Vegetative Compatibility and Self-Incompatibility within *Fusarium oxysporum* f. sp. *melonis*

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ABSTRACT

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A worldwide collection of *Fusarium oxysporum* f. sp. *melonis* isolates was characterized by virulence and vegetative compatibility. Sixty-five isolates comprised five distinct vegetative compatibility groups (VCGs). There is a complex pattern of association between race, VCG, and geographic distribution; a VCG contained either one or several races, while a race was either unique to one VCG or divided among multiple VCGs. California isolates were placed in two VCGs, one unique to the San Joaquin Valley (0130) and the other distributed over North America (0131). In one case, isolates from both VCG 0130 and 0131 were recovered from the same field. Seven isolates were identified as vegetatively self-incompatible based on their inability to form heterokaryons between complementary nitrate nonutilizing mutants and between nitrate nonutilizing and sulfate nonutilizing mutants. The partial or complete absence of intra-isolate fusion cells, as determined microscopically, was also characteristic of vegetatively self-incompatible isolates. Four of these isolates were unable to form heterokaryons with other isolates; however, the other three isolates were able to form heterokaryons with tester strains and were included in VCG 0134. VCG analysis combined with race determination provides a more complete description of sub-forma specialis groups within *F. o.* f. sp. *melonis*. Vegetative self-incompatibility must be taken into account in such classifications.

Fusarium oxysporum Schlect. f. sp. *melonis* (Leach & Currence) Snyd. & Hans., the cause of Fusarium wilt of muskmelon (*Cucumis melo* L.), exhibits host specialization. With one notable exception (20), members of this forma specialis attack only muskmelon and not the related cucurbits watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai), squash (*Cucurbita* spp. L.), or cucumber (*Cucumis sativus* L.). There is differing opinion on the classification of races within *F. o.* f. sp. *melonis*. Armstrong and Armstrong (2) report seven races based on six differential cultivars, while Risser et al (27) suggest four races (0, 1, 2, and 1,2) based on three differentials. The latter system of nomenclature will be followed here because it is based on resistance genes characterized in the differential cultivars (Table 1).

Strains of *F. oxysporum* are grouped into formae speciales and race solely on the basis of their ability to cause disease on certain hosts (31). Additional characterization of subspecific groups in *F. oxysporum* was reported by Puhalla (24), who developed the techniques necessary for identifying vegetative compatibility groups (VCGs) within this species. He found that these VCGs were correlated to forma specialis and suggested that they may represent genetically isolated populations. More in-depth studies have since been conducted focusing on VCGs within specific formae speciales [*F. o.* f. sp. *apii* (6), *F. o.* f. sp. *asparagi* (13), *F. o.* f. sp. *conglutinans* (3), *F. o.* f. sp. *lycopersici* (12), *F. o.* f. sp. *pisi* (8)], and among nonpathogenic forms (7). The results of these studies support the hypothesis that *F. oxysporum* consists of distinct populations that are strongly correlated to formae speciales. Thus, pathotypes may now be identified using the genetic marker of vegetative compatibility combined with virulence. Classification by means of VCGs does, however, have limitations. Certain isolates of *F. oxysporum* have been found that are not vegetatively compatible with themselves or other isolates, and thus cannot be placed into a VCG (3,6,23). This phenomenon of vegetative self-incompatibility must be taken into account when examining the population biology of *F. oxysporum*.

Fusarium wilt of muskmelon has been reported in North America, Europe, India, East Asia, and the Middle East (2,11,14,17,19,21,28), but the distribution of races is not uniform. Before 1985, only race 2 was found in North America, and race 1 was limited to Europe and Israel. In 1985, race 1, previously unknown in North America, was discovered in Maryland (11) and race 0 was found in 1986 in the Rio Grande Valley in Texas (18). Using VCGs to determine the identity of distinct populations may provide valuable insight into the relationships between new and established infestations and the pattern of disease spread.

This study reports the characterization of vegetative compatibility groups within *F. o.* f. sp. *melonis* as a first step toward understanding the relationship between races within this forma specialis. A partial account of this work has previously been published (15).

MATERIALS AND METHODS

Strains. A collection of 29 strains of *F. o.* f. sp. *melonis* was received from various investigators (see acknowledgments and Table 2). Included in this collection are the cultures Armstrong and Armstrong (2) deposited with the American Type Culture Collection (ATCC), Rockville, MD, as well as representatives from the race system of Risser et al (27).

An additional 45 isolates of *F. oxysporum*, representing 15 melon fields in Fresno and Stanislaus counties, California, were collected from either diseased or asymptomatic plants during 1986.

TABLE 1. Classification of *Fusarium oxysporum* f. sp. *melonis* races according to disease reaction with differential cultivars of *Cucumis melo*[a]

Races of *F. o.* f. sp. *melonis*	Differential cultivars and their gene for resistance				
	Charentais/T	Doublon (*Fom* 1)	CM 17187 (*Fom* 2)	Topmark	Perlita (*Fom* 3)[b]
Race 0	C[c]	I	I	C	I
Race 1	C	C	I	C	C
Race 2	C	I	C	C	I
Race 1,2[d]	C	C	C	C	C

[a] According to Risser et al (27).
[b] Described by Zink and Gubler (32).
[c] C = compatible, I = incompatible.
[d] Race 1,2 is further divided into wilt strains (1,2w) and yellows strains (1,2y).

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Segments of petiole, stem, or taproot, 1 cm long, were surface sterilized by dipping in 70% ethanol for 5 sec then submerging in 0.5% sodium hypochlorite for 3 min. The tissue was plated on Komada medium (16) amended with 1 ml/L of Tergitol NP-10 to further restrict colony size (23). Plates were incubated at ambient temperature (23 ± 2 C) and under fluorescent illumination (two 34W daylight tubes) 12 hr/day. Colonies exhibiting the characteristic morphology of *F. oxysporum* on this medium (16) were identified after 6 days. Confirmation of isolate identity was based on colony morphology on potato-dextrose agar and conidia morphology on carnation leaf agar (22). Single spore or hyphal tip subcultures of these colonies were recovered and stored as dried filter paper cultures (6) and also as spore suspensions in 25% glycerol at −70 C.

Virulence tests. To confirm the race identity of *F. o.* f. sp. *melonis* strains, virulence tests were performed using the differential muskmelon cultivars Charentais T, Doublon, CM17-187, Topmark, and Perlita (Northrup-King Seed Co.)(Table 1). Strains received from other investigators and a representative California isolate (P-2) were tested. Seedlings were grown in steamed soil mix (equal parts fine sand and peat moss) at 26 C for 7–10 days until the first true leaf began to emerge. Inoculations were made by a root dip method (32). Seedlings were shaken to remove excess soil and the roots trimmed to a length of 3.4 cm. Inoculum consisted of a suspension of 2.5×10^5 conidia per milliliter prepared from cultures grown on potato-dextrose agar for 7 days at ambient temperature under lights. The roots were submerged in the inoculum (about 1 min) and the seedlings transplanted to plastic cell-type trays (cells 5 cm diameter × 5 cm deep) containing fresh soil mix with one seedling per cell. Seedlings with trimmed roots dipped in sterile water were planted as controls. Plants were incubated in the greenhouse where temperatures fluctuated between 24 and 40 C. For each strain tested, five seedlings of each cultivar were inoculated and arranged randomly on a single greenhouse bench. Disease symptoms progressed through stunting, chlorosis, necrosis, and finally death of the seedling. Plants that were stunted, as compared with the water-treated controls, and also showed chlorosis and/or necrosis were considered to be diseased. Symptoms were recorded at 7-day intervals up to 28 days after inoculation; virulence is expressed as the percentage of diseased seedlings. The remaining California isolates were tested, as described above, for pathogenicity on muskmelon using the susceptible cultivar Topmark and the race 2 resistant cultivar Perlita (Table 1).

TABLE 2. Isolates used to determine vegetative compatibility groups within *Fusarium oxysporum* f. sp. *melonis*

Isolate	Race[a]	Location	VCG[b]
ATCC[c] 16418	2	Ontario, Canada	0131
ATCC 28856	0	France	0134
ATCC 28857	1	France	013-
ATCC 28858	1,2w	France	0133
ATCC 28859	1,2y	France	0134
ATCC 28861	2	Japan	0132
ATCC 28862	1	Israel	013-
ATCC 32669	2	Michigan	0131
B-1	2	San Joaquin Valley, California	0130
B-2	2	Indiana	0131
E-465A	1	Caroline Co., Maryland	013-
E-466A	0	Caroline Co., Maryland	0134
E-468A	1	Caroline Co., Maryland	0134
E-660A	1	Wicomico Co., Maryland	0134
E-661C	1	Wicomico Co., Maryland	0134
E-662B	1	Wicomico Co., Maryland	0134
E-662C	1	Wicomico Co., Maryland	0134
F-112	0	Italy	0134
F-123	2	Italy	0134
Fm-103	2	San Joaquin Valley, California	0130
Fo-8	2	Michigan	0131
M-1	2	Michigan	0131
0-1127	2	New York	0131
P-2	2	Fresno Co., California	0130
Pt-1	2	Stanislaus Co., California	0131
R-1	1	France	013-
R-12w	1,2w	France	0133
R-12y	1,2y	France	0134
R-21	2	San Joaquin Valley, California	0130
Tx-388	0	Rio Grande Valley, Texas	0134
X-22	2	Riverside Co., California	0131

[a] Race of the pathogen according to Risser et al (27).
[b] Vegetative compatibility group numbered according to Puhalla (24). 013-: an artificial group containing vegetatively self-incompatible isolates.
[c] American Type Culture Collection, Rockville, MD.

Determination of vegetative compatibility groups. Vegetative compatibility groups (VCGs) were determined through the complementation of nitrate nonutilizing (*nit*) mutants as a visual indicator of heterokaryon formation (24). Potato-sucrose agar containing 1.5% $KClO_3$ was used initially to generate *nit* mutants (6). The concentration of $KClO_3$ was increased to 3–5% when needed for isolates that were not restricted with 1.5% $KClO_3$. Corn meal agar with dextrose (Difco Laboratories, Detroit, MI) containing 1.5% $KClO_3$ was used as an alternative medium to increase the production of sectors where necessary. Chlorate resistant sectors were screened on Puhalla minimal medium (MM) containing sodium nitrate ($NaNO_3$) as the sole nitrogen source (24). Those chlorate resistant colonies that grew thinly but expansively on this medium were considered to be *nit* mutants.

The formation of heterokaryons was recognized as a line of aerial mycelium where two complementary *nit* mutants grew together on MM. *Nit* mutants were generated from each isolate until two complementary *nit* mutants were found that formed a vigorous heterokaryon when paired on MM. These *nit* mutants were used as heterokaryon tester *nit* mutants for that isolate in subsequent inter-isolate pairings. When testers from two different isolates successfully formed a heterokaryon they were placed in the same VCG.

Nitrogen utilization phenotypes. Growth on five defined media containing different nitrogen sources was used to assign *nit* mutants to separate phenotypic classes (4). MM, withou $NaNO_3$, was supplemented with one of the following nitrogen sources at 1.2 mM: sodium nitrate, sodium nitrite, hypoxanthine, uric acid, or ammonium chloride. A mass transfer (a cube 2 mm on a side) of each *nit* mutant, growing on MM, was placed on all five media, with the wild type as a control. The plates were incubated in the dark at ambient temperature (23 ± 1 C). Growth was rated qualitatively at 3 and 7 days as either positive (similar to the wild type) or negative (thin and expansive growth).

Sulfate nonutilizing mutants. Selenate is a toxic analog of sulfate and interrupts normal sulfur metabolism (10). To obtain sulfate nonutilizing (*sul*) mutants (5), mass transfers of wild-type isolates were placed on MM supplemented with 1.0 g/L of sodium selenate and 0.1 g/L of taurine (Sigma Chemical Co., St. Louis, MO), a reduced form of sulfur. *F. o.* f. sp. *melonis* grew slowly or not at all on this medium. Fast-growing selenate resistant sectors appeared in 7–28 days. These sectors were transferred to MM, which contained sulfate as the sole sulfur source. *Sul* mutants were distinguished by thin and expansive growth on MM as compared with the wild type. *Sul* mutants were paired with *nit* mutants on MM to visualize heterokaryon formation.

Microscopic examination of anastomosis. Wild-type isolates were grown on 1.75% water agar, which was overlaid with about 3 cm^2 of sterilized cellophane. After 3–7 days, segments of the colonized cellophane were removed from the plate and mounted on a glass slide in water. The mycelium was examined at 400× magnification under phase contrast illumination. The number of hyphal fusions per field was counted in each of 20 randomly selected fields 2–4 mm behind the growing margin of the colony.

RESULTS

Virulence. The pathogenicity tests resulted in clear virulence reactions; at least 80% of the plants of susceptible cultivars were diseased, while resistant cultivars showed no symptoms and were indistinguishable from the controls. Among the 74 isolates of *F. oxysporum* tested in this study, 69 were pathogenic to one or more

cultivars of muskmelon. Of the five nonpathogens, two were isolated from diseased melon stems and three were isolated from roots of nonsymptomatic plants; these plants were collected in Fresno County, CA. The race identity of the strains received from other investigators was confirmed in our virulence test (Table 2). The race determination of isolate Tx-388 was made by Dr. F. W. Zink, Department of Vegetable Crops, University of California, Davis. The cultures received from ATCC were placed into the four-race system as expected from the data of Armstrong and Armstrong (2). The distinction between wilt and yellow strains of race 1,2 as described by Risser et al (27) was also apparent by the inoculation method used here. Consequently, these variants are herein referred to separately as race 1,2w and 1,2y.

The representative California isolate P-2, as well as the four California isolates received from other investigators, were consistent with the virulence pattern of race 2. The other 39 pathogenic isolates collected in California during 1986 were virulent on the cultivar Topmark but avirulent on the race 2 resistant cultivar Perlita.

Vegetative compatibility groups. Complementary tester *nit* mutants were generated from 22 of the 29 strains obtained from other researchers and ATCC. In addition, testers were generated from one of the Fresno County isolates (P-2) and from the Stanislaus County isolate (Pt-1). This gave a total of 24 tester pairs. These testers were paired in all combinations, revealing five distinct VCGs that were designated, as suggested by Puhalla (24), 0130 to 0134 (Table 2).

At least three *nit* mutants were generated from each of the remaining California isolates. These *nit* mutants were initially paired with the testers of isolate P-2; 38 of the 39 pathogenic isolates formed heterokaryons and were placed into VCG 0130 (Table 3). The remaining isolate (V-2) was paired with testers from the other four VCGs. Isolate V-2 formed a heterokaryon with testers from VCG 0131. This is noteworthy since another isolate from the same field (V-1) is included in VCG 0130. Thus, isolates V-2 and Pt-1 were both placed, along with X-22, in VCG 0131. These three were the only California isolates not included in VCG 0130.

TABLE 3. Sub-forma specialis organization of *Fusarium oxysporum* f. sp. *melonis* by vegetative compatibility and virulence

VCG[a]	Race[b]	Number of Isolates	Location
0130	2	38[c]	Fresno Co., California
		3	San Joaquin Valley, California
0131	2	1[c]	Stanislaus Co., California
		1[c]	Fresno Co., California
		1	Riverside Co., California
		1	Indiana
		3	Michigan
		1	New York
		1	Ontario, Canada
0132	2	1	Japan
0133	1,2w	2	France
0134	0	1	France
		1	Italy
		1	Texas
		1	Caroline Co., Maryland
	1	1	Caroline Co., Maryland
		4	Wicomico Co., Maryland
	2	1	Italy
	1,2y	2	France
013-	1	1	Caroline Co., Maryland
		2	France
		1	Israel
Total		69	

[a] Vegetative compatibility groups numbered according to Puhalla (24). 013-: an artificial group containing vegetatively self-incompatible isolates.
[b] Race of the pathogen according to Risser et al (27).
[c] These isolates are presumed to be race 2 based on virulence to Topmark and avirulence to Perlita. This conclusion is supported by virulence tests of other isolates from the same fields (F. W. Zink, *unpublished*).

Nit mutants from the five nonpathogenic isolates did not form heterokaryons with the P-2 testers. Tester *nit* mutants were generated from two of these isolates and paired with testers from the five VCGs of *F. o.* f. sp. *melonis*. No heterokaryons were formed between pathogenic and nonpathogenic isolates.

To establish whether the VCGs within *F. o.* f. sp. *melonis* overlap a previously characterized VCG, all testers were paired with testers from *F. o.* f. sp. *niveum* (E. F. Sm.) Snyd. & Hans. VCG 0080 (24), which attacks watermelon. None of the *F. o.* f. sp. *melonis* strains used in this study formed a heterokaryon with *F. o.* f. sp. *niveum*.

Heterokaryon-forming tester *nit* mutants could not be obtained for seven isolates. Up to 230 *nit* mutants were generated for each of these isolates and paired together without forming a heterokaryon. Three of the isolates (R-12y, ATCC 28856, and E-468A), although incapable of forming intra-isolate heterokaryons, did form weak heterokaryons (limited aerial mycelium) with at least one other tester. However, four isolates (R-1, ATCC 28857, ATCC 28862, and E-465A) would not form heterokaryons with themselves, or any other isolate. Because these four isolates shared virulence characteristics (all are race 1); they were designated VCG 013-, for convenience.

Nitrogen utilization phenotypes. The nitrogen utilization phenotypes were determined as a first step in explaining the inability to obtain complementary *nit* mutants from the seven isolates described above. A small sample (4–20 *nit* mutants) from each of the seven isolates was grown on MM with various nitrogen supplements. The pattern of growth on these five media indicated three distinct phenotypes. *Nit* mutants of at least two different phenotypes were identified within each isolate. These putative testers were paired again on MM and rated after 28 days. In no case was a heterokaryon formed. These seven isolates were therefore considered to exhibit vegetative self-incompatibility. The tester *nit* mutants for each VCG were also examined, and, in all cases, the two testers were of different phenotypes.

Sulfate nonutilizing mutants. At least one *sul* mutant was recovered from each of the self-incompatible isolates and the self-compatible isolates P-2 and E-660A. Each *sul* mutant was paired separately with two phenotypically different *nit* mutants from the same isolate. The *sul* mutant of P-2 and E-660A formed heterokaryons with each of their respective *nit* mutant testers. The pairings of *nit* and *sul* mutants within the self-incompatible isolates did not result in heterokaryons. When *sul* mutants were paired with tester *nit* mutants of other isolates, the results were as expected: R-1, ATCC 28857, ATCC 28862, and E-465A formed no heterokaryons, while *sul* mutants from R-12y, ATCC 28856, and E-468A formed heterokaryons with their respective VCG tester *nit* mutants. No *sul* mutant had a positive reaction with strains outside the VCG defined by heterokaryon formation using *nit* mutant testers.

Microscopic examinations of anastomosis. Two self-compatible isolates (P-2 and E-660A) and the seven self-incompatible isolates were examined. In both P-2 and E-660A anastomosis in the wild-type colony was similar to that described by Puhalla (23); secondary branches behind the growing margin of the colony met and anastomosed with considerable regularity. The average number of fusions seen per 0.04 mm^2 field for isolates P-2 and E-660A were 7.0 and 5.6, respectively. In contrast, no anastomosis was apparent within wild-type colonies of the four isolates in VCG 013- or isolates ATCC-28856 and R-12y. One self-incompatible isolate, E-468A, showed hyphal fusions, with an average of only 0.5 fusions per field.

DISCUSSION

Results indicate that there is substantial genetic diversity in *F. o.* f. sp. *melonis* as reflected by both multiple races and multiple VCGs. The relationship between race and VCG is complex; race 2 is found in four different VCGs while VCG 0134 includes all four races. Although there is no simple correlation, the following trends are considered significant.

The presence of multiple physiological races within a single VCG

is noteworthy since, based on studies of sexually reproducing fungi such as *Gibberella fujikuroi* (26) and *Aspergillus nidulans* (9), a high degree of genetic homology is required for isolates to be vegetatively compatible. This homology suggests that pathogenic races within a VCG may differ at a relatively small number of loci. A similar, if less extreme, situation has been reported for *F. o.* f. sp. *conglutinans* (3), in this case two pathogenic races belong to the same VCG. Pathogenic diversity within a VCG renders the prospect of parasexual interaction potentially significant (29). If a parasexual cycle occurs among isolates in VCG 0134, it may have contributed to the variation that now exists. For example, race 1,2 could have arisen through the recombination of virulence factors in races 1 and 2. Parasexuality might also lead to the development and spread of new races in the future.

The occurrence of race 2 in four different VCGs raises interesting questions concerning the phylogeny of subspecific groups with *F. oxysporum*. More information on the genetic relationships among VCGs will be required before it is possible to adequately address these questions. Nevertheless, it is clear that race 2 does not constitute a homogeneous group of isolates; this underscores the limitations of the present system for naming races. Race 2 isolates are unified solely by their pathogenicity to a small number of host genotypes (27). If additional differential cultivars were available, differences in virulence might become apparent. Subtler differences may also exist, such as the distinction between the wilting (VCG 0133) and yellows (VCG 0134) strains of race 1,2. Though no such differences have as yet been documented within race 2, it is apparent that no single isolate may safely be regarded as representative of the pathogenic potential of this race. This consideration bears directly on the selection of isolates for use in screening muskmelon germ plasm for resistance to Fusarium wilt.

Although race 2 is represented in four VCGs, in a given geographic area a single VCG may prevail. This appears to be the case in the San Joaquin Valley. The 40 pathogenic isolates collected from Fresno and Stanislaus counties were all virulent on Topmark and avirulent on Perlita and are therefore presumed to be *F. o.* f. sp. *melonis* race 2. This conclusion is supported by virulence tests in a concurrent survey where only *F. o.* f. sp. *melonis* race 2 was found in the San Joaquin Valley (F. W. Zink, *unpublished*); included in this survey are isolates representing the same 15 fields from which our collection was made. Thirty-eight of the 40 isolates, as well as the San Joaquin Valley isolates received from other workers, were identified as belonging to VCG 0130. High temperatures prevail during the growing season in the San Joaquin Valley, and the disease is commonly seen in mature fields during the warmest part of the season (14). Reports from other areas, however, describe Fusarium wilt of muskmelon as a cool weather disease (17,19,21). The predominance of VCG 0130 in one area and its apparent absence in other melon-growing regions may reflect its unique adaptation to the conditions in the San Joaquin Valley.

The intercontinental distribution of VCG 0134 is of potential importance. Both the Maryland and Texas isolates are included with European isolates in VCG 0134 (Table 3), and it is possible that these infestations resulted from recent introductions of the pathogen from Europe. These observations, however, are based on very few isolates and must be substantiated by more extensive collections and further characterization of this VCG.

Some of the isolates tested could not be assigned to a VCG. This problem, which has also been reported by other investigators (3,6,23), occurs when tester *nit* mutants cannot be obtained for an isolate and that isolate will not form a heterokaryon with testers from any other isolate. This can result from a failure to obtain complementary *nit* mutants or the inherent inability of an isolate to form a heterokaryon. Data on nitrogen utilization phenotypes reported here show that complementary *nit* mutants were obtained from isolates that did not form heterokaryons. Moreover, sulfate nonutilizing mutants generated from these same isolates also were unable to form heterokaryons with *nit* mutants. Therefore, it was concluded that the isolates that could not be assigned to a VCG were vegetatively self-incompatible. This conclusion was strengthened by the observation that intra-isolate hyphal fusions were absent within these isolates. Vegetative self-incompatibility was also observed in three isolates from which testers could not be obtained but which were assigned to a VCG based on the formation of heterokaryons with testers from other isolates. Of the three isolates in this category, two did not form hyphal fusions while one, E-468A, produced hyphal fusions at a greatly reduced rate when compared with fully self-compatible isolates. Thus, vegetative self-incompatibility seems to result from the inability of an isolate to initiate or complete heterokaryon formation.

F. o. f. sp. *melonis* is a genetically diverse group unified by the common trait of pathogenicity to muskmelon. In other studies, VCG analysis has proved useful in identifying subspecific groups within a morphological species (1,9,25,30). This is also true within *F. o.* f. sp. *melonis*, and although the relationship between virulence and VCG is complex, interesting patterns have emerged. The five VCGs described here may not represent the total number of distinct populations within *F. o.* f. sp. *melonis*; additional VCGs may be discovered. Vegetative self-incompatibility further complicates VCG analysis of *F. o.* f. sp. *melonis*; it must also be considered and its limitations taken into account in future studies.

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