Formae Speciales and Races of Fusarium oxysporum Causing Wilts of the Cucurbitaceae

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ABSTRACT

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Fusarium oxysporum f. sp. *cucumerinum* from the U.S., Germany, and Japan; f. sp. *melonis* from Canada, France, Israel, Japan, and the U.S.; f. sp. *niveum* from Florida and South Carolina; f. sp. *lagenariae* and f. sp. *luffae* from Japan were used, respectively, in inoculations of 16 cultivars or breeding lines of cucumber, 49 of muskmelon, 23 of watermelon, eight of gourds, and one each of citron and colocynth. Variations in virulence for a specific host occurred, but each forma specialis showed sufficient selective pathogenicity for the host from which it was derived to be retained as a valid forma specialis. No races were identified with ff. sp. *cucumerinum*, *lagenariae*, or *luffae*, nor could the races of f. sp. *niveum* reported from the U.S. be clearly separated. In addition to the four clearly defined races of f. sp. *melonis* from France, three new races; viz., race 5 from the U.S.-Canada, race 6 from Israel, and race 7 from Japan, were found among the 24 isolates in the collection of f. sp. *melonis*. Fifty other different wilt fusaria were nonpathogenic on a cultivar of cucumber, muskmelon, watermelon, and dishrag gourd, each of which was susceptible to its respective forma specialis. A forma specialis causing wilt of cucumber, muskmelon (race 5), watermelon, and dishrag gourd, respectively, was nonpathogenic on plants of 46 other species and cultivars that have been helpful in differentiating formae speciales and races of *F. oxysporum*.

We have reclassified some formae speciales (ff. sp.) of *Fusarium oxysporum* that cause vascular wilts owing to common hosts. Further investigations have been made to determine if those that cause wilts of the Cucurbitaceae are sufficiently distinct in pathogenicity to be retained as formae speciales or if they should be reclassified; viz., *F. oxysporum* Schlecht. emend. Snyd. & Hans. f. sp. *cucumerinum* Owen (39), f. sp. *melonis* (Leach & Currence) Snyd. & Hans. (28), f. sp. *niveum* (E. F. Sm.) Snyd. & Hans (49), f. sp. *luffae* Kawai, Suzuki, & Kawai (22), and f. sp. *lagenariae* Matuo & Yamamoto (31). The status of races in these formae speciales also has been examined.

When our first inoculations were made of watermelon [*Citrullus lunatus* (Thumb.) Mansf.] in 1949, muskmelon (*Cucumis melo* L.) in 1950, and cucumber (*Cucumis sativus* L.) in 1957, no pathogenic races of the formae speciales attacking these hosts had been found. Later, three races of f. sp. *niveum* were reported (14, 15, 38) and races 1, 2, 3, 4 of f. sp. *melonis* (44, 45). We (5) designated 11 isolates of f. sp. *melonis* from Canada and the United States as another race in 1970. Leary and Wilbur (29) recently reported race 2 and probably race 3 of f. sp. *melonis* in California. Banihashemi and deZeeuw (9), in reporting a new race (race 4) of f. sp. *melonis* in 1975, did not mention the earlier description of race 4 by Risser et al. (45) in 1969. The validity of the report will be discussed later. However, Gubler and Grogan (19) more recently designated their isolates from California as the race 4 of Banihashemi and deZeeuw.

Presented here are the results of our inoculations of cultivars of cucumber, muskelon, watermelon, dishrag gourd (*Luffa aegyptiaca* Mill.), and bottle gourds (*Lagenaria leucantha* Rusby, and *L. siceraria* Mol.) with formae speciales that cause wilts of these cucurbits, as well as with 50 wilt fusaria from other hosts. Plants of 46 other species and cultivars that have been helpful in differentiating forms and races of *F. oxysporum* also were inoculated with the formae speciales that cause wilts of cucumber, muskmelon (race 5), watermelon, and dishrag gourd. Chiefly considered in our investigation were (i) differential hosts, which could indicate genetic differences in pathogenicity rather than mere differences in virulence of the isolates; (ii) an inoculum concentration to give a full measure of their virulence; (iii) age of plants at inoculation that would give results comparable to the behavior of the plants in the field; and (iv) a medium for growth of plants, especially muskmelon, to avoid physiological disorders that might occur after steam sterilization.

MATERIALS AND METHODS

Source of cultures.—The isolates of f. sp. *cucumerinum*

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included three from Florida, six from Japan, and five from Germany [four of which were labeled f. *melonis* (24, 25)] that caused wilt of cucumber but were avirulent on muskmelon.

Eight isolates of f. sp. *melonis* represented collections in the United States: viz., Michigan (M4); Minnesota (M55); and two each from North Carolina, Washington, and Wisconsin. Also included were isolates from three collections in Canada; one in Belgium; two in Israel; five in Japan; and races 1, 2, 3, 4 in France. One isolate from Israel (188/3) was obtained from a wilted cucumber (40) but, with our methods, caused no wilt of cucumber, was virulent on muskmelon, and, therefore, was placed in f. sp. *melonis* as race 6 (Tables 1, 3).

Isolates of f. sp. *niveum* were race 1 (60-3A) and race 2 (62-8) from Florida (14) and 17 isolates from various locations in South Carolina.

One isolate each of f. sp. *lagenariae* and f. sp. *luffae* came from Japan. Fifty other different wilt fusaria were used to inoculate one or more cultivars of cucumber, muskmelon, watermelon, and *L. aegyptiaca*.

Sources of seed.—Seed of the 16 cultivars of cucumber were from England, Israel, Japan, and the United States. Thirty-five cultivars or breeding lines of muskmelon were from France, Israel, Japan, and the United States; and 14 Plant Introductions (P. I.) each were from a different country. Twenty-three cultivars of watermelon from the U.S. were used during the investigations, but one from Israel was used only in a few tests. One cultivar each of citron [*Citrullus lunatus* (Thunb.) Mansf. var. *citroides*] and colocynth (*Citrullus colocynthis* Schrad.) were inoculated in a few tests with f. sp. *niveum* and f. sp. *melonis*.

Growth and inoculation of plants.—Since the soils available to us were toxic to all plants after steam sterilization (2, 7), the plants (except muskmelon) were grown in sand in 8-liter glazed pots (22 cm diameter) that had been sterilized at 121 C for 8 hr or more. A 2-cm-diameter lateral hole at the bottom of the pots provided drainage. A considerable range in size of sand particles was permissible, but extreme variations were avoided. Since muskmelons showed a severe physiological disorder in sand, they were grown in nonsterilized vermiculite, plasterers'-grade Zonolite® (W. R. Grace & Co., Atlanta, GA 30300).

Usually 20 seeds, treated with a 5% calcium hypochlorite solution for 5 min, were planted per pot, spaced evenly in a circle 2.5 cm from the periphery and 2.5 cm or less deep. Later, the plants in each pot were thinned to 10 to 12 of uniform size.

The roots of all plants were cut by pressing an inverted Büchner funnel (100 mm in diameter) into the sand in the center of the pot and then pouring the liquid inoculum around the roots. Roots were cut for the first inoculation when the plants had the first true leaves and were past the stage when damping-off might be confused with wilt. A second inoculation was given 5 to 7 days later. Most plants of the cucurbits, especially those of muskmelon, were grown in the fall, winter, and spring in a greenhouse with the temperature usually at 27 to 28 C, but variations from 17 to 39 C occurred occasionally for short periods of time. The nutrient solution for growing plants (1) and for the fungus inoculum (3) are given elsewhere.

The possible ill-effects of unequal ion absorption by the plants were prevented by flushing each pot with at least 1 liter of water every 7 to 10 days. Noninoculated plants of the appropriate cultivar were included as checks in each experiment. Precautions were taken to prevent cross-contaminations.

Monoconidial isolates, derived chiefly from microconidia, were the source of the inoculum, and the corresponding mass cultures were tested for comparison. The isolates were maintained on Parafilm-sealed, potato-dextrose agar (PDA) slants and stored at about 5 C.

In preparing the inoculum, 10 ml of sterile water was added to a fresh agar slant culture, and conidia and mycelium were lossened with a sterile needle. One ml of this suspension was added to 500 ml of the liquid medium in a 2-liter flask, which was shaken several times daily and kept at approximately 28 C for 72 hr. A visual index was used to estimate the density of growth in the flasks and to give approximately the same concentration of the inoculum throughout the experiments. If the density was judged insufficient, incubation was continued, usually no more than 24 hr. This liquid inoculum, which was poured around the cut roots, consisted of fragments of hyphae, microconidia, and bud cells. There was no indication that toxic staling products accumulated in the medium since inoculated nonsusceptible plants grew normally.

Plants were removed from the pots when they showed severe wilt. Only the percentages of plants with external wilt symptoms are given, although at the end of an experiment, plants without external symptoms were cut to determine the extent of vascular discoloration. In our experiments, vascular discoloration has proven an unreliable criterion for evaluating the degrees of virulence of the fungal isolates or for distinguishing races. Throughout the investigation, sections of a representative number of plants were surface sterilized and plated on water agar. A typical *F. oxysporum* was usually isolated, and the pathogenicity was verified from a random selection.

RESULTS

Inoculations of cucumber with Fusarium oxysporum ff. sp. cucumerinum, -melonis, and -niveum.—Seven cultivars of cucumber from the United States; viz., Ashley, Cubit, Marketer, Palmetto, Straight Eight, Wauchula, and White Wonder, were highly susceptible to all isolates of f. sp. *cucumerinum* from Germany and Florida and resistant to four isolates of f. sp. *niveum* and seven isolates of f. sp. *melonis* race 5. Four isolates with varying degrees of virulence on cucumber were received from Germany in 1957 as f. sp. *melonis* (24, 25); however, they caused no wilt of six muskmelon cultivars, but were pathogenic on the seven cucumber cultivars mentioned above. Another isolate from a different source in Germany in 1964 which was labeled as a cucumber wilt *Fusarium* was virulent on cucumber but caused no wilt of muskmelon. In 1973, six isolates of f. sp. *cucumerinum* from several locations in Japan and seed of five cultivars were supplied by Komada (23). The cultivars, Aofushinari A, Hyuga 2 Improved, Kurume Ochiai, and Saitama Ochiai 4, were resistant to one isolate each from Japan and Florida and to a random selection of the other five isolates from Japan. Ashley (U.S), Bet Alpha (Israel), and Shimoshirazujihai (Japan) were susceptible to the two isolates used on all four cultivars above. No races of the fungus were evident in the preceding experiments, but their probable existence is being investigated further.

Inoculation of muskmelon with Fusarium oxysporum f. sp. melonis.—The reactions of 35 cultivars of muskmelon to f. sp. *melonis* are given in Table 1. Charentais T and Hale's Best Jumbo were susceptible to isolates of all races; Ein-dor, Honey Rock, Makdimon, and Casaba were susceptible to those tested on them. Delicious 51 showed intermediate resistance (53% wilted plants) in six tests with five U.S.-Canada isolates (Table 1, subtitle 1). The isolates from Canada and the United States (Table 2) were classified as race 5 (Table 1) since some host reactions differed from those caused by either race 1, 2, 3, or 4, differentiated by Risser et al. (44, 45). Twelve cultivars reacted similarly to races 1 and 5 (Table 1, subtitle 2), but the reactions of five others (Table 1, subtitle 3) showed the differences between them. A Belgian isolate was placed in race 1, although it seemed to have reduced virulence. Isolate #498 from Israel reported as race 1 (29, 38) also was placed in race 1 after our inoculations of 14 cultivars, including the seven in Table 3. This isolate was a different pathogen from the one (188/3) received earlier from Israel, race 6 (Tables 1, 3).

Risser et al. (45) separated races 3 and 4 on the basis of symptom expression; race 3 caused wilt without loss of green color and race 4, wilt and yellowing of leaves similar to that caused by races 1 and 2. We found that Ogon 9 and Oriental Kinpyo were susceptible (S) to race 3 and resistant (R) to race 4 and that Edisto 47 was moderately resistant to race 3 and highly susceptible to race 4 (Table 1).

The results in Tables 1 and 3 show that in addition to the four races in France, a fifth race occurs in the U.S. and Canada, a sixth in Israel, and a seventh in Japan. These can be separated by the differential reactions of six cultivars given in Table 3.

Inoculations of muskmelon with Fusarium oxysporum ff. sp. cucumerinum, -niveum, -lagenariae, and -luffae.—Cultivars of muskmelon in Table 1 numbered 1, 3, 7, 8, 9, 11, 12, 15, 16, and 20 were not susceptible to ff. sp. *cucumerinum*, *-niveum*, *-lagenariae*, and *-luffae*. A reciprocal pathogenicity of the Elegans fusaria isolated from cucumber and muskmelon was reported (24, 25, 43). To check further if this relation could be found, muskmelons from different countries with P. I. numbers 176503, 181748, 182936, 190184, 190554, 193495, 194054, 199681, 201581, 207009, 208741, 211725, 213184, and 224785 were inoculated with f. sp. *cucumerinum*. None was susceptible.

Smith's Perfect (Tables 1, 5) was resistant to ff. sp. *cucumerinum*, *-niveum*, and *-lagenariae* but was susceptible to f. sp. *luffae* (Table 5) in 17 tests with 81% wilt of 200 plants before 1972. Since then inoculations of 103 plants in nine pots with isolates of this clone have resulted in only 39% wilted plants (range 20-55%); however, this reduced virulence was not apparent in inoculations of the original host, *Luffa* sp. When *Luffa* sp. was inoculated with f. sp. *luffae*, there was little or no decay at the soil line, vascular discoloration extended far up the vines, and yellow areas with final necrosis occurred in leaves. When Smith's Perfect was inoculated with the same isolate, the symptoms included decay at the soil line, internal browning for only a short distance up the vines, and drooping of leaves (often without yellowing), which resembled the symptoms caused by *F. solani*. Morphologically, however, we classified f. sp. *luffae* as an *F. oxysporum*. It might seem logical to reduce f. sp. *luffae* to a race of f. sp. *melonis* with Smith's Perfect muskmelon a common host. Also, Kawai et al. (22) reported that f. sp. *luffae* caused wilt of muskmelon (cultivar unknown). It is retained as a forma specialis since we have found that it also caused wilt of a noncucurbitaceous host (Armstrong and Armstrong, *unpublished*) as well as causing symptoms on Smith's Perfect that usually are associated with *F. solani*.

Inoculation of watermelon with Fusarium oxysporum f. sp. niveum.—As early as 1949, watermelon was included in our inoculations to see if races of f. sp. *niveum* could be found. One or more of the 17 isolates from South Carolina were used randomly from 1949 to 1959 to inoculate the cultivars listed in Table 4. The pathogenicity and, presumably, the relative virulence of the isolates was checked on the susceptible cultivar Garrison. A complete loss of virulence occurred in one single-spored clone. The reactions of the cultivars to the various isolates agreed with their ratings as susceptible or resistant, but no clues indicating races of the isolates were found.

Crall (14, 15) reported races 1 and 2 of f. sp. *niveum* in Florida in 1963. After receiving these isolates from him in 1969, they were compared with a freshly isolated clone (SC) of f. sp. *niveum* from South Carolina. Each of the three isolates was used in five inoculations at different times on each of the resistant cultivars, Charleston Gray, Crimson Sweet, Klondike, and Summit, and the susceptible cultivars, Florida Giant and Sugar Baby. Judged by the rapidity of wilting in most experiments, the isolates showed different degrees of virulence with isolate SC being most virulent and races 2 and 1 less virulent in descending order, but there was insufficient evidence to distinguish them as races.

Inoculation of watermelon with Fusarium oxysporum ff. sp. cucumerinum and melonis.—When the cultivars listed in Table 4 were inoculated with f. sp. *cucumerinum* and f. sp. *melonis*, respectively, no damping-off or wilting occurred, although vascular discoloration frequently was noted in the basal 2.5-cm of stem. Three to nine repetitions of the test were made with cultivars numbered 2, 5, 6, 8, 9, 13, 14, and 17 in which the vascular discoloration was most apparent. Only single-pot tests were made with the other cultivars in which the discoloration was least evident. A typical *F. oxysporum* was recovered from random samples of surface-sterilized stems plated on water agar. Also, no damping-off or wilting occurred when a wilt-susceptible cultivar of watermelon was planted in nine pots, each with 10 plants, where cucumber had wilted after inoculation with f. sp. *cucumerinum* or in six pots in which muskmelon had wilted after inoculation with f. sp. *melonis*.

Inoculation of colocynth, cucumber, muskmelon, watermelon, and gourds with Fusarium oxysporum ff. sp. lagenariae and -luffae.—One cultivar of colocynth, two of cucumber, one of muskmelon, and three of watermelon were resistant to the formae speciales from gourds in random inoculations. The gourds, *Lagenaria siceraria* (P. I. 247681) and *L. leucantha* (P. I. 256069), were susceptible only to f. sp. *lagenariae*. *Luffa aegyptiaca* (P.

TABLE 1. Reactions and percentages of wilted plants (external symptoms) of 35 cultivars of muskmelon after inoculation with isolates of seven races of *Fusarium oxysporum* f. sp. *melonis*

Susceptibility groups of cultivars[a]	Origin of isolates and reaction of cultivars to races															
	Israel (498)		France								US-Canada		Israel (188/3)		Japan	
	Race 1		Race 1		Race 2		Race 3		Race 4		Race 5		Race 6		Race 7	
	R/I/S	(%)	R/I/S	(%)	R/I/S	(%)	R/I/S	(%)	R/I/S	(%)	R/I/S	(%)	R/I/S	(%)	R/I/S	(%)
Susceptible:																
1. Charentais T	S[b]	82	S_3	83	S_2	89	S	100	S_3	98	S_5	74	S_4	94	S_3	81
2. Delicious 51	...		S_2	83	S_2	95	S_2	86	...		I_6	53	...		...	
3. Hale's Best Jumbo	S	100	S_9	97	S_9	84	S_{10}	95	S_6	90	S_{51}	95	S_{10}	79	S_4	97
4. Ein-dor	S	100	S	100	...		S	100	S	94	S	100	S	100	...	
5. Honey Rock	...		S	83	S	83	S	78	...		S_2	96	...		...	
6. Makdimon	S	100	S	100	...		...		...		S	92	S	100	...	
7. Casaba Golden Beauty	...		S	100	S_2	92	S_2	90	S_2	89	S_5	94	S_2	100	S_2	100
Resistant to races 1 and 5:																
8. Ananas Yokneam	R_2	30	R_2	22	R_2	35	S_2	100	S_2	95	R_3	13	S_2	92	R_2	0
9. CM17.187	...		R	13	R	0	S	100	S_2	68	R_2	29	...		...	
10. CM17.187 Calif. sibs	...		R	0	R	0	S	100	...		R_2	0	...		...	
11. Crenshaw	...		R_3	3	S_4	84	S_4	84	...		R_6	0	...		...	
12. Doublon	R_2	0	R_2	0	S_3	91	S_2	87	S_2	93	R_8	0	R_5	31	R_2	0
13. Georgia 47	R	0	R	0	S	100	S	100	S	100	R_4	3	S	93	R	0
14. Iroquois	...		R	27	R	0	I	56	...		R_2	0	...		...	
15. Ogon 9	R	0	R	0	R	0	S_2	76	R_7	12	R_{18}	31	R_4	0	S_4	94
16. Oriental Kinpyo	...		R_2	29	R_2	30	S_2	85	R_2	28	R_7	43	R_3	27	S_3	89
17. Persian Small	...		R_3	11	S_3	94	S_3	92	S_2	77	R_6	0	S_2	92	R_2	25
18. Saticoy Hybrid	...		R	0	S	100	S	100	...		R_3	0	...		...	
19. Smith's Perfect	R	0	R_2	0	S_3	97	S_3	97	S_2	100	R_{20}	2	S_4	98	R_3	3
Susceptible to race 1, Resistant to race 5																
20. Earl's Favorite	S	100	S_5	100	S_2	100	S_3	97			R_{14}	7	I_6	51	S_2	68
21. Edisto 47	S_2	100	S_3	100	S_2	100	R_3	37	S_2	96	R_5	30	S	100	S	100
22. Honey Dew	S	92	S_2	88	S_2	65	S_2	89	S_2	72	R_8	13	R_2	20	S_2	76
23. Harvest Queen	S	100	S	100	S	100	S	100	S_2	94	R_4	38	S	100	S	100
24. Haogen	S	100	S	100	...		...		...		R	0	S	75	...	

[a]Cultivars Banana, Charentaiser, Early Watters, Edisto, Hearts of Gold, and Texas Mildew Resistant No. 1 were susceptible to race 5 in single tests. Cultivars Berliner, Golden Gopher, Persian Large, Seed Breeder's, and Von de Bellegrade were resistant to race 5 in single tests.

[b]Letter symbols represent symptoms (as percentage of wilted plants): R = resistant, 0-46%; I = intermediate, 47-56%; and S = susceptible, 57-100%. Subscripts = number of tests; no subscript = one test.

TABLE 2. Reactions and percentages of wilted plants (external symptoms) of 11 cultivars of muskmelon after inoculation with 11 isolates of *Fusarium oxysporum* f. sp. *melonis* from the United States and Canada

	Numbers and origin of isolates and host reaction to isolates from:											
	Canada		Wisconsin		Michigan		Minnesota		North Carolina		Washington	
Cultivar / Number of isolates	3		2		(1 (M4)		1 (M55)		2		2	
	R/I/S	(%)	R/I/S	(%)	R/I/S	(%)	R/I/S	(%)	R/I/S	(%)	R/I/S	(%)
Charentais T	S[a]	64	S	83	...		...		...		S_3	74
Hale's Best Jumbo	S_{25}	93	S_{18}	98	S_2	100	S	100	S_3	91	S_2	100
Ananas Yokneam	R	20	...		...		...		...		R_2	10
Crenshaw	R_2	0	R_2	0	R	0	R	0	...		...	
Doublon	R	0	R	0	R	0	R	0	R_2	0	R_2	0
Earl's Favorite	R_2	0	R_4	23	R	0	R_2	0	R_3	0	R_2	0
Honey Dew	R_2	9	R_3	32	R	0	R_2	0	...		...	
Ogon 9	R	0	R	0	R	0	R	10	R_2	0	R_{12}	44
Persian Small	R_2	0	R_2	0	R	0	R	0	...		...	
Saticoy	R	0	R	0	...		...		R	0	...	
Smith's Perfect	R_6	3	R_8	0	R	0	R	0	R_2	0	R_2	10

[a]Letter symbols represent symptoms (as percentage of wilted plants): R = resistant, 0-46%; I = intermediate, 47-56%; S = susceptible, 57-100%. Subscripts = number of tests; no subscript = one test.

I. 174878) was susceptible only to f. sp. *luffae* (Table 5).

Inoculation of colocynth with Fusarium oxysporum ff. sp. cucumerinum, -melonis, and -niveum and citron with the latter two formae speciales.—Colocynth was susceptible to f. sp. *niveum* only, and citron was resistant to both ff. sp. *melonis* and *niveum* (Table 4).

Inoculation of plants other than cucurbits with Fusarium oxysporum ff. sp. cucumerinum, -melonis, -luffae, and -niveum.—The plants listed in Table 2 of Armstrong and Armstrong (4) were inoculated with each of the preceding formae speciales. Only those of the Cucurbitaceae were susceptible. Additional nonsusceptible plants were castor bean (*Ricinus communis* L. 'Red Spire'), gladiolus (*Gladiolus* spp. 'Picardy'), gourd (*Lagenaria leucantha* Rusby 'P. I. 256069'), and Bambarra groundnut (*Voandzeia subterranea* L. 'BA/4/1').

Inoculation of cucumber, muskmelon, Luffa, and watermelon with other formae speciales and races of F. oxysporum.—Fifty formae speciales and races were nonpathogenic on cucumber Ashley or Palmetto; *Luffa aegyptiaca* P. I. 174878; muskmelon Hale's Best Jumbo; and watermelon Garrison, Sugar Baby, or Watson. These formae speciales and races were *apii*; *asparagi*; *batatas*

TABLE 3. Seven races of *Fusarium oxysporum* f. sp. *melonis* differentiated by the reactions of six cultivars

Cultivar	Race 1	2	3	4	5	6	7
Charentais T or	S_3[a]	S_2	S	S_3	S_5	S_4	S_3
Hale's Best Jumbo[b]	S_9	S_9	S_{10}	S_6	S_{51}	S_{10}	S_4
Ananas Yokneam	R_2	R_2	S_2	S_2	R_3	S_2	R_2
Doublon	R_2	S_3	S_2	S_2	R_8	R_5	R_2
Earl's Favorite	S_5	S_2	S_2	S_3	R_{14}	I_6	S_2
Ogon 9	R_2	R	S_2	R_7	R_{18}	R_4	S_4
Smith's Perfect	R_2	S_3	S_3	S_2	R_{20}	S_4	R_3

[a]Letter symbols represent symptoms (as percentage of wilted plants): R = resistant, 0-46%, I = intermediate, 47-56%; and S = susceptible, 57-100%. Subscripts = number of tests; no subscript = one test.

[b]Both cultivars susceptible to isolates of all races; Charantais T is readily available in France and Hale's Best Jumbo is readily available in the USA. The last seed lot of Hale's Best Jumbo showed appreciable resistance to *F. oxysporum* f. sp. *melonis*.

TABLE 4. Reactions (external symptoms) of watermelon, citron, and colocynth inoculated with *Fusarium oxysporum* ff. sp. *niveum*, *-cucumerinum*, and *-melonis*

Plants	*Fusarium oxysporum* f. sp. *-niveum* South Carolina	*-cucumerinum* US-Germany	*-melonis* US-Canada Race 5
Watermelon cultivars:			
1. Black Diamond	S	...	R
2. Black Diamond Yellow Flesh	S_2	R_5	R_3
3. Blacklee	I	R	R
4. Chris Cross	R	R	R
5. Clara Lee	S_2	R_3	R_4
6. Cole's Allheart	S	R_{10}	R_4
7. Congo	R	R	R
8. Florida Favorite	S	R_{10}	R
9. Garrison	S_{14}	R_3	R_5
10. Golden Sweet	S	R	R
11. Kleckley	S	...	R
12. Klondike R7	R	...	R
13. Miles	R	R_3	R_3
14. New Hampshire Midget	S	R_5	R_3
15. Royal Golden	S	R	R
16. Tender Sweet	S	R	R
17. Willhite Wonder	S_7	R_9	R_3
Citron	R_2	...	R
Colocynth	S	R	R_2

[a]Letter symbols represent symptoms (as percentage of wilted plants): R = resistant, 0-46%; I = intermediate, 47-56%; and S = susceptible, 57-100%. Subscripts = number of tests; no subscript = one test.

races 1, 2; *betae* (*spinaciae* race 2); *callistephi* race 1; *carthami* races 1, 2, 3; *cassiae*; *chrysanthemi*; *cepae*; *conglutinans* races 1, 2, 3, 4; *cubense* race 1; *cyclaminis*; *dianthi*; *fragariae*; *gladioli*; *glycines*; *hebe*; *lagenariae*; *lilii*; *lupini* race 2; *lycopersici* races 1, 2; *medicaginis*; *melongenae*; *narcissi*; *passiflorae*; *perniciosum* race 1; *phaseoli*; *pisi* races 5, 6; *pyracanthae*; *rhois* (*callistephi* race 3); *ricini*; *sesami*; *spinaciae* race 1; *tracheiphilum* races 1, 2, 3; *tuberosi*; *tulipae*; *vasinfectum* races 1, 2, 3, 4; and *voandzeiae*. The exceptions were: no inoculations of f. sp. *pyracanthae* on cucumber; ff. sp. *chrysanthemi*, *cubense* race 1, *cyclaminis*, *fragariae*, *hebe*, and *tuberosi* on *Luffa*; and f. sp. *carthami* races 2 and 3 on cucumber, muskmelon, or watermelon.

DISCUSSION

Owing to the large volume of literature on the Fusarium wilts of the cucurbits that has appeared since the first report of watermelon wilt in 1899 (49), our citations have had to be restricted to papers that are most pertinent to the objectives of this investigation. For example, over 40 citations would be required in a comprehensive review of the results of merely the cross inoculations by other workers.

There are contradictions among the studies, which no doubt are due, in part at least, to the diversity of methods and environmental conditions in the investigations. Among the more important factors influencing the results are (i) media for the growth of the plants; (ii) variations in temperature; (iii) nature and concentration of the inoculum; (iv) variation in pathogens; (v) differential hosts of unknown genomes; (vi) stages of growth at which inoculated, as seedlings or more mature plants; (vii) inoculations with or without transplanting into naturally or artificially infested media, and with or without cutting the roots or dipping them in inoculum. Some of these are discussed briefly.

Bouhot (12) produced biochemical mutants of ff. sp. *melonis* and *niveum* that showed an overlapping of genes for pathogenicity, which indicates that they have potentialities for attacking both hosts. This in part might account for some of the variable host-pathogen interactions that have been reported.

Media for growth of plants.—Most workers have used soil of numerous types with various additions of inoculum for growth of the plants and generally agree that more wilt occurs in sterilized than in nonsterilized soil (16, 35, 36, 52). Also, the toxic effects of sterilized soil alone (2, 28) or with the addition of organic matter such as corn-meal, oat hulls, and wheat-oats mixtures have been noted (2, 16, 47, 52). Sand with the addition of a nutrient solution has been a good medium for normal growth of all plants in our experiments except those of muskmelon, in which the plants showed a severe physiological disorder similar to that reported by Ivanoff (21) and Pierce and

TABLE 5. Reactions of colocynth, cucumber, muskmelon, watermelon, and gourds inoculated with *Fusarium oxysporum* ff. sp. *lagenariae* and *-luffae*

Plants	*F. oxysporum* f. sp.	
	lagenariae	*luffae*
Colocynth:		
Paddy melon (Australia)	R[a]	R
Cucumber:		
Ashley	R	R
White wonder	...	R
Muskmelon:		
Hale's Best Jumbo	R	R_3
Smith's Perfect	R	S_{26}
Watermelon:		
Florida Favorite	...	R
Sugar Baby	R	R
Willhite Wonder	...	R
Gourds:		
Lagenaria siceraria P. I. 247681	S_2	...
L. leucantha P. I. 256069[b]	S_{11}	R_2
L. cucumis anguineous 'Serpent'	...	R_2
L. cucumis anguineous 'Giant bottle'	...	R_2
L. ovifera 'Apple-Small'	...	R_2
L. ovifera 'Nest Egg'	...	R
Luffa aegyptiaca P. I. 174878	R	S_{39}
Italian Edible Gourd	...	R

[a]Letter symbols represent symptoms (as percentage of wilted plants): R = resistant, 0-46%; I = intermediate, 47-56%; and S = susceptible, 57-100%. Subscripts = number of tests; no subscript = one test.

[b]*Lagenaria leucantha*, duplicate pots, R to f. sp. *cucumerinum*; *melonis* races 1, 2, 3, 4, 5; f. sp. *niveum* (SC); and in single pots R to ff. sp. *ricini* and *voandzeiae*.

Stoddard (41). A coarse sand was mentioned (41) as the superior medium, but we found the disorder severe in an acid-washed coarse sand passing a 0.97-mm (20-mesh) sieve. However, sand has been used by others as a growth medium for muskmelon (52) or for growth to the transplant stage (44, 45). Since excellent plants of muskmelon were grown in vermiculite, it has been used in our experiments. Others have used this material for direct seeding into plastic pots and subsequent inoculation (40), or as the medium for growth of the plants in which a potato-dextrose broth culture of the fungus had been incorporated as inoculum (13).

Variation in temperature.—Although the optimum temperature for the growth of f. sp. *melonis* is similar to that for practically all formae speciales of *F. oxysporum* causing wilt diseases; viz., 26-28 C, Leach (26, 27) reported the disease was most severe at lower temperatures, and the optimum was placed at 21-25 C by Leach and Currence (28). An increase in disease severity at temperatures below 30 C was noted (35, 36, 42), but Reid (42) found this true chiefly for resistant cultivars since there was a high disease incidence in the susceptible Bender's Surprise at 30 C. At 30-35 C, Veldeman and Welvaert (51) found that infected muskmelons grew for a month without wilting, but, by lowering the temperature, they wilted in 10 days. Mortensen (37) found that the disease was inhibited by high summer temperatures, but 30 C was better for testing the resistance of muskmelon, than was 16 C since many resistant plants were killed at the lower temperature. Mas and Risser (30) found the aggressiveness of three races of f. sp. *melonis* decreasing with high temperature and high light intensity. Only the results from the inoculations of muskmelon during the fall, winter, and spring are presented here since we also found that, in the greenhouse, the high summer temperatures reduced or inhibited the disease.

Nature and concentration of the inoculum.—Numerous methods for growing the inoculum have been employed. In using an organic base for growing f. sp. *melonis* as inoculum, a low inoculum concentration used in dilution experiments was shown to result in severe wilt (35, 36); a factor or factors other than the population of the fungus affected the wilt potential of a soil (53); the fungus in a 10-day-old inoculum caused higher percentages of wilt than when grown for 2 or 5 mo, supposedly due to toxic metabolites (47); and the resistance reactions of cultivars as R or S could be detected only at an intermediate concentration, since higher concentrations caused wilt of the resistant cultivars (17). A liquid inoculum suspension filtered through cheesecloth and with a final concentration of 10^6 conidia/ml gave best results (9). The liquid inoculum in our experiments has been used over a long period with many hosts and fusaria. Dilutions of 1:1 or 1:2 of the inoculum of several formae speciales did not change significantly the percentages of wilt of their respective hosts. Furthermore, the undiluted inoculum of the wilt fusaria of cotton and cowpea had been shown to give the same relative susceptibility ratings of their respective hosts in the greenhouse as in separate heavily infested field plots. The many tests on both susceptible and resistant cultivars of the cucurbits in which there was consistently no wilt of the resistant ones and 80-100% wilt of the susceptible ones indicated that the inoculum concentration was not too high nor too low (Table 1). This inoculum has provided a concentration in a range whereby the full pathogenic potentialities of a wilt *Fusarium* could be determined.

Variation in pathogens.—Storing cultures of f. sp. *melonis* in sterilized soil to maintain the wild type and presumably the virulence was recommended (32, 33, 35); however, mutation in sterile soil culture has been reported (34). The reduction in virulence or complete loss of pathogenicity of isolates on laboratory media has been stressed in several of our papers (3, 4, 7). Virulent isolates have been maintained chiefly through constant checking and passing through the host in inoculations. However, when a virulent isolate was lost, a replacement was obtained from the American Type Culture Collection where they have been preserved by freezing techniques.

Host-pathogen specialization.—Differences in virulence of isolates of f. sp. *niveum* without clear host-specific pathogenicity to indicate races have been reported (10, 20, 48). Sleeth (48) made an extensive collection of isolates of f. sp. *niveum*, apparently in search of races, but concluded that they differed merely in degrees of virulence. Crall (14, 15) reported races 1 and 2 in Florida. Netzer and Dishon (38) reported race 3 in Israel.

We found no races among a fairly large number of isolates of f. sp. *niveum* collected in the U.S. during a 10-yr period. The most recent studies with a freshly collected isolate from South Carolina and races 1 and 2 from Florida (14) showed differences in degrees of virulence but were inconclusive in the differentiation of races. However, the isolates from Florida had been in culture for several years.

Welty (52), using 17 isolates of f. sp. *melonis* on three cultivars, and Rodriquez (47), using 10 isolates on three other cultivars, found no host-pathogen specialization. Eide and Makila (18) found what appeared to be pathogenic specificity of f. sp. *melonis* for cultivar Iroquois. Douglas (17) found apparent race-specific resistance in one breeding line but concluded that further tests were necessary to determine if this was so. We found no evidence of host-pathogen specialization among 11 isolates of f. sp. *melonis* from the U.S. and Canada used at random among 35 lines or cultivars (Table 2). However, after the addition of isolates and cultivars from France, Israel, and Japan, pathogenic races were apparent (Table 1).

Proposal for races of F. oxysporum f. sp. melonis.—The International Code of Botanical Nomenclature 1972 (50 Art. 4, Note) states that the formae speciales shall not be covered by the Code. However, the importance of formae speciales and races of the wilt fusaria to pathologists, plant breeders, and others suggests that, if rules can be established under which the validity of names for such categories can be shown by adequate differentiation, proper preservation, and effective publication, it seems desirable to try to have them accepted by the International Congress. Our ideas on some phases of the problem have been presented (6, 7). The recently proposed nomenclature for races of f. sp. *melonis* by Risser et al. (46) follows the system devised for *Phytophthora infestans* (11); however, Risser et al. suggested that this system probably could cause confusion if additional races are found. Until the genes for resistance in the cultivars of muskmelon are known, we shall follow a numerical system for races of f. sp. *melonis*; i.e., 1, 2, 3, and 4 as originally and validly proposed (44, 45).

The resistance of one cultivar, Persian Small, after inoculation with a Michigan isolate (M4) led Banihashemi (8) to suggest a fourth race in 1968 in a Dissertation Abstract. If he had inoculated this cultivar with races 1, 2, 3, and 4, its resistance to race 1 also would have been apparent, and there would have been no basis for a new race. Based on our inoculations in 1967, Persian Small is resistant to race 1, susceptible to races 2 and 3 (Table 1), and resistant to isolate M4, which was supplied by Banihashemi (Table 2).

In 1975, Banihashemi and deZeeuw (9) reported the M4 isolate to be a new race (race 4) but did not mention the earlier description of race 4 by Risser et al. (45). According to the rules of priority, therefore, the use of race 4 by Banihashemi and deZeeuw (9) and by Gubler and Grogan (19) is invalid. If the M4 isolate is a new race, another number is necessary. We reported in 1970 (5) that an additional race was known, but since it was in an abstract, no number was given.

Due to the new races, additional cultivars are needed as differentials; viz., Ananas Yokneam, Earl's Favorite, and Smith's Perfect (Table 3). Therefore, races 1, 2, 3, and 4 Risser et al. (44, 45) are revised to include these differentials and races 5, 6, and 7 are proposed. In the following list of differentials for each race the capital letters S, I, and R indicate susceptible, intermediate, and resistant, respectively.

Race 1. Differentials: Charentais T and Earl's Favorite, S; Ananas Yokneam, Doublon, Ogon 9, Smith's Perfect, and CM17.187, R.

Race 2. Differentials: Charentais T, Doublon, Earl's Favorite, and Smith's Perfect, S; Ananas Yokneam, Ogon 9, and CM17.187, R.

Race 3. Differentials: Ananas Yokneam, Charentais T, Doublon, Earl's Favorite, Ogon 9, Smith's Perfect, and CM17.187, S. This is the only race that causes complete wilting without yellowing.

Race 4. Differentials: Ananas Yokneam, Charentais T, Doublon, Earl's Favorite, and Smith's Perfect, S; Ogon 9, R. Symptoms are similar to those caused by races 1 and 2.

Race 5. Differentials: Charentais T, S; Ananas Yokneam, Doublon, Ogon 9, and Smith's Perfect, R (also R to race 1); Earl's Favorite, R (but S to race 1).

Race 6. Differentials: Ananas Yokneam, Charentais T, and Smith's Perfect, S; Earl's Favorite, I; Doublon and Ogon 9, R.

Race 7. Differentials: Charentais T, Earl's Favorite, and Ogon 9, S; Ananas Yokneam, Doublon, and Smith's Perfect, R.

Plants from the last lot of seed of Hale's Best Jumbo have shown an appreciable degree of resistance to all races.

Isolates of the formae speciales of *Fusarium oxysporum* mentioned have been deposited with the American Type Culture Collection, Rockville, Maryland and are catalogued as follows: f. sp. *cucumerinum*, ATCC 16416; f. sp. *lagenariae*, ATCC 18143; f. sp. *luffae*, ATCC 26860; f. sp. *melonis*, race 1 ATCC 28856; f. sp. *melonis*, race 2 ATCC 28857; f. sp. *melonis*, race 3 ATCC 28858; f. sp. *melonis*, race 4 ATCC 28859; f. sp. *melonis*, race 5 ATCC 16418; f. sp. *melonis*, race 6 ATCC 28862; f. sp. *melonis*, race 7 ATCC 28861; f. sp. *melonis* M-4 from Michigan, ATCC 32669; f. sp. *niveum*, ATCC 18467.

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