Biological Characteristics of Elsinoë fawcetti Pertaining to the Epidemiology of Sour Orange Scab

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ABSTRACT

Hyaline conidia of *Elsinoë fawcetti* required liquid water for their production, dispersal, survival, and germination, and a minimum wetting period of 2.5 to 3.5 hours to cause infection. Colored conidia, representing a morphologically distinct asexual spore form produced by this fungus, were liberated from conidiophores both by wind in excess of approximately 2 m/second and by water. Conidiophores that had previously borne colored conidia produced only hyaline conidia when wetted. Apparently, these conidiophores require some unknown environmental factor, in addition to high humidity, to produce colored conidia. When dispersed dry by wind, most colored conidia remained viable at least until the following night and then germinated with dew. Colored conidia dispersed by water in the daytime survived drying until the following night only if they remained attached to each other following detachment from the conidiophores. Because of the ability of colored conidia to survive postdispersal desiccation until dew was available for germination, some infection still ensued when the periods of canopy wetting by rain, overhead irrigation, or nonfungicidal sprays were too short to permit infection prior to drying.

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Moisture is an important factor contributing to the severity of sour orange scab which is caused by *Elsinoë fawcetti* Bitanc. and Jenkins. In Florida, severe scab infection on susceptible *Citrus* spp. cultivars has been associated mostly with unusually wet springs, especially if rainy spells occur soon after bloom (12). Scab infection is also favored by overhead sprinkler irrigation (6). Doubt remained, however, whether rainfall or overhead irrigation are essential for scab epidemics, or whether moisture from heavy dew or fog may suffice.

In Florida citrus groves on elevated areas with deep, well-drained soils (sandhills), scab tends to be serious only in years of above-average rainfall. In lower-lying areas with wetter soils (low-lying hammocks and flatwoods) where dew tends to be heavier and more prolonged, scab can be severe even during years with a relatively dry spring. These observations led Winston (12) and Ruehle (10) to suggest that moisture did not have to be in the form of rain for scab epidemics to occur, and raised the question whether substantial conidial dispersal, apart from localized spread by dew itself, could occur without a water splashing action. Previous literature on sour orange scab has left this question unanswered. Widespread dispersal of *E. fawcetti* would be feasible by wind-blown ascospores, but the perfect stage [which was described from Brazil (1)] has not been found in Florida.

In Florida, *E. fawcetti* produces two distinct asexual spore forms which were originally described by Jenkins (5) as hyaline elongate conidia and colored spindle-shaped conidia, the latter with a development like *Cladosporium* spp. Hereafter, the two forms will be described as hyaline and colored conidia, respectively.

In a report on scab epidemiology, Yamada (13) concluded that conidia are rain-dispersed, and that the distance of dispersal is rather short. Yamada made no mention of colored conidia, which suggests that they may

not be a universal feature of *E. fawcetti.*

This paper reports the effects of some environmental factors on the development, dispersal, survival, and germination of each conidial type produced by *E. fawcetti*, and the overall requirements for infection of young shoots.

MATERIALS AND METHODS.—One isolate of *E. fawcetti* was used. It was obtained from a diseased rough lemon (*Citrus jambhiri* Lush.) tree growing at Lake Alfred, Florida, and was maintained on potato-dextrose agar (PDA).

Container-grown plants were used for infection studies and as traps to detect wind- or water-dispersed conidia. They were propagated by cuttings from the same rough lemon clone that yielded the fungal isolate. The clone was highly susceptible to scab, but atypical for rough lemon in that it was resistant to Alternaria leaf spot, which by severely damaging young shoots would have rendered a susceptible clone unsatisfactory for outdoor studies. The plants were maintained scab-free in the greenhouse, and pruned prior to use to promote the development of new scab-susceptible shoots.

For tests on the effect of relative humidity (RH) on fungal activity, microscope slides with deposits of mycelia, conidia, or excised scab lesions were supported in modified desiccator jars over solutions of sulfuric acid providing 90 to 100% RH. Temperature and RH were monitored periodically with a Hygrodynamics Inc. Model 5 15-3001 Electric Hygrometer Indicator. Temperature was held at 25 C. Maximum RH was reached 6-8 hours after closing the lids.

Wind speeds required to liberate and disperse conidia were studied in simulated laboratory experiments. Scab lesions were excised from diseased leaves and held with forceps 2-4 cm inside the entrance of the tunnel portion of a spore trap-impactor system similar to that described by Brook (2). A 2-mm (internal diameter) tube connected to a compressed air supply was directed at a 45-degree angle to the base of the tunnel with its outlet 5 mm from the surface of the scab lesions. The velocity of air from the jet was estimated by connecting the tube to a 250-ml burette and observing the rate of air displacement as indicated by the movement of introduced soap bubbles. The vacuum pump attached to the impactor created an air speed through the 50-mm-long tunnel of 0.13 m/second.

Airborne conidia were trapped in the field using the portable spore trap designed by Schenck (11). Duration of dew wetting periods was recorded with the device developed by McCoy et al. (8).

Conidial production counts were based on 16 fungal colonies or scab lesions per treatment. Germination and survival percentages were based on a minimum of 100 conidia per test. In plant inoculation and field trapping studies, a minimum of four plant-replicates, each containing > 8 susceptible shoots were used for each treatment.

RESULTS.—*Production of conidia on artificial media.*—Colonies of *E. fawcetti* did not sporulate on PDA, but after fragmenting the compact stromatic growth in a Waring Blendor and transferring fragments to a film of distilled water on a microscope slide, a few hyaline conidia were produced. This led to the development of the following method for producing deposits of hyaline conidia for survival and germination studies.

Portions of fungal growth were extracted aseptically from the center of 4- to 6-week-old colonies on PDA and chopped into small pieces in a 100-mm diameter petri dish. Ten milliliters of a liquid medium, similar to the modified Fries' medium (7), were poured into the petri dish. The medium consisted of 5 g $(NH_4)_2\ C_4H_4O_6$ (ammonium tartrate), 1 g NH_4NO_3, 1 g K_2HPO_4 0.5 g $MgSO_4 \cdot 7\ H_2O$, 0.1 g $CaCl_2$, 0.1 g NaCl, and 20 g sucrose in 1 liter of distilled water. Because of its sticky consistency, the chopped deposit had to be stirred into the medium vigorously to separate the hyphal fragments. Mucous secretions from the fungus soon caused most hyphal pieces to become affixed to the bottom of the petri dish. After 2-3 days at 25 C, the medium and any unattached hyphal fragments were decanted and the affixed colonies were flushed three times with sterile distilled water. Colonies which measured approximately 0.2 mm in diameter (microcolonies) were scraped from the glass with a scalpel and transferred to drops of distilled water on microscope slides.

No conidia were produced on colonies growing in Fries' medium, but after being washed and transferred to water, the colonies started to release conidia in 2-3 hours at 25 C (Fig. 1-3). These conidia were identical to the hyaline conidia produced on scab lesions.

The percentages of microcolonies that had commenced conidial production, when observed 5 hours after being transferred from Fries' medium to water, were 37 at 18 C, 87 at 21 C, 94 at 24 C, 87 at 27 C, and 6 at 30 C.

No conidia developed on washed microcolonies transferred to drops of 2% sucrose solution, 10% orange juice, decoction of rough lemon leaves (prepared by autoclaving 20 g young leaves in 100 ml water), or to Fries' medium minus sucrose.

The washed microcolonies survived drying and exposure to 50-60% RH for 2 days at 24 C and resumed conidial production after rewetting.

Colored conidia were never produced on the microcolonies. Attempts to induce their formation by holding the microcolonies at 95, 98, or 100% RH failed.

Production of conidia on naturally produced scab lesions.—During early stages of lesion development, the conidiophores were poorly defined and produced only hyaline conidia. Generally, the conidiophores remained short and continued to produce only hyaline conidia. On some lesions, mostly on the lower leaf surface, the conidiophores elongated (Fig. 4) and produced chains of colored conidia. Observations made shortly after sunrise, before dew dissipated, indicated that hyaline conidia were present on wetted lesions, whereas longer conidiophores with chains of colored conidia developed mostly on lesions that had escaped dew wetting because of their different orientation.

Chains of colored conidia were easily detached by lightly touching drops of water on microscope slides with the lesion surface (Fig. 5, 6). In 30-45 minutes, the colored conidia germinated to form hyaline conidia. These arose at the point or just to the side of the point (Fig. 7) of the conidia as previously described by Jenkins (5).

The hyaline conidia, whether produced directly from the conidiophores or indirectly from colored conidia, measured mostly 4-8 $\times$ 3-4 μm. No microconidia of

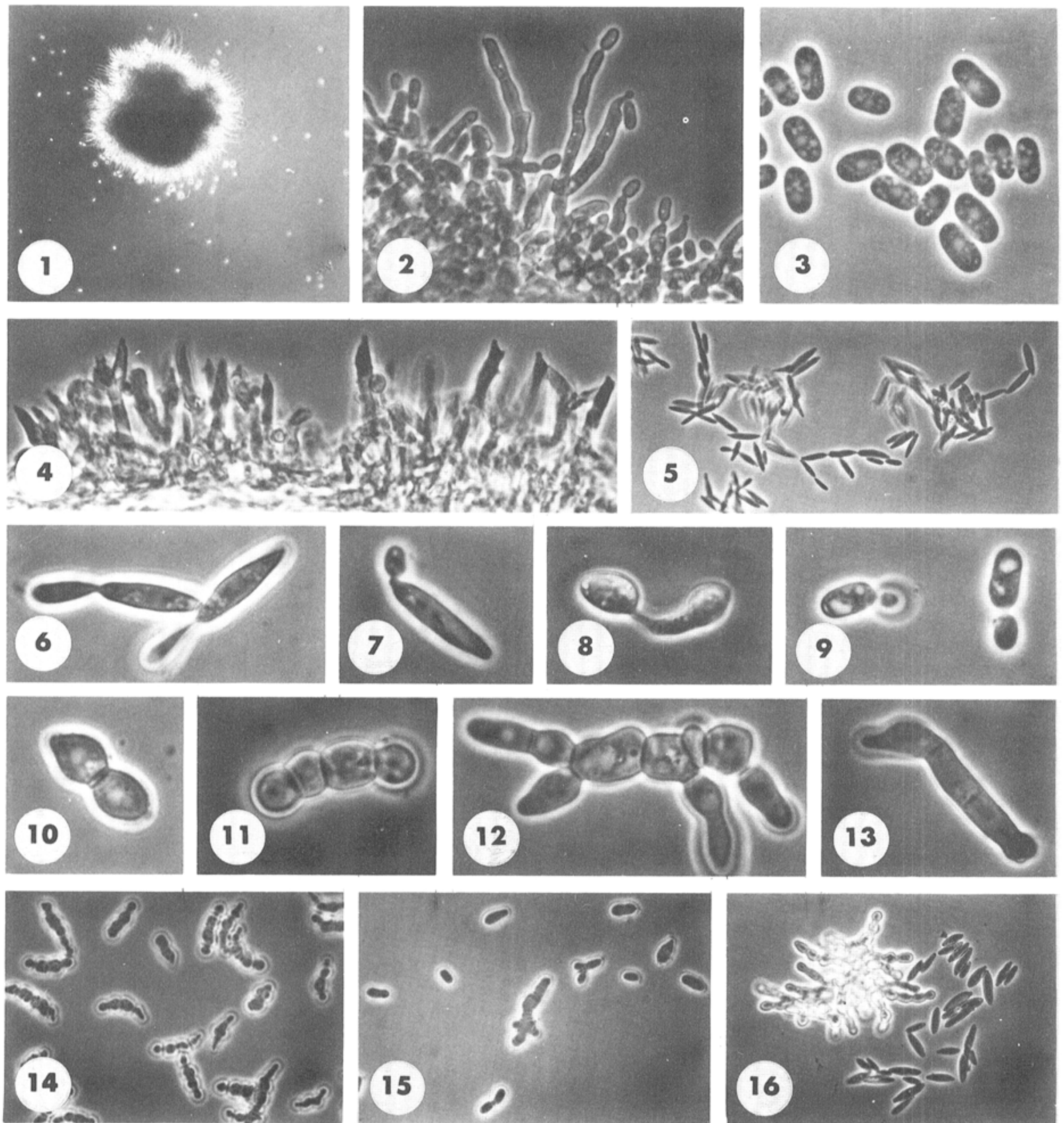

Fig. 1-16. Photomicrographs by phase-contrast optics on preparations of *Elsinoë fawcetti* colonies, conidiophores, conidia, and germinating conidia mounted in water. **1)** Microcolony from Fries' medium producing hyaline conidia as observed 4 hours after being washed and transferred to a drop of water on a microscope slide (× 90). **2)** Production of hyaline conidia from tips of unmodified hyphae on microcolony shown in Fig. 1 (× 360). **3)** Deposit of hyaline conidia from microcolony (×900). **4)** Conidiophores on a scab lesion that had produced colored conidia (× 450). **5)** Clumps of colored conidia, with some still in chains, following removal from conidiophores by gently brushing the lesion surface against a drop of water on a microscope slide (× 360). **6)** Branching chain of colored conidia (×900). **7)** Colored conidium producing hyaline conidium to the side of the apex, 45 minutes after wetting (×900). **8)** Germination of hyaline conidium by germ tube on leaf secretion medium (× 900). **9)** Budding of hyaline conidia on leaf secretion medium (× 900). **10-12)** Germination of hyaline conidia on Fries' medium at 25 C showing development of septa at 8 and 16 hours, respectively, and branching growth at 30 hours (×900). **13)** Germination of colored conidium after 15 hours in Fries' medium at 25 C, showing enlargement and septation of conidium prior to hyphal growth (× 900). **14-15)** Showing, respectively, after 24 hours, the relatively uniform germination of hyaline conidia in Fries' medium, and the uneven germination of hyaline conidia in 2% sucrose solution (× 360). **16)** Fries' medium viability test on deposit of water-liberated colored conidia following 24 hours of desiccation, showing that detached conidia were all dead and that the clump on the left, where some conidia had remained attached to each other, contained viable conidia (× 360).

diameter < 2 µm as described by Jenkins (5) were observed. The colored conidia were almost hyaline when young, and became light yellowish-brown with age. Mature, colored conidia mostly measured 10-16 × 4 µm, but were sometimes longer. They were single-celled or occasionally 1-septate. Conidial measurements were essentially similar to those reported by Jenkins (5).

For studies on the effect of RH and water on production of conidia, leaves carrying abundant colored conidia were submerged and agitated in water for 2 hours, washed under a jet of water to remove any remaining conidia, and allowed to dry naturally before being exposed to different RH levels. Below 95% RH, the conidiophores were inactive. Above this level they continued their growth as hyphae or, if wetted, they produced hyaline conidia. Similarly washed and dried lesions produced a new crop of colored conidia while exposed outdoors from 2200 to 0800 hours on nights when there was a dew wetting period of approximately 8 hours.

Dispersal of conidia.—Both types of conidia were readily washed off scab lesions by rain, overhead irrigation, and during spraying operations.

In laboratory experiments, the threshold wind velocity required to dislodge colored conidia from the acervuli was approximately 2 m/second. Air jets of different velocities were directed for 10 seconds on each of 10 lesions, each measuring approximately 25 mm^2. The comparative numbers of conidia impacted onto microscope slides in the trapping device, including those still attached to each other, were 47 at an air speed of 2 m/second, 131 at 4 m/second, and 873 at 8 m/second. Conidiophore breakage occurred when the wind speed exceeded 10 m/second. At velocities above 8 m/second, a few hyaline conidia were also detached, but none of these was viable when tested after being held for 6 hours at 50% RH.

On dry days, colored conidia were sometimes trapped 1 m away from the canopy on the leeward side of a heavily infected rough lemon tree. Evidence that conidia liberated by wind can play a role in spreading the pathogen was established by the following plant trapping tests.

In the first test, 14 trap plants were placed on the ground 3 m from the canopy perimeter of a 1.5-m-high, heavily infected rough lemon tree. The plants were placed in position at 0800 hours and moved at 1600 hours to an isolation site 400 m from the nearest inoculum source and left exposed to dew overnight. This operation was repeated for five consecutive rainless days and nights before returning the plants to the greenhouse. Another 14 plants were left continuously in position at the isolation site throughout the 5-day period. None of these check plants developed any scab lesions. Among the plants that had been exposed near the diseased trees, single scab lesions appeared on four plants and another plant had 15 lesions, all on one shoot. This high number possibly resulted from budding of conidia prior to germination.

In a second test, also performed during a rainless period, 15 plants were spaced 2 m apart in a line proceeding west (prevailing leeward side) from a diseased 2-m-high rough lemon tree. Plants were left continuously in position for 8 days, and over the same period another 15 plants were exposed as checks at the isolation site. Again, no disease appeared on any check plant. Numbers of lesions per trap plant, proceeding from the source of inoculum, were 5, 16, 6, 2, 0, 1, 0, 1, 2, 0, 0, 5, 0, 0, and 1, respectively.

Germination of conidia.—Germination of conidia on the surface of young leaves was variable and often poor. Hyaline conidia either germinated by producing a germ tube (Fig. 8), by budding to produce more conidia (Fig. 9), or by becoming septate to form two- to four-celled short-lived filaments. Colored conidia did not produce germ tubes; they only gave rise to hyaline conidia. Liquid water was essential for all types of germination.

The effect of different media on germination was tested on deposits of hyaline conidia produced from microcolonies on microscope slides. After sufficient conidia had been produced, the microcolonies were removed by drawing them to the edge of the microscope slide with a mounted needle, thus leaving a mycelium-free conidial deposit. The original drop of water in which the conidia formed was reduced to a shallow film by absorbing the excess onto filter paper. Before the deposit had a chance to dry, drops of test medium were added. Most conidia sank and stuck to the glass surface and were undisturbed during these procedures. Results of these tests are summarized in Table 1. Germination by germ tube occurred consistently only in the leaf secretion

TABLE 1. Amount and type of germination by hyaline conidia of *Elsinoë fawcetti* in different liquid media

Medium	Number of tests	Germination[a] by germ tube (%)	Germination[a] by septation (%)	Observations on budding[b]
Distilled water	8	0-17	0	+
2% sucrose	2	0	60-90	+
0.2% sucrose	2	1-9	0	+
Modified Fries' medium	8	0	95-100	0
Modified Fries' medium diluted 1:7 (v/v)	2	0	90-93	0
Modified Fries' medium diluted 1:15 (v/v)	2	2-3	42-51	0
Leaf decoction[c]	2	0	59-95	0
Leaf secretion[d]	8	19-90	4-6	++

[a]Counts made after 18-24 hours.

[b]Budding rating scale: 0 = no budding, + = occasional budding, ++ = budding variable but heavy in some tests.

[c]Prepared by boiling 20 g of young shoot apices in 100 ml H_2O.

[d]Prepared by cutting and immersing 10 actively growing shoot apices, with their cut ends above water, in 4 ml water for 1 hour.

extract, but even in this medium germination was sometimes very poor. Conidia germinated more uniformly in Fries' medium than in 2% sucrose (Fig. 14, 15), and this uniformity was maintained even when this medium was diluted 1:7 with water.

The leaf secretion medium induced most hyaline conidia to germinate by a germ tube (Table 1). Because this type of germination is very rapid and possibly solely responsible for plant infection, this medium was used to study the effects of temperature on germination. In one test, percentage of germination after 4 hours was 14 at 18 C, 30 at 21 C, 46 at 24 C, 39 at 27 C, and 22 at 30 C, and it reached 82 at 18 C, 89 at 21 C, 88 at 24 C, 85 at 27 C, and 61 at 30 C after another 4 hours. These ratings are approximations, because no allowance could be made for any conidial budding that may have occurred. Similar germination-temperature relationships were recorded in other tests.

An important reason for testing germination in different media was to find a reliable medium for determining conidial viability: one that would prevent budding, yet promote consistently high germination. Fries' medium proved to be best for this purpose. In this medium, both hyaline and colored conidia enlarged, became septate (Fig. 10-13), and formed an easily identified stromatic growth.

Survival of conidia.—Conidia were considered viable if they became septate in Fries' medium after 18-24 hours at 25 C.

Of the numerous hyaline conidia that developed on nights with heavy dew, some perished when the dew evaporated; others were still viable after 3 days of continuous exposure of the acervuli to 50% RH. Following liberation by water, hyaline conidia or the resulting germ tubes perished immediately if the water evaporated.

For survival tests with colored conidia, following simulated liberation by water, the conidia-bearing surface of selected scab lesions was lightly brushed against drops of water on microscope slides. The water was allowed to evaporate and the conidial deposit was exposed to different periods of desiccation. Survival tests were also made on conidia that had been blown from scab lesions and impacted onto slides by means of the aforementioned trapping device (2), thus simulating sensitivity to desiccation following naturally induced wind dispersal.

Half of the colored conidia released by wind and held thereafter at 50% RH and 25 C were still viable 24 hours later. Sensitivity of colored conidia to desiccation, following release by water, depended on whether they had been liberated singly or had remained attached to each other during dispersal. Separated conidia perished within 30 minutes, but some of those that remained in chains were still viable 1 day later. In one test, 42% of conidial chains deposited on microscope slides still contained viable conidia after 24 hours of exposure at 50% RH (Fig. 16). Similar results were obtained in other tests.

Plant infection.—Inoculum used to evaluate the effect of temperature on infection contained a mixture of naturally produced hyaline and colored conidia obtained by agitating scab-infected shoots in distilled water. The plants were atomized with the conidial suspension, enclosed individually in polyethylene bags, and placed in dark incubators for 7 hours. The bags were then removed, the foliage was dried with a fan within 30 minutes, and the plants were retained in the greenhouse for development of symptoms. In one such test, the numbers of lesions per shoot that developed were 0.15 at 16 C, 0.62 at 20 C, 0.62 at 24 C, 0.69 at 28 C, and 0.11 at 32 C. In another test, using a higher inoculum concentration, lesion counts per shoot were 1.6 at 16 C, 3.1 at 20 C, 3.3 at 24 C, 3.2 at 28 C, and 0.6 at 32 C.

Tests to determine minimum continuous wetting requirements for infection were made by placing plants under heavily diseased trees and exposing them to an overhead irrigation-induced spore rain for various periods. Plants were dried in the sun before returning them to the greenhouse. In different tests conducted between 24 and 28 C, the minimum wetting period for infection varied from 2.5 to 3.5 hours. In a later more critical test, plants were exposed to a spore rain for only 1 hour. They were then covered with polyethylene bags to preserve the water droplets and brought indoors. After various periods, the covers were removed and the shoots were dried quickly with a fan. Numbers of lesions per shoot that developed following exposure to 2, 2.5, 4.0, 5.5, and 7.0 hours of wetting were 0.00, 0.02, 0.50, 1.34, and 2.24, respectively.

Tests were also made to determine whether plants exposed during the daytime to a spore rain and short wetting period, followed by a lengthy dry period, can still become infected the following night if there is sufficient dew. In one test, 30 plants were exposed to an irrigation-induced spore rain for 3 hours starting at 0800 and then dried within 30 minutes indoors. Ten plants were then placed in the greenhouse, 10 were left indoors, and the remainder were placed outdoors overnight and exposed to 5 hours of dew-wetting with minimum temperature of 18 C. At 1000 hours the next day, all plants were returned to the greenhouse. Plants exposed outdoors developed 7.7 lesions per shoot, whereas only 0.3 and 0.2 lesions per shoot, respectively, were produced on those plants kept indoors or in the greenhouse on the night following inoculation. In another test in which the plants were exposed to an irrigation-induced spore rain for 3.5 hours, commencing at 1100 hours and then dried by 1500 hours, 9.3 lesions per shoot appeared on plants placed outdoors the first night when 6 hours of dew-wetting occurred with minimum temperature 24 C, and only 0.2 lesions per shoot appeared on plants placed immediately in the greenhouse.

An experiment was conducted to determine whether dispersal of conidia during spraying operations could lead to infection during dew-wetting the following night. Trap plants were placed beneath severely diseased trees and the tree canopies were then sprayed to drip-off with water alone or with benomyl [methyl 1-(butylcarbamoyl)-2-benzimidazolecarbamate] 50 WP at 0.3 g/liter, which is very effective in controlling scab (4) or with 1 ml/liter Ethion 4 EC which is a commonly used miticide in Florida citrus groves. After dripping had ceased, the trap plants were removed and dried with a fan. Total period of wetting was < 1.5 hours. Some of the plants exposed to the water-only-sprays were placed in the greenhouse immediately after drying. Others were placed outdoors for one night along with the chemically sprayed plants and exposed to 8 hours of dew-wetting (minimum

temperature 24 C) before being returned to the greenhouse at 1000 hours the next day. Plants exposed to the water-only-sprays and placed directly in the greenhouse and those plants exposed to benomyl and left outdoors for the following night showed no disease. Plants sprayed with water and exposed outdoors had 99% shoots infected and those sprayed with Ethion and exposed outdoors had 98% shoots infected. Results were expressed in this manner because very heavy infection made lesion counting impractical.

DISCUSSION.—Results concerning the effect of temperature on fungal activity and shoot infection are similar to those reported by Yamada (13). They contradict earlier reports (3, 9) that the optimum and maximum temperatures are so low that scab would be inhibited in areas with prolonged periods above 23 C. From 20 to 28 C, little difference in rate of production and germination of hyaline conidia was discernible. A marked decline occurred at 30 and 32 C, but in Florida this would have little or no epidemiological significance because when shoots or fruit are wetted by dew or by rain, the temperature would usually be below 30 C.

Environmental requirements for the production of colored conidia were not determined, but observations suggested that special RH-temperature regimes occurring naturally at night might be involved. Liquid water apparently inhibited formation of colored conidia. Conidiophores that had previously borne colored conidia, produced only hyaline conidia when wetted.

Of epidemiological importance was the relatively short period of wetting required for conidia formation and germination. Hyaline conidia were produced in 2-3 hours after washed and previously nonsporing, young colonies were transferred to drops of water. On scab lesions, Yamada (13) showed that conidia could be formed in 1.5-2.0 hours. I found that 2.5 hours continuous wetting was sufficient for infection. Thus, even if there were no viable conidia on a scab lesion when rain or irrigation commenced, a new crop of conidia could be formed, dispersed, and initiate infection, all within 4-6 hours.

The observation that colored conidia can be liberated and dispersed dry by wind and then germinate the following night with dew certainly raises the question as to whether this phenomenon could be of sufficient magnitude in itself to cause serious scab epidemics. Field observations suggest that this is unlikely because scab tends to be very localized; disease incidence usually varies considerably between neighboring trees and even between different parts of the same tree. This distribution suggests that splash dispersal is more significant epidemiologically than dry, airborne dispersal. The latter, however, might cause more distant dispersal than wind-blown splash-liberated inoculum.

Data presented here on the behavior of *E. fawcetti* indicate that heaviness and frequency of dew probably increases scab incidence as previously suggested by Winston (12) and Ruehle (10). Wetting of leaves by dew, even for a few hours, can promote abundant conidial development thereby increasing the inoculum potential. Also established was the fact that colored conidia liberated in chains by water during the daytime and then subjected to temporary desiccation, can still germinate and cause infection the following night if wetted with dew.

The studies reported here also demonstrated the danger of liberating and dispersing the inoculum during spraying operations. Thus, it is desirable to include an effective fungicide in the spray mix whenever infected groves must be sprayed before the fruit reaches a resistant stage of development.

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