Overwintering Hosts, Compatibility Types, and Races of *Phytophthora infestans* on Tomato in Southern California

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ABSTRACT

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Although 11 solanaceous species of plants were susceptible to local isolates of *Phytophthora infestans* in the greenhouse, only tomato, potato, and *Solanum sarrachoides* were infected in the field. Tomato was the most common host. Although potato is not grown commercially in coastal southern California, potato occasionally was found infected in home gardens. Blighted plants of *S. sarrachoides* were encountered commonly in field surveys throughout the year. In cross-inoculation tests, isolates of *P. infestans* recovered from tomato, potato, and *S. sarrachoides* were pathogenic on all three hosts. Thirty-eight isolates of *P. infestans* from tomato, potato, and *S. sarrachoides* collected from southern California coastal counties, the lower San Joaquin Valley, and Baja California, Mexico, were evaluated for their race composition on tomato differential hosts. Ninety-five percent were tomato race 1 (T1) and 5% were tomato race 0 (T0). When 57 isolates were evaluated for their compatibility type, 54 were A1, one was neuter, and two presumably were homothallic.

After an absence of 32 yr, late blight, caused by *Phytophthora infestans* (Mont.) de Bary, appears to have become an annual threat to tomatoes (*Lycopersicon esculentum* Mill.) in coastal regions of southern California from Santa Maria to San Diego (Fig. 1). This is because the mild winters since 1979 have permitted the fungus to overwinter on infected solanaceous plants and because the temperate coastal climate with its frequent fogs favor both the fungus and the disease.

If integrated control measures are to be developed against late blight, information is needed on how the fungus overwinters and what races and compatibility types of the pathogen are present.

Of the six southern California coastal counties, only in the southernmost county, San Diego, are three crops of tomatoes grown per year. In the remaining counties, only one crop is grown; it is planted in March through June and harvested from August into November. During periods when tomatoes are being grown, the fungus survives mainly on tomato, but it is not evident how the fungus overwinters in the absence of commercial crops of tomatoes since potatoes are not grown commercially in the coastal areas.

Information is also needed on the occurrence and relative prevalence of the A1 and A2 compatibility types of *P. infestans* in southern California because oospore formation is dependent on the presence of both compatibility types. Both compatibility types are known to occur together only in Mexico; in other areas of the world, only the A1 compatibility type has been reported (5).

This paper deals not only with a determination of the tomato races and compatibility types of *P. infestans* in southern California but also with its overwintering solanaceous hosts.

MATERIALS AND METHODS

Field surveys. The major tomato production areas of coastal southern California were surveyed during 1981 and 1982 for the occurrence of late blight on cultivated and uncultivated host plants. Special attention was directed to solanaceous weed species growing within and around fields of blighted tomato, and seeds of these weeds were collected for greenhouse host range studies. When lesions suggestive of late blight were found, isolations were made by surface-disinfesting the lesions for 2–5 min in 0.5% NaOCl solution and plating them on rye seed medium A (RSA-A) (2) supplemented with pimaricin, ampicillin, rifampicin, and pentachloronitrobenzene (7). Representative lesions also were placed in a moist chamber to induce sporulation typical of *P. infestans*.

Greenhouse inoculations. Since the race identity of *P. infestans* in southern California was unknown, eight isolates of the pathogen from blighted plants of

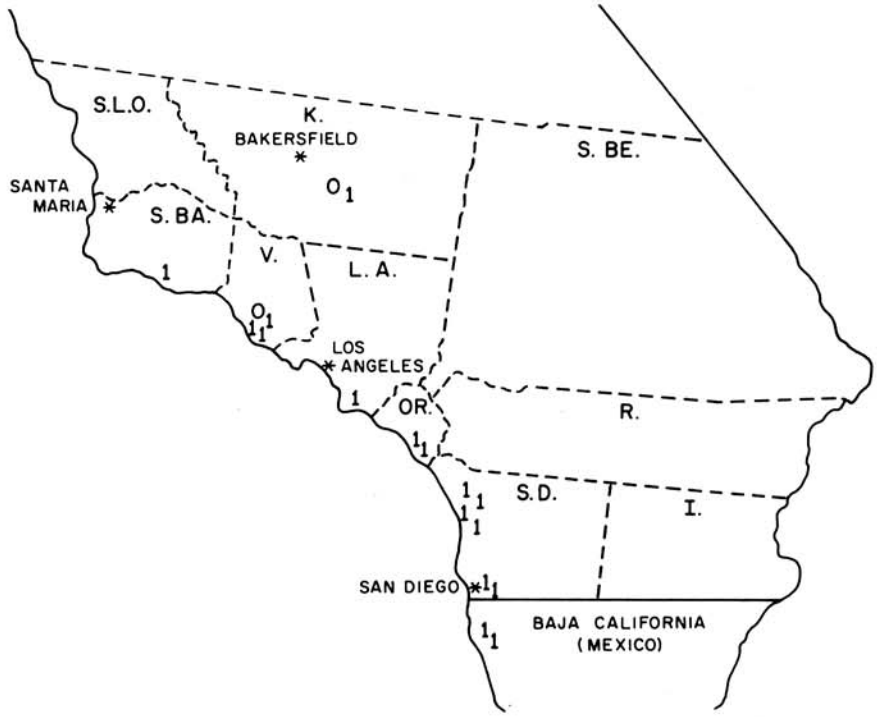

Fig. 1. Distribution of tomato races 0 and 1 of *Phytophthora infestans* in southern California counties in 1981–1982: S.L.O. = San Luis Obispo, K. = Kern, S. BE. = San Bernardino, S. BA. = Santa Barbara, V. = Ventura, L.A. = Los Angeles, OR. = Orange, R. = Riverside, S.D. = San Diego, and I. = Imperial.

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Solanum sarrachoides Sendt. ex. Mart., tomato, and potato (*S. tuberosum* L.) were mixed and used as inoculum for the host range studies. In subsequent studies, two of the isolates were identified as race 0 and six as race 1.

A total of 39 solanaceous plant species growing in California and the susceptible tomato cultivar Casino Royale were inoculated in the greenhouse for the host range studies. Of these, 30 species grow in southern California. Twenty-eight of the seeds or cuttings of the test plants were obtained from local sources; the others, from various herbaria in the United States. Plants were grown from seeds or cuttings in 10-cm-square pots in steamed U.C. soil mix (1) in the greenhouse at 18–24 C. When plants were 8–12 wk old, they were spray-inoculated with a sporangial suspension (10^4 sporangia per milliliter); the plants were placed in a mist chamber (16–21 C, 10 hr of fluorescent illumination per day) for 48 hr, then moved to the greenhouse. In addition, detached leaves and stem segments in petri dish moist chambers were inoculated with two to four drops of inoculum (10^4 sporangia per milliliter) per leaf or stem; control plants were treated with double-distilled water. The petri dishes were placed in a growth chamber set at 20 ± 1 C and received 8 hr of fluorescent illumination per day.

Inoculated plants were observed daily for symptom development. If lesions developed on whole plants, they were placed in the mist chamber for 24 hr to induce sporulation. Detached leaves and stem pieces were observed for 7 days after inoculation for the appearance of lesions. The reaction of a species was considered incompatible or resistant if no visible lesions or sterile, nonsporulating lesions were produced or compatible or susceptible if necrotic lesions were produced that bore sporangia.

Cross-inoculations were conducted with isolates of the fungus recovered from tomato, potato, and hairy nightshade to each of the three hosts. Isolations and inoculations were carried out as described previously.

Determination of tomato races. Isolates of *P. infestans* that were evaluated for their tomato race composition were isolated from lesions taken from blighted fruits, stems, or leaves of tomato, potato, or hairy nightshade collected from different locations within coastal southern California, the lower San Joaquin Valley, and Baja California, Mexico. Isolations were made onto the RSA-A medium as described previously.

Two tomato accessions, WV 63 and WV 700, were used to distinguish between tomato race 0 (T0) and tomato race 1 (T1) following the recommendation of R. J. Young (*personal communication*), Division of Plant and Soil Sciences, West Virginia University, Morgantown, who also supplied seeds of the differential host plants, the susceptible cultivar Success, and cultures of races T0 and T1. Differentiation of the two races is based on incompatibility responses induced in the two differential hosts by each of the two races.

Seeds of all cultivars were placed individually in steamed U.C. soil mix held in fiber pots (10 × 10 cm) and the plants were grown on a greenhouse bench (18–24 C). The 38 isolates of *P. infestans* used in the race identification studies, plus the known isolates of races T0 and T1, were grown on RSA-A medium for 10–12 days at 18 C in the dark. Inoculum was prepared as follows: Sporangia were rinsed off the culture plates and filtered through one layer of cheesecloth, then the inoculum concentration was adjusted to 10,000 sporangia per milliliter. Plants 6–8 wk old were sprayed with a sporangial suspension until runoff, placed in a mist chamber (16–19 C) for 24 hr, and then placed on a bench in the greenhouse (17–22 C). If symptoms developed, the plants were placed in the mist chamber for 24 hr to induce sporulation. Young, detached leaflets from plants 6–8 wk old were also inoculated by placing them on a moist filter paper in petri plates. Two to four drops of the inoculum were applied to both the upper and lower surfaces of the leaflets, and the leaflets incubated at 19 ± 1 C with 10 hr of light. The final results were recorded 7 days after inoculation.

Determination of compatibility types. A total of 57 isolates of *P. infestans* were individually paired with each of two compatibility types of the fungus. Both compatibility type A1 (isolate WV 473) and A2 (isolate WV 445) were obtained from the *Phytophthora* culture collection of the Department of Plant Pathology, University of California, Riverside. Matings were made as follows: Agar disks (3 mm in diameter) were cut from the edges of 7-day-old RSA-A cultures of *P. infestans* of unknown compatibility type and placed singly on the RSA-A medium 4 cm from a similar agar disk of either the A1 or A2 compatibility type. Control matings consisted of similar pairings of the A1 and A2 compatibility types. Cultures were incubated at 21 C in the dark for 4–5 wk, then microscopic readings for the presence or absence of oospores were made.

RESULTS

Field surveys. Only tomato, potato, and hairy nightshade were observed to be infected with *P. infestans* in the field in the six southern California coastal counties. All developed abundantly sporulating lesions on all aerial parts of the plants throughout the year.

Tomato was the most common host. A unique situation was found in San Diego County, the only county where three crops of tomatoes are grown annually. The fall crop of fresh market and cherry tomatoes is harvested from September into December. Since the crop is grown on poles, depoling, destringing, and plowing under are frequently delayed until labor is available. In the absence of killing frosts, many of the plants persist until early March. Since the weather from January to March was ideal for late blight, holdover plants developed the disease in both the winters of 1982 and 1983. From the holdover plants, *P. infestans* was transmitted by sporangia to tomato transplants of the spring crop planted under plastic tunnels in southern San Diego County, to tomato transplants grown in unheated plastic greenhouses owned by growers or transplant nurserymen in northern San Diego County, and to tomato seedlings grown outside in transplant trays by nursery workers for sale to the public. Blighted transplants became widely distributed in home gardens during the winters of 1982 and 1983 because transplants were sold to homeowners in San Diego, Orange, and Los Angeles counties. Blighted plants also became widespread in growers' fields in San Diego County because infected seedlings with latent infections were transplanted.

Another unusual situation involving blighted tomato plants was observed on four occasions in San Diego and Ventura counties during the very wet winters of 1982–1983. Blighted seedlings were observed emerging in clumps from infected tomato fruits lying on the ground. Since lesions and sporulation were located at the bases of the stems, the infected seedlings probably had arisen from seeds infected or infested with *P. infestans* and not from aerially disseminated sporangia (V. G. Vartanian, *unpublished*).

Infected tomato plants were observed in three additional situations: 1) on volunteer tomato plants arising in the winter in and around old tomato fields, 2) on volunteers arising from tomato cull piles, and 3) on holdover tomato plants and volunteers in the gardens of homeowners.

Although potatoes are not grown commercially along the coast of southern California, potato plants were found infected under two situations. The first occurred in San Diego County at Camp Pendelton, where several acres of potatoes were grown annually during the winter by the extension services of several western states to determine whether seed tubers were free of virus. Late blight occurred severely in these plots during the winters of 1982 and 1983, and the inoculum presumably came from an adjacent 100-acre holdover field of blighted tomatoes. In the second situation, blighted potatoes were found during the winter in home gardens in San Diego and Ventura counties.

Other potential hosts (solanaceous weeds, eggplant, pepper, and ornamentals)

were observed, but late blight was found only on the common annual weed hairy nightshade. It developed lesions on the stems, petioles, and leaves, and the fungus produced abundant sporangia throughout the year. Although seven other solanaceous plants occurring in southern California were found susceptible to *P. infestans* in the host range studies conducted in the greenhouse, none were found infected in the field.

Greenhouse inoculations. Of 39 species of solanaceous plants inoculated, 11 were susceptible to the composite inoculum that consisted of a mixture of races T0 and T1 (Table 1). No differences in response were detected between whole plants and detached plant parts after inoculation.

Table 1. Reactions of 37 solanaceous plant species growing in California to tomato races 0 and 1 of *Phytophthora infestans* inoculated in the greenhouse[a]

Plant species	Reaction to *P. infestans*[b]
Browallia speciosa Hook.	R
Brugsmansia sanguinea (Ruiz & Pav.) D. Don	R
Capsicum annuum L.	R
Cestrum elegans Schlecht.	R
C. nocturnum L.	R
C. parqui L'Her	R[c]
Datura meteloides	S
D. stramonium	S
Lycium chinense	S[d]
L. halimifolium Mill.	R
Nicandra physalodes	S
Nicotiana acuminata	S[d]
N. alata Link & Otto	R
N. bigelovii (Torr.) Wats.	R
N. clevelandii	S
N. glauca Graham	R
N. sanderae W. Wats.	R
N. sylvestris Speg. & Comes	R
N. trigonophylla Dunal	R
Nierembergia hippomanica Miers	R
Petunia hybrida	S
P. parviflora Juss.	R
Physalis ixocarpa Brot.	R
P. peruviana L.	R
Salpiglossis sinuata Ruiz & Pav.	R
Schizanthus pinnatus	S
Solandra guttata Don	R
Solanum aviculare	S
S. douglasii Dunal	R
S. elaeagnifolium Cav.	R
S. jasminoides Paxt.	R
S. melongena L.	R
S. nigrum L.	R
S. nodiflorum Jacq.	R
S. pseudocapsicum L.	R
S. sarrachoides	S
S. sisymbriifolium	S

[a] Sporangial inoculum (10^4 sporangia per milliliter) consisted of a mixture of eight isolates of *P. infestans* that included the two tomato races, T0 and T1.

[b] R = resistant: no visible lesions, or sterile nonsporulating lesions produced after inoculation. S = susceptible: sporulating lesions produced after inoculation.

[c] Flowers and fruits were susceptible but foliage was resistant.

[d] Susceptible plants that grow outside southern California.

The 11 susceptible plant species were *Datura stramonium* L., *Lycium chinense* Mill., *Nicandra physalodes* (L.) Gaertn., *Nicotiana acuminata* (R. C. Grah.) Hook., *N. clevelandii* Gray, *Solanum aviculare* Forst., *S. sarrachoides, S. sisymbriifolium* Lam., *Petunia hybrida* Vilm., *Schizanthus pinnatus* Ruiz. & Pav., and *D. meteloides* DC. *D. meteloides* was an unusual host in that only the flowers and fruits were susceptible. Of the 11 susceptible species, only *L. chinense* and *N. acuminata* grow outside of southern California.

Five nonsolanaceous hosts were inoculated because they had been reported to be susceptible to *P. infestans* (9,10) but were not found to be hosts of the local isolates of the pathogen. These were *Galinsoga parviflora* Cav., *Ipomoea hederacea* (L.) Jacq., *I. purpurea* (L.) Roth., *Mirabilis jalapa* L., and *Sonchus oleraceous* L.

Ten of 10 tomato isolates of *P. infestans* were pathogenic to the potato cultivar Red La Soda, and nine of 10 were pathogenic to *S. sarrachoides*. Four of four potato isolates of *P. infestans* were pathogenic to *S. sarrachoides* and to tomato; one potato isolate was only slightly pathogenic to tomato. Two of two isolates from *S. sarrachoides* were highly pathogenic to potato and tomato.

Race composition. Thirty-six of the 38 isolates evaluated were race T1. The cultivars Success and Casino Royale were highly susceptible to race T1, whereas WV 63 was moderately resistant and WV 700 was highly resistant. The remaining two isolates were race T0. The cultivars Success and Casino Royale were susceptible to race T0, whereas WV 63 and WV 700 manifested a high degree of hypersensitive resistance. Plants and detached leaflets of Casino Royale and of Success inoculated with T1 isolates developed symptoms several days earlier than when inoculated with T0 isolates. The disease reaction of detached leaflets of each of the differential hosts to an isolate was very similar to that expressed by whole plants.

The colony morphology and growth rate of all the T1 isolates grown on RSA-A and incubated at 18 or 21 C in the dark were very similar to the T0 and T1 isolates obtained from West Virginia. However, the two T0 cultures from California grew more slowly and produced fewer sporangia than the other isolates.

The 36 isolates that were race T1 were isolated from tomato, potato, and *S. sarrachoides* collected from coastal southern California, the lower San Joaquin Valley and Baja California, Mexico (Fig. 1). Thus race T1 appeared to be generally distributed throughout the southern part of the state. In contrast, race T0 was isolated only from a pear tomato fruit collected from midcoastal southern California and from a potato stem collected from the southern San Joaquin Valley.

Compatibility types. Assuming that sexual compatibility in *P. infestans* is controlled by two alleles of a single locus (A1 and A2) (2), none of the 59 isolates evaluated was of the A2 compatibility type, including the three isolates from tomatoes collected from Baja California. Fifty-four of the 57 isolates were compatibility type A1. One of the tomato isolates from Baja California did not produce oospores when paired with either of the two compatibility types. The remaining two isolates were apparently homothallic since the oospores produced in single cultures were morphologically very similar to the ones produced in paired cultures, the antheridia were amphigynous, and the oospores were thick-walled. Contrary to observations made by Gallegly and Galindo (5), the number of oospores produced homothallically in single cultures did not increase when paired with either the A1 or the A2 isolates.

To ensure that production of oospores was homothallic and that the colonies were not mixed cultures of compatible strains, single-spore (sporangium) colonies of the homothallic isolates were established on the RSA-A medium. Six colonies of both homothallic isolates were studied. All 12 cultures arising from a single sporangium produced oospores that were morphologically similar to the ones formed by the original cultures.

Although the oospores of the homothallic isolates appeared normal morphologically, the parent cultures grew somewhat atypically; cultures were slightly appressed rather than cottony and hyphal swellings were present.

The two homothallic isolates were isolated from a stem lesion and a tuber lesion from potato plants collected from Bakersfield, CA (southern San Joaquin Valley) (Fig. 1). The isolate from the stem lesion was identified as race T0; the race of the second isolate was not characterized.

DISCUSSION

Although 11 of the 30 solanaceous species inoculated in the greenhouse were susceptible to *P. infestans, S. sarrachoides* was the only species found infected in the field. These observations agree with those of Sztejnberg and Wahl (11), who reported that the host range of *P. infestans* in the field was more restricted than that observed in their greenhouse studies. Infected *S. sarrachoides* was found throughout the year only in cultivated fields, and isolates of *P. infestans* from hairy nightshade readily infected tomato. Barring killing frosts, therefore, *P. infestans* can overseason in infected *S. sarrachoides*. Effective herbicides are currently available to control *S. sarrachoides* in most crops but

not in tomato.

Field surveys showed that barring killing frosts, tomato is the most important overwintering host of *P. infestans* in southern California. The fungus not only overwintered on holdover plants growing in abandoned commercial fields (San Diego County only) and in home gardens but also on volunteer plants arising in old tomato fields, home gardens, and cull piles. Primary sources of inoculum occurred only rarely in the field when infected or infested tomato seeds gave rise to blighted seedlings in moist soil. Obviously, to reduce the number of infected tomato plants carrying the fungus over mild winters, growers must plow under or destroy all holdover tomato plants and volunteers as soon as possible. However, sufficient blight may overwinter on holdover tomato plants in home gardens to reinitiate the disease in the spring.

Potato probably plays a minor role in overwintering since it is not grown commercially along the coast and late blight was found in only two home gardens. Each year in the southern San Joaquin Valley near Bakersfield, several thousand acres of potatoes are planted that become blighted, apparently because infected tubers are planted and the crop is grown under sprinkler irrigation. Since Bakersfield is 90 mi. northeast of the nearest coastal tomato-growing area, it is doubtful whether viable sporangia can be wind-disseminated over this distance.

Prevalence of race T1 in southern California may be due to its biological and pathological properties. The local T1 isolates grew much faster, sporulated more abundantly, and were more virulent than the T0 isolates. These factors plus the continuous presence of susceptible host plants in the area, the occurrence of cool, foggy periods, and the recent absence of winter frosts could allow for the buildup of race T1 and the gradual reduction of race T0.

Since both tomato races are present, a breeding program for tomatoes in California must be designed to control both races. Resistance in the genus *Lycopersicon* against *P. infestans* is rare (8). There are tomato accessions possessing the Ph 1-gene for hypersensitive resistance against race T0 of *P. infestans* (6), but accessions with a gene for hypersensitivity against race T1 are not available (12). Resistance against race T1 in tomato is only partial and is present in very few accessions (9,12).

Since the A2 compatibility type is absent, most isolates of *P. infestans* in southern California are incapable of forming oospores and surviving by these means. Since two isolates of *P. infestans* were apparently homothallic in culture, experiments are in progress to determine whether these single-strain isolates also produce infectious oospores in solanaceous hosts in the field.

In conclusion, a considerable reduction in the numbers of overwintering blighted plants could be obtained by sanitation, which would reduce effectively the amount of inoculum produced during the growing season. According to Fry (3), control of the polycyclic late blight disease is best achieved by reducing large amounts of initial inoculum, thereby lowering the rate of disease increase. Keeping down the rate of disease increase appears feasible in coastal southern California from May to September because the weather is characterized by very low rainfall and only occasional, favorable periods of fog. Any practice that reduces moisture formation and retention during that period has been observed to keep late blight under control. Examples of such techniques are growing tomatoes on poles, use of drip irrigation, elimination of sprinkler irrigation, reducing the number of furrow irrigations to a minimum, and not overfertilizing with nitrogen. Keeping down the rate of blight increase from October to December is more difficult because rains may occur, temperatures are cool, and the tomato canopy is well developed. However, the occasional and prompt use of fungicides will help to control the disease at this time.

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