Rootstock Influence on Occurrence of *Homalodisca coagulata*, Peach Xylem Fluid Amino Acids, and Concentrations of *Xylella fastidiosa*

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ABSTRACT

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The influence of three *Prunus* rootstocks—a domestic plum, a domestic peach, and a peach from Brazil—on the occurrence of the vector of phony peach disease, *Homalodisca coagulata*, was assessed in a 4-yr study in an experimental block of Flordaking peach (*P. persica*). Relationships between the amino acid profile of xylem fluid from scions, the concentration of *Xylella fastidiosa* in xylem fluid from roots, and leafhopper occurrence were also assessed. The vector was less numerous in trees on the Brazilian rootstock than in those on the domestic rootstocks. The concentration of the bacterium in root xylem fluid was lower in the peach rootstocks than in the domestic plum. The occurrence of the leafhopper, the amino acid profile of scion xylem fluid, and the concentration of *X. fastidiosa* were influenced by the rootstock. The amino acid profile of xylem fluid was not correlated with the concentration of *X. fastidiosa* in root xylem fluid.

Phony peach disease (PPD) is a major factor limiting the production of peaches (*Prunus persica* (L.) Batsch) in the southeastern United States. Symptomatic trees appear dwarfed, as a result of the shortening of stem internodes. Other symptoms include early bloom and fruit-set and reduced fruit size (15). PPD is caused by one or more of a group of gram-negative, xylem-limited, rod-shaped bacteria, typified by convoluted cell walls, terminal fimbriae, and fastidious nutritional requirements (14,25). Phenotypic and genotypic similarities of these xylem-limited bacteria prompted classification in a single species, *Xylella fastidiosa* Wells et al (24).

In the southeastern United States, both PPD and plum leaf scald (PLS), another disease caused by *X. fastidiosa* (10,19), are vectored principally by the xylem-feeding leafhopper *Homalodisca coagulata* (Say) (Homoptera: Cicadellidae); several other species of leafhoppers may also transmit the bacterium (3,22,23). *H. coagulata* feeds on over 100 different host plants (22), many of which harbor *X. fastidiosa* and may serve as reservoirs (13,18). Peach is not a preferred host of *H. coagulata*, and the survival of the insect is reduced in peach trees manifesting PPD symptoms (17). Previous work showed that leafhopper feeding and plant host selection are influenced by the amino acid content of xylem fluid, which is influenced by the rootstock (4).

PLS occurs in South America on Japanese plum (*P. salicina* Lindl.) (10). Despite an abundance of leafhopper vectors, PPD has not been observed in South America, even in trees with U.S. scion material (9). No differences in growth rate, colony characteristics, cell morphology, or immunofluorescent staining have been noted in *X. fastidiosa* strains from the United States and Brazil (5). The objectives of this study were to determine if a rootstock obtained from South America influences 1) the acceptability of the scion to vector feeding and 2) resistance to colonization by *X. fastidiosa*.

MATERIALS AND METHODS

Experimental material. Rootstock seedlings of 1–1 plum, Nemaguard peach (a southeastern U.S. industry standard), and A82 peach (a Brazilian industry standard) were budded with Flordaking peach at the University of Florida Agricultural Research and Education Center in Monticello in 1983 and 1984. In February 1985, five to nine of the 1- and 2-yr-old trees on each rootstock were transplanted in a 1-ha block, in a completely randomized factorial design. Standard cultural and management practices were used. The trees were irrigated from April to October with microjet-type emitters, which delivered 42 L/day to each tree in 1985 and 1986 and 48 L/day in 1987 and 1988. In June 1987, the length (in centimeters) of the current season's growth on 10 limbs per tree was measured. The canopy width of each tree was measured at the widest points along the tree row and perpendicularly to the row, and the two measurements were averaged. The trunk was measured with a diameter tape measure approximately 15 cm from the soil line.

Estimation of leafhopper occurrence. Visual counts of *H. coagulata* per tree were recorded three times weekly from May to September in 1985–1988. Counts were made from 8:00 to 11:00 A.M., the lowest point of leafhopper flight activity (R. F. Mizell, 1989, *unpublished data*).

Incidence of PPD. Concentrations of *X. fastidiosa* in the roots were determined by sampling three roots (in different zones) per tree in June 1987 and four roots (one from each quadrant) per tree in June 1988. Sample dates were chosen to correspond to the time of peak leafhopper occurrence in the block. Samples were collected 0.5–1.0 m from the trunk of each tree. Xylem fluid was extracted by vacuum infiltration with 0.5 ml of 0.1 M KOH (8). The collection procedure extracted about 82% of the total *X. fastidiosa* (2). A 10-µl sample of the filtrate was examined with a phase-contrast compound microscope at 400×. The number of bacteria in 10 randomly selected microscopic fields was recorded, and the number per cubic centimeter of root xylem was calculated. If *X. fastidiosa* was recovered from the root xylem fluid of a tree, that tree was considered to have PPD whether or not it showed symptoms.

Amino acid analysis. Xylem fluid samples from three or four limbs per tree were collected from 5:00 to 8:30 A.M. on 16 and 18 June 1987. Fluid was extracted from exposed xylem tissue in stem sections 10–15 cm long, in a pressure chamber (20) with a pressure of 0.5–1.5 MPa. The samples were frozen until the amino acid concentrations could be determined. Thawed samples and appropriate amino

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acid standards were prepared essentially according to the procedure of Heinrickson and Meredith (11). Samples and standards were injected into a reverse-phase high-performance liquid chromatography gradient system (Waters Associate) equipped with a PicoTag column (11).

Statistical analysis. Dependent variables were analyzed by analysis of variance as a function of rootstock or tree age. The number of leafhoppers and the number of *X. fastidiosa* per cubic centimeter of root xylem were log-transformed prior to analysis. A one-way analysis of variance was performed to compare leafhopper populations or amino acid levels in trees from which *X. fastidiosa* was recovered or was not recovered.

Spearman correlation analysis was performed on data from all rootstocks combined to examine relationships between leafhopper occurrence, the concentration of *X. fastidiosa* per cubic centimeter of root xylem, concentrations of amino acids in scion xylem fluid, and tree parameters. Statistical Analysis Systems (SAS) software was used in data analyses (12).

RESULTS

Tree growth parameters. In 1987, the Flordaking scions on both peach rootstocks (Nemaguard and A82) had greater growth of limbs than those on the plum rootstock (1–1) (Table 1). Trees on the 1–1 rootstock had a greater average trunk diameter than the others. The age of the tree (the year in which it was budded) made little difference in limb growth or canopy width. Trunk diameter was greater in the older trees (Table 1).

Leafhopper occurrence. *H. coagulata* was the leafhopper observed almost exclusively in the experimental block throughout the study. Averaged weekly, the observed number of *H. coagulata* attained a maximum during early to mid-June in 1985–1987 (Fig. 1A–C). In 1988 leafhopper occurrence peaked twice, once in mid-June and again in mid-July (Fig. 1D). More leafhoppers were observed in trees on the domestic rootstocks (1–1 and Nemaguard) than in those on the Brazilian rootstock (A82) when leafhopper occurrence was greatest (Table 2). The total number of leafhoppers observed in 1985 was approximately 40% of that in each year from 1986 to 1988. Except in 1986, leafhoppers occurred in similar numbers in trees budded in 1983 and 1984 (Table 2).

Incidence of PPD. Trees were not sampled for *X. fastidiosa* in 1985 and 1986. From 1987 to 1988, the number of trees with detectable *X. fastidiosa* increased from 17 to 26% (Table 3). In 1988, bacteria were recovered from six of 13 trees (46%) on the 1–1 rootstock and from fewer trees on the peach rootstocks, Nemaguard and A82 (25 and 11%, respectively) (Table 3). The number of trees on the A82 rootstock from which *X. fastidiosa* was recovered did not change from 1987 to 1988.

The concentrations of *X. fastidiosa* recovered per cubic centimeter of root xylem from the peach rootstocks, Nemaguard and A82, were low, compared with those from the plum rootstock (Table 3). Most trees in the experimental planting remained asymptomatic; by the end of the study period, only one tree in the block (on the 1–1 rootstock) was visually symptomatic for PPD. All trees on the Brazilian rootstock remained asymptomatic for PPD the year following the completion of the study (J. H. Aldrich, 1989, *unpublished data*).

On the domestic rootstocks, 1–1 and Nemaguard, trees infected with *X. fastidiosa* had fewer leafhoppers than uninfected trees during the peak periods of leafhopper occurrence in 1987 and 1988 (Table 4). On the Brazilian rootstock, infected and uninfected trees did not differ in leafhopper populations (Table 4).

Amino acid analysis. In 1987, the amides, plus their associated acids, constituted 93, 89, and 91% of the total amino acids in 1–1, Nemaguard, and A82, respectively (Table 5). (The pre-hydrolysis ratio of amides to the respective acids was 84% for *P. salicina* and 68% for *P. persica*.) The concentrations of asparagine, glutamine, histidine, alanine, threonine, arginine, proline, valine, methionine, isoleucine, leucine, lysine, and the total amino acids in xylem fluid were greater in the trees on the plum rootstock (1–1) than in those on the peach rootstocks, Nemaguard or A82 (Table 5). The concentrations of serine, glycine, tyrosine, cysteine, and phenylalanine did not differ in trees on the different rootstocks.

With the exception of the asparagine concentration, the amino acid profiles of scion xylem fluid from infected and uninfected trees were similar (data not shown). For trees on the Nemaguard rootstock, the asparagine concentration was lower in infected than in uninfected trees (1.9 and 4.0 mM, respectively).

Relationships between leafhopper occurrence, *X. fastidiosa* concentration, amino acid concentration in scion xylem fluid, and tree parameters. A highly significant relationship ($P = 0.0001$) was found between the number of leaf-

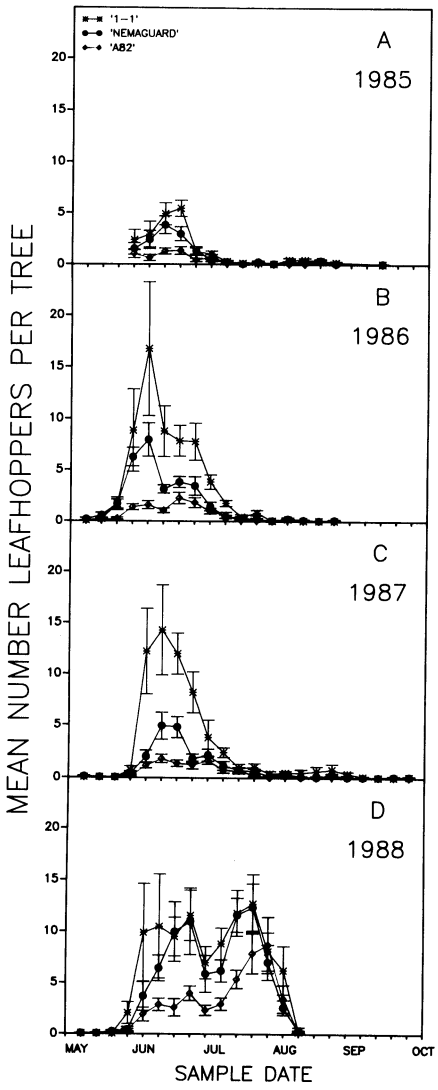

Fig. 1. Seasonal variation of the mean number of leafhoppers observed on Flordaking scions on 1–1 plum, Nemaguard peach, and A82 peach rootstocks, averaged weekly from May to October, 1985–1988.

Table 1. Growth of Flordaking peach scions on different rootstocks in 1987

	Limb growth (cm)[x]	Canopy width (m)	Trunk diameter (cm)
Rootstock			
1–1 plum	52.7 b	3.79 a	11.9 a
Nemaguard peach	74.6 a	3.92 a	10.1 b
A82 peach	71.5 a	4.01 a	10.4 b
Year budded			
1983	64.5 a	3.91 a	11.4 a
1984	70.9 a	3.92 a	10.0 b
Interaction	NS[y]	NS	**[z]

[x] Means in a column followed by the same letter are not significantly different ($P < 0.05$) (least square means).
[y] Not significant.
[z] $P < 0.01$.

hoppers and the concentrations of asparagine, glutamine, the amides (asparagine and glutamine combined), arginine, and total amino acids (Table 6). Leafhopper occurrence was also correlated with other amino acids, but to a lesser degree. Alanine, cysteine, glycine, proline, phenylalanine, serine, and valine were not significantly related to leafhopper occurrence.

A significant positive relationship between tree trunk diameter and leafhopper occurrence was evident; however, there was no relationship between leafhopper occurrence and limb growth or canopy width (Table 6).

The concentration of *X. fastidiosa* recovered per cubic centimeter of root xylem was only weakly related to the concentrations of glycine and cysteine in scion xylem fluid (Table 6). There was an inverse relationship between the bacterial concentration and limb growth and canopy width.

No relationship between leafhopper numbers and the bacterial concentration was found (data not shown).

DISCUSSION

Seasonal patterns of leafhopper occurrence on *Prunus* in 3 of the 4 yr of the experimental period were similar and are in accordance with published results for *H. coagulata* in Florida (3). Leafhopper occurrence during peak periods was influenced by the rootstock and was consistently lowest in trees on the Brazilian rootstock. Since the scions on both peach rootstocks (Nemaguard and A82) exhibited similar phenological development, it is unlikely that differences in leafhopper occurrence on them were due to differences in tree phenology.

Mizell and French (17) noted that the occurrence and survival of *H. coagulata* are reduced in trees with PPD symptoms. Changes in leaf elemental concentration, leaf gas exchange, and xylem water potential have been observed with the development of PPD symptoms (2,6,7). In this study, factors that influence leafhopper occurrence in infected peach trees were present prior to the expression of PPD symptoms, as leafhopper occurrence in trees on domestic rootstocks was lower in those with detectable levels of bacteria than in those from which bacteria were not recovered. The presence of less attractive infected trees may increase vector pressure on uninfected trees, enhancing their probability of infection.

Xylem-limited bacteria occur in low concentrations in peach orchards. This and the lack of attraction of the vector to infected trees may account for slow or nonexistent secondary spread within peach orchards (16). New infections may depend on inoculum from various plant species outside the orchards (16). The use of more resistant rootstocks, such as the Brazilian rootstock, which was found to be a less suitable host for leafhopper abundance and bacterial colonization, could reduce disease incidence.

Previous work showed that the chemistry of xylem fluids of *Vitis* spp. (21) and *P. persica* (4) are greatly influenced

Table 2. Number of *Homalodisca coagulata* observed on Flordaking peach scions per week during periods of leafhopper population peaks (early to mid-June)

	Number of *H. coagulata* per tree[z]			
	1985	1986	1987	1988
Rootstock				
1-1 plum	5.4 ± 0.8	16.7 ± 6.5	14.2 ± 4.4	11.5 ± 2.5
Nemaguard peach	2.9 ± 0.7	7.9 ± 1.6	4.9 ± 1.3	10.9 ± 3.3
A82 peach	1.3 ± 0.4	1.6 ± 0.4	1.8 ± 0.4	3.9 ± 0.7
Year budded				
1983	3.6 ± 0.6	5.4 ± 1.4	5.4 ± 1.2	8.0 ± 1.8
1984	2.3 ± 0.6	10.8 ± 2.4	7.4 ± 2.2	9.0 ± 2.2

[z] Mean number per week, plus or minus standard error.

Table 3. Number of peach trees from which *Xylella fastidiosa* was recovered and concentration of the bacterium in root xylem during periods of leafhopper population peaks

Rootstock	Trees in block	Trees with *X. fastidiosa*		*X. fastidiosa* per cubic centimeter of root xylem[z]	
		1987	1988	1987	1988
1-1 plum	13	3 (23%)	6 (46%)	30.7 a	38.7 a
Nemaguard peach	16	3 (19%)	4 (25%)	0.6 b	1.2 b
A82	18	2 (11%)	2 (11%)	0.6 b	0.5 b
Total	47	8 (17%)	12 (26%)		

[z] Means in a column followed by the same letter are not significantly different ($P < 0.05$).

Table 4. Number of *Homalodisca coagulata* observed on peach trees from which *Xylella fastidiosa* was recovered (infected) or not recovered (uninfected) during periods of leafhopper population peaks

	Number of *H. coagulata* per tree[z]		
	1-1 plum rootstock	Nemaguard peach rootstock	A82 peach rootstock
1987			
Infected	4.3 b	1.1 b	1.3 a
Uninfected	13.8 a	3.7 a	1.4 a
1988			
Infected	6.7 b	6.4 b	2.3 a
Uninfected	13.2 a	10.5 a	4.4 a

[z] For each year, means in a column followed by the same letter are not significantly different ($P < 0.05$).

Table 5. Mean concentration of amino acids in peach scion xylem fluid in 1987

Amino acid	Concentration (mM)[z]		
	1-1 plum rootstock	Nemaguard peach rootstock	A82 peach rootstock
Asparagine/aspartic acid	7.91 a	3.18 b	2.40 b
Glutamine/glutamic acid	3.14 a	1.13 b	0.94 b
Histidine	0.041 a	0.020 b	0.015 b
Alanine	0.049 a	0.136 b	0.080 ab
Threonine	0.116 a	0.043 b	0.039 b
Arginine	0.082 a	0.031 b	0.025 b
Proline	0.092 a	0.022 b	0.034 b
Valine	0.112 a	0.052 b	0.037 b
Methionine	0.035 a	0.019 b	0.018 b
Isoleucine	0.070 a	0.034 b	0.024 b
Leucine	0.028 a	0.015 b	0.011 b
Lysine	0.064 a	0.022 b	0.015 b
Serine	0.048 a	0.028 a	0.044 a
Glycine	0.033 a	0.029 a	0.023 a
Tyrosine	0.023 a	0.012 a	0.009 a
Cysteine	0.006 a	0.008 a	0.004 a
Phenylalanine	0.016 a	0.010 a	0.007 a
Total amino acids	11.87 a	4.82 b	3.69 b

[z] Means in a row followed by the same letter are not significantly different ($P < 0.05$) (least square means).

Table 6. Spearman correlation analysis of relationships between total number of leafhoppers, concentration of *Xylella fastidiosa*, amino acid concentrations in xylem fluid, and tree measurements in 1987

	X. fastidiosa per cubic centimeter of root xylem		Leafhopper number	
	r^2	P^x	r^2	P
Amino acid ($n = 28$)[y]				
Asparagine/aspartic acid	...	NS[z]	0.83	0.0001
Glutamine/glutamic acid	...	NS	0.74	0.0001
Glycine	0.39	0.04	...	NS
Histidine	...	NS	0.61	0.0006
Threonine	...	NS	0.42	0.03
Arginine	...	NS	0.48	0.01
Tyrosine	...	NS	0.51	0.006
Methionine	...	NS	0.38	0.04
Cysteine	0.48	0.01	...	NS
Isoleucine	...	NS	0.54	0.003
Leucine	...	NS	0.54	0.003
Lysine	...	NS	0.55	0.003
Total amino acids	...	NS	0.82	0.0001
Total amides	...	NS	0.84	0.0001
Tree measurement ($n = 47$)				
Limb growth	−0.44	0.002	...	NS
Canopy width	−0.33	0.022	...	NS
Trunk diameter	...	NS	0.43	0.002

[x] Probability that r is not significant.
[y] The correlation coefficients for the amino acids alanine, proline, phenylalanine, serine, and valine are not significant for either variable ($P < 0.05$).
[z] Not significant ($P = 0.05$).

by the rootstock. In this study, the profiles of amino acids in xylem fluid of scions were influenced by the rootstock; thus the use of a single scion on different rootstocks obviates confounding effects of tree anatomy, morphology, or physiology on leafhopper occurrence. The strong relationship observed in 1987 between leafhopper occurrence and the amino acid profile, particularly the concentrations of asparagine and glutamine in xylem fluid, agrees with results obtained by Brodbeck et al (4). Chemical profiles may vary over time, but these high correlations are consistent with the hypothesis that the nutrient status of xylem fluid is an important determinant of host selection by *H. coagulata* (4).

Although both peach rootstocks were poorly colonized by *X. fastidiosa* and have similar sap profiles, the leafhopper vector was more attracted to the domestic rootstock. Apparently, factors addressed in this study do not entirely account for the responses observed. Organic acids are present in approximately the same concentrations as amino acids and are major sources of carbon in xylem fluid (1). The amount of xylem fluid collected in this study precluded the quantification of organic acids; yet it is possible that their concentrations affect host selection by the vector and colonization by *X. fastidiosa*.

The explanation for the presence of PLS but not PPD in South America remains obscure. Peach trees infected with *X. fastidiosa* in South America may not become symptomatic because of environmental or other constraints. One year following the completion of this study A82 trees remained asymptomatic for PPD. Research on trees symptomatic for PPD may reveal further relationships between vector behavior and disease incidence. Alternatively, different strains may be responsible for PPD and PLS; peach trees in the United States may have both strains, but only the PLS strain may exist in South America.

This study indicates that the occurrence of leafhoppers and the incidence of PPD are influenced by the rootstock. Whether differential susceptibility of *Prunus* germ plasm (plum vs. peach) to colonization by *X. fastidiosa* is associated with specific nutritional requirements of the pathogen is not clear from the data. If chemical profiles in xylem fluid associated with bacterial colonization can be identified, *Prunus* germ plasm may be screened for resistance to colonization by *X. fastidiosa.*

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