Comparison of Germination of Pathogenic Fusarium oxysporum Chlamydospores in Host Rhizosphere Soils Conducive and Suppressive to Wilts

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ABSTRACT

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The germination of chlamydospores and subsequent growth of hyphae of *Fusarium oxysporum* f. sp. *vasinfectum* and *F. oxysporum* f. sp. *tracheiphilum* were less in soils known to be suppressive to Fusarium wilts than in wilt-conducive soils, whether in host rhizospheres or in response to added nutrients (300 μg glucose and 300 μg asparagine per gram of soil). Germination and growth in seedling rhizospheres usually continued longer than germination following a single introduction of nutrients to the soils, but even in these rhizosphere soils, germination often decreased after 24-60 hr. An *Arthrobacter* sp. was associated with the *F. oxysporum* germlings in the wilt-suppressive soils, but was rare in the wilt-conducive soils that were studied. This bacterium increased markedly as the chlamydospores germinated and the germlings grew.

Additional key words: cotton, cowpea.

Some field soils are restrictive to the progress of Fusarium wilts, even when the pathogens have been repeatedly introduced. Such soils were designated as "Fusarium wilt-suppressive" (2, 27) in comparison to "wilt-conducive" soils of fields where these diseases progress readily. A previous paper (21) compared the germination of *Fusarium oxysporum* chlamydospores in a wilt-suppressive and a wilt-conducive soil in response to nutrients added to the moistened soils. Isolates pathogenic to sweet potato, banana, and tomato were compared with nonpathogenic isolates in two soils from Monterey County, California. The present study was initiated to observe chlamydospore germination in *F. oxysporum* Schlecht. f. sp. *vasinfectum* (Atk.) Snyd. & Hans. and *F. oxysporum* f. sp. *tracheiphilum* (E. F. Smith) Snyd. & Hans., pathogens of cotton and cowpea, respectively, in host plant rhizospheres in these same two soil types; and to compare these observations with those following addition of nutrients to the soils. Certain soil bacteria were noted to increase during experiments, and these also were investigated further.

MATERIALS AND METHODS

The soils studied were the two described (21) as "wilt-suppressive" (S) and "wilt-conducive" (C). Both were sandy loams from fields cultivated to vegetable crops in Monterey County. Fusarium wilt diseases have not been observed in the vicinity where the S soil was collected in spite of a warmer summer climate and many years of cultivation of wilt-susceptible crops (e.g., tomatoes, blackeyed beans, common beans, crucifers, spinach, and alfalfa). The C soil, on the other hand, was collected from a field nearer the Pacific coast, and in spite of generally lower temperatures in this area, the field was heavily infested with the radish wilt pathogen (*F. oxysporum* f. sp. *raphani*), adjoining fields were heavily infested with the spinach wilt pathogen (*F. oxysporum* f. sp. *spinaciae*), and the pathogenic formae speciales that cause Fusarium wilts of various crucifers in addition to radish occurred in the vicinity.

Two other soils were collected from a field in Kern County in which Fusarium wilt of cotton was known to occur since 1960 (9). *Fusarium oxysporum* f. sp. *vasinfectum* had been isolated since 1965 from sites throughout the field. However, in certain locations in this field, propagule counts of the pathogen were consistently low and wilt was rare, while in other areas there was virtually a 100% cotton crop loss due to *F. oxysporum* f. sp. *vasinfectum* and propagule counts of the pathogen exceeded 1,000/g of soil (22). Soils from this field and representing the extremes in disease potential were considered S and C soils for Fusarium wilts, and were used in chlamydospore germination experiments. Some physical and chemical characteristics of these four soils are given in Table 1.

Conidial suspensions of recent field isolates of *F. oxysporum* f. sp. *tracheiphilum* and f. sp. *vasinfectum* were seeded into each freshly-collected soil sample, where they quickly converted to chlamydospores. Glucose was added to the soils (300 μg/g) along with the conidia; this increased the numbers of chlamydospores that formed. The soil samples (usually 50- to 100-g amounts) were dried slowly, remoistened to approximately the maximum water-holding capacity, and allowed to dry again; by this time few viable *Fusarium* sp. conidia or intact hyphal fragments remained, but chlamydospores

were numerous.

All soils again were moistened to approximately field capacity and held for 1 day prior to the addition of nutrients or the placement of intact seedling roots into them. Where nutrients were employed, the soil samples were held in individual tubes (12-16 g soil/tube) in a Haines apparatus (10) for the duration of the experiment. In this device one end of a soil tube (open at both ends) was pressed against the fritted disk of a 600-ml Büchner funnel, beneath the sintered glass disk. The flow of water through the disk determined soil moisture, and was regulated by raising or lowering the two funnels in relation to one another. Thus, the soil samples of a given experiment were under the same tension (40-70 cm water), so that the water potential was similar in all samples, even when there was a variation in soil type. A beaker was placed over the top of the funnel to prevent drying of the soil surface.

Chlamydospores in these soils were stimulated to germinate by pipetting 0.4-0.8 ml of 1% glucose-asparagine solution onto the surface of the soil in each tube. At intervals, soil plugs of approximately 0.5 g were withdrawn (usually in duplicate) with a sterile 7-mm diameter (No. 3) cork borer for chlamydospore observations. Sometimes plugs were halved longitudinally; one-half was used for microscopic observations, and the other was diluted for bacterial plate counts. The soil on a glass slide was lightly stained with cotton blue in lactophenol. Two hundred to 300 chlamydospores were counted per slide. Soil dilutions (10^{-6} to 10^{-8}) were spread onto the hardened surfaces of tryptone-glucose-yeast extract agar plates (21) that had been poured 6-8 days previously; bacterial colonies were examined and counted 7 days later.

The kinds of bacteria associated with *Fusarium* sp. germlings in S soil were compared with the total soil bacterial population by the following method. Ten to 12 hours after addition of the glucose-asparagine (300 μg/g soil), a soil suspension, prepared by gently mixing 0.5 g of soil with molten (50 C) 2% water agar, was quickly poured in 1-ml aliquots onto sterilized slides and examined microscopically (×70) for *Fusarium* germlings. Once found, the germlings' position was marked with a fine needle and transferred, with the aid of a dissecting microscope, to a dilution blank, which was shaken and plated.

Bacterial plate counts also were prepared from soils not fortified with *Fusarium* chlamydospores, but (i) similarly treated with glucose-asparagine solution in the Haines apparatus, or (ii) taken from the rhizospheres of cowpea seedlings. This was done to determine the influence of fortifying the soils with unusually high populations of *F. oxysporum* f. sp. *tracheiphilum* upon the soil bacteria present.

Seedling plants of cotton (*Gossypium hirsutum* L. 'Acala SJ-2') and cowpea [*Vigna sinensis* (L.) Savi 'California Blackeye #5'] were cultured in sand for 6-9 days prior to use. The roots were thoroughly washed and then each plant root was encased in a square petri dish filled with wet vermiculite and held on edge so that the hypocotyl protruded through a hole in one edge, and the root tip through a hole at the opposite edge (Fig. 1). The root tip (less than 15 mm long) was inserted into moistened test soil (2-3 g) contained in a tube (35 mm high × 10 mm diameter) that had a small plastic sponge placed in the opposite end. These tubes had been filled with dry soils and tamped down before moistening, to lessen

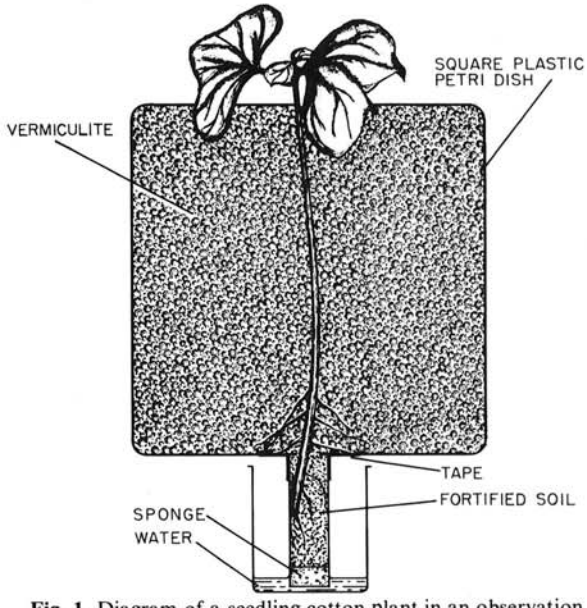

Fig. 1. Diagram of a seedling cotton plant in an observation made from a square plastic petri dish and used for laboratory germination studies of *Fusarium oxysporum* f. sp. *vasinfectum* chlamydospores in seedling rhizospheres.

TABLE 1. Analyses (dry weight basis) of experimental soils conducive (C) and suppressive (S) to wilts caused by *Fusarium oxysporum*

Soil source	Organic matter[a] (%)	pH[b]	Chemical analyses					Mechanical analysis		
			Total N (μg/ml)	NO_3 (μg/ml)	NH_4 (μg/ml)	P (μg/ml)	K (μg/ml)	Sand (%)	Silt (%)	Clay (%)
Monterey County										
C	2.84	6.0	860	33	70	52	315	82	6	12
S	2.46	7.3	470	23	23	14	137	72	14	14
Kern County										
C	1.86	5.9	510	17	29	24	118	68	18	14
S	2.49	6.3	670	26	37	29	215	51	27	22

[a]Measured by loss of weight upon ignition.
[b]pH was measured on a water-saturated paste of the soil.

moisture variation between them. The sponge ends were kept immersed in a few millimeters of water to maintain soil moistures. The roots grew about 1 cm/day, after the first 24 hr. When chlamydospore germination was to be observed in rhizosphere soil for more than 36 hr, only a few millimeters of root were inserted into test soils to allow room for growth. These individual plant growth chambers were incubated upright in a rack under cool-white fluorescent or "Gro-Lux" lamps (1,830 lux).

Rhizosphere soil was checked for chlamydospore germination at intervals after insertion of the root into the soil. Roots from two to four replicate plants were severed at the soil surface. The soil with the root intact was then pushed out of the tube so that root with rhizosphere could be gently removed. Soil adhering to the root was stained with cotton blue in lactophenol, then washed off the root into a 5-ml beaker with a few drops of water. One or two drops on a slide constituted a sample for observation of chlamydospore germination.

Bacterial counts in soils surrounding root tips were performed as done on soil plugs from the Haines apparatus.

Scanning electron microscope observations.—Surface details of germlings and their associated microflora were observed with a scanning electron microscope (S.E.M.) using preparations made as follows: Pieces of fine-mesh, nylon screening cloth were pressed against growing cultures of wilt fusaria. After 1 wk the cloths were removed from the cultures and buried in either a C or S soil that had been moistened previously and allowed to dry for a few weeks. Before each experiment the soils were remoistened for 24 hr or more and then treated with 0.03% glucose-asparagine to induce chlamydospore germination. After another 10-12 hr, the pieces of cloth that contained germinated and nongerminated chlamydospores were removed from the moist soils, fixed in osmium tetroxide or glutaraldehyde, dehydrated in series of alcohol and Freon, critical-point dried, and coated with gold in the manner described by Duafala and Nemanic (6). The preparations were mounted with "silverdag" and stored at room temperature in a desiccator until viewed in a S.E.M.

RESULTS

Germination of F. oxysporum f. sp. vasinfectum and f. sp. tracheiphilum in C and S soils.—The percentage germination of the chlamydospores of the two pathogens was consistently less and growth of the germ tubes was slower in S soils compared to C soils (Fig. 2). Lysis of the

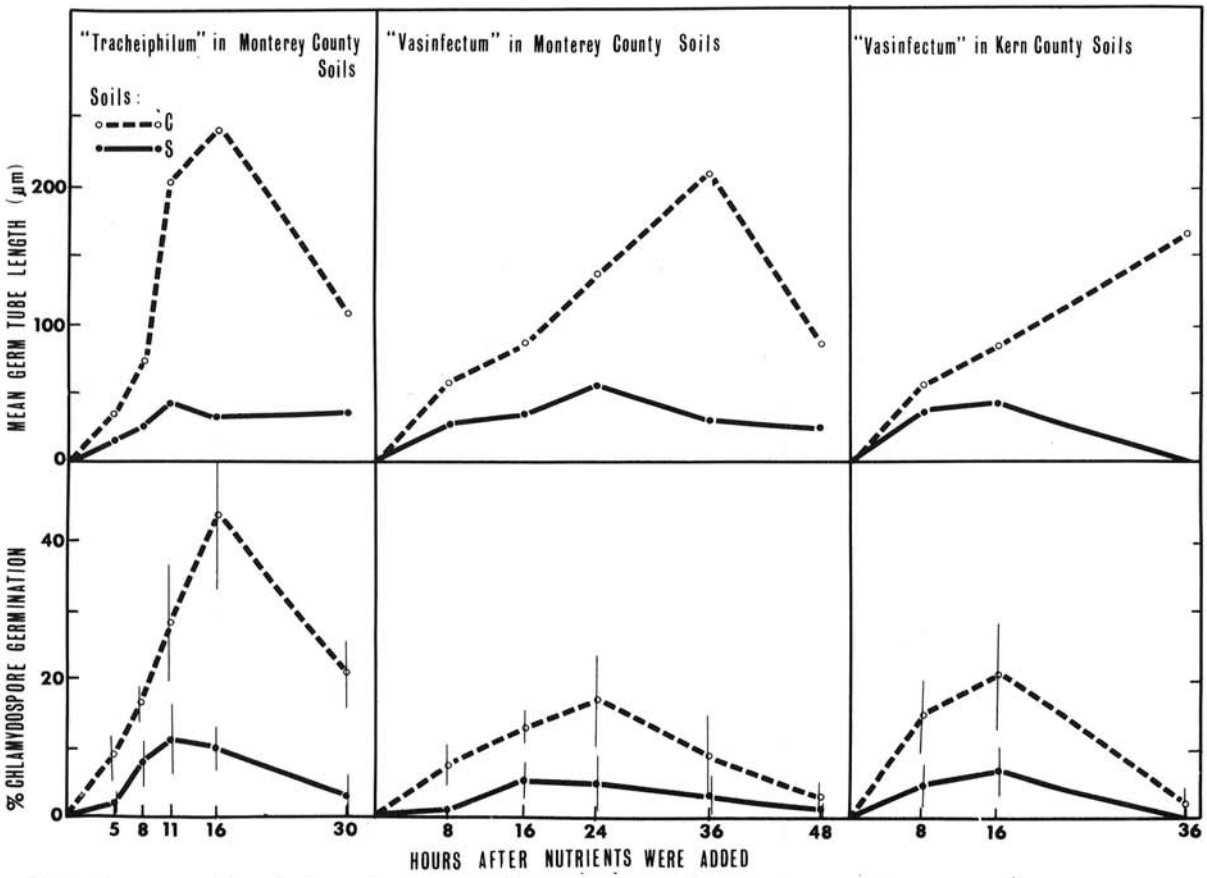

Fig. 2. Percentages of germination and mean germ tube lengths produced in chlamydospores of pathogenic *Fusarium oxysporum*, incorporated into soils "conducive" (C) or "suppressive" (S) to wilts. The soils were incubated in a Haines apparatus (60 cm water tension) and observed following the addition of 300 μg/g soil and asparagine. The bars indicate the standard deviation in percentages of germination in the 2-3 slide observations of each time interval.

hyphae often was observed within 8 hr after addition of nutrients and was earlier and in greater frequency in the S than the C soils. Lysis of hyphae was manifested first as short, nonstaining segments usually adjacent to septa; later the germ tubes stained very lightly and disappeared altogether in portions. Cell walls were the last remnants.

Lysis was observed in all soils by 11-24 hr after addition of the nutrient. Presumably most of the energy available for germ tube initiation and growth would have been used by that time. Maximum percentages of spores with germ tubes in C soils were higher and occurred later (18-45% at 16-24 hr) than in the S soil samples (5-11% at 11-16 hr) following addition of nutrient. Generally growth also continued longer in the C soils; an occasional hypha well over 1,000 μm was measured in soil sampled after 16 hr. Some branching occurred, which indicated healthy germlings on the way to formation of more extensive thalli (5). Some chlamydospores produced two or three germ tubes; often one such tube was observed to be growing while another was lysing.

Although most growth had stopped 36-48 hr after the addition of nutrient, an occasional sporeling in C soil continued to grow and formed a colony with profusely-branched hyphae in the thallus. Sometimes a weft of mycelium visible to the naked eye was observed on the surface of C soil after a few days of incubation. Such growth was not observed in S soil incubated simultaneously in the same apparatus.

There was considerable variation among experiments in chlamydospore germination and germ tube growth of pathogens in C and S rhizosphere soils. The data presented (Fig. 3) were from experiments where germination was optimum. These percentages usually were lower than in soil where nutrients were applied, but hyphae persisted in the rhizosphere much longer in C than in S soil. Germination percentage was not maximal until 20-24 hr after root tip placement and germlings were still present after 60 hr. Nevertheless, differences still were detectable in chlamydospore germination percentage in C rhizosphere soil compared to S rhizosphere soil, 18 and 8%, respectively. Germ tubes averaged 60-140 μm in length by 20-48 hr. Many were several hundred micrometers long after 60 hr in C soil, while in S soils, few living germlings were observed by 36 hr. Lysis was observed as early as 8 hr after roots were inserted in S soil. Some new germ tubes continued to appear in both soils, although to a lesser extent in S soil samples. Thus, some germlings were nearly completely lysed and others, nearby in the same preparation, looked vigorous and stained deeply.

The germ tubes produced in S soils frequently remained short and appeared to have a "rough" outer surface when viewed under the light microscope (Fig. 4-a, b, and c). They were similar to those observed in soils following the addition of nutrients (21). Tiny coccoid or pleomorphic rod-shaped bacteria were visible singly or in

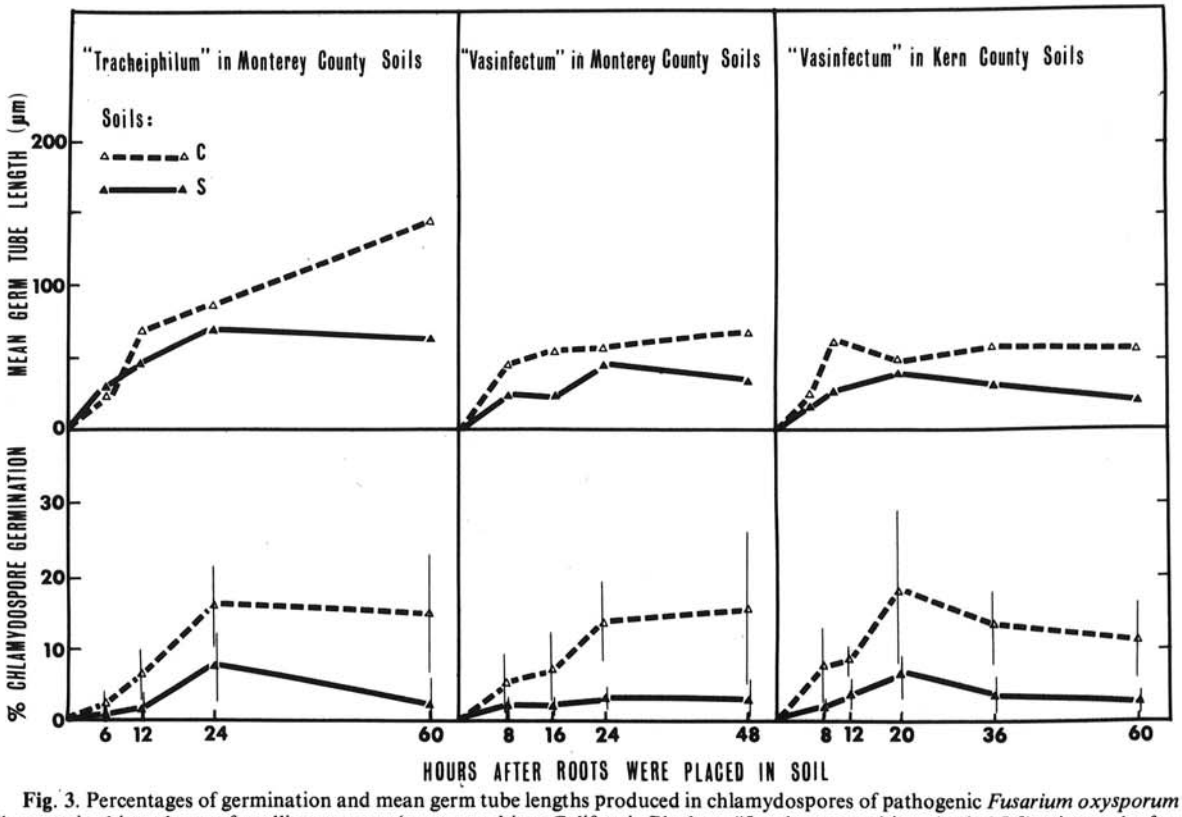

Fig. 3. Percentages of germination and mean germ tube lengths produced in chlamydospores of pathogenic *Fusarium oxysporum* in root-tip rhizospheres of seedling suscepts (cowpea cultivar California Blackeye #5 and cotton cultivar Acala SJ-2) at intervals after the seedlings had been transplanted into artificially-infested soil samples "conducive" (C) or "suppressive" (S) to wilt. The bars indicate the standard deviation in percentage germination in observations at each time interval.

small colonies associated with the germ tubes. Apparently they were attached to the germ tubes because they did not float away in these preparations in spite of ample opportunity to do so. The S.E.M. preparations of similar S soil germlings revealed the individual cells and small colonies of the pleomorphic bacteria closely adhering to the germlings (Fig. 4-d, e, and f); they were particularly prevalent on or near the chlamydospore and the tip of the germ tube. Figure 4-f shows the unevenness of the hyphal wall and a deep constriction at a septum; these are often signs that a germling had stopped growing shortly after germination in an S soil.

Bacteria were also observed near germlings from C soils, but these often consisted mostly of short rods or long slender rods in chains.

Bacterial plate counts.—A large number of *Arthrobacter* sp. colonies appeared in the S soil following some chlamydospore germination, but they were absent or present only in low numbers in similarly treated C soils. The most common type in the two S soils formed white, opaque, medium-sized colonies on the medium used. After 7-8 days, sectors of the colonies of this pleomorphic bacterium became dry and rather flat, and consisted of tiny Gram-positive cocci. The more mucoid portions of the colonies consisted of larger rod-, or sometimes club-shaped Gram-variable cells.

Increases in numbers of bacteria, particularly of *Arthrobacter* sp. were evident in *Fusarium*-fortified S soils after 16-24 hr, in both rhizosphere soils or soils with 0.03% glucose and asparagine added (Table 2). *Arthrobacter* sp. reached 10^9 cells/g in the S soil from Monterey County when nutrients were added (about 50-fold increase), but did not exceed 7×10^6 in any C soil (only a 15-fold increase) under the same conditions. In host rhizospheres in S soil from Kern County, *Arthrobacter* sp. reached 3.9×10^7/g after 20 hr

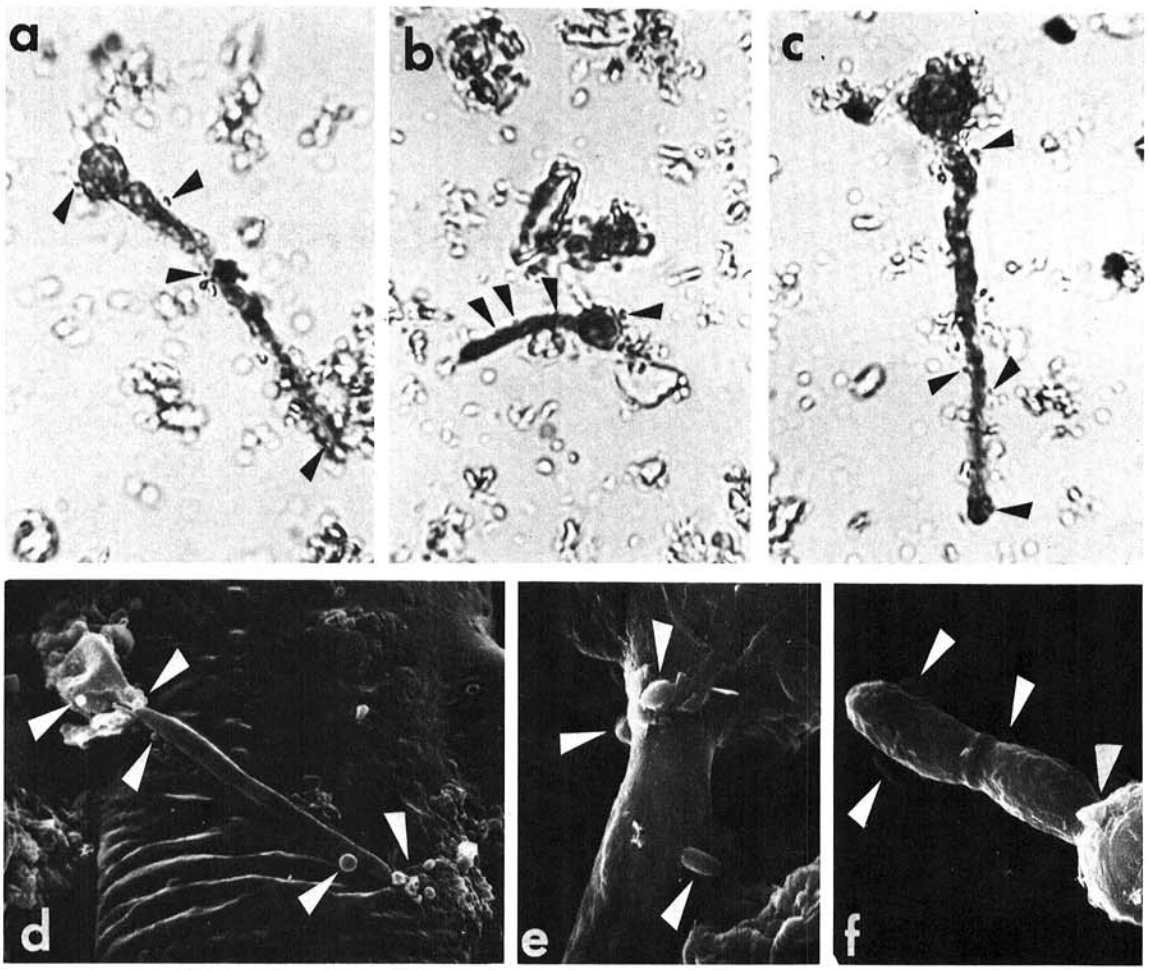

Fig. 4-(A to F). Chlamydospores of pathogenic *Fusarium oxysporum* germinating in "suppressive" soils in response to 0.03% glucose and asparagine. The *F. oxysporum* sporelings shown in **A**), **B**), and **C**) were viewed with a light microscope at ×900. Markers point to single bacterial cells (not well resolved) and small colonies close to hyphae. Elements **D**), **E**), and **F**) are similar sporelings viewed with scanning electron microscope showing the attachment of pleomorphic bacteria. **D**) shows small colonies (× 1,000); **E**) shows a portion of a chlamydospore at a point of germ tube emergence (×4,400), and **F**) shows an irregular wall of a "stunted" hypha, a septum constriction, and adhering bacteria (× 2,500).

TABLE 2. Bacterial counts in soils conducive (C) and suppressive (S) to wilts caused by *Fusarium oxysporum* enriched with chlamydospores of *F. oxysporum* f. sp. *vasinfectum* and *F. oxysporum* f. sp. *tracheiphilum*

Enrichment with *Fusarium oxysporum* f. sp.:	Soil source (Calif. County)	Time (hr)[a]	Bacteria per gram soil ($\times 10^6$)			
			C soils		S soils	
			Total (no.)	*Arthrobacter* (no.)	Total (no.)	*Arthrobacter* (no.)
In bulk soil[b]						
vasinfectum	Monterey	0	87	0.86	11.6	2.14
		16	126	1.4	178	103
	Kern	0	35	0.42	68	. . .
		16	177	6.3	149	47
tracheiphilum	Monterey	0	7.2	<0.05	25.4	3.7
		16	74.8	<0.2	220	70.6
In host rhizospheres[c]						
vasinfectum	Monterey	0	. . .	0.45	. . .	0.68
		24	. . .	1.2	. . .	18.0
	Kern	0	. . .	. . .	. . .	. . .
		20	88.3	5.6	214	39.1
tracheiphilum	Monterey	0	6.9	<0.1	16.9	5.2
		24	53.8	<0.3	130	16.0

[a]Samples were taken before (0 time) and after (16-24 hr) either the addition of 300 μg of glucose and asparagine per gram of soil, or the insertion of roots of seedlings of host plants into test soils.
[b]Amended with glucose and asparagine and maintained in a Haines apparatus at 60 cm of water tension.
[c]Root inserted into soil sample containing the pathogens.

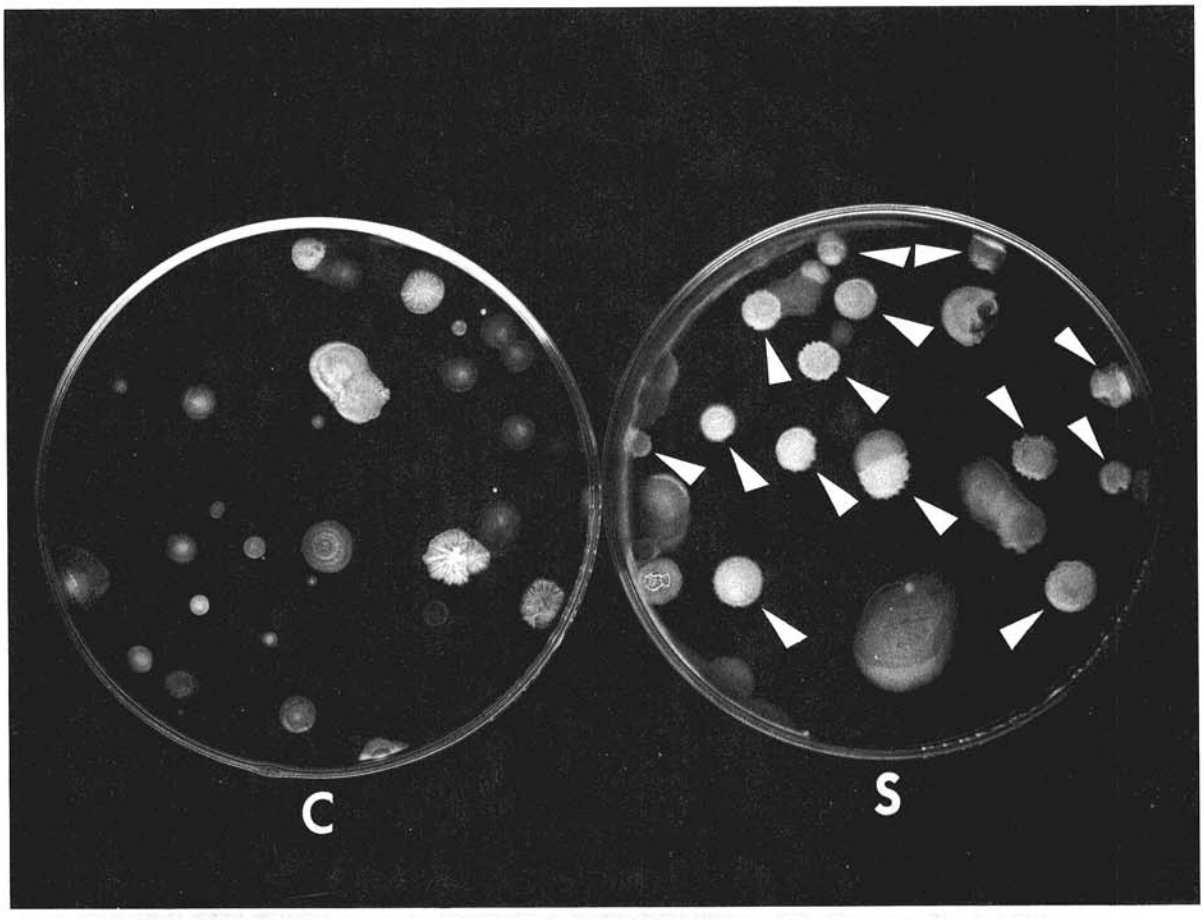

Fig. 5. Bacterial dilutions of *Fusarium oxysporum* f. sp. *tracheiphilum*-enriched "conducive" (C) (left) and "suppressive" (S) soil (right) plated 12 hr after addition of glucose and asparagine (300 μg/g). Note the many Arthrobacter sp. colonies (marked) in 'S' soil. The dilution factors of the two soils were similar ($\sim 2 \times 10^6$).

compared with only 5.6×10^6 in the corresponding fortified C soil. *Arthrobacter* sp. was barely detectable in C soils from Monterey County. Figure 5 shows how numerous *Arthrobacter* colonies can be in S soil from Monterey County after only 16 hr of incubation.

The association of an *Arthrobacter* sp. with *F. oxysporum,* was further documented by dilution platings of the bacteria adhering to germlings of *F. oxysporum;* the bacteria in close proximity to germlings of *F. oxysporum* predominantly resembled *Arthrobacter* sp. In addition, the percentages of bacterial colonies identified as *Arthrobacter* sp. were higher in cowpea rhizosphere or nutrient-treated soil which had been fortified with *F. oxysporum* f. sp. *tracheiphilum* chlamydospores than in soil containing only the normal complement of *Fusarium* species and clones from the field (Table 3).

DISCUSSION

It has been reported (2) that continuous growth of thalli of *F. solani* f. sp. *phaseoli* near bean hypocotyls for 60 hr is sufficient for host penetration to occur. If this is true also for *F. oxysporum* under field conditions, it is evident why some soils are not suitable for the spread of Fusarium wilts. The data presented in this paper show that hyphal growth in rhizospheres often proceeds for 60 hr or more in one soil, but is suppressed soon after 24 hr in another. Investigations of factors responsible for pathogen suppressiveness are of interest from the standpoints of both biological control and for predicting whether wilt-susceptible crops may be grown repetitively with impunity on a given site.

Soil bacteria have often been implicated as deterrents to fungal pathogens. Some produce perforations in the heavy walls of resting structures, which leads to rapid lysis of these structures (4, 18), whereas others (e.g., *Bacillus subtilis*) produce potent, lysis-inducing antibiotics that reduce disease (1, 3, 29, 30). However, factors that act to deter *F. oxysporum* in soil seem to be less drastic. Chlamydospores are no more vulnerable in S than in C soils, although they are prevented from germinating, and lysis occurs only when rather high populations of certain inhibitory bacteria are present in close proximity to the germlings. The termination of germ-tube growth and onset of lysis of hyphae may be as described by Lingappa and Lockwood (13); namely, increased growth of the microorganisms on or close to fungus hyphae, in response to specific substances exuded by the fungus, followed by fungitoxicity and finally lysis.

As early as 1938, Starkey (23) described the presence of tiny, lightly-staining coccoid bacteria in close contact with fungal mycelium on Cholodny slides. He conjectured that the relatively short period of existence of fungal mycelium in soil was due to susceptibility to bacterial attack.

Old and Schippers (19), working with *F. solani* f. sp. *cucurbitae,* found that bacteria of different morphological types (rods, spheroids, helically lobed, and spiral forms) were present on the surface of chlamydospore walls and also imbedded in the wall matrices. Examination of S.E.M. preparations of chlamydospore germlings in S soil revealed that many of the bacteria associated with the *F. oxysporum* germ tubes came from the surfaces of chlamydospore walls, and that they multiply as the germ tube elongated. Observations of nongerminated chlamydospores showed that bacteria appeared to cling to the rough walls.

Venkat Ram (28) observed stimulation of chlamydospore formation by soil bacteria in a nonpathogenic *F. solani* isolate. Ford et al. (7) found that an *Arthrobacter* sp. (or even its culture filtrates) and certain other soil bacteria induced chlamydospore formation in *F. solani* f. sp. *phaseoli. Fusarium oxysporum* forms chlamydospores readily even in distilled water. Nevertheless, in field soils the resting structures of fusaria and soil bacteria, such as *Arthrobacter* sp., appear to be harbored together.

Frequently *F. oxysporum* colonies appeared in close proximity with *Arthrobacter* sp. colonies on the dilution plates. In these instances, the inhibition or lysis of *Fusarium* mycelium was slight (compared to the large zones of inhibition near Actinomycete or *Bacillus* sp. colonies). However, growth and inhibition of colonies on nutritionally-rich agar plates may not be relevant to the prevailing situation with the same combination of organisms in soil.

Mitchell and Hurwitz (17) isolated a rhizosphere *Arthrobacter* that was capable of extensively lysing mycelium of *F. oxysporum* f. sp. *lycopersici* when the two organisms were co-cultured. Vascular wilt of tomato was greatly suppressed if sterilized seeds were inoculated with these bacteria and planted in sterile soil, but severity was not reduced if seeds inoculated with the bacterium were

TABLE 3. Percentages of *Arthrobacter* sp. among the total bacteria plated from nonfortified field soil, from the same soils fortified with chlamydospores of *Fusarium oxysporum* f. sp. *tracheiphilum,* and from the close proximity of germinating chlamydospores

	Bulk soil amended with glucose and asparagine[a]			Cowpea rhizosphere soils[a]	
		Fortified with chlamydospores			
Kern County soils	Native Fusaria only	Fortified	Surrounding germlings[b]	Native Fusaria only	Fortified with chlamydospores
Conducive	<0.2	6 ± 3.5		<0.1	1.6 ± 1.2
Suppressive	2.4 ± 1.5[c]	26 ± 9	83 ± 12	1.6 (0-5.3)	9.2 ± 6

[a]Figures represent averages of three soil sample replicates made: 12 hr after glucose-asparagine addition in the Haines apparatus (60 cm water tension) for bulk soil, and 20 hr after transplanting cowpea seedlings for rhizosphere soil.

[b]Bacteria were washed from the surfaces of three chlamydospore germlings.

[c]Fluorescent pseudomonads made up 13% of this nonfortified soil sample, but were not found in the soil fortified with *Fusarium.*

grown in nonsterile soil. It is not known if the soil used was "wilt-conducive". Other *Arthrobacter* sp. strains isolated by these authors lysed mycelium of *Pythium debaryanum*. None was found, however, which lysed spores.

Koths and Gunner (12) described a bacterium, later identified as an *Arthrobacter* sp. (25), that partially controlled pathogenicity of *F. roseum* f. sp. *cerealis* to carnations when roots of cuttings were dipped into a culture of it (P35) in a slurry of milled lobster shell (rich in chitin). P35 had ability to lyse *Fusarium* mycelium only when other carbon sources were not added. In a later paper Szajer and Koths (25) reported that culture P35 used several complex carbohydrates including chitin, cellulose, lamarin, gelatin, and pectin. They also noted a tendency of the bacterium to attach to *Fusarium* mycelium, which they attributed to the chitin constituency in the walls. Their data support the premise that chitin in *Fusarium* cell walls encourages chitinase-producing organisms, which in turn attack the fungus. This corroborates earlier reports of controlling *Fusarium* diseases in the greenhouse (14, 15, 16) with chitin, cellulose, and other complex carbohydrates.

Chlamydospore germination and hyphal growth of pathogenic *F. oxysporum* in relation to soil type do not alone determine wilt severity in the field. The presence of root knot nematodes is also important in the occurrence of the two wilt diseases of this study in California soils (8, 26). In addition, Stover and Malo (24) described increases in Panama disease of bananas with factors that stress the plants, such as poor drainage, lack of soil depth or permeability, etc. Stress factors, and perhaps also nematodes, alter host susceptibility to Fusarium wilts (11, 20), breaking down resistance in plants. In our observations Fusarium wilts, even in plants under stress, seldom occur in soils known to be "wilt-suppressive".

The present work points to an important role of *Arthrobacter* spp. as a deterrent to the activity of pathogenic *F. oxysporum* in soils currently recognized as "wilt-suppressive". However, since antagonists can be effective only in environments where they can proliferate, soils unfavorable to antagonists may remain "conducive" to disease, unless means are found to alter them and encourage growth of antagonists.

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