Comparative Pathogenicity and Host Ranges of *Fusarium oxysporum* Isolates Causing Crown and Root Rot of Greenhouse and Field-Grown Tomatoes in North America and Japan

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The author would like to thank Mrs. Deborah Murray for extensive technical assistance throughout this study as well as Hajimu Komada, Ronald Sonoda, and William Jarvis for arranging collecting trips in Japan, Florida, and Ontario, Canada, respectively. I would also like to thank James Farley, Ohio State University, and Paul Nelson, Pennsylvania State University, for advice in preparation of the manuscript.

Approved for publication as Journal Article 52-80 of the Ohio Agricultural Research and Development Center, Wooster.

Accepted for publication 15 May 1980.

ABSTRACT

ROWE, R. C. 1980. Comparative pathogenicity and host ranges of *Fusarium oxysporum* isolates causing crown and root rot of greenhouse and field-grown tomatoes in North America and Japan. Phytopathology 70:1143-1148.

Forty-two isolates of *Fusarium oxysporum* isolated from crown and root rot-affected tomato plants in 20 locations in North America and Japan were inoculated to four differential tomato lines. The symptoms and pattern of infection on these lines were similar for all isolates tested, and differed from that of *F. oxysporum* f. sp. *lycopersici (Fol)* races 1 and 2. Results from inoculation of 15 hosts representing five botanical families indicated that many legumes were moderately susceptible to the crown and root rot isolates tested, while cucurbits, crucifers, and cereals were unaffected. *Fol* isolates were host specific to tomato. These tests show that isolates of *F. oxysporum* from crown and root rot-affected tomato plants derived from many areas produce similar symptoms and that the pathogen involved is not a race of *Fol*, but a new forma specialis of *F. oxysporum*.

Additional key words: tomato wilt, *Fusarium* taxonomy

Fusarium crown and root rot of greenhouse tomatoes (*Lycopersicon esculentum* Mill.) was first reported from Ohio and Ontario, Canada in 1974 (11,17). Since then it has become a major limiting factor in the production of greenhouse tomatoes in the eastern USA, having been reported from six states (15,24,30). A similar disease was reported from Japan in 1974 (31,39) and has become a serious problem there in the production of greenhouse tomatoes (28,38). A crown and root rot of winter-grown field tomatoes was reported from southern California in 1971 (22). A similar disease was noted in outdoor, staked tomatoes in Florida in 1975 (33) and in central Mexico in 1979 (W. L. George, Jr., *personal communication*). The problem has not become economically limiting in field-grown tomatoes, except in a few localized areas.

Research on the biology and control of this pathogen has been conducted in our laboratory since 1974 (29, 30). Collections made in Ohio, Florida, and Ontario, Canada as well as isolates obtained from cooperators yielded a large collection of *F. oxysporum* Schl. isolates from both field and greenhouse grown-tomatoes affected with crown and root rot. Additional isolates were collected during a survey of greenhouse vegetables in Japan in 1979. This report summarizes results from pathogenicity tests of these *F. oxysporum* isolates on a set of differential tomato lines, and other hosts, and compares these data with the reactions of races 1 and 2 of *F. oxysporum* f. sp. *lycopersici* (Fol). A preliminary report of this work has been published (27).

0031-949X/80/12114306/$03.00/0
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MATERIALS AND METHODS

Collection and storage of isolates. Isolates of *F. oxysporum* were collected from mature tomato plants with symptoms of Fusarium crown and root rot. Stem sections with characteristic chocolate-brown vascular and cortical discoloration were excised 2–8 cm above the soil line and placed in plastic bags. In most cases, isolations were made within 2 days of collection. Stem sections were surface sterilized in 0.5% NaOCl for 30–60 sec and small segments placed on potato dextrose agar acidified to approximately pH 3.5 (APDA) or Komada's agar (KA), a medium selective for *F. oxysporum* (21). Plates were incubated at ~25 C under cool-white fluorescent lights with a 12-hr photoperiod at ~90 hlx. After 2–4 days, colonies of *F. oxysporum* obtained from these isolations were subcultured onto non-acidified PDA. Monoconidal isolates were prepared and microspore suspensions of these were added to sterile

soil in small vials and incubated at ~25 C for 10–14 days. For long-term storage, soil cultures were kept at 5 C.

Inoculation of tomato differential lines. To compare pathogenic reactions of *F. oxysporum* crown and root rot isolates with each other and with standard cultures of *Fol* races 1 and 2, a series of four tomato differential lines was selected. Cultivar Vendor was the susceptible control, while Ohio MR-13 (a commercial greenhouse cultivar resistant to *Fol* race 1) and cultivar Walter (resistant to both races of *Fol*) were used to identify isolates of *Fol*. The Japanese breeding line IRB-301-31 contains resistance to Fusarium crown and root rot derived from *L. peruvianum* PI 126944 (38). Crown and root rot isolates can easily be distinguished from those of *Fol* when compared on Walter, which is susceptible to crown and root rot (Table 1).

Inoculum of isolates to be tested consisted of microspores produced in potato dextrose broth shake culture at ~25 C for 3–4 days. Microspore suspensions were filtered through cheesecloth and final concentrations were adjusted to $\sim 5 \times 10^6$/ml. The roots of 15- to 20-day-old tomato seedlings grown in a greenhouse in steam-disinfested soil (Wooster silt loam) were carefully uprooted and freed of soil by immersion in water and gentle shaking. Then they were dipped into a microspore suspension for 15–30 sec and planted, 10 per box, in 20 × 40 × 12 cm deep plastic boxes containing steam-disinfested soil. Boxes were only two-thirds filled with soil and spaced at least 10 cm apart on steel-mesh benches to guard against cross-contamination of isolates during watering. Inoculated plants were grown in a greenhouse for 8 wk at 20–25 C under supplemental fluorescent light with a 14-hr photoperiod at 100–200 hlx.

After 8 wk, when most plants were 30–45 cm tall, they were uprooted and the lower stem and tap root was longitudinally sectioned for examination of internal tissues. Each plant was rated on a scale of 0 to 3 as follows: 0 = no internal browning; 1 = slight internal browning (usually at the tip of the tap root); 2 = moderate to severe internal browning of the entire tap root; or 3 = severe internal browning extending from the tap root into the lower stem above the soil line. In the case of *Fol*, races 1 and 2, severe reactions often resulted in collapse and death of the test plants 1–2 wk after inoculation. This reaction also was given a rating of 3.

Host range tests. Host range studies were initiated in an attempt to futher differentiate the *F. oxysporum* crown and root rot isolates from *Fol*, races 1 and 2, which are specific to tomato (35). Seventeen crop plants from five botanical families were selected for testing (Table 2). Steam-disinfested soil was reinfested with a spore suspension of a single isolate of *F. oxysporum* immediately after cooling and incubated at ~25 C for 10–15 days to allow colonization and the formation of chlamydospores. Final chlamydospore concentrations as determined by dilution plating on KA ranged from 10^5–10^7/gm soil. Seeds of host range plants were soaked 4 hr in a microspore suspension (10^6/ml) of each test isolate and then planted in a soil previously colonized with the same isolate. Plants were grown in a greenhouse for 8–10 wk under the conditions previously described. Plants were then uprooted and basal stem and tap root areas were longitudinally sectioned to observe internal brown discoloration and root rot symptoms. Stem sections from plants with internal discoloration were surface sterilized 30–60 sec in 0.5% NaOCl and small, excised sections were placed on APDA for reisolation of the pathogen. Isolates of *F. oxysporum* recovered in this manner were used to reinoculate cultivar Vendor tomato seedlings by the root dip method to confirm their identity as crown and root rot pathogens.

TABLE 1. Susceptibility of four differential tomato lines to *Fusarium oxysporum* isolates

Tomato line	Isolate: Fol[a] Race 1	Isolate: Fol[a] Race 2	Isolate: Crown and root rot[b]
Vendor	S[c]	S	S
Ohio MR-13	R	S	S
Walter	R	R	S
IRB-301-31	S	S	R

[a] *Fusarium oxysporum* f. sp. *lycopersici*.
[b] Isolates from tomato plants with typical crown and root rot symptoms.
[c] Plant reactions: S = susceptible, R = resistant.

TABLE 2. Test host plants used to compare pathogenicities of *Fusarium oxysporum* isolates and *F. oxysporum* f. sp. *lycopersici*

Botanical family and common names	Latin name	Cultivar tested
Solanaceae		
Tomato	*Lycopersicon esculentum* Mill.	Ohio MR-13
Pepper	*Capsicum frutescens* L.	California Wonder
Eggplant	*Solanum melongena* var. *esculentum* Nees	Black Beauty
Cucurbitaceae		
Squash	*Cucurbita maxima* Dcne.	Butternut
Watermelon	*Citrullus vulgaris* Schrad.	Sugarbaby
Cucumber	*Cucumis sativus* L.	Straight Eight
Cruciferae		
Cabbage	*Brassica oleracae* var. *capita* L.	Danish Ballhead
Chinese cabbage	*Brassica campestris* var. *pekinensis* (Lour) Rupr.	Michili
Radish	*Raphanus sativus* L.	Scarlet Knight
Leguminosae		
Soybean	*Glycine max* (L.) Merr	Amsoy 71
Green bean	*Phaseolus vulgaris* L.	Tendergreen
Pea	*Pisum sativum* L.	Wando
Peanut	*Arachis hypogea* L.	Florigiant
Lima bean	*Phaseolus limensis* Macf.	Baby Lima
Red clover	*Trifolium incarnatum* L.	Unknown
Gramineae		
Sweet corn	*Zea mays* var. *saccharata* (Sturtev.) Bailey	Unknown
Wheat	*Triticum aestivum* L.	Michigan Amber

RESULTS

Inoculation with a total of 42 isolates of *F. oxysporum* from crown and root rot-affected tomato plants from 20 locations in North America and Japan resulted in a similar pattern of infection and symptomatology on the four differential tomato lines. The isolates tested varied considerably in virulence, but the pattern of infection on the differential lines was always consistant. Data from 16 of these isolates is presented in Table 3. Cultivar Vendor plants were susceptible to all isolates tested. Cultivar Ohio MR-13 plants were susceptible to all crown and root rot isolates and to *Fol* race 2. A few plants also showed a susceptible reaction to *Fol* race 1 in many tests, resulting in a disease index greater than zero. Though this cultivar is considered resistant, incomplete resistance to race 1 has been noted previously in other cultivars (2,19). Cultivar Walter plants were resistant to both races of *Fol*, but were quite susceptible to all crown and root rot isolates from all sources tested. Japanese breeding line IRB-301-31 plants were consistently resistant to all crown and root rot isolates, but were extremely susceptible to *Fol* race 1 and moderately susceptible to race 2.

Differences in pathogenicity between the crown and root rot isolates and isolates of *Fol* races 1 and 2 were apparent, both in varietal reaction and symptomatology. Characteristically, plants inoculated with crown and root rot isolates had no abnormal aboveground symptoms 8 wk after inoculation. When uprooted and sectioned, however, browning of the vascular system, and sometimes the cortex, usually could be seen. This was typically confined to the tip of the tap root in mild infections but extended upward to 3–6 cm above the soil line in severe cases (Fig. 1). Severely infected plants often showed a proliferation of adventitious root initials on the first 10 cm of stem above the soil line. This was absent in uninfected or lightly infected plants. Wilt and subsequent death, symptoms characteristic of this disease under commercial conditions, occur only in mature, fruit-bearing plants. In the case of susceptible plants inoculated with *Fol* races 1

and 2, above ground symptoms commonly became apparent within 2 wk after inoculation. Plants often were severely stunted and wilted, and some collapsed and died within 3–4 wk after inoculation. When sectioned, these plants usually showed severe vascular discoloration extending well up the stem, and in many cases, into the petioles of the lower leaves (Fig. 2). This contrasted with the discoloration in crown and root rot-affected plants which was limited to the lower stem near the soil line.

Host range tests in early phases of this study confirmed an observation made by Yamamoto et al (39) that some isolates of the crown and root rot organism were slightly pathogenic to pepper and eggplant. Inoculation studies of 15 host plants representing five botanical families indicated that many legumes also were moderately susceptible, but the cucurbits, crucifers, and cereals tested were not infected (Table 4). Symptoms on infected legumes were similar to those of tomato and included necrosis of the tip of the tap root, severe rot of lateral roots and the tap root cortex, and (in some cases) discoloration of the vascular system. A second test comparing susceptibility of Ohio MR-13 tomato with six legumes confirmed that these hosts could be infected, to a limited extent, by greenhouse crown and root rot isolates from Ohio and Japan as well as by field crown and root rot isolates from Florida. *Fol* race 1 and 2 isolates, however, were specific to tomato (Table 5).

DISCUSSION

Consistent pathogenic reactions of four differential tomato lines to isolates of *F. oxysporum* recovered from crown and root rot-affected tomatoes indicates that cases of crown and root rot reported under field and greenhouse conditions in diverse areas of North American and Japan are the same disease. In all cases, the pathogen is a strain of *F. oxysporum* that causes root and cortical decay resulting in a chocolate-brown discoloration of internal tissues extending no more than 10–15 cm above the soil line. Mature plants under heavy fruit load often wilt on sunny days and may eventually die. Wilting, however, is probably due to root dysfunction and stem girdling, and not strictly to obstruction of the vascular system. The symptoms typical of Fusarium wilt (epinasty, nonuniform wilt of certain leaves or branches, and vascular discoloration extending well above the soil line) were never observed with this disease.

TABLE 3. Pathogenicity of *Fusarium oxysporum* from crown and root rot-affected greenhouse and field-grown tomato plants and of *F. oxysporum* f. sp. *lycopersici* (Fol) races 1 and 2 on four differential tomato lines

Isolate designation	Origin		Disease index[a]			
	Locality	Country	Vendor	MR-13	Walter	IRB-301-31
Greenhouse						
315	Cleveland, OH	USA	1.6	0.9	1.6	0.1
317	Cleveland, OH	USA	3.0	2.6	2.3	0.0
327	Niagara Co., NY	USA	1.4	1.1	2.1	0.1
330	Ashville, NC	USA	2.0	2.5	1.3	0.5
267	Northumberland Co., PA	USA	1.3	1.8	2.1	0.1
319	Leamington, Ontario	Canada	2.0	1.3	1.9	0.0
322	Leamington, Ontario	Canada	1.6	1.8	0.9	0.0
286	Kurume, Kyushu	Japan	2.4	2.3	2.0	0.0
289	Kochi, Shikoku	Japan		2.5	2.2	0.1
292	Kisozaki, Mie	Japan		2.1	2.0	0.2
294	Toyakawa, Aichi	Japan		2.1	1.7	0.0
295	Fujioka, Gumma	Japan		2.1	1.8	0.1
Field						
296	Jupiter, FL	USA		2.7	2.5	0.1
297	Jupiter, FL	USA	2.0	2.3	2.1	0.0
311	San Diego Co., CA	USA	2.8	2.0	2.2	0.0
304	Culiacon	Mexico		2.6	2.6	0.1
Fol						
242	Race 1 Florida	USA	2.6	0.8	0.1	3.0
247	Race 2 California	USA	2.3	1.4	0.2	1.7

[a] Root and crown necrosis rated visually on a scale of 0 (no visible root browning) to 3 (severe browning and necrosis). Figures represent an average rating of 20–30 plants.

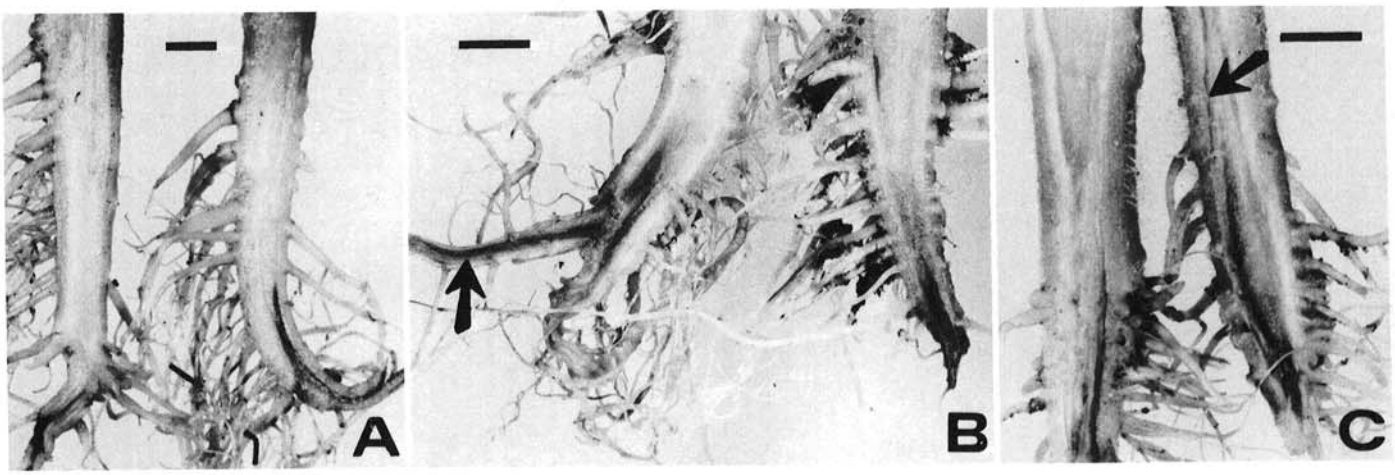

Fig. 1. Symptoms of Fusarium crown and root rot in tomato plants 8 wk after seedling roots were dipped in microspore suspensions of *Fusarium oxysporum*. **A,** Slight infection—necrosis only at the tip of the tap root. **B,** Moderate infection—internal necrosis is apparent throughout tap root; note severely infected lateral root (arrow). **C,** Severe infection resulting in some vascular discoloration above the soil line (arrow). Scale bars represent 1 cm.

Differences of opinion regarding the pathogen involved in this disease and its taxonomic status have led to confusion. Grogan et al (13) disputed the original designation by Leary and Endo (22) of *F. oxysporum* as the pathogen involved in crown and root rot of field tomatoes in southern California. Grogan et al (13) claimed that the disease was caused by a virulent pathotype of *Alternaria alternata* specifically pathogenic to certain tomato cultivars. Although the disease described in their report obviously was caused by *Alternaria,* the symptoms described were not those typical of Fusarium crown and root rot. A culture of *F. oxysporum* isolated from a crown and root rot-affected tomato in San Diego County, California, was pathogenic in our tests and fits the pattern of pathogenesis of other crown and root rot isolates on the set of differentials (Table 3). Since the symptoms Leary and Endo (22) described were identical to those of crown and root rot-affected plants and their culture was pathogenic, it seems possible that both diseases may have been present simultaneously in the California situation, resulting in the confusion.

When Yamamoto et al (39) originally described the crown and root rot of greenhouse tomato in southern Japan, they named the pathogen as a new race (J3) of *Fusarium oxysporum* f. sp. *lycopersici*, based on its pathogenicity to cultivar Walter which is resistant to both known races of *Fol* (35). Sato and Araki (31), describing the disease in northern Japan, later agreed. Since then, there has been some disagreement with the designation of this pathogen as a new race of *Fol* because the symptoms are not those typical of a vascular wilt but of a crown and root rot disease (15,24,30). This designation now seems especially inappropriate with the evidence presented here that the crown and root rot isolates are pathogenic to hosts outside the Solanaceae. Although other genera have been shown to be latent hosts of *Fol* (20), the fungus causes disease only in species of *Lycopersicon* (20,35).

In 1978, Jarvis and Shoemaker, in a letter to the editor (16), designated this pathogen as a new *forma specialis* and named it *F. oxysporum* f. sp. *radicis-lycopersici*, citing the precedent of Weimer (37). Weimer described a root rot of lupine and named the pathogen *F. oxysporum* f. sp. *radicis-lupini* to differentiate it from *F. oxysporum* f. sp. *lupini* which causes a vascular wilt of lupine. Jarvis et al (17) present no data to support their new designation and stated the fungus was restricted to the genus *Lycopersicon* and attacked all cultivars of *L. esculentum* tested. The forma specialis concept within *F. oxysporum* has not been used uniformly throughout the literature. Although the designation was intended to differentiate among pathogenic forms which could not be distinguished morphologically, usage within *F. oxysporum* has often restricted it to those forms causing vascular wilts (4,18,32). Armstrong and Armstrong (4), in fact, excluded f. sp. *radicis-lupini* from their list of forma speciales of *F. oxysporum* because it does not cause a vascular wilt. Gordon (12), however, used the concept in a broader sense to include pathogenic forms not causing vascular wilts and included f. sp. *radicis-lupini*.

Although most pathogenic forms of *F. oxysporum* cause vascular wilts, a number of recent studies describe root, crown, and bulb rots caused by this species (1,9,18,23,25,34,36). Authors of these studies have handled the taxonomic problem in various ways.

TABLE 4. Pathogenicity of three *Fusarium oxysporum* crown and root rot isolates to 15 test host plants from five botanical families

Botanical families and test hosts	Number of infected plants[a] Ohio 315	Ohio 317	Pennsylvania 267
Solanaceae			
Tomato	6	6	8
Pepper	0	0	0
Eggplant	0	7	4
Curcurbitaceae			
Squash	0	0	0
Watermelon	0	0	0
Cucumber	0	0	0
Cruciferae			
Cabbage	0	0	0
Chinese cabbage	0	0	0
Radish	0	0	0
Leguminosae			
Soybean	1	1	7
Green bean	3	6	1
Pea	1	6	5
Peanut	9	2	11
Gramineae			
Corn	...[b]	0	0
Wheat	...	0	0

[a] Number of plants of 30 tested that developed moderate to severe stem-browning and vascular necrosis from which *Fusarium oxysporum* cultures were reisolated which caused crown and root rot symptoms when reinoculated to cultivar Vendor tomato plants.
[b] ... = not tested.

TABLE 5. Pathogenicity of five *Fusarium oxysporum* crown and root rot isolates and *Fusarium oxysporum* f. sp. *lycopersici* (Fol), races 1 and 2, to tomato and six legumes

	Number of infected plants[a]						
						Fol	
Host	Ohio 317	Japan 286	Japan 289	Florida 296	Florida 297	race 1 242	race 2 247
Tomato	5	5	7	4	9	0	8
Pea	1	0	1	0	2	0	0
Lima bean	0	0	0	0	0	0	0
Red clover	2	0	1	1	1	0	0
Soybean	2	0	2	0	0	0	0
Peanut	1	1	0	4	0	0	0
Green bean	1	0	0	0	0	0	0

[a] Number of plants of 20 with moderate to severe stem-browning and vascular necrosis from which *Fusarium oxysporum* was reisolated.

Fig. 2. Vascular discoloration caused in tomato plants by *Fusarium oxysporum* f. sp. *lycopersici* 8 wk after tomato seedling roots were dipped in a microspore suspension of the pathogen. Discoloration is visible even in leaf petioles of infected plants (arrow). Scale bar represents 1 cm.

Some have used only *Fusarium oxysporum* (9,18,23,36) in spite of the fact that this is a collective species and does not really define a specific pathogen. In support of this, Joffe (18) expressed the opinion that since a wide range of Fusaria affect roots of many crops, the use of forma specialis designations should be restricted to those that cause vascular wilts. Other authors, however, have used forma specialis designations for certain bulb and stem rots caused by *F. oxysporum*, preferring to apply subspecific epithets to forms attacking certain hosts (1,25,34).

Although the forma specialis concept originally was associated with host specificity, this too has changed (6,10). There are examples of host-specific forms other than f. sp. *lycopersici* (14,26), but many forms are pathogenic to a wide range of hosts either within a botanical family (3,7) or across many families (5,8).

The tomato crown and root rot disease is definitely not a vascular wilt, nor is the pathogen host specific. But, since it is well defined in its pathogenic capabilities on tomato, subspecific designation as a forma specialis of *F. oxysporum* seems appropriate to separate it from other members of this diverse species. For this reason, I concur with Jarvis and Shoemaker's (16) designation of this pathogen as *F. oxysporum* f. sp. *radicis-lycopersici*. Their description, however, must be modified to include pathogenicity to various hosts in the Leguminosae and resistance to infection in *L. esculentum* in the Japanese breeding line IRB-301-31. Breeding studies suggest this resistance is controlled by a single dominant gene (Farley and Rowe, *unpublished*). The use of this gene in the development of commercial crown and root rot resistant tomato cultivars is presently underway in the USA and Japan (38).

Although the disease is under control in Ohio greenhouses (29), it remains a serious problem in Canada and Japan (28,38). It is economically important in field-grown tomatoes only in limited areas in Florida and Mexico where the crop is produced on fumigated beds during the winter months. This parallels the development of crown and root rot in tomato greenhouses during the winter following steam disinfestation of soil (29). In most cases the disease is favored by production in cool soils (below 20 C). Indeed, it could be considered a "man-made" disease that is favored when competing microorganisms are removed by soil disinfestation and tomatoes are produced at suboptimal temperatures.

Although the spread of crown and root rot has been dramatic in the last decade, the source of inoculum remains unclear. In greenhouses, the use of organic mulches between the rows is common practice; rice straw is used in Japan and wheat straw and peanut hulls in the USA and Canada. The fungus was recovered from old wheat straw mulch in an infested greenhouse (29). Evidence that this fungus has a host range broader than originally thought leads to the possibility it may have been introduced with organic mulches. *F. oxysporum* f. sp. *radicis-lycopersici* may be a "low grade" pathogen, associated with many crop plants in the field, but not causing damage until it is present with plants growing under sub-optimal temperatures in recently disinfested soil. Further research is underway to investigate this possibility.

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