Etiology of Phony Peach and Plum Leaf Scald Diseases

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ABSTRACT

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Rickettsialike bacteria (RLB), previously associated with phony peach disease (PPD) and plum leaf scald (PLS), were transmitted from peach trees with PPD symptoms to plum and from plum trees with PLS symptoms to peach by grafts of root sections. Symptoms of PLS appeared on plants of plum cultivars Ozark Premier, Methley, Santa Rosa, and Shiro 9 mo after they had received root grafts from Dixiland peach with PPD symptoms. Grafted plum had RLB that appeared to be identical to those associated with PPD, measuring 0.35 × 2.0 μm, and shared similar ultrastructural details, including an outer (rippled) trilaminar membrane in the cell wall profile. Graft-transmitted RLB from plum and from peach reacted positively to immunofluorescence and enzyme-linked immunosorbent assays conducted with antiserum prepared against RLB associated with PPD.

Additional key words: symptomatology, alternate hosts, electron microscopy.

Phony disease (PPD) of peach (*Prunus persica* (L.) Batsch) has recurred in orchards in the southeastern United States since 1890 (14). Rickettsialike bacteria (RLB) have only recently been associated with the disease. The bacteria were described as xylem-limited, rod-shaped cells measuring 0.35 × 2.3 μm (13), slightly smaller than those found in grape affected by Pierce's disease (4,12,20). Peach trees infected with RLB eventually show typical symptoms of phony disease: a flattened and umbrellalike canopy caused by shortening of terminal internodes, foliage darker green and denser than normal, and production of progressively smaller, unmarketable fruit 3–5 yr after symptom appearance (14).

Phony peach disease is transmitted by xylem-feeding sharpshooter leafhoppers and by grafting (14). Several additional hosts and natural reservoirs of the RLB have been identified including other members of the genus *Prunus* (2,15,24) and the common perennial weed, Johnson grass, *Sorghum halapense* (L.) Pers. (25). Disease symptoms on weed or wild hosts have been observed only on Japanese-type plums, a mixed group derived from *Prunus salicina* Lindl. alone or hybridized with such other diploid species as *P. americana* Marsh., *P. cerasifera* Ehrh., *P. simonii* Carr., *P. munsoniana* Wright and Hedr., and *P. angustifolia* Marsh.

Plum leaf scald disease (PLS) was first reported in Argentina in 1954 (6), and also in Paraguay and Brazil in 1978 (9). Xylem vessels of plums affected by leaf scorch or scald contain bacterial cells similar to RLB, measuring 0.5 × 1–3 μm (16) are also transmissible by grafting. It has since been observed in the southeastern United States by French et al (8) on plum hybrids and cultivars in association with xylem-limited RLB. Diseased trees show moderate to severe marginal leaf necrosis and mortality is high (18).

Although the symptomatology of PPD bears little resemblance to that of PLS, the two diseases appear to share elements of a common etiology. Peaches and plums are generally cultivated together or in the same geographical areas, RLB have been associated with both diseases, both diseases are graft transmissible, and both hosts are closely related. However, there is little direct evidence in the literature other than in preliminary reports (10) to establish a closer relationship between the diseases. This report presents several lines of evidence, including transmission and serological tests, to demonstrate that PPD and PLS are caused by the same pathogen.

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MATERIALS AND METHODS

Disease ratings. Peach trees were determined to be symptomatic or symptomless for PPD according to criteria previously described (24). Plum trees were rated for PLS according to percentage of foliage affected: none (0%), light (1–20%), moderate (20–50%), and severe (over 50%). A collection of plum trees on or adjoining the Southeastern Fruit and Tree Nut Research Laboratory, U.S. Department of Agriculture (USDA), Byron, GA, were used for study. The group consisted of a 6-yr-old planting of plum cultivar Frontier, a 5-yr-old planting of cultivar Bruce, and an extensive planting of 2- and 3-yr-old hybrids and cultivars from the USDA Southeastern Plum Breeding Project. Hybrids were offspring of open-pollinated crosses of diverse pedigree (fully described in Table 1).

Quantification of RLB in tissues. Tissues of symptomatic and symptomless trees were examined for RLB by the method of French et al (7) with slight modifications. Root and twig sections approximately 0.5-cm-diameter were trimmed to 6 cm, and 1 ml 0.1 M KOH was drawn through by vacuum infiltration. To reduce variability, KOH extracts from three root or twig samples per tree were combined. A drop of the combined KOH extract (approximately 10 μl) was placed on a microscopic slide and dried. Slides were examined at ×800 with a microscope (Universal Microscope, Carl Zeiss, Inc., New York, NY 10018) equipped with phase-contrast optics and a wide-angle (20-mm) objective lens. Three representative fields per slide were examined and particles with light transmittance and morphological characteristics of typical RLB were counted. Occasionally, leaf petioles were examined for RLB by macerating 0.5-cm sections in 1 ml of 0.1 M KOH with a mortar and pestle. The RLB were then counted in the KOH supernatants. Ratios of RLB counts in roots vs twigs

were statistically analyzed by a transformation of averages to square root of ($\sqrt{\bar{x} + 0.5}$) and by chi-square tests, $P = 0.05$.

Transmission tests. Cross-transmission tests were conducted by root grafts due to our high percentage of successful grafts (*unpublished*) and due to the reported concentrations of RLB in the root systems of diseased trees (24). In January 1980, wedge grafts of 7.6-cm (3-in.) root sections from a 4-yr-old Dixiland peach tree infected with PPD and from a 5-yr-old Shiro plum tree (interspecific Prunus hybrid) infected with PLS were made onto healthy 1-yr-old peach and plum trees. Only root sections from roots that tested positive for RLB were used in grafting. Five plum trees each of cultivars Methley, Shiro, Ozark Premier, and Santa Rosa received phony-infected peach root grafts, and five peach trees of cultivar Dixiland received grafts from diseased plum. An equal number of checks received grafts of root material from symptomless 1-yr-old Lovell peach rootstocks or Ozark Premier plum. Grafted trees were planted in an insect-proof screenhouse. In June, August, and October twigs were assayed for RLB, and the trees were monitored for symptom development. Additional evidence for the identity of RLB detected in tissues was gathered by serology and electron microscopy.

Electron microscope studies. Symptomatic leaves from plum grafted with roots of peach trees with PPD symptoms were prepared for electron microscopy by the method of Lowe et al (19). Portions of midveins were removed and cut into 2×2-mm pieces in 2% glutaraldehyde, and then fixed in 2% osmium tetroxide. Fixed samples were dehydrated in a graded series of acetone (10–100%) and embedded in Spurr's medium (23). Ultrathin sections were cut with a diamond knife, mounted on copper grids, and stained with both uranyl acetate and lead citrate prior to transmission electron microscopic examination. Similar sections were prepared from peach twigs from trees grafted with root sections of plum showing symptoms of PLS.

Serology. Antiserum prepared against the RLB associated with PPD was obtained from W. J. French, University of Florida, Monticello 32344. Graft-inoculated plum and peach samples were tested against this antiserum by immunofluorescence (IMF) and by enzyme-linked immunosorbent assay (ELISA).

Immunoglobulins were separated from bulk sera with a DEAE Sephadex A-50 column and conjugated with fluorescein isothiocyanate by the method of Dedmon et al (5). Plant tissues were prepared and stained with the fluorescein-labeled γ-globulin (1), and observed at 405 nm (A_{405nm}) with a Zeiss GFL microscope equipped with an HB 200-W mercury vapor lamp and filters.

Plant samples for ELISA were prepared by the method of Nomé et al (21), and γ-globulin purification and enzyme conjugation were by the method of Clark and Adams (3). The tests were carried out by using flat-bottomed micro-ELISA(R) plates (Dynatech Laboratories Inc., Alexandria, VA 22314) (21).

Positive controls for IMF and ELISA tests consisted of RLB isolated from peach and plum symptomatic for PPD and PLS acquired by natural infection in the field. Extracts of healthy, symptomless peach and plum tissues were included as negative controls. In the ELISA, peach and plum affected by bacterial canker (*Pseudomonas syringae*) and root rot (*Armillaria mellea*) were also included as negative checks.

RESULTS

Presence of RLB in diseased plum and peaches. Plum trees showing symptoms of leaf scald contained RLB in either root or twig tissues during the time of sampling (Table 1). Average numbers of RLB in twigs of 3-yr-old hybrids showing severe scald symptoms were remarkably high, well over 500 per microscopic field. In general, RLB were significantly ($P = 0.05$) more numerous in the twigs than in the roots of the 3-yr-old hybrids. Five-yr-old Bruce and 6-yr-old Frontier plums also contained RLB in roots and in some twigs of moderately to severely scalded trees. Root tissues in these older trees, however, had consistently higher numbers of RLB than in twig tissues ($P = 0.05$). In most cases, RLB were not observed in tissues of symptomless plum trees. When they were observed, there were only one or two cells per microscope field in

TABLE 1. Leaf scald severity and rickettsialike bacteria (RLB) counts in roots and twigs of plum (*Prunus* spp.) trees in Byron, GA

Tree designation	Age in years	Cultivar	Scald rating[a]	RLB detected[b]	
				Roots	Twigs
7760-23	3	Hybrid[c]	Severe	1	48
7760-43	3	Hybrid[c]	Severe	1	45
7760-46	3	Hybrid[c]	Severe	38	74
7761-38	3	Hybrid[d]	Severe	5	3
7761-56	3	Hybrid[d]	Severe	12	604
7761-66	3	Hybrid[d]	Severe	24	2,477
7840-114	2	Hybrid[e]	None	0	0
7840-121	2	Hybrid[e]	None	0	0
7840-160	2	Hybrid[e]	None	0	0
R6T4	5	Bruce	Severe	168	0
R7T11	5	Bruce	Severe	290	3
R7T11	5	Bruce	Severe	48	10
R5T3	5	Bruce	Moderate	25	5
R6T12	5	Bruce	Moderate	10	0
R5T1	5	Bruce	Moderate	375	0
R5T6	5	Bruce	None	0	0
R7T2	5	Bruce	None	1	2
R7T3	5	Bruce	None	0	0
F4	6	Frontier	Severe	0	5
F2	6	Frontier	Moderate	14	6
F3	6	Frontier	Moderate	10	2
F5	6	Frontier	Moderate	1	3
F6	6	Frontier	Light	0	1
F7	6	Frontier	Light	1	4
F8	6	Frontier	None	1	0
F1	6	Frontier	None	0	0

[a] Based on visual estimations of percentage of leaves affected in October 1980. None = 0%, light = 1–20%, moderate = 25–50%, severe = over 50%.
[b] Average RLB per microscopic field in 0.1 M KOH extracts of three roots and twig samples per tree.
[c] Open-pollinated seedling of cultivar Friar.
[d] Open-pollinated seedling of cultivar Queen Ann.
[e] Open-pollinated seedling of FL 1-1.

the roots. In peach, RLB were more numerous in roots than in twigs, consistent with data in a previous report (24). Typical averages of RLB per field were 325 for roots and 28 for twigs (*unpublished*).

Symptoms of PLS were more frequently observed on plum hybrid seedlings with pedigree origins from California than from Georgia or any other region represented (Table 2). At least 10% of the offspring of the four high quality cultivars from California showed symptoms of PLS in the third summer. On the whole, PLS incidence in the Byron, GA, seedling was 50% less than in those from California.

Fig. 1. Marginal necrosis typical of plum leaf scald on a leaf of cultivar Ozark Premier 9 mo after the tree received a root graft from a peach tree infected with phony disease.

Transmission tests. Nine months after healthy, 1-yr-old plum trees were grafted with roots from a Dixiland peach tree infected with phony disease, leaf scald symptoms had developed (Fig. 1) and RLB were present in the xylem (Table 3). Rickettsialike bacteria were found in KOH extracts of twigs of some graft-inoculated plum trees as early as June, 5 mo after grafting (*unpublished*). Leaf scald symptoms were confined to the older leaves and did not appear in late-summer growth. All five of the inoculated Ozark Premier trees had scalded leaves but only one or two of the inoculated trees of other plum cultivars had symptoms. However, RLB were present in all but two of the 20 plum trees inoculated. In uninoculated check trees, no RLB could be detected and scald or scaldlike symptoms could be found in only one to two leaves of four of the 20 trees. In each cultivar, the inoculated tree with the highest RLB counts also had the greatest number of scalded leaves.

Four of the five peach trees graft-inoculated with root sections from plum trees with symptoms of PLS contained low numbers of RLB in KOH extracts of twigs (Table 4). Symptoms of PPD, however, were not evident in these trees by the end of the 1980 growing season.

Serology. Bright-green fluorescence was observed in extracts from all of 12 Methley and Ozark Premier plum petioles from trees that had received grafts of root sections from peach with PPD symptoms, then sampled and tested by IMF (Table 4). Slight fluorescence was observed in extracts of all of 12 Shiro and Santa Rosa petioles tested and in extracts of all of 10 Dixiland peach stem sections from plants grafted with root sections from plums with PLS symptoms. Bright fluorescence also was observed in extracts of all 20 petiole and stem sections of peach and plum with symptoms of PPD and PLS (*unpublished*).

Strong color reaction obtained in ELISA with antiserum prepared against PPD-associated RLB was observed with all of the

TABLE 2. Incidence of visible symptoms of plum leaf scald on 3-yr-old hybrids of cultivars and selections used in the USDA Southeastern Plum Breeding Project

Region of origin	Cultivar or selection	Pedigree	Number of seedlings	Trees with scalded leaves	Trees with scalded leaves by region (%)
USA, CA	Casselman	Bud spot of Late Santa Rosa	44	17	
	Queen Ann	Gaviota × Eldorado	119	23	
	Nubiana	Gaviota × Eldorado	21	3	
	Friar	Gaviota × Nubiana	60	6	
	K5-70	USDA, Fresno, selection	132	8	
Totals			376	87	15.2
USA, Byron, GA	BY69-339	Mariposa × Morris	30	5	
	BY4-587	Queen Ann × Santa Rosa	62	6	
	BY69-924	Queen Ann × Santa Rosa	138	13	
	Robusto	(Queen Ann × Barstow) × (Ozark Premier × *P. angustifolia*	258	19	
	BY69-624	Redheart, open-pollinated (OP)	39	2	
	BY69-350	Mariposa × Morris	36	1	
	BY68-87	Gaviota, OP × (Ozark Premier × *P. angustifolia*)	111	3	
Totals			674	49	7.1
USA, MO	Ozark Premier	Burbank × Methley	101	11	
USA, TX	Bruce	*P. salicina* × *P. munsomana* × *P. angustifolia*	52	3	
USA, TN	*Prunus americana*	Native species	140	3	
USA, TN	Six Weeks	Abundance × *P. angustifolia-varians*	20	0	
Totals			313	17	5.2
So. Africa	Methley	*P. salicina* × *P. cerasifera*	68	2	
So. Africa	Haleardi	*P. salicina* × *P. cerasifera*	40	0	
Totals			108	2	1.9

TABLE 3. Counts of rickettsialike bacteria (RLB) and number of scalded leaves on second-leaf trees of four cultivars of plum (*Prunus salicina*) receiving grafts of root sections from symptomless peach trees or trees with symptoms of phony peach disease (PPD)

Root graft source[a]	Ozark Premier		Methley		Shiro		Santa Rosa	
	RLB in twigs[b]	Leaves scalded[c]	RLB in twigs	Leaves scalded	RLB in twigs	Leaves scalded	RLB in twigs	Leaves scalded
Diseased tree	3	1	4	0	4	0	2	0
Diseased tree	6	4	23	11	57	4	8	0
Diseased tree	5	7	0	0	3	0	1	0
Diseased tree	20	11	7	0	0	0	53	18
Diseased tree	1	6	1	0	2	0	1	2
Symptomless tree	0	2	0	0	0	1	0	1
Symptomless tree	0	0	0	0	0	0	0	0
Symptomless tree	0	0	0	0	0	0	0	0
Symptomless tree	0	1	0	0	0	0	0	0
Symptomless tree	0	0	0	0	0	0	0	0

[a]Grafts wedged onto roots of healthy 1-yr-old plum trees in January 1980.
[b]Average number of RLB per microscopic field from three twigs per tree sampled in October 1980.
[c]Number of leaves per tree showing distinct leaf scald symptoms (Fig. 1).

TABLE 4. Serological reactions by immunofluorescence (IMF) and enzyme-linked immunosorbent assay (ELISA) of KOH extracts of plum petioles from trees grafted with peach root sections from trees with symptoms of phony peach disease (PPD) and of peach twigs from trees grafted with plum root sections from trees with symptoms of plum leaf scald disease (PLS)

Grafted tree[a]	Source of root graft[b]	IMF[c]	ELISA[d]	Numbers of RLB[e]
Plum cultivar	Peach:			
Methley	PPD-affected	++++	++++	3
Methley	Symptomless	−	−	0
Ozark Premier	PPD-affected	++++	++++	5
Ozark Premier	Symptomless	−	−	0
Shiro	PPD-affected	++	++	1
Shiro	Symptomless	−	−	0
Santa Rosa	PPD-affected	++	++	1
Santa Rosa	Symptomless	−	−	0
Peach cultivar	Plum:			
Dixiland	PLS-affected	++	++	2
Dixiland	Symptomless	−	−	0

[a]Trees grafted January 1980; serological and RLB counts completed October 1980.
[b]Phony-infected peach cultivar Dixiland; scald-infected plum cultivar Shiro; healthy plum cultivar Ozark Premier.
[c]Fluorescent reaction visually rated as negative (−), light (++), or bright (++++) on 12 samples from each cultivar.
[d]Optical density readings (A_{405nm}) ranging from 0.0–0.1 (−), 0.1–1.0 (++), to 1.0–1.8 (++++) on eight samples from each cultivar.
[e]Average number of rickettsialike bacteria (RLB) per microscopic field from one plum petiole or peach twig of five plants tested.

eight leaf and stem samples of Methley and Ozark Premier plums that received grafts of root sections from peach with PPD symptoms (Table 4). Slight color reaction from ELISA was observed with all of eight leaf and stem samples of Santa Rosa and Shiro plum that also had been grafted with root sections from peaches with PPD symptoms. Slight color reaction was also observed in ELISA of all of three Dixiland peaches that received root grafts from Shiro plum with PLS symptoms. Positive color reaction in ELISA was similarly observed with extracts of all 10 leaf and stem samples of peach and plum trees with symptoms of PPD and PLS, respectively (*unpublished*). No color reaction was observed in extracts of plum or peach trees that had received grafts from roots of healthy peach or plum. The A_{405nm} values of samples from trees with symptoms were significantly higher than those obtained with samples from symptomless trees ($P = 0.01$). Results of ELISA were negative (no color reaction) in samples of peach and plum trees affected by bacterial canker or root rot. Negative results were also observed from peach and plum leaves showing scorching due to dehydration or senescence.

Electron microscopy. Numerous bacteria were found in sections of xylem vessels from midveins of plum leaves with PLS symptoms on trees that had received grafts from peach trees with PPD symptoms. The occupied vessels were densely packed with organisms embedded in a low-electron-density matrix (Fig. 2A). "Free" particles, short strands, and amorphous "debris" in the matrix were common. Similar phenomena have been observed in specimens of grape affected with Pierce's disease (PD) (20), in almond affected with leaf scorch (ALS) (19), and in peach with symptoms of PPD (22). Broad osmiophilic bands were observed at the periphery of some cells (Fig. 2). These bands have also been noted in cells occupied by the organism associated with PPD (22).

The bacteria in plum with PLS symptoms were rod-shaped, approximately 0.35 μm in diameter, and 2.0 μm long. In transverse section they appeared ovoid or spherical, and possessed a prominently rippled cell wall (Fig. 2E), best seen in longitudinal view (18), similar to RLB in grape with PD, almond with ALS, and peach with PPD (17,18,20). The wall profile consisted of an outer (rippled) trilaminar membrane (OM) and an inner cytoplasmic membrane (CM). In the periplasmic space between the OM and CM was a distinct electron-dense layer (Fig. 2C) which is characteristic of Gram-negative bacteria and probably composed of peptido-glycan (11). Other components observed in the cytoplasm included ribosomes, a nuclear region with DNA-like fibrils (Fig. 2D), and occasional particles resembling polyglucoside granules (19).

Similar organisms were observed in xylem vessels of plum trees with PLS symptoms, and in peach grafted with root sections from plum with PLS symptoms

DISCUSSION

RLB with similar morphology have repeatedly been associated with PLS and PPD (8,13,18). In this study, however, evidence is presented to indicate that both diseases may be caused by the same organism. Reciprocal transmission between peach and plum by root grafts was evident within 9 mo. In addition, PLS symptoms appeared on all inoculated cultivars of plums within that time. Rickettsialike bacteria from both hosts reacted with antisera prepared against RLB associated with PPD and were detected in infected tissues by ELISA. Finally, similarity in ultrastructure of the RLB associated with PPD and PLS was established, and electron microscopy indicated that the organism associated with PLS was Gram-negative.

The etiology of PLS, however, differs in some ways from that of PPD. In young hybrid plums with symptoms of PLS, RLB occurred in remarkably high numbers in twig tissues. The observed RLB counts from hybrid twigs (Table 1) were higher than any recorded from previous studies (24). In peach, with symptoms of PPD, root extracts generally contained greater numbers of RLB than twigs.

Our observations of cultivar differences in response to graft transmission of PLS is consistent with observations of other authors that plum varieties differ in their susceptibility to PLS (16,18). There are no analogous observations made among peach cultivars.

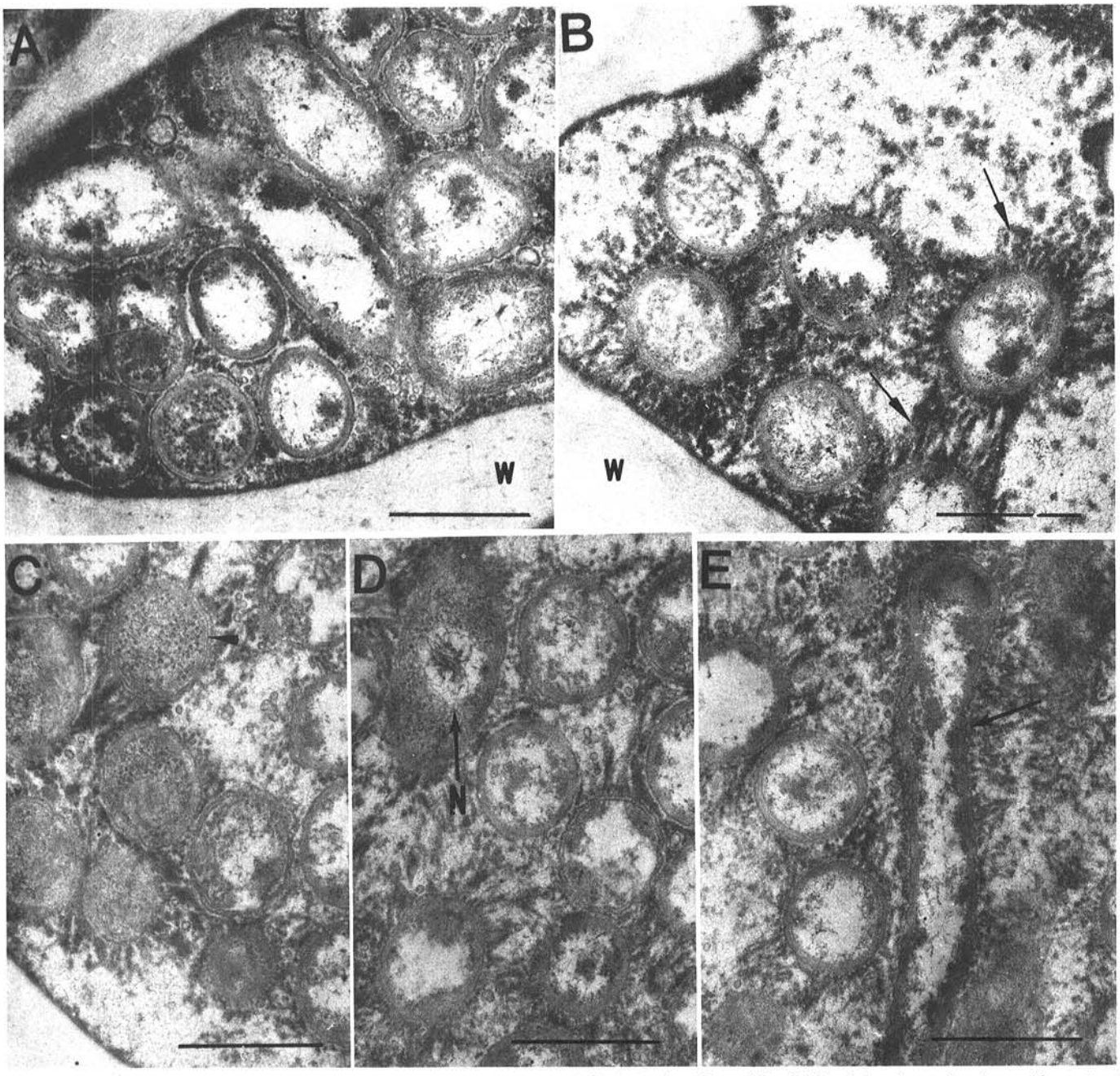

Fig. 2. Electron micrographs of rickettsialike bacteria (RLB) embedded in a matrix in the lumina of vessels in midribs of plum leaves showing scald symptoms. Leaves came from plum trees that received grafts from peach trees with symptoms of phony peach disease. Numerous "free" particles, and amorphous "debris," were seen in the matrix. W = vessel wall. Scale bars = 0.5 μm. **A,** RLB in transverse and longitudinal in an occupied vessel. **B,** A group of organisms with broad osmiophilic bands (arrows) at the cell periphery. **C,** An RLB cell possessing a distinct electron-dense peptidoglycan or R layer (arrowhead) in the periplasmic space between the outer membrane and the cytoplasmic membrane. Some cells were rich in ribosomes. **D,** A nuclear region (N) was observed in the ribosome-rich cytoplasm of an RLB cell (arrow). Note the DNA-like fibrils. **E,** The rippled wall profile of an RLB (arrow) is evident in longitudinal view.

Preliminary evidence from the breeding collection of 3-yr-old seedlings indicated that at least a portion of the variation in expression of PLS is under genetic control and passes from parent to offspring (Table 2). Most of the selections derived from the Byron plum breeding program apparently transmitted more resistance, or at least tolerance, to PLS than did the California cultivars, even though there was a high degree of consanquinity between the groups.

Our graft inoculations with PLS and PPD are in their first year; thus, the PLS symptoms on grafted plums were mild compared to disease expression found on some trees in the orchard. Presumably, symptom severity will increase in subsequent growing seasons.

Graft inoculations of peach with scorch-infected plum did not produce symptoms of PPD within the time frame of this study. A latent period of 18–24 mo prior to symptom development is typical with PPD (14). The presence of RLB in graft-inoculated trees and their absence in the checks is an indication that symptoms may eventually develop. In a previous study (24) we found that symptoms of PPD occurred 3–12 mo after detection of RLB.

The proximity of peach and plum plantings in orchards in the southeastern United States adds importance to the relationship between the two diseases. The similarities between the RLB reported here suggest that similar disease control measures may be useful. These measures include removal of affected trees to prevent spread of RLB by insect vectors, and selection of resistant or tolerant plum cultivars.

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