FIG ENDOSEPSIS

An Old Disease Still a Dilemma for California Growers

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The common edible fig (Ficus carica L., Moraceae), one of the oldest fruits for which we have written records, is in many ways unusual. It bears a morphologically unique fruit called a "syconium," which is almost entirely vegetative peduncular tissue with true fruits, tiny, pedicellate druplets, within (Fig. 1A). It is a gynodioecious species with two distinct forms: the monoecious, nonedible caprifig, which serves as a pollenizer, and the pistillate edible fig. Pollination is achieved through the female fig wasp (Blastophaga psenes L., Chalcidoidea) (Fig. 2A), which develops in the syconium of the caprifig. The symbiotic relationship between fig and fig wasps is an example of coevolution between plant and insect (6,17), which is still progressing (4,5).

In an immature syconium, tightly packed florets line the inner wall of a fleshy, hollow receptacle. For reproduction, fig wasps depend on the ovaries of the figs, in which their larvae develop after the wasps gain access via an apical ostiole (eye), which is lined with overlapping scales (Fig. 1A). Syconia of the inedible caprifigs bear both female and male flowers (hermaphrodites) (Fig. 1A), while the syconium of the Calimyrna fig bears only female flowers. Caprifig trees produce three to four crops of syconia annually (Fig. 3) (8). The winter crop (mamme) is

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initiated in the fall and matures in late winter (middle to late March), and the spring crop (profichi), initiated in late winter, matures in mid-spring (beginning of June). The scant summer crop(s) (mammoni) develops either single or double fruits during late summer and autumn. The spring crop syconia contain the most pollen and are used for the pollination of the edible Calimyrna figs (Fig. 3). Although the various crops of the fig and caprifig trees are given different names in different countries, the convention observed in this review is to refer to the edible, pistillate, cultivated members of F. carica as "figs" and the inedible, monoecious forms that serve as pollinators as "caprifigs."

History

The literature on figs is voluminous and dates from ancient times. In an exhaustive 663-page bibliography, Condit and Enderud (12) compiled all known fig literature prior to 1956. Figs have been prized for both medicinal and dietary value. The early Greeks so highly rated figs that it was considered an honor to bestow either the foliage or the fruit; winning athletes in the original Olympic games were crowned with fig wreaths and given figs to eat. Because figs were so highly valued, their export from areas of production (Attica and Sikyon in ancient Greece) was forbidden, keeping them solely for the Greeks. Athenians who informed authorities about those illegally exporting figs from Attica were named "sycophants," a practice from which the word took its modern meaning. (Sykon in Greek means fig fruit; sykea is the fig tree; and sykeón is the fig orchard.) Today, since figs have recently been described as the fruit with the highest fiber content (3,15), their consumption is increasing. It is essential, therefore, to continuously produce healthy figs of high quality. However, because of their very nature, fig fruit are infected by a number of microorganisms.

An early reference to fig spoilage is found in chapter 24 of Jeremiah (Old Testament). "The Lord shewed me, and, behold two baskets of figs were set before the temple of the Lord.... One basket had very good figs, even like the figs that are first

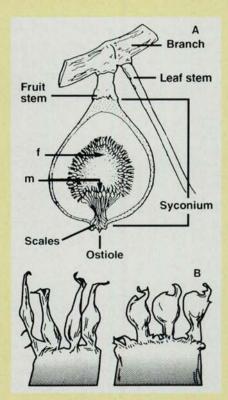


Fig. 1. (A) The fig syconium, depicting the various parts of female (f) and male (m) inflorescences, and (B) short-styled inflorescences of caprifigs (right, these will be converted to flower-gall habitat of wasps) and long-styled inflorescences of edible (Calimyrna) figs (left, these will be converted to seeds after pollination).

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ripe: and the other basket had very naughty figs, which could not be eaten, they were so bad. Then said the Lord unto me, What seest thou, Jeremiah? And I said, Figs; the good figs, very good; and the evil, that cannot be eaten, they are so evil..." As the reference indicates, figs were early recognized for their proclivity to spoil, although it is difficult to specify the kind of disease to which these biblical records refer.

Figs were introduced into the New World by Spanish and Portuguese missionaries, first in Cuba and then in the eastern United States. The spread of figs to the western United States probably came about through Spanish missions to Mexico, since it is generally accepted that the figs were subsequently spread from Mexico to California through Franciscan missionaries. The first California figs were planted in 1769 in the gardens of the mission in San Diego. From there these same figs, all of the cultivar Mission or Franciscan, spread northward to Sonoma, Santa Clara, and Ventura counties about two centuries ago (1793). Half a century later, in 1850, American settlers from the east imported a wide variety of figs from the eastern United States and Europe. By 1867, there were about 400 ha under cultivation in the Sacramento Valley and about 15 ha in the San Joaquin Valley. The White Adriatic was the most widely planted and remained the most popular California fig until the twentieth century. The true Smyrna (Lob Injir) fig cultivar was introduced in 1880, and it is still growing in popularity. No fruit was produced initially because of the absence of caprifigs. The introduction of caprifigs (containing the pollinator wasps) from Greece in April 1899 and Algeria in June of that year produced the first successful hatching of wasps and initiated the California commercial fig industry.

Present Hectarage and Fig Cultivars

The beginning of the twentieth century through 1943 saw the heyday of the California fig industry, with 14,000 ha in pro-

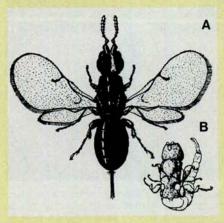


Fig. 2. Pollinator wasp (Blastophaga psenes) of fig (Ficus carica). (A) Adult female, and (B) adult male.

duction. Today there are 6,300 ha, producing a crop valued at \$21.8 million (10). Currently, California ranks third in world fig production, after Turkey and Greece, providing 100% of domestic fig production, 65% of which is consumed within the country. It is a small industry in California (ranking 22nd in value and 18th in hectarage), but it is an important specialty crop (16). Although fig hectarage in California declined in the past, the discovery of figs as a nutritious and nutrient-dense food has reversed this trend, and fig production in California today is estimated to be nearly 70% greater than it was just 10 years ago. Based on market demands, the hectarage devoted to the various cultivars changes over time. In the past 5 years, fig hectarage averaged 55% Calimyrna, 20% Black Mission, and 20% Adriatics and Conadrian figs, and the rest other minor cultivars.

Caprifigs. Caprifigs are essential for pollination of the edible fruit of the Calimyrna-type cultivars, because the caprifig syconia contain staminate flowers and short-styled pistillate flowers (Fig. 1B), which provide the habitat of the fig wasp that transfers pollen to pistillate

flowers of the edible fig, a process known to the growers as caprification (see below). The caprifig is generally regarded as a single type with 20 cultivars. However, only Roeding 3, the main cultivar, and Stanford, a later, midseason cultivar, are now grown commercially in California. In years when severe frost damages flowers on trees maintained as pollenizers, growers collect and use wild caprifigs of unidentified cultivars to supplement the shortage of the frozen winter crop caprifigs.

Edible figs. Fig fruits are enjoyed fresh in areas where they are grown and dried throughout the world. Edible fig cultivars are divided into three horticultural categories, Smyrna, San Pedro, and Common, with more than 600 named cultivars, many of which are synonymous (11). Although all three possess the long-styled pistillate flower (Fig. 1B) unique to edible figs, they are generally distinguished by their crops and pollination requirements.

Smyrna-type figs do not usually produce a first crop (or breba crop). Produced in July by cultivars normally requiring pollination, breba figs mature without pollination since pollen is not available at that time. The major California cultivar can

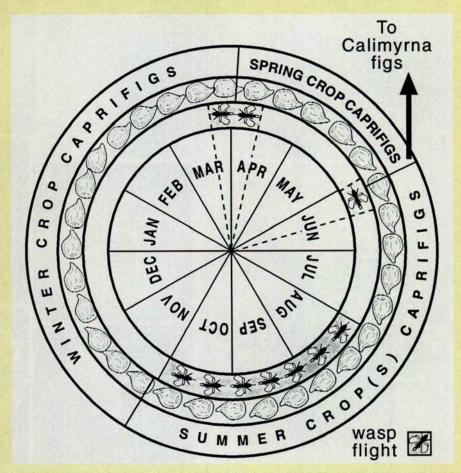


Fig. 3. A diagram of *Blastophaga psenes* flights and caprifig crops during a calendar year. The fig wasp has at least three major flights in late March to early April, early June, and during August through September. Caprifig trees produce at least three major crops per year: winter crop (mamme), spring crop (profichi), and summer crop (mammoni). The spring crop caprifigs are collected by the growers and hung on the trees in Calimyrna orchards.

produce fair breba crops, but the mature fruits are seedless. The main crop of fruit will not set unless pollinated, since the syconia will shrivel and abscise following anthesis without pollination. After pollination, the multiple ovules each produce a viable seed within thin, brittle endocarp with endosperm surrounding the embryo. This process results in the characteristic crunchy quality of dried figs. Of the 116 Smyrna cultivars, only the Sari Lop, renamed Calimyrna (California plus Smyrna) for promotional purposes, has achieved any prominence.

The San Pedro-type figs initiate moderate to large parthenocarpic breba crops and an adequate main crop (which requires

pollination) on the same branch within one season. Except for the cv. King, which is of only minor importance in California, none of the other 21 named cultivars (11) has any significance for the California fig industry (16).

Since almost all California figs (except Mission, which serves as a fresh and dried cultivar) are grown for dried utilization, they are allowed to fully ripen and partially dry on the tree. After summer irrigations end, figs fall to the ground, where they continue to dry. Later, they are mechanically swept into windrows, where they dry until mechanically collected. Commercial figs have multiple (every 2 weeks) harvests, which exacerbate disease and insect

infestation because the figs come in contact with the soil. Field debris is removed at this point. Grade standards specify that acceptable figs may contain no more than 13% insect infestation and 33% total defects. Grade defects include insect infestation, smut and mold (which includes endosepsis), sour rot, and filthy or worthless fruit (large, foreign material such as dried mud, etc.).

In the past 40 years, the California fig industry has experienced significant problems from substandard quality production. Calimyrna figs, because of the necessity of pollination, have the highest rate of substandard production. Over the past 40 years, Calimyrna figs have averaged 25%

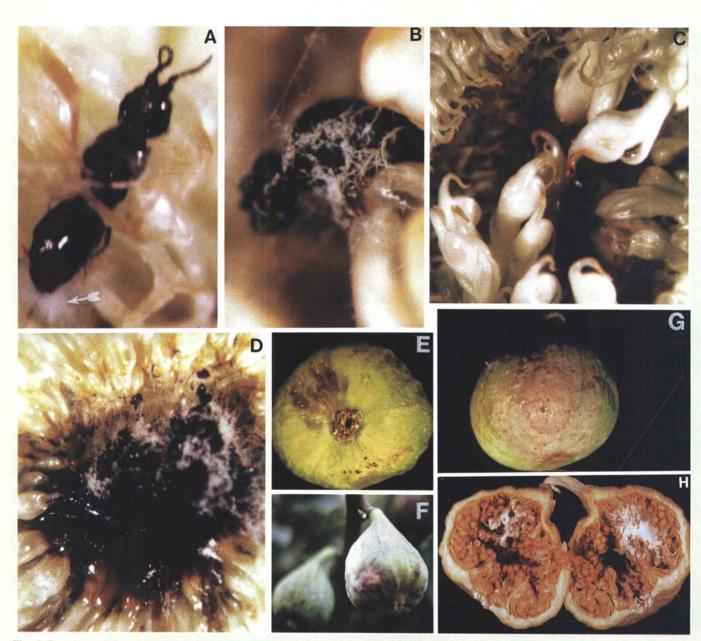


Fig. 4. Development and symptomatology of endosepsis in caprifigs and Calimyrna figs. (A) Growth of Fusarium moniliforme on a dead wasp. (B) Extensive sporulation of the pathogen on wasp. (C) Rusty to golden discoloration of inflorescences surrounding a dead wasp infested with F. moniliforme. (D) Cavity of a summer crop caprifig syconium filled with dead wasps infested with F. moniliforme (also note golden to brown discoloration and extensive growth of the pathogen). (E) External symptoms of endosepsis close to the ostiole of a spring crop caprifig. (F) Sporulation of the pathogen on an external lesion of a spring crop caprifig. (G) Large pink lesions on a winter crop caprifig. (H) Internal signs of endosepsis in a dry Calimyrna fig.

substandard production, followed by Adriatics (14%), Missions (6%), and Kadotas (4%) (10). During the last 5 years, 14% of the dried fruit production was lost due to smut and mold (2).

Pollination (Caprification)

Because the pollination of figs is idiomatic and closely related to the fig endosepsis disease, the process is described here in some detail. The fig wasps usually complete three, sometimes four, generations in the three or four caprifig crops, respectively, produced successively by caprifig trees in California (Fig. 3). Among these crops, it is only the spring crop caprifigs that contain pollen, and it is this caprifig crop that is used to pollinate fig trees. The main crop of Calimyrna figs is produced on current-season wood between May and July, requires pollination, and matures from August through November.

The male fig wasps (Fig. 2B) never leave the caprifig syconia; they emerge from the florets first (2 to 10 days before the female) and fertilize the female wasps while they are still in the ovaries. This same procedure is repeated throughout the season in each crop (winter, spring, and summer) (Fig. 3). The process of caprification is initiated when the female fig wasp deposits eggs in the ovaries of spring crop caprifigs after having passed the winter as larvae within the pistillate flowers, which are then transformed to galls (flower-galls) of the winter crop caprifig. The pupal stage develops in early spring, and the females emerge as winged adults (Fig. 2A) while the spring crop is developing. Only females leave the winter crop through the ostiole, enter the spring crop syconia through their ostioles, and deposit eggs in the pistillate flowers. The eggs in the spring crop caprifigs hatch about June (Fig. 3), and the adult leaves the spring crop syconia, taking on her body numerous pollen grains as she makes her way out through the ostiole (Fig. 1A). These female wasps enter the developing summer crop syconia through the ostiole to lay eggs in the short-styled pistils (Fig. 1B, right) of the next summer crop. If an edible pistillate cultivar is present (e.g., Calimyrna trees), the female wasp will enter the developing edible figs and try unsuccessfully to lay eggs in their long-styled flowers (Fig. 1B, left) by inserting her ovipositor into the stylar end. In her repeated attempts, however, she involuntarily deposits pollen from her body on the stigma of the florets, thus completing pollination.

The discovery that the fig wasp vectors Fusarium moniliforme J. Sheld. microconidia from the caprifig to the edible Calimyrna fig, causing endosepsis (9,37,38), led to legislation to culture caprifig trees and the Calimyrna trees in separate locations (33). Typically, growers of Calimyrna figs either maintain separate, isolated caprifig orchards or purchase spring crop

caprifig fruit that have been cleaned to reduce endosepsis (see control approaches below). By law, growers are allowed to maintain an area of caprifigs equal to 1.5% of the area of the Calimyrna figs they grow

Calimyrna fig flowers are receptive to wasps when the young figs are 9.5 to 13 mm in diameter, and caprifigs are ready when the pollen sheds and wasps emerge. Because Calimyrna receptivity within a production area generally precedes caprifig pollen shedding, most caprifigs are obtained from a district where maturation is early (usually from orchards close to the foothills of the Sierra Nevada in Central Valley). The spring crop caprifigs containing wasps ready to hatch are gathered and hung on Calimyrna trees, four to five per tree, in small paper bags, nylon nets, or baskets made from wire mesh, at 3- to 5day intervals over a 2- to 3-week period. Emergence of fig wasps from the hung caprifigs begins almost immediately and continues for 1 to 2 days. Growers monitor the efficiency of pollination either by checking the presence of wasps in the fruit cavity after splitting several arbitrarily collected figs or by detecting detached wasp wings attached to the ostiolar scales

Diseases of Figs Grown in California

Although figs are afflicted by a complex of disease-causing molds (Alternaria, Penicillium, Eurotium, Cladosporium, and Aspergillus spp.) or souring (caused by various species of yeasts [37]), figs of the edible Calimyrna cultivar are particularly susceptible to two very damaging diseases, endosepsis (caused mainly by F. moniliforme) (9) and smut (caused by Aspergillus niger Tiegh. [36] and other Aspergillus spp. [14]). More than 20 different Aspergillus spp. decayed figs in California orchards, but only A. niger occurred in more than 0.2% of the figs (14). The blackspored Aspergillus isolates cause smut, which along with endosepsis, causes major losses for growers (1). In this paper, however, we emphasize only endosepsis.

Fig Endosepsis

Endosepsis of Calimyrna figs, also called pink rot, brown rot, soft rot, and eye-end rot, has puzzled fig growers for almost three-quarters of a century. The name "endosepsis" was proposed as more appropriate and less confusing than the other names by Caldis (9), since endosepsis derived from Greek adverb endos, meaning internal, and the noun sepsis, meaning rot. Growers now usually refer to the disease as endosepsis. Caldis (9) was also the first to describe the transmission of endosepsis by the fig wasp pollinator in the early twentieth century. In the early 1900s, endosepsis, along with smut and souring diseases of figs, cost fig growers

an estimated annual loss of 50% (18). In addition, hand-picking and sorting of the fruit for later treatment frequently raised the costs of production so much that the industry in some districts was severely reduced for lack of profits. As a result, endosepsis poses a major dilemma for the fig industry in California as well as in other countries such as Greece, Turkey, and Algeria, where Smyrna type figs are grown. One wonders if this disease was introduced into the United States from these countries along with the first wintercrop caprifigs brought to California for the successful release and establishment of the first generation of fig wasps.

Causal agent(s). Initially, the causal agent was characterized as a distinct taxonomic variety of F. moniliforme, based on the presence of shorter micro- and macroconidia, and loose and aerial mycelia of various hues of white, pink, maroon, or reddish purple, and designated as F. m. var. fici Caldis (9). Subbarao and Michailides (39), after showing that the morphological characteristics used by Caldis (9) to delineate the pathogen causing fig endosepsis as F. m. var. fici are not unique to the pathogen and that the fungus does not show specificity to figs, dropped the variety name fici for the fig endosepsis pathogen, F. moniliforme.

In 1988, an extensive collection of more than 200 isolates from figs showing endosepsis obtained from different locations in the San Joaquin and Sacramento valleys in California showed that at least three distinct species of Fusarium cause endosepsis. These included F. moniliforme, F. solani, and F. episphaeria (=F. dimerum) (29,40). Recently, two additional species were identified (F. proliferatum and F. subglutinans) (W. F. O. Marasas, personal communication). The F. proliferatum isolate from figs was also confirmed by an-



Fig. 5. Mummies of summer crop caprifigs infected by Fusarium moniliforme surviving until April of the following year. The surface and the interior of these mummified caprifigs are covered with the pathogen's mycelia and sporulation.

other *Fusarium* expert in Germany (H. Nirenberg, *personal communication*). The majority of *F. moniliforme* and *F. solani* isolates have a temperature optimum of 25°C, but optimum temperature for colonization of fruit by *F. moniliforme* was 30°C (40–42).

F. moniliforme usually produces microconidia in false heads or in chains of white to light pink aerial hyphae, which are ovoid-fusoid, 5 to 11 μm long, and 2 to 3 μm wide. Macroconidia are not produced in the fruit; however, when the fungus is grown on synthetic media, some macroconidia develop that are sickle-shaped, with three to five septa, 20 to 52 μm long, and 2 to 5 μm wide. Although perithecia

were produced in cultures with crosses of mating types of *F. moniliforme* (40), they were never observed in infected fresh fruit or on mummified winter crop caprifigs in the field overwintering on the trees or on the ground (T. J. Michailides, *unpublished*).

Symptomatology. Endosepsis affects all caprifigs, Calimyrna figs, and to a lesser degree, parthenocarpic figs when wasps accidentally enter figs of the latter cultivars. The first indication that an immature green fruit will develop endosepsis is the growth and sporulation of *Fusarium* on dead wasps trapped in the cavity of the syconium or along the ostiolar bracts (Fig. 4A and B). Initially, there is no obvious

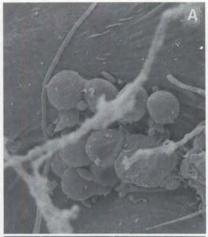
indication that the fungus has colonized the fruit tissues. However, a yellow to rusty discoloration may be present on the stigma of the inflorescences in the proximity of the dead wasp (Fig. 4A and C). This rusty discoloration can be very extensive when several wasps have colonized the syconium's cavity, a frequent occurrence with the summer crop caprifigs (Fig. 4D). Immature caprifigs infected with endosepsis show yellow, brown, or rusty discoloration on the base of one or more flowers. As the fig ripens, and depending on the locus of infection, these colored areas can first be found in the pulp near the ostiole or on any part of the fig pulp (37). Isolations from these golden yellow or brown discolored

Calimyrna fig Caprifig (Edible fig cultivar) (Nonedible fig pollinator) Aug-Sept Summer crop (mammoni) Some contamination Mummy of of wasps with summer crop propagules of caprifig Fusarium spp. and other fungal species on plant surfaces may occur **Fusarium** propagules contaminate the surface Winter crop of plants (mamme) which contaminate the wasps Spring crop Pollination (profichi) March Winter crop treatments Some contamination June of wasps with 1. Fungicide propagules of Fusarium spp. and 2. Sanitation Treated Sanitation Some refigs are (first step) treatment other fungi on plant contamination of (second step) hung surfaces Biocontrol wasps with Mummies back on may occur propagules of of summer the crop caprifig Fusarium spp. and Fig endosepsis cycle caprifigs other fungal species eventually on plant surfaces Wasp cycle fall onto the may occur Fig wasp ground

Fig. 6. A diagram depicting pollination in nonedible caprifigs and edible Calimyrna figs (*Ficus carica*), the life cycle of fig wasp (*Biastophaga psenes*), and the disease cycle of fig endosepsis caused by *Fusarium moniliforme* and other *Fusarium* spp. Depending on weather conditions, one to two additional wasp and disease cycles can be completed during the summer and early autumn. The circular arrows inside the caprifigs indicate successful development and emergence of adult female wasps through the fig ostiole.

florets or pulp almost always yield Fusarium spp. No external symptoms are noticeable at this stage of the infection. Later on, the fungus develops rapidly, with the pulp of the fig discolored amber, considerably darker in color than the beige color of uninfected fruit. Typical symptoms of endosepsis in Calimyrna fruit include disintegration of pulp, watersoaked purple or pink skin spots, eye and stem end rot, the "slip-skin" condition, and the production of yellow or amber-colored gum exuding through the eye.

As the fig ripens more and softens, the skin appears water-soaked in indefinite areas, usually initiated around the eye (Fig. 4E and F) in a circular spot and extending down the sides to the neck of the fig. The water-soaked areas gradually turn pink or purple (Fig. 4G). In other cases, only a small, water-soaked ring appears around the eye, and a drop of clear or amber-colored, dense syrup is exuded. (This last symptom is common in the Calimyrna but never occurs in caprifig fruit since these figs usually do not develop sugary tissues.) However, figs can dry before the internal rot reaches the external surface (Fig. 4H). Thus, a portion of infected Calimyrna fruit



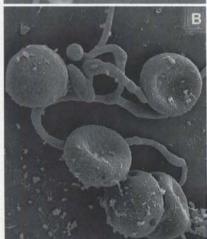


Fig. 7. (A) Microconidia, mycelium, and pollen grains (875x), and (B) germinated microconidia among fig pollen (1,460x) on the body of a female wasp.

will dry out and may be considered a good fruit, but even partial infection of the pulp causes off flavors in taste. In healthy Calimyrna figs, only occasionally does a small, water-soaked ring appear around the eye and a drop of clear or amber-colored liquid (syrup) exude. However, this exudate neither drips onto the foliage nor solidifies in long drops, as it does with figs that are infected by souring (9). Summer crop caprifigs infected late in the season overwinter on the tree and become mummified, covered with pinkish sporulation (Fig. 5). Characteristically, these mummified figs are distinct among the green winter and spring caprifig crops and may provide sources of contamination of the surface of caprifig trees (Fig. 6). Mummified fruit are rarely found on Calimyrna

Ecology, epidemiology, and life cycle. The fungus normally overwinters in the mamme crop of the caprifig (Fig. 6), but propagules of the pathogen have been found on the surface of both caprifig and Calimyrna trees (29). Conidia of the pathogen are introduced into the winter crop (mamme crop) during fall by the female fig wasps as they enter to lay eggs (Fig. 6). By similar methods, the pathogen is then transferred to the following spring crop (profichi) and then to the summer crop (mammoni) (Fig. 6). In this way, all successive caprifig crops can be infected, and endosepsis can be transmitted from year to year, becoming an endemic disease in both cultivated and wild caprifig trees (Fig. 6). In the first detailed description of the transmission of fig endosepsis by the fig wasp pollinators, Caldis (9) suggested that the wasps carried F. moniliforme propagules on their wings. However, the wings and the greater part of the antennae detach as the female wasp enters a syconium via the tight ostiole (7,25). The wasps, therefore, carry microconidia and sometimes mycelial fragments of F. moniliforme (Fig. 7A) along with pollen grains (Fig. 7B) directly into the syconium cavity on their body and leg parts. Germinating microconidia and pollen grains have also been observed on body parts of female wasps (Fig. 7B).

In the field, incidence of endosepsis increases when high populations of wasps coincide with limited availability of receptive fruit (25). This explains why the highest levels of endosepsis are recorded in summer crop syconia, when the flying wasps are the most numerous and syconia few, a situation that leads to more wasps entering the syconia and many becoming trapped among the ostiolar scales or packed on top of the ostiole (Fig. 8).

Because the pathogen sporulates before adult wasps emerge, the wasps become heavily contaminated with the numerous microconidia of F. moniliforme after emerging from infected syconia and transfer the fungus to the next healthy caprifig crop (9). Fruit not entered by the wasps (noncaprified caprifigs or nonpollinated Calimyrna figs) remain free of the fungus, but these fruit do not develop to maturity. Partially caprified caprifigs, which are retained on the trees, can support the development of only a few wasps. Since the pathogen has never been isolated from wasps forcibly removed from the flower galls, it has been concluded that there is no transovarian transmission (25).

Endosepsis is not a major disease of parthenocarpic cultivars unless these trees are next to a caprifig orchard and their fruit have been entered inadvertently by the wasps. For example, after splitting and examining microscopically 9,000 Conadria and 12,600 Black Mission figs, respectively, only <0.5% and <1% incidence of endosepsis in these parthenocarpic varieties was recorded.

The female wasps enter the Calimyrna fruit when the figs are still green and the ostioles are still closed. When wasps emerged from spring crop caprifigs enter Calimyrna syconia, they not only transfer



Fig. 8. A sectioned syconium of a summer crop caprifig in which several wasps have entered the cavity successfully, many are trapped among the ostiolar scales, and some are packed on top of the ostiole.

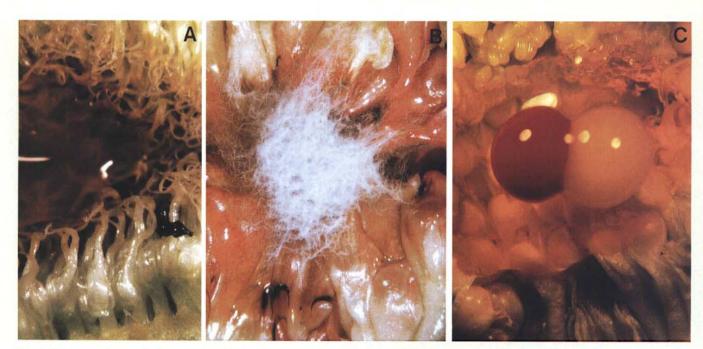


Fig. 9. The agar-drop technique used mainly to detect endosepsis in spring crop caprifigs. (A) Solidified agar devoid of any fungal growth (clean syconium). (B) A colony of Fusarium moniliforme growing on solidified agar (infected syconium). (C) A Serratia sp. and a creamy yeast growing side by side on solidified agar in the cavity of a fig syconium.

Table 1. Comparison of three methods for determining incidence of fig endosepsis on mamme caprifigs

Technique	Endosepsis (%)	Time to process figs (min:sec)	Potato-dextrose agar per 20 figs (ml)
Agar-drop ^y	67	12:30	7.5
Scoop-out ^z	52	32:30	300.0
5 scoops/agar dishz	47	44:00	300.0
LSD $(P < 0.05)$	9.4	3:04	

y Each fig received 4 to 5 drops of melted potato-dextrose agar.

pollen for pollination but also carry microconidia of the pathogen (Fig. 6). As in caprifig syconia, the pathogen develops profusely and sporulates easily on the dead wasp's body, but it is unable to invade the fig tissue. Infection and sporulation of the fungus on the fruit tissues occur only when fruit begins to ripen. The female wasps journey from one fruit to the next, land, and walk on leaves, shoots, or the surface of fruit before entering the Calimyrna cavity. During these activities, they acquire bacteria and fungal conidia commonly found on plant surfaces (Fig. 6). Propagules of Paecilomyces lilacinus (Thom) R.A. Samson, Cladosporium herbarum, C. cladosporioides, and other Cladosporium spp., and Alternaria and Aspergillus spp. are commonly recovered from healthyappearing figs. In addition, propagules of yeasts and bacteria can be recovered from both wasps and interior flower tissues of caprifigs or Calimyrna figs. Some of these fungi can cause other diseases, and a number of yeasts can cause souring of figs because of fermentation of the sugary pulp before drying.

Spread. The spread of fig endosepsis from a caprifig source was studied in both commercial and experimental Calimyrna orchards. The levels of fig endosepsis were the same in fruit collected from both the lower and upper canopies, the north and south sides of the trees, and the outer and inner tree canopies (27). More wasps entered syconia of fig trees located 3 to 5 m from the caprifig source than syconia of trees 70 to 80 m away from the source (24). Spread of fig endosepsis in fig orchards is closely related to the distance from the source and depends strongly on the incidence of contaminated wasps. Incidence of endosepsis of fruit on shoots protected from infestation by insects was not significantly different from that on nonprotected shoots, suggesting that there is no secondary spread of fig endosepsis (20). Therefore, the levels of endosepsis are determined by the population levels of contaminated wasps and the number of wasps entering the syconia. The presence of three or more wasps in the fruit cavity resulted in 100% F. moniliforme on the ostiole, while the presence of five or more

wasps resulted in 100% contamination of the syconium cavity (25).

New Developments

Improved method for determining contamination in spring crop caprifigs. The fig industry requires that growers check the cleanliness of spring crop caprifigs prior to their use for pollination. Growers annually submit three to five 30fruit samples for analysis. The method of analysis involves scooping out the contents of each fig and placing them in a sterile petri dish, then pouring about 15 ml of potato-dextrose agar (PDA) over them and incubating the dishes at 25°C. The colonies of Fusarium and other molds are then recorded, and the dishes are rated as having low, medium, or heavy contamination. Because caprifig contents contain a variety of bacteria, the PDA is acidified with 2.5 ml of a 25% (vol/vol) solution of lactic acid to prevent the growth of bacteria. The California Fig Institute (CFI) is now using acidified PDA for plating contents from the caprifigs to determine their cleanliness, but even in this medium, a species of the genus Serratia, which is a common inhabitant of fig syconia (35), commonly thrives.

In cooperation with the CFI, representing the California fig industry, Michailides et al. (26) developed an agar-drop technique (Fig. 9A) that, when performed at the right developmental stage of caprifigs, is as efficient as the traditional scoop-out technique used by the CFI for determining levels of fig endosepsis. Propagules of Fusarium spp. (Fig. 9B), as well as yeasts and certain bacteria (Fig. 9C), grow well on the solidified PDA. The agar-drop technique is preferable since it requires approximately one-third of the time and only

² Twenty dishes, each containing 15 ml of agar medium and one fig.

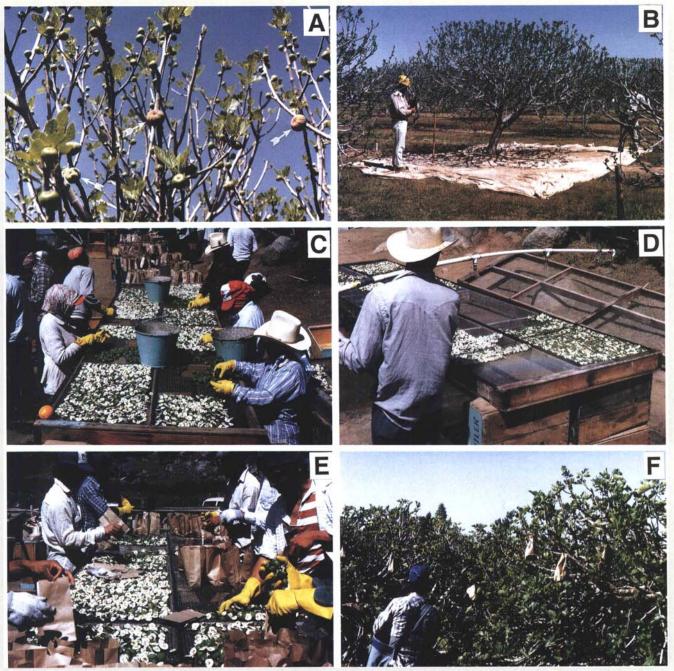


Fig. 10. Method for cleaning winter crop caprifigs. (A) During March, caprifig fig trees bear both the winter caprifig crop (larger fruit, arrows) and the developing spring crop caprifigs (smaller fruit) on the same branches. (B) Caprifig trees are stripped of all their winter crop caprifigs, which are collected on canvas placed under the trees. (C) Winter crop caprifigs are split in half and placed cut surface up on wire screens. (D) Split caprifigs are sprayed with a fungicide mixture (see text for details) on the upper and lower surfaces. (E) Treated caprifigs are allowed to drain for about 1 h, then 20 to 30 caprifig halves are placed in small paper bags. (F) Several of these paper bags are stapled on the caprifig trees so that the clean emerging wasps will enter the developing, receptive spring crop caprifigs.

one-fortieth of the acidified PDA (Table 1). It is now used routinely in our laboratory for assessing levels of endosepsis for various experiments using caprifigs and figs of pollinated or parthenocarpic cultivars. For dry figs, splitting the figs in half and observing the characteristic presence of white mycelia and sporulation on the surface of the fruit flesh and seeds (Fig. 4H) is a satisfactory procedure for identifying endosepsis.

Old and New **Disease Control Methods**

Cultural control. In California at one time, the male tree pollinators (caprifigs) were planted in rows or in groups among the Calimyrna trees. However, in the 1930s, Smith and Hansen (37,38) suggested that, because endosepsis is endemic in caprifigs, they should be kept as far away as possible from any cultivar of edible figs requiring pollination. Following this recommendation, fig growers now plant their caprifigs in separate areas, usually far from Calimyrna orchards, and destroy caprifig trees in abandoned orchards. In addition, growers scout wild areas close to their orchards, mainly near creeks and riverbanks, and remove the wild caprifigs that are common in these areas, since isolates of F. moniliforme from wild caprifigs are more virulent than those from culti-

Table 2. Incidence of Fusarium spp. (mainly F. moniliforme) isolated from winter crop (mamme) caprifigs of several cultivars and percentage of benomyl-resistant isolates

County	Caprifig	Caprifigs tested	Incidence of Fusarium spp. (%)x	Fusarium spp. resistant to benomyly	
(field)	cultivar	(no.)w		1 μg/ml	4 μg/ml
Tulare	Maslin 150	101	27	100	0
Tulare	Stanford	105	60	58	4
Tulare	Wild	106	41	100	48
Tulare	Roeding	102	51	75	4
Madera	Stanford	100	23	100	24
Madera	Stanford ^z	20	100	100	11
Merced	Selection 01-757-06	104	18	82	13
Merced	Wild	103	42	60	20
Merced	Stanford	97	36	84	12
Merced	Roeding	100	54	100	20
Yolo	Stanford	20	24	8	8

w Isolations were made on acidified potato-dextrose agar by plating five scoops of inflorescences after splitting each caprifig in two. The plates were incubated at $24 \pm 1^{\circ}$ C for 6 to 8 days.

Nother fungi isolated included Cladosporium herbarum, Alternaria alternata, Botrytis cinerea, Aspergillus niger, and Penicillium spp.

y Resistance to benomyl was determined after 5 to 10 days growth of Fusarium spp. on amended agar media.

² Summer crop (mammoni) caprifigs.

Table 3. Incidence of Fusarium moniliforme in spring crop caprifigs caged with fungicidetreated and nontreated winter crop caprifigs

	F. moniliforme (%)			
Method/fungicide treatment of winter crop caprifigs ^r	On winter caprifigss	On wasps from spring caprifigs ^t	In Calimyrna figs ^u	
Dipping	NO FEET	10 - 10 10		
Benomyl + dicloran + chlorothalonil + nacconol + NaOCl ^v	13 f ^w	52 bc	20 ef	
K-sorbate + captan + nacconol + NaOCl	23 ef	11 cd	27 de	
E-0858 + nacconol + NaOCl	19 ef	8 d	18 fg	
Iprodione + nacconol + NaOCl	36 с-е	22 cd	18 fg	
Iprodione + NaOCl	76 a	77 b	55 b	
Puratized Agric. Spray + nacconol	38 с-е	17 cd	40 c	
Spraying				
Benomyl + dicloran + chlorothalonil + nacconol + NaOCl ^v	42 cd	41 b-d	18 fg	
K-sorbate + captan + nacconol + NaOCl	31 c-f	55 bc	36 cd	
E-0858 + nacconol + NaOCl	46 c	5 d	32 cd	
Iprodione + nacconol + NaOCl	32 с-е	7 d	17 f-h	
Iprodione + NaOCI	49 bc	21 cd	21 ef	
Puratized Agric. Spray + nacconol	26 d-f	29 b-d	27 de	
Untreated control (arbitrarily selected)*	65 ab	35 b-d	13 h	
Untreated control (selected healthy) y	25 d-f	11 cd	16 gh	
Untreated control (selected diseased) z	76 a	100 a	88 a	

⁷ Concentrations of chemicals used were in g a.i./liter as follows: benomyl, 0.6; dicloran, 1.6; chlorothalonil, 1.8; nacconol, 0.2; sodium hypochlorite (NaOCl), 2.52; K-sorbate, 20; captan, 1.2; E-0858 (experimental chemical), 0.6; iprodione, 0.6; and Puratized Agricultural Spray (Semesan), 0.2.

s Six 20-fig replications (240 half figs) were tested using the agar-drop technique (26).

Average of 50 plated wasps (10 wasps per plate) for each of three 5-fig replications per treatment; caprifigs were incubated in sealed paper bags at 23°C for 15 days; plates were incubated at 23°C for 4 to 5 days.

^u Seventy (seven replications of 10 fruit each) mature Calimyrna figs were used for each treatment, using the agar-drop technique; numbers represent the average of two harvests (on 5 and 26 August).

Prepared from common household NaOCI solution source.

* Numbers followed by different letters are significantly different using Fisher's protected least significant difference test at P < 0.05.

x Figs were selected in a manner similar to growers' criteria.

y Selected figs without any brown symptoms inside the syconium after splitting.

² Selected caprifigs with yellow to brown discoloration in their inflorescences.

vated caprifigs (40). If removing these trees is not permitted by the county Agricultural Commissioner's office, growers can spray them with ethephon to enhance ripening and abscising of the spring crop caprifigs before maturation and normal emergence of the fig wasps (13). If a caprifig orchard is next to an edible fig orchard, surplus spring crop caprifigs should be destroyed before they are mature to avoid overcaprification and uncontrollably high levels of endosepsis (38). Some growers allow excess fruit to fall on the ground. This practice is not recommended because these figs can serve as a source of highly (99%) contaminated wasps, which continue emerging for 1 to 2 days after figs drop onto the ground (28).

The recommended procedure for cleaning up caprifigs involves the following five steps:

- All winter crop caprifigs (Fig. 10A) should be removed from the orchard by hand or by knocking them down on canvas placed under the trees before wasp emergence begins in March (Fig. 10B).
- All harvested figs should be stored at 10°C in a room with sufficient ventilation and used as needed for caprifying the developing spring crop caprifigs, completing item 3 below.

 Figs should be split in half (Fig. 10C) and sprayed with or dipped for 10 min in a solution of registered fungicides (see below) (Fig. 10D).

 Treated caprifigs should be placed in small paper bags (30 to 40 halves per bag) (Fig. 10E) and hung on the caprifig trees periodically (Fig. 10F).

 Steps 3 and 4 should be repeated as needed, depending on weather. Cool, rainy weather slows down both receptivity of the developing spring crop caprifigs and emergence of wasps, and warm weather speeds up these processes.

Although a statewide cleanup program of winter crop caprifigs was established early this century (18) and state regulations have been imposed, endosepsis is still a problem for California growers. Sanitation of the orchard by removing and destroying fruit should reduce disease as it has for winter crop caprifigs. In orchards where a few caprifig trees are growing among the Calimyrna trees, the spring crop caprifig fruit should be removed from the orchard or destroyed before wasp maturation and emergence.

Chemical control. In controlling endosepsis, researchers more than 70 years ago suggested, along with the cultural methods they developed, a cleanup program that consisted of harvesting the winter crop and splitting and dipping the fruit in proper fungicide solutions (38), believing that the emerging wasps would then be clean and able to set a spring crop with less endosepsis. The treatment of the winter

crop caprifigs initially utilized chemicals such as Puratized Agricultural Spray (Semesan, a mercuric fungicide; [18]) (43), but since the mercuric compounds have been prohibited by EPA, growers have started dipping or spraying the winter crop caprifigs after splitting with a solution of benomyl, chlorothalonil, dicloran, and potassium sorbate. This change of treatment has resulted in reduction of the incidence of F. moniliforme, Rhizopus, and Alternaria on treated winter crop caprifigs (34). However, none of these studies examined the resulting cleanliness of the wasps that emerged from treated caprifigs. Since the late 1980s, fig growers have been using a combination of all four chemicals or combinations of benomyl with one or two of the other fungicides, a mixture to which some growers added a surfactant to improve penetration of fungicides among the dense inflorescences of winter crop caprifigs. However, a 1987 survey of Fusarium isolates from cultivated and wild caprifig trees (mainly from winter crop caprifigs) showed that 8 to 100% of isolated Fusarium spp. were resistant to 1 µg of benomyl and 4 to 48% resistant to 4 µg of benomyl (Table 2).

Spraying caprifig trees prior to the beginning of wasp emergence from the winter crop caprifigs reduced significantly (35 to 50%) the incidence of endosepsis in the spring crop caprifigs but did not affect the levels of disease in the summer crop caprifigs (21). However, placing the winter crop caprifig halves on screens, cut surface facing up, then spraying them with the fungicide mixture reduces contamination of the uninfected figs and of the emerging wasps by the pathogen, thus reducing the disease in spring crop caprifigs compared with the dipping procedure.

During 1987 to 1992, we tested several fungicide combinations and methods of treating winter crop caprifigs (Table 3). In most instances, sanitation (see below) resulted in identical or even lower levels of disease than did fungicide treatments (19,23,27-29). Spraying trees with various

fungicides just before pollination provided inconsistent results (21).

Sanitation. Winter crop caprifigs that show any yellow or brown discoloration when split for dipping or spraying with fungicides should be discarded, because wasps issuing from such caprifigs usually show a high incidence of contamination with conidia of Fusarium spp. (23). Any caprifigs with water-soaked or rotted spots and caprifigs with sporulating Alternaria or Cladosporium on a surface damaged by frost (greenish black spots) should also be removed before the figs are treated with the fungicides. Although sanitation had been practiced along with chemical control of winter crop caprifigs (see chemical control above), it was not until 1988 that sanitation was shown experimentally to reduce fig endosepsis in Calimyrna figs (Table 4). In all experiments, spring crop caprifigs caged with "selected healthy" winter crop caprifigs resulted in significantly cleaner spring crop caprifigs and lower levels of contaminated wasps than other tested treatments (28). Furthermore, a two-step sanitation approach (the first step with winter crop caprifigs and the second with spring crop caprifigs) (Fig. 6) showed the greatest reduction in fig endosepsis in Calimyrna figs (30). Calimyrna figs pollinated with spring crop caprifigs (second step of sanitation) that had been caprified with winter crop caprifigs with no yellow symptoms (first step of sanitation) had the lowest detectable incidence of F. moniliforme of any of the treatments tested (Table 4). More importantly, significantly more wasps per fig emerged from caprifigs with no obvious yellow or brown symptoms than from figs of any of the other treatments, and the wasps showed the

Table 4. Effects of sanitation and fungicide treatments in winter crop caprifigs on the incidence of Fusarium moniliforme in Calimyrna figs in two commercial orchards (Merced and Fresno counties)

	Incidence of F. moniliforme (%)s		
Treatment	Merced County	Fresno County	
Commercial fungicide dip ^t	52 ab ^u	26 c	
Selected chemical dip ^v	50 ab	24 c	
Healthy control (1st step sanitation) w	38 b	31 bc	
Untreated commercial control*	53 ab	52 ab	
Selected diseased ("dirty") controly	74 a	55 a	
Contrast sums of squares			
Sanitation vs. no sanitation	3,000*z	2,464*	
Sanitation vs. chemical control	779 ns	140 ns	

- s Average of 57 to 231 Calimyrna figs in seven replications.
- Winter crop caprifigs dipped in a mixture of benomyl (0.6 g a.i./liter) + chlorothalonil (1.8 ml/liter) + dicloran (1.6 g a.i./liter).
- ^u Numbers in each column followed by different letters are significantly different using Fisher's protected least significance difference test at P < 0.05.
- v Winter crop caprifigs dipped in a mixture of a 0.25% NaOCl solution and a surfactant, nacconol (0.2 g/liter).
- w Healthy control refers to winter crop caprifigs (mamme) that do not show any brown discoloration symptoms in the syconium after splitting and that are used to pollinate (caprify) the spring crop caprifigs, which in turn are used to pollinate the Calimyrna crop.
- x Refers to untreated figs selected with the growers' criteria.
- y Refers to figs selected for the presence of brown discoloration in the syconium.
- z * = significant at P < 0.05, and ns = not significant.



Fig. 11. Paecilomyces lilacinus covering the body of a wasp trapped among the ostiolar scales.

Table 5. Number of wasps emerged from spring crop caprifigs that were caprified with winter crop caprifigs from different treatments, and incidence of wasp infestation by Fusarium moniliforme

Treatment	No. of wasps emerged ^w	Wasps with F. moniliforme (%)x
Commercial fungicide dip	359 b ^y	12 c
Selected chemical ^z	328 b	54 b
Healthy control (1st step of sanitation)	809 a	22 c
Untreated commercial control	495 b	57 b
Selected diseased ("dirty") control	274 b	93 a

- w Averages from five spring crop caprifig replications after 9 days incubation at 23 ± 1°C.
- * Mean of six 10-wasp replications.
- y Numbers in each column followed by different letters are significantly different using Fisher's protected least significance test at P < 0.05.
- ² Winter crop caprifigs dipped in a mixture of a 0.25% NaOCl solution and a surfactant, nacconol (0.2 g/liter).

lowest level of *Fusarium* infestation (Table 5).

Harvesting all the overwintering winter crop (mamme) of caprifigs, splitting them in half, and treating them with fungicides reduces endosepsis (38). But removing all the winter crop caprifigs from a tree is almost impossible, and growers initially were indifferent or even hostile and opposed to removal of the winter crop. However, in time, and because chemical treatments provided satisfactory control of endosepsis, this practice predominated in the fig industry and is now routinely followed to reduce endosepsis.

Once the winter crop caprifigs have been treated, they are placed back in the caprifig orchard in white or brown paper bags (Fig. 10F) so that the emerging clean wasps pollinate (caprify) the spring crop (profichi) caprifigs. Wild caprifigs in the proximity of cultivated caprifig orchards should be removed. Otherwise, caprifig growers have to collect all the winter crop fruit from the wild caprifig trees to avoid intrusion of unwanted, contaminated wasps. If caprifig trees are located in or near a Calimyrna orchard, the spring crop caprifigs should be completely removed from the trees before wasp emergence to prevent an outbreak of endosepsis (22,25).

Sanitation of winter crop caprifigs is equivalent to, if not better than, the fungicide treatment. Although distinguishing infected spring crop caprifigs visually is difficult initially, late-harvested caprifigs can have external lesions and should not be used for pollination of Calimyrna figs, since almost all the wasps that emerge from these figs show contamination by Fusarium spp. Although several improvements have been made in the original chemical cleanup and sanitation methods, growers traditionally continue testing profichi caprifigs by the scooping-out process before using them to pollinate the Calimyrna figs. Lots of spring crop caprifigs that show high levels of contamination are an indication of areas of caprifig orchards to avoid for use in pollination of Calimyrna fruit. Growers consider checking the spring crop caprifigs in anticipation of a high potential of endosepsis.

Biocontrol. The microflora from cavities of fig syconia (both caprifigs and Calimyrna figs) include several commonly isolated fungi, yeasts, and bacteria (32,35). Similar microflora, including Fusarium spp., are frequently recovered from the surfaces of shoots, leaves, petioles, and fruit of Calimyrna and caprifig fruits (29). In addition, the same microorganisms are frequently isolated from the ostiole of figs (T. J. Michailides and D. P. Morgan, unpublished). Among commonly isolated microflora, P. lilacinus was frequently associated with the dead bodies of wasps trapped in the fruit cavity or among the ostiolar or channel scales (Fig. 11). This fungus does not cause decay of figs but instead colonizes the dead wasps and somehow excludes the growth of F. moniliforme (31). In addition, P. lilacinus sprayed on caprifig trees in the spring before caprification of spring crop caprifigs significantly reduced fig endosepsis. P. lilacinus was ineffective, however, when sprayed on Calimyrna figs in the summer, when drier conditions prevented its growth (42). Isolations from wild and cultivated caprifigs from different counties as well as from Calimyrna figs showed that this fungus is a natural inhabitant of the syconia of all types of figs grown in California (T. J. Michailides, unpublished).

The fig wasp pollinators successfully carried propagules of *P. lilacinus* from the winter crop caprifigs to the spring crop caprifigs. Depending on the cleanliness of caprifigs used, *P. lilacinus* treatments reduced fig endosepsis by 55 to 60%. Recovery of *P. lilacinus* from wasps emerged from spring crop caprifigs injected with the biocontrol agent ranged from 45 to 58%

and was significantly (P < 0.05) higher than from wasps emerged from untreated caprifigs (31). Fig wasps picked up P. lilacinus conidia from the surface of caprifig trees and transmitted them to the spring crop caprifigs and then to the summer crop caprifigs or the Calimyrna figs, reducing endosepsis. P. lilacinus has been established in caprifig orchards, where it is now naturally found in 5 to 10% of the figs. The incidence of naturally occurring P. lilacinus was only 1 to 2% before establishment of the fungus in these orchards. Furthermore, coinoculation of sterilized wasps with P. lilacinus and F. moniliforme resulted in a sixfold reduction in F. moniliforme sporulation (Fig. 12). If the body of the dead wasp, which serves as the initial nutrient source for development of F. moniliforme, is occupied by P. lilacinus, F. moniliforme growth is significantly attenuated, thus reducing endosepsis by excluding the initial growth of F. moniliforme on the wasp's body (Figs. 11 and 12). Although P. lilacinus did not cause specific inhibition of F. moniliforme in culture, P. lilacinus grows faster than the pathogen when they grow side by side on the wasps. Water agar amended with wasp bodies supported greater growth and more abundant sporulation of P. lilacinus than nonamended water agar media.

Cultivar resistance. The healthy Calimyrna fruit is a high-quality cultivar and is used mainly for high-value, attractive gift packages in California (Fig. 13) and abroad. However, because of its unique method of pollination and the relatively large opening of the ostiole when fruit is mature, it is very susceptible to endosepsis and a number of other internal rots (smut, Alternaria, Rhizopus, Cladosporium, Penicillium, various Aspergillus rots, including rots caused by A. flavus and A. parasiticus, and sour rot). Since a disproportionate amount of the annual Calimyrna crop is lost due to these defects,

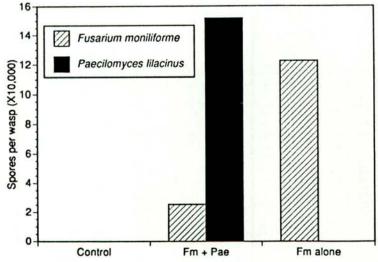


Fig. 12. Effect of *Paecilomyces lilacinus* (Pae) on *Fusarium moniliforme* (Fm) sporulation 6 days after coinoculation of dead wasps.



Fig. 13. A high-value, attractive gift pack that includes, among other fruits, dried Calimyrna figs from California.

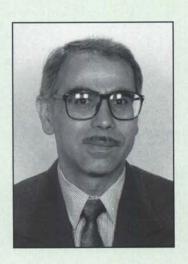
the available pool of high-quality fruit is unpredictable from year to year, limiting the industry's ability to build long-term markets for the Calimyrna crop. An improved Calimyrna-type fig should have the following characteristics: (i) it should still look like Calimyrna (light brown to golden color); (ii) it should still taste like Calimyrna, crunchy and flavorful; (iii) it should be self-pollinated so that problems associated with pollination in Calimyrna do not occur; and (iv) it should not have the wide-open ostiole, which serves as the Achilles heel of the variety's internal defects. The quality issues related to the Calimyrna fig have long been known to the industry and early on were addressed by various researchers from the USDA and the University of California (Department of Plant Pathology, Berkeley [9,18,36-38]) with the support of the California Fig Institute. Currently, the California fig industry supports research with the University of California at the Kearney Agricultural

Center in Parlier (located in the center of the San Joaquin Valley) on breeding an ideal cultivar that will have the desirable quality characteristics of the Calimyrna fig as listed above but will have a small ostiole to prevent access to insects and soil dust, and thus reduce internal molds.

Industry Prospects

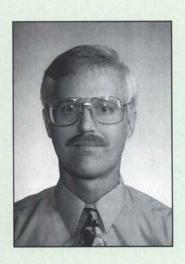
In the last 6 years, fig research has taken a two-pronged approach: first, attempting to improve the quality and yield of the Calimyrna fig, and second, trying to develop improved Calimyrna-type fig cultivars. As part of the first objective, research at the University of California is attempting to develop an early-pollinating caprifig (having winter crop caprifigs with pollen) that can fertilize the breba (first) crop of Calimyrna figs. These breba figs would have the advantage of developing at an earlier date, when conditions for the development of endosepsis and other internal molds are still unfavorable. To accomplish

the second objective of developing a Calimyrna-type fig, breeders are trying to get a fruit with a tight ostiole, which would prevent molds and insects from invading the internal cavity. Breeders are using the cultivar Tena as a female parent that shows a characteristically tight ostiole covered well by overlapping scales. Another desirable characteristic would be a self-fertile cultivar similar to the Calimyrna fig. Although a self-fertile Calimyrna look-alike does appear to be on the horizon, it will take at least 5 to 7 years before a superior fig is available to growers. Currently, the California fig industry is stable but expanding slightly in hectarage. The potential economic benefit of obtaining an improved fig cultivar was shown after the development by breeders of the cultivar Conadria (Condit's Adriatic), a fig whose quality approaches that of Calimyrna, but which does not require pollination. The majority of new California dried-fig plantings are Conadria.



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