Etiological Role of the Xylem-Limited Bacterium Causing Pierce's Disease in Almond Leaf Scorch

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ABSTRACT

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A xylem-limited bacterium resembling the bacterium that causes Pierce's disease (PD) of grapevines was isolated from 17 of 20 almond trees (*Prunus amygdalus*) with almond leaf scorch (ALS) symptoms but not from 16 symptomless trees in two orchards in California. The bacterium was isolated from symptomatic trees in both orchards throughout one summer on 22 of 23 (95.7%) and 34 of 60 (56.7%) attempts. PD or ALS symptoms developed in their respective hosts when inoculated with bacterial strains from either host. Injections with a syringe and hypodermic needle were an efficient means of inoculating both hosts. ALS symptoms were more extensive and the bacteria were reisolated more frequently when trees in varietal blocks were inoculated with bacteria by injection than by leafhopper (*Draeculacephala minerva*) transmission. Few first-year infections survived the winter.

Additional key words: rickettsialike bacteria, alfalfa dwarf disease.

Almond leaf scorch (ALS) was first described as a disease of unknown etiology in 1974 (13,16). Subsequently, leafhopper transmission and electron microscope studies (12) revealed ALS to possibly be caused by the same xylem-limited bacterium previously associated with Pierce's disease (PD) of grapevines and alfalfa dwarf (AD) disease (6,7).

Recently a xylem-limited bacterium isolated from grapevines with PD and almond trees with ALS incited PD in inoculated grapevines (1). Ultrastructurally, the bacteria in culture were indistinguishable from those in diseased almond and grapevines, and a positive serological relationship between the bacteria in culture and in naturally infected grapevines with PD was established. In this paper we present evidence that the same xylem-limited bacterium is responsible for causing both PD and ALS. The efficiency of isolation from naturally infected almond with ALS was examined as were various techniques for inoculating both grapevine and almond. A short account of portions of this study has been published (3).

MATERIALS AND METHODS

Medium. The PD2 medium with cycloheximide was used throughout this study. The medium was made as follows: To 980 ml of double distilled water add Bacto-tryptone, 4 g; Phytone (BBL), 2 g; trisodium citrate, 1 g; disodium succinate, 1 g; hemin chloride stock solution, 10 ml; $MgSO_4 \cdot 7H_2O$, 1 g; K_2HPO_4, 1.5 g; KH_2PO_4, 1.0 g; and Bacto-agar, 15 g. The hemin chloride stock solution consisted of 0.1% hemin chloride in 0.05 N NaOH. This basal medium was heated to dissolve the agar and then autoclaved at 121 C and 1.27 kg/cm^2 for 20 min. Bovine serum albumin fraction five at 20% and cycloheximide at 0.5% were dissolved in double-distilled water and filter sterilized by passage through a 0.22-μm Millipore membrane filter. Ten milliliters of the bovine serum albumin fraction five and cycloheximide solution were added to the autoclaved portion of the medium cooled to 45–50 C. The medium was then dispensed in 90-cm-diameter plastic petri dishes at 20 ml per dish.

Isolations. PD and ALS strains were isolated from leaf petioles. The petioles were surface sterilized in 1% sodium hypochlorite for 2.5 min followed by four rinses in sterile distilled water. In most isolations, the petioles were aseptically cut into five or six sections and the end sections were discarded. Sap was then expressed from each remaining petiole section with forceps and blotted onto the medium leaving four-to-six slight impressions in the agar. In some isolations from almond, six petioles per tree were triturated in 10 ml of phosphate buffer (K_2HPO_4, 1.5 g/L; KH_2PO_4, 1.0 g/L; pH 6.9) and six serial 10-fold dilutions of the resulting suspension were used to spot-inoculate the medium with 0.01-ml samples. Inoculated medium was incubated aerobically at 28 C for 7–14 days.

Isolations were attempted from almond trees in two orchards in Contra Costa County, CA. Approximately 50-yr-old cultivar Long IXL trees in orchard 1 and 20-yr-old cultivar Jordonola trees in orchard 2 were sampled. In 1977, 10 symptomatic and nine nonsymptomatic trees were sampled in orchard 1. In 1978, an additional five symptomatic and two nonsymptomatic trees were sampled in orchard 1, and five symptomatic and five non-symptomatic trees were sampled in orchard 2. Samples were taken from each tree on 23 June and 30 August in 1977, and on 30 June, 26 July, 29 August, 26 September, and 24 October in 1978, except that only the trees in orchard 2 were sampled on 29 August. In 1977, one branch in each tree was sampled and in 1978, three branches in each tree were sampled. Samples were taken from the same branches on each isolation date. Small twigs with attached leaves were removed from the branches, moistened with water and transported to the laboratory in plastic bags. Isolations were attempted from six petioles from each tree within 24 hr of collection. When symptomatic leaves were present, their petioles were used in the isolations.

Cultural and serological identification of isolates. Preliminary identification upon isolation was based on the following colony characteristics: not apparent with the unaided eye prior to 3 days after inoculation; diameter less than 1 mm after 1 wk unless several colonies had coalesced; circular, with entire margins; white-to-opalescent in reflected light; leaving a slight pit on the solid medium when removed; and located only on the inoculation site (petiole imprint). The indirect fluorescent antibody technique (2,5) or the tube agglutination technique was used to confirm the identity of some isolates. Tube agglutination tests were performed at room temperature in the wells of microtiter trays with antisera for PD and ALS bacterial isolates (1). PD and ALS strains obtained in this and in an earlier study (1) were maintained on the PD2 medium by weekly subculture. Each strain was given a coded label designating its source and strain number. The first letter of the code designates

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the original host, thus V = *Vitis vinifera* and A = *Prunus amygdalus*. The second letter stands for the geographic location of the host, thus P = greenhouse strain from Napa County maintained in grapevine by leafhopper transmission, N = Napa County, T = Tulare County, and C = Contra Costa County. The VT1 and AC1 strains were submitted to the American Type Culture Collection (Rockville, MD) and catalogued as ATCC 29980 and ATCC 29981, respectively.

Inoculations. Suspensions of ALS and PD strains were used to inoculate almond trees and grapevines in a greenhouse. The inoculum was prepared by either heavily streaking plates of the PD2 medium in several directions or by spreading 0.5 ml of a 3- to 4-day-old suspension culture in PD2 broth onto each plate of medium with a bent glass rod. After 4–6 days of growth at 28 C, each isolate was removed from the medium with a spatula and suspended in 10 ml of either one-third strength liquid PD2 medium or in 10 ml of a phosphate buffered citrate-magnesium solution (K_2HPO_4, 1.5 g/L; KH_2PO_4, 1.0 g/L; trisodium citrate, 1.0 g/L; $MgSO_4 \cdot 7\ H_2O$, 1.0 g/L; pH 6.9). The turbidity of each suspension was adjusted to approximately 5×10^8 colony forming units (cfu) per milliliter.

Approximately 1-yr-old cultivar Mission almond on Nemaguard rootstocks in the greenhouse were inoculated by a modification of the xylem-infiltration technique (1,3). The plants, pruned earlier to obtain lateral branching, were pruned again leaving four or five nodes per branch. Two or three lateral branches measuring 8–15 mm in diameter were inoculated on each tree. An oblique knife cut was made toward the end of each branch between the second and third node from the base of the branch. The knife was twisted to split the branch to the third node leaving a flap of tissue approximately 2 cm in length. This flap was inserted into a 12 × 75-mm test tube, and the test tube was filled with inoculum suspended in one-third strength PD2 broth. A vacuum pump was attached to the acropetal end of the branch with rubber tubing and 0.1–1.0 ml of inoculum was drawn into the branch by 600–650 mm Hg vacuum pressure. After inoculation the branch was bound together with a budding rubber.

Both grapevine and almond seedlings were inoculated with suspensions of bacterial isolates in the phosphate-buffered citrate-magnesium solution. Three methods of inoculation were tested: syringe injection, wounded root uptake, and a modified leaf infiltration technique. The open pollinated Long IXL almond seedlings were approximately 6 mo old and the open-pollinated Pinot Noir grapevine seedlings were approximately 6 wk old. The seedlings were maintained throughout the experiments in a greenhouse. In the injection method, the main stem at 2–5 cm above the soil was pierced with a 0.71-mm-diameter (22-gauge) hypodermic needle and the inoculum was injected into the wound with a syringe as the needle was withdrawn. The procedure was repeated 3–5 times for each plant. In the wounded root uptake method, roots were washed free of soil, the lower half of the roots were cut off, the remaining roots were submerged in inoculum for 2 hr at 32 C, and then the plants were repotted. In the leaf infiltration method, the lower surfaces of the leaves on each plant were sprayed with an artists' airbrush until they became congested with inoculum and then the plants were kept overnight in a humidity chamber (100% RH). All plants were maintained in the greenhouse until symptoms developed, usually 2–4 mo, or until discarded after 6 mo.

Inoculation of almond trees in orchards. Syringe injection and leafhoppers were used to inoculate mature almond trees in an established varietal block at the University of California's Kearney Horticultural Field Station and Westside Field Station in the central San Joaquin Valley. A total of 11 trees were inoculated including eight of cultivar NePlus, two of NonPareil, and one of Peerless. Six trees and five trees were inoculated on 28 March and 15 June 1978, respectively. Each tree was inoculated with the VT7 and VT8 strains from two grapevines with PD. The grapevines had been inoculated by naturally infective leafhoppers (*Draeculacephala minerva* Ball) which were collected from a permanent mixed-vegetation pasture within 20 km of the Kearney Field Station. The bacteria were grown on PD2 medium and suspended in phosphate buffer (KH_2PO_4, 1.0 g/L and K_2HPO_4, 1.5 g/L; pH 6.9) in the field to obtain suspensions of approximately 10^7 cfu/ml. Each strain was used to inoculate 4–5 shoot tips at different sites on each tree. Two to five sites on each tree also were exposed to leafhopper inoculation. *D. minerva* were collected from the same pasture as before and (without determining whether they were naturally infective) fed for 24 hr on the same grapevines from which the VT7 and VT8 strains were isolated. Two or three leafhoppers were placed into either 2.5 cm plastic and mesh clip cages or 15-cm-diameter organdy sleeve cages over the leaves of terminal shoots. Symptoms in inoculated trees were recorded in June and October of 1977 and 1978. Approximately six leaves were collected on 11 October 1978 and 4 October 1979 from each inoculation site in the 11 trees for attempts to reisolate the bacteria.

TABLE 1. The results of isolation attempts from 20 almond trees with almond leaf scorch (ALS) in two orchards in Contra Costa County, California. Isolations were attempted on seven dates in 1977 and 1978

Date	No. of trees from which bacteria were isolated / No. of trees from which isolations were attempted	
	Orchard No. 1	Orchard No. 2
1977		
23 June	6/10	ND[a]
30 August	5/10	ND
1978		
30 June	10/15	4/4
26 July	8/15	5/5
29 August	ND[a]	5/5
26 September	8/15	5/5
24 October	8/15	3/4
Totals	45/80 (56.3%)	22/23 (95.7%)

[a]ND = not done.

RESULTS

Isolations from naturally infected almond trees. The ALS bacterium was isolated from 12 of 15 (80.0%) symptomatic Long IXL trees in orchard 1 and all five Jordonola trees with ALS in orchard 2. Bacteria were isolated from symptomatic trees during 45 of 80 (56.3%) attempts in orchard 1 and 22 of 23 (95.7%) attempts in orchard 2 (Table 1). Nine symptomatic trees in orchard 1 yielded

TABLE 2. The results of inoculating grapevines and almond trees with Pierce's disease and almond leaf scorch bacterial strains by three different inoculation methods

Inoculation method	Strain	Plant inoculated	Ratio (diseased/inoculated)
Xylem infiltration	VP1	Grapevine	0/5
		Almond	0/5
	VT1	Grapevine	4/5
		Almond	5/5
	AC1	Grapevine	19/19
		Almond	5/5
	AC3	Grapevine	0/5
		Almond	0/5
	AC6	Grapevine	3/4
		Almond	5/5
Injection	VP2	Grapevine	6/6
		Almond	3/4
	VT3	Grapevine	6/6
		Almond	4/4
	AC6	Grapevine	6/6
		Almond	4/4
Wounded root uptake	VN1	Almond	0/3
	VP2	Grapevine	1/10
		Almond	0/2
	VT3	Grapevine	2/10
		Almond	0/3
	AC6	Grapevine	5/10
		Almond	0/2

bacteria during 42 of 48 (87.5%) attempts while only three of 32 (9.4%) attempts from the remaining six symptomatic trees sampled in orchard 1 were successful. In both orchards the frequency that trees yielded bacteria remained approximately the same from June through October (Table 1). The ALS bacterium was not isolated during a total of 66 attempts from 11 non-symptomatic trees in orchard 1 and five such trees in orchard 2 which were sampled on the same dates as were the symptomatic trees (Table 1).

Serological comparison of PD and ALS bacterial isolates. All of the ALS bacterial isolates from naturally infected trees in 1977 reacted positively when tested with the indirect fluorescent antibody technique and antisera either to a Napa Valley PD strain (VN1) or an ALS strain (AC1). All ALS isolates obtained in 1978 reacted positively with antisera to the VN1 PD strain when tested by the tube agglutination method.

Pathogenicity of ALS and PD strains. Two ALS and three PD strains incited typical symptoms of ALS in almond trees and PD in grapevines within 2–4 mo after inoculation regardless of the original host species (Table 2). None of the strains infected one host species and not the other. The xylem-infiltration and injection methods were used successfully to inoculate both grapevines and almond trees, while only grapevines were successfully inoculated by the wounded root uptake method (Table 2). Inoculation by the leaf infiltration method did not result in disease in any of eight almonds and 12 grapevines inoculated with either the VP2, VT3, or AC6 strain. ALS symptoms did not develop in five almond trees inoculated with one-third concentrated PD2 medium by the xylem-infiltration method. A total of 24 uninoculated almond trees and seven uninoculated grapevines were maintained adjacent to the inoculated plants during the experiments and none became diseased.

In all greenhouse inoculation experiments, the PD or ALS strains were reisolated from every plant that developed symptoms. Neither the uninoculated plants nor the inoculated plants that did not become diseased yielded PD or ALS isolates.

Inoculation of almond trees in orchards. ALS developed in inoculated almond trees under field conditions in the central San Joaquin Valley. Six trees in March and five trees in June were inoculated. The trees inoculated in March did not have ALS symptoms in June, but all 11 trees inoculated in either March or June had developed symptoms by October (Table 3). Symptoms were only apparent within 10–30 cm of the inoculation site on each branch. No evidence of spread to other branches was observed. In the 11 trees, 29 of 94 (30.9%) branches inoculated by the injection method and 2 of 37 (5.4%) branches inoculated by leafhopper transmission developed symptoms. The VT7 and VT8 strains incited symptoms in almost the same proportion of branches (Table 3). The bacteria were reisolated in October from inoculated branches with and without symptoms (Table 3). The bacteria were isolated regardless of symptoms from 41 of 94 (43.6%) branches inoculated by the injection method and eight of 37 (21.6%) branches inoculated by leafhoppers. Bacteria were isolated at a greater frequency from symptomatic branches than from nonsymptomatic branches.

The overwinter survival of the bacteria in the inoculated branches apparently was poor. By October the following year, symptoms had developed in only two of the 131 inoculated branches. These symptomatic branches were in different trees and had been inoculated by the injection method. The bacteria were reisolated from both symptomatic branches but not from any of the nonsymptomatic branches inoculated by either the injection method or by leafhoppers.

DISCUSSION

A constant association was demonstrated between ALS and a xylem-limited bacteria by isolating the organism from diseased but not from healthy trees. The xylem-limited bacteria were consistently isolated in orchard 2, but not in orchard 1; however, nine of the 15 trees sampled in orchard 1 also consistently yielded bacteria in 87.5% of the isolation attempts during 1977 and 1978. Two trees in orchard 1 failed to yield isolates despite being strongly symptomatic. Varietal differences do not explain the differences between overall isolation frequencies in the two orchards, since the bacteria consistently were isolated from individual trees of cultivars Jordonola and Long IXL. The Jordonola trees were younger, more vigorous, and had larger, more succulent petioles from which isolations were attempted, and this might partially account for the greater frequency of isolations obtained from orchard 2. Other factors may have been involved in the inability to isolate bacteria from some trees. Mircetich et al (12) suggested that ALS symptoms may be caused by a toxin and more recently a toxin was implicated in the production of symptoms in PD (10). Possibly under some circumstances leaf symptoms are caused by a translocated toxin without bacteria being immediately present.

Both PD and ALS strains were pathogenic in almond trees and grapevines. No differences in symptomology were observed after inoculating with either PD or ALS strains. The failure of some strains to infect either host species may have been due to either a loss of virulence or pathogenicity in culture or unsuccessful inoculations. Since strains shown to be pathogenic infected most if not all of the plants inoculated in the greenhouse by either the xylem-infiltration or injection methods, these inoculation methods appear to have been adequate for demonstrating pathogenicity. Bacteria were only reisolated from plants that developed symptoms; thus, no strains were observed that could infect plants without inciting symptoms.

Of the inoculation techniques employed, the syringe injection method of inoculation was very efficient and simple. The xylem infiltration technique, although also very efficient, was more complicated and not as convenient for inoculating plants in the field. However, a more precise amount of inoculum can be introduced into grapevine cuttings and possibly almonds using the xylem infiltration technique. Neither the wounded root uptake nor the leaf infiltration methods of inoculation were satisfactory. Grapevine seedlings recovered more rapidly than the almond seedlings from the root damage incurred during inoculation by wounded root uptake, and only a few of the grapevines and none of the almonds were successfully inoculated. None of the grapevines or almonds became infected following inoculations that utilized the modified leaf infiltration technique, suggesting that wounding to expose tracheary elements is a prerequisite for infection.

TABLE 3. The results of inoculating 11 almond trees in the central San Joaquin Valley of California by injection of bacterial isolates and by leafhopper transmission. The trees were inoculated on 28 March and 15 June 1978 and the data were obtained in October 1978

Inoculation method	Strain[a]	Symptomatic trees (no.) / Trees inoculated	Symptomatic branches (no.) / Branches inoculated (no.)	Successful isolations / Symptomatic branches (no.)	Successful isolations / Non-symptomatic branches (no.)
Injection	VT7	10/11 (90.9%)	15/48 (31.3%)	13/15 (86.7%)	7/33 (21.2%)
	VT8	7/11 (63.6%)	14/46 (30.4%)	11/14 (78.6%)	10/32 (31.3%)
Total		10/11 (90.9%)	29/94 (30.9%)	24/29 (82.8%)	17/65 (26.6%)
Leafhopper transmission[b]		2/11 (18.2%)	2/37 (5.4%)	1/2 (50.0%)	7/35 (20.0%)

[a] The VT7 and VT8 strains were isolated from grapevines with PD which had been inoculated by naturally infective leafhoppers from a pasture in the central San Joaquin Valley.

[b] *Draeculacephala minerva* were collected from the same pasture as those leafhoppers which had inoculated grapevines from which the VT7 and VT8 strains were isolated, and fed 24 hr on these same grapevines before they were allowed to feed on the almond trees.

PD but not ALS frequently is observed in the central San Joaquin Valley of California even when PD is present in vineyards in close proximity to almond orchards. Our inoculations show that almond is susceptible to infection by strains causing PD from naturally infective leafhoppers and from the same geographical area. However, few infections survived the winter and then only in branches inoculated by injection. The injection method presumably introduced more inoculum into the trees than did transmission by *D. minerva*, since there was a higher frequency of successful inoculations and the severity and extent of the symptoms were greater. *D. minerva* is an abundant and principle vector of PD in the central San Joaquin Valley and is a possible natural vector of ALS. Only 5.4% of the branches inoculated by *D. minerva* developed symptoms during the first summer which is comparable to the equally poor transmission rate of PD by *D. minerva* to grapevines (15). A low vector transmission rate together with poor overwinter survival following current season infections may account for the infrequent occurrence of ALS in the central San Joaquin Valley.

In this study, Koch's postulates were fulfilled, which proved that the same xylem-limited bacterium caused both PD and ALS. The same or very similar bacterium was isolated from alfalfa suspected of having alfalfa dwarf disease, and although isolates from alfalfa were not used in this study, their ability to cause ALS in inoculated almond has been briefly described elsewhere (18). The xylem-limited bacteria were indistinguishable in culture, and were Gram-negative, oxidase-negative, catalase-positive, small, rod-shaped, non-motile, aerobic organisms (1).

The xylem-limited bacteria associated with Phony disease of peach (8,14), plum leaf scald (4,9), elm scorch (17), and periwinkle wilt (11) have not been isolated in pure culture. Thus, the completion of Koch's postulates as "proof" of their pathogenicity has not been possible. Recent attempts to isolate these bacteria on the PD2 medium (JD3 medium) also have failed, suggesting that at least two pathotypes and perhaps species of xylem-limited bacteria exist. Serological studies using the indirect fluorescent antibody staining technique have not differentiated the bacteria associated with phony disease of peach from those causing PD and ALS (2), but have shown that these bacteria are serologically distinct from representatives of a number of genera of taxonomically characterized bacterial phytopathogens (2,5).

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