The Behavior of Fusarium oxysporum f. sp. melonis in the Presence and Absence of Host Plants

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ABSTRACT

Both the rhizosphere population and the colonization of roots of susceptible host plants by *Fusarium oxysporum* f. sp. *melonis* increased with time. The increase in population was caused mainly by sporulation on infected roots. The population of *F. oxysporum* f. sp. *melonis* and other fungi was greater in the rhizosphere of wilted host plants than in the rhizosphere of healthy plants. The pathogen was able to colonize roots of many nonhost plants under field conditions, but there was no accompanying increase of *F. oxysporum* f. sp. *melonis* in soil.

The population of *F. oxysporum* f. sp. *melonis* in soil increased in the presence of a living host and decreased in its absence, and was greater at the site of wilted plants and on the soil surface than between rows and at lower soil levels. Sporulation of the pathogen on infected vines and the sloughing away of decomposing infected tissues contributed to the increase in population on the soil surface, and to the root-zone effect at the lower depths. Infected vines were an important source of overwintering of the pathogen. In Michigan, the population of *F. oxysporum* f. sp. *melonis* was not greatly affected by low winter temperatures, but declined sharply in spring with the advent of milder weather. The drop in population was assumed to coincide with the progressive decomposition of infected plant residues.

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The importance of nonhost plants on soil-borne plant pathogens has been emphasized by various workers (5, 11, 14, 16, 18, 20). Reyes and Mitchell (16) found that *Fusarium* was stimulated in the rhizosphere of susceptible plants, but not in that of nonhosts. However, they did not indicate the kind of propagules that were stimulated. Fusarium wilt pathogens have been isolated from roots and stems of nonhost plants under field conditions (1, 20).

Wensley and McKeen (24, 25) found that the population of melon wilt Fusarium increased at the site of muskmelon plants and declined shortly after harvest. In the greenhouse studies, only susceptible cultivars of melon caused a site increase in inoculum, whereas the population remained constant or even decreased slightly in the case of resistant cultivars.

In the present report, the activity of *Fusarium oxysporum* f. sp. *melonis* (Leach and Currence) Snyder and Hansen was studied in the root zone of host and nonhost plants and also in soil both in the field and under more closely controlled greenhouse conditions.

MATERIALS AND METHODS.—Sandy loam top soil was collected from a melon field (near Belleville, Michigan) that was heavily infested with *F. oxysporum* f. sp. *melonis*. This soil was screened to remove stones and trash and stored at 14% moisture in closed cans for at least 3 months before use. At saturation, the water-holding capacity (WHC) was 35-40% moisture by weight. The pH was 6.5.

For greenhouse studies, plants were grown in 1-liter white opaque containers at 25 C in temperature tanks. Aliquots of soil (1,100 g oven-dry basis) were apportioned to each container. The units were irrigated by means of clear plastic (Nalgene) tubes about 15 cm long. The lower end of each tube was closed and ten holes 2 mm in diameter were made along the length. Tubes were placed in the soil diagonally from bottom to top. To reduce evaporation, the containers were usually covered with a plastic top containing two 2-cm diameter holes, one for the plant stem and one for the irrigation tube. Pots were weighed daily and deionized water was added as required. A day-length of 14 hours was maintained using supplemental illumination at 4,300 lux from cool-white fluorescent bulbs. Greenhouse temperature was controlled between 18-22 C.

One experiment was conducted in 1966 in the Belleville field, where there had been severe Fusarium wilt of melon in 1965. Part of the field was planted to soybean and the remainder to corn. Root samples of both soybeans and corn were taken between June 1966 and April 1967. Soil samples for assay were collected with a soil auger at intervals throughout the 20-month experimental period. Assays were begun within 1 day of sampling.

Rhizosphere samples were obtained by shaking a weighed sample (1-2 g) of roots with adhering soil in sterile 500-ml flasks containing 100 ml of sterile distilled water (SDW). After 30 minutes on a reciprocal shaker at 280 cycles per minute, the contents of each flask was filtered through cheesecloth. This filtrate, with plant particles eliminated, was the "rhizosphere soil suspension". Samples of rhizosphere soil suspension were further diluted with 0.1% water agar (WA), and each seeded on three to six plates of assay medium. The amount of rhizosphere soil in a given suspension was determined by calculation after drying a 20-ml sample at 105 C for 12 hours. By subtracting the weight of rhizosphere soil from the original sample weight, the fresh weight of roots in the gross root-soil sample was determined. The results of assays of propagules in the rhizosphere was expressed as numbers per gram fresh weight of root and/or numbers per gram of oven-dry rhizosphere soil.

A standardized soil-dilution-plate method was employed throughout this work. Individual soil samples were thoroughly mixed, and all visible organic particles removed. One gram (oven-dry equivalent) of soil was placed in 100 ml of SDW and mixed for 10 minutes with a magnetic stirrer. Further dilutions were made as required with 0.1% WA. Five-to-ten plates of selective medium were used for each assay.

Root-surface populations were determined on the same roots used for rhizosphere assay after washing nine more times on the shaker (3). Each assay sample consisted of about 300, 2- to 3-mm-long segments cut aseptically from randomly selected washed roots.

Potato-dextrose agar (PDA) with 500 μg/ml Tergitol TMN (trimethylnonanol) at pH 4.2, a selective medium for *Fusarium oxysporum* (3), was used for soil, rhizosphere, and root-surface studies.

Numbers of *F. oxysporum* f. sp. *melonis* in each treatment as distinct from total population of *F. oxysporum* were estimated by index pathogenicity tests on subcultures. A representative group of isolates, usually between 10-40 per sample, were tested in various experiments. If the sample being assayed was from a known high-disease situation, a small index sufficed. Four- to five-day-old cultures of *F. oxysporum* from soil or plant material were transferred to medicine bottles with PDA slants and incubated 7 days at room temperature. Inoculum was prepared by adding 30 ml of deionized water to each culture bottle and shaking for 30-60 seconds to suspend the spores. This inoculum suspension was then used in either of two procedures: (i) the method used by Wensley and McKeen (23) in which roots of seedlings were placed in vials containing spore suspension on a shaker (60 cycles per minute), (ii) the root-dip method in which the roots were dipped in the inoculum and transplanted to 7.6-cm (3-inch) diameter pots of steamed soil. Three 10- to 14-day-old melon seedlings (cultivar, Hale's Best Jumbo) grown in autoclaved vermiculite were used for each isolate. The appearance of each plant (yellow, wilted, or dead) was recorded daily for 15 days in the shaker method and for 3-4 weeks in the root-dip method.

RESULTS.—*Root zone of host plants.*—Root zone activities of *F. oxysporum* f. sp. *melonis* were studied at 16 and 28% moisture (40% and 70% WHC) using wilt-susceptible Hale's Best Jumbo muskmelon. Data were obtained 2, 4, 6, and 8 weeks after planting. After an initial delay, root colonization and propagule numbers of *F. oxysporum* f. sp. *melonis* in the rhizosphere increased with time at both moisture levels, but higher populations occurred at the lower soil moisture (Table 1). No rhizosphere effect was noticed at 2 weeks, and root colonization was detectable only at the lower soil moisture. Disease symptoms had appeared at this time, but the pathogen could be isolated from stems of some symptomless plants growing at the lower soil moisture. The number of propagules of *F. oxysporum* f. sp. *melonis*

TABLE 1. Rhizosphere population of *Fusarium oxysporum* f. sp. *melonis* and root colonization of wilt-susceptible melon cultivar Hale's Best Jumbo grown for 2-8 weeks in naturally infested soil[a] at 25 C, and either 40 or 70% water-holding capacity (WHC)[a]

Time after planting (weeks)	WHC of soil (%)	Propagules (thousands/g)		Root segments colonized (%)
		Fresh root	Rhizosphere soil	
2	40	0.15[b]	0.95	8.8
	70	0.15	0.77	0.0
4	40	33.00	278.00	31.6
	70	14.00	79.00	15.6
6	40	79.00	853.00	72.5
	70	1.60	34.00	14.5
8	40	...[c]	...	...
	70	25.60	158.00	64.0

[a]Population of *F. oxysporum* f. sp. *melonis* in naturally infested soil ranged from 900 to 1,100, and from 700 to 1,000 per gram dry soil in 40 and 70% WHC, respectively.
[b]Average of three replicates.
[c]All plants were dead.

TABLE 2. Comparison of rhizosphere population of *Fusarium oxysporum* f. sp. *melonis* and root colonization of healthy and infected muskmelon plants at 25 C and 70% water-holding capacity (WHC)

Time after planting (weeks)	Propagules in rhizosphere soil (thousands/g)		Root segments colonized (%)	
	Healthy[a]	Infected[b]	Healthy	Infected
2	0	3	0	0
4	3	235	44	4
6	80	100	14	7
8	31	280	51	87

[a]The pathogen could not be isolated from the stem.
[b]Plants were systemically infected with *F. oxysporum* f. sp. *melonis*.

in the rhizosphere was appreciable at 4 weeks with both moisture levels and the pathogen could also be isolated from aerial parts of the plants. Plant wilt symptoms showed at 3-4 weeks in the lower soil moisture treatments, but not until 6-8 weeks in the higher moisture treatments. The lower soil moisture caused growth reduction of the host plant. In this experiment, populations of the pathogen remained relatively constant in nonplanted control soil.

Rhizosphere population and root colonization of systemically infected plants which were either wilted (but not decayed) or apparently healthy (but with the pathogen in the stem) were compared with those of healthy plants (in which the pathogen could not be isolated from stem). Infected plants harbored greater numbers of propagules of *F. oxysporum* f. sp. *melonis* and other fungi in their rhizosphere than did the healthy plants (Table 2).

Microscopic examination of infected roots with adhering soils of artificially inoculated 2-month-old melon plants growing in steamed soil in clay pots revealed heavy sporulation on roots. Scattered or grouped sporodochium-shaped structures with conidia and detached macroconidia were observed. Little mycelium was evident in the surface of infected roots. No such attempts were made with infected plants in naturally infested soil. When wilt-susceptible melons were grown in naturally infested soil in root observation boxes, it was found that large proportions of absorptive roots were killed by *F. oxysporum* f. sp. *melonis* prior to the appearance of wilt symptoms.

Root zone of nonhost plants.—The multiplication and survival of *F. oxysporum* f. sp. *melonis* in the presence of nonhost plants was studied in fields with histories of muskmelon wilt. Roots of soybean, corn, and several species of grasses were collected throughout the year and assayed. Results are summarized in Table 3. *Fusarium oxysporum* f. sp. *melonis* could be isolated from soybean and corn roots throughout the experiment. The percentage of soybean root segments colonized by *F. oxysporum* f. sp. *melonis* was about 21% in the seedling stage and decreased to about 8% for the remainder of the

TABLE 3. The isolation of *Fusarium oxysporum* f. sp. *melonis* from the roots of field-grown soybean and corn at various times after planting[a]

Sample date	Growth stages	Weeks after planting	Root segments colonized (%)	
			Soybean	Corn
June 1966	Seedling	2	21	0
July 1966	Flowering	6	8	3
September 1966	Fruit set	11	6	2
October 1966	Postharvest	16	6	...[b]
April 1967	Plant residues	42	9	7

[a]Howard Gerst Farm, Belleville, Michigan. Population of *F. oxysporum* f. sp. *melonis* in soil was 200 propagules per gram of soil (see Table 5).
[b]No assay.

TABLE 4. Population of *Fusarium oxysporum* f. sp. *melonis* in soil around wilted melons, nonwilted melons, and in soil between rows of melons

	Organism assayed and soil depth sampled (cm)						
	F. oxysporum f. sp. *melonis*			Other *F. oxysporum*			Other fungi
Soil sample source	0-5	5-15	15-30	0-5	5-15	15-30	0-30
Wilted melons	313[a]	37	16	0	9	4	2,440
Healthy melons[b]	11	8	0	9	2	3	440
Between melon rows	0	1	0	28	19	8	395

[a]Hundreds of propagules per gram of soil. Average of three replicates.
[b]*Fusarium oxysporum* f. sp. *melonis* was not isolated from vines.

experiment. There was very low recovery of *F. oxysporum* f. sp. *melonis* and other forms of *F. oxysporum* from actively growing corn, but colonization of corn roots by *F. oxysporum* f. sp. *melonis* tended to increase with age. *Fusarium oxysporum* f. sp. *melonis* could be recovered from undisturbed overwintered roots of both soybean and corn.

Population of *F. oxysporum* f. sp. *melonis* in corn and soybean rhizospheres were too low to be measured reliably with the assay employed. This was due to the low population of *F. oxysporum,* most cultures of which were nonpathogenic to melon, and the populations and high recoveries of other soil fungi.

Different species of grasses were collected from various fields either currently or recently cropped to melon and their roots assayed. The roots of weed grasses (mostly crabgrass) supported the pathogen to some extent (0-8% of root segments colonized by *F. oxysporum* f. sp. *melonis*). Usually roots of grasses in early and active growth stages (which harbored few if any *F. oxysporum*) were apparently not colonized to any extent by that species.

When plantings were made in autoclaved soil infested with chlamydospores of race 2 and 4 of *F. oxysporum* f. sp. *melonis* (4), heavy colonization occurred in roots of peas, soybean, cowpea, and corn; but apparently there was no sporulation, since no increase of the pathogen could be detected in the rhizosphere of these plants. In another experiment, when soybeans were planted in artificially infested steamed soils at different moisture levels 87, 72, 45, and 17% of roots were colonized by *F. oxysporum* f. sp. *melonis* at 30, 40, 60, and 80% WHC, respectively.

The effect of host or nonhost and of a crop-free period on population of Fusarium oxysporum f. sp. melonis in soil.—The amount of *F. oxysporum* f. sp. *melonis* in field soil is influenced by the crop grown. Soil samples were taken from within and between rows at various depths throughout the experiment. After the melon crop had been harvested, the field was ploughed until the following spring (1966). Soil samples were obtained at three depths from row containing melon residues during March 1966. The number of propagules of *F. oxysporum* f. sp. *melonis* per gram of soil were 6,000, 1,200, and 1,800, respectively at 0-2.5, 2.5-7.5, and 7.5-20.0 cm depths. Although more than 60% of the *F. oxysporum* colonies obtained from the surface soil (0-2.5 cm) were pathogenic to melon, the proportion was lower at the other levels. The increased populations on the soil surface were accounted for by sporulation of *F. oxysporum* f. sp. *melonis* on infected vines in late summer and sloughing of infected stem tissues. The increase in the lower levels was the result of sporulation on roots.

TABLE 5. Population of *Fusarium oxysporum* f. sp. *melonis* in soil of a single field at intervals during a 20-month period[a]

Sample date	Crop or residue	Propagules/g soil (no.)
August 1965	Melon plants (wilted)	9,100
January 1966	Melon residue (under snow)	3,300
March 1966	Melon residue (thawing)	3,000
June 1966	Soybean plants (seedling)	200
October 1966	Soybean residue	200
April 1967	Soybean residue	200

[a]Howard Gerst Farm, Belleville, Michigan. Soil samples from August 1965 to March 1966 were collected within melon rows. Samples from June 1966 to April 1967 were from soybean rows.

The distribution of propagules of the pathogen was studied at the Michigan State University Botany Farm in the fall of 1966. Before harvest, a few wilted and nonwilted plants were marked and tissue isolations were made. No *F. oxysporum* f. sp. *melonis* could be isolated from nonwilted plants. A week after harvest (October 1966) soil samples were taken from around wilted and nonwilted plants or between rows and at three depths (0-5, 5-15, and 15-30 cm). More colonies of *F. oxysporum* f. sp. *melonis* were obtained from soil taken around wilted than nonwilted plants, and least from soil between the rows (Table 4). Soil around wilted plants had 20 times as many *F. oxysporum* f. sp. *melonis* propagules as that around nonwilted plants, and about 500 times as much as intra-row soils. Both diseased and nonwilted plants increased the pathogen considerably in comparison to control soils. Of the *F. oxysporum* colonies obtained around diseased plants, 97% were pathogenic to melon, while from control soils only 1% was pathogenic. The highest populations were obtained from surface soil.

Population changes of *F. oxysporum* f. sp. *melonis* were also studied during a 20-month period, both in the presence and absence of susceptible host plants. Soil samples were obtained 6 times from the top 10-cm soil layer of a single field between August 1965 and April 1967 (Table 5). The presence of susceptible melon increased *F. oxysporum* f. sp. *melonis*. Maximum numbers of propagules were reached in August when most melons were badly infected with the pathogen. By January 1966, the pathogen population had decreased about 30% from its August high and subsequently remained unchanged until early spring. This indicated that the population of *F. oxysporum* f. sp. *melonis* remained almost unchanged

despite a period of freezing. In early June, half of the field was planted with soybean (cultivar Harosoy 63) and the other half with corn. Shortly after planting (June 1966), the populations of *F. oxysporum* f. sp. *melonis* in samples of soil from between rows of corn and soybean had dropped considerably from the January population, and then remained relatively constant to the end of the experiment (April 1967). The ratio of pathogenic to nonpathogenic *F. oxysporum* decreased after melon residues had decomposed. In the earlier period (August 1965 to March 1966) more than 50% of the *F. oxysporum* isolates were pathogenic to melon, but later (June 1966 to April 1967), populations contained only about 12% of the *F. oxysporum* f. sp. *melonis* forms. The sharp drop in population was thought to be due to loss of viability of propagules following the decomposition of most of the infected melon residues during early June.

Soil samples were collected within and between rows of soybeans and corn in April 1967 to compare the effect of those two crops on changes of *F. oxysporum* f. sp. *melonis* in soil. Populations from these were then compared with those determined in the initial assays of the field made in June 1966. *Fusarium oxysporum* f. sp. *melonis* populations both within and between soybean rows, were similar and remained unchanged throughout the experiment. None of the 40 isolates of *F. oxysporum* obtained from within corn rows in April 1967 was pathogenic to susceptible melons.

DISCUSSION.—The present investigation revealed that only the host plants contribute greatly to the increase of pathogen inoculum in nature. Some of the nonhost plants (symptomless carriers), however, are important perhaps in activating germination of *F. oxysporum* f. sp. *melonis* propagules and colonization of roots. It appears that the association of *F. oxysporum* f. sp. *melonis* with nonhost plants is in the form of commensalism which ensures a continuous survival in the absence of a susceptible host. The importance of nonhosts as symptomless carriers have been demonstrated in other fusarial diseases (1, 9, 17).

The present study revealed that nonhost plants such as soybean and possibly other legumes, are more favorable substrates for *F. oxysporum* f. sp. *melonis* than grasses (such as corn and crabgrass) at least in the early and active stages of growth. The importance of root exudates on spore germination of *Fusarium* spp. and its subsequent activities in the root zone have been emphasized (17, 18). Schroth and Hildebrand (18) have indicated that germination of propagules in the rhizosphere is relatively nonspecific. The nutritional value of root exudates which enable certain root pathogens to overcome general soil fungistasis is of major importance. Root exudates are qualitatively different in different plants and under various conditions (18). Roots of some nonhost plants serve as a better substrate for colonization of given organisms. In this study, it was shown that soybean was better than corn under field conditions. Failure of propagules of *F. oxysporum* f. sp. *melonis* to increase in the rhizosphere of nonhosts, and failure of the fungus to become established on the root surface of certain plants, may be important phenomena applicable to biological control of the pathogen under natural conditions. In this work, corn and some other grasses are representative of such nonhosts. Mechanisms responsible for the decrease in population of *F. oxysporum* f. sp. *melonis* propagules in soil near these plants were not investigated. We might speculate that some nonhost plants are able to stimulate germination of nearby propagules and yet resist root colonization. The germinated spore would then shortly lyse in the soil environment.

Soil moisture influenced disease development, root colonization, and rhizosphere population by *F. oxysporum* f. sp. *melonis*. Although higher soil moisture (70% WHC) delayed the onset of the disease, it did not prevent it. Lower soil moisture levels (40% WHC) increased disease development and rhizosphere population in host plants. It also increased root colonization in both host and nonhost plants. These increases appeared to have resulted from physiological changes brought about by reduced water. Increases of soil microorganisms in the rhizosphere of plants growing at lower soil moisture have been attributed to increased exudation and root hair formation (10, 15, 19). In the present experiments, wilted melon plants supported greater numbers of other soil microorganisms in the rhizosphere of infected than in that of healthy plants. This is probably due to increased exudation as a result of injuries and the presence of morbid roots previously infected by the pathogen. Miller (13) found that growth of the melon was less at lower soil moisture levels and concluded that lower moisture affected disease severity through predisposition. Crozier (8) concluded that the major factor in the appearance of sudden wilt (Fusarium wilt) of muskmelon was drought in many of the melon-growing areas of New York. Other fusarial diseases are also reported to be favored by dry soil, but the results on some wilt fusaria are not conclusive and difficult to interpret (6, 7, 21).

Soil populations of *F. oxysporum* f. sp. *melonis* increased in the presence of a susceptible host and decreased in its absence. Maximum population was obtained when most of the melon plants were severely infected by the pathogen. Low winter temperature did not much effect the population of the pathogen, but it declined sharply in spring. This drop in population appears to be due to progressive decomposition of infected melon residue, which perhaps is an important source of inoculum in the field. Although the origin of colonies of *F. oxysporum* f. sp. *melonis* on plates were not studied, the possibility of the survival of naked propagules such as conidia during cold periods can not be ruled out. Warcup (22) indicated that in soil assays *Fusarium* spp. was one of the small groups of fungi more often isolated from humus particles than as naked spores, and that the spores were resistant types. It is, therefore, possible to assume that the amount of pathogen survival in soil appears to depend on its association with plant materials that are at least partially intact. Complete decomposition of invaded tissues reduces chances of the propagule survival if the organism does not soon become reestablished in another nearby substrate. Chlamydospores are considered to be the principal survival propagules of *F. oxysporum* f. sp. *melonis* (2, 12), but they also cannot survive long in the soil environment if not sheltered within the plant tissues (2). Humus particles or especially intact tissues are, therefore, important resident substrates which shelter the chlamydospores against long-term environmental stress.

Recovery of *F. oxysporum* f. sp. *melonis* from partially disintegrated overwintered tissues of nonhost plants under field conditions demonstrates the importance of decay-resistant tissues in the biology of the pathogen.

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