Colonization of Crop Residue by *Fusarium oxysporum* f. sp. *melonis* and Other Species of *Fusarium*

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ABSTRACT

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Colonization of decomposing roots, and shoot tissue buried in field soil, by the muskmelon wilt pathogen race 2 of *Fusarium oxysporum* f. sp. *melonis* was quantified as colony-forming units per gram of tissue. Colonization of the same substrates by *F. equiseti*, *F. solani*, and nonpathogenic *F. oxysporum* was also quantified. *F. o. melonis* was isolated from roots of the following seven crops both before and 5 days after shoots were severed at the soil line: the muskmelon cultivar PMR-45 (susceptible to Fusarium wilt), the muskmelon cultivar Greenflesh Honey Dew (resistant to Fusarium wilt under field conditions), alfalfa, tomato, sugar beet, cotton, and wheat. The proportion of total root colonization represented by each of the four fungi was the same before and after shoot removal except that, under some conditions, *F. equiseti* represented a significantly greater proportion of total colonization after shoot removal. Averaged over seven different residue sources (i.e., crops), population densities of *F. o. melonis* on buried shoot tissue were greater than those of nonpathogenic *F. oxysporum*. This difference could not be attributed to differences in soil inoculum density of the two fungi or to prior colonization of the shoot tissue by *F. o. melonis*.

Additional keywords: soilborne pathogen.

Formae speciales of *Fusarium oxysporum* Schlectend. ex Fr. cause vascular wilt diseases affecting a large number of economic hosts (16). These pathogens are known to persist through long intervals between susceptible crops (3,6). Persistence in the absence of a susceptible host has been attributed to the production of long-lived chlamydospores (6,14,17), the colonization of nonsusceptible crops (9,10,20), and the colonization of wounded tissue and crop residue (1,15).

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All these modes of persistence have been documented for *Fusarium oxysporum* f. sp. *melonis* W. C. Snyder & H. N. Hans., which causes Fusarium wilt of muskmelon (*Cucumis melo* L.). Fusarium wilt is an important disease affecting melon production in the San Joaquin Valley of California (8) and throughout North America (5,13). In Michigan, *F. o. melonis* has been shown to colonize roots of corn and soybeans and residue derived from both crops (1,2). In California, *F. o. melonis* colonizes living roots of at least six different crops commonly grown in rotation with susceptible cultivars (7); however, we have no information concerning the ability of this pathogen to colonize residue of these crops.

Numerous researchers have shown that formae speciales of *F. oxysporum* can colonize crop residue (1,15,18,21). However, for saprophytic growth to be important in the long-term persistence of a pathogen, the pathogen must compete effectively with other soilborne fungi. This study was undertaken to characterize the ability of race 2 of *F. o. melonis* to compete with *F. equiseti* (Corda) Sacc., *F. solani* (Mart.) Sacc., and nonpathogenic strains of *F. oxysporum* as a colonizer of decomposing roots and buried shoot tissue.

MATERIALS AND METHODS

Plant materials and growth conditions. The following crops were included in this study: wheat (*Triticum aestivum* L. 'Yecora Rojo'), alfalfa (*Medicago sativa* L. 'Moapa 69'), sugar beet (*Beta vulgaris* L. 'SS-Y1'), cotton (*Gossypium hirsutum* L. 'SJ-2'), tomato (*Lycopersicon esculentum* Mill. 'UC 82'), a western shipping-type muskmelon susceptible to Fusarium wilt (*C. melo* 'PMR 45-SJ'), and Honey Dew muskmelon (*C. melo* 'Greenflesh Honey Dew'). Greenflesh Honey Dew is susceptible in a root dip assay (23) but does not develop Fusarium wilt in the field. Plants were grown from seed under greenhouse conditions in a Panhill clay loam soil naturally infested with race 2 of *F. o. melonis*. Before seeding, this soil was combined with sterile coarse sand (3:1, soil:sand) to improve drainage. Plants were grown in 150-cm^3 pots, each of which contained approximately 300 g of the soil and sand mixture. Pots were set in clay saucers, which were filled with water whenever the soil surface became dry. Unless otherwise indicated, plants were maintained in a greenhouse with a temperature regime of 28 ± 8 C during the day and 18 ± 3 C at night. Mean colony-forming units per gram (cfu/g) of air-dried soil (± standard errors), estimated by dilution plating (7), were as follows: *F. o. melonis*, 270 ± 25; nonpathogenic *F. oxysporum*, 250 ± 20; *F. equiseti*, 390 ± 55; *F. solani*, 685 ± 160.

Colonization of roots. Roots of all seven crops were sampled when plants were 4–5 wk old. The entire root system was harvested from each pot, except that roots growing against the bottom or sides of the pot were cut off and not included in the sample. Soil was removed from roots with repeated washings in sodium hexametaphosphate (7). Washed roots were blotted dry, weighed, suspended in 50–75 ml of sterile distilled water, and homogenized in a blender for 30 sec. One milliliter of undiluted root homogenate was spread over the surface of Komada's selective medium (11) and amended with 1 ml of Tergitol NP-10 (Sigma Chemical Co., St. Louis, MO) per liter of medium (KM). Plates of KM were also inoculated with 1 ml of both 1:10 and 1:100 dilutions of each root homogenate. Plates were incubated for 6 days, and *Fusarium* spp. were identified based on colony morphology on KM (7). These plates were used to estimate the number of colony-forming units per gram of root tissue represented by *F. o. melonis, F. equiseti, F. solani*, and nonpathogenic *F. oxysporum*.

The abundance of these fungi was estimated before and 5 days after shoots were severed at the soil line. After shoot removal, the soil surface was covered with coarse sand. Water was supplied from below as needed to maintain soil moisture near field capacity. Roots from which shoots were removed (detached roots) were taken from two replicate pots of each crop. For comparison, living (attached) root samples were taken from two different pots of each of the same seven crops; these plants were of the same age as those from which shoots were removed. Average fresh weights of the detached and attached root samples ranged from 0.3 to 1.8 and 0.7 to 4.6 g per replicate, respectively. Roots were harvested, washed, and blended as previously described. This experiment was arranged in a completely randomized design and repeated once. Data from both experiments were included in a two-way analysis of variance (ANOVA) to test for significant differences in population densities of each fungus on attached as compared with detached roots of each crop. A three-way ANOVA was used to evaluate differences in colonization of attached and detached roots by each fungus, averaged over all seven crops in both experiments.

The muskmelon cultivar PMR-45 and one of the nonsusceptible crops (tomato) were also used in additional experiments to evaluate the relative abundance of *F. o. melonis, F. equiseti, F. solani*, and nonpathogenic *F. oxysporum* before and after shoot removal. Half of the shoots in each pot were severed at the soil line, and 5 days later a sample of both attached and detached roots was recovered from each pot. Root samples were washed, homogenized, and assayed as previously described. Four replicates were included for each crop in a randomized complete block design, with each pot representing a block. The experiment was repeated, and a three-way ANOVA was used to test for significant differences in the proportion of total colonization represented by each fungus on attached and detached roots.

Colonization of detached roots was examined by burying washed roots in field soil. Roots from 5-wk-old seedlings (17.5 and 14.5 g fresh weight for PMR-45 and tomato, respectively) grown in Panhill clay loam soil were washed and bulked as a single sample for each crop. Four subsamples were homogenized and assayed as previously described. Four additional subsamples were buried in each of four 150-cm^3 pots of Panhill clay loam field soil. After 5 days in moist soil at 23 ± 2 C, roots were removed from soil, washed, and assayed. There were four replicates in a completely randomized design. The experiment was repeated, and data from both experiments were analyzed in a two-way ANOVA.

Colonization of buried shoot tissue. Shoot material was taken from 5-wk-old seedlings of all seven crops, buried in Panhill clay loam soil, and incubated as previously described for roots. Buried shoot material was largely intact, with cuts made only as required to allow for complete coverage of shoot tissue (5–10 g per sample) with soil in the confines of a 150-cm^3 pot. Before burial, a cross section was taken from the lowest portion of each shoot, surface-disinfested, and plated on KM. Surface-disinfestation was accomplished by rinsing with tap water to remove any adhering soil, followed by sequential treatment with 70% ethanol for 30 sec and 0.5% sodium hypochlorite for 1.5 min.

Buried shoots were recovered 5 days later, washed in the same manner as the root samples, blotted dry, weighed, and homogenized in a blender. The resultant suspensions were plated on KM. Pots containing the buried shoots were incubated in an unlighted growth chamber at 24 ± 3 C. This experiment included four replicates in a completely randomized design. When the experiment was repeated, pots containing buried shoots were incubated in a greenhouse with a temperature regime of 28 ± 6 C during the day and 20 ± 2 C at night. For each experiment, ANOVA was used to test for significant differences in the population densities of *F. o. melonis, F. equiseti, F. solani*, and nonpathogenic *F. oxysporum* on buried shoots of each crop; differences in fungal population densities averaged over all seven crops were evaluated in a two-way ANOVA. A three-way ANOVA was used to analyze data from both experiments.

The ability of *F. o. melonis* to colonize field-grown shoot tissue was examined with leaves of cotton and the muskmelon cultivar PMR-45 collected at the University of California's West Side Field Station in Fresno County. Fully expanded leaves were collected in the field and transported to the laboratory in plastic bags at approximately 15 C. An experimental treatment consisted of three disks (16.5 cm^2 per disk) from a single leaf buried in Panhill clay loam soil in a 150-cm^3 pot. There were four replicates, and the experiment was repeated once. The soil in which leaf

disks were buried was maintained near field capacity in a growth chamber at 25 C during a 12-hr light period and at 18 C during a 12-hr dark period. Four days later, the leaf disks were recovered, washed, homogenized, and assayed as previously described for greenhouse-grown shoot tissue.

When the leaf disks were buried, the petiole of each leaf was surface-disinfested and placed on KM to assay for the presence of *Fusarium* spp. Additional disks were removed from each leaf and placed directly on water agar plates. These plates were incubated at 22 ± 3 C under 12 hr of fluorescent light per day for 5–7 days. Leaf disks were then examined under 10–140× to identify fungi sporulating on the leaf tissue and surrounding agar.

Data analysis. Before statistical analysis, colonization data expressed as colony-forming units per gram were log-transformed, and data expressed as proportions were transformed to the arcsine of the square root of the proportion; nontransformed data are reported. Statistical computations were performed with NCSS version 5.0 (J. L. Hintze, Kaysville, UT) on an IBM PC-AT.

RESULTS

Colonization of roots. Root samples taken 5 days after shoot removal included both discolored and apparently healthy roots. Thus, these detached roots represented a composite of roots in various stages of decomposition. With incubation periods longer than 5 days, root decomposition was so extensive that adequate samples frequently could not be recovered.

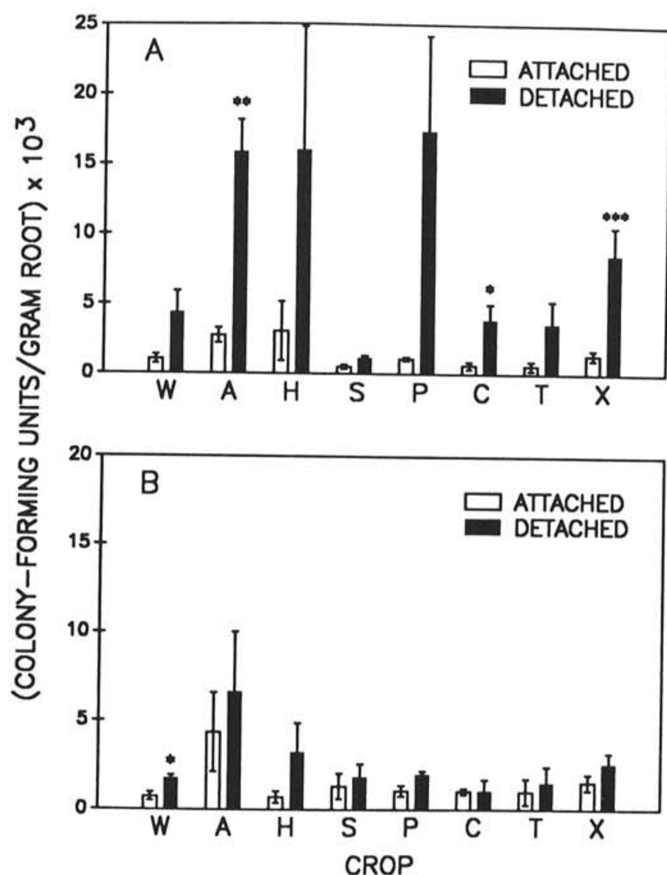

Fig. 1. Colonization of attached and detached roots by *Fusarium oxysporum* f. sp. *melonis*, **A**, and nonpathogenic *F. oxysporum*, **B**. Detached roots were taken from plants 5 days after shoot removal. Each bar represents the mean of four replicates of a single crop (W = wheat, A = alfalfa, H = Greenflesh Honey Dew, S = sugar beet, P = muskmelon cultivar PMR-45, C = cotton, T = tomato, and X = average for the seven crops). Mean population densities on attached roots were significantly different from those on detached roots of the same crop at $P = 0.05$ (*), $P = 0.01$ (**), or $P = 0.001$ (***). Vertical lines represent twice the standard error.

Species of *Fusarium* were the predominant fungi recovered from root suspensions plated on KM. On this medium, *F. o. melonis* could be distinguished from nonpathogenic strains of *F. oxysporum* on the basis of colony morphology. Pathogenicity tests were conducted to confirm this observation, and the results have been reported elsewhere (7). Other fungi identified on isolation plates, in order of decreasing frequency, were *Penicillium* spp. (found on fewer than 10% of the plates), *Cylindrocarpon* spp., *F. proliferatum* (T. Matsushima) Nirenberg, *Trichoderma* sp., and *Aspergillus* spp.

Because there were no significant experiment × treatment interactions, data from two experiments were combined to give the mean values shown in Figure 1A and B. Significantly larger population densities of *F. o. melonis* were recovered from detached than from attached roots of alfalfa ($P = 0.01$) and cotton ($P = 0.05$) (Fig. 1A). Averaged over all seven crops, significantly larger population densities of *F. o. melonis* were recovered from detached than from attached roots ($P = 0.001$).

Nonpathogenic strains of *F. oxysporum* were significantly more abundant on detached than on attached roots of wheat ($P = 0.05$), but, on all other crops, no significant difference was found between attached and detached roots (Fig. 1B). No significant differences were found in the population densities of *F. equiseti* or *F. solani* between attached and detached roots of any crop evaluated individually or for the average population densities on all seven crops (data not shown).

No significant effects of root condition (attached versus detached) were found on the proportion of total colonization represented by *F. o. melonis*, *F. equiseti*, *F. solani*, or nonpathogenic *F. oxysporum* in the muskmelon cultivar PMR-45 (Fig. 2A) and tomato (Fig. 2B). Similar results were obtained when this experiment was repeated, and no significant experiment × treatment interactions occurred. Consequently, the mean

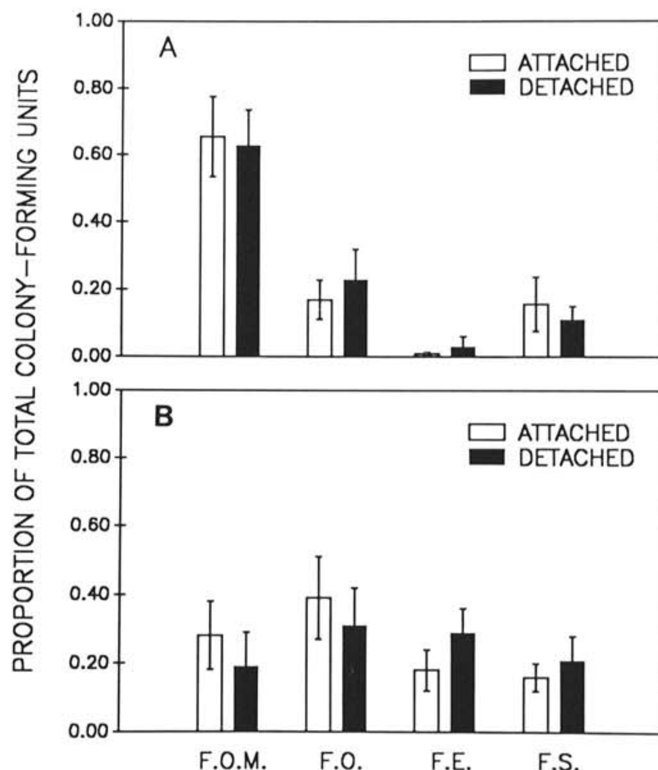

Fig. 2. Colonization of attached and detached roots of muskmelon cultivar PMR-45, **A**, and tomato, **B**, by *Fusarium oxysporum* f. sp. *melonis* (F.O.M.), nonpathogenic strains of *F. oxysporum* (F.O.), *F. equiseti* (F.E.), and *F. solani* (F.S.). Detached roots were taken from plants 5 days after shoot removal; attached roots were taken from intact plants of the same age. Each bar corresponds to the mean proportion of total colonization by *Fusarium* spp. represented by one of the four fungi; mean of eight replicates. Vertical lines represent 2 × the standard error.

proportions shown in Figure 2 are based on data from both experiments.

F. equiseti represented a significantly ($P = 0.05$) greater proportion of total colonization on detached buried roots as compared with attached roots in both the muskmelon cultivar PMR-45 (Fig. 3A) and tomato (Fig. 3B). None of the other fungi represented a significantly different proportion of total colonization between attached and detached buried roots. Similar results were obtained when the experiment was repeated, and, because no significant treatment × experiment interactions occurred, data from both experiments were averaged to obtain the mean values shown in Figure 3.

Colonization of buried shoot tissue. After 5 days in moist soil in a growth chamber, significantly ($P = 0.05$) greater population densities of *F. o. melonis* relative to nonpathogenic *F. oxysporum* were recovered from residue of sugar beet, alfalfa, and tomato (Fig. 4). Averaged over all seven residue types, the population density of *F. o. melonis* was significantly ($P = 0.01$) greater than that of nonpathogenic *F. oxysporum*. Residue source had a significant effect on total colonization levels, but the residue source × colonizer (pathogen or nonpathogen) interaction was not significant ($P = 0.05$). Isolations from shoot tissue before burial indicated no colonization by any species of *Fusarium*.

Results from the residue colonization test conducted in the greenhouse (Fig. 5) were similar to those from the growth chamber experiment. However, a significant difference ($P = 0.001$) was found between the experiments conducted in different locations. This difference could be attributed to larger final populations of both pathogen and nonpathogen in the greenhouse trial because of more extensive tissue decomposition at the higher greenhouse temperatures. The location × colonizer interaction was not significant, indicating that the difference between experiments did not differentially affect saprophytic growth by *F. o. melonis* and nonpathogenic *F. oxysporum*. However, the residue source × location interaction was significant ($P = 0.05$), and, consequently, fungal population densities were not averaged over all types of residue across locations.

F. equiseti was generally the most abundant of the four fungi on shoot residue (data not shown). *F. equiseti* was recovered at significantly higher densities than the other three species of *Fusarium* on residue from sugar beet, wheat, cotton, and tomato ($P = 0.01$).

Disks taken from field-grown leaves of both cotton and the muskmelon cultivar PMR-45 and incubated for 4 days in moist soil were colonized more extensively by nonpathogenic *F. oxysporum* than by *F. o. melonis* (data not shown), but these

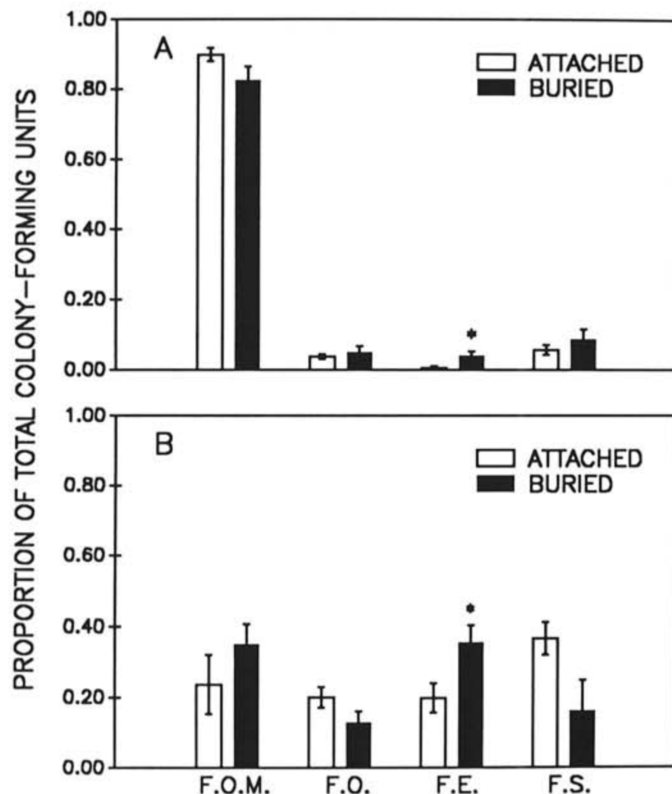

Fig. 3. Colonization of attached and detached roots of muskmelon cultivar PMR-45, **A**, and tomato, **B**, by *Fusarium oxysporum* f. sp. *melonis* (F.O.M.), nonpathogenic *F. oxysporum* (F.O.), *F. equiseti* (F.E.), and *F. solani* (F.S.). Attached roots were washed and assayed immediately. Detached roots were washed and then buried in field soil; 5 days later, they were removed, washed, and assayed. Each bar corresponds to the mean proportion of total colonization by *Fusarium* spp. represented by one of the four fungi, mean of eight replicates. Mean proportions of colonization on attached as compared with detached roots differed significantly at $P = 0.05$ (*). Vertical lines represent 2 × the standard error.

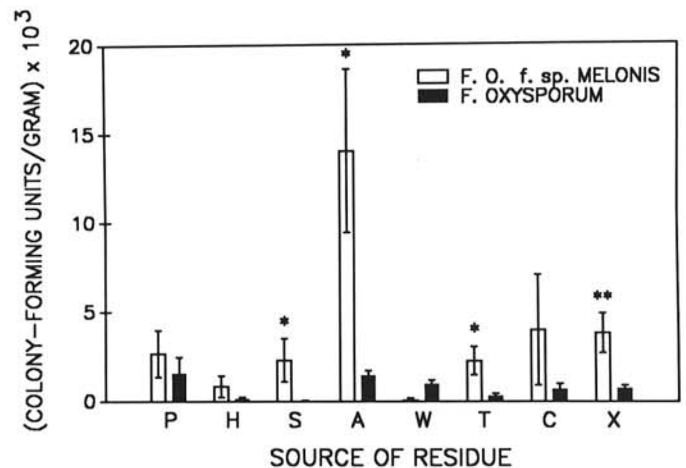

Fig. 4. Colonization of shoot tissue of seven crops (P = muskmelon cultivar PMR-45, H = muskmelon cultivar Greenflesh Honey Dew, S = sugar beet, A = alfalfa, W = wheat, T = tomato, C = cotton, and X = average for seven residue sources) by *Fusarium oxysporum* f. sp. *melonis* and nonpathogenic *F. oxysporum* in a growth chamber held at 24 ± 3 C. Each bar represents the mean of eight replicates. Mean population densities of *F. o. melonis* were significantly different from those of nonpathogenic *F. oxysporum* on the same type of residue at $P = 0.05$ (*) or $P = 0.01$ (**). Vertical lines represent 2 × the standard error.

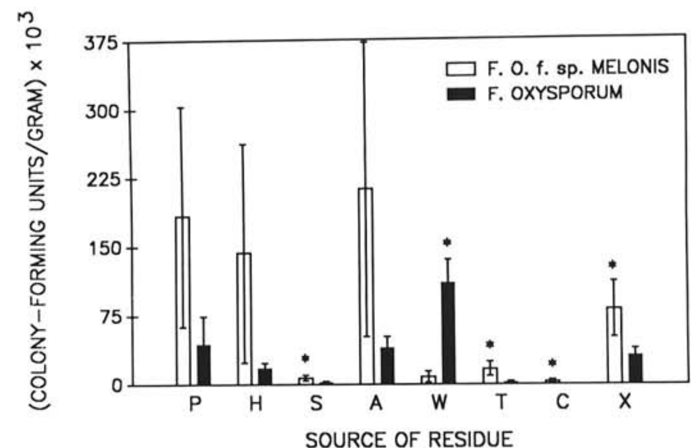

Fig. 5. Colonization of shoot tissue of seven crops (P = muskmelon cultivar PMR-45, H = muskmelon cultivar Greenflesh Honey Dew, S = sugar beet, A = alfalfa, W = wheat, T = tomato, C = cotton, and X = average for seven residue sources) by *Fusarium oxysporum* f. sp. *melonis* and nonpathogenic *F. oxysporum* under greenhouse conditions. Each bar represents the mean of eight replicates. Mean population densities of *F. o. melonis* were significantly different from those of nonpathogenic *F. oxysporum* on the same type of residue at $P = 0.05$ (*). Vertical lines represent 2 × the standard error.

differences were not significant. Isolation from petioles of the sampled leaves indicated no prior colonization by either *F. o. melonis* or nonpathogenic strains of *F. oxysporum*. Leaf disks incubated on water agar revealed a diversity of imperfect fungi, including *Alternaria alternata* (Fr. ex Fr.) Keiss., seen on every leaf disk and, in order of decreasing frequency, *Ulocladium* sp., *Stemphylium* sp., *Cladosporium* sp., *Penicillium* sp., and *Aspergillus* sp.

DISCUSSION

Nonpathogenic strains of *F. oxysporum* have been described as aggressive saprophytes (15,19,22), whereas pathogenic strains have been reported as both poor and effective saprophytes (18,20,21). It has been suggested that, as specialized pathogens, formae speciales of *F. oxysporum* will generally be less competent saprophytes than nonpathogenic fungi (6). However, data to support this hypothesis are relatively scarce. Direct comparisons between pathogenic and nonpathogenic strains of *F. oxysporum* are often problematic, because pathogenicity tests are required to distinguish most formae speciales from nonpathogenic strains.

Smith and Snyder used colony morphology in culture to distinguish *F. oxysporum* f. sp. *vasinfectum* (Atk.) W. C. Snyder & H. N. Hans. from nonpathogenic strains isolated from soil and plant material in the San Joaquin Valley of California (20). They found that *F. o. vasinfectum* was generally more abundant in barley tissue fragments than were nonpathogenic strains of *F. oxysporum*, even though soil populations of the nonpathogen were greater than those of the pathogen. In an earlier study, Nash and Snyder (15) assessed the frequency of *F. o. vasinfectum* and nonpathogenic *F. oxysporum* as secondary invaders of bean root lesions in soil naturally infested by these fungi; the pathogen was isolated from 10% of the lesions examined, whereas 4.5% were colonized by nonpathogens. In this case, pathogen propagules in the soil outnumbered those of the nonpathogens.

We have shown that *F. o. melonis* is capable of colonizing detached roots and buried shoot tissue of both susceptible and nonsusceptible crops. Although the population density of *F. o. melonis* differed on residue of the six nonsusceptible crops, these differences were influenced by rates of tissue decomposition and, therefore, may not reflect comparable differences in the amount of inoculum each crop would contribute to soil populations of the pathogen. Differential rates of survival in the colonized tissue would also influence the amount of carryover inoculum in different sources of residue.

The most important conclusion from our study is that *F. o. melonis* is saprophytically competitive with nonpathogenic strains of *F. oxysporum*. On roots allowed to decompose in situ and on washed roots buried in field soil, *F. o. melonis* grew or, at least, persisted to the same extent that nonpathogenic *F. oxysporum* did. On shoot tissue, *F. o. melonis* was at least as abundant as nonpathogenic strains of *F. oxysporum* on six of the seven crops tested. This result cannot be attributed to prior colonization of the shoot tissue by the pathogen, nor can it be explained by a greater abundance of propagules of *F. o. melonis* in the soil, because the soil population density of each fungus was nearly identical.

Our interpretation of the data is based on the assumption that colony-forming units per gram of tissue is an unbiased measure of the extent of tissue colonization by *F. o. melonis* and nonpathogenic *F. oxysporum*, which is probably a valid assumption, provided that results are not influenced by differential rates of sporulation. Direct microscopic observations of isolation plates indicated that over 90% of the colonies of both *F. o. melonis* and nonpathogenic *F. oxysporum* were intimately associated with, and presumably originated from, plant tissue pieces (data not shown). Thus, colonies arising directly from spores appeared to represent a small fraction of those counted on isolation plates; consequently, if a differential rate of sporulation had occurred, it would have had a correspondingly small effect on our results.

Mature field-grown leaves commonly carry propagules of numerous saprophytic fungi (4), which are capable of colonizing decomposing tissue. For this reason, *F. o. melonis* may colonize shoot tissue less extensively under field conditions than the data from our greenhouse experiments would suggest. However, we have shown that *F. o. melonis* is capable of colonizing leaf tissue in the presence of a diverse foliar mycoflora and remains competitive with nonpathogenic *F. oxysporum* under these conditions.

Garrett (6) suggested that some characteristics required to confer a high degree of competitive saprophytic ability will be lost by vascular wilt pathogens. If *F. o. melonis* suffers from inherent deficiencies as a saprophyte, perhaps these deficiencies were offset by nutritional factors, reflecting age differences between propagules of the pathogen and nonpathogens. The soil used in our experiments was collected in 1988 from a field cropped to cotton the preceding year. In 1986, a muskmelon crop in this field was devastated by Fusarium wilt. Thus, most of the pathogen propagules in this soil probably were produced in 1986. In contrast, the soil population of nonpathogenic *F. oxysporum*, presumably, would be represented by propagules of a much broader age range. Such a difference in age may result in pathogen propagules being ensconced within relatively large pieces of plant tissue, providing them with a superior food base (12). However, this distinction should diminish with time after a susceptible melon crop, as the age distribution of pathogen propagules becomes progressively more like that of the nonpathogens.

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