Development of Phenological Scales for Figs and Their Relative Susceptibilities to Endosepsis and Smut

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ABSTRACT

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The relative susceptibilities of figs to infection by *Fusarium moniliforme*, which causes endosepsis, and *Aspergillus niger*, which causes smut, were evaluated on figs sampled at weekly intervals. Both caprifigs and Calimyrna figs were resistant to endosepsis infection up to 7 weeks prior to maturity, whereas smut could occur at any time on injured Calimyrna figs. Several morphological and physiological factors affecting the two pathogens during the development of figs were studied, and phenological scales for caprifigs and Calimyrna figs were developed. The effects of fig latex and different carbon sources on germination of conidia, germ tube elongation, and linear growth of the two pathogens were evaluated. Fig latex significantly inhibited all three variables on *F. moniliforme* but had no effect on *A. niger*. Of the carbon sources tested, lactose, mannose, maltose, and starch supported more growth of *F. moniliforme* than other carbon sources, although not more than on water agar ($P \leq 0.05$). Growth of *A. niger* on fructose-, mannose-, and maltose-amended agar was greater than on the other sugars tested. Of the two principal sugars (glucose and fructose) in figs, *A. niger* grew better on fructose than on glucose, whereas *F. moniliforme* grew equally well on both sugars. The linear growth of both pathogens also was evaluated on media amended with 9, 18, 36, 54, and 72% glucose or fructose. Radial growth of *A. niger* increased with increasing fructose concentrations of up to 36%, whereas growth of *F. moniliforme* increased only up to 18% fructose. In contrast, radial growth of *F. moniliforme* decreased at glucose concentrations of greater than 9%, whereas *A. niger* growth was reduced at greater than 18% glucose concentration. The relationships between the radial growth of the two pathogens and increasing glucose or fructose concentrations were quadratic ($P = 0.0001$), although the slopes for fructose were not as steep as for glucose. Other factors, such as the timing of ostiole opening, determined when smut infection occurred.

Additional keywords: caprification, *Ficus carica*, internal rot, pink rot

All figs (*Ficus carica* L.) are characterized by an inflorescence called a "syconium" that produces a multiple fruit. Horticulturally, fig syconia can be classified as persistent (self-fertile) or caducous. Caducous figs require pollination (=caprification) to produce mature fruits. The process of pollination in caducous figs is complex and has been described previously in detail (3,4). Briefly, caducous figs consist of botanically distinct male (caprifig) and female (edible nonparthenocarpic cultivars, i.e., Calimyrna) figs, which have different types of flowers in the syconia. Caprifigs provide pollen for the female crop and the hibernating site for the fig wasp (*Blastophaga psenes* L.), which matures in ovaries of modified pistillate flowers (flower galls) (4). Pollination is accomplished by the fig wasp (3,4). Caprifigs produce winter (mamme), spring (profichi), and summer (mammoni) crops of syconia. The spring-crop syconia have the highest number of staminate flowers and, consequently, the largest amount of pollen; as a result, the syconia of the spring crop are used to pollinate edible Calimyrna figs.

Endosepsis, caused mainly by *Fusarium moniliforme* J. Sheld. (also caused by *F. solani* and *F. dimerum*), and "smut," caused by *Aspergillus niger* Teigh., are two of the most important diseases of edible Calimyrna figs (3,4,10); however, only endosepsis is considered an important disease for caprifigs. Microconidia and mycelia of *F. moniliforme* carried from infected caprifigs by the fig pollinator are the primary sources of inoculum for endosepsis infection in Calimyrna figs (3). *A. niger* is primarily soilborne; soil dust deposited on the fruit and infested insects (such as nitidulid beetles) that feed and reproduce in figs are considered the primary vectors of the fungus (8,9). Higher levels of smut in Calimyrna figs are correlated with increased dust in orchards (8). Whereas the spores of *A. niger* can land on Calimyrna figs anytime during the crop season, the relative susceptibilities of Calimyrna figs at different growth stages are unknown. Similarly, the endosepsis pathogen is introduced into the Calimyrna fig cavity by the fig wasp at the time of caprification (3,4); however, the fungus remains dormant through much of the growing season, and endosepsis symptoms are not observed until several weeks before harvest.

Monosaccharides, such as glucose and fructose, are the major constituents of the sugar content in figs (1). During the growing season, sugar content gradually increases in Calimyrna figs and reaches a maximum at maturity. As caprifigs mature and as the sugar content in Calimyrna figs increases, the amount of latex in the syconia decreases. Information on how these two corresponding changes affect *F. moniliforme* and *A. niger* is unavailable. Although linear growth of *F. moniliforme* (6) and production of gibberellins and fusaric acid (14,15) as related to nutrition and physiology have been studied extensively, their significance in disease epidemiology has not been determined.

The objectives of this study were to develop phenological scales for caprifig and Calimyrna fruits, determine their relative susceptibilities to endosepsis and smut infection at different developmental stages, and elucidate the effects of latex, carbon sources, and levels of glucose and fructose on the growth and sporulation of *F. moniliforme* and the growth of *A. niger*. Preliminary results have been reported (11).

MATERIALS AND METHODS

Effect of carbon sources on growth and sporulation. Carbon sources tested were lactose, mannose, maltose, starch, fructose, glucose, sucrose, and xylose. Culture media were prepared with 1% of each carbon source and 2% agar. Media (15 ml) were dispensed into 9-cm-diameter petri plates. Five plates of each medium were inoculated centrally with a 0.4-cm-diameter agar disk from an actively growing colony of *F. moniliforme* (isolate F50). Because of the hydrophobic nature of *A. niger* spores, a spore suspension was prepared in 0.1% agar with 4 drops of Tween 20 per liter. A 5-µl spore suspension was placed centrally on five plates of each medium. The cultures of *F. moniliforme* were incubated in the dark at 25 ± 1°C, and those of *A. niger* were incubated in the dark at 30 ± 1°C. When the edge of the colony in any one carbon source reached the side wall of the plates for each fungus, colony diameters on all plates were measured. To assess sporulation of *F. moniliforme*, plates were flooded with 10 ml of sterile deionized water, and spores were dislodged with a rubber po-

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liceman and placed on a hemacytometer for counting. The experiment was repeated once.

Analysis of variance was used to determine the effects of carbon sources, and a least significant difference ($P = 0.05$) was calculated to compare means (SAS release 6.03, SAS Institute, Cary, NC). Effects of carbon sources on sporulation of *A. niger* were not determined.

Dosage effect. Experiments were conducted to determine how levels of glucose and fructose, the major sugars in fig syconia, affect the growth of the two fig pathogens and sporulation by *F. moniliforme*. Mature figs contain about 58% sugar, of which 32% is glucose and 23% is fructose (1). Preliminary experiments, conducted twice, revealed increased growth of *A. niger* and *F. moniliforme* on media amended with increments of 1% glucose and fructose up to 8%; therefore, in this experiment we evaluated the growth of *A. niger* and *F. moniliforme* at concentrations higher than 8%. Agar media amended with 9, 18, 36, 54, and 72% of either glucose or fructose were prepared, and five plates were inoculated with each fungus and incubated, as described, for the effect of carbon sources. Colony diameters of each fungus were measured when the edge of the colony at any one sugar level reached the side wall of the plate. Sporulation by *F. moniliforme* also was determined, as described. The experiment was repeated once. Polynomial regression analysis was used to study the relationships between doses of glucose or fructose and linear growth of the two pathogens or sporulation by *F. moniliforme*.

Effects of latex. Generally, a long lag period occurs between the time of *F. moniliforme* propagule introduction into the cavity and the appearance of endosepsis symptoms in figs. We hypothesized that fig latex may play a role in delaying fruit infection and symptom development. To investigate the effects of latex on radial growth, spore germination, and germ tube elongation of *F. moniliforme* and *A. niger*, latex was collected from the cut ends of the fig stalk. Latex was undiluted (10^0) or serially diluted to 10^1, 10^2, 10^3, or 10^4 in sterile distilled water. Five 4-mm-diameter agar disks from an actively growing *F. moniliforme* culture were placed separately in sterile distilled water, transferred into each latex dilution, and agitated for 15 s. Similarly, a spore suspension of *A. niger* was prepared in 0.1% agar with 4 drops of Tween 20 per liter, and 5 drops of this suspension was added to a separate set of each dilution and sterile distilled water. To study the effect of latex dilutions on growth rate, 5 µl of each suspension was placed in the center of five potato dextrose agar plates. Plates inoculated with *F. moniliforme* and *A. niger* were incubated at 25 and 30°C, respectively. Colony diameters in all dilutions were measured as soon as the colonies in any dilution reached the side walls of the plates.

To determine the effects of latex on spore germination and germ tube elongation, spore suspensions of each fungus in different latex dilutions were spread uniformly on four replicate water-agar plates. The inoculated plates were incubated as described above. Germination of *F. moniliforme* and *A. niger* conidia was determined in five microscopic fields (250×) per plate after 24 h of incubation. In each microscopic field, the total number of spores and the number that germinated were determined and expressed as a percentage of all spores present. Similarly, germ tube length was measured on 10 germinated spores per microscopic field per replicate. Percent inhibition of germination, germ tube elongation, and radial growth at different dilutions was calculated as: Percent inhibition = $[(X_w - X_d)/X_w] \times 100$, where X_w is either germination, germ tube elongation, or radial growth in water and X_d is the corresponding variable in different latex dilutions. Latex dilutions were transformed to $\log_{10}$ values. Linear regression analysis was used to study the relationships between latex dilutions and conidial germination, germ tube elongation, and radial growth in *F. moniliforme* and *A. niger*.

Phenological scales for figs and their relative susceptibilities to infection. Experiments were conducted on both spring-crop caprifigs and Calimyrna figs during 1991 and 1992. In addition to determining

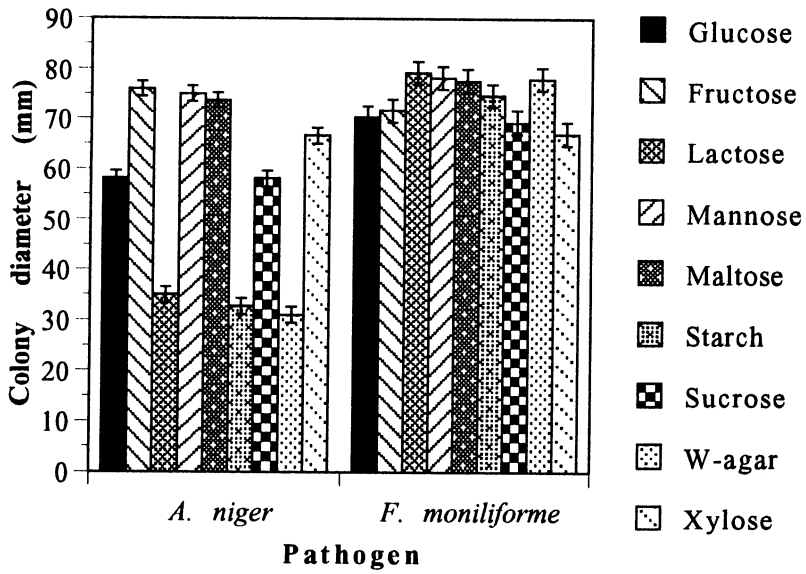

Fig. 1. Colony diameters of *Aspergillus niger* and *Fusarium moniliforme* on agar media amended with 1% of different carbon sources after incubation at 30 and 25°C, respectively.

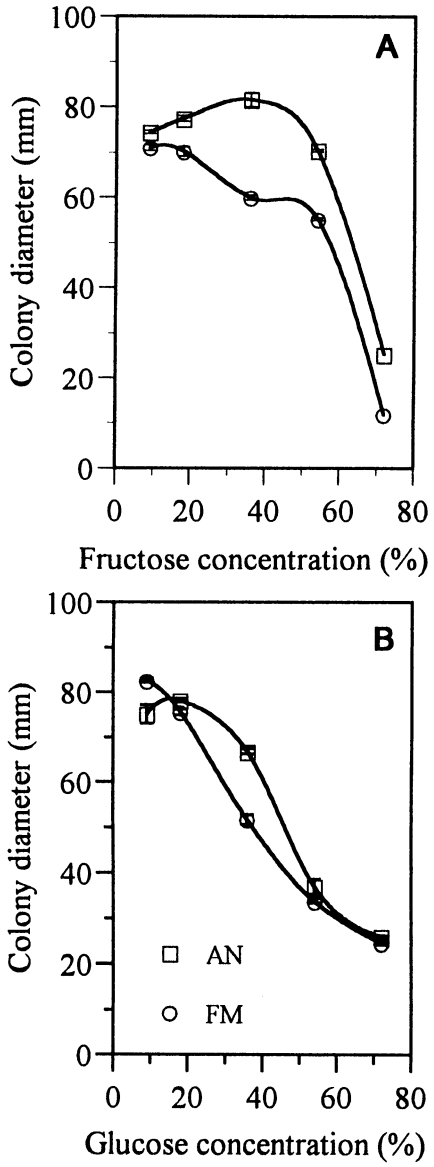

Fig. 2. Colony diameters of *Aspergillus niger* and *Fusarium moniliforme* on media amended with different levels of **(A)** fructose or **(B)** glucose and incubation at 30 or 25°C, respectively. The regression equations for the colony diameter of *A. niger* to increasing levels of fructose and glucose were $Y = 54.5 + 1.9X - 0.03X^2$ with an r^2 of 0.96 ($P = 0.0001$) and $Y = 82.5 - 0.44X - 0.005X^2$ with an r^2 of 0.91 ($P = 0.0001$), respectively. Similarly, for *F. moniliforme*, the equations were $Y = 70.3 + 0.3X - 0.16X^2$ with an r^2 of 0.89 ($P = 0.0001$) for fructose and $Y = 92.9 - 1.17X - 0.002X^2$ with an r^2 of 0.95 ($P = 0.0001$) for glucose.

the relative susceptibilities of figs at weekly intervals, we also recorded physical characteristics that are useful in developing a phenological scale for both caprifigs and Calimyrna figs. Beginning with the spring-crop caprifigs and continuing later with the Calimyrna figs, 20 fruits were sampled arbitrarily from 20 trees at weekly intervals. Caprifig characteristics, such as fruit diameter, dimensions and condition of internal cavity, condition of the ostiole, and thickness of rind, were recorded for each fruit. In addition, because of the structural and functional differences of Calimyrna figs, the amount of latex per 20 fruits, firmness of the fruit, and the amount of sugars (soluble solids) also were recorded. Fruit firmness was measured with a Hunter spring-force gauge (Ametek, Testing Equipment Systems, Lansdale, PA). The total amount of soluble solids was determined from juice squeezed from five arbitrarily chosen figs and measured with a hand refractometer (Atago, NSG Precision Cells, Hicksville, NY).

To determine relative weekly susceptibility, 20 fruits (each of spring-crop caprifigs and Calimyrna) similar to those whose various physical characteristics were recorded were split in half, arbitrarily divided into two groups, and each group was inoculated with *F. moniliforme* on the external surface or in the cavity. Fruit halves were placed over wire screens (20 × 29.5 cm) in separate, clear plastic containers (23.5 × 32 × 10 cm). Inoculum was prepared from a 9-day-old culture of *F. moniliforme* flooded with sterile distilled water and dislodged with a rubber policeman. Fruit halves were inoculated with a 5-µl suspension of 10^6 spores per ml placed either in the cavity or on a wound 2 mm wide × 2 mm deep for surface inoculations. About 250 ml of deionized water was added to each container to create a saturated atmosphere, and containers were incubated at 25 ± 1°C. Inoculated fruits were scored for the presence or absence of endosepsis symptoms, and lesion sizes were measured only on surface-inoculated fruit halves after 5 days of incubation.

Inoculation experiments with *A. niger* were done only on Calimyrna figs, because smut seldom appears on caprifigs. Because *A. niger* spores can be deposited on the fruit at any stage of development by various means, four methods of inoculation were used. To determine the period when Calimyrna fruit becomes susceptible to *A. niger* infection, 20 fruits were collected weekly from 7 July to 15 September and inoculated by the following methods: (i) the external fruit surface was wounded (2 × 2 × 2 mm) with a nail; (ii) the fruit cavity was wounded; (iii) the fruit cavity was not wounded; and (iv) fruits were inoculated directly in the ostiole. A 5-µl suspension of 10^6 *A. niger* spores per ml was used to inoculate the fruits by the above methods.

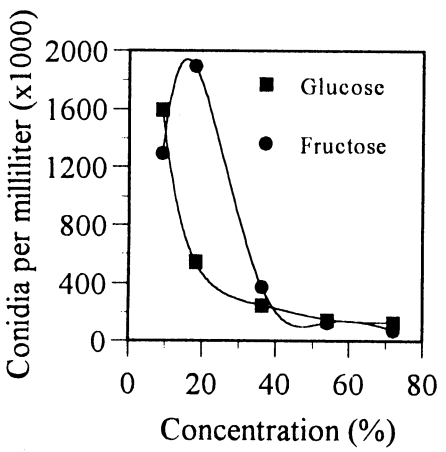

Fig. 3. Sporulation by *Fusarium moniliforme* at different levels of either fructose or glucose after incubation at 25°C.

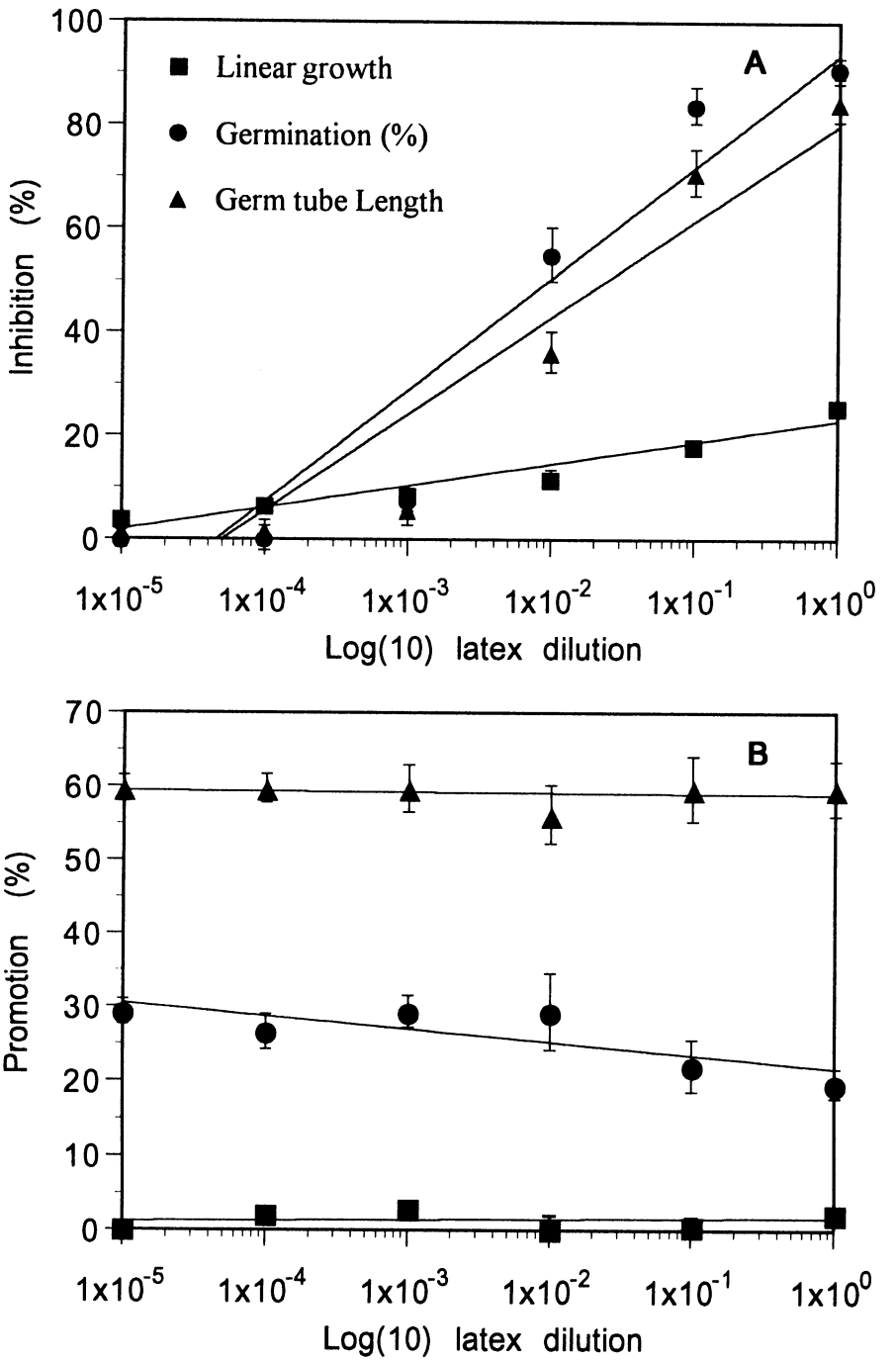

Fig. 4. Percent **(A)** inhibition or **(B)** promotion of conidial germination, germ tube elongation, and radial growth of **(A)** *Fusarium moniliforme* and **(B)** *Aspergillus niger*, respectively, in different dilutions of fig latex. The regression equations for *F. moniliforme* were germination = 80.13 + 8.1 $\log_{10}$ latex dilution (r^2 = 0.89, P = 0.0001); germ tube elongation = 93.6 + 9.4 $\log_{10}$ latex dilution (r^2 = 0.90, P = 0.0001); and colony diameter = 7.6 + 19.1 $\log_{10}$ latex dilution (r^2 = 0.63, P = 0.0001). Similarly, for *A. niger* germination = −21.7 + 0.8 $\log_{10}$ latex dilution (r^2 = 0.61, P = 0.0519); germ tube elongation = −58.9 + 0.04 $\log_{10}$ latex dilution (r^2 = 0.02, P = 0.6899); and colony diameter = −1.2 − 0.14 $\log_{10}$ latex dilution (r^2 = 0.11, P = 0.1291).

Inoculated fruits were incubated as described for *F. moniliforme*. After 3 days of incubation, the presence or absence of *A. niger* growth was recorded on each fruit, and lesion sizes were measured on the surface-inoculated fruits.

RESULTS

Carbon sources. Overall, both *F. moniliforme* and *A. niger* grew well on most of the sugars tested. Lactose, mannose, maltose, and starch supported significantly more growth of *F. moniliforme* than did the other carbon sources, although growth was not significantly greater than on water agar (Fig. 1). Growth of *A. niger* on fructose, mannose, and maltose was significantly greater than on other sugars (Fig. 1). Of the two principal sugars (glucose and fructose) in figs, *A. niger* growth was significantly better on fructose, but *F. moniliforme* grew equally well on both sugars (Fig. 1). Sporulation by *F. moniliforme* on different sugars was similar to radial growth.

Dosage effect. The two pathogens responded differently to increasing fructose concentration. Radial growth of *A. niger* significantly increased with increasing fructose concentration up to 36% and declined with further increase (Fig. 2A). *F. moniliforme* grew similarly on plates amended with 18 or 9% fructose; however, growth decreased significantly with further increase in fructose concentration (Fig. 2A). Radial growth of *F. moniliforme* decreased significantly with each incremental increase in the level of glucose beyond 9% (Fig. 2B); however, radial growth of *A. niger* was promoted by increasing glucose concentration up to 18% and declined with further increase. The relationships between the radial growth of the two pathogens to increasing glucose or fructose concentrations were quadratic ($P = 0.0001$), although the slopes for fructose were not as steep as for glucose (Fig. 2). Sporulation by *F. moniliforme* at increasing concentrations of glucose or fructose was similar to that of radial growth (Fig. 3).

Effects of latex. Fig latex inhibited conidial germination, germ tube elongation, and radial growth of *F. moniliforme* (Fig. 4A) and appeared to promote growth in *A. niger* (Fig. 4B). There was an inverse linear relationship between latex dilutions and percent inhibition of conidial germination, germ tube elongation, and radial growth of *F. moniliforme* (Fig. 4A), with the highest inhibition occurring with latex in its original concentration (undiluted). Conidial germination was inhibited the most, followed by germ tube elongation and radial growth (Fig. 4A). Undiluted and diluted latex did not have a deleterious effect on conidial germination, germ tube length, or radial growth of *A. niger*. Conversely, all three variables appeared to be favored by latex (Fig. 4B).

Growth and morphology of profichi caprifigs and susceptibility to infection. Spring-crop caprifigs expanded continuously at varying rates until they were ready to shed pollen. During February, March, and April, they expanded at an average rate of 9 mm/week; further expansion was slower (2 mm/week). The single largest weekly expansion of profichis occurred during June during the last week before harvest (15 mm) (Table 1). The fruit rind also increased continually in thickness. Associated with the increase in size were many noticeable internal changes.

Until caprification, fruits were externally green and internally hollow with a large cavity. The cavities were lined with developing florets. Until mid-March, anthers did not develop. Between mid-March and mid-April, development of anthers was completed, and by the end of April, all fruits had been caprified. Soon after caprification, the hollow internal cavity began shrinking with the development of flower galls (the habitat of wasps). The anther stalks elongated, and the anthers themselves were aligned in a ziplike fashion beneath the internal bracts near the ostiole.

Changes after caprification also were noticeable externally and were marked by blue-green skin with deposition of wax near the stalk. The ostioles in fig fruits remained tightly closed during this period. Approximately 1 month after caprification, the ostiolar scales around the ostiole began loosening, internal bracts shrank, and anthers swelled. Two weeks after these changes, the ostioles were open in the majority of fruits, the anther stalks were further elongated, and the anthers began shedding pollen. By this time, the hollow internal cavity had completely disappeared (Table 1).

Despite inoculations with *F. moniliforme* prior to the development of anthers, no visible signs of infection occurred. Inoculations after the development of anthers re-

Table 1. Characteristics of caprifigs collected at weekly intervals and their susceptibility to infection by *Fusarium moniliforme*

Date collected	Fruit diameter (mm)	Internal cavity (mm)[a]	Condition of ostiole	Condition of stamens	Rind width (mm)	Endosepsis susceptibility	
						Surface inoculated[b]	Cavity inoculated[c]
13 Feb.	9.8	4.4	Closed	Not developed	1.1	–	–
20 Feb.	14.1	6.5	Closed	Not developed	2.8	–	–
27 Feb.	17.7	9.3	Closed	Not developed	3.9	–	–
6 Mar :h	20.7	10.4	Closed	Not developed	5.0	–	–
13 March	24.4	12.7	Closed	In 10% of fruits	5.7	–	–
20 March	29.1	13.7	Closed	Developed	6.7	+	+
27 March	31.4	15.4	Closed	Developed	6.6	+	+
3 April	32.9	15.5	Closed	Developed	7.3	+	+
11 April[d]	34.2	17.4	Closed	Developed	7.0	+	+
17 April[e]	37.5	18.9/9.2/5.3	Closed	Developed	8.2	+	+
25 April[f]	41.1	21.9/10.5/5.1	Closed	Anthers ziplike	9.1	+	+
1 May[g]	42.1	22.5/10.5/3.0	Closed	Anthers ziplike	9.1	+	+
8 May	44.4	24.0/11.9/2.7	Closed	Anthers well dev.[h]	9.7	120.3	Typical symptoms
15 May	45.5	25.5/12.3/1.5	Closed	Anthers well dev.	8.9	20.5	Typical symptoms
23 May	45.0	26.0/13.8/0.9	Closed	Swollen anthers	9.1	59.2	Typical symptoms
31 May	46.6	27.3/12.9/0.3	Loose bracts	Elongated stalks	8.9	115.8	Typical symptoms
5 June	45.6	26.1/14.2/0.1	Loose bracts	Almost dehiscent	8.5	85.5	Typical symptoms
13 June	46.1	26.4/16.2/0.0	Open	Shedding pollen	8.9	424.7	Typical symptoms
21 June	50.9	27.9/17.9/0.0	Open	Dehiscent	9.9	298.4	Typical symptoms

[a] Before caprification only the width of the fig cavities was measured. After caprification the length, width, and height of the cavities were measured.
[b] – indicates no browning and no lesion development; + indicates development of localized browning of the spongy tissue without lesions. Lesion size was measured beginning during the week when symptoms were first noticed; size expressed in square millimeters.
[c] – indicates no browning and no lesion development. + indicates development of localized browning in the cavity. When typical endosepsis symptoms appeared, actual sizes of the lesions could not be measured because of their irregular nature.
[d] Less than 10% of the fruits had been caprified.
[e] About 50% of the fruits had been caprified.
[f] About 75% of the fruits had been caprified, anther stalks were turned toward the eye, and anthers were arranged in a ziplike fashion.
[g] Caprification was complete.
[h] Anthers well developed.

sulted in localized browning around the point of inoculation. Approximately 2 weeks after caprification, measurable lesions appeared in fruits inoculated on the external surface, and typical endosepsis symptoms with irregular lesions appeared in fruits inoculated in the cavity. After this period, the profichis remained susceptible to endosepsis infection (Table 1). The salient features of these developments were categorized into during, pre- and postcaprification, and a phenological scale was developed for caprifigs (Fig. 5).

Growth and morphology of Calimyrna figs and susceptibility to infection. Calimyrna figs also expanded at an average rate of 9 mm/week through most of the season. Unlike caprifigs, mature Calimyrna figs were reduced in size due to shrinkage, shriveling, and drying toward the end of the season. The hollow cavity that existed prior to caprification disappeared soon after caprification, similarly to the hollow in caprifigs. However, in Calimyrna figs the hollow cavity reappeared in mature figs due to shrinking and drying of the fruit.

Postcaprification changes were marked by hardening of the fruit and an increase in the amount of latex. The figs remained green prior to caprification and immediately after caprification. Approximately 45 days after caprification, the fruits turned yellowish-green and became softer, the ostioles began opening, the sugar content in fruits increased, and the amount of latex decreased. This stage also was marked by the appearance of typical endosepsis symptoms in inoculated fruits (Table 2).

After this stage, there was a rapid reduction in the amount of latex, an increase in total sugar content, and further softening of the fruits. The average lesion sizes in inoculated fruits also increased linearly (Table 2), and the color of the skin turned amber to brown. The salient features of these developments were categorized into during, pre-, and postcaprification, and a phenological scale was developed for Calimyrna figs (Fig. 6).

Uninjured Calimyrna fruit cavities inoculated with an *A. niger* spore suspension did not result in fruit infection from 7 July to 1 August. Fruits inoculated from 8 August to 9 September were infected and showed abundant sporulation by *A. niger*. All fruits that were injured and inoculated with *A. niger* were infected regardless of the growth stage at which inoculation was performed. Fruits inoculated in the ostiole remained uninfected from 7 to 25 July, but all fruits inoculated between 1 August and 9 Sep-

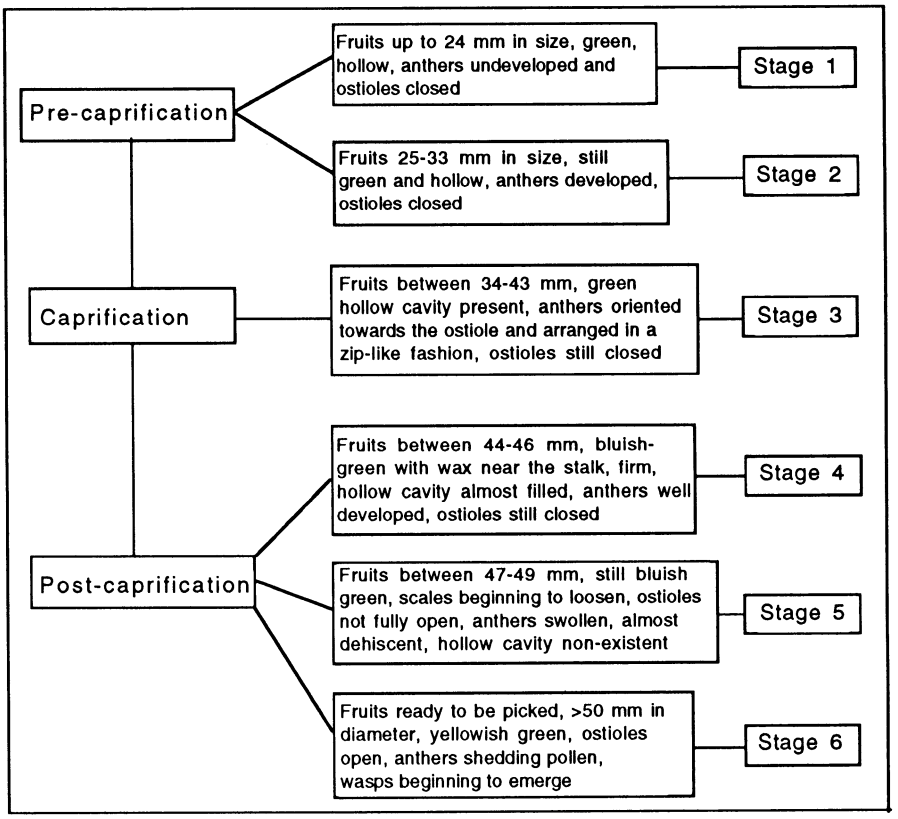

Fig. 5. Proposed growth scale for spring-crop (profichi) caprifigs.

Table 2. Characteristics of Calimyrna figs collected at weekly intervals and their susceptibility to infection by *Fusarium moniliforme*

Date collected	Fruit diameter (mm)	Internal cavity (mm)[a]	Ostiole	Firmness (kg/cm²)[b]	Rind width (mm)	Sugar (°Brix)[c]	Amount of latex (ml)[d]	Susceptibility	
								Surface inoculated[e]	Cavity inoculated[f]
13 June	25.2	15.6/11.5/5.7	Closed	24.9	3.2	12.0	1.0	–	–
20 June	33.3	22.5/12.7/5.1	Closed	30.6	4.0	10.0	1.8	–	–
27 June[g]	37.9	26.8/14.5/1.7	Closed	39.7	4.5	10.0	2.4	–	–
3 July	40.4	31.3/18.7/0.2	Closed	40.0	4.2	10.0	2.2	–	–
10 July	42.3	33.4/20.4/0.0	Closed	48.0	4.2	10.0	3.1	+	+
17 July	43.7	33.7/20.5/0.0	Closed	46.0	3.7	10.0	3.6	+	+
25 July	45.5	34.2/21.7/0.0	Closed	46.0	3.8	10.0	3.6	+	+
1 Aug.	44.9	34.8/21.3/0.0	Closed	46.3	3.5	10.0	2.8	40.1	Symptoms
8 Aug.	46.3	35.2/23.5/0.0	50% open	16.3	3.6	15.8	2.9	115.2	Symptoms
15 Aug.	49.3	37.9/25.2/0.3	Open	16.0	3.8	12.0	2.4	139.0	Symptoms
23 Aug.	54.0	42.6/27.1/0.0	Open	4.9	4.1	19.0	1.0	254.2	Symptoms
30 Aug.	51.1	39.5/25.9/0.5	Open	4.3	3.7	24.0	0.3	404.3	Symptoms
9 Sep.	50.9	41.6/25.5/0.0	Open	1.4	5.1	27.0	0.2	609.8	Symptoms
17 Sep.	41.7	29.8/30.1/2.0	Open	12.3	2.4	38.0	0.0	–	–

[a] Length, width, and height of internal cavities.
[b] Mean firmness from 20 fruits.
[c] Mean sugar content from 20 fruits.
[d] Total amount of latex per 20 fruits collected from stalks immediately after fruit harvest.
[e] – indicates no browning and no lesion development. + indicates development of localized browning of the spongy tissue without lesions. Lesion size was measured beginning during the week when symptoms were first noticed.
[f] – indicates no browning and no lesion development. + indicates development of localized browning in the cavity. Symptoms indicates appearance of typical endosepsis symptoms; actual sizes of the lesions could not be measured because of their irregular nature.
[g] Caprification completed in most fruits.

tember were infected. Regardless of the method of inoculation, dried fruits were not infected (data not shown).

DISCUSSION

In this study, we developed phenological scales for both caprifigs and Calimyrna figs and determined the factors that affect the dynamics of fig endosepsis and smut within a season. We also determined the relative susceptibilities of these two types of figs to infection by *F. moniliforme* and *A. niger*. In earlier studies, we characterized nonhost factors that determine the seasonal dynamics of these two pathogens (12,13).

Even though *F. moniliforme* is introduced into both types of figs by a wasp at the time of pollination (very early in fruit growth), symptoms of endosepsis are not evident until near maturity. The inhibition of *F. moniliforme* growth by fig latex explains the inability of the pathogen to cause endosepsis immediately after its introduction into the fig cavity. Latex is usually abundant at earlier stages of fruit growth and becomes scant as fruits mature.

The inhibitory effects of latex were greatest on germination of conidia and germ tube elongation. These two growth parameters perhaps account for the reduced linear growth. Whereas latex even at the original concentration was not completely inhibitory to linear growth of the pathogen, it showed a fungistatic effect on *F. moniliforme*.

In general, all *Ficus* spp. and other members of the family Moraceae are characterized by the presence of latex. The latex from other *Ficus* spp. contain alkaloids (2) and enzymes (7) that have been reported to possess antimicrobial properties. It is possible that the latex in figs (*F. carica*) also contains alkaloids and enzymes that have antimicrobial properties.

Three factors differentiate edible Calimyrna figs and inedible caprifigs: (i) structure; (ii) development or lack of pollinator insect within the cavity; and (iii) accumulation of sugars. Edible Calimyrna figs contain only pistillate florets in the cavity, in contrast to caprifigs, which contain both staminate and pistillate florets. Whereas the development of the pollinator insect occurs in all crops of caprifigs, the only pollinator insect found in the edible Calimyrna fig cavity is the one that enters it for pollination. Sugar accumulation occurs in Calimyrna figs (edible) and not in caprifigs (inedible). In Calimyrna figs, at least, the types and amounts of various sugars may affect infection by *F. moniliforme*.

Of the carbon sources we evaluated, lactose, mannose, and maltose supported growth of *F. moniliforme* to the greatest extent. The two principal sugars in mature Calimyrna figs, glucose and fructose at 1%, supported growth of *F. moniliforme* equally well; growth on either was nearly 90% of that observed on lactose, mannose, or maltose. Similar results were obtained by Hsieh et al. (6). Concentrations of more than 9 and 18% glucose significantly decreased growth of *F. moniliforme* and *A. niger*, respectively, but both fungi grew well at higher concentrations of fructose. Mature figs contain about 58% sugar, with glucose and fructose as major constituents in a 3:2 ratio. Determination of the ratio of glucose and fructose in edible fruits throughout their development would provide further insights into the interactions between these two pathogens and Calimyrna figs within a given season.

Because of the structural and functional differences between caprifigs and Calimyrna figs, development of different phenological (growth) scales are necessary. The parameters reflecting both the structural and functional differences between the caprifigs and Calimyrna figs described in this study were useful in developing phenological scales. Some of the advantages of growth scales are standardization of terminology, definition of the development of fig fruits in relation to seasonal conditions and variety, indication of stage of development of diseases, and recommendation of fungicide spray schedules. Currently, growers use vernacular terms to characterize stages of fig growth.

The phenological scales developed for both spring-crop caprifigs and Calimyrna figs indicate that the greatest changes occur after caprification, characterized by rapid growth and internal changes in the fruit. Caprifigs remain resistant to endosepsis infection until 4 weeks after caprification. This stage is marked by softening of the fruit and reduction in the amount of latex. The susceptibility of Calimyrna figs to endosepsis infection is marked by softening of the fruits, increase in sugar content, and reduction in the amount of latex; however, the total sugar content in Calimyrna figs close to maturity is higher than glucose and fructose concentrations that decreased the growth of *F. moniliforme*. Our inoculations of Calimyrna figs close to maturity failed to produce observable symptoms, probably because the moisture of the fruit is very low.

Smut seldom occurs in caprifigs, partially because of unsuitable temperatures (12) and perhaps because of limited inoculum levels; however, smut is very common in Calimyrna figs. Our four methods of inoculation at different growth stages indicated that *A. niger* infections can occur on injured fruits at any stage of development. Furthermore, fig latex had no inhibitory effect on germination of conidia, germ tube elongation, or linear growth.

Fruit injury at earlier growth stages is uncommon in fig orchards, and the ostiole, which remains closed until the first week of August, is the only opening through which the pathogen can gain entry. Our inoculations of ostioles of Calimyrna fruit at various stages indicated that *A. niger*

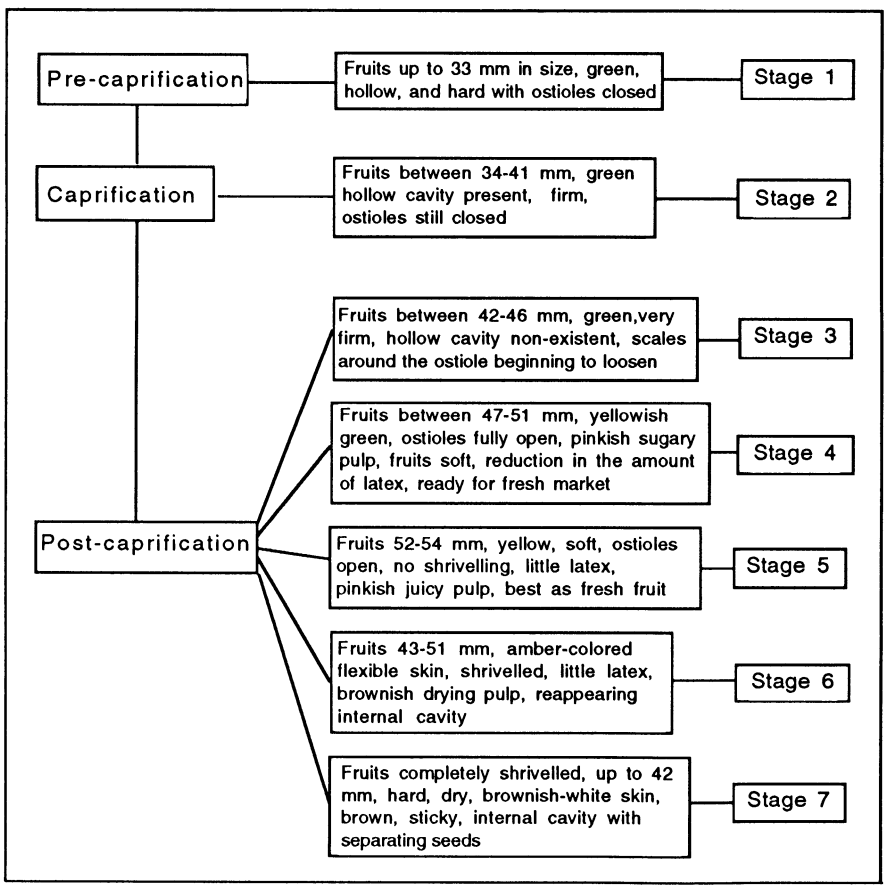

Fig. 6. Proposed growth scale for Calimyrna figs.

infection does not occur when the ostiole is closed. The opening of the ostiole and susceptibility of the fruit to infection occur simultaneously during the first week of August, although propagules of *A. niger* can be vectored into the syconium cavity before the ostiole opens (5). Infection of uninjured fig cavities coincided with increased sugars, reduced firmness, and an open ostiole. This is also the period of increased visits by nitidulid beetles, which may injure the fruit cavity and vector propagules of *A. niger*. These results partially explain why *A. niger* can be a serious late-season pathogen.

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