# Vegetative Compatibility, Pathogenicity, and Virulence Diversity of *Fusarium oxysporum* Recovered from Spinach

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## ABSTRACT

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Four hundred thirty-nine isolates of *Fusarium oxysporum* recovered from symptomatic spinach seedlings and mature plants from Arkansas, California, New York, Oklahoma, South Carolina, Tennessee, and Washington in the United States as well as from Canada, Japan, and Sweden were examined for vegetative compatibility. A total of 110 isolates also were tested for pathogenicity on spinach. A minimum of 23 vegetative compatibility groups (VCGs) were identified among the 439 isolates in the collection. However, 216 (49%) of the isolates belonged to one of three vegetative compatibility groups (VCGs 1, 2, or 3). Of these 216 isolates, 125 (58%) belonged to VCG 1, 58 (27%) to VCG 2, and 33 (15%) to VCG 3. Fifty-five geographically diverse isolates from VCGs 1, 2, and 3 and 55 isolates vegetatively incompatible with VCGs 1, 2, and 3 were tested for pathogenicity on the spinach cultivar Grandstand. Of the 55 isolates in VCGs 1, 2, and 3 tested, 53 were pathogenic on spinach seedlings, while the 55 remaining isolates were not pathogenic on spinach. Among the three VCGs of *Fusarium oxysporum* f. sp. *spinaciae* identified, two distinct virulence phenotypes were detected. Isolates in VCGs 1 and 3 were significantly more virulent on the cultivar Grandstand than isolates in VCG 2. The *F. o.* f. sp. *spinaciae* population was composed of three VCGs that have a worldwide distribution, including the United States, Canada, Japan, and Sweden.

*Fusarium oxysporum* Schlechtend.:Fr. f. sp. *spinaciae* (Sherb.) W.C. Snyder & H.N. Hans., an important soilborne pathogen of spinach (*Spinacia oleracea* L.), causes seedling damping-off and wilt of mature plants (1,10,11,13,15,21,22). *F. o.* f. sp. *spinaciae* has been reported in Arkansas, Arizona, California, Idaho, Vermont, and Ontario, Canada (1,10,11,13,21). It also has been reported to be part of a seedling disease complex of spinach in Georgia, Japan, and Sweden (15,18,22). In Arkansas, isolations from symptomatic spinach indicate that *F. o.* f. sp. *spinaciae* is a major component of a seedling disease complex as well as a pathogen of mature plants (3). Typically, *F. o.* f. sp. *spinaciae* causes seedling damping-off when the spinach crop is planted in warm soils in late summer to early fall (August to September) in Arkansas. It is more of a problem on mature plants in the spring crop, which is planted in early spring (February to March). Bassi and Goode (3) hypothesized that *F. o.* f. sp. *spinaciae* was introduced into both seed and commercial production areas by infected or infested seed.

Armstrong and Armstrong (2) reported two races of *F. o.* f. sp. *spinaciae*. Race 1 was pathogenic on spinach, sugar beet (*Beta vulgaris* L.), and Maltese-cross (*Lychnis chalcedonica* L.), was less pathogenic than race 2 on Swiss chard (*Beta vulgaris* L. subsp. *cicla* (L.) W. Koch), and was nonpathogenic on mangel (*Beta vulgaris* L.). Race 2 was pathogenic on sugar beet, beet (*Beta vulgaris* L.), mangel, and Swiss chard, and nonpathogenic on spinach.

Efforts to identify spinach cultivars, breeding lines, or plant accessions with immunity to *F. o.* f. sp. *spinaciae* have been unsuccessful (11,19). However, some differences in disease resistance have been observed among spinach accessions (19). Several spinach cultivars, including Virginia Savoy, Ozarka, Greenvalley, and Fall Green, are reported to have field resistance to *F. o.* f. sp. *spinaciae* (4,5,12).

With the exception of pathogenicity tests, very little work has been done to characterize *F. oxysporum* associated with spinach. A better understanding of the genetic diversity of *F. oxysporum* attacking spinach should allow plant breeders to more effectively screen for *Fusarium* resistance in spinach. The objective of this study was to characterize isolates of *F. oxysporum* associated with spinach seed, seedlings, and mature plants on the basis of vegetative compatibility, pathogenicity, and virulence. A preliminary report of this work has been published (9).

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## MATERIALS AND METHODS

**Isolations.** Isolations were made primarily from symptomatic spinach seedlings (four or fewer true leaves) and mature plants (more than six true leaves) in 1991 and 1992. Most seedlings were recovered from fields with a long history of spinach production in the Arkansas River Valley in Arkansas and Oklahoma. Several isolates of *F. oxysporum* also were recovered from plants in a reproductive stage (bolting). Isolates were recovered on water agar or Komada's medium (14). Monoconidial isolates were subcultured onto potato-dextrose agar (PDA) and stored on desiccated filter paper as previously described (8). Several isolates were received as pure cultures from other researchers and the American Type Culture Collection (ATCC). The ATCC isolates included three spinach isolates from Arkansas, California, and Canada and a sugar beet isolate from Colorado. In addition, 150 seeds from each of three commercially produced spinach cultivars were placed on Komada's medium and examined for contamination by *F. oxysporum*.

**Vegetative compatibility tests.** Nitrate nonutilizing (*nit*) mutants were generated on 1.5% chlorate medium (20). The phenotypes of the *nit* mutants were determined by growing *nits* on several media amended with different nitrogen sources

**Table 1.** Number and geographic distribution of vegetative compatibility groups of *Fusarium oxysporum* from spinach

| VCG[y] | No. of isolates | Geographical origin |
|---|---|---|
| 1 | 94 | Arkansas |
| 1 | 1 | New York |
| 1 | 17 | Oklahoma |
| 1 | 3 | South Carolina |
| 1 | 1 | Tennessee |
| 1 | 2 | Japan |
| 1 | 7 | Sweden |
| 2 | 34 | Arkansas |
| 2 | 1 | California |
| 2 | 4 | Oklahoma |
| 2 | 1 | Tennessee |
| 2 | 7 | Washington |
| 2 | 1 | Canada |
| 2 | 2 | Japan |
| 2 | 8 | Sweden |
| 3 | 24 | Arkansas |
| 3 | 1 | Arkansas or Virginia |
| 3 | 4 | Oklahoma |
| 3 | 1 | Washington |
| 3 | 2 | Japan |
| 3 | 1 | Sweden |
| 4 - 23 | 66 | Arkansas and Oklahoma |
| NC[z] | 157 | ... |

[y] VCG = Vegetative compatibility group.
[z] Isolates were not vegetatively compatible with isolates in VCGs 1, 2, or 3.

(6). *Nit*1 and NitM tester strains were generated from all isolates. Appropriate *nit* mutant testers were paired on minimal agar medium (MM) to determine which isolates were vegetatively compatible (6). Isolates were scored for complementation over a 2-week period. Complementation was scored as weak, intermediate, or strong depending on how robust a heterokaryon was formed. Isolates that were vegetatively compatible were assigned to the same vegetative compatibility group (VCG). VCGs were only assigned to isolates when two phenotypically distinct *nit* mutants from a given isolate were recovered and were capable of complementation.

**Pathogenicity test.** Isolates for pathogenicity tests were selected on the basis of VCG diversity, geographic origin, and host age diversity. One hundred ten isolates representing at least 23 different VCGs from seven states (Arkansas, California, New York, Oklahoma, South Carolina, Tennessee, and Washington) and three other countries (Canada, Japan, and Sweden) were tested for pathogenicity on spinach seedlings in a greenhouse inoculation test. The majority of the isolates were recovered from spinach seedlings. Four isolates (MF231, MF257, MF263, MF264) were recovered from 5- to 6-week-old spinach plants with more than six true leaves. Seven isolates (MF210, MF213, MF214, MF219, MF220, MF240, MF241) were recovered from three flower-

**Table 2.** Vegetative compatibility group, origin, and pathogenicity of *Fusarium oxysporum* recovered from spinach

| VCG[w] | Isolate | Origin | Pathogenicity[x] | VCG[w] | Isolate | Origin | Pathogenicity[x] |
|---|---|---|---|---|---|---|---|
| 1 | MF5*[y] | Arkansas | + | 4 | MF6 | Arkansas | – |
| 1 | MF15* | Arkansas | + | 4 | MF71 | Arkansas | – |
| 1 | MF84 | Arkansas | + | 5 | MF77 | Arkansas | – |
| 1 | MF210 | Arkansas | + | 6 | JB1 | Arkansas | – |
| 1 | MF213 | Arkansas | + | 7 | JB6 | Arkansas | – |
| 1 | MF220 | Arkansas | + | 8 | JB7 | Arkansas | – |
| 1 | MF241 | Arkansas | + | 9 | JB10 | Arkansas | – |
| 1 | MF257 | Arkansas | + | 10 | JB16 | Arkansas | – |
| 1 | NY1* | New York | + | 11 | JB18 | Arkansas | – |
| 1 | OK11* | Oklahoma | + | 12 | JB21 | Arkansas | – |
| 1 | SC15* | South Carolina | + | 13 | KB9 | Arkansas | – |
| 1 | SC30 | South Carolina | + | 14 | MF2 | Arkansas | – |
| 1 | MF68* | Tennessee | + | 14 | MF7 | Arkansas | – |
| 1 | SP1 | Japan | + | 14 | MF154 | Oklahoma | – |
| 1 | SP6* | Japan | + | 14 | MF158 | Oklahoma | – |
| 1 | ML4 | Sweden | + | 15 | MF 37 | Arkansas | – |
| 1 | ML7 | Sweden | + | 16 | MF1 | Arkansas | – |
| 1 | ML10* | Sweden | + | 17 | MF99 | Arkansas | – |
| 1 | ML11 | Sweden | + | 17 | MF100 | Arkansas | – |
| 1 | ML14 | Sweden | + | 17 | MF169 | Oklahoma | – |
| 1 | ML15 | Sweden | + | 18 | MF67 | Arkansas | – |
| 1 | ML17 | Sweden | + | 18 | MF152 | Oklahoma | – |
| 2 | MF12 | Arkansas | + | 19 | MF118 | Arkansas | – |
| 2 | MF34* | Arkansas | + | 19 | MF160 | Oklahoma | – |
| 2 | MF35 | Arkansas | + | 19 | MF167 | Oklahoma | – |
| 2 | MF44 | Arkansas | + | 19 | MF191 | Oklahoma | – |
| 2 | MF219 | Arkansas | – | 20 | MF125 | Arkansas | – |
| 2 | MF240 | Arkansas | + | 21 | MF143 | Oklahoma | – |
| 2 | MF263 | Arkansas | – | 22 | MF162 | Oklahoma | – |
| 2 | ATCC34299* | California | + | 23 | MF164 | Oklahoma | – |
| 2 | OK7* | Oklahoma | + | NC[z] | MF72 | Arkansas | – |
| 2 | MF69* | Tennessee | + | NC | MF76 | Arkansas | – |
| 2 | AC2* | Washington | + | NC | MF214 | Arkansas | – |
| 2 | ATCC38620 | Canada | + | NC | MF231 | Arkansas | – |
| 2 | SP3* | Japan | + | NC | MF221 | California | – |
| 2 | SP5* | Japan | + | NC | MF224 | California | – |
| 2 | ML2* | Sweden | + | NC | MF225 | California | – |
| 2 | ML3 | Sweden | + | NC | MF233 | California | – |
| 2 | ML9 | Sweden | + | NC | MF242 | California | – |
| 2 | ML12 | Sweden | + | NC | MF234 | California | – |
| 2 | ML18 | Sweden | + | NC | MF243 | California | – |
| 2 | ML20 | Sweden | + | NC | MF245 | California | – |
| 3 | MF3 | Arkansas | + | NC | MF230 | California | – |
| 3 | MF9* | Arkansas | + | NC | MF222 | California | – |
| 3 | MF20 | Arkansas | + | NC | MF229 | California | – |
| 3 | MF21 | Arkansas | + | NC | ATCC36331 | Colorado | – |
| 3 | MF42* | Arkansas | + | NC | MF73 | Oklahoma | – |
| 3 | MF58 | Arkansas | + | NC | SC1 | South Carolina | – |
| 3 | MF63 | Arkansas | + | NC | SC5 | South Carolina | – |
| 3 | MF264* | Arkansas | + | NC | SC24 | South Carolina | – |
| 3 | ATCC18780* | Arkansas | + | NC | SC31 | South Carolina | – |
| 3 | FO23* | Washington | + | NC | ML1 | Sweden | – |
| 3 | SP2* | Japan | + | NC | ML5 | Sweden | – |
| 3 | SP4* | Japan | + | NC | ML6 | Sweden | – |
| 3 | ML16* | Sweden | + | NC | ML8 | Sweden | – |

[w] VCG = vegetative compatibility group.

[x] Each inoculation experiment was conducted on 10–20 seedlings per replicate with three replicates on the cultivar Grandstand. Disease rating scale of 0–2 was used: 0 = no symptoms, 1 = wilt symptoms, 2 = dead plant. An isolate was considered pathogenic (+) if the mean disease rating was ≥0.5 for both tests.

[y] An asterisk (*) denotes isolates used in experiments to compare virulence between pathogenic vegetative compatibility groups.

[z] NC = not vegetatively compatible with isolates in VCGs 1, 2, or 3.

ing spinach plants. A sugar beet isolate (ATCC36331) also was included. Each isolate was streaked on PDA and grown under fluorescent light (24-h photoperiod) for 2 to 5 days. Spores were rinsed off the plates with sterile distilled water, and the spore concentration was adjusted to $1 \times 10^6$ spores per ml. Pregerminated seed (cv. Grandstand) were planted in Todd planter flats (model 100A, Speedling Corp., Sun City, FL) with 200 cells and a cell size of 2.5 × 2.5 × 7.6 cm. Flats were drenched with a solution of metalaxyl (0.066 ml a.i./liter), once at planting and once after 7 days, to control *Pythium* sp. Spinach seedlings (11 to 14 days old) were inoculated by placing 10 ml of inoculum in the root zone using a repeating syringe. The experiment was conducted as a randomized complete block design with three replicates and 10 plants per replicate. All isolates were tested twice. Seedlings were rated for disease severity on a scale of 0–2, where 0 = no disease, 1 = wilting of foliage, and 2 = dead seedlings. Seedlings were rated every 2 days for 15 days after inoculation. An isolate was considered pathogenic if the mean disease rating was ≥0.5 after 3 weeks. Isolates were compared within pathogenicity tests by the general linear model procedure using the Statistical Analysis System (SAS) (SAS Institute, Inc., Cary, NC 27511).

Greenhouse temperatures fluctuated daily during seedling pathogenicity tests. The average daily minimum and maximum temperatures for the pathogenicity tests were 20 and 35°C, respectively.

**Virulence test.** Isolates for virulence tests were selected on the basis of VCG diversity and geographic origin. Eight isolates from each of the three pathogenic VCGs (VCGs 1, 2, and 3) were tested for virulence on spinach seedlings. Most of these isolates were recovered from symptomatic spinach seedlings. Isolates were tested for virulence as previously described. Seedlings were rated every 2 days for 3 weeks after inoculation. Areas under the disease progress curve (AUDPC) also were calculated for each VCG and analyzed using the general linear model procedure of the SAS. Least square means were used to compare VCGs by a multiple *t* test. Standard errors were generated for each VCG based on variation among isolates within a VCG.

Temperatures fluctuated daily during the seedling virulence tests. The average daily minimum and maximum for the two virulence tests were 18 to 23°C and 24 to 32°C, respectively.

**Table 3.** Isolates of *Fusarium oxysporum* recovered from soil and plants at different stages of maturity

| Source of isolate | Isolates examined | Number of isolates (%) | | |
|---|---|---|---|---|
| | | VCG 1 | VCG 2 | VCG 3 |
| Seedlings | 263 | 69 (26.2) | 21 (8.0) | 22 (8.4) |
| Mature plants | 70 | 29 (41.4) | 4 (5.7) | 5 (7.1) |
| Flowering plants | 16 | 8 (50.0) | 6 (37.5) | 1 (6.3) |
| Soil | 16 | 2 (12.5) | 0 (0.0) | 0 (0.0) |
| Plant (age unknown) | 74 | 17 (24.3) | 27 (38.6) | 5 (7.1) |

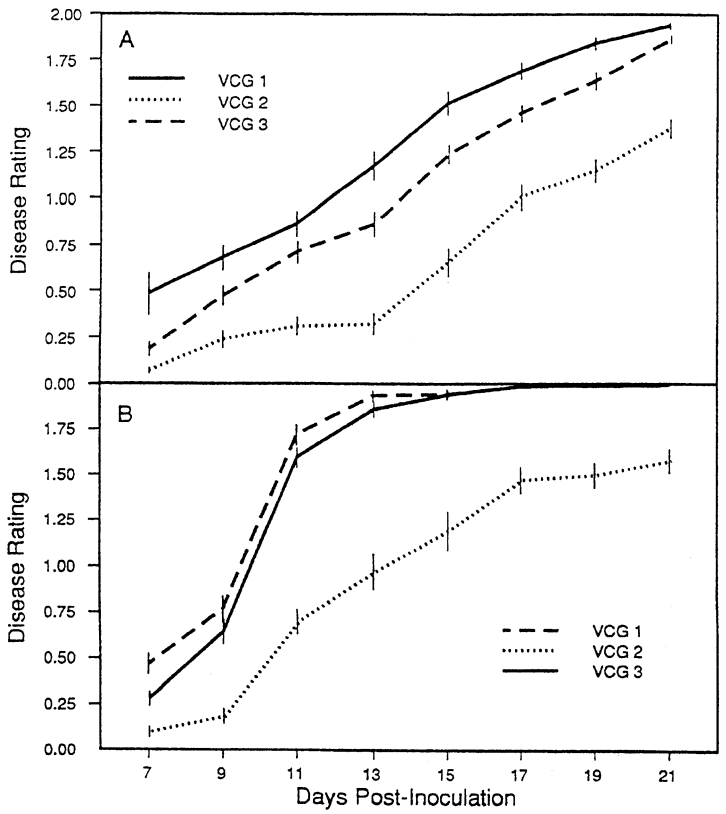


**Fig. 1.** Mean disease progress for VCGs 1, 2, and 3 of *Fusarium oxysporum* f. sp. *spinaciae*. Disease rating scale of 0–2, where 0 = no symptoms, 1 = wilting, and 2 = dead. Vertical lines represent ±1 standard error (A = experiment 1 and B = experiment 2).

## RESULTS

**Isolations.** A total of 439 isolates of *F. oxysporum* was examined for vegetative compatibility in this study. Two hundred sixty-three isolates were recovered from spinach seedlings, 70 from mature plants, 16 from plants with a seed stalk, 16 from spinach rhizosphere soil, and 74 from plants of undetermined age.

Of 439 isolates of *F. oxysporum* examined, 216 (49%) of the isolates belonged to one of three VCGs (VCGs 1, 2, and 3) (Table 1). Twenty additional VCGs (VCGs 4–23) were identified, with one to 16 isolates per VCG. The remaining 157 isolates were vegetatively incompatible with isolates in VCGs 1–3 but were not given a VCG designation because complementary *nit* mutants were not recovered from these isolates.

Of the 216 isolates in VCGs 1, 2, and 3, 125 (58%) were in VCG 1, 58 (27%) in VCG 2, and 33 (15%) in VCG 3 (Table 2). All three VCGs were recovered from the United States, Japan, and Sweden. A VCG 2 isolate also was recovered from Canada. In the United States, all three VCGs were recovered from Arkansas and Oklahoma. VCG 1 also was recovered from New York, South Carolina, and Tennessee, VCG 2 from California, Tennessee, and Washington, and VCG 3 from Washington.

A total of 58 isolates of *F. oxysporum* was recovered from 150 seed of each of three commercial spinach cultivars. However, none of the 58 isolates recovered

**Table 4.** Area under the disease progress curve (AUDPC) for VCGs 1, 2, and 3 of *Fusarium oxysporum* f. sp. *spinaciae*

| VCG[x] | AUDPC[y] | |
|---|---|---|
| | Test 1 | Test 2 |
| 1 | 18.1 b[z] | 23.1 b |
| 2 | 8.9 a | 13.7 a |
| 3 | 14.8 b | 22.3 b |
| Standard error | 1.1 | 0.6 |

[x] VCG = vegetative compatibility analysis.
[y] AUDPC = area under the disease progress curve in rating*day units.
[z] Data were analyzed using the general linear model of SAS. Least square means were used to compare VCGs by multiple *t* tests. Means within a column followed by a different letter are significantly different ($P > 0.05$).

were vegetatively compatible with VCGs 1, 2, or 3.

VCGs 1, 2, and 3 were recovered from symptomatic seedlings, mature plants, and plants in a reproductive stage (Table 3). However, only 43% of the isolates recovered from seedlings were in VCGs 1, 2, or 3. Fifty-four percent and 94% of the isolates recovered from mature plants and reproductive stage plants, respectively, were in VCGs 1, 2, or 3.

**Pathogenicity test.** In the greenhouse pathogenicity tests, 53 of the 55 isolates in VCG 1, 2, and 3 tested were pathogenic on spinach seedlings (Table 2). All isolates in VCGs 1 and 3 tested were pathogenic on spinach seedlings. Two isolates from VCG 2 (MF219 and MF263) were not pathogenic on spinach seedlings. All 55 isolates from VCGs 4–23 tested were not pathogenic on spinach seedlings.

The majority of the pathogenic isolates of *F. o.* f. sp. *spinaciae* were recovered from symptomatic seedlings or mature plants. However, six of the seven isolates (MF210, MF213, MF219, MF220, MF240, MF241) recovered from plants with seed stalks that were tested were pathogenic on spinach, and one isolate (MF214) was not pathogenic. Three of the four isolates (MF257, MF263, MF264) recovered from mature plants tested were pathogenic on spinach seedlings, while isolate MF231 was not pathogenic.

**Virulence test.** Preliminary observations indicated that isolates in VCGs 1 and 3 were more virulent than isolates in VCG 2. When virulence was compared, the mean disease ratings for isolates in VCGs 1 and 3 were greater than the ratings for isolates in VCG 2 throughout the duration of the rating period (Fig. 1). This was also reflected in the AUDPC. The AUDPC was significantly greater for VCGs 1 and 3 than VCG 2 when isolate variation within a VCG was used as the error term (Table 4). No significant differences in AUDPC were observed between VCGs 1 and 3.

## DISCUSSION

Damping-off of spinach seedlings is an important disease in most spinach producing areas, particularly when fields have been cropped to spinach for successive years (7,15,18). Although a number of damping-off pathogens, including *Pythium aphanidermatum*, *P. irregulare*, *P. ultimum*, *P. dissotocum*, *Pythium* sp., *Aphanomyces cochlioides*, *Phytophthora* spp., and *Rhizoctonia solani,* are known to cause damping-off of spinach, *F. o.* f. sp. *spinaciae* also is an important component of the damping-off complex (7,15,22; M. B. Fiely and J. C. Correll, *unpublished*). In addition, *F. o.* f. sp. *spinaciae* can cause wilting of mature plants, particularly those in a reproductive stage of development (7). In this study, *F. oxysporum* was readily recovered from symptomatic seedlings, mature plants, and plants in a reproductive stage of development. Of the 439 isolates of *F. oxysporum* recovered, 216 (49%) belonged to one of three pathogenic VCGs (VCGs 1, 2, or 3). Fifty-three of the 55 isolates in VCGs 1, 2, and 3 tested were pathogenic on spinach seedlings in a greenhouse pathogenicity test. The pathogenic isolates included six of seven isolates recovered from plants in a reproductive stage and three of four isolates recovered from mature plants.

None of the isolates from all of the other VCGs tested were pathogenic on spinach seedlings. Most of the nonpathogenic isolates of *F. oxysporum* were recovered from symptomatic spinach seedlings (Table 3). It is likely that the nonpathogenic isolates were growing on spinach seedlings as root colonizers and/or as secondary invaders.

In the current study, isolates of *F. o.* f. sp. *spinaciae* were confined to three distinct VCGs, all of which have a worldwide distribution, being recovered from throughout the United States, Japan, and Sweden. VCG 2 also was recovered from Canada. *F. o.* f. sp. *spinaciae* has been recovered from spinach seed and may be a source of pathogen migration (3). However, none of the isolates of *F. oxysporum* recovered from a limited sampling of commercial spinach seed were in VCGs 1, 2, or 3.

Within the *F. o.* f. sp. *spinaciae* population, there was a difference in virulence between isolates in VCG 2 and isolates in VCGs 1 and 3. VCG 2 isolates were significantly less virulent than the isolates in VCGs 1 and 3 on the cultivar Grandstand in a greenhouse pathogenicity test. In addition, two VCG 2 isolates were even classified as avirulent under these inoculation conditions. Examination of molecular diversity within the *F. o.* f. sp. *spinaciae* population also indicates that VCG 2 is distinct from VCG 1 and 3 (10,23).

The genetic relationship between isolates of *F. oxysporum* attacking hosts in the *Chenopodiaceae* has not been thoroughly addressed (2,16,17). Armstrong and Armstrong reported that there were two races of *F. o.* f. sp. *spinaciae,* with race 1 being pathogenic on spinach and beet (*B. vulgaris*), whereas race 2 was not pathogenic on spinach (2). Examination of the VCGs among the isolates of *F. oxysporum* pathogenic on spinach and those pathogenic on beet, as well as cross-inoculation tests, may help to resolve the degree of host specificity that occurs among isolates within *F. o.* f. sp. *spinaciae* and *F. o.* f. sp. *betae* populations.


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