]	22 September	83.3 ± 11.2
A	1	18 October	64.5 ± 2.8
	2	18 October	42.6 ± 8.5
	Wasps	18 October	77.6 ± 4.4
B		20 October	21.5 ± 8.8

[a] Average of four to six 20-fruit replications determined by using the agar-drop technique (19) ± standard deviation.
[b] Average of six replications each of five petri dishes containing acidified potato-dextrose agar and ten wasps per dish; the dishes were incubated at 23–25 C for 4–5 days.

in the fruit cavity (Fig. 8A-B). As wasp numbers in the cavity increased, incidence of *F. moniliforme* also increased. Five or six wasps per syconium resulted in a 100% incidence of *F. moniliforme* in the cavity (Fig. 8A and B). In general, *F. moniliforme* incidence was higher on ostioles than in cavities. Sixty to 67% of pollinated Calimyrna syconia were infested with *F. moniliforme* in the ostiole when no wasps were detected in the fruit cavity. The relationships of the numbers of wasps counted in the fig cavity and the incidence of infestation by *F. moniliforme* in the cavity or the ostiole were best described by second-degree polynomial equations ($P < 0.01$).

DISCUSSION

This study shows that *F. moniliforme*, causing fig endosepsis, is not transmitted transovarily by the fig wasp (Table 1). Instead, the wasps become contaminated with spores of the fungus either in the cavity of figs or from their contact with plant surfaces. Interestingly, wasps collected from the upper surface of leaves had significantly higher incidences of both *F. moniliforme* and *Alternaria* spp., including *A. alternata*. Michailides et al (21) observed propagules of *Fusarium* spp. on 1- to 2-yr-old shoots of Calimyrna and 1- to 3-yr-old shoots of Roeding 3 caprifig trees. In addition, *Fusarium* spp. propagules were found on young and old fig leaves, petioles, and on surfaces of infected fruit (advanced stages of infection). This suggests that the chance of contamination of a clean wasp increases as the wasp walks on shoots, leaves, petioles, and fruits before reaching the ostiole of a receptive fig. Contamination of the wasps with *Alternaria* and *Cladosporium* spp. probably occurs similarly as these fungi are not commonly found sporulating in the cavity of caprifigs. The incidences of contamination with *F. moniliforme* of wasps collected from plant surfaces were significantly ($P < 0.05$) smaller than those of wasps collected from diseased syconia (Table 1) because emerged wasp populations represent individuals from both healthy and diseased spring crop syconia.

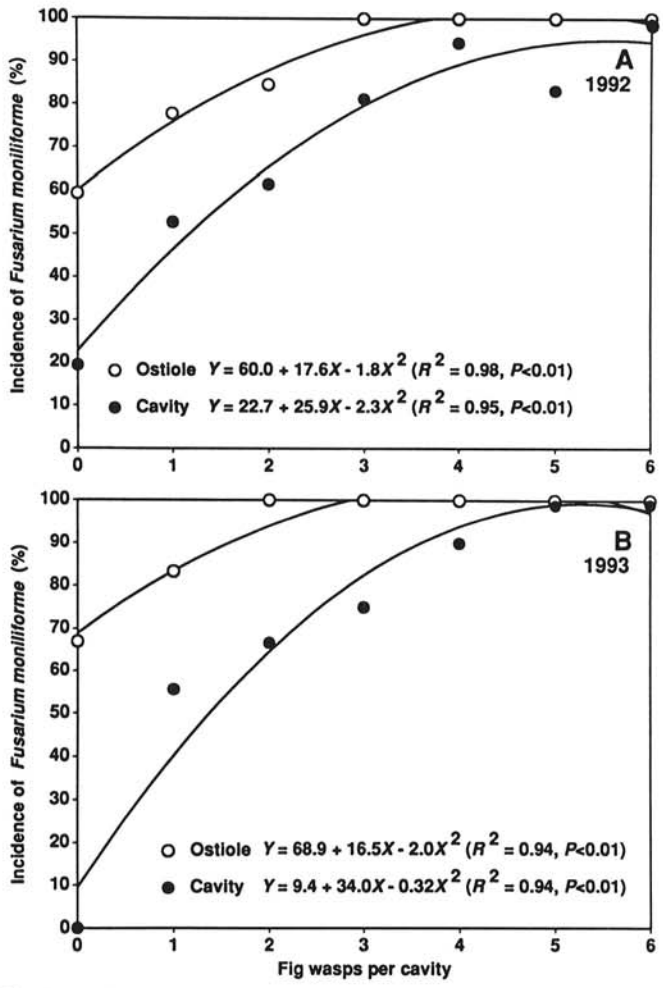

Fig. 8. Relationship of number of fig wasps (*Blastophaga psenes*) observed in the cavity of Calimyrna fig fruits and incidence of *Fusarium moniliforme* determined in the fruit cavity or ostiole. Data are the means of three 20-fruit samples (**A**) in 1992 and (**B**) in 1993.

Several species of yeasts were associated with the fig wasp pollinator in previous studies (29) and in this study. Contamination of wasps with yeasts results in contamination of the cavity of Calimyrna figs with yeast propagules that can cause fermentation and souring of the fruit tissues containing sugars (9,32). However, other insects (dried fruit beetles and vinegar flies) can also vector yeasts in the fig cavity, resulting in souring of figs (14,22). Incidence of sour figs is one of the tests when figs are inspected for separating the merchantable product (1).

Scanning electron microscopy showed that microconidia of *F. moniliforme* could be found easily on almost all parts of male and female wasps. Male wasps emerge earlier than the females, move around within the cavity of the caprifig syconium, and impregnate the females while still in the inflorescence galls (2,16,24). It is at this time that the male wasps can become contaminated from a sporulating colony of *F. moniliforme* in the cavity and spread its spores over the cavity. Female wasps probably become contaminated in the cavity of the syconium as they emerge from the flower galls. The behavior of male and female wasps explains the very high levels of contaminated wasps (up to 100%) emerging from diseased caprifigs (Table 1).

The bagging experiments in the laboratory clearly showed that enclosing more than one winter caprifig resulted in higher contamination levels of emerging fig wasps with *F. moniliforme*. This is because the chance of including symptomless infected caprifigs in the bag increases as more figs are used. In the third experiment with symptomless caprifigs (Table 3), however, the incidence of *F. moniliforme* on wasps emerged from 5 and 10 caprifigs was greater than in experiments one and two, suggesting that incidence of disease was higher in this batch of figs than in the caprifigs used in experiment one and two. When symptomatic figs were used there was no relationship between the number of caprifigs and incidence of *F. moniliforme* on emerged wasps, suggesting that symptomatic figs contained abundant sporulation of *F. moniliforme*. An average of 1.5×10^6 spores of *F. moniliforme* are present in the cavity of a symptomatic fig (T. J. Michailides, *unpublished*), explaining the high levels of contamination on wasps emerging from these figs.

All wasps detected in fruit cavities were wingless and 71% of the caprifigs observed 2–3 wk after pollination had detached wasp wings either on top of the outer ostiole or among the ostiolar scales (17). About 50% of caprifigs that did not have any wings on the outside of the ostiole had wings trapped among the ostiolar scales. Brostein (3) and Galil (10) also observed in syconia of other *Ficus* spp. tufts of detached wings of fig wasps pushing through the tight ostiolar opening and suggested that this was direct evidence that wasps had entered the syconium. The high incidence of detached wings on the ostioles of summer crop caprifigs and Calimyrna figs can be explained by the fact that these syconia were scarce at a time when a peak of emerging wasps imposed greater competition for these limited sites for oviposition. Because pollinator wasps have a lifespan only 1–3 days (4,15,28) and individual syconia lose their attractiveness to pollinators within 1–2 days of the first entry (4), the wasps have to find a syconium as soon as they emerge from a syconium of a previous caprifig crop. Kjellberg et al (16) observed dozens of wasps trying to enter syconia at the same time of the season. We also observed dozens of wasps trying to enter the scarce syconia of summer caprifigs and the syconia of a Calimyrna tree (the only one) found in the caprifig orchard in Tulare County (T. J. Michailides, *unpublished*). Wings on the ostioles are easily detected by their reflection of sunlight and their presence is used by growers to monitor the progress of pollination.

The number of wasps that hatched from syconia of spring crop pollinated with 10 winter crop caprifigs was significantly smaller than when one to five winter crop caprifigs were used. Brostein

(3) reported that total wasp offspring maturation is influenced by the number of pollinator wasps per syconium and the number of mature wasps is often low when pollinator entries are high. Emergence of fewer wasps in these syconia can result in lower activity in the fruit cavity. This may explain why the incidence of contamination with *F. moniliforme* of spring crop caprifigs that had been pollinated with 10 winter crop caprifigs and on the wasps that had emerged from these caprifigs was about the same as when five winter crop caprifigs were used for pollination (curvilinear lines in Fig. 6).

This study presents the first experimental evidence from the field showing that overpollination of caprifigs (using more winter crop caprifigs than necessary) resulted in significantly higher incidence of *F. moniliforme* in the spring crop caprifigs. This increase in disease incidence led to greater numbers of emerged wasps infested by *F. moniliforme* (Fig. 6B). This suggests that, when more than the sufficient number of winter crop of caprifigs is used, there is a greater chance of including symptomless (but infected by *F. moniliforme*) caprifigs in the pollination process. Most importantly, when spring crop caprifigs that were pollinated with five to 10 winter crop caprifigs were used to pollinate Calimyrna fruit, significantly more endosepsis developed on the mature, dry fruit of Calimyrna figs (Fig. 7). Thus, increases in disease as a result of overpollination can occur at two different stages: 1) pollination of spring crop with more winter crop caprifigs than necessary; and, 2) pollination of the Calimyrna with spring crop caprifigs (Fig. 2). Growers, therefore, should avoid overpollination at either stage in order to keep endosepsis at manageable levels.

To avoid overpollination, the process of pollination should be monitored closely either by recording the incidence of wings attached to the ostiole or by determining the number of wasps present in the fruit cavity. If a large number of split figs show no signs of fertilization, additional caprifigs should be added to the bags hung on the trees. Experience in recognizing the receptive stages of development of figs in both caprifigs and Calimyrna crops is, of course, helpful in achieving optimum pollination.

Because of the limited numbers of available caprifigs (summer crop) in early July and the very high numbers of flying wasps (Fig. 3), strong competition for sites was observed. This intense competition is shown by 1) the numerous wasps surrounding the eye of developing fruit and trying to enter through the scales in the cavity, 2) the high numbers of wasps recorded in the cavities of fruits during this period, and 3) the unusually high incidence of *F. moniliforme* propagules in the cavity of these figs (Table 5). Incidence of *F. moniliforme* in Calimyrna figs was similarly affected by the number of wasps trying to gain entry. The presence of three wasps in the cavity was associated with 100% contamination of ostioles but five to six wasps in the cavity were required to result in 100% *F. moniliforme* contamination in the fig cavities. Microconidia of *F. moniliforme* attached to the wasps' bodies are probably more important for causing disease than are those attached to their wings. A higher incidence of fig endosepsis in the ostiole than in the cavity, and the smaller number of wasps required for contaminating the ostiole than the cavity of the syconium, suggest that propagules of *F. moniliforme* can be deposited among the scales of the ostiole. In addition, wasps' wings or wasps (10) contaminated with *F. moniliforme* trapped among the ostiolar scales may contribute to the higher incidence of endosepsis disease on the ostiole (eye) than in the cavity of figs (Figs. 6B and 8A-B).

Nonpollinated caprifigs or Calimyrna fruits quickly dehisced from the plant and dropped. The fact that the cavity of these figs is sterile is yet another strong indication that initially the microflora detected in the cavity of the figs is brought in by the fig wasp. Miller and Phaff (23) were unable to isolate any microorganisms from the fig cavity until after pollination. Furthermore, the more wasps entering the fig, the higher the chances for figs to become contaminated with propagules of *F. moniliforme* and develop endosepsis. Although various species of thrips have been detected in cavities (13) and nitidulid beetles (*Carpophilus* spp. [14,31]), it is believed that thrips enter the cavity after the ostiolar scales of figs become loose and the nitidulid beetles when figs start ripening (14,22). Thrips, however, have been reported to carry other microorganisms causing decay in figs (13).

Prior to this study experimental evidence that overpollination results in higher incidence of fig endosepsis in Calimyrna figs was missing. Although there is a general belief among growers that overpollination results in more diseased fruit, this is the first study to show the effects of overpollination on incidence of fig endosepsis and the relationships of population dynamics of fig wasp to disease incidence, explaining how the disease became endemic in both cultivated and wild caprifig pollinators. In cultivated figs, overpollination affects the number of wasps entering the cavity, thus influencing the chance of contamination of the cavity by *F. moniliforme*. Optimum pollination should reduce the disease. For instance, in wild caprifigs where pollination is done without human interference, the incidence of endosepsis in these figs is lower than in the cultivated ones (T. J. Michailides, *unpublished*).

LITERATURE CITED

1. Anonymous. 1992. Amendments to the administrative rules and regulations for the marketing order for dried figs, as amended effective 25 August. California Fig Institute, Fresno.
2. Bouček, Z., Watsham, A., and Wiebes, J. T. 1981. The fig wasp fauna of the receptacles of *Ficus thonningii* (Hymenoptera, Chalcidoidea). Tijdschr. Entomol. 24:149-233.
3. Bronstein, J. L. 1992. Seed predators as mutualists: Ecology and evaluation of the fig/pollinator interaction. Pages 1-44 in: Insect-Plant Interactions, E. Bernays, ed. CRC Press, Boca Raton, FL.
4. Bronstein, J. L., and Patel, A. 1992. Temperature-sensitive development: Consequences for local persistence of two subtropical fig wasp species. Am. Midl. Nat. 128:397-403.
5. Buscalioni, L., and Grandi, G. 1938. Il *Ficus carica* L., la sua biologica, la sua coltivazione ei suoi rapporti con l'insetto pronubo (*Blastophaga psenes* L.). Boll. Ist. Entomol. Univ. Stud. Bologna 10:223-280.
6. Caldis, P. D. 1927. Etiology and transmission of endosepsis (internal rot) of the fruit of the fig. Hilgardia 2:287-328.
7. Domsch, K. H., Gams, W., and Anderson, T.-H. 1980. Compendium of Soil Fungi. Vol. I. Academic Press, New York. 859 pp.
8. Dowdy, S., and Wearden, S. 1985. Statistics for Research. 2nd ed. John Wiley & Sons, New York.
9. Ferguson, L., Michailides, T. J., and Shorey, H. H. 1990. The California fig industry. Hortic. Rev. 12:409-490.
10. Galil, J. 1977. Fig biology. Endeavour (Engl. ed.) 1:52-56.
11. Gilman, J. C. 1957. A Manual of Soil Fungi. 2nd ed. Iowa State College Press, Ames.
12. Hansen, H. N. 1928. Endosepsis and its control in caprifigs. Phytopathology 18:931-938.
13. Hansen, H. N. 1929. Thrips as carriers of fig-decaying organisms. Science 79:356-357.
14. Howard, B. J. 1933. The influence of insects in the souring of figs. J. Econ. Entomol. 26:917-918.
15. Kjellberg, F., Doumesche, B., and Brostein, J. L. 1988. Longevity of a fig wasp (*Blastophaga psenes*). Proc. K. Ned. Akad. Wet. Ser. C. Biol. Med. Sci. 91:117-122.
16. Kjellberg, F., Gouyon, P.-H., Ibrahim, M., Raymond, M., and Valdleyron, G. 1987. The stability of the symbiosis between dioecious figs and their pollinators: A study of *Ficus carica* L. and *Blastophaga psenes* L. Evolution 41:693-704.
17. Michailides, T. J. 1990. Comparison of commercial treatments of mamme figs on the development of fig endosepsis and transfer of the disease by the fig wasp (*Blastophaga psenes*). Annu. Fig. Res. Rep. Crop Year 1989. California Fig Institute, Fresno.
18. Michailides, T. J., and Morgan, D. P. 1990. A correlation of numbers of fig wasp (*Blastophaga psenes*), availability of caprifig crop, and fig endosepsis levels. Annu. Fig. Res. Rep. Crop Year 1989. California Fig Institute, Fresno.
19. Michailides, T. J., Morgan, D. P., and Klamm, R. 1994. Comparison of three methods for determining fig endosepsis caused by *Fusarium moniliforme* and other molds in caprifigs and Calimyrna figs. Plant Dis. 78:44-50.
20. Michailides, T. J., and Ogawa, J. M. 1989. Investigations on the correlation of fig endosepsis on Calimyrna fig with caprifig infestations by *Fusarium moniliforme*. Annu. Fig. Res. Rep. Crop Year 1988. California Fig Institute, Fresno.

21. Michailides, T. J., Ogawa, J. M., and Ferguson, L. 1988. Investigations on the correlation of fig endosepsis on Calimyrna fig with caprifig infestations by *Fusarium moniliforme*. Annu. Fig. Res. Rep. Crop Year 1987. California Fig Industry, Fresno.
22. Miller, M. W., and Mrak, M. E. 1953. Yeasts associated with dried-fruit beetles in figs. Appl. Microbiol. 1:174-178.
23. Miller, M. W., and Phaff, H. J. 1962. Successive microbial populations in Calimyrna figs. J. App. Microbiol. 10:394-400.
24. Murray, M. G. 1990. Comparative morphology and mate competition of flightless male fig wasps. Anim. Behav. 39:434-443.
25. Nelson, P. E., Tossoun, T. A., and Marasas, W. F. O. 1983. *Fusarium* Species. An Illustrated Manual for Identification. The Pennsylvania State University Press. University Park.
26. Obenauf, G., Gerdts, M., Leavitt, G., and Crane, J. 1978. Commercial dried fig production in California. Div. of Agric. Sci., University of California, Berkeley. Lfl. 21051.
27. Obenauf, G. L., Ogawa, J. M., Lee, K., and Frate, C. A. 1982. Fungicide control of molds that attack caprifigs. Plant Dis. 66:566-567.
28. Patel, A., Hossaert-McKey, M., and McKey, D. 1993. *Ficus*—pollinator research in India: Past, present, and future. Curr. Sci. (Bangalore) 65:243-253.
29. Phaff, H. J., and Miller, M. W. 1961. A specific microflora associated with the fig wasp, *Blastophaga psenes* Linnaeus. J. Insect Pathol. 3:233-243.
30. Phillips, E. H., Smith, E. H., and Smith, R. 1925. Fig smut. University of California Agric. Exp. Stn., Berkeley, Bull. 378.
31. Smilanick, I. M. 1979. Colonization of ripening figs by *Carpophilus* spp. J. Econ. Entomol. 72:557-559.
32. Smith, R. L., and Hansen, H. N. 1931. Fruit spoilage diseases of figs. University of California Agric. Expt. Stn., Berkeley, Bull. 506.
33. Smith, R. L., and Hansen, H. N. 1935. Directions for control of endosepsis in figs. 1934-1935. University of California Agr. Expt. Stn.
34. Wiebes, J. T. 1979. Co-evolution of figs and their insect pollinators. Annu. Rev. Ecol. Syst. 10:1-12.