Persistence of Fusarium oxysporum f. sp. vasinfectum in Fields in the Absence of Cotton

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ABSTRACT

When formae speciales of *Fusarium oxysporum,* which cause vascular wilts, are introduced into a conducive soil, the pathogen usually persists there indefinitely. In a California cotton field soil planted for several years to cereals, the population of the pathogen, *F. oxysporum* f. sp. *vasinfectum,* increased more rapidly in the absence of cotton than when previously planted to cotton. Small barley roots remaining after the grain crop was harvested contained high populations of the pathogen. Likewise, roots and crowns of yellow nutsedge contained populations of the pathogen in epidermal and outer cortical cells which were as much as 20 times greater than those of nonpathogenic *F. oxysporum.* Nonsuscepts of the cotton pathogen, such as barley, may increase populations of *F. oxysporum* f. sp. *vasinfectum* under field conditions at a faster rate than does the continuous planting of cotton. Thus a crop rotation that does not take into consideration the manner in which the Fusarium wilt pathogen persists in field soil cannot be relied upon to reduce its numbers in the field.

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Pathogenic formae of *Fusarium oxysporum* Schlecht. are known to persist in field soils long after the susceptible crop has been removed from the field. Stover (16) reported that after 25 years of cocoa being grown on a banana plantation infested with *F. oxysporum* f. sp. *cubense* (E.F.Sm.) Sny. & Hans., Fusarium wilt rapidly appeared again when the plantation was replanted to the susceptible 'Gros Michel' banana. Armstrong and Armstrong (2) observed that *F. oxysporum* f. sp. *vasinfectum* (Atk.) Sny. & Hans. also persisted in soil for a long time. In instances where cotton was replanted into infested fields after intervening periods of as long as 12 years, the Fusarium wilt incidence was still high. This persistence was attributed, at least in part, to the ability of the wilt Fusaria to parasitize many plants other than those usually considered to be susceptible, without causing external disease symptoms (2). Sweet potato cuttings were invaded by cotton wilt Fusarium when they were planted into a field infested with that fungus, and *F. oxysporum* f. sp. *batatas* (Wr.) Sny. & Hans. was isolated from cotton plants grown in a field in which sweet potatoes had wilted. Although these fungi could occasionally move into the xylem of the nonwilt-susceptible hosts, most of the invasion was of the cortex, and the fungus did not move up the stem very far (2). Hendrix and Nielson (8) obtained many *F. oxysporum* isolates from roots of nine crop plants other than sweet potatoes, which were planted into two fields infested with *F. oxysporum* f. sp. *batatas.* A few of these isolates proved to be very pathogenic to sweet potatoes.

Occasionally, a little vascular browning was noted in the field-grown plants, but otherwise the plants were symptomless.

Not only crop plants, but also common weeds in the fields have been found capable of harboring pathogenic *F. oxysporum*. Waite and Dunlap (17) reported the isolation of *F. oxysporum* f. sp. *cubense* from roots of common grasses growing in banana plantations. Abawi and Lorbeer (1) found *F. oxysporum* f. sp. *cepae* (Hanz.) Sny. & Hans. consistently in roots of *Oxalis corniculata* L. in infested onion fields. Ebbels (5) reported that *F. oxysporum* f. sp. *vasinfectum* was able to infect a number of weed species of the orders Malvales and Tiliales, when the roots were dipped or stems inoculated. Eight of the species, all common weeds in the cotton-growing areas of Tanzania, showed no visual symptoms, but *Abutilon grandiflorum* G. Don. and *Hibiscus calyphyllus* Cav. showed interveinal browning on the leaves.

In the present investigation, the numbers of propagules of *F. oxysporum* f. sp. *vasinfectum* surviving in field soils several years after a cotton crop had last been grown were determined, and the means of their survival were investigated.

MATERIALS AND METHODS.—Populations of pathogenic *F. oxysporum* were estimated in composite soil samples taken from measured stations in a field known to have been infested before 1960 (6). Most of the stations sampled were those previously described (14), in which populations of the pathogen had been determined over a period of years during the culture of cotton, and were found to vary from < 20 to > 800 propagules per gram of soil at different stations within the field. Considerable variation was also reported at single stations sampled at different dates. However, the pathogen had been isolated at least sometimes from every site sampled in the field, even where Fusarium wilt had not been observed in the cotton (14). In addition to continued sampling of these stations in this field, stations in other fields mentioned in the Results section were sampled.

At each field site, a composite soil sample (consisting of 10 individual samples of 50-100 g) was taken and hand mixed. From each such sample, three weighed replica subsamples were diluted with 0.1% water agar and blended 3-4 minutes in a Waring Blendor. Further dilutions were made of soil suspensions such that final dilutions ranged from 1:150 to 1:700, depending upon the concentration of all Fusaria at the site.

In preparing peptone-PCNB agar plates, hydrolysis of both agar and peptone were prevented by autoclaving only the water and 2.0% agar together. The other ingredients, 1.5% peptone (Difco), 0.05% $MgSO_4 \cdot 7H_2O$, 0.1% KH_2PO_4, 0.05% streptomycin SO_4, and 0.1% "Terraclor" (75% pentachloronitrobenzene W.P.) were added to the water agar shortly after it was removed from the autoclave, when the temperature was about 90 C. Plates were poured at approximately 60 C and then held 5-6 days before seeding; any contaminated plates were discarded at that time. One ml of the final soil dilution suspension was pipetted on to the agar and spread evenly over the surface by tilting and rotating each plate. Colonies were examined after the plates had been incubated 4-5 days on the laboratory table. Ideally each plate contained from 15 to 50 colonies.

In order to recognize colonies of the pathogen on plates from among colonies formed by the large populations of nonpathogenic *Fusarium oxysporum* prevalent in cultivated soils (10), they were compared with plates seeded with cultures known to be pathogenic. We recognize two distinct cultural types of *F. oxysporum* f. sp. *vasinfectum* obtained from diseased host plants in San Joaquin Valley cotton fields (Fig. 1-C), although clones of the fungus intermediate between these two types may occasionally be isolated. Conidial suspensions from potato-dextrose agar (PDA) cultures of these isolates of known pathogenicity were spread over the surface of peptone-PCNB agar plates at several concentrations and incubated for the same period as the soil dilution plates (Fig. 1-D), and were used to obtain "known colonies" of the pathogen. All colonies on the soil dilution plates that resembled the known colonies were transferred to a poured PDA plate by cutting out a tiny agar block near the colony margin. Similar transfers were made from colonies of the known pathogen. Plates with seven to nine such transfers were incubated at room temperature for 60-80 hours. At this time, colonies from the soil-dilution plates which appeared identical to those of the known pathogen were transferred to PDA slants and kept until

TABLE 1. Average numbers of *Fusarium* propagules in naturally infested soil at several stations within one field several years after cotton was last grown

Station	Last year in cotton	Fusarium propagules per gram of soil: *F. oxysporum* f. sp. *vasinfectum* 1973	*F. oxysporum* f. sp. *vasinfectum* 1969	Other *F. oxysporum* 1973	Total Fusaria 1973	*F. oxysporum* f. sp. *vasinfectum* per total Fusaria (%)
18	1966	3,130 ± 800	1,015	6,370 ± 840	10,915 ± 1,100	28.9
19	1966	1,230 ± 390	770	4,160 ± 630	7,870 ± 1,530	15.6
1	1967	760 ± 185	805	3,310 ± 320	7,540 ± 500	10.1
7	1966	600 ± 65	. . .	8,670 ± 1,660	18,275 ± 4,700	3.28
2	1967	465 ± 120	403	7,120 ± 700	12,390 ± 970	3.75
4	1967	180 ± 100	. . .	. . .	8,100 ± 680	2.22
9	1966	98 ± 38	35	9,830 ± 3,400	11,500 ± 205	0.85
8	1966	27 (<9-64)	<20	4,110 ± 820	16,980 ± 4,500	0.16

TABLE 2. *Fusarium oxysporum* f. sp. *vasinfectum* propagules in barley residues as compared with those in soil samples

Stations		Propagules per gram				
		Barley residues[a]				
		Straw fragments		Root fragments		Soil samples[b]
		Shaken	Blended	Shaken	Blended	
18, 19, and 20 (loamy sand)	AVERAGE:	12,000	36,000	10,000	85,000	825
	RANGE:	1,000-42,000	2,500-150,000	2,000-24,000	23,000-200,000	585-994
8, 9, and 10 (sandy loam)	AVERAGE:	2,000	8,800	3,000	20,000	44
	RANGE:	<1,000-3,000	3,000-14,000	<1,000-5,000	5,000-35,000	<20-91

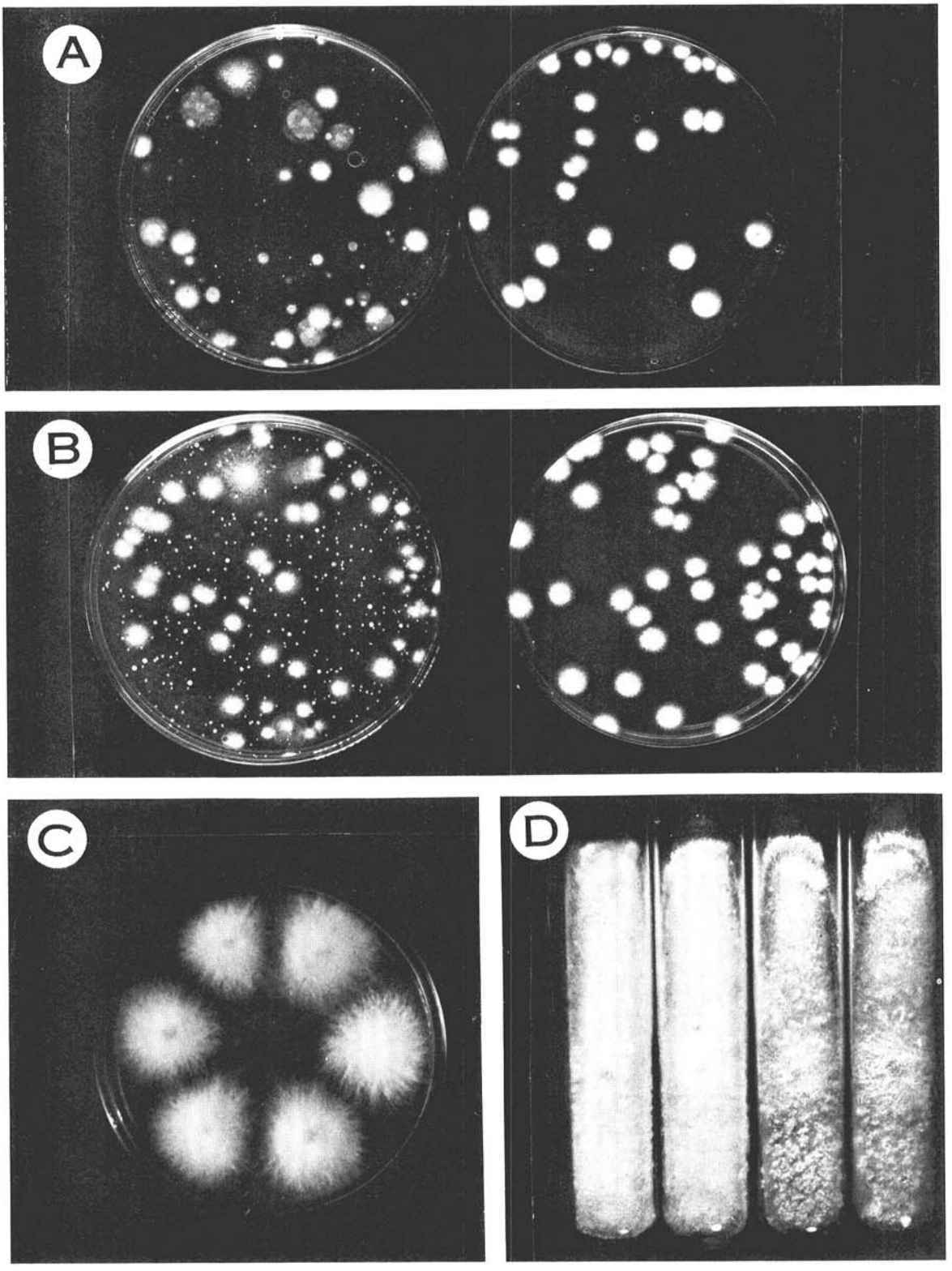
[a] Average number and range of propagules per gram in barley residue fragments that were removed from field soil.
[b] Average number and range of propagules per gram in soil sampled in the respective areas of the field from which the fragments were removed.

greenhouse pathogenicity tests were run. In addition, some colonies dissimilar to those known to be "vasinfectum" were tested. Greenhouse pathogenicity tests were made by dipping week-old cotton seedlings with root tips severed into slurries made from the conidia of each test slant suspended in 40-50 ml. of distilled water. Then, after being transplanted to U.C. Mix, the seedlings were incubated at 90 C until either symptoms appeared, or a period of 3 weeks had elapsed. If a test isolate was *F. oxysporum* f. sp. *vasinfectum,* seedling transplants showed vascular symptoms in the above-ground stem within 10 days of inoculation, were severely stunted, and usually all were dead after 15 days. Common soil forms of *F. oxysporum* occasionally caused a slight vascular browning in the tap root only; no external symptoms were observed, no stunting, discoloration, nor other differences from uninoculated controls.

Isolations made from barley, certain weeds and fragments of these plants removed from soil samples.—Isolations were made from roots and other parts of plants not ordinarily thought of as hosts, but which were growing in heavily infested field soils. Also, residues, consisting of roots, straw and seeds of barley, were removed from field soil in which the count of the pathogen had been observed to increase after the cereal crop had been grown. Isolations of *F. oxysporum* f. sp. *vasinfectum* were made from such barley recovered from soil in a plowed field (Fig. 1-A, B) in September, more than two months after the crop had been harvested. Field soil was sampled in areas of the field where wilt was prevalent (14), namely stations 18, 19, and 20, and also where wilt was not obvious, stations 8 and 9. In the laboratory, visible fragments of barley were picked from the soil samples with forceps, classifying them as root, straw or seed as they were removed. These fragments were then weighed, diluted, vigorously shaken, and then plated to obtain estimates of the numbers of propagules of the pathogen in the soil and small pieces of sloughed-off tissue adhering to the fragments. Propagules more likely to be truly colonizing the barley itself were determined next by draining the fragments, rediluting and comminuting them, and then making more dilution plates. However, it is not known how many chlamydospores, formed on the surface of the plant material, were removed in the shaking, and of course some of the fibrous material was not well homogenized in the blender.

Upon finding high populations of the pathogen present in this residue, fresh plant material, gathered from the barley crop of the following year, was plated. A few green barley plants were examined, as were numerous crowns and roots of stubble just after the cutting. This material in

Fig. 1-(A to D). The method used for isolation of *Fusarium oxysporum* f. sp. *vasinfectum* propagules from soil and barley residue. **A)** A soil dilution plated on PCNB-peptone agar (left) compared with a plate (right) seeded with a spore suspension of a mixture of the clones of *F. oxysporum* f. sp. *vasinfectum* isolated from the field being studied. All colonies resembling the pathogen on the soil dilution plate were marked and transferred to PDA. On this particular plate, 13 colonies considered as "possible" *F. oxysporum* f. sp. *vasinfectum* isolates were transferred; eight proved to be pathogenic. Plates with similar numbers of colonies were used in these comparisons. **B)** The plate on the left was spread with a suspension of comminuted barley fragments recovered from soil. The plate on the right, as in (A), was spread with spores of known isolates, and used for identifying colonies likely to be pathogenic. Typically there was a high number of *F. oxysporum* propagules in this material, and often many pathogens. On this particular plate, 29 of the 48 colonies picked proved to be *F. oxysporum* f. sp. *vasinfectum.* **C)** A PDA (pH 6.2) transfer plate showing some of the colonies picked 60 hours earlier from the plate in (B). The colony in the one o'clock position was picked from the plate on the left, and known, therefore, to be *F. oxysporum* f. sp. *vasinfectum.* The colony right of it, at the 3 o'clock position, obviously was not the pathogen. All other colonies were transferred to PDA slants for later pathogenicity tests. (At the times when many of the isolations were made, only 20% were tested on greenhouse plants.) **D)** PDA slants, 25 days old, of the two common clonal types of the pathogen found in all of the infested fields known in California. Each tube shown is a different isolate. All of the pathogenic isolates, whether from cotton plants, soil or residues, resembled these two cultural types or were intermediate between them. The types become distinguishable when sporodochia appear.


A
B
C
D

some cases was dipped briefly in 0.25% Na-hypochlorite between shaking and comminuting, but this treatment appeared to reduce counts.

In addition to barley, the pathogen was sought in some of the common weeds found among the cotton. Aboveground tissue from cheeseweed (*Malva parviflora* L.), and several composites, were cultured. Roots and crowns of yellow nutsedge (*Cyperus esculentus* L.), which is particularly prevalent in the very areas of the fields where wilt occurs, were cultured using the method described above for barley plants.

RESULTS.—*Build-up of F. oxysporum f. sp. vasinfectum in field soils in the absence of a cotton crop.*—The population of the pathogen in field soils did not decrease in the absence of cotton during the 5-6 years that the field had been planted to barley or wheat. At some stations there was a definite increase (Table 1). An increase was noted after the first year (14), at which time only a portion of the field had been planted to barley (stations 6 to 20), due to a cut in cotton acreage allotment that year. At that time the count had increased more in some areas (stations 18, 19 and 20) which were planted to barley than in those remaining in cotton (stations 1 and 2). Five years later, the count was higher than ever in some areas (stations 7, 18 and 19).

At other stations (8 and 9) the population still was not very high, even after many years of infestation, the fungus having been first isolated at these stations 10 years ago. Nevertheless, total populations of *F. oxysporum* in these soil samples were found to be as great, even though wilt Fusaria failed to become established in high populations, as occurred where wilt had been severe. This observation illustrates the futility of trying to correlate total numbers of *F. oxysporum* propagules present with the population of a specific wilt pathogen in a field soil.

Occurrence of F. oxysporum f. sp. vasinfectum in plants and residues other than cotton.—Barley root and straw fragments that were removed from field soil samples at a heavily infested site contained high populations of the pathogen (Table 2). The samples, when collected, were very dry, probably because the field had been harvested and disked several weeks earlier and was lying fallow and unirrigated. The dryness of the soil and plant residues precluded vigorous growth of soil fungi, and it was assumed that the propagules were in a resting state at that time. However, the possibility exists that some of the invasion by *F. oxysporum* f. sp. *vasinfectum* had occurred at a time when the plant material had been too dry for most of the competitors in the soil, especially bacteria, to grow in it.

Fusaria other than the pathogen, usually *F. oxysporum,* were isolated in and on the barley straw and roots, but in the heavily infested areas, *F. oxysporum* f. sp. *vasinfectum* made up 20-45% of the isolates obtained from the straw, and 30-65% of those obtained from the root. Fig. 1-A illustrates a typical barley fragment isolation plate from one such area. On this particular plate most of the colonies, excepting bacteria, were *F. oxysporum,* and in further testing it was found that 29 out of 48 of them were the pathogen. The numerous bacterial colonies present on this plate were frequently encountered on dilution plates of soil organic matter. However, these bacteria were usually dead by the fourth or fifth day of incubation and did not interfere with identifications nor contaminate transfers. The pathogen was less frequently isolated from fragments sampled from less heavily infested parts of the field. Usually the *F. oxysporum* clones other than those of f. sp. *vasinfectum* encountered in root and straw residue culturally resembled ubiquitous isolates of many cultivated soils in California (10). The types which were most frequently isolated from the fragments described here and from soil samples were tested and found to be nonpathogenic to blackeyed beans, tomatoes, and sweet potatoes, the most usual hosts of Fusarium wilts in the valley. Because of this, and of their ubiquity, even in soils which are not conducive to wilts, it was assumed that these isolates were nonpathogenic to any hosts. *F. roseum,* cultivars 'Gibbosum' and 'Culmorum', and *F. solani* were isolated

TABLE 3. *Fusarium oxysporum* f. sp. *vasinfectum* propagules in and on barley roots and rhizospheres per gram of material

Growth stage of barley	No. propagules per gram (fresh wt.) of root material[a]	
	Roots diluted and shaken	Roots diluted and comminuted
Green plants	200	0
Cut stubble	13,750	7,500

[a] The plant material was first shaken vigorously in a dilution blank and this sample (rhizosphere) was plated separately from the subsequently rewashed, rediluted, and comminuted sample.

TABLE 4. Fusarium propagules from nutsedge roots and crowns in cotton field soils in which both nutsedges and Fusarium wilt of cotton were prevalent

Field No.		*F. oxysporum* f. sp. *vasinfectum* propagules per g.		*Fusarium* sp. propagules per gram of nutsedge roots and crowns (Total no.)	*F. oxysporum* f. sp. *vasinfectum* per total Fusaria (%)
		in soil sample	in nutsedge roots and crowns		
1	AVERAGE:	1,577	30,200	68,500	
	RANGE:	. . .	500-188,000	6,000-340,000	<8-88
2	AVERAGE	3,170	64,000	97,000	
	RANGE:	. . .	2,500-420,000	18,700-660,000	21-92

from the barley root and straw fragments of this field in lesser numbers than *F. oxysporum,* but nearly all of the Fusaria present within and on seeds in the soil were *F. roseum.*

In the following year's barley crop, the cotton wilt Fusarium was abundant in the rhizosphere and in roots and crowns of mature plants examined just after they were cut for grain (Table 3). Green plants prior to heading did not appear to harbor high populations of the fungus. Thus, it appeared that barley was usually colonized in the mature and senescent stages, and that the pathogen remained in the residue returned to the soil after the harvest.

Presence of F. oxysporum f. sp. vasinfectum in weeds common in cotton fields.—F. oxysporum f. sp. *vasinfectum* was isolated from above-ground stems of 8 out of 48 cheeseweed plants obtained from heavily infested field sites. Some of the infected cheeseweeds matured earlier and were smaller than those from which the pathogen was not isolated, but external wilt symptoms were not noted on such plants.

Nutsedge plants from two fields at different locations harbored high populations of *F. oxysporum* f. sp. *vasinfectum* in their roots, and (as observed in barley) the build-up increased as the plants reached maturity and senescence. Although the numbers of propagules found among individual plants pulled at the high-infestation sites varied considerably, because of the high population in many plants (Table 4), it appears that this weed may be contributing much to the build-up of the cotton wilt Fusarium in soil.

Microscopic examinations of [air-dried and lightly stained (briefly washed with 1% acid fuchsin in 85% lactic acid and rinsed with water)] root fragments of nutsedge plants from the field revealed numerous structures which closely resembled chlamydospores of Fusaria. Structures resembling spores and resting structures of other fungi, cysts of amoebae, and structures unidentifiable to us also were observed. Fusarium resting spores usually appeared to be intercellular and upon or near the surface. Some were epidermal and some within the first few layers of the cortex.

The pathogen was not isolated from the limited number of Compositae weeds examined.

DISCUSSION.—After numerous and detailed microscopic examinations of California field soil samples, we concluded that the chlamydospores of Fusarium species in these soils are usually found adhering to or imbedded within a piece of organic matter (9). Furthermore, this organic matter may have been invaded by various Fusaria when it was still a viable plant root. The present study indicates that roots of several kinds of senescent plants are frequently invaded by a *F. oxysporum* pathogen, and also by nonpathogenic forms.

In 1962, Christou and Snyder (4) reported that chlamydospores of three formae speciales of *F. solani* and of *F. roseum* f. sp. *cerealis* (Cke.) Sny. & Hans. 'Culmorum' produced abundant chlamydospores both within and on the surface of tissues of their respective hosts at the time the plants became senescent. Nash, Christou, and Snyder (9) further reported that such chlamydospores were not observed in the deeper cortical tissues, and that the chlamydospores formed on the surfaces of root tissues were larger and had thicker walls than those formed inside the tissue. The present work suggests that many plant species, besides those that show external symtoms, are frequently parasitized late in their lives, and that chlamydospores form in and on root and crown tissue, where they remain after the harvest.

Other workers have reported that the species *Fusarium oxysporum* is a frequent invader of cereal roots. Gordon (7) and Warren and Kommedahl (18, 19, 20) found *F. oxysporum* to be the predominant Fusarium species isolated from roots, rhizospheres, crop residues, and soil in cereal plots. The latter authors reported further, however, that in a year when seedling blight was severe in Minnesora, *F. roseum* comprised 90% of the root isolates in their plots. Removal of cereal residue, mainly from the soil surface, increased the proportion of *F. oxysporum* surviving. They further reported (21) that in a field which had grown soybeans for 10 years, *F. oxysporum* was by far the most frequently isolated Fusarium species from soil, plant rhizospheres, roots, and residues, and suggested that it may be an aggressive secondary invader of soybean roots, or a co-invader with *Rhizoctonia solani.*

Evidence suggests that pathogens as well as nonpathogens may invade roots of a variety of plants, probably at a time when the hosts are in a senescent stage or as secondary invaders (11, 12).

Long rotations do not necessarily mean that a soil-borne pathogen, deprived of its specific host, will gradually decrease in the soil by attrition. Populations of *F. oxysporum* f. sp. *vasinfectum* increased in the field described here during the years that cereals were cropped. On the other hand, the classical experimental plot of the Rothamsted Experimental Station, "Broadbalk", where wheat has been grown continuously for over 100 years, yielded relatively few isolates of any types of *F. oxysporum* (15). These plots, however, were probably extroardinary because of the long history of continuous wheat. Other wheat fields in the vicinity, such as those at Woburn, contained relatively high populations of *F. oxysporum.*

More work should be done to find crops which do not harbor *F. oxysporum,* especially the wilt pathogens. Another alternative that might be investigated as a possible practical means of reducing soil populations of wilt Fusaria is the use of long fallow with periodic irrigation and with especial attention to removing weeds.

A recent report by Bird and Högger (3) showed that two common nutsedges served as reservoirs for two nematode species that were severely pathogenic to cotton, *Meloidogyne incognita* (Kofoid & White) Chitwood and *Hoplolaimus columbus* Sher. They attributed the recent increase in severity of nematode diseases of cotton to the widespread use of herbicides not effective against nutsedges. The evidence here presented that *F. oxysporum* f. sp. *vasinfectum* also increased on nutsedges may mean that this weed is an important contributor to the complex of Fusarium wilt and nematode diseases of cotton.

Many Malvaceous weeds are somewhat susceptible to Fusarium wilt caused by the cotton pathogen, and the fungus may be isolated from both above and below-ground plant parts.

Not all of the *F. oxysporum* clones reported here from roots and residues of plants as well as those from soil dilutions were causative agents of wilts known to occur in the area. The ecological role of these ubiquitous, presumably nonpathogenic *F. oxysporum* has yet to be clarified, but they would appear to be important agents in breaking down crop residues.

Distribution of pathogenic forms of *F. oxysporum* fortunately is still much more limited and regional than that of nonpathogenic forms. The establishment of these special forms in soils depends on their introduction, and on their ability to spread through field soils. In some fields, the pathogenic Fusaria spread rapidly and in others they are slow to establish (13, 16). In the field most often cited in this report, *F. oxysporum* f. sp. *tracheiphilum* was the only other pathogenic *Fusarium* sp. thus far encountered. It is present in low population levels and has only very recently built-up to countable levels. The establishment of this later-introduced pathogen in relation to the pattern of the well-established cotton wilt form of Fusarium should be interesting to follow.

LITERATURE CITED

1. ABAWI, G. S., and J. W. LORBEER. 1972. Several aspects of the ecology and pathology of Fusarium oxysporum f. sp. cepae. Phytopathology 62:870-876.
2. ARMSTRONG, G. M., and J. K. ARMSTRONG. 1948. Nonsusceptible hosts as carriers of wilt Fusaria. Phytopathology 38:808-826.
3. BIRD, G. W., and C. HÖGGER. 1973. Nutsedges as hosts of plant-parasitic nematodes in Georgia cotton fields. Plant Dis. Reptr. 57:402.
4. CHRISTOU, T., and W. C. SNYDER. 1962. Penetration and host-parasite relationships of Fusarium solani f. phaseoli in the bean plant. Phytopathology 52:219-226.
5. EBBELS, D. L. 1971. Plant pathology. Pages 19-27 *in* L. C. Hughes, ed. Progress reports from Experiment Stations for the season 1968-69 Tanzania. Cotton Research Corp. 12 Chantrey House, Eccleston St., London, S.W.1. 58 p.
6. GARBER, R. H., and G. A. PAXMAN. 1963. Fusarium wilt of cotton in California. Plant Dis. Rep. 47:398-400.
7. GORDON, W. L. 1954. The occurrence of Fusarium species in Canada. IV. Taxonomy and prevalence of Fusarium species in the soil of cereal plots. Can. J. Bot. 32:622-629.
8. HENDRIX, F. F., JR., and L. W. NIELSON. 1958. Invasion and infection of crops other than the forma suscept by Fusarium oxysporum f. batatas and other formae. Phytopathology 48:224-228.
9. NASH, S. M., T. CHRISTOU, and W. C. SNYDER. 1961. Existence of Fusarium solani f. phaseoli as chlamydospores in soil. Phytopathology 51:308-312.
10. NASH, S. M., and W. C. SNYDER. 1965. Quantitative and qualitative comparisons of Fusarium populations in cultivated fields and noncultivated parent soils. Can. J. Bot. 43:939-945.
11. NASH, S. M., and W. C. SNYDER. 1967. Comparative ability of pathogenic and saprophytic Fusaria to colonize primary lesions. Phytopathology 57:293-296.
12. PALMER, L. T., and T. KOMMEDAHL. 1969. Root-infecting Fusarium species in relation to rootworm infestations in corn. Phytopathology 59:1613-1617.
13. SMITH, S. N., and W. C. SNYDER. 1971. Relationship of inoculum density and soil types to severity of Fusarium wilt of sweet potato. Phytopathology 61:1049-1051.
14. SMITH, S. N., W. C. SNYDER, and F. MOYNIHAN. 1970. Populations of Fusarium oxysporum f. vasinfectum in field soil in relation to cotton wilt. Pages 69-70 *in* Proc. Beltwide Cotton Prod. Res. Conf., Houston, Texas. January 1970.
15. SNYDER, W. C., and S. M. NASH. 1968. Relative incidence of Fusarium pathogens of cereals in rotation plots at Rothamsted. Trans. Br. Mycol. Soc. 51:417-425.
16. STOVER, R. H. 1962. Fusarial wilt (Panama Disease) of bananas and other Musa species. Commonw. Mycol. Inst. Phytopathol. Pap. No. 4. Kew, Surrey, England. 117 p.
17. WAITE, B. H., and V. C. DUNLAP. 1953. Preliminary host range studies with Fusarium oxysporum f. cubense. Plant Dis. Rep. 37:79-80.
18. WARREN, H. L., and T. KOMMEDAHL. 1973. Fertilization and wheat refuse effects on Fusarium species associated with wheat roots in Minnesota. Phytopathology 63:103-108.
19. WARREN, H. L., and T. KOMMEDAHL. 1973. Prevalence and pathogenicity to corn of Fusarium species from corn roots, rhizosphere, residues and soil. Phytopathology 63:1288-1290.
20. WARREN, H. L., and T. KOMMEDAHL. 1973. Root infecting species of Fusarium in soil and in the roots, rhizospheres, and residue of oats. Phytopathology 63:1401-1403.
21. WARREN, H. L., and T. KOMMEDAHL. 1973. Fusarium species in roots and soil associated with monoculture of soybeans in Minnesota. Plant Dis. Rep. 57:912-914.