Several Aspects of the Ecology and Pathology of Fusarium oxysporum f. sp. cepae

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Accepted for publication 2 February 1972.

ABSTRACT

A direct correlation was found between inoculum density of *Fusarium oxysporum* f. sp. *cepae* and damping-off of onion seedlings in artificially infested organic soil under controlled environment (26-C day and 21-C night; 60-70% relative humidity; 16-hr fluorescent light/day at 2,000 ft-c). A population of 5×10^4 or more propagules/g of oven-dry soil was needed before significant disease development could be detected in field soil; 100 propagules caused extensive disease development in a sterilized soil. Seedling damping-off increased with temperature from 10 to 32 C. Poor germination occurred when conidia were added to field soil and germ tubes formed were either lysed or converted to chlamydospores, the form in which the fungus exists in organic soils cropped to onion. The fungus population decreased in the absence of onion and increased in its presence. Roots of *Oxalis corniculata* were heavily infected by the fungus when grown in artificially infested organic soils containing 5×10^4 propagules/g of oven-dry soil.

Phytopathology 62:870-876.

Additional key words: Allium cepa, Fusarium basal rot of onion, root rot diseases.

Fusarium oxysporum Schlecht. emend. Snyd. & Hans. f. sp. *cepae* (Hanz.) Snyd. & Hans. is composed of four morphological types; sporodochial, ropy, pionnotal, and mycelial (1). In naturally infested organic soils cropped to onion in New York, the fungus exists only as the sporodochial type and is unevenly distributed, with average population counts for fields ranging from 300 to 6,500 propagules/g oven-dry soil (2). Soils with a history of Fusarium basal rot of onion generally were found to have a higher population of the fungus than soils with histories of light or no known outbreaks of the disease. The fungus attacks seedlings, causing pre- and postemergence damping-off, root rot of older plants, and stem plate discoloration and basal rot of bulbs in the field and in storage (3, 4).

The objectives of the present investigation were: (i) to determine the effect of temperature and inoculum density on disease development under controlled environment; (ii) to observe germination, growth, and establishment of the pathogen in organic soils; (iii) to determine the propagule form in which the pathogen exists in organic soils; and (iv) to make a limited host range study.

MATERIALS AND METHODS.—Sporodochial-type isolates of *F. oxysporum* f. sp. *cepae* isolated from naturally infected onion plants collected in western New York were used. The cultures were maintained on potato-dextrose agar (PDA) in a Lab-Line No. 844 incubator at a temperature of 24 C and 12 hr of fluorescent light (500 ft-c) per day. The cultures were transferred frequently by the single spore technique. Conidial suspensions used for inoculum were obtained from 3- to 4-week-old cultures, filtered through four sterile layers of cheesecloth, and washed three times by centrifugation at ca. 3,300 *g*. The concentration of washed conidial suspensions was determined by hemacytometer count. A representative suspension of washed conidia used consisted of 75% macroconidia and 25% microconidia. Chlamydospores were present in 4% of the suspensions of both conidial forms.

Seeds of onion (*Allium cepa* L.) cultivars Elba Yellow Globe, Autumn Spice Improved, Grandee, and Treasure were surface-sterilized by wetting for 20 to 30 sec in 30% ethyl alcohol, placement for 5 min in 10% Clorox (5.25% by weight sodium hypochlorite), or by rinsing several times in sterile distilled water.

Temperature and disease development.—The growth of *F. oxysporum* f. sp. *cepae* in culture at different temperatures was studied by making monoconidial transfers to PDA plates which were incubated in the dark for several days. Temperatures tested were at 3-degree intervals from 0 to 36 C. All treatments were replicated 5 times. Colony diameter was measured every 24 hr, and colony dry weight was determined at 166 hr of incubation. The agar-mycelial suspension was filtered through Whatman No. 13061 filter paper in a Büchner funnel attached to a faucet water pump. Mycelial fragments were washed several times with hot water and dried for 30 min in an oven at 100 C, and the dry weight was recorded.

Surface-sterilized seeds of the onion cultivars Elba Globe and Treasure were planted in steam-treated soil artificially infested with the fungus (5×10^3 propagules/g oven-dry soil) and placed in growth chambers maintained at the desired temperatures, a relative humidity of 60 to 70%, and 16 hr of 2,000 ft-c fluorescent light/day. Twenty-five seeds were planted in each 4-inch pot of artificially infested soil with four replications for each treatment and each cultivar. Emergence and stand counts were recorded as percentage of the control 2 and 4 weeks after planting, respectively.

Inoculum density and disease development.—Inoculum density of *F. oxysporum* f. sp. *cepae* as the number of propagules per gram oven-dry soil was determined in all experiments. Conidia of the fungus were added to soil with an atomizer, and the soil was thoroughly mixed.

Four-inch pots were filled with the infested soil, and 25 surface-sterilized onion seeds of the cultivar Treasure were planted in each. Each test was replicated 4 times. All pots were placed in a growth chamber with a diurnal temperature of 21 to 26 C night and day, respectively, 60 to 70% relative humidity, and 16 hr of 2,000 ft-c fluorescent light/day. Emergence and stand counts were recorded as percentage of the control 2 and 5 to 6 weeks after planting, respectively. Recovery of the fungus from infested soils was accomplished by both the dilution plate count method using a specific selective medium (2) and the most probable number method (11).

The effect of incubation time and the presence or absence of the host plant on inoculum density of the fungus when added to both steam-treated and nontreated organic soil was determined. Each soil sample analyzed was divided into four equal parts. Two parts were infested with 10^5 propagules of the fungus/g soil, and two were not infested. One sample of infested and one of noninfested soil were planted with onion seeds at the rate of 25 seeds/pot while the others were left fallow. All treatments were incubated in the dark for 14 days, watered lightly, then transferred to a growth chamber at 24 C and 12 hr fluorescent light (500 ft-c)/day. The population of the fungus was estimated at 0, 7, 14, and 35 days after infestation.

The population of the fungus in the rhizosphere-rhizoplane region of onion roots was determined by planting surface-sterilized seeds of the cultivar Treasure in artificially infested soil (10^5 propagules/g oven-dry soil) as described above. Two weeks after planting, the soil ball was removed from the pot and the soil was removed carefully, leaving the rhizosphere soil on the roots. Roots were weighed and placed in 100-ml sterile distilled water in flasks on a Burrell Wrist-Action shaker for 30 min, removed, and weighed again to determine the weight of the soil sample used. Recovery of the fungus from infested soils was accomplished on the selective medium (2) for both the dilution plate count and the most probable number methods (11).

Fate of the conidia and the propagule form in organic soil.—The fate of conidia added to soil and the propagule form in which the fungus exists in soil were studied with the soil-agar-smear technique (12). Three grams of soil were mixed in 50 ml of 1.5% warm water agar. Several drops of this suspension were placed on a slide and stained with 1% cotton blue in lactophenol or 1% aqueous phloxine, a cover slip was added, and the slides were examined microscopically. For identification of the structures, hyphal tip transfers from the germinated structures on unstained slides were made to PDA slants. Organic soils naturally and artificially infested with *F. oxysporum* f. sp. *cepae* as well as artificially infested steam-treated organic and greenhouse-prepared soils were used. The greenhouse soil consisted of 1 part peat moss:1 part sandy loam soil:1 part river sand. Conidial germination also was determined in sterile distilled water and potato-dextrose broth and compared with that in the soils.

Host range study.—A number of clones of *F. oxysporum*, morphologically and culturally similar to *F. oxysporum* f. sp. *cepae*, were isolated from *Oxalis corniculata* L. (oxalis), *Portulaca oleraccea* L. (purslane), *Amaranthus* sp. (pigweed), and onion. The oxalis isolate was obtained from apparently healthy plants growing in the greenhouse in soil artificially infested with *F. oxysporum* f. sp. *cepae*. The onion, purslane, and pigweed isolates were obtained from plants growing in organic soils cropped to onion from western New York. Vascular tissues of pigweed roots exhibited a dark brownish discoloration. The pathogenicity of these isolates was measured by the onion slice method of inoculation (1) and by their ability to cause damping-off of onion seedlings growing in artificially infested soils. An isolate of *F. oxysporum* f. sp. *cepae* was used as the control. Each treatment was replicated 5 times.

To investigate the possible role of oxalis as a symptomless host of *F. oxysporum* f. sp. *cepae*, surface-sterilized oxalis seeds were planted in both steam-treated and nontreated artificially infested (5×10^3 propagules/g oven-dry soil) organic soils. Twenty seeds were planted in 4-inch pots, and three pots were used/treatment. Stand and fresh weight as percentage of the control were recorded 4 and 8 weeks after planting, respectively.

RESULTS.—*Temperature and disease development.*—The optimum temperature range for the growth of *F. oxysporum* f. sp. *cepae* in culture is 24 to 27 C as determined by measurement of colony diameter and dry weight after 146 and 166 hr, respectively (Fig. 1-C). No growth occurred on plates incubated at 0, 3, 6, 9, and 36 C. When transferred to an incubator at 25 C for several days, growth resumed on those plates initially incubated at 3, 6, and 9 C, and on one of the five plates at 0 C, but not in those incubated at 36 C.

A close correlation occurred between temperature and damping-off of onion seedlings growing in organic soil artificially infested with *F. oxysporum* f. sp. *cepae* under controlled conditions. A higher percentage of seedling damping-off developed as the temperature was increased from 10 to 32 C (Fig. 1-C). Emergence and stand of onion seedlings at temperatures of 15 to 10, 21 to 15, 21 to 21, 27 to 21, and 32 to 27 C (day and night, respectively) were 95 and 92, 82 and 58, 80 and 5, 33 and 0, and 38 and 0%, respectively. Virtually no disease developed when plants were grown in a growth chamber at 15 C during the day and 10 C at night, 60 to 70% relative humidity, and 14 hr of 2,000 ft-c fluorescent light/day. A range of from 32 to 27 C was not optimum for the growth of the fungus in culture; however, the stand of onion seedlings growing in infested soil at this temperature was reduced to zero. Higher temperatures caused a low percentage of seed germination and poor growth of onion seedlings in the control treatments, and thus their effect could not be determined.

Inoculum density and disease development.—Close correlation existed between inoculum density of *F. oxysporum* f. sp. *cepae* and disease development as

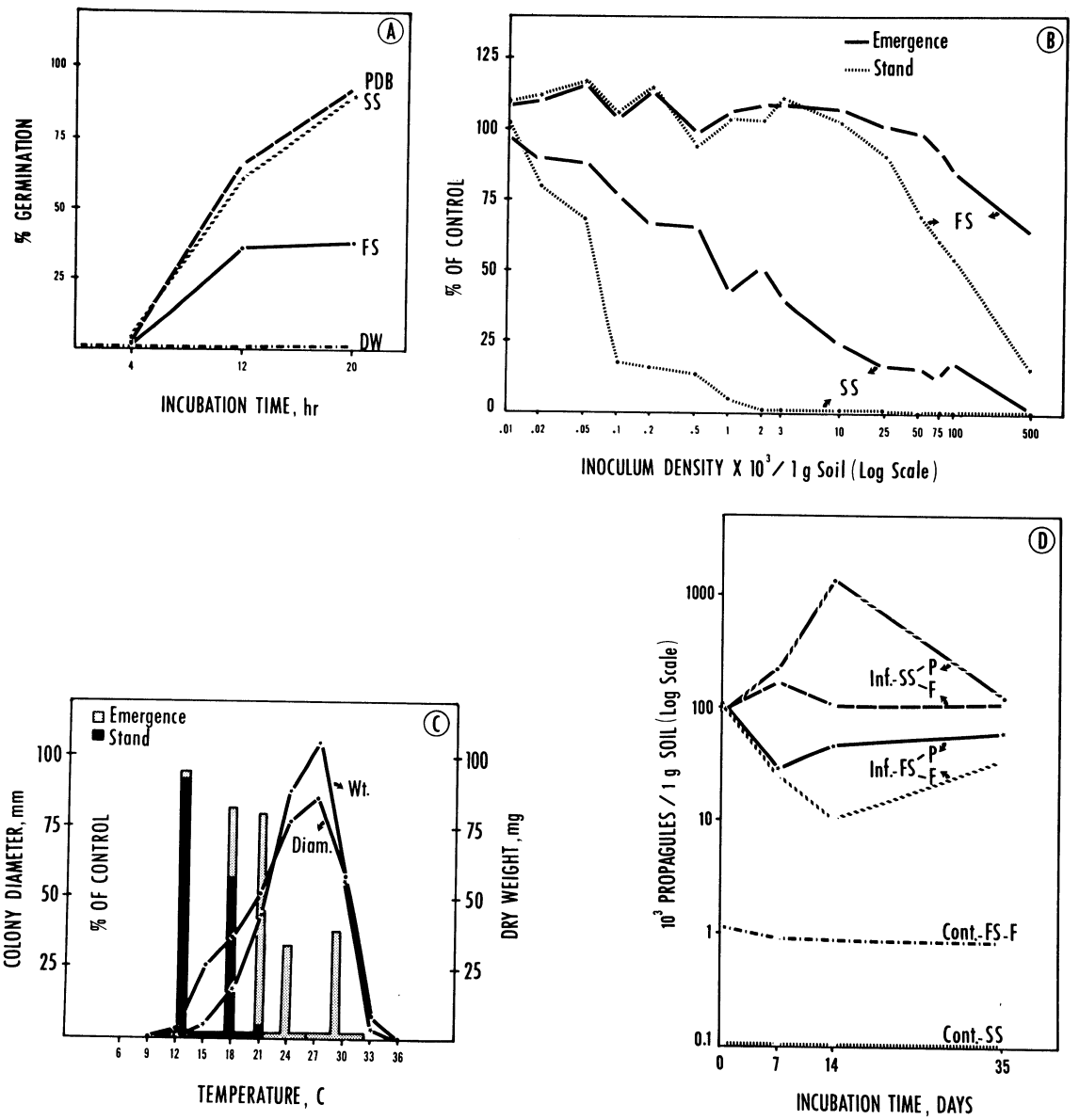

Fig. 1. Biological activity of *Fusarium oxysporum* f. sp. *cepae* in organic soils. **A)** Conidial germination in sterile distilled water (DW), field soil (FS), steam-treated soil (SS), and potato-dextrose broth (PDB). **B)** Effect of inoculum density on seedling emergence and stand in field soil (FS) and steam-treated soil (SS). **C)** Effect of temperature on conidial growth of *F. oxysporum* f. sp. *cepae* in culture and disease incidence in onion seedlings growing in artificially infested soils. Colony diameter and dry weight of the fungus were recorded at 146 and 166 hr of incubation, respectively. **D)** Population changes of *F. oxysporum* f. sp. *cepae* in artificially infested steam-treated soil (SS) and field soil (FS) in the presence (P) and absence (F) of the host plant (onion seedlings) as affected by incubation time. Control (Cont.) consisted of noninfested soils.

measured by emergence and stands of onion seedlings growing in artificially infested soils. In a typical experiment, fifteen inoculum levels (0.01 to 500 X 10^3 propagules/g oven-dry soil) were tested in steam-treated and untreated organic soil which had been cropped to onions for only 1 year (Fig. 1-B). As few as 100 propagules/g oven-dry soil caused about 80% reduction in seedling stand in steam-treated soil. However, 5 X 10^4 propagules/g oven-dry soil were needed before seedling damping-off was detected in field soil. Stands were actually better than the control when low levels of fungus inoculum were added to nontreated organic soil.

In another typical experiment, the relationships of five inoculum levels (0.1, 1, 10, 100, and 1,000 X 10^3 propagules/g oven-dry soil) and damping-off were investigated both in steam-treated and nontreated organic soils (Table 1). The stands of onion seedlings in steam-treated soils were 24, 2, 0, 0, and 1% of the control, respectively. Stands in nontreated soils were

TABLE 1. The relationship between inoculum density of *Fusarium oxysporum* f. sp. *cepae* and disease development in steam-treated and nontreated organic soils using the onion cultivar Treasure as measured by seedling emergence and stand 2 and 4 weeks after planting

Inoculum density[a]	Steam-treated soil			Nontreated soil		
	% of control		Recovery counts[a]	% of control		Recovery counts[a]
	Emergence	Stand		Emergence	Stand	
0.1	90	24	13	99	100	0.5
1.0	67	2	28	103	106	2.1
10.0	37	0	74	98	86	6.6
100.0	53	0	876	92	36	20.5
1,000.0	44	1	1,250	85	10	158.2

[a] Times 10^3 propagules/g oven-dry soil.

TABLE 2. The relationship between inoculum density of *Fusarium oxysporum* f. sp. *cepae* and disease development in steam-treated and nontreated organic field soils using the onion cultivar Autumn Spice Improved, as measured by seedling emergence and stand recorded 2, 4, and 22 weeks after planting. Percentage smut (*Urocystis colchici*) was recorded 4 weeks after planting to show the masking effect in organic soils cropped to onions

Inoculum density[a]	Steam-treated soil				Nontreated soil			
	%				%			
	Emergence	Stand		Smut	Emergence	Stand		Smut
0	89	89[b]	88[c]	0	83	81[b]	32[c]	61
199	56	29	16	0	80	78	24	50
498	52	21	9	0	79	74	20	72
996	42	17	3	0	72	67	12	79
1,993	50	21	10	0	70	58	11	76
2,990	22	5	3	0	76	72	24	74
5,981	24	5	3	0	60	48	12	73
11,961	31	8	4	0	79	65	19	86

[a] Number of propagules/g oven-dry soil.
[b] Recorded 4 weeks after planting.
[c] Recorded 22 weeks after planting.

100, 106, 86, 36, and 10, respectively. In the treated soil, a population of 100 propagules/g of soil was high enough to cause 76% reduction of onion seedlings, while in nontreated soil, more than 1,000-fold of this population was needed to cause as much disease. In addition, the population of the fungus at the termination of the experiment was determined for each level. A much higher population of the fungus was recovered from treated than nontreated soil at any inoculum level used.

Organic soils cropped to onions for many years were initially used in this study. However, high percentages of onion smut generally developed under experimental conditions which masked the effect of the inoculum levels of the *F. oxysporum* f. sp. *cepae* tested in nontreated soils (Table 2). The use of fungicides for onion smut control is a routine practice on most onion farms in New York, and this practice may reduce the amount of seedling infection by *F. oxysporum* f. sp. *cepae* under field conditions. Therefore, an organic soil only recently cleared and brought under cultivation was used in most of the experiments, and the onion smut problem was obviated.

The effect of incubation time and presence or absence of the onion plant on the population of *F. oxysporum* f. sp. *cepae* was investigated in artificially infested, steam-treated and nontreated organic soils (Fig. 1-D). Higher populations of the fungus were recovered from treated than nontreated infested soils at 7, 14, and 35 days after soil infestation. Significant differences were not found between the populations of the fungus recovered from both soils immediately after infestation. Later, the presence of onion seedlings caused a considerable increase in the population of the fungus as compared to the fallow treatment in both treated and nontreated soils. There was a net increase and decrease in the original population of the fungus when added to treated and nontreated organic soils, respectively.

Populations of the fungus were higher (38.3×10^5 propagules/g) in soil samples obtained from the rhizosphere-rhizoplane region of onion roots than in those obtained from composite soil samples (0.5×10^5 propagules/g) of similar treatments (Table 3). These samples were obtained from organic soil artificially infested with 10^5 propagules of the fungus/g oven-dry soil 3 weeks before sampling.

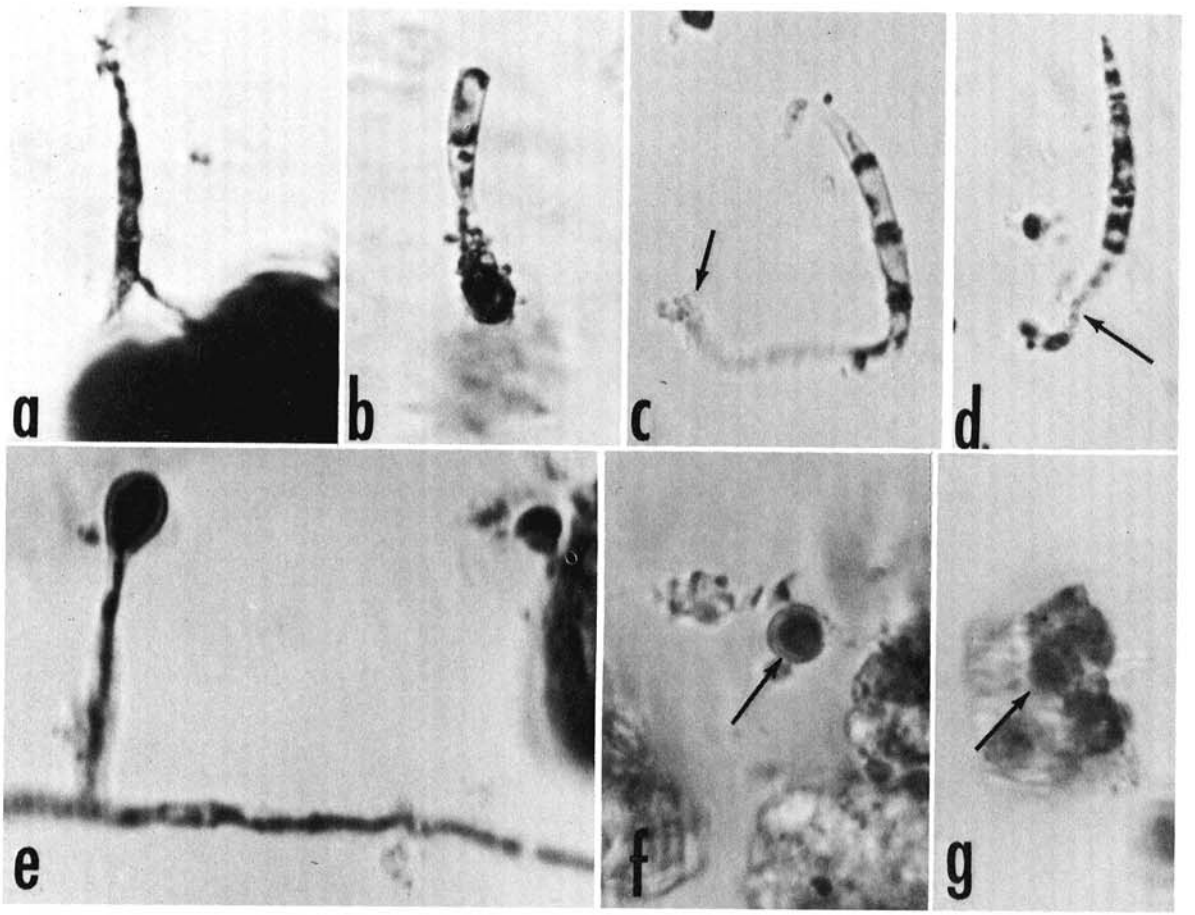

Fig. 2. Germination and subsequent growth in soil of conidia of *Fusarium oxysporum* f. sp. *cepae*. **a)** A macroconidium with a narrow and short germ tube penetrating an organic particle in nontreated soil. **b)** A chlamydospore formed at the end of a short germ tube produced by one cell of a broken macroconidium in nontreated soil. **c)** A germ tube produced by a macroconidium in the process of lysing (arrow) in nontreated soil. **d)** An immature chlamydospore formed at the end of a germ tube in a stage of lysis (arrow) in nontreated soil. **e)** A terminal chlamydospore produced by a hypha growing in a steam-treated soil. **f)** A chlamydospore between soil particles in a nontreated soil. **g)** A chlamydospore embedded in an organic particle in nontreated soil.

TABLE 3. Population of *Fusarium oxysporum* f. sp. *cepae* in a soil sample obtained from the rhizosphere-rhizoplane zones of onion roots and in a composite soil sample from an artificially infested field soil

Soil sample	Population[a] (10^3 propagules/g oven-dry weight)
Check-composite sample	1
Check-rhizosphere-rhizoplane sample	3
Infested-composite sample	50
Infested-rhizosphere-rhizoplane sample	3,830

[a] All colonies morphologically and culturally similar to *F. oxysporum* f. sp. *cepae* were recorded.

Germination, growth, and establishment of F. oxysporum f. sp. cepae in organic soil.—Germination of conidia of *F. oxysporum* f. sp. *cepae* in organic soils was much lower in nontreated soil than in steam-treated soil or in potato-dextrose broth (Fig. 1-A). Highest conidial germination observed in nontreated organic soil was 40%. Germ tubes formed in nontreated organic soils generally were short and narrow. They either penetrated an organic particle, lysed, or formed chlamydospores (Fig. 2-a, b, c, d). Germ tubes formed in steam-treated soils were long, wide, branched, and produced abundant mycelial growth which eventually formed a large number of chlamydospores (Fig. 2-e). Within 2 weeks, all conidia added to field soils either converted to chlamydospores or lysed. Conidia added to nontreated organic soil which was left fallow were reduced in number by 90.2% between 0 and 14 days after soil infestation. This indicated that the conversion of conidia to chlamydospores in nontreated organic soils occurs at a ratio of about 10:1. These findings may explain, at least in part, the

need for a high number of conidia in nontreated organic soils as compared to treated soils to produce a high incidence of onion seedling infections. The ratio of the conversion of conidia to chlamydospores becomes especially important when chlamydospores are the only form of this fungus capable of infecting onion seedlings in nontreated organic soils.

Propagule form in which F. oxysporum f. sp. cepae exists in organic soils.—Chlamydospores were the only structures of the pathogen observed in naturally infested organic soils or in artificially infested nontreated organic soils 2 weeks after infestation. Chlamydospores were the only units found when conidia were stored in sterile distilled water for 5 years with or without the addition of small pieces of leaf blades of grasses. Complete conversion of conidia to chlamydospores was observed in an artificially infested, sterilized organic soil which was left for several months under laboratory conditions, receiving no water except at the time of infestation. However, in artificially infested, steam-treated greenhouse soil stored for several years under laboratory conditions, the pathogen existed as chlamydospores (73.8%), macroconidia (6.6%), microconidia (9.8%), and hyphal fragments (9.8%). In old cultures of the pathogen on several media, chlamydospores are formed in large numbers. We conclude that the pathogen exists in naturally infested soils in the form of chlamydospores. In naturally infested soils, chlamydospores generally were globose to subglobose in shape and 7.5 to 10.0 μ in diam. Chlamydospores were either free between soil particles (Fig. 2-f) or embedded in organic tissues (Fig. 2-g).

Host range.—When the pathogenicity to onion of *F. oxysporum* f. sp. *cepae* (isolate 156) and four other isolates of *F. oxysporum* obtained from oxalis, purslane, pigweed, and onion was compared, the forma specialis *cepae* and the oxalis isolate were highly pathogenic to onion as measured by both the onion slice and seedling damping-off methods (Table 4). The purslane and pigweed isolates were found slightly pathogenic, as indicated by the onion slice method of inoculation, whereas the onion isolate caused no detectable symptom by either method.

The oxalis isolate was designated as *F. oxysporum* f. sp. *cepae* because it was morphologically, culturally, and pathogenically identical with isolate 156 used in the present study, which is typical of *F. oxysporum* f. sp. *cepae*. The oxalis isolate caused no apparent symptoms or significant damage to oxalis, although it colonized the plant. In one experiment, stand and wet weight of oxalis plants growing in artificially infested soil were 96 and 107% of the control, respectively. In a second experiment, stand and wet weight were 92 and 91% of the control, respectively. The fungus repeatedly was isolated from oxalis plants growing in the infested soil, but was never isolated from those growing in the noninfested soil.

TABLE 4. Pathogenicity to onion of four isolates of *Fusarium oxysporum* (morphologically and culturally similar to *F. oxysporum* f. sp. *cepae* isolate 156). Pathogenicity as measured by the onion slice method of inoculation and the ability of these isolates to cause damping-off of seedlings 4 weeks after planting

Isolate	Disease index[a] (166 hr)	Stand (% of control)
Onion (No. 156)	4.5	10
Oxalis	4.8	25
Purslane	2.6	96
Pigweed	2.3	99
Onion	0.0	101
Check	0.0	100

[a] Pathogenicity index: 0 = no visible discoloration, rotting, or mycelial growth observed; 5 = complete rotting of the onion slice with abundant mycelial growth covering both sides of the slice.

DISCUSSION.—Abawi & Lorbeer (2) reported that levels of natural infestation of *F. oxysporum* f. sp. *cepae* in organic soils of New York onion farms ranged from 300 to 6,500 propagules/g oven-dry soil. Higher counts were obtained for individual samples, and undoubtedly still higher counts may exist in the microenvironments of the soil. Under controlled environmental conditions maintained for the experiments conducted in the present study, a close correlation between inoculum density of *F. oxysporum* f. sp. *cepae* and onion seedling infection occurred in organic soils (steam-treated and nontreated) artificially infested with the fungus. The present findings further substantiate the conclusion made earlier (2) that biotic and physical factors in addition to the size of the population of the fungus determine the basal rot potential of nontreated, naturally infested organic soil under field conditions. These findings are in general agreement with the many other reports in the literature on the ecology of different species of the genus *Fusarium* (6, 7, 12, 13, 14, 15). They illustrate the poor competitive ability of *F. oxysporum* f. sp. *cepae* with the natural soil microflora. Adapting the concept of Garrett (8), the fungus may be considered as a root-inhabiting fungus.

Soil temperature could be the major factor responsible for the late appearance of Fusarium basal rot of onion under field conditions in New York, which generally are cool in the early part of the growing season. Temperatures favorable for growth of the fungus in culture and for pathogenicity to onion in the present study were similar to those described earlier by Walker & Tims (18). During unseasonably warm spring weather, a higher incidence of damping-off and early stem plate infection has been observed and underscores the effect of temperature in disease regulation. These observations concur with those of Szatala (16), who showed that in Hungary, infection of onion with *F. oxysporum* f. sp. *cepae* appears first in early July when the temperature is above 25 C. He reported that nearly all onions inoculated and stored at 25 to 30 C were killed. Twenty per cent infection occurred at 15 C, and the fungus did not develop below 5 C. Kehr et al. (10) reported that isolates of *F. oxysporum* f. sp. *cepae*

were pathogenic over the temperature range of 22 to 38 C, and that stand of onion seedlings decreased as temperature increased. They also suggested that infection and injury could occur below 22 and above 38 C. However, they observed that germination and growth of onion seedlings were impaired and the plants injured at 38 C.

Fusarium oxysporum f. sp. *cepae* parasitized oxalis plants, but caused no detectable symptoms under greenhouse and growth chamber conditions. Oxalis could be considered as a symptomless host for the fungus, and may play a significant role in the survival of the fungus under field conditions. Invasion of nonhosts for a number of formae speciales of *F. oxysporum* has been reported (5, 9, 17).

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