Nature of Cultural Variability in *Fusarium oxysporum* f. sp. *apii* Race 2

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ABSTRACT

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Fusarium oxysporum f. sp. *apii* race 2 was characterized by abundant aerial mycelium (mycelial cultures) when isolated from diseased celery plants and cultured on chloramphenicol-amended potato-dextrose agar (CPDA). Two-week-old mycelial isolates cultured on CPDA at 24–27 C (12-hr photoperiod; fluorescent cool-white light; 3,875 lx) produced abundant microconidia but few macroconidia. When single microconidia were repeatedly transferred from mycelial cultures and grown on CPDA as above, cultures lacking aerial mycelium (pionnotal cultures) frequently were produced. These either originated directly from mycelial cultures or indirectly from intermediate cultures possessing both mycelial and pionnotal patches. Mycelial cultures were more virulent on celery than pionnotal cultures. Twenty-nine percent of plants infected with mycelial cultures developed vascular dicoloration and 3% died after 8 wk. None of the plants infected with pionnotal cultures developed any of these symptoms. In a sterile soil extract solution, mycelial cultures significantly produced more chlamydospores than pionnotal cultures. Mycelial cultures were less stable than pionnotal cultures and produced fewer macroconidia on CPDA. Radial growth and dimensions of conidia were similar for both culture types. Mycelial and pionnotal cultures maintained their morphological identity when passed through the host and reisolated on CPDA. It appears that only the mycelial type occurs in nature and that the intermediate and pionnotal forms are only of cultural significance.

A previous study (6) has indicated that *Fusarium oxysporum* f. sp. *apii* race 2, causal agent of Fusarium yellows of celery (*Apium graveolens* L. var. *dulce* DC.) in New York, is characterized by abundant production of aerial mycelium and microconidia when isolated from diseased celery plants and grown on chloroamphenicol-amended potato-dextrose agar (CPDA). Variation in cultural characteristics of the fungus after periodic subculturing on CPDA also was observed. Even though cultural and pathogenic variability is well established for a number of *Fusarium* spp. (1,19,21–23), little has been done to investigate this phenomenon extensively in *F. o.* f. sp. *apii* race 2. Ryker (15) obtained evidence of cultural and pathogenic variability in race 1 of the fungus. However, his study was not conclusive because it did not characterize culture variants, their stability on culture media, and their relative pathogenicity.

The present study was undertaken to determine the range and direction of variability in the fungus, compare the virulence of the predominant cultural types, and characterize the wild type of the fungus.

MATERIALS AND METHODS

Direction of variability. The direction of cultural variability in *F. o.* f. sp. *apii* race 2 was studied by making sequential single-microconidial transfers of each generation of the fungus on chloramphenicol-amended Difco potato-dextrose agar (CPDA) in large test tubes (4 × 20 cm) and characterizing the morphological features of the resulting 2-wk-old cultures. Chloroamphenicol had been used routinely and without any deleterious effect in media used previously for isolating the fungus from infected celery plants (6). Three representative and typical monoconidial isolates of the fungus (R-1, P-13, and P-3) selected from a large culture collection of isolates of *F. o.* f. sp. *apii* obtained from infected celery plants in Orange County, NY, were used. Most of these isolates had shown a degree of variability during maintenance on CPDA slants. Mycelial cultures of each of the three typical isolates were grown on CPDA for 8–22.5 wk (duration depending on isolate). The first generation then was established by single-microconidial transfers from a true-to-type culture (wild type), and the progenies were grown on CPDA. After 2 wk, phenotypic scoring was conducted in which cultures were classified as mycelial, intermediate, or pionnotal. They were then grown for an additional period before the next single-microconidial transfers were made. If all progenies in a particular generation were morphologically similar, only one was used to initiate the next generation. However, when a variant was present, the variant and the mycelial type culture were carried into the next generation. In this manner, the isolates were propagated through four to eight test-tube generations. Fifteen monoconidial transfers from a typical mycelial culture as well as 15 for each variant in each generation were made. All cultures were grown at 24–27 C with a 12-hr photoperiod (fluorescent cool-white light; 3,875 lx). Two Sylvania fluorescent tubes (F30T12-CW RS) set 45 cm above the cultures served as the light source.

Pathogenic variation. Pathogenicity of mycelial and pionnotal cultures was determined for cultures derived from four wild types (R-1, P-13, JC-1, NR-1) of *F. o.* f. sp. *apii* race 2. In a typical experiment, single microconidia from 2-wk-old mycelial cultures and corresponding 2-wk-old pionnotal cultures were placed separately in 20 ml of 2.4% potato-dextrose broth (PDB) in 50-ml Erlenmeyer flasks. Each culture was incubated for 2 wk under the light and temperature regimes described previously. The resulting mycelial mat and culture solution then were homogenized in a Waring Blendor with 300 ml of distilled water and used to infest 750 g of steamed Cornell University Plant Pathology greenhouse mix (16.6% sand, 41.7% compost, and 41.7% peat moss) in a plastic bag. The infested soil was placed in three 12.7-cm plastic pots. Three-week-old seedlings of celery cultivar Florida 683 were transplanted into the infested soil (four seedlings per pot). The plants were grown at 24–26 C with a 16-hr photoperiod and watered as needed for 8 wk. They were then rated for disease as described previously (6).

Fate of mycelial and pionnotal cultures after passage through host. Two-week-old mycelial and pionnotal cultures of each of three isolates (JC-1, R-1, and P-13) were grown on PDB and used to inoculate susceptible celery plants as previously described. Plants were grown for a sufficient period (5–10 wk) to permit the pathogen to enter the vascular system of the roots, crown, and at times petioles. Isolation of the pathogen on CPDA plates then was attempted from these areas as previously described (6). Plated tissue sections were incubated in light for 3–5 days, and fungal colonies growing from them were characterized as either mycelial or pionnotal.

Growth rate. Radial growth of mycelial and pionnotal cultures of three isolates (NR-1, JC-1, and P-13) was measured to

investigate its relationship to pathogenicity. Mycelial and pionnotal cultures of each isolate used in the experiment were stored in sterile soil columns (20). A few grains of a soil culture of each culture type were aseptically sprinkled on CPDA plates, which then were incubated on laboratory benches (diffuse sunlight, 27–30 C). Single-microconidial transfers were made after 5 days from the margins of the resulting true-to-type (mycelial or pionnotal) colonies to CPDA plates (10 plates per culture type) and incubated on laboratory benches as described previously. At 4 and 6 days, colony radius was estimated from a measurement of colony diameter taken at two perpendicular planes.

Sporulation intensity. Conidial production in mycelial and pionnotal cultures for three isolates (NR-1, JC-1, and P-13) was determined. In a typical experiment replicated three times, a 7-mm-diameter culture plug was removed from each culture type with a cork borer from the periphery of a 6-day-old colony growing on CPDA in diffuse sunlight at 27–30 C. The plug was shaken vigorously in 10 ml of sterile distilled water (30 up-and-down strokes) in a capped test tube. Macroconidia and microconidia were counted with a hemacytometer. Results were expressed as the number of conidia per square millimeter of culture plug. Any conidium with a septum was counted as a macroconidium.

Chlamydospore production. The capacity of mycelial and their corresponding pionnotal cultures to produce chlamydospores was determined in a soil extract solution by a method modified from Alexander et al (4). The soil extract solution was prepared by shaking 50 g of organic soil (previously cropped to celery and naturally infested with *F. o.* f. sp. *apii* race 2) in 500 ml of distilled water for 1 hr at high speed on a variable-speed reciprocating platform shaker (model 6000, Eberbach Corp., Ann Arbor, MI). The slurry was partially clarified by filtration under suction through Whatman No. 9 filter paper. The crude extract was sterilized by passage through a 0.20-μm Millipore filter under suction. A loopful of the filtrate was streaked on CPDA and nutrient agar, and no microbial growth occurred. The sterile filtrate was refrigerated at 5 C until use (usually 1–2 days). Conidia used to seed the soil extract solution were obtained from mycelial and pionnotal cultures grown on CPDA. These were established from soil cultures as described previously. Five 7-mm-diameter culture plugs were removed with a cork borer from 1-wk-old CPDA cultures and placed in 10 ml of sterile distilled water in capped test tubes. These were shaken vigorously by hand for 10 sec. Mycelial fragments were filtered off through four layers of cheesecloth. Conidia were counted with a hemacytometer and adjusted to 4×10^4 conidia per milliliter. Half a milliliter of the adjusted conidial suspension was used to seed 6 ml of sterile soil extract solution in sterilized 5-cm-diameter glass petri dishes (four replicates per culture type), which were incubated on a laboratory bench. After 7 days of growth, chlamydospore formation was observed directly with a compound microscope (10× objective) and the chlamydospores were counted. For each replicate, chlamydospores in 10 microscopic fields were counted. In a typical experiment, three isolates were used.

Dimensions of conidia. The dimensions of conidia from mycelial and pionnotal cultures were determined. CPDA cultures of mycelial and their corresponding pionnotal cultures were grown from soil cultures as previously described. After 7 days, mycelial bits were taken from the periphery of each culture plate and mounted in cotton blue and lactophenol. Conidia (microconidia and only one-septate macroconidia) were measured with a compound microscope (25× objective).

RESULTS

Range and direction of cultural variability. The wild type of isolate P-3, when grown on CPDA under light for 2 wk, was mycelial (Fig. 1) and produced abundant microconidia. Production of macroconidia was scanty. Culture propagation by single microconidial transfers and incubation under fluorescent light resulted in production of pionnotal cultures (Fig. 1). Pionnotal cultures originated either directly from parental mycelial cultures or indirectly from intermediate cultures that possessed both pionnotal and mycelial patches (Fig. 1). Isolates R-1 and P-13 were similar to P-3 in their cultural behavior. Of the three cultural classes, pionnotal cultures, characterized by the absence of aerial mycelium, intense orange to light purple pigmentation of the culture medium, and a slimy growth form, were the most stable on CPDA (Fig. 2). Mycelial cultures were intermediate in stability, and intermediate type cultures were the least stable (Fig. 2).

Pathogenic variation. Mycelial cultures of isolates R-1, P-13, JC-3, and NR-1 were more pathogenic to celery than their corresponding pionnotal cultures (Table 1). Twenty-nine percent of the plants inoculated with mycelial cultures developed vascular discoloration in the roots and crown region, and 3% died after 8 wk (data not shown). None of the plants inoculated with pionnotal cultures developed any of these symptoms. Top growth of plants grown in soil artificially infested with mycelial cultures generally was less than in those plants inoculated with pionnotal cultures (Table 1). Eighty-four to 93% of isolations from plants infected with mycelial cultures yielded true-to-type mycelial cultures and no pionnotal cultures (data not shown). On plants inoculated with pionnotal cultures, 87–95% of isolations yielded true-to-type pionnotal cultures and no mycelial cultures (data not shown).

Growth rate, spore production, and dimensions of conidia. Mycelial and pionnotal cultures of isolates NR-1, JC-1, and P-13 did not differ in their radial growth on CPDA at 27–30 C (diffuse sunlight). Colony radius of both culture types ranged from 18.6 to 20.9 mm after 4 days and from 29.9 to 30.9 mm after 6 days (Table 2). Production of microconidia in mycelial cultures did not differ significantly from that in pionnotal cultures (Table 2). Macroconidia, however, were more numerous in pionnotal cultures than in mycelial cultures. Dimensions of conidia for both culture types were similar. Size ranges for microconidia of the three isolates were 3.1–3.7 μm × 6.8–7.8 μm. Macroconidia (only those with one septum) were 4.1–4.8 μm × 17.8–18.6 μm (Table 3). Significantly more chlamydospores were produced in soil extract solution by mycelial cultures than by pionnotal cultures (Table 2). Chlamydospores typically were produced either terminally on germ tubes or on growing hyphae. Occasionally, a microconidium would round up to form a chlamydospore. Germ tube tip swelling was very common in pionnotal cultures.

DISCUSSION

Based on this study, the naturally occurring cultural type of *F. o.* f. sp. *apii* race 2 in organic soils cropped to celery in New York is the mycelial type. Cultural variability common in *Fusarium* spp. also occurs in this fungus. Ryker (15) suggested that cultural stability in *F. o.* f. sp. *apii* race 1 occurred when cultures were propagated by monoconidial transfer, but he did not describe the

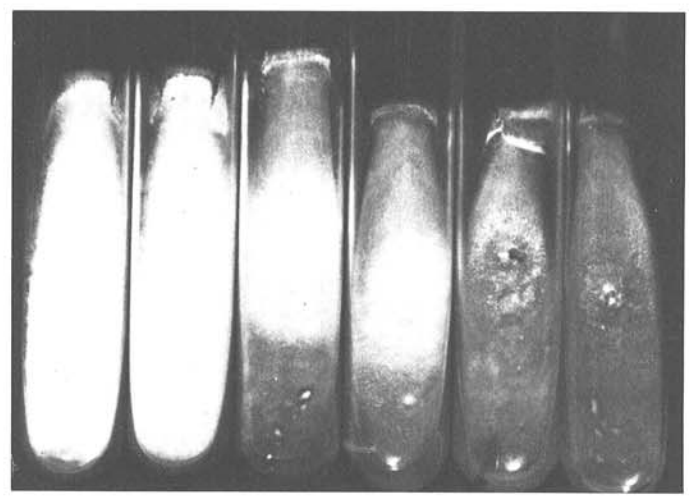

Fig. 1. Cultural forms of *Fusarium oxysporum* f. sp. *apii* race 2. Left to right: two tubes each of mycelial, intermediate, and pionnotal cultures.

nature of the wild type, the variant cultures involved, and their relative stability on culture media. Because all isolations from diseased celery plants in the present study yielded mycelial cultures, it appears that this culture type, characterized by abundant production of microconidia and few macroconidia, represents the wild type of *F. o.* f. sp. *apii* race 2. Intermediate and pionnotal cultural forms of the pathogen probably are only significant on agar media and appear to be rare in nature.

The occurrence of one morphological type of *F. o.* f. sp. *apii* race 2 in nature is consistent with similar findings for *F. o.* f. sp. *apii* race 1 (11), *F. o.* f. sp. *cubense* (22), *F. o.* f. sp. *cepae* (2), and *F. o.* f. sp. *melonis* (7). However, it contrasts with the occurrence of multiple types in nature for *F. solani* f. sp. *phaseoli* (19) and for *Fusarium* spp. (12) associated with cereal root rots. It is possible that a pionnotal form of *F. o.* f. sp. *apii* race 2 occurs in nature and that this form reverts to a mycelial form after passage through the host. This seems unlikely, however, because passage of pionnotal cultures through celery and reisolation on CPDA yielded a high frequency of true-to-type pionnotal cultures and no mycelial cultures in the present study. Maintenance of cultural identity of *Fusarium* spp. after passage through the host plant also has been reported by other investigators (15,21). Pionnotal cultures showed a reduced capacity to produce the levels of chlamydospores needed for long-term survival of *Fusarium* spp. in natural soils (3,10), and this indirectly suggests the probable absence of pionnotal forms of *F. o.* f. sp. *apii* race 2 in natural soils. Because storage of *Fusarium* spp. in soil reduces variant production (8,20), this suggests that variability is either eliminated or minimized in the natural soil environment. Thus, the possibility that variants of *F. o.* f. sp. *apii* race 2 persist in nature is doubtful.

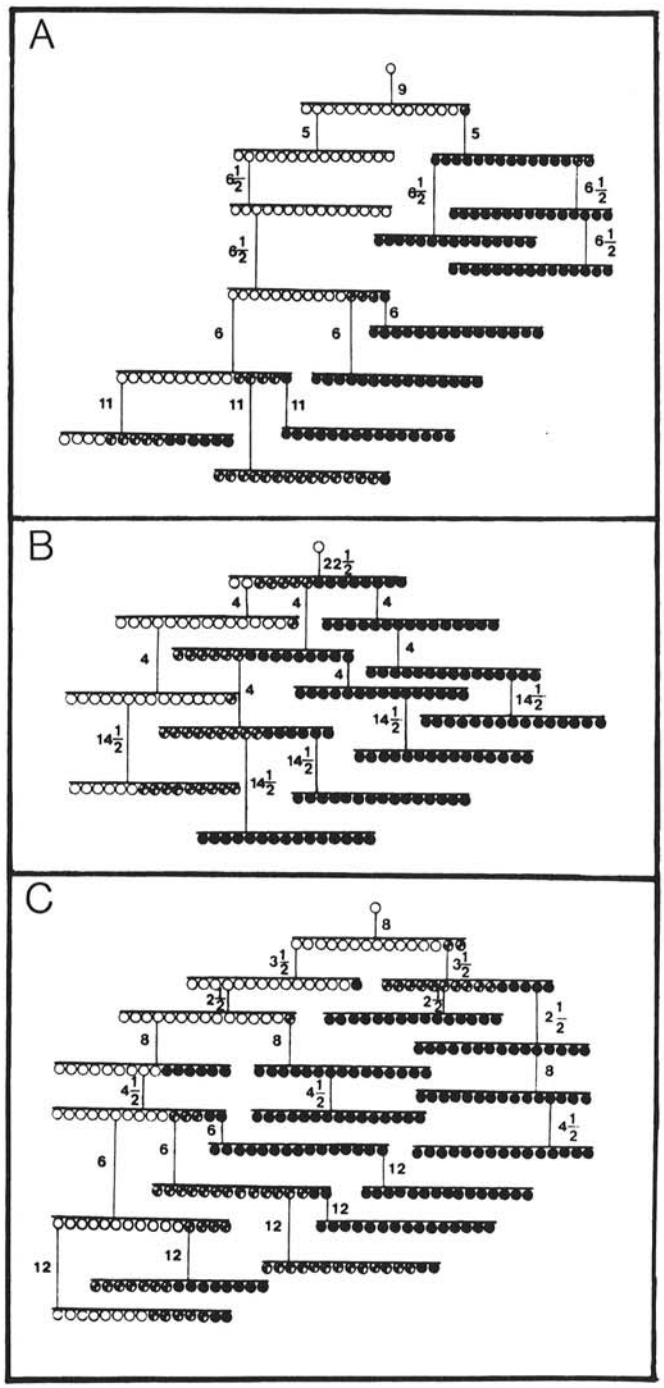

Fig. 2. Schematic representation of the direction of cultural variability in *Fusarium oxysporum* f. sp. *apii* race 2. **A,** Isolate P-3, **B,** isolate R-1, and **C,** isolate P-13. Circles represent progenies of test-tube generations. Time intervals (weeks) between transfers are indicated along vertical lines connecting the generations. Cultures were grown with a 12-hr photoperiod at 24–27 C (fluorescent cool-white light; 3,875 lx). o = Mycelial culture, ⊖ = intermediate culture, and ● = pionnotal culture.

Studies on cultural variability in *Fusarium* spp. indicate that in general, a loss of aerial mycelium occurs (13) and that pionnotal and appressed cultures, which are highly stable under normal laboratory conditions, can result (5,7,12,22,23). This trend in cultural variability is corroborated by the findings in the present study. Repeated monoconidial propagation of pionnotal cultures and growth of these progenies under fluorescent light did not result in morphological changes. Abawi (1), however, reported that pionnotal cultures of *F. o.* f. sp. *cepae* were unstable and frequently produced ropy and ultimately mycelial cultures.

Pionnotal cultures of the four isolates of *F. o.* f. sp. *apii* race 2 tested were less pathogenic to celery than their corresponding parental mycelial cultures. This parallels reports (5,7,21,23) indicating that when mycelial cultures of *Fusarium* spp. change to pionnotal cultures, a loss in pathogenicity generally occurs. Ryker (15) obtained several variants of *F. o.* f. sp. *apii* race 1 on culture media that varied in their virulence on celery, but he did not indicate which were the more virulent variants. Because the loss of pathogenicity accompanies the loss of aerial mycelium in *F. o.* f. sp. *apii* race 2, use of inoculum from pionnotal cultures in either pathogenicity studies or for cultivar evaluation for resistance to Fusarium yellows is not appropriate. Therefore, great care must be taken to preserve the morphological integrity of isolates of the pathogen. Storage of cultures in sterile soil columns following the method of Toussoun and Nelson (20) could achieve this goal.

TABLE 1. Pathogenicity of mycelial and pionnotal cultures of *Fusarium oxysporum* f. sp. *apii* race 2 to celery[y]

Isolate	Culture type	Disease index[z]	Shoot dry wt (% of control)
JC-1	Mycelial	3.5 a	59 e
	Pionnotal	1.9 b	83 bc
R-1	Mycelial	3.1 a	66 de
	Pionnotal	1.7 b	89 ab
P-13	Mycelial	3.3 a	66 de
	Pionnotal	1.9 b	78 bcd
NR-1	Mycelial	3.0 a	71 cde
	Pionnotal	2.0 b	83 bc
Control		0.0 c	100 a

[y] Data represent averages of two experiments. Each treatment in each experiment consisted of three replicates (four plants per replicate). Means in each column followed by the same letter are not significantly different (Duncan's multiple range test; $P = 0.05$).

[z] Based on a disease rating scale of 0–5: 0 = clean roots, healthy top, no disease; 1 = slight vascular discoloration limited primarily to secondary and tertiary roots; 2 = pronounced vascular discoloration of secondary and tertiary roots, healthy top; 3 = leaves chlorotic or slightly blanched; 4 = blanching, brittleness and curling of leaves, stunted growth, vascular discoloration of the primary roots (or remnants) or crown, discoloration extending into petiole occasionally; and 5 = dead plant.

TABLE 2. Growth characteristics of mycelial and pionnotal cultures of *Fusarium oxysporum* f. sp. *apii* race 2[w]

Isolate	Culture type	Number of chlamydospores produced[x]	Radial growth (mm)[y] Day 4	Radial growth (mm)[y] Day 6	Microconidia/mm² of culture[z]	Macroconidia/mm² of culture[z]
NR-1	Mycelial	15.5 a	18.6 a	30.9 a	20,791 a	228 a
	Pionnotal	0.6 c	18.9 a	30.5 a	18,181 a	553 a
JC-1	Mycelial	4.3 b	18.4 a	30.9 a	19,511 a	665 a
	Pionnotal	0.4 c	18.9 a	30.4 a	14,012 a	1,922 b
P-13	Mycelial	7.5 b	19.1 a	30.4 a	15,007 a	673 a
	Pionnotal	0.4 c	18.7 a	29.9 a	17,629 a	6,157 c

[w] Cultures grown on CPDA under diffuse sunlight at 27–30 C. Numbers in each column followed by the same letter are not significant (Duncan's multiple range test; $P = 0.05$).
[x] Each number is an average of four replicates. A replicate consisted of the total number of chlamydospores in 10 microscopic fields (10× objective).
[y] Each number is an average of 10 replicates. Cultures were started from single conidia.
[z] Data taken after 6 days of growth. Each number is an average of three replicates (four to eight hemacytometer counts per replicate).

TABLE 3. Dimensions (μm) of conidia from mycelial and pionnotal cultures of *Fusarium oxysporum* f. sp. *apii* race 2[a]

Isolate	Culture type	Microconidia Average size	Microconidia Range	Macroconidia[b] Average size	Macroconidia[b] Range
NR-1	Mycelial	7.8 × 3.1	7.4–9.3 × 3.0–4.1	18.6 × 4.8	15.2–22.6 × 3.7–5.6
	Pionnotal	7.8 × 3.5	6.7–9.3 × 3.0–4.1	18.6 × 4.2	16.7–22.2 × 3.7–4.8
JC-1	Mycelial	7.5 × 3.6	6.7–8.1 × 3.0–4.4	18.0 × 4.3	16.7–20.0 × 3.7–5.2
	Pionnotal	7.6 × 3.6	7.4–7.8 × 3.0–3.7	18.6 × 4.1	15.9–22.2 × 3.7–4.8
P-13	Mycelial	6.8 × 3.6	6.7–8.1 × 3.3–4.1	17.8 × 4.1	15.9–19.6 × 3.7–4.4
	Pionnotal	7.5 × 3.7	7.0–8.1 × 3.3–4.1	18.2 × 4.1	15.9–18.9 × 3.7–4.8

[a] Samples taken from the growing margins of 7-day-old cultures grown on CPDA with diffuse sunlight at 27–30 C.
[b] Only one-septate (two-celled) macroconidia.

Because pionnotal and mycelial cultures of *F. o.* f. sp. *apii* race 2 grew at similar rates on CPDA but showed different pathogenicity to celery, growth rate of cultures on agar media cannot be used to explain the difference in pathogenicity between the two culture types. Lack of correlation between culture growth rate and pathogenicity in *F. o.* f. sp. *apii* race 1 also has been demonstrated (15). Recently, Rappaport et al (14) reported that celery tissue infected with *F. o.* f. sp. *apii* race 2 contains highly polar substances that inhibit or kill celery cells in suspension cultures and on solid media. It is possible that pathogenic mycelial type cultures of *F. o.* f. sp. *apii* race 2 are capable of producing these polar substances in infected celery tissue. Pionnotal cultures could lack this capacity. The two culture types might then be used as tools in elucidating physiological aspects of postpenetration pathogenesis in the *F. o.* f. sp. *apii*-celery system.

Mycelial and pionnotal cultures of *F. o.* f. sp. *apii* race 2 differed in their capacities to produce macroconidia on CPDA and chlamydospores in soil extracts. Pigmentation on CPDA also was different. It is possible that physiological variation including nutrient requirement, tolerance to different chemicals, and production of enzymes and/or toxins necessary for pathogenesis also occurs in the two culture types of the fungus. The extreme variability in *F. o.* f. sp. *apii* race 2 could present a taxonomic problem in that different culture types of the fungus differing in a number of characteristics (morphological and physiological) could be mistakenly placed in different taxa by different investigators. This point has been stressed by other investigators with regard to other *Fusarium* spp. (9,12,16–18). Thus, it is important to use a wild type culture in identifying and testing this pathogen.

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