Characterization of Pathogenic Races of *Fusarium oxysporum* f. sp. *melonis* Causing Fusarium Wilt of Melon in New York

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ABSTRACT

Zuniga, T. L., Zitter, T. A., Gordon, T. R., Schroeder, D. T., and Okamoto, D. 1977. Characterization of pathogenic races of *Fusarium oxysporum* f. sp. *melonis* causing Fusarium wilt of melon in New York. Plant Dis. 81:592-596.

Forty-six isolates of *Fusarium oxysporum* f. sp. *melonis* obtained from soil samples throughout melon-producing areas in New York State were identified on the basis of pathogenicity and colony morphology. Physiological races 1 and 2 were identified by their reaction on a set of differential melon cultivars. Race 1 was widely distributed, occurring in six of the seven New York counties surveyed. Twenty-seven of the 28 race 1 isolates were associated with vegetative compatibility group (VCG) 0134, whereas one was incompatible with all known VCGs of *F. oxysporum* f. sp. *melonis*. Twelve out of 18 race 2 isolates were associated with VCG 0131, and occurred in four counties in eastern and western New York. Five isolates of race 2, associated with VCG 0130, were recovered from a farm in Washington County, as was a single race 2 isolate which was incompatible with all known VCGs of *F. oxysporum* f. sp. *melonis*. Restriction fragment length polymorphisms in the nuclear DNA revealed variability among the isolates examined, but race 1/VCG 0134 isolates from New York and Maryland were identical or nearly so, as were race 2/VCG 0131 isolates from the two states. These findings suggest a close relationship between the populations of *F. oxysporum* f. sp. *melonis* in New York and Maryland. Race 2 isolates were more virulent than race 1 isolates, based on the number of days to first symptoms and death of melon seedlings.

Additional keywords: cantaloupe, *Cucumis melo*, muskmelon

Fusarium wilt of melon (*Cucumis melo* L.) is caused by the fungus *Fusarium oxysporum* Schlechtend.:Fr. f. sp. *melonis* W. C. Snyder & H. N. Hans. Identification to forma specialis is dependent upon a pathogenicity assay on a susceptible melon cultivar such as Top Mark. Of the seven formae speciales attacking cucurbits, *F. oxysporum* f. sp. *melonis* is one of the most important on a worldwide scale (9).

Four races of Fusarium wilt infecting melons have been designated 0, 1, 2, and 1,2 (18). Two genes for resistance, *Fom 1* and *Fom 2*, are currently used to identify races of the pathogen (22). Race 2 predominates in the United States, and was the only race known in North America until 1985, when race 1 was discovered in Maryland (3). Race 0 was found in Texas in 1986 (13). More recently, race 1 was identified in New York (23) and race 1,2 in Maryland (1).

Once introduced into a field, *F. oxysporum* f. sp. *melonis* can remain indefinitely, even after rotation to nonsusceptible crops (4). The fungus survives as chlamydospores, and is capable of colonizing crop residue and roots of most crops likely to be grown in rotation with melon (4). It can enter the host through root tips, primarily in the area of elongation, and is aided by wounding (14). As a result of the persistence of the pathogen in the soil, the disease is best controlled with cultivars that carry multiple resistance (11,16,21).

Currently, eight vegetative compatibility groups (VCGs) are recognized in the forma specialis *melonis* worldwide. Some VCGs are associated with one or more physiological races (6); in Europe, all four races of *F. oxysporum* f. sp. *melonis* have been associated with VCG 0134. Because the recently identified isolates of races 1 and 1,2 in North America were associated with VCG 0134, which was previously unknown in North America, it seems likely these new races were introduced from Europe, where VCG 0134 is common (7).

The principal objective of this project was to identify the race or races of *F. oxysporum* f. sp. *melonis* in the melon-producing areas of New York state. Because the survey revealed the occurrence of race 1, not previously known in New York State,

we sought to make a preliminary assessment of the population structure of *F. oxysporum* f. sp. *melonis* to gain a better understanding of the origin of this new race in the state. A portion of this study has previously been reported (19,24).

MATERIALS AND METHODS

Soil survey and isolation of *F. oxysporum*. Three hundred ninety soil samples were collected in June and July 1993 from three geographical regions of New York State; eastern (Columbia, Rensselaer, Schoharie, and Washington counties), central (Onondaga County), and western (Erie and Niagara counties) (Fig. 1). For each sample, approximately 500 g of soil was collected at a depth of 10 to 20 cm in an area of 1 m² using a soil-sampling probe. The probe was dipped in alcohol and flamed after each sampling to avoid contamination. Sampling sites were areas where melons were grown during 1991 to 1993; 10 to 20 samples were taken per field. A repeating W-shaped pattern was used to adequately cover a field.

Each soil sample was assayed by transplanting 10-day-old seedlings of the susceptible melon cv. Top Mark into 7.5-cm clay pots. Plants were maintained in a greenhouse at 27 to 29°C, day, and 18 to 24°C, night. Seedlings were observed daily for symptom development. Those exhibiting yellowing or wilting were uprooted and surface-disinfested with a 1:10 dilution of Clorox for 1 min. Individual stem and root pieces were plated on Komada's medium (10) and incubated for 7 days. Individual colonies resembling *F. oxysporum* were transferred to potato dextrose agar (PDA) plates, single-spored, and transferred to PDA slants for further identification to species and forma specialis. Final identification of *F. oxysporum* to species was based on colony morphology (cottony white aerial mycelium with purplish pigmentation) on PDA and morphology of micro- and macroconidia and chlamydospores on carnation leaf agar (15). For long-term storage, the isolates were stored as filter paper cultures (2).

Pathogenicity and race determination. Each recovered *F. oxysporum* isolate was used to inoculate two Top Mark seedlings to establish pathogenicity and to identify the forma specialis *melonis*. Fungal isolates were grown on PDA plates for 7 to 8

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Accepted for publication 14 February 1997.

Publication no. D-1997-0422-09R
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days at room temperature under two 20 W fluorescent lights for 14 h. Conidial suspensions were standardized to 1×10^6 spores/ml. Seedlings were inoculated by dipping the roots in the inoculum suspension for 1 min. Seedlings potted in 10-cm clay pots with steamed potting mix (1 part each soil:sand:peat moss:compost) were held in a greenhouse at 27 to 29°C, day, and 18 to 24°C, night. Inoculated seedlings were observed daily for symptom development over a 4-week period. Race determination was made by observing symptom development on two inoculated seedlings of the differential cultivars Top Mark, Doublon (or Top Mark FR), and CM17-187 (18,22). The test was performed under the same environmental conditions previously described.

Comparison of virulence for *F. oxysporum* f. sp. *melonis* races 1 and 2. Fifteen isolates each of *F. oxysporum* f. sp. *melonis* races 1 and 2 were used to inoculate 5 10-day-old seedlings of Top Mark to determine differences in virulence between the two pathotypes. The isolates chosen for each race were randomly selected to represent the three sampled geographical regions of the state. Procedures for inoculum preparation, concentration, and inoculation were the same as previously described. The experiment was conducted in a controlled environment chamber set at 23°C, day, and 18°C, night, with 14 h fluorescent light. Isolates were selected to represent a state-wide distribution of *F. oxysporum* f. sp. *melonis*. Differences in virulence were measured by recording the number of days to first symptoms (DTFS) and the number of days to death (DTD). Readings were taken daily for a period of two weeks. Calculations of DTFS and DTD were made when 50% of the seedlings showed symptoms and died, respectively. Means of these two parameters for both races were compared using a *t* test (12).

Vegetative compatibility groups. Nitrate nonutilizing mutants (*nits*) were obtained from the 46 soil isolates of *F. oxysporum* f. sp. *melonis* as described by Gordon and Okamoto (5). *nits* from each isolate were paired on a minimal medium (17) with complementary *nits* representing previously characterized VCGs of *F. oxysporum* f. sp. *melonis* (8). A pairing reaction was scored as positive when complementing *nits* produced wild type growth (aerial mycelium) along the line of contact.

Restriction fragment length polymorphisms in nuclear DNA of races 1 and 2. To obtain the probe used to visualize restriction fragments, nuclear DNA of *F. oxysporum* f. sp. *melonis* isolate Pt-1 was separated from other fractions by cesium chloride centrifugation. Fragments resulting from digestion of the nuclear DNA with *Eco*R1 were cloned into a pUC vector using cloning kit 1013 084, as per the manufacturer's instructions (Boehringer Mannheim Biochemicals, Indianapolis, IN). A 6.0 kb-fragment thus obtained, designated as pnFOM-9, was found to hybridize with multiple bands in restriction digests of *F. oxysporum* f. sp. *melonis* isolates (20).

Each isolate to be examined was grown in liquid culture, mycelium was harvested and lyophilized, and DNA was extracted as described by Appel and Gordon (1). Total DNA was digested for 1 h with *Eco*R1 and treated with RNase for an additional half hour. Fragments were separated electrophoretically in 1% agarose at a current of 20 Ma for 18 h. Agarose gels were blotted and stored under vacuum at room temperature. Bands were visualized using a DIG DNA labeling and detection kit (Genius 1) according to the manufacturer's instructions (Boehringer Mannheim Biochemicals). Similarities among isolates of *F. oxysporum* f. sp. *melonis* were assessed by determining the extent to which the

restriction fragments of the same mobility, which hybridized to pnFOM-9, were shared.

RESULTS

Race survey of *F. oxysporum* f. sp. *melonis* from soil. One hundred twenty-five isolates of *F. oxysporum* were recovered from the 390 soil samples collected (Fig. 1), and 46 were identified as *F. oxysporum* f. sp. *melonis* (Table 1). Twenty-eight of the isolates were identified as race 1, and 18 were identified as race 2. A majority of the isolates (39 of 46) came from eastern New York; where race 1 was recovered from Washington, Columbia, and Schoharie counties (23 isolates) and race 2 was recovered from Washington, Columbia, Rensselaer and Schoharie counties (16 isolates) (Fig. 1). Three isolates of race 1 were recovered from Onondaga County in central New York, and one each from Erie and Niagara counties in western New York. Two isolates of race 2 were also identified in Erie County.

Four of the 28 race 1 isolates were recovered from a field in Washington County that had not grown melons since 1991, 17 from fields that had been planted to melons in 1992, and the remaining 7 isolates from fields where melons were growing during the 1993 soil sampling period (Table 1). Five of the 18 race 2 isolates were recovered from fields that produced melons in 1992, and 13 from fields cropped to melons in 1993. On four of the nine farms from which *F. oxysporum* f. sp. *melonis* was recovered, both race 1 and 2 were present, representing four different counties in eastern and western New York (Table 1).

Race 1 and 2 virulence study. Races 1 and 2 were statistically different ($P = 0.05$) with respect to DTFS and DTD. Seedlings inoculated with 15 race 2 isolates showed symptoms an average 1.3 days sooner than the seedlings inoculated with 15 race 1 isolates (Table 2). The same plants inoculated with race 2 died an average 1 day sooner than those inoculated with race-1 isolates.

Vegetative compatibility groups. Twelve race 2 isolates were associated with VCG 0131, 10 of which were from eastern New York (Columbia, Rensselaer, and Schoharie counties); the remaining 2 isolates were from western New York (Erie County) (Table 1). Five race 2 isolates were associated with VCG 0130, which was previously known only from California. All 5 isolates in VCG 0130 were isolated from one field in Washington county where melons were produced in 1992 and 1993. The remaining race 2 isolate was paired with tester strains representing all other known *F. oxysporum* f. sp. *melonis* VCGs (7,8) and was not compatible with any of them.

Twenty-seven race 1 isolates were associated with VCG 0134, including 2 (isolates

Fig. 1. Location and number of *Fusarium oxysporum* isolates collected in New York State in 1993, where E = Erie, N = Niagara, O = Onondaga, R = Rensselaer, S = Schoharie, and W = Washington.

84 and 105 in Table 1) that were not compatible with the original tester strains but did pair with other isolates associated with VCG 0134. Twenty-three of the 27 race 1 isolates associated with VCG 0134 were from eastern New York (Columbia, Schoharie, and Washington counties), 2 were from central New York (Onondaga County), and 2 were from western New York (Erie and Niagara counties). A single race 1 isolate was not compatible with any *F. oxysporum* f. sp. *melonis* tester strains.

Restriction fragment length polymorphisms in nuclear DNA of races 1 and 2. Variation in nuclear DNA, based on restriction fragment length polymorphisms (RFLPs) revealed by a multi-locus probe, was characterized for 19 isolates (Table 3). Four RFLP patterns were evident among the 19 isolates (Fig. 2). Ten VCG

0134/race 1 isolates, 8 from New York and 2 from Maryland, were associated with pattern A (Fig. 2). Eight isolates from New York, including 84 and 105, were compatible with some but not all other 0134 isolates. One 0134/race 1 isolate from New York had a banding pattern very similar to A, sharing all but two of the major bands; this pattern was designated A1. Five 0131/race 2 isolates, 3 from New York and 2 from Maryland, were associated with pattern C (Fig. 2). Three 0130/race 2 isolates were associated with pattern B, which included several prominent bands not seen in the 0131/race 2 isolates.

DISCUSSION

The presence of *F. oxysporum* f. sp. *melonis* races 1 and 2 in New York has

already been reported, based on a limited number of isolates (23). The present survey found race 1 to be more widely distributed than was originally thought, with the greatest frequency of occurrence in eastern New York (86%) compared to central or western locations (7% each). Race 1 was recovered from six of the seven counties surveyed; Rensselaer was the only county in eastern New York where race 1 was not found. Race 2, the most prevalent race in the United States, was also recovered in eastern and western New York, but it accounted for only 18 of the 46 isolates of *F. oxysporum* f. sp. *melonis* (39%). Race 2 was recovered from all four eastern counties but only from Erie county in western New York.

The presence of race 1 is of particular importance because resistance to this race in eastern-type melons is present in only a few commercial cultivars, and they are only now being evaluated by growers for horticultural features. Many more cultivars with resistance to race 2 are available for the eastern markets.

We previously reported the recovery of race 1 from severely wilted plants in a field in Washington County in 1992 (23). The recovery of 4 race 1 isolates from a field not planted to melons since 1991 suggests it has been in New York at least since 1991. Race 1 was readily recovered from soil, accounting for 57% of the isolates obtained from fields cropped to melons in 1992 and for 29% of the isolates recovered from fields planted to melons in 1993. Currently, race 1 is responsible for heavy losses on the farm where this race was first detected, and the grower has shifted the majority of his acreage to rented land which is not infested.

Although race 1 is now widely established in New York and is readily recovered from soil, race 2 isolates produced symptoms and killed inoculated seedlings sooner than did race 1 isolates.

Race 1 of *F. oxysporum* f. sp. *melonis* was only recently discovered in New York, whereas race 2 has been recognized in this state since the 1930s (14). The appearance of a new pathotype indicates either a change in the local population (through

Table 1. *Fusarium oxysporum* f. sp. *melonis* races recovered from 1993 soil samples, the year planted to melons, the vegetative compatibility group (VCG), and location and county in New York

Isolate number	Location	County ^y	Year in melon	Race	VCG ^z
1	Ransomville	N	92	1	0134
3	Hudson	C	93	2	0131
9	Phoenix	O	93	1	0134
11	Hamburg	E	93	2	0131
26	Greenwich	W	92	1	0134
27	Greenwich	W	92	1	0134
33	Hudson	C	93	2	0131
37	E. Greenbush	R	93	2	0131
38	Hudson	C	93	2	0131
40	Greenwich	W	91	1	0134
44	Middleburg	S	92	1	0134
55	Middleburg	S	93	1	0134
59	Middleburg	S	92	1	0134
60	Schoharie	S	92	1	0134
61	Hudson	C	92	1	0134
62	Schoharie	S	92	1	0134
64	Hudson	C	93	2	0131
65	Phoenix	O	93	1	0134
67	Middleburg	S	92	2	0131
69	Hudson	C	93	2	0131
73	Hudson	C	92	1	0134
75	Hudson	C	93	2	0131
77	Greenwich	W	92	1	0134
78	Hudson	C	92	1	0134
80	Eagle Bridge	W	93	2	0130
81	Eagle Bridge	W	93	2	NA
82	Eagle Bridge	W	93	2	0130
84	Greenwich	W	91	1	0134
86	Greenwich	W	91	1	0134
88	Greenwich	W	91	1	0134
92	Greenwich	W	92	1	0134
100	Eagle Bridge	W	92	2	0130
101	Eagle Bridge	W	92	2	0130
103	Eagle Bridge	W	92	2	0130
105	Eagle Bridge	W	92	1	0134
112	Middleburg	S	93	1	0134
114	Schoharie	S	92	1	0134
115	E. Greenbush	R	93	2	0131
116	Schoharie	S	92	1	0134
117	Middleburg	S	93	1	0134
118	Phoenix	O	93	1	0134
119	Hudson	C	92	2	0131
122	Schoharie	S	92	1	0134
123	Hamburg	E	93	2	0131
125	Hudson	C	92	1	NA
126	Hamburg	E	93	1	0134

^y C = Columbia, E = Erie, N = Niagara, O = Onondaga, R = Rensselaer, S = Schoharie, W = Washington.

^z NA indicates the isolate was not assigned to a VCG because compatibility with testers representing known VCGs could not be demonstrated.

Table 2. Difference in virulence between 15 isolates each of races 1 and 2 of *Fusarium oxysporum* f. sp. *melonis* in growth chamber studies

	Parameters	
	DTFS ^x	DTD ^y
Race 1	6.3 a ^z	8.9 a
Race 2	5.0 b	7.9 b

^x Days from inoculation to first symptom appearance on the universally susceptible cultivar Top Mark.

^y Days elapsed from inoculation until death of Top Mark seedlings.

^z Means separated with *t* test (*P* = 0.05, 15 degrees of freedom).

Fig. 2. An autoradiograph showing restriction fragment length polymorphisms in *Fusarium oxysporum* f. sp. *melonis* isolates from New York and Maryland. Total DNA from each isolate was cut with *Eco*R1 and probed with a repetitive element cloned from an isolate of *F. oxysporum* f. sp. *melonis* (see text for details). Isolates, from New York unless otherwise indicated, were assigned to lanes as follows, beginning with lane 1: 88, VCG 0134/race 1 (pattern A); 660A, VCG 0134/race 1 from Maryland, Jacobson and Gordon (7) (pattern A); 84, VCG 0134/race 1 (pattern A1); 105, VCG 0134/race 1 (pattern A); 123, VCG 0131/race 2 (pattern C); 82, VCG 0130/race 2 (pattern B); and B7-9S, VCG 0131/race 2 from Maryland, Appel and Gordon (1) (pattern C). Approximate size references, in kilobase pairs, are given to the left of lane 1.

Table 3. Cross reference of *Fusarium oxysporum* f. sp. *melonis* isolates used for restriction fragment length polymorphism analysis

Isolate	County	Region	Race	RFLP pattern ^w	VCG ^x
59	Schoharie	Eastern NY	1	A	0134
60	Schoharie	Eastern NY	1	A	0134
82	Washington	Eastern NY	2	B	0130
84	Washington	Eastern NY	1	A1	0134
88	Washington	Eastern NY	1	A	0134
100	Washington	Eastern NY	2	B	0130
103	Washington	Eastern NY	2	B	0130
105	Washington	Eastern NY	1	A	0134
9	Onondaga	Central NY	1	A	0134
118	Onondaga	Central NY	1	A	0134
126	Erie	Western NY	1	A	0134
1	Niagara	Western NY	1	A	0134
11	Erie	Western NY	2	C	0131
123	Erie	Western NY	2	C	0131
MC1-1S ^y	Caroline	Maryland	1	A	0134
B3-3S ^y	Wicomico	Maryland	2	C	0131
B8-2S ^y	Wicomico	Maryland	2	C	0131
B7-9S ^y	Wicomico	Maryland	2	C	0131
660A ^z	Wicomico	Maryland	1	A	0134

^w Restriction fragment length polymorphisms revealed by probing *Eco*R1 digest of total DNA with a repetitive element cloned from isolate Pt-1 of *F. oxysporum* f. sp. *melonis*. Isolates sharing all clearly resolved fragments were given the same letter designation. Pattern A1 was a subtle variant of pattern A (Fig. 2).

^x VCG = vegetative compatibility group.

^y Refer to Appel and Gordon (1).

^z Refer to Jacobson and Gordon (6).

mutation or selection of a previously rare variant) or a recent introduction. Because race 1 and race 2 were not found to be associated with the same VCG in New York, it is unlikely that race 1 originated from the indigenous race 2 population. Alternatively, most race 1 isolates in New York are associated with VCG 0134, suggesting an introduction from Maryland, where this same VCG/race combination was already known to occur (7). This interpretation is supported by the similarity in nuclear DNA among 0134/race 1 isolates found in New York and Maryland. The repetitive element used to generate the RFLPs in nuclear DNA reveals variation among isolates associated with the same VCG (20; D. T. Schroeder and T. R. Gordon, *unpublished*) and thus provides a more sensitive measure of identity than does vegetative compatibility.

Notwithstanding the similarity between race 1 isolates in New York and Maryland, the occurrence in New York of an isolate associated with race 1 which could not be assigned to a known VCG indicates that the origin of race 1 in New York involves more than a single introduction from Maryland, where race 1 has been associated only with VCG 0134. Although our findings show a clear connection between the infestations in New York and Maryland, they leave open the question of where race 1 occurred first.

The VCG diversity in the population of *F. oxysporum* f. sp. *melonis* in New York is apparently greater than what has been described for other parts of the United States. Only two VCGs of *F. oxysporum* f. sp. *melonis* are found in both Maryland (0131 and 0134) and California (0130 and 0131)

(1,6,7). Outside the United States, the greatest VCG diversity has been observed in France, where three VCGs are known to occur. Most of the characterized isolates of *F. oxysporum* f. sp. *melonis* from France have been assigned to VCG 0134 (7), as have all isolates in South Africa (W. Schreuder, *personal communication*). In Israel, two VCGs have been identified (8). These situations are consistent with clonal propagation of one or more strains, which in some cases may be recent introductions.

In New York, we have identified 3 VCGs from a sample of 46 isolates, including VCG 0130, previously known only from California. Moreover, 2 isolates were incompatible with each other and tester strains representing all known VCGs of *F. oxysporum* f. sp. *melonis* and may therefore be associated with 2 new VCGs. The observed incompatibility is not definitive, however, given the lack of fidelity in intra-VCG pairings observed with 2 isolates of VCG 0134. Thus, pairings with additional isolates will be required before erecting new VCGs to accommodate these isolates. Nevertheless, even if the isolates in question can be assigned to a known VCG, the complexity of the pattern of inter-isolate compatibility is further testimony to the diversity in the population of *F. oxysporum* f. sp. *melonis* in New York State. Similar patterns of inter-isolates pairings were observed among isolates associated with *F. oxysporum* f. sp. *melonis* VCG 0138 in Israel (8). The diversity observed in the New York population, coupled with the fact that New York was one of the first locations where *F. oxysporum* f. sp. *melonis* was identified, suggests that more intensive sampling of *F. oxysporum* populations in New York, expanded to include strains not pathogenic to melon, may provide considerable insight into the evolutionary and geographic origins of *F. oxysporum* f. sp. *melonis*.

ACKNOWLEDGMENTS

This study was supported by funds allocated by the New York State College of Agriculture and Life Sciences for Hatch Project NYC 153-417. We thank J. Drennan for technical assistance, the melon growers who participated in this study, and E. Rutkowski, D. Young, and D. Riggs of Cornell Cooperative Extension for locating the fields used in this survey.

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