

Reactions of Solanaceous Species to *Pseudocercospora fuligena*, the Causal Agent of Tomato Black Leaf Mold

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ABSTRACT

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A total of 137 accessions representing 26 species and five genera of solanaceous plants were inoculated with *Pseudocercospora fuligena*, the causal agent of tomato black leaf mold, under controlled conditions (growth room) and in the field. Twenty of 26 species developed symptoms after inoculation under controlled conditions. Black nightshade (*Solanum nigrum*) developed symptoms when inoculated under controlled conditions, but not in the field. Ground cherry (*Physalis* sp.), five Irish potato (*Solanum tuberosum*) cultivars, and eight tobacco (*Nicotiana tabacum*) lines remained symptomless following inoculation both under controlled conditions and in the field. Of 40 pepper accessions representing four species of *Capsicum* tested under controlled conditions, 32 developed lesions and eight were symptomless. Of 33 eggplant (*Solanum melongena*) accessions and related species representing seven *Solanum* spp. tested under controlled conditions, 24 developed symptoms and nine were symptomless. Two commercial eggplant cultivars, Pingtung Long and Farmers Long, were highly susceptible under controlled conditions and in the field. Among 46 *Lycopersicon* accessions representing 10 species that were evaluated, accessions of *L. esculentum* were the most susceptible and accessions of *L. hirsutum* were the most resistant. Five *Lycopersicon* spp., three *Solanum* spp., and four *Capsicum* spp. are reported as new hosts of *P. fuligena*.

Black leaf mold of tomato (*Lycopersicon esculentum* Mill.), caused by *Pseudocercospora fuligena* (Roldan) Deighton (Syn. *Cercospora fuligena* Roldan) (12), is widespread in the tropics (1-3,10-14), where it develops under warm, humid conditions (1,5,14). Disease symptoms begin with the development of irregularly shaped chlorotic spots on the leaves, with sporulation evident mainly on the lower surface. In advanced stages, the lesions enlarge and coalesce, with abundant dark sporulation on both surfaces. The leaves roll upward, die prematurely, and generally remain hanging on the plant with a

soot-covered appearance. The fruit are not attacked. Recent reports from Taiwan demonstrated that black leaf mold can cause extensive damage to tomatoes (4,5). A yield loss of 32% was reported during the 1989-90 season on tomato cultivar Tainan Selection No. 2 (TN-2). Yield loss was due to fewer and smaller fruits produced on infected plants (5). More recently, a yield loss of more than 40% was observed in a planting of four commercial cultivars (T. C. Wang and L. L. Black, unpublished).

Little is known about the epidemiology of black leaf mold. For example, it is not known whether primary inoculum of *P. fuligena* originates from infected crop debris or from alternative host species. Conidia have been found to survive up to 6 months on infected tomato leaves stored in a dried condition but did not survive for 40 days on leaves maintained in moist conditions (14). Known hosts of *P. fuligena* include tomato, cultivated eggplant (*Solanum melongena* L.), and black nightshade (*Solanum nigrum* L.) (4,7). Although there has been some question as to whether the pathogen on *S. nigrum* is a different species (*Pseudocercospora atromarginalis* (Atk.) Deighton) (9), cross-

inoculation studies (4,7), in addition to isozyme and polymerase chain reaction (PCR) studies (7), suggest that *P. atromarginalis* is synonymous with *P. fuligena*. The objectives of our study were to evaluate a range of solanaceous weed and crop species for their potential to serve as alternative hosts for *P. fuligena* and to evaluate accessions of crop species for potential sources of resistance.

MATERIALS AND METHODS

A series of experiments was conducted in which representatives of 26 greenhouse-grown solanaceous species were inoculated with *P. fuligena*. Inoculum consisted of a 5×10^3 conidia per ml suspension of two tomato isolates, Pf-2 and Pf-14, that were mixed in equal proportions. These isolates were collected from western and eastern Taiwan, respectively. Cultures were established by making streak transfers from stock cultures to tomato-oatmeal agar (TOA) (4). They were grown at 28°C in a fluorescent-lighted ($57 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) incubator with alternating 12-h light/dark periods. Conidia were harvested from 7- to 10-day-old cultures by adding sterile distilled water to each plate and scraping the surface lightly with the edge of a glass microscope slide to dislodge conidia, which were filtered through a 40- μm -mesh sieve to remove mycelial fragments. The conidial concentration was determined using a hemacytometer and diluted to 5×10^3 conidia per ml. Plants were atomized with the inoculum to the point of runoff and maintained for a minimum of 1 week in a growth room at $95 \pm 2\%$ relative humidity and $28 \pm 2^\circ\text{C}$ with 14 h of light ($49.3 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Disease severity was assessed by averaging visual estimates of the percent leaf area affected on individual plants based on a modified Horsfall-Barratt scale (8). Incubation period, postincubation maintenance of plants, days to disease evaluation, and numbers of plants inoculated are detailed for each experiment. Data were analyzed by analysis of variance (ANOVA) and means were separated by LSD ($P \leq 0.01$).

Experiment 1: Solanaceous species. The following solanaceous species were inoculated with *P. fuligena*: pepper, *Cap-*

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sicum annuum L. cvs. Blue Star and Szechwan; a susceptible tomato, *L. esculentum* Mill. cv. TN-2; a resistant wild tomato, *L. hirsutum* Humb. & Bonpl. (AVRDC accession L733, PI127827) (6); tobacco, *Nicotiana tabacum* L. cv. Van-Hicks; ground cherry, *Physalis* sp.; eggplant cvs. Pingtung Long and Farmers Long; black nightshade; and Irish potato, *Solanum tuberosum* L. cv. Feng-White. Plants were grown in the greenhouse in a steam-sterilized soil mixture (three parts soil, one part rice hulls, one part sand, and one part compost) in 15-cm-diameter clay pots. The potato plants were grown from three 3-cm-diameter tubers planted directly in each pot; tobacco plants were transplanted, three per pot, at the two-leaf stage; and all other plants were directly seeded on 31 January 1992 and thinned to three plants per pot after emergence. Each pot of three plants represented one of four

replicates for each entry arranged in a randomized complete block design (RCBD). Plants were inoculated 4 weeks after seeding or transplanting, incubated in a growth room for 7 days as described previously, and returned to the greenhouse for 12 days prior to rating for disease severity. Infected leaves were sampled; the technique used to reisolate the fungus was described elsewhere (4).

Experiment 2: *S. tuberosum* and *Nicotiana* species. Five Irish potato cultivars, Feng-White, Scangre, Cardina, Kennebec, and Omega; five tobacco cultivars, Havana, Xanthi, Samsun, Burley, and Van-Hicks; and single accessions of *Nicotiana benthamiana* Domin., *N. glauca* Graham, and *N. rustica* L. were inoculated with *P. fuligena*. A susceptible tomato cultivar, Taichung ASVEG No. 4, was included as a positive control. Seeds were sown on 12 December 1992 and propagated as de-

scribed in the previous section. Experimental units consisted of a single 15-cm-diameter pot with three plants, and entries were replicated four times in an RCBD. Plants were inoculated 56 days after seeding and incubated in the growth room for 20 days. Disease severity was rated at 15 and 20 days after inoculation.

Experiment 3: *Capsicum* species. Twenty-five accessions of *C. annuum* and five accessions each of *C. baccatum* L., *C. chinense* Jacquin, and *C. frutescens* L. were inoculated with *P. fuligena*. Three susceptible tomato cultivars, Taichung ASVEG No. 4, Known You 301 (KY301), and TN-2, and a resistant *L. hirsutum* line, PI127827, were included as controls. Plants were seeded in 9-cm-diameter black plastic pots on 1 September 1993, thinned to one plant per pot after emergence, and maintained in the greenhouse. Two plants (pots) represented one of four replicates for each entry in an RCBD. Plants were inoculated 4 weeks after seeding and incubated for 16 days in the growth room prior to disease severity evaluations.

Experiment 4: *Solanum* species. Ten violet-colored eggplant cultivars, including elliptical (Onita, Enda, Queen of Sheba, Florida High Bush, Megal, Kokutonaga, Bentenmaru, and Market Supreme) and long (Black Jack and Sanshi Nega) fruit shapes were inoculated with *P. fuligena*. Three susceptible tomato cultivars (Taichung ASVEG No. 4, KY301, and TN-2) were inoculated for comparison. Plants were seeded in 9-cm-diameter black plastic pots on 1 September 1993, thinned to one plant per pot after emergence, and maintained in the greenhouse. Two plants (pots) represented one of four replicates of each entry. They were inoculated 4 weeks after seeding and incubated in the growth room for 16 days prior to disease severity evaluations.

In a second part of the experiment, 23 accessions of eggplant and related species, including *Solanum aethiopicum* L., *S. indicum* L., *S. macrocarpon* L., *S. melongena*, *S. petinatum* Dunal, *S. pseudocapsicum* L., and *S. torvum* Sw., plus one susceptible tomato cultivar, TN-2, were seeded in 9-cm-diameter black plastic pots on 3 November 1993 and thinned to one plant per pot after emergence. Plants were maintained in the greenhouse for 41 days. They were moved to the growth room for inoculation and arranged in an RCBD with four plants per three replicates for each accession. Plants were incubated in the growth room for 17 days prior to disease severity evaluations.

Experiment 5: *Lycopersicon* species. Forty-six accessions representing 10 *Lycopersicon* species and an interspecific hybrid were inoculated with *P. fuligena*. Three known susceptible cultivars, KY301, Taichung ASVEG No. 4, and TN-2, were included as positive controls. Seeds were soaked for 1 min in 1% so-

Table 1. Percent leaf area affected of eight solanaceous species inoculated with *Pseudocercospora fuligena* and incubated in a growth room at 95 ± 2% relative humidity, 28 ± 2°C, and 14 h of light

| Crop | Cultivar/accession | Species | Leaf area affected (%) ^a |
|----------------------------|--------------------|--------------------------------|-------------------------------------|
| Black nightshade | Local weed | <i>Solanum nigrum</i> | 5 |
| Eggplant | Farmers Long | <i>S. melongena</i> | 30 |
| Eggplant | Pingtung Long | <i>S. melongena</i> | 27 |
| Ground cherry | Local weed | <i>Physalis</i> sp. | 0 |
| Hot pepper | Szechwan | <i>Capsicum annuum</i> | 0 |
| Irish potato | Feng-White | <i>Solanum tuberosum</i> | 0 |
| Sweet pepper | Blue Star | <i>C. annuum</i> | 27 |
| Tobacco | Van-Hicks | <i>Nicotiana tabacum</i> | 0 |
| Tomato (susceptible check) | TN-2 | <i>Lycopersicon esculentum</i> | 90 |
| Tomato (resistant check) | L733 (PI127827) | <i>L. hirsutum</i> | 17 |
| LSD (<i>P</i> < 0.01) | | | 4.8 |

^a Mean of four replicates; three plants per replicate.

Table 2. Percent leaf area affected of *Solanum* spp. accessions and a commercial tomato variety Known You 301 inoculated with *Pseudocercospora fuligena* in a growth room at 95 ± 2% relative humidity, 28 ± 2°C, and 14 h of light

| Species | Cultivar | AVRDC accession code | Mean leaf area affected (%) ^a |
|--------------------------------|--------------------|----------------------|--|
| <i>S. aethiopicum</i> | ... | TS-05 | 35 |
| <i>S. indicum</i> | Perat | TS-11 | 35 |
| <i>S. indicum</i> | Kapal | TS-18 | 18 |
| <i>S. indicum</i> | Arupa | TS-19 | 0 |
| <i>S. macrocarpon</i> | Macrocarpon | TS-52 | 0 |
| <i>S. macrocarpon</i> | ... | TS-54 | 10 |
| <i>S. melongena</i> | Brinjal | TS-01 | 46 |
| <i>S. melongena</i> | ... | TS-02 | 13 |
| <i>S. melongena</i> | Mte-1 | TS-06 | 13 |
| <i>S. melongena</i> | Mte-2 | TS-07 | 35 |
| <i>S. melongena</i> | Terong Lalap | TS-55 | 6 |
| <i>S. melongena</i> | Sapi | TS-65 | 0 |
| <i>S. melongena</i> | ... | TS-76 | 15 |
| <i>S. melongena</i> | Ihijan | TS-88 | 3 |
| <i>S. melongena</i> | ... | TS-106 | 7 |
| <i>S. melongena</i> | ... | TS-123 | 12 |
| <i>S. melongena</i> | Farmers Long | ... | 27 |
| <i>S. melongena</i> | Pingtung Long | TS-1462 | 40 |
| <i>S. petinatum</i> | Petinatum | TS-51 | 0 |
| <i>S. pseudocapsicum</i> | ... | TS-206 | 0 |
| <i>S. pseudocapsicum</i> | ... | TS-207 | 0 |
| <i>S. torvum</i> | Mangool | TS-12 | 0 |
| <i>S. torvum</i> | ... | TS-26 | 0 |
| <i>Lycopersicon esculentum</i> | Known You 301 (ck) | ... | 75 |
| LSD (<i>P</i> < 0.01) | | | 7.8 |

^a Mean of three replicates; four plants per replicate.

dium hypochlorite, rinsed with water, transferred onto moist filter paper in petri dishes, and germinated at 24°C with a 12-h daylight period. Seedlings were transplanted into a steam-sterilized soil mix in 9-cm-diameter black plastic pots on 5 June 1993, with one plant per pot in each of three blocks, each of which included from one to 22 plants, depending on availability. Plants were placed on the greenhouse bench, where they were shaded with a black net during the first 2 weeks. Inoculation and disease severity evaluations were made on 5 and 22 July, respectively.

Experiment 6: Field evaluation. Seedlings of two susceptible tomato entries, cv. KY301 and AVRDC accession L194; two resistant tomato AVRDC accessions, L733 and L3718; two susceptible eggplant cultivars, Pingtung Long and Farmers Long; one hot pepper cultivar, Szechwan; one sweet pepper cultivar, Blue Star; and two solanaceous weeds, black nightshade and ground cherry, were transplanted to the field on 24 September 1992 in an RCBD with 10 plants per plot replicated three times. Plots were 6 × 1.5 m raised beds on which plants were arranged in a single row in the center of each bed. A single row of the susceptible tomato cv. Taichung AS-VEG No. 4 was planted on the field perimeter. A suspension of 1 × 10⁵ conidia per ml was sprayed on the foliage of all the plants on 14, 19, and 28 October and 3 November 1992. Plots were furrow irrigated about every 10 days. Visual estimates of the percentage of foliage affected were made on a per plot basis at 2-week intervals from 28 October 1992 to 3 February 1993.

RESULTS

Experiment 1: Solanaceous species. Black leaf mold affected 90 and 17% of the foliage on the susceptible TN-2 tomato cultivar and the resistant L733 accession, respectively (Table 1). The two eggplant cultivars, the sweet pepper cultivar, and black nightshade also developed symptoms. Symptoms on eggplant were similar to those observed on the susceptible tomato, but fungal sporulation was restricted to the lower leaf surface. Blue Star sweet pepper developed numerous small necrotic lesions with little sporulation. Lesions on black nightshade were also somewhat restricted, but the fungus sporulated abundantly. Szechwan hot pepper, ground cherry, potato, and tobacco remained symptomless. *P. fuligena* was reisolated from black nightshade, eggplant, sweet pepper, and tomato.

Experiment 2: *S. tuberosum* and *Nicotiana* species. None of the potato or tobacco plants developed black leaf mold symptoms following inoculation. The susceptible tomato cultivar Taichung AS-VEG No. 4 developed severe symptoms under the same conditions, with 70% of the leaf area affected at 20 days after inoculation.

Experiment 3: *Capsicum* species. Several, but not all, *Capsicum* accessions developed black leaf mold symptoms following inoculation. When symptoms occurred, they appeared as irregular necrotic spots with little or no sporulation. No symptoms developed on eight *C. annuum* hot pepper AVRDC accessions: C00679 (NUM-598), C00948, C02049 (PI-174114), C02138 (PI177293), C02151 (PI179195), C02156 (PI179201), C02179 (PI181863), and C02657; or on one *C. baccatum* accession, C00948. Seven accessions, including C00307, C00873, C00942, C02006 (PI169130), C02024

(PI172768), C02084 (Angeli Emleke F₁), and C02128 (PI176476), had less than 10% of their total leaf areas covered by lesions, compared to 7.5% for the resistant tomato accession L733. Three susceptible tomato checks had over 65% of their leaf areas affected by black leaf mold lesions.

Experiment 4: *Solanum* species. Nine of the 10 eggplant cultivars that were inoculated developed black leaf mold symptoms. A single cultivar, Megal, remained symptomless. The amount of leaf area affected on symptomatic eggplant cultivars ranged from 7.5% (Edna) to 80.0% (Onita). The three susceptible tomatoes

Table 3. Evaluation of *Lycopersicon* spp. accessions for their responses to black leaf mold following inoculation with *Pseudocercospora fuligena*, isolate Pf-2, in a growth room at 95 ± 2% relative humidity, 28 ± 2°C, and 14 h of light

| Species | Entry | Plants tested | Leaf area affected (%) | |
|-----------------------------|----------------------------|---------------|------------------------|---------|
| | | | Each entry | Average |
| <i>L. cheesmanii</i> | L 4253 (PI379039) | 41 | 20 | |
| <i>L. cheesmanii</i> | TL 1044 | 35 | 3 | |
| <i>L. cheesmanii</i> | TL 1052 | 24 | 30 | |
| <i>L. cheesmanii</i> | TL 1078 | 15 | 6 | |
| <i>L. cheesmanii</i> | TL 1082 | 40 | 12 | |
| <i>L. cheesmanii</i> | LA 317 | 23 | 36 | |
| <i>L. cheesmanii</i> | LA 1402 | 13 | 12 | 17 |
| <i>L. chilense</i> | TL 1169 | 11 | 30 | |
| <i>L. chilense</i> | TL 1171 | 14 | 13 | |
| <i>L. chilense</i> | TL 1175 | 20 | 11 | |
| <i>L. chilense</i> | LA 1932 | 4 | 10 | |
| <i>L. chilense</i> | LA 2884 | 10 | 20 | 17 |
| <i>L. chmielewskii</i> | LA 1028 | 10 | 6 | |
| <i>L. chmielewskii</i> | LA 1306 | 20 | 2 | |
| <i>L. chmielewskii</i> | LA 2663 | 15 | 10 | 6 |
| <i>L. esculentum</i> | L 1 | 34 | 25 | |
| <i>L. esculentum</i> | L 2 | 48 | 24 | |
| <i>L. esculentum</i> | L 3 | 48 | 26 | |
| <i>L. esculentum</i> | KY 301 (ck) | 24 | 55 | |
| <i>L. esculentum</i> | Taichung AS-VEG No. 4 (ck) | 24 | 46 | |
| <i>L. esculentum</i> | TN-2 (ck) | 24 | 60 | 39 |
| <i>L. e. v. cerasiforme</i> | LA 1546 | 24 | 13 | |
| <i>L. e. v. cerasiforme</i> | LA 1673 | 22 | 25 | 19 |
| <i>L. esculentum</i> | | | | |
| × <i>pimpinellifolium</i> | L 457 (PI108245) | 14 | 40 | |
| <i>L. esculentum</i> | | | | |
| × <i>pimpinellifolium</i> | L 483 (PI112855) | 49 | 27 | |
| <i>L. esculentum</i> | | | | |
| × <i>pimpinellifolium</i> | L 486 (PI114038) | 46 | 24 | 30 |
| <i>L. glandulosum</i> | L 634 (PI126434) | 41 | 7 | |
| <i>L. glandulosum</i> | L 639 (PI126440) | 38 | 16 | |
| <i>L. glandulosum</i> | L 641 (PI126443) | 36 | 11 | 11 |
| <i>L. hirsutum</i> | L 643 (PI126445) | 36 | 8 | |
| <i>L. hirsutum</i> | L 645 (PI126449) | 33 | 9 | |
| <i>L. hirsutum</i> | L 733 (PI127827) | 67 | 1 | |
| <i>L. hirsutum</i> | LA 1353 | 20 | 10 | |
| <i>L. hirsutum</i> | LA 1908 | 16 | 1 | |
| <i>L. h. f. glabratum</i> | LA 1223 | 15 | 2 | 5 |
| <i>L. parviflorum</i> | LA 1326 | 12 | 9 | 9 |
| <i>L. pennellii</i> | LA 1505 | 11 | 6 | 6 |
| <i>L. peruvianum</i> | L 631 (PI126431) | 40 | 17 | |
| <i>L. peruvianum</i> | L 635 (PI126435) | 22 | 10 | |
| <i>L. peruvianum</i> | L 638 (PI126439) | 32 | 6 | |
| <i>L. peruvianum</i> | LA 111 | 67 | 19 | |
| <i>L. peruvianum</i> | LA 385 | 4 | 5 | |
| <i>L. p. f. glandulosum</i> | LA 1292 | 16 | 9 | 11 |
| <i>L. pimpinellifolium</i> | L 139 | 45 | 22 | |
| <i>L. pimpinellifolium</i> | L 140 | 46 | 23 | |
| <i>L. pimpinellifolium</i> | L 141 | 48 | 9 | |
| <i>L. pimpinellifolium</i> | LA 722 | 20 | 9 | |
| <i>L. pimpinellifolium</i> | LA 2184 | 7 | 37 | |
| <i>L. pimpinellifolium</i> | LA 2584 | 10 | 26 | 21 |
| Mean | | | 17.5 | |

used for comparison had 65 to 69% of their leaf areas affected.

In the second part of this experiment, in which accessions of seven *Solanum* spp. were inoculated, a wide range of disease responses was observed (Table 2). Eleven of the 12 *S. melongena* accessions developed symptoms, with disease severity ranging from 3 to 46% of their leaf areas affected. The cultivar Sapi did not develop symptoms. Two of three *S. indicum* accessions, one of two *S. macrocarpon* accessions, and a single *S. aethiopicum* accession developed symptoms. One *S. peruvianum* accession, two *S. pseudocapsicum* accessions, and two *S. torvum* accessions did not develop symptoms.

Experiment 5: *Lycopersicon* species. All 46 accessions of the 10 *Lycopersicon* spp. developed symptoms to some degree following inoculation. Responses of the accessions to black leaf mold ranged from 2 to 60% of their leaf areas affected (Table 3). Sources with high levels of black leaf mold resistance (<10% leaf area affected) were found among entries of *L. cheesmanii*, *L. chmielewskii* Rick et al., *L. glandulosum*, *L. hirsutum*, *L. pennellii* (Corr.) D'Arcy (*S. pennellii*), *L. parviflorum* Rick et al., *L. peruvianum*, and *L. pimpinellifolium* (Table 3). None of the *L. esculentum* or *L. esculentum* × *pimpinellifolium* entries were resistant.

Experiment 6: Field evaluation. Following repeated inoculations with *P. fuligena* conidia, black leaf mold symptoms

developed only on the two susceptible tomato entries and the two susceptible eggplant entries. Blue Star sweet pepper, tomato accessions L733 and L3718, and black nightshade, previously observed with symptoms under certain conditions, remained symptomless in this study. Szechwan hot pepper and ground cherry did not develop symptoms in this experiment nor in previous ones.

DISCUSSION

Black leaf mold of tomato was first described in 1938 (12). Other than a report on screening *Lycopersicon* spp. for resistance (6), there have been no extensive studies to determine the hosts of *P. fuligena*. In this report, 137 accessions representing 26 species and five genera of solanaceous plants were inoculated with *P. fuligena*. Disease developed on 106 accessions, representing *C. annuum*, *C. baccatum*, *C. chinense*, *C. frutescens*, *S. aethiopicum*, *S. indicum*, *S. macrocarpon*, *S. melongena*, *S. nigrum*, and 10 species of *Lycopersicon* (Table 4). All but five *Lycopersicon* spp. (6), *S. melongena* (7), and *S. nigrum* (4,7) are newly reported hosts of *P. fuligena*. Black leaf mold did not develop on *Nicotiana* spp., *Physalis* sp., *S. petinatum*, *S. pseudocapsicum*, *S. torvum*, or *S. tuberosum*.

Previous cross-inoculation studies using isolates from *S. nigrum* and tomato (4) suggested that *S. nigrum* was a host of *P. fuligena*. In our study, *S. nigrum* devel-

oped limited symptoms when inoculated with tomato isolates under controlled conditions, but not in the field. These studies show that our isolates of *P. fuligena* from tomato are much more aggressive on tomato than on *S. nigrum*. Whether this means that tomato isolates of *P. fuligena* are better adapted to tomato or that *S. nigrum* is in general more resistant than tomato to black leaf mold cannot be answered from our data, because isolates from *S. nigrum* were not used for comparison. However, *S. nigrum* plants growing in nature in Taiwan often develop extensive black leaf mold symptoms, which suggests the occurrence of wild types of the pathogen that are better adapted to *S. nigrum* than our tomato isolates.

With all species that developed symptoms except *Capsicum* spp., leaf lesions were first covered with white fungal growth that turned gray to black as the fungus sporulated, typical of *P. fuligena* sporulation on field-grown tomato (4). Pepper symptoms were atypical and appeared as irregular necrotic spots with limited conidial production. Field-grown peppers were not observed to develop black leaf mold symptoms in these studies, nor in other fields located adjacent to tomato fields with extensive black leaf mold symptoms (T. C. Wang, unpublished).

In the studies with eggplant-related species, both susceptible and resistant accessions were identified among entries from *S. indicum*, *S. macrocarpon*, and *S. melongena*. A single entry of *S. aethiopicum* was susceptible. All entries representing *S. petinatum*, *S. pseudocapsicum*, and *S. torvum* were resistant. Although cultivated eggplant developed symptoms in the field after inoculation, thus far no natural infection has been observed on eggplant in Taiwan's production areas. The differential responses among the *Solanum* spp. accessions are not surprising because of the genetic diversity of this genus.

All of the *Lycopersicon* spp. accessions developed some black leaf mold symptoms, but the range in the percent leaf area affected among wild tomato accessions varied greatly. It appears that the preferred host for *P. fuligena* is tomato. Besides *L. hirsutum* (6), there may be other sources like *L. chmielewskii* or *L. cheesmanii* that could be crossed with tomato as potential sources of resistance. These studies may serve as the basis for further work on host plant resistance as a component of an integrated system for management of black leaf mold of tomato.

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Table 4. Summary of the black leaf mold responses by accessions following inoculation with *Pseudocercospora fuligena* in a growth room at 95 ± 2% relative humidity, 28 ± 2°C, and 14 h of light per day

| Common name | Species | Accessions tested | Disease response ^a |
|------------------|---|-------------------|-------------------------------|
| Black nightshade | <i>Solanum nigrum</i> | 1 | + |
| Eggplant | <i>S. aethiopicum</i> ^b | 1 | + |
| Eggplant | <i>S. indicum</i> ^b | 3 | +(2/3) |
| Eggplant | <i>S. macrocarpon</i> ^b | 2 | +(1/2) |
| Eggplant | <i>S. melongena</i> | 22 | +(20/22) |
| Eggplant | <i>S. petinatum</i> | 1 | - |
| Eggplant | <i>S. pseudocapsicum</i> | 2 | - |
| Eggplant | <i>S. torvum</i> | 2 | - |
| Ground cherry | <i>Physalis</i> sp. | 1 | - |
| Pepper | <i>C. annuum</i> ^b | 25 | +(18/25) |
| Pepper | <i>C. chinense</i> ^b | 5 | + |
| Pepper | <i>C. baccatum</i> ^b | 5 | +(4/5) |
| Pepper | <i>C. frutescens</i> ^b | 5 | + |
| Potato | <i>S. tuberosum</i> | 5 | - |
| Tobacco | <i>Nicotiana</i> spp. | 8 | - |
| Tomato | <i>Lycopersicon cheesmanii</i> | 7 | + |
| Tomato | <i>L. chilense</i> ^b | 5 | + |
| Tomato | <i>L. chmielewskii</i> ^b | 3 | + |
| Tomato | <i>L. esculentum</i> | 5 | + |
| Tomato | <i>L. glandulosum</i> ^b | 3 | + |
| Tomato | <i>L. hirsutum</i> | 6 | + |
| Tomato | <i>L. parviflorum</i> ^b | 1 | + |
| Tomato | <i>L. pennellii</i> ^b | 1 | + |
| Tomato | <i>L. peruvianum</i> | 6 | + |
| Tomato | <i>L. pimpinellifolium</i> | 9 | + |
| Tomato | <i>L. esculentum</i> × <i>pimpinellifolium</i> | 3 | + |
| Total | 7 | 26 | 137 (106+) |

^a + = Developed lesions with sporulation or the fungus was reisolated from nonsporulating lesions; - = no symptom development.

^b First report as a host of *P. fuligena*.

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