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THE EPIDEMIOLOGY OF FIG SPOILAGE¹ A. E. DAVEY² AND RALPH E. SMITH³

INTRODUCTION

The high percentage of spoilage which occurs in figs grown for drying has been the subject of much investigation. It is generally recognized that this trouble originates internally in the hollow, fleshy body of the fig. (fig. 1) while it is still on the tree in an immature state. In California three specific types of spoilage are distinguished by growers and packers of figs. These are popularly designated as "smut and mold," "souring," and "endosepsis." "Smut" is often considered as a distinct disease. All of these are caused by common saprophytic microorganisms which in some manner are able to invade the central cavity of the fruit previous to its maturity. The possibility of control of spoilage in figs is closely tied up with the question of *how* and *when* these molds, bacteria, and yeasts get into the fig. Of particular importance is the problem of the relation of insects to the transmission and effects of these organisms.

The disease called endosepsis has not been considered in the present work since its etiology and epidemiology were thoroughly established by Caldis (1927), who showed that this particular type of spoilage affects only caprified (pollinated) figs, that it is caused by the fungus *Fusarium* moniliforme Sheld., and that it is transmitted exclusively by the figcaprifying (pollen-carrying) insect Blastophaga psenes L. The types of spoilage regarding the transmission of which there is still uncertainty are the others above-mentioned, smut and mold, and souring. The former trouble is characterized by the presence inside the ripe fig of a mass of moldy material, representing various fungus types like Alternaria,

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Fig. 1. Stages of fig development Nos. 1 to 4. (From Bul. 387.)



Fig. 2. Stages of fig development Nos. 5 to 7. (From Bul. 387.)

Aspergillus, Cladosporium, Hormodendrum, Macrosporium, and Penicillium. "Smut" is the name specifically applied to the type of fig spoilage caused by the black fungus Aspergillus niger v. Tieg. It is in nowise different from the other types of molding except for its characteristic appearance. Souring is a wet, gassy fermentation of the contents of the fig, supposedly caused by certain yeasts. "Soft rot," a decay of figs on the tree, caused by species of Rhizopus or Mucor is also a rather typical form of spoilage which is sometimes fairly abundant.

Previous Work on Fig Spoilage.—Newton B. Pierce, as early as 1892, suggested the relation of cryptogamic microorganisms and insect carriers to fig souring. Eisen (1901) came to similar conclusions and was the first to call attention to the possible function of the eye of the fig as a barrier to insects and microorganisms entering the interior cavity. Howard (1901) and Condit (1919) also suggested insect transmission of fig souring. Condit (1917) and Hodgson (1918) mentioned a similar possibility in the case of fig smut. Coit (1921), on the other hand, expressed the opinion "Inasmuch as the atmosphere is filled with spores of many kinds of yeasts, molds, smuts and bacteria, and since the eye of the Smyrna fig is open, it is unavoidable that these agents gain access to the interior of the majority of the figs."

In all the work referred to, the idea of insect transmission had to do with scavenger insects, particularly the dried-fruit beetle (Carpophilus) and the vinegar fly (Drosophila), both of which are very common in ripening figs and decaying fruit. Phillips (Phillips, Smith, and Smith, 1925) undertook the first comprehensive investigation of the subject by means of cultures and systematic laboratory methods. Second-crop Adriatic figs were classed into ten successive stages of maturity, based on the opening of the eye, and the interior of large numbers of figs of each stage was examined. The particular object of this work was the study of the smut disease. The examination of nearly 10,000 figs in this investigation was made, mostly with the hand lens and microscope, for the purpose of detecting the earliest development of Aspergillus. Only a comparatively small number of the figs were cultured before the opening of the eye. From this study it was concluded that A. niger is not present in figs until after the eye opens (stage 5, fig. 2) and the fig is nearly mature.

When green, immature figs with closed eyes were inoculated with spores of the smut fungus, very active infection and decay resulted. This was found to be true in the Mission and Kadota fig varieties as well as in the Adriatic. Since, under natural conditions, figs in the early stages are not attacked by these mold fungi and since those of the Mission and Kadota varieties are practically never affected, the conclusion was again drawn that spores are not present in figs before the eyes open. These investigators also found that if the internal tissues of the fig were injured, as with a needle or pipette, in the process of inoculation, infection was more apt to result.

On the basis of all this work Phillips, Smith, and Smith (1925) concluded that "Under summer conditions in the San Joaquin Valley, before the eve of the Adriatic fig opens and the fruit begins to soften, the interior cavity is sterile and neither smut spores nor any other organisms enter." Since a large percentage of the immature figs were not cultured the word "sterile" is apparently used here in a comparative sense to indicate freedom from tissue-destroying fungus colonies visible to the eye or microscope, rather than absolute sterility. In mature figs after the eyes had opened (stage 5, fig. 2) the fruit from some trees showed as high as 50 per cent infection with Aspergillus niger. Many figs which were cultured after the eyes opened showed a considerable variety of fungi, Aspergillus, Rhizopus, Alternaria, Cladosporium, Penicillium, Hormodendrum, various species of yeast, and a number of forms of bacteria. From rather circumstantial evidence it was concluded that the usual carrier of spores of Aspergillus and other microorganisms into ripening figs after the eye opens, is the dried-fruit beetle (Carpophilus). In a previous article (Smith and Phillips, 1922) the statement is made that "Ants, fruit flies and beetles are able to make their way into very green figs with closed eyes, but of course the major part of these visitations occurs after the fruit becomes attractive to them."

Caldis (1927) reported culturing 274 figs of eight parthenocarpic varieties previous to the opening of the eye (stages 1-3, fig. 1), and found them all sterile. Of these figs, 154 were of the Adriatic variety, 67 of these being first crop and 87 of the second crop. By caging *Carpophilus* beetles on ripening figs on the tree, Caldis found that of 54 figs confined in 7 cages with beetles, 50 per cent soured; while of 663 figs in 128 cages with no beetles, none soured. This work was done in two different seasons and in two places.

Hansen (1929) first suggested the importance of thrips as vectors of fig-spoilage organisms and the possibility of their introducing infections before the opening of the eye. In several thousand hard, green figs of four varieties, collected from various parts of California in May, 1928, slightly in excess of 20 per cent were found to be infested with thrips. Figs collected at this time would be of the first crop which ripens in June. Commercial drying figs come entirely from the second crop and commence to form in May and to ripen in August. In 1929, thrips were

again found by Hansen to be common in immature figs. Concerning the cryptogamic flora of the thrips-infested figs collected in May he reports "The interior of 200 of the figs showing evidence of insect invasion were cultured individually on nutrient media to determine their cryptogamic flora. Each of the 200 thrips-infested figs yielded one or more of the following organisms: various species of bacteria, *Rhizopus* spp., *Asper-gillus* spp., *Penicillium* spp., *Fusarium* spp., *Verticillium* spp., *Spicaria* sp., *Hormodendrum* spp., and a number of yeasts.⁴ The 10 figs showing no evidence of insect invasion yielded no cryptogamic flora in culture." Smith and Hansen (1931) state that "Culturing of thrips taken from figs has repeatedly given the same results, namely, that they carry an abundant flora of yeasts, bacteria, and mold fungi." They also cite several instances of crops of figs which showed a high percentage of smut and mold, correlated with an abundance of thrips in the figs, but no beetles. The thrips yielded in culture the same flora found in the figs.

Smith and Hansen also directed attention to a new vector of fig-spoilage organisms, of the type known as predaceous mites. Several species of these almost microscopic creatures are now known to be common in the interior of green figs where they apparently prey upon the fig mite (*Eriophyes fici* Ewing). Smith and Hansen showed by cultures that the bodies of predaceous mites taken from overwintering caprifigs were contaminated with the same molds and other organisms that are carried by thrips.

Hansen and Davey (1932) studied in more detail the relation of thrips and predaceous mites to cryptogamic infestation of figs. Green, second-crop Adriatic figs were taken at various maturity stages from the hazelnut size up to the time when the eye scales begin to loosen. This was done in four different fig districts at intervals of 4 to 7 days between July 1 and August 15, 1930. All the figs were split open and examined for insect infestation.

In regard to cryptogamic infestation, the following statement is made: "During the progress of this examination mites and thrips taken from the interior of the figs were cultured on nutrient agar from time to time to determine the abundance and diversity of flora carried by them.... The cryptogamic flora... on mites and thrips cultured included the following species named in the order of the frequency of their occurrence: Miscellaneous fungi, bacteria, *Hormodendrum* spp., *Asper*-

⁴ We are able to state from personal knowledge and information that the "yeasts" referred to in the work of Hansen and associates with thrips and predaceous mites were yeastlike fungi, not those forms which cause fermentation and souring in figs. These yeastlike fungi form a membranous, wrinkled, dry surface growth on solid media.

gillus spp., Penicillium spp., Alternaria spp., Rhizopus spp., Acrostalagmus sp., and a few yeasts⁵." The figs themselves were not cultured in this work; the exact dates or fig stages at which the mites and thrips were cultured is not stated but the inference is that it was all before the eyes were open.

In the same work Hansen introduced a new technique to determine the time when figs become infested with microorganisms. "In order to show the effect of maximum infestation of mites and thrips and, at the same time exclude larger insects (mainly Carpophilus hemipterus and Drosophila ampelophila) from entering the figs, the following experiment was devised. During August 10-15 the still unopened eyes of 1,557 Adriatic figs were effectively sealed by placing on the eye scales of each a small dab of Tanglefoot preparation. Such treatment did not appear to injure the fruit in any way, as it developed and matured in normal manner and season. The treated figs were allowed to mature on the trees and were not collected until they had dropped to the ground, after which they were taken to the laboratory, split open, and examined for smut and molds. As control, 400 mature figs were picked from the ground under surrounding trees and examined likewise." These figs were not cultured. Of the figs which were sealed before the eyes opened, 16.6 per cent contained visible development of molds.

Varietal Relations.—The fact has frequently been mentioned in the literature that there is a decided difference in the susceptibility of different varieties of figs to these diseases. In particular it has been stated, and from common knowledge may be accepted as true, that the Mission and Kadota varieties are usually immune or free from smut and mold, and souring, whereas the Adriatic and Calimyrna are commonly affected with these troubles. The reasons for this difference need further study and might throw light on the present problem. It has been commonly assumed that the lesser opening of the eye of the Mission and Kadota figs is responsible but in the light of present knowledge this explanation is not well supported. Phillips, Smith, and Smith (1925) found that Mission and Kadota figs were very susceptible to smut (Aspergillus) when artificially inoculated with the fungus.

Discussion of Previous Work.—In the basic work on the epidemiology of fig spoilage carried out by Phillips, Smith, and Smith, by Caldis, and by Hansen and Davey, several questions stand out as being of fundamental importance. Some of them are: (1) To what extent is the entrance of microorganisms into the interior of the fig dependent upon insects and what are the species concerned? (2) Is there any other mode

⁵ See footnote 4, page 528.

of entrance? (3) What is the importance of the eye of the fig in relation to infection? (4) When are the various spoilage microorganisms introduced into figs? The conclusions of the various workers mentioned seem to be at variance on some of these points. Phillips, Smith, and Smith, and Caldis are in essential agreement that the interior cavity of figs remains in a sterile condition until it is entered by insects; that insects



Fig. 3. Interior of nearly mature Calimyrna fig, twice enlarged, at the stage when ripening begins and pulp is about to soften and liquefy. It is at this stage that decay and souring begin. The whole problem of fig spoilage depends upon knowing what organisms cause this, when and how they get into the fig, and how they may be kept out or their development prevented. (From Bul. 506.)

are the principal if not the sole carriers of infection; that the driedfruit beetle is the usual vector of the organisms which cause smut and souring, as well as of various other fungi; and that, since this insect seldom enters figs until the eye opens, the infection is not introduced until that time, previous to which the fig cavity is sterile. The fact that Caldis actually cultured 274 immature figs and found them all sterile is difficult to reconcile with some of the facts and conclusions of later workers. These workers (Hansen and Davey, 1932) conclude that "The major part of smut and mold loss is due to cryptogamic organisms carried into the green figs by predaceous mites and thrips long before the eye scales begin to loosen," and that "The presence of C. hemipterus and D. ampelophila is not at all necessary for the occurrence of this type of spoilage."

An examination of the data and methods given by the various workers discloses several factors which might account, to some extent at least, for discrepancies in their results. Conditions may have been actually different in different seasons. Phillips, Smith, and Smith worked in 1921, Caldis in 1923, 1924, and 1925, Hansen and others in 1928, 1929, and 1930. The studies were also made in several different places. There was some difference in the variety and crop of fig studied. At least eight different kinds of figs were used by the various workers and the figs were partly of the first crop and partly of the second crop. The examination of figs for evidence of infection was made in part by the naked eye, by the microscope, and by means of cultures. In culturing the interior tissues of figs subsequent experience has emphasized the fact that the exact method of sampling the flesh is of much importance. Referring to figure 3, which illustrates the interior of a nearly mature fig in the condition in which it is cultured, two facts are of particular significance. (1) The method by which the fig is opened or split and handled may affect the possibility of contaminating the inside with organisms from the surface or atmosphere. The various investigators whose work is discussed state that the figs were "split," "opened," "cut in two" or merely that the interior was cultured. (2) The exact region or portion of the flesh which is sampled for culturing might affect the results. Whatever may be the time or method of inoculation the probability can scarcely be doubted that entrance is made through the eye of the fig. If, therefore, in one case the cultures were made from a small portion of pulp from the basal region of the cavity, farthest from the eye, and in another case from tissue near the eye or even including portions of the eye and eye scales, it may readily be seen that the results might be very different. In the previous literature most of the information on this point is vague or entirely lacking, but it is known that there was considerable variation in the methods used. It appears therefore that in order to obtain comparable results in this work a uniform or standard technique should be adopted on these and all other important details.

New Work.—The present work was intended to determine more comprehensively and accurately than has been attempted heretofore the occurrence of insects, mites, and cryptogamic microorganisms in figs throughout their period of development, and endeavor to explain some of the apparent discrepancies in past work. The problem was attacked in two ways: first, by following the progress of insect infestation and cryptogamic flora in the developing fruit by observation and cultures; second, by the application of methods directed at the exclusion of insects and microorganisms from the inside of the figs.

The observations to be reported were made during 1932 almost entirely in a block of eight acres of Adriatic figs in the Tuttle district, Merced County. The trees were on heavy clay soil underlain at a depth of 2 or 3 feet by material of a more open consistency and gradually changing to sand at a depth of about 5 feet. A boring at the eastern boundary showed the water table in August, and continuously thereafter until the end of September, to be at a depth of 9 to 10 feet. Irrigations had been made in May and again on June 15. The foliage remained green and the trees appeared not to suffer to any marked extent for want of soil moisture until the crop had been harvested. Figs used in this work came almost altogether from 24 trees. The material examined for infestation, and that of which the eyes were sealed, was produced on two blocks of 9 trees, each comprising 3 trees in 3 adjacent rows in different parts of the orchard.

MICROORGANISMS FOUND ON CULTURING DEVELOPING FIGS IN RELATION TO INSECT INFESTATION

Methods.---In attempting to determine their fauna and cryptogamic flora, uncaprified second-crop Adriatic figs were gathered from the trees at various stages of development for examination and culture. Since on the fig tree there is a continual formation of new fruit throughout the summer it is possible to obtain specimens of the same stages or states of maturity over a period of several weeks, after those stages have once been reached. Theoretically, therefore, the various samples of stage 1 gathered at intervals from June 20 to August 6 (table 1) would all be of the same age. The same would be true of the different batches of each of the other stages. Actually, however, it is conceivable that the later batches of each stage might contain some older, more slowly developed figs than the earlier samplings. Five more or less critical stages of development from the standpoint of disease infection were chosen. Thus stage 1 included figs in which the eye scales were tightly closed and the texture was hard. Stage 2 included figs in which the eye scales had pulled slightly apart in the growth of the fruit but still did not give an uninterrupted passage to the central cavity. Such figs while firm in texture were somewhat softer than those selected as representing stage 1. These stages correspond with those of the same numbers of Phillips, Smith, and Smith (1925) (fig. 1). Stage 3 included figs in which the eye was distinctly open providing clear access to the central cavity; at the same time the fruit was firm and smooth in outline although yielding slightly to pressure of the thumb in picking (stages 4 and 5, figs. 1 and 2). Stage 4 included figs which presented a more or less wrinkled exterior. In these the eye was distinctly enlarged by the drying of the eye scales so that the maximum opportunity was given either insects or organisms to be carried to the interior (stage 6, fig. 2). They still retained their green color. Stage 5 included figs which had dried to a considerable extent upon the tree sufficiently to become thoroughly yellow. The later samples of stages 1, 2, and 3 were obtained from more vigorous trees in another section of the orchard owing to the lack of late figs in the area under observation. Only figs which appeared sound were taken, thus eliminating in the later stages a large number of figs which had become infected with the trouble called souring and undoubtedly reducing materially the number of figs in which causative organisms or vectors associated with that trouble were present.

The samples after being collected were taken to the field laboratory at Planada, about three miles distant, where they were examined and plated the day on which they were gathered. In making the examination each fig was first wiped off with a cloth soaked in 95 per cent alcohol. A shallow longitudinal cut was made with a sterile scalpel through the stem, and the fig split by pulling the halves apart. Examination of the interior for insects was then made by the use of a bi-objective binocular. The florets were then cut out with a sterile scalpel and placed in petri dishes. Referring to figure 3, the technique adopted as standard was to remove all the florets as completely as possible, including the tissue at the base of the eve closely enough so that an occasional eve scale from this point was taken with the sample. Upon each petri dish was recorded the kinds of infestation discovered in the examination. Melted standard potato dextrose agar was then poured from flasks over the fig tissue in each plate, endeavoring to distribute the florets as evenly as possible through the medium. It was not possible, however, in every case to distribute and submerge all the florets in the agar so perfectly as to insure positively the development of every spore or microorganism which might be present. The plates were then stored at the comparatively high summer temperature of the San Joaquin Valley until the observations were completed. Record was made of the number of insectinfested figs and of the kinds of insects observed, but not of the number of individuals in each fig. The cryptogamic organisms which developed from the figs were identified, at least as to genera, as accurately as possible, giving particular attention to those of possible pathological significance. The number of colonies was not recorded.

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THE INSECT FAUNA AND CRYPTOGAMIC FLORA OF UNCAPRIFIED, SECOND-CROP ADRIATIC FIGS

AT DIFFERENT STAGES AND SEASONS

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TABLE 1 (Concluded)

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Results.—Under the conditions described the results cannot be expected to be of absolute accuracy. Most of the insects recorded are of a free-moving character and some might easily have entered and left the figs before the observations were made. Others are small and a few individuals might have been overlooked, especially since it was necessary to manipulate the fig as little as possible on account of the subsequent culturing. Although no record was attempted of the number of individual insects in each fig, it was evident that, in the case of predaceous mites especially, there was much variation in this respect. This may have affected the degree of infection with microorganisms. Since each fig before culturing had to be split open and examined for insects in the open laboratory a considerable chance of contamination could not be avoided and it is probable that this sometimes occurred. Since, however, figs of different stages were usually being cultured simultaneously a check on air-borne contamination was provided and it is not believed that this was a serious source of error. To a considerable extent also the characteristic flora of the figs was different from that of the room. As a rule it is probable that the results for microorganisms were too low rather than too high, for the reason noted above relating to the difficulty of thoroughly distributing and submerging the fig material in the culture medium. This would apply especially in the early part of the season when the number of spores per fig was small. It is to be expected, however, that determinations made by culturing the figs will be higher and reveal more kinds of organisms than those made by simply examining the figs with the eye or microscope. Many spores or latent infections might be present in the figs which would never develop under natural conditions but come to light only in the culture plate. Table 1 gives the data of the entire experiment with the number and percentage of figs in each batch found infested with insects (which are listed in separate columns) and the same data for the cryptogamic flora. No attempt was made to record the amount or location of contamination in individual figs.

The figures under "Figs with fig mite" indicate that these were abundantly present in figs of all stages from the beginning of the observations up to the latter part of August. A large percentage of the figs examined from mid-July to the end of August showed extensive damage to the florets as a result of this infestation. From then on the mites noticeably decreased in figs of all 5 stages, indicating possibly that they begin to leave the fruit at that season.

"Predaceous mites," so far as the data show, were comparatively scarce in the figs until late in June but by September 1 were present in practically all green figs. As the figs ripened these mites apparently left them. According to notes not included in the table it may be stated that early in June the predaceous mites were present in the fruit in much lesser numbers as well as in a smaller percentage of the figs than later in the season. In the earlier cases often only a single mite or at most only a few were found per fig, while later, when the eyes opened, a pronounced increase was apparent both in the number of figs infested and the number of predaceous mites found in each fig. The mites were of two or more species but no attempt was made to identify them or record their relative abundance. Smith and Hansen (1931) give some information regarding the species of such mites found in figs.

Thrips were not found abundant in figs at any time during the season. Compared with the figures of Hansen (1929) for 1928 and 1929, and those of Hansen and Davey (1932) for 1930, it appears that there is a wide variation in the occurrence of thrips in figs in different places and seasons. Here again, as with predaceous mites, several different species were concerned but their identity or relative abundance was not determined. Hansen (1929) and Smith and Hansen (1931) discuss this, mentioning six different species of thrips found in figs. The few cases of thrips found in this work were scattered throughout most of the season. Fewer thrips were observed in figs the latter part, which appears to be the rule except in the case of one species, the black thrips of bean and cotton (*Heliothrips fasciatus* Perg.). This species is often found very abundantly in green figs late in the fall.

The dried-fruit beetle was never found abundantly, but all the infestation occurred after August 20 and only in figs in which the eye was open. The same was true of the vinegar fly, which occurred even less frequently. Both the beetle and fly may have passed into and out of some of the figs without being observed or recorded. The fact also that only sound figs were examined, those showing signs of spoilage being rejected, must have eliminated many which contained or had been entered by beetles and vinegar flies.

The data under the heading, "Sterile figs" represent only figs which gave no growth in agar plate cultures containing most of the interior portion of the fig. Although these figures show considerable fluctuation (due partly perhaps to difficulties of technique) they seem to display certain well-marked trends. In general the figs (stage 1) cultured during the month of June appeared to be nearly all sterile, after which figs with closed eyes (stage 1 and stage 2 in part) showed an average contamination with microorganisms of about 50 per cent. Of the open-eye figs of stage 3, about 25 per cent remained sterile until September, after which nearly all developed a cryptogamic flora.

The figures given under the heading "Figs with smut fungus" show a small, scattering but definite occurrence of *Aspergillus niger* in sound, closed figs of stage 1 from the beginning of the observations. Of the 946 figs which were cultured less than 2 per cent developed this fungus. In 8 of the 17 batches all of the figs were free from the smut fungus and only one fig with *Aspergillus* was found in each of three other lots. In stage 2 (eyes commencing to open) the smut fungus was found in a small but rather uniformly increasing percentage of the figs. In stage 3 (eyes open) smut showed a very marked increase, becoming even more pronounced in stages 4 and 5, where more than 50 per cent of the figs contained this fungus. These, it may be repeated, were all selected, sound figs which showed little if any smut development.

Under "Figs with other molds" are grouped together the fungi which cause visibly moldy figs (*Alternaria, Cladosporium, Hormodendrum, Macrosporium,* and *Penicillium*). The situation here showed an almost total absence of these fungi from figs during most of June, a small percentage of contaminated figs during the first part of July, and a pronounced increase occurring about the middle of July. The most mature figs up to this time were all of stage 1, having tightly closed eyes. After July 16 the percentage of figs containing these mold fungi did not increase significantly in figs of any stage, even those with open eyes.

"Figs with *Rhizopus* and *Mucor*" showed a very light and scattering occurrence previous to the opening of the eye, a marked increase at that time (stage 3) and some further development in the later stages.

Under "Figs with miscellaneous fungi" is included a variety of forms which have no known significance in fig spoilage. Most of them are of the yeastlike fungi referred to in the footnote on page 528, together with species of *Acrostalagmus*. These forms constitute a rather characteristic flora in green figs. The data show that the miscellaneous fungi were present very early in a considerable percentage of green, closed figs and that the percentage increased after the opening of the eyes.

"Figs with souring yeasts" includes forms of *Mycoderma*, *Pseudo-saccharomyces*, *Hansenia*, and *Pichia* which were found associated with typical fig souring. Such yeasts were entirely absent from all the figs of stage 1 and the first three batches of stage 3. Two figs of stage 2 were found to contain souring yeasts. About the middle of August these organisms began to appear commonly in figs of stage 3 and, in the last batch examined on September 16, were found in over 50 per cent of the fruit. No figs showing visible souring were included in the samples.

The figures for "Figs with bacteria" include several types which were fairly constant in most of the cultures but which, so far as known, are of no primary importance in fig spoilage. These organisms appeared to be the first to invade green figs. They were present in 50 per cent of figs of stage 1 soon after July 1, following the earlier period when most of the figs were sterile.

Conclusions and Correlations from Examination and Culturing of Figs.—The results reported in table 1 suggest some fairly definite conclusions as to the epidemiology of fig-spoilage diseases. The high percentage of sterile figs found during June indicates that there was a period at that time of year when the interior of young, closed figs was comparatively free from microorganisms. Gradually, however, contamination took place until, after July 1, less than 50 per cent of figs in the same stage of development (stage 1) were sterile. Figs of stage 1 continued in about this degree of contamination throughout the season. The earliest contamination consisted of a rather specific flora of bacteria, yeastlike fungi, and certain other miscellaneous fungi which never cause visible injury to figs. Regarding insect vectors of this early contamination three possible agents may be considered: fig mites, predaceous mites, and thrips. The fact that figs of stage 1 (eye tightly closed) were nearly all sterile during June and at the same time all heavily infested with the fig mite, confirms previous conclusions that this mite is not a carrier of microorganisms (Phillips, Smith, and Smith, 1925, p. 32; Smith and Hansen, 1931, p. 28). "Predaceous mites," so far as these data show, were present in very few figs when the first two batches of stage 1 were examined, but the percentage of infestation materially increased during the period (June) when most of these figs of stage 1 were still sterile. Of the 60 figs examined on June 27, for example, 23, or 38.4 per cent, were infested with predaceous mites; but 54, or 90 per cent of the same figs were sterile. On June 28, 60 similar figs were examined and 15, or 25 per cent, showed predaceous mites, yet all but one (98.3 per cent) were sterile. The mites in individual figs were fewer in number at this time than later and it may be true also that they had not as yet penetrated the interior of the figs very extensively. Attention may also be directed to the showing of Hansen and Davey (1932) that of 226 predaceous mites cultured by them, 122, or 43.5 per cent, were free from cryptogamic organisms. It is not unlikely that the percentage of infection of the mites, or in other words the abundance of mold spores, may be less in the earlier part of the season. Unless some of these factors are significant it is difficult to reconcile the low percentage of cryptogamic infection in figs of stage 1 in June and the high infestation with predaceous mites at the same time, with the idea that these mites are important vectors of spoilage organisms. Thrips were present in such small and irregular numbers that no conclusions could be drawn as to their importance.

The next striking development was the marked increase in molds which took place in closed figs (stage 1) after July 15. No correlation of this with any insect vector is apparent, unless it be the increased abundance of predaceous mites in individual figs, a difference in the species present, increase in their cryptogamic contamination, or more extensive penetration of the inside of the figs.

The small amount of smut present in figs of stages 1 and 2 might be correlated with predaceous mites or, to a slight extent, with thrips. The large and sudden increase of Aspergillus and Rhizopus which occurred early in August in figs of stage 3, followed closely by the development of souring, correlates with the time of the opening of the eye of the fig, the ripening of the first figs, and the appearance in numbers of the dried-fruit beetle. No evidence is afforded, however, as to whether there was any connection between these events or if it was merely a coincidence. Vinegar flies were not sufficiently abundant to justify any conclusions. The conclusion of previous workers that thrips, predaceous mites, and fig mites are not vectors of souring yeasts is supported by the results given in this table. The nonsouring yeasts or yeastlike fungi previously mention by Hansen, by Smith and Hansen, and by Hansen and Davey as being carried by thrips are included here under "Miscellaneous fungi." Of the true souring yeasts (Mycoderma, Pseudosaccharomyces, Hansenia, Pichia) not a single colony developed from the 946 figs of stage 1 in which fig mites and predaceous mites were abundant.

The older figs of stages 4 and 5 are probably of no additional significance. At the latter stage the fig commences to dry, the infection period is passed, and the high concentration of sugar in the fig makes it no longer a favorable medium for the growth of microorganisms, or for the insects which attack green figs. To such causes, and the fact that all figs showing spoilage were rejected, is probably due the apparent decrease of infection in the later stages.

EXPERIMENTS IN EXCLUDING INSECTS AND MICROORGANISMS

Sealing the Eyes of Figs.—The use of Tanglefoot to seal the eyes of figs has already been mentioned (Hansen and Davey, 1932). In the present work this method was used on four trees and on a much larger number of figs than before. The sealing was carried out at two periods: figs with closed eyes on two trees were sealed between June 22 and June 25, and those on two other trees between July 28 and August 4, hoping at the early period to forestall the infestation by predaceous mites. Examination of green figs at about the first time of sealing, however, indicated that a considerable percentage was already infested (see table 1) by the time the sealing was completed on June 25. The figs were allowed to mature and fall, and were gathered from the ground about once a week. A number of unsealed figs from the same trees, together with the crop from two adjacent trees were picked up at the time by way of controls. All of these trees, as described on page 532, were adjacent to those from which the figs were taken for culturing (table 1). In making the examinations of the figs and in reporting results, all with broken seals were carefully segregated and reported separately. The figs were not cultured but simply examined for spoilage. Consequently most of the miscellaneous fungi and all of the bacteria reported in table 1, as determined by culturing the figs, would fail to be detected in these figs. The percentages of smut, Rhizopus, and other molds would also be expected to be lower here than in the experiments where the figs were cultured. In the latter case the presence of a few spores would be responsible for a record of the fungus, while, in the method used here, visible growth and spoilage in the fig was required. In so far as simple, microscopic examination of the growth within the fig could determine, the molds were assigned to the same groups as in table 1.

Results.—The results obtained in this experiment are presented in table 2. The tables gives the figures for the crop of each tree, considering separately the figs in which seals were intact, those with broken seals, those on the same trees not sealed, and figs from adjacent trees on which none were sealed. In regard to smut it will be noted that on all the trees the percentages in the unsealed figs were very much greater than in the fruit which had been sealed. On trees 1 and 2 on which the figs were sealed early, less than 2 per cent of the figs with unbroken seals developed smut, while the average of unsealed figs was more than 10 per cent. Similar figs sealed later on trees 3 and 4 averaged about 3 per

TABLE	c1	
	TABLE	

RESULTS OF SEALING EVES OF FIGS PREVIOUS TO OPENING

h souring	Per cent	0.00	0.00	0.00	0.20	0.00	00.00	0.00	0.20	0.00	0.00	0.20	0.15	0.00	0.0		0.15
Figs wit	Number	0	0	0	5	0	0	0	5	0	0	5	9	0	0	4	9
Rhizopus Mucor	Per cent	0.1	0.1		1.3	0.2	0.0		1.3	0.4	0.4		0.86	0.2	0.0		0.86
Figs with and <i>l</i>	Number	2	-	. 1	29	ę	0	:	29	4	1		35	3	0	:	35
th other Ids	Per cent	15.2	5.0	6.0	4.0	20.0	10.6	3.3	4.0	10.0	12.0	9.2	2.0	6 .6	6.0	2.5	2.0
Figs wit mo	Number	321	63	32	92	344	177	12	92	103	33	83	462	78	14	`36	62
mut fungus lus niger)	Per cent	1.5	2.1	13.5	10.6	1.8	2.9	6.7	10.6	3.5	2.2	13.6	6.8	2.6	2.9	4.9	8 [.] 9
Figs with s (Aspergil	Number	32	26	70	219	32	48	24	219	36	9	124	277	31	7	72	277
Date of sealing)	June 22–25	June 22-25.	Not sealed	Not sealed	June 22–25	June 22–25.	Not sealed	Not sealed.	July 28–Aug. 4	July 28–Aug. 4	Not sealed	Not sealed	July 28–Aug. 4	July 28-Aug. 4	Not sealed	Not sealed
Number	of figs	2,108	1,253	517	2,322	1,730	1,668	358	2,322	1,031	274	906	4,053	1,180	240	1,468	4,053
Condition of seal when	examined	Intact	Broken.	Not sealed	Not sealed	Intact	Broken	Not sealed	Not sealed	Intact	Broken	Not sealed	Not sealed.	Intact	Broken	Not sealed	Not sealed
Tree	number	1	1	1	5	2	2	67	5	ę	ŝ	ŝ	9	4	4	4	9

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cent smut while the percentage in the unsealed was much higher. These results indicate that there was a small and slowly increasing percentage of smut infection in the figs before the eyes opened, but that the great bulk of the infection entered after the opening of the eyes. In the case of other molds, on the contrary, it appears that the maximum amount of infection took place early in the development of the fruit before the opening of the eye, and could have had no relation to the entrance or exclusion of insects as large as the dried-fruit beetle. In fact, the sealed



Fig. 4. Tent over fig tree to exclude insects.

figs show a decidedly greater percentage of spoilage by mold than those with open eyes. This may have been due to increased humidity within the fig. *Rhizopus* was present in very small amounts in these figs, both sealed and unsealed. No souring took place in the figs with sealed eyes and only a very few of the control figs were sour.

Screening of Trees.—In 1922 an experiment was undertaken by Phillips, Smith, and Smith (1925) in which two large Adriatic fig trees were screened from infestation by the dried-fruit beetle by tenting them over with unbleached muslin. Such a measure was effective in keeping out the insect but a large amount of molding occurred on the exterior of the fruit. Dried-fruit beetles were introduced into one of the tents but apparently failed to enter the fruit upon the tree.

In 1932 a similar experiment was conducted in the present investigation. The exterior molding of the fruit was avoided by permitting freer air movement through the selection of smaller trees and the use of more open material as a screen. Six trees were selected. Four of these were completely enclosed on sides and top with a screen (fig. 4) of absorbent gauze (cheesecloth) which had a denseness of weave of 14 threads to

Tree	Type of screening	Beetles intro-	Number of	Figs with si (Aspergili	mut fungus lus niger)	Figs wit mo	h other Ids	Figs with	ı souring	Figs wit]	n beetles
number)	duced	figs	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent
7	Complete	No	753	24	3.2	21	2.8	0	0.0	0	0.0
80	Complete	No	632	34	5.4	26	4.1	0	0.00	0	0.0
6	Complete	No	869	86	9.9	36	4.1	0	0.00	0	0.0
10	Complete	Yes	688	28	4.1	28	4.1	10	1.50	11	1.6
11	Open top	No	1,037	102	9.4	53	5.0	10	0.90	œ	0.7
12	Open top	No	808	51	6.3	41	5.2	0	0.0	0	0.0
5	None	No	2,322	219	10.6	92	4.0	5	0.20	:	
9	None	No	4,053	277	6.8	79	2.0	9	0.15	•	

TABLE 4

THE RELATION OF ANTS TO FIG SPOILAGE

souring	Per cent	2.2 1.6
Figs with	Number	18 15
other molds	Per cent	5.3 7.2
Figs with c	Number	43 58
Rhizopus	Per cent	4.1 4.0
Figs with	Number	33 32
mut fungus (us niger)	Per cent	5.2 5.6
Figs with si (Aspergill	Number	42 45
Infestation with ants		Infested Not infested
Number of	figs	800 800
Number of	trees	8 8

TABLE 3

RESULTS OF SCREENING FIG TREES TO CONTROL DRIED FRUIT BEETLES

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the inch. A floor of unbleached muslin was provided and fitted closely around the tree trunk, the whole structure being made as tight as possible. The dimensions of these tents were: sides 12 feet, height 9 feet. Two other trees were similarly screened except that no top was provided; the sides were 12 feet in height. All figs approaching ripeness were removed before screening with the object of precluding any chance of infestation with dried-fruit beetles. The construction of the screens was completed between July 30 and August 2. On August 11, 70 sour figs containing adult beetles and larvae were placed in a shallow granite dish within a 50-pound lug box. The lug box contained a layer of soil 2 to 3 inches deep, was loosely covered by brown wrapping paper, and the whole introduced within the screen over one tree. The crop on the trees was allowed to drop and was not gathered until August 21, when the figs were removed from the floor and the trees were stripped of any fruit on the branches.

Results.—Table 3 shows the numbers of smutty and moldy figs, sour figs, and figs infested with the dried-fruit beetle in the crop from each tree, including the two adjacent unscreened trees (Nos. 5 and 6) which have already appeared in table 2. It will be seen that the percentage of smut in the figs from screened trees, which are believed to have been entirely free from dried-fruit beetles, ranged as high as in those of unscreened trees; and the screened tree into which beetles were introduced ranked next to the lowest in amount of smut. The amount of mold also showed no relation to the presence or absence of beetles. Souring occurred on screened trees only where beetles were present within the screen. On such trees beetles were discovered in both normal immature figs and figs already sour.

Ants as Carriers of Fig-Spoilage Organisms.—The presence of black ants in numbers on fig trees drew attention to them as possible carriers of fruit-spoilage organisms. It was noted that many trees were badly infested with ants while others were apparently free from such infestation. The crops of 8 infested and 8 uninfested trees were therefore sampled, 100 mature figs being taken from the ground beneath each tree. Table 4 gives the results of this experiment.

Results.—The figures show that spoilage troubles were almost identical in the crops from ant-infested and noninfested trees and that the dissemination of these troubles can probably therefore not be attributed to this agency.

DISCUSSION

The results obtained by the three different lines of attack upon the problem of the epidemiology of fig spoilage are essentially in agreement and suggest a number of conclusions in relation to previous work and ideas on this subject.

Sterility of Immature Figs.-The former conception of the epidemiology of fig spoilage was based largely upon the following hypotheses, first formulated by Phillips, Smith, and Smith (1925), that (1) "In the climate of the San Joaquin Valley, the interior cavity of Adriatic figs usually remains sterile until it has been entered by insects." (2) "The smut fungus is usually carried into figs by insects, of which the driedfruit beetle, Carpophilus hemipterus (Linn.) appears to be the most important." (3) "Indications point to the dried-fruit beetle as being also an important carrier of some other forms of decay." (4) "Figs become infected with smut when they are still on the tree, just at the time when the eye opens and the fruit begins to soften." The work of Caldis (1927), (1930), supported this point of view. Subsequently, the work of Hansen (1929), Smith and Hansen (1931), and Hansen and Davey (1932) established the fact that a considerable percentage of the figs which they examined were not sterile previous to the opening of the eye and presumably could not have been inoculated with organisms introduced by insects as large as the dried-fruit beetle. These investigators directed attention to thrips and predaceous mites as possible vectors.

The present work establishes very plainly the fact that many figs are not sterile just previous to the opening of the eye, and that closed figs may gradually become contaminated during the growing season. In table 1, for example, the 946 figs which reached stage 1 and were examined and cultured at intervals during June and July indicate a gradual progress from 100 per cent sterile in those which were of this stage of maturity early in June, to less than 50 per cent in those which reached the same stage of development about August 1. It is noticeable that much of this early contamination, and practically all of it previous to about July 15, was due to bacteria and the organisms listed as miscellaneous. This flora was a characteristic one and did not indicate haphazard, air-borne contamination. As to vectors, it may be assumed that the figs of stage 1, table 1, had not been entered by dried-fruit beetles, and the same is nearly as positive concerning the figs with sealed eyes, in table 2, and those in the enclosed cages, in table 3. It therefore seems

safe to conclude that Carpophilus is not the sole carrier of cryptogamic infection and that if a living vector is involved it must be of sufficiently small size to penetrate the closed eye of the fig. According to the data in table 1 the fig mite (Eriophyes), and various species of predaceous mites and thrips are possibilities in this connection. The fig mite as a possible carrier has already been practically eliminated by previous work of others and by the data in table 1 where figs 100 per cent heavily infested with fig mite were practically all sterile. Thrips cannot be excluded as potential carriers of infection, but during the season when this work was done they did not seem abundant enough (table 1) to account for much of the cryptogamic flora. Predaceous mites seem then to be the only remaining possibility, since, with the amount of work which has been done upon the fauna of green figs, it is doubtful if any other important vector has been overlooked. Allusion has already been made (page 539) to the situation which was found (table 1) in figs of stage 1 near the end of June, when almost all were sterile as to cryptogamic flora and yet from 25 to 40 per cent were infested with predaceous mites. Although a plausible explanation of this condition has been suggested, it is still evident that final and complete proof has not yet been established regarding insect transmission of fig-inhabiting microorganisms.

Smut.—In this work it seems to be clearly shown that the idea of the dried-fruit beetle's being the sole vector of fig smut (Aspergillus niger) is no longer tenable. Table 1 shows definitely that a small percentage of figs which had never been entered by this or any other comparatively large insect contained the spores of this fungus.⁶ From this table it appears, however, that the percentage of figs entered by the smut fungus was very low until after the fruit had reached that stage of maturity when the eyes open and ripening began, whereupon a very large increase in the percentage of invasion took place. The coincidence of this with the entrance of the beetle naturally suggests a connection between the two events and from the data in table 1 alone it might easily be concluded that Carpophilus is the principal vector of smut. Table 3, however, seems to show very plainly that when the beetle was entirely excluded from figs by screening the percentage of smut developed was just as great as in fruit which was fully exposed to this insect. If it be assumed that the possibility of the beetle as a primary carrier of smut

⁶ One fig of stage 2, in which the eye was still practically closed, contained a beetle, and Smith and Phillips (1922) record finding a few cases of ants, beetles, and flies in green closed figs. These cases are too exceptional to seem of any significance in the present connection.

is eliminated by these experiments, then the fact of the presence of Aspergillus spores in closed-eye figs may be looked upon as a similar situation to that which has just been discussed in regard to miscellaneous fungi. Predaceous mites seem to be the only carriers which could have been extensively involved but it cannot yet be said that the case against them is a complete one. It is not entirely impossible that the small numbers of thrips present in closed figs might have had some significance regarding this early smut infestation. The fact of the increase of Aspergillus in figs with open eyes (tables 1 and 2), taken with the showing in table 3 that excluding the Carpophilus beetle did not prevent this, might be taken to suggest that the opening of the eye provides access to the interior of the fig for large numbers of Aspergillus spores from the atmosphere. It is, however, also true that the population of predaceous mites and fig mites and the injury to fig tissue by the latter are all at their height at this time and other complicating factors no doubt exist. Further work is needed upon this important point. Phillips, Smith, and Smith (1925) reported negative results from their limited experiments on air-borne infection. It should of course be remembered that the figures in table 1 are based on cultures and represent figs all of which appeared to be sound and free from visible smut, while the figs listed under "Smut" in tables 2 and 3 showed visible development of the disease. There is considerable uncertainty, therefore, as to how much significance the late-entering, abundant invasion of open-eye figs by Aspergillus spores has in the development of visible smut or commercial spoilage of this type.

Other Molds.—In the figs from which the figures presented in table 1 were obtained it is fairly definite that the fungi which cause what is commonly called "mold" (Alternaria, Hormodendrum, Cladosporium, etc.) became abundant in closed figs of stage 1 about the middle of July, but were not present during the first part of the season in figs which had reached stage 1 at that time. No marked increase took place after the eyes opened. Sealing the eyes or screening the trees (tables 2 and 3) did not affect development of mold except that sealing increased it somewhat. The question of insect transmission or the method of the introduction of these molds into figs with closed eyes has the same aspects as in the case of other fungi. Predaceous mites and the few thrips which were present seem to be the only possible vectors but further proof is needed in regard to them.

Souring.—The figures given in table 1 corroborate the conclusion of previous workers that souring yeasts do not enter the fig until after the eye opens and that this time coincides with the appearance of the driedfruit beetle. This, however, does not give proof that these facts have any relation to each other. Tables 2 and 3 indicate that when beetles were excluded, either by sealing or screening, no souring occurred, whereas a certain amount developed in beetle-infested figs. The data are too meager, however, to be taken as final. The results coincide with those of Phillips, Smith, and Smith (1925) and those of Caldis (1930).

SUMMARY

The epidemiology of spoilage diseases of uncaprified, second-crop Adriatic figs was studied at Merced, California, by three different methods with particular reference to insect transmission.

The internal fauna of developing figs was found to consist of the fig mite, *Eriophyes fici* Ewing, various species of predaceous mites, various species of thrips, the dried-fruit beetle (*Carpophilus hemipterus* L.), and the vinegar fly (*Drosophila ampelophila* Loew.). The last two mentioned were found to enter the figs only after the eyes had opened; the others were found throughout the season in immature figs with the eyes still closed. Ants were also found to infest ripening figs in some cases.

Up to about July first, green, nearly full-grown figs with closed eyes (stage 1) were found to be nearly all internally sterile. In the successively developing figs which reached this stage after that time an increasing percentage was found to contain cryptogamic microorganisms.

The earliest flora to appear in figs of stage 1 consisted mostly of bacteria and certain yeastlike fungi.

In figs of stage 1 the fungi which cause moldy figs (*Alternaria*, *Hormodendrum*, *Cladosporium*, etc.) were first found abundantly in fruit which reached that stage about July 15. No marked increase thereafter in the percentage of figs of any stage infected with these fungi was found.

The fig-smut fungus (*Aspergillus niger*) was found to be present in a small percentage of figs previous to the opening of the eye. After the eyes opened this percentage was much increased.

The yeasts which cause fig souring were found to be entirely absent from figs until after the eyes had commenced to open.

No relation could be seen between the presence in figs of the fig mite (*Eriophyes fici*) and any type of infection.

Evidence was obtained that the dried-fruit beetle (*Carpophilus*) is not an important factor in the transmission of smut and mold, but may be the principal carrier of the yeasts associated with souring. During the season when this work was done thrips were not present in figs in sufficient numbers to warrant any final conclusions as to their importance as carriers of infection.

Predaceous mites and, to a much less extent, thrips, were the only living vectors to which the transmission of smut and mold could be attributed.

No relation was found between the activities of ants in figs and the spread of smut and mold, and souring.

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