Host Range, Specificity, and Biometrical Measurements of *Leveillula taurica* in California

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ABSTRACT

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Powdery mildew of tomato caused by *Leveillula taurica* (= *Oidiopsis taurica*) was found on tomato in all of the major tomato-growing regions of California during 1983–1985. In addition to tomato, the pathogen was found on four crop hosts (pepper, cotton, artichoke, and onion) and six weed species. The morphological characteristics of *L. taurica* were similar on all hosts and included endophytic mycelium, dimorphic conidia (pyriform and cylindrical), long and often branched conidiophores, and conidia borne singly or in short chains. Isolates from artichoke had both endophytic and epiphytic mycelium. Conidial size varied considerably among the isolates. The range of mean conidial measurements was 71.4–49.7× 24.1–16.6 and 65.2–44.6× 22.7–16.2 μm for the pyriform and cylindrical conidia, respectively. All isolates tested except the one from artichoke were able to infect tomato and apparently represent one physiological race of the pathogen.

The powdery mildew fungus, *Leveillula taurica* (Lév.) Arn. (=*Oidiopsis taurica* (Lév.) Salmon), is a unique foliar pathogen in its ability to infect a large and diverse number of plant species. Hirata (13) reported *L. taurica* on some 710 host species from 59 plant families. Additional reports indicate that the host range of *L. taurica* includes a minimum of 750 plant species including 27 economically important crop hosts (22). Most of the reports of this pathogen have been from warm arid to semiarid climatic zones in Asia, the Mediterranean, and Africa (21).

Until recently, there have been relatively few reports of *L. taurica* in North America (13). The first report of this pathogen in the United States was by Salmon on the host *Diplacus aurantiacus* Jeps. (=*Mimulus glutinosus*) in 1906 (24). This was followed by reports of *L. taurica* on mesquite (*Prosopis chilensis* Stuntz., *P. juliflora* (Swartz) DC., and *P. glandulosa* Torr.) in Texas (26), *Hibiscus cannabinus* L. in Florida (10), and again on *D. aurantiacus* in California (28). Subsequently, *L. taurica* has been reported on several economically important crop hosts in the United States including tomato (*Lycopersicon esculentum* Mill.) (15), pepper (*Capsicum annuum* L.) (27), onion (*Allium cepa* L.) (16), cotton (*Gossypium hirsutum* L.) (6), and guar (*Cyamopsis tetragonoloba* (L.) Taub.) (18).

There has been some debate over the identity of *L. taurica* as a species. Some workers have split *L. taurica* into several species and formae speciales on the basis of conidial size and host association (1,11,14,29). However, the validity of this nomenclature has been questioned (3) and has not been generally accepted (21). This has been due, in part, to the variability in conidial size of *L. taurica* and the somewhat contradictory results of cross-inoculation tests. In a recent taxonomic treatment of powdery mildews, Boesewinkel (2) recognized four species of *Leveillula*, with *L. taurica* having a host range spanning 18 plant families.

The objective of this investigation was to identify the hosts of *L. taurica* in California. Isolates from several diverse hosts were tested for their ability to infect tomato (*Lycopersicon esculentum*). Observations also were made on the morphological characteristics of the fungus from different hosts.

MATERIALS AND METHODS

Identification and biometrical measurements. *L. taurica* was identified on each host according to the description of Boesewinkel (2). Morphological characteristics such as the location of the mycelium on the host, the presence of dimorphic conidia, branching of the conidiophores, and size and shape of the conidia were recorded.

Conidia from several hosts were collected by dislodging them from the host tissue onto a strip of clear tape or by collecting spores on a piece of clear tape with a field-portable spore sampler (9). The tape was mounted on a microscope slide for measurements. The slides were stored at 4 C after returning them to the laboratory, and conidia were measured within 72 hr. The conidia were measured at either 320 or 640× with a calibrated ocular micrometer. A minimum of 100

Table 1. Crop and weed hosts of *Leveillula taurica* in California

Plant family	Common name	Plant species	Cross-infectivity to tomato[a]
Amaryllidaceae	Onion	*Allium cepa*	+
Compositae	Annual sowthistle	*Sonchus oleaceus*	+
	Artichoke	*Cynara scolymus*	−
	Wild artichoke[b]	*C. cardunculus*	NT
	Cocklebur	*Xanthium strumarium* L.	NT
	Common groundsel	*Senecio vulgaris* L.	NT
Cruciferae	Shepherd's purse	*Capsella bursa-pastoris* (L.) Medic.	NT
Geraniaceae	Whitestem filaree	*Erodium moschatum* (L.) L'He'r.	NT
Malvaceae	Cotton	*Gossypium hirsutum*	+
Solanaceae	Groundcherry	*Physalis* sp.	+
	Chili pepper	*Capsicum annuum* L. var. *longum*	+
	Tomato	*Lycopersicon esculentum*	+

[a] + = Positive infection (minimum of one lesion per plant), − = no infection, and NT = not tested.
[b] Reported by Sims and Esparza (25) in San Diego County.

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conidia were measured from each host, and no more than five conidia were measured from any one lesion.

Cross-inoculations. Isolates were collected from tomato (*L. esculentum*), pepper (*C. annuum* var. *longum* Bailey 'Jalapeno'), onion (*A. cepa* 'Henry's Special'), cotton (*G. hirsutum* 'GC-510'), sowthistle (*Sonchus oleraceus* L.), groundcherry (*Physalis* sp.), and artichoke (*Cynara scolymus* L. 'Globe') plants growing under field conditions during the 1983–1985 growing seasons. Host tissue showing evidence of infection and sporulation was collected, stored in a plastic bag under cool conditions (about 15 C), and transported to the laboratory. Host tissue was incubated for 24–48 hr at 20 C before use as an inoculum source. Inadequate inoculum from several hosts prevented testing the pathogenicity of those isolates on tomato.

Tomato plants (cultivars Royal Flush or Bonny Best) used for inoculation experiments were grown as follows: 6-wk-old tomato seedlings were transplanted into 0.5-L pots containing pasteurized potting soil mix. Plants were fertilized daily with half-strength Hoagland's solution (12). All plants were inoculated at the eight- to 20-leaf stage and were blooming but had no fruit when inoculated.

Inoculations were made in the evening (1700–2200 hours), as suggested by Reuveni and Rotem (23). Plants were put in a settling tower (0.8 × 1.6 m) that was open at the top. A stream of forced air was passed over infected host tissue so that dislodged conidia were carried into the settling tower. All inoculations were done on six to 12 plants, and each inoculation experiment was repeated once. Only one inoculation experiment was under way at any given time to eliminate the possibility of contaminating inoculum being present. Also, uninoculated control plants were incubated in the same greenhouse room as the inoculated plants during each experiment to verify the absence of contaminating inoculum.

After inoculation, plants were moved to the greenhouse for incubation. The temperature during a 12-hr period immediately following all inoculations was 20 ± 5 C. The relative humidity was maintained between 85 and 100% during this 12-hr period. Lesion development per plant was recorded over a 30- to 40-day period after inoculation. The maximum and minimum temperatures during this incubation period were 29 ± 6 and 23 ± 5 C, respectively. The relative humidity fluctuated daily, 60 ± 10% during the day and 85 ± 8% at night.

RESULTS AND DISCUSSION

Tomato is a major host of *L. taurica* in many countries that have a warm arid to semiarid climate during the growing season (21). *L. taurica* has been reported on tomato in the Imperial Valley (15), the San Joaquin Valley (5), and the San Diego area (25) in California. We found the pathogen in all of the major tomato-growing regions of California during the 1983–1985 growing seasons. Our findings extend the earlier reports of the occurrence of *L. taurica* to the Sacramento, Salinas, Ventura, and Santa Clara valleys. Thus, *L. taurica* is now widespread in California.

The fungus was also found on numerous weed and crop hosts growing in the vicinity of tomato plantings (Table 1). In general, sporulating lesions were predominantly, but not exclusively, restricted to the oldest leaves of each host. Infected weeds were more common in the late summer and early fall (August through October) in the San Joaquin Valley as daily maximum temperatures decreased. Nour (20) reported similar findings and suggested that certain hosts may be more susceptible to infection by *L. taurica* under cooler environmental conditions.

L. taurica has been found on several crop hosts in California, including onion (16), pepper (8), cotton (6), and artichoke. The pathogen was found on onion

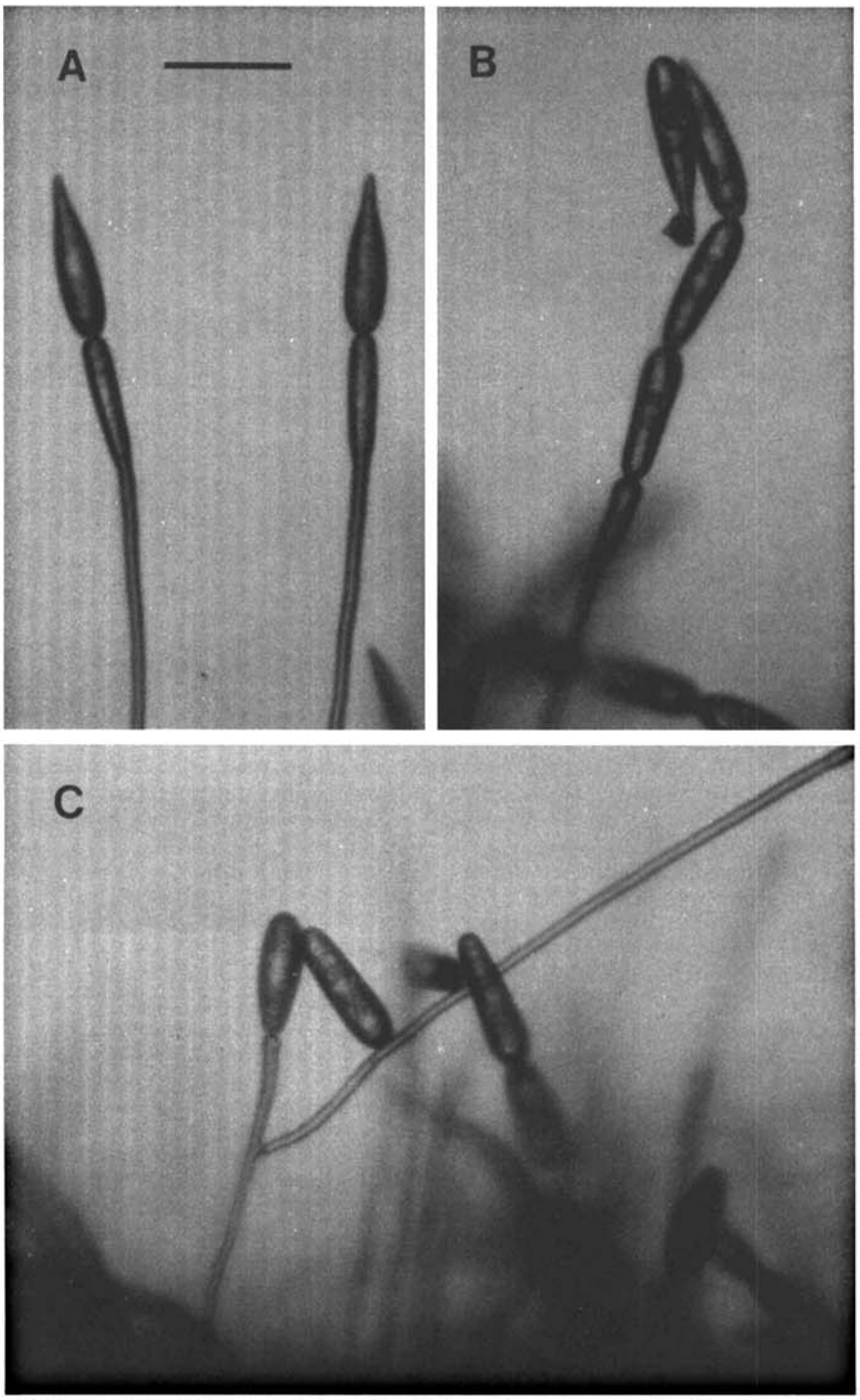

Fig. 1. Morphological characteristics of *Leveillula taurica* on tomato. **(A)** Dimorphic conidia (terminal conidium pyriform to obclavate and secondary conidium cylindrical). **(B)** Conidia borne in short chains. **(C)** Branched conidiophore. Scale bar = 50 μm.

Table 2. Conidial sizes of *Leveillula taurica* from various hosts and locations in California

Host	County	Spore type[a]	L × W[b]	L × W (SD)[c]	Range L max.	Range L min.	Range W max.	Range W min.
Tomato	Merced	1	60.8 × 17.6	5.7 × 1.8	73.8	45.4	22.7	12.8
		2	54.1 × 16.6	5.7 × 1.4	69.6	38.3	19.2	14.2
Tomato	Stanislaus	1	61.9 × 19.1	7.3 × 1.6	76.7	44.7	23.4	14.9
		2	56.9 × 18.2	6.8 × 1.6	77.4	46.2	22.0	14.2
Tomato	San Quintin[d]	1	63.1 × 16.6	9.0 × 2.7	78.1	35.5	24.8	10.6
		2	54.3 × 16.2	7.5 × 3.0	71.0	39.8	20.6	8.5
Pepper	Santa Clara	1	60.6 × 20.8	5.2 × 2.3	72.9	51.5	24.3	15.7
		2	57.6 × 19.4	5.2 × 2.1	67.2	45.8	22.9	15.7
Onion	Imperial	1	49.7 × 17.9	4.8 × 3.7	60.3	39.1	27.7	12.1
		2	44.6 × 17.7	4.4 × 2.2	58.9	35.5	21.3	14.2
Cotton	Fresno	1	65.9 × 18.5	8.1 × 2.7	81.5	51.5	22.9	14.3
		2	57.1 × 18.0	6.5 × 2.7	71.5	45.8	24.3	14.3
Artichoke	Santa Maria	1	52.8 × 24.1	4.3 × 2.9	68.6	42.9	30.0	17.2
		2	56.0 × 22.7	6.5 × 3.0	75.8	45.8	27.2	14.3
Sowthistle	Stanislaus	1	56.8 × 17.1	4.9 × 1.8	68.2	47.6	21.3	11.4
		2	48.9 × 16.9	5.4 × 1.8	59.6	35.5	21.3	12.8
Sowthistle	Stanislaus	1	69.0 × 17.7	4.1 × 1.3	77.2	60.1	20.0	15.7
		2	64.8 × 16.2	6.7 × 1.3	81.5	55.8	18.6	12.9
Cocklebur	Stanislaus	1	71.4 × 18.2	4.2 × 2.0	77.2	60.1	21.5	14.3
		2	65.2 × 17.5	6.3 × 1.5	75.8	52.9	21.5	15.7

[a] 1 = Pyriform conidium and 2 = cylindrical conidium.
[b] L = length and W = width of conidia in micrometers.
[c] SD = standard deviation of the mean.
[d] Baja California, Mexico.

in the Imperial Valley (16) in 1983 and 1985 and in the central San Joaquin Valley in 1985. Cotton (6) also was found infected with *L. taurica* in the central San Joaquin Valley in 1985. Only one cotton field was found with powdery mildew, and this field was adjacent to and downwind of a tomato field that had a very high incidence of powdery mildew. Chili peppers (*C. annuum* var. *longum*) were found infected by *L. taurica* in the Santa Clara Valley in 1983 and 1985. However, we have not seen the pathogen on sweet peppers (*C. annuum* var. *grossum* Bailey) in the central San Joaquin Valley, even though many fields observed were adjacent to heavily infected tomato fields. Artichokes observed in the Santa Maria and Salinas valleys in the summer and fall of 1985 and 1986 were heavily infected by *L. taurica*.

Based on morphological characteristics, the isolates closely match Boesewinkel's description of *L. taurica* (2). The characteristics observed on all the hosts were endophytic mycelium, dimorphic conidia (terminal conidium pyriform to obclavate and secondary conidium cylindrical) (Fig. 1A), conidia borne singly or in short (fewer than six conidia) chains (Fig. 1B), and long (147–236 μm) and often branched conidiophores (Fig. 1C). Mean conidial measurements were 71.4–49.7 × 24.1–16.6 and 65.2–44.6 × 22.7–16.2 μm for the pyriform and cylindrical conidia, respectively (Table 2). The conidia we observed were slightly wider (1–3.4 μm) than those reported by Boesewinkel (2). The teleomorph of this pathogen, which has been reported on numerous hosts (22), has not been reported in the United States and was not found in California.

There was considerable variation in the size of conidia among isolates from different hosts. The length and width of conidia from various hosts in California clearly overlap and therefore do not justify the designation of different species for isolates on the basis of conidial size as suggested by Laudanski (17). In addition, conidia on sowthistle from two locations varied in size considerably (Table 2). Moreover, Caesar and Clerk (4) have shown that conidial morphology also may be affected if the host is water-stressed.

The isolate from artichoke differed from other isolates in several characteristics. The mycelium of *L. taurica* on artichoke was both endophytic and epiphytic on the abaxial leaf surface rather than entirely endophytic as observed on all other hosts. Conidia of the artichoke isolate also were considerably wider than those found on the other hosts, and the apical conidium was more cylindrical with a much less pronounced "point."

The data suggest that in California, *L. taurica* is capable of infecting a diverse group of plant species and has a broad host range. Isolates from six hosts in four plant families were able to infect tomato under controlled greenhouse conditions (Table 1). Lesions developed within 11–26 days of inoculation, with longer latent periods occurring under cooler conditions. The resulting lesions induced by the various isolates were indistinguishable from those induced by isolates originating from tomato. Lesions were not observed on any of the uninoculated control plants. Although Palti (21) has speculated on the probable occurrence of races or specialized forms of *L. taurica*, this has not been demonstrated. With the exception of the artichoke isolate, all tested isolates in California have been able to infect tomato and probably represent one physiological race.

Although the artichoke isolate was unable to infect tomato, caution should be used in evaluating negative results of cross-inoculation tests. Environmental conditions have been shown to influence infection by the pathogen (19,21). Moreover, cross-inoculation tests also are dependent on the viability of inoculum. Isolates obtained from artichoke were only recently discovered, and infected artichoke leaves were collected at a time when the plants were not actively growing. This may have had an effect on the viability of the conidia collected from artichoke.

Many of the weed hosts of *L. taurica* are present throughout the winter months in California and may allow the pathogen to overwinter in the absence of the tomato host. Consequently, these hosts may serve as the source of primary inoculum in the initiation of early-season epidemics of powdery mildew of tomato (7). Onion, planted as a winter crop in many of the tomato-growing regions, also may be an important overwintering host.

Environmental conditions appear favorable for *L. taurica* in California throughout the summer months, and we suspect that with closer scrutiny, more crop and weed hosts will be found infected with *L. taurica*.

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