Characteristics of Strains of *Pseudomonas solanacearum* from the French West Indies

P. PRIOR, Research Plant Pathologist, Institut National de la Recherche Agronomique, Station de Pathologie Végétale, de Phytoécologie et de Malherbologie, BP 1232, 97184, Pointe à Pitre Cedex, Guadeloupe, French West Indies; and H. STEVA, Research Plant Pathologist, Institut de Recherches Agronomiques Tropicales et des Cultures Vivrières, CIRAD, BP 427, 97204, Fort de France, Martinique, French West Indies

ABSTRACT

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Twenty-four strains of *Pseudomonas solanacearum* isolated from five host plants at different locations in Martinique and Guadeloupe were compared with respect to results of physiological and biochemical tests and to pathogenicity on seven different hosts. On the basis of Hayward's classification, six strains were placed in biovar I, one in biovar II, and 17 in biovar III. On the basis of pathogenicity tests, all but one of the 24 strains were placed in race 1; the exception (from Guadeloupe) was placed in race 3.

Bacterial wilt caused by *Pseudomonas solanacearum* E. F. Smith is one of the most important and widespread bacterial diseases of crops in the tropics, subtropics, and warm temperate regions of the world. Two major classification systems have been used for characterization of *P. solanacearum* at the subspecific level. Races have been defined by host range (6); race 1 strains have a broad host range, race 2 strains are pathogenic only to Musaceae, and race 3 strains are pathogenic to potato. Biovars are defined by the ability of strains to oxidize three sugar alcohols and three disaccharides (21).

In the French West Indies (FWI), located in the Caribbean area, Escudié and Digat surveyed solanaceous crops for the disease in 1965 (13) and isolated the causal organism from tomato, pepper, eggplant, and potato growing in Guadeloupe and Martinique in 1967 (12). Twenty strains from different locations in the FWI were typed for race; strains from tomato and tobacco were grouped into race 1 (biovars I and III) (10). An initial concern that strains pathogenic to Musaceae (banana) were present in the FWI was not confirmed (2). Recently, however, bacterial wilt was observed on ornamental banana (*Ensete ventricosum* (Welw.) Cheesman); strains pathogenic to this host might represent a threat to banana crops. Since 1983, losses of nearly 100% of eggplant crops have been reported from Martinique (29); in Guadeloupe, 150 miles away, bacterial wilt of the same crop has not been so damaging.

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Although variation within the species is great worldwide (5,20,35), it is not known if such variation occurs among strains indigenous to islands in a specific geographic region. This research was undertaken to determine the variation among strains of *P. solanacearum* from Martinique and Guadeloupe.

MATERIALS AND METHODS

Cultures. Twenty-four strains of *P. solanacearum* were isolated from tomato, eggplant, pepper, potato, and ornamental banana collected at different locations in Martinique and Guadeloupe (Table 1). These were compared with seven known strains (K60, K105, K136, S225, S236, S247, and 1000) obtained from the collection at the Department of Plant Pathology, University of Wisconsin, Madison. According to L. Sequeira (*unpublished*), strains K60, S247, and 1000 were typed as biovar I, strains S225 and S236 as biovar III, and strain K105 as biovar IV. The newly isolated strains have been deposited in the Collection Nationale des Bactéries Phytopathogènes (INRA, Station de Pathologie Végétale et de Phytobactériologie, Angers, France).

For inoculum preparation, single colonies of the virulent, fluidal type grown on tetrazolium chloride (TZC) medium (24) at 28 C for 48 hr were streaked on TZC-free medium. After 48 hr of incubation, cells were harvested in distilled water and suspensions were adjusted to 10^9 cfu/ml (10^7 cfu/ml had an optical density of 0.01 at 650 nm). Working stock cultures were maintained as suspensions in distilled water in capped test tubes (25) at room temperature.

Plant production and inoculation. Inoculations were made on a range of plants, including tomato (*Lycopersicon esculentum* Mill. 'Floradel'), eggplant (*Solanum melongena* L. 'Florida Market'), pepper (*Capsicum annuum* L. 'California'), peanut (*Arachis hypogea* L. 'Brésilien'), tobacco (*Nicotiana tabacum* L. 'Xanthi'), potato (*S. tuberosum* L. 'Claustar'), and bean (*Phaseolus vulgaris* L. 'Contender'). Seeds and seedlings were planted in vegetable mold in 10-cm pots. Seedlings of tomato, pepper, and tobacco were transplanted, and seeds of peanut and bean were sown directly. Pieces of potato tuber with a growing bud were planted directly into pots, and one stem was allowed to develop (18). All plants were grown in a greenhouse at 27 ± 4 C.

When 20–25 cm tall, plants were inoculated by a stem technique (36). An alcohol-flamed needle was forced into the stem through a 25-µl drop of bacterial suspension (10^9 cfu/ml in sterilized tap water) placed in the axil of the third leaf below the stem apex. Ten plants of each host were inoculated with each strain. Inoculated plants were placed in a glasshouse at 28 ± 2 C under supplemental lighting (8×10^3 lx) provided by Mazdafluor tubes and watered daily with tap water. Severity of wilting was rated daily on the scale of He et al (22): 1 = no symptoms, 2 = inoculated leaf wilted, 3 = two or three leaves wilted, 4 = four or more leaves wilted, and 5 = plant dead. The last observation was at 3 wk after inoculation.

Hypersensitivity in tobacco. Hypersensitive reaction (HR) in tobacco was tested by injection of 10^8 cfu/ml of an aqueous suspension of each strain into a panel of three leaves (27). Plants were incubated in a glasshouse as described above. Reactions were recorded at 24, 48, 72, and 96 hr.

Physiological and biochemical tests. To test for production of melanin pigments, strains were transferred to casamino acids-peptone-glucose (CPG) medium (9) containing 0.1% tyrosine. Oxidase reaction was determined by Kovacs's (26) method, catalase production by Digat's (11) procedure, gelatin

liquefaction by Frazier's (15) technique, and production of nitrate reductase, urease, and indole by Fahy and Hayward's (14) method. Production of arginine dihydrolase and of tryptophan deaminase was tested according to the methods of Thornley (34) and Cassagne (7), respectively, and esterase activity was tested with Tween 80 medium (30). Pectate degradation tests were completed according to Prunier and Kaiser (32), and the carboxymethyl cellulose (medium viscosity, Sigma) medium (31) was used to detect cellulolytic activity. The ability of the strains to hydrolyze starch also was tested (14). Salt tolerance was examined by incubation of each strain for 7 days at 28 C in test tubes of nutrient broth (0.3 g of yeast extract, 0.5 g of bactotryptone) containing 1.0, 1.4, 1.7, or 2% NaCl. Growth in the broth tubes was judged by comparisons with the turbidity of controls.

Utilization (acid production and bacterial growth) of lactose, maltose, cellobiose, fructose, trehalose, arabinose, sucrose, mannitol, sorbitol, and dulcitol was tested as sole carbon source with the medium of Hayward (21). Carbohydrates were first sterilized according to He et al (22), and metabolism of glucose was tested according to Hugh and Leifson (23). Tests were performed at 28 C, and cultures were observed for acid production over a 21-day period.

Sensitivity to antibiotics was tested with bioMérieux antibiotic sensitivity disks (1) (Marcy l'Etoile, France). Strains were cultivated on Mueller-Hinton medium (1), and inhibition zones were recorded after 5 days at 30 C. Other tests included in this study are described in Table 2.

RESULTS

Cultural, physiological, and biochemical characteristics. On CPG medium, the 48-hr cultures of all strains were smooth, opaque, and highly fluid; one strain, MA4, produced a brown pigment. On TZC medium, colonies were creamy white with pink or light red centers; differences were observed, however, in colony size and shape, formazan pigmentation patterns, and slime deposition. On tyrosine medium, all strains except MT4, MA2, and GT5 produced a brown, diffusible pigment. All the FWI and reference strains were negative for arginine dihydrolase and tryptophan deaminase activity, indole production, gelatin liquefaction, starch hydrolysis, and pectate degradation. They were all positive for production of nitrate reductase and presence of oxidase, catalase, and urease, and all oxidized acetate and citrate. Other results are given in Table 2.

Strains from the FWI differed in ability to oxidize sugar alcohols and disaccharides (Table 3). According to Hayward's (21) classification, six of the 24 strains from the FWI were biovar I, one (MA4) was biovar II, and 17 were biovar III. Host and geographic origin of most strains were not related to their biovars, but all strains isolated from potato were typed as biovar I. Strains differed in antibiotic sensitivity, as susceptibility to colistin separated two groups (Table 4). All were susceptible to streptomycin (10 μg), kanamycin (30 μg), doxycycline (30 μg), and nalidixic acid (30 μg).

Hypersensitivity in tobacco. Most strains of *P. solanacearum* from the FWI caused a typical HR (19) in tobacco leaves (Table 5). The exceptions were strains MT5, GT1, GP1, MPT1, MPT3, and GPT1, which caused a slow, spreading necrosis similar to that caused by strain K60 from the United States (isolated from tomato) and by strain S247 from Colombia (isolated from tobacco). Strain MA4 caused no symptoms 72 hr after infiltration; the

Table 1. Source and host range of French West Indies and reference strains of *Pseudomonas solanacearum*

Strain	Host	Location	Year isolated	Severity of wilting[a]							Race	Group
				Potato	Tomato	Eggplant	Pepper	Bean	Peanut	Tobacco		
Martinique												
MT1	Tomato	Basse Pointe	1986	H	H	H	H	H	M	H	1	1
MT2	Tomato	Lamentin	1983	H	H	H	H	H	L	M	1	1
MT3	Tomato	Lamentin	1984	H	H	H	H	H	L	H	1	1
MT4	Tomato	Lamentin	1985	H	H	H	H	M	L	L	1	1
MT5	Tomato	Case Pilote	1987	H	H	H	L	M	L	H	1	1
MA1	Eggplant	Morne L'Etoile	1985	H	H	H	H	H	L	H	1	1
MA2	Eggplant	Case Pilote	1984	H	H	H	M	M	L	M	1	1
MA3	Eggplant	Morne Vert	1985	H	H	H	M	H	M	M	1	1
MA4	Eggplant	Schoelcher	1983	0	0	M	0	0	0	0	1	4
MPT1	Potato	Lamentin	1986	M	H	H	L	H	0	L	1	2
MPT2	Potato	Carbet	1987	H	H	H	H	H	M	H	1	1
MPT3	Potato	Morne Vert	1987	H	H	H	L	M	H	H	1	1
MP1	Pepper	Fort de France	1985	H	H	H	H	H	M	H	1	1
MB1	Ornamental banana	Lamentin	1987	H	H	H	H	H	M	M	1	1
Guadeloupe												
GT1	Tomato	Saint-François	1985	H	H	H	L	M	L	H	1	1
GT4	Tomato	Petit-Bourg	1984	H	H	H	H	M	H	H	1	1
GT5	Tomato	Saint-Claude	1984	H	H	M	L	L	0	0	3	5
GA1	Eggplant	Petit-Bourg	1984	H	H	H	M	M	H	M	1	1
GA2	Eggplant	Sainte Rose	1986	H	H	H	H	M	H	M	1	1
GA3	Eggplant	Matouba	1984	H	H	H	M	M	0	L	1	2
GA4	Eggplant	Vieux-Habitants	1983	H	H	H	H	H	M	M	1	1
GA5	Eggplant	Saint-François	1983	H	H	H	H	H	M	H	1	1
GPT1	Potato	Petit-Bourg	1987	H	H	H	M	H	M	M	1	1
GP1	Pepper	Petit-Bourg	1984	H	H	H	0	H	0	M	1	3
Reference												
K136	Tomato	BWI, Trinidad	1957	H	H	H	L	L	L	H	1	1
S225	Tomato	Peru, Lupuna	1966	H	H	H	H	L	H	H	1	1
1000	Tomato	F. Guyana, Kourou	1966	H	H	H	M	M	0	M	1	2
K60	Tomato	USA, North Carolina	1953	H	H	H	H	H	0	M	1	2
K105	Tobacco	USA, Florida	1955	H	H	H	L	L	0	H	1	2
S236	Tomato	Australia, Nambour	1965	H	H	H	L	L	0	H	1	2
S247	Tobacco	Colombia	···	H	H	L	0	M	0	H	1	3

[a]Rated on a scale where 1 = no symptoms, 2 = inoculated leaf wilted, 3 = two or three leaves wilted, 4 = four or more leaves wilted, and 5 = plant dead and expressed as average disease indices of 10 plants: H = high (4.1–5.0), M = medium (2.6–4.0), L = low (1.1–2.5), and 0 = none (1.0).

infiltrated area became chlorotic 4 days after infiltration, but symptoms differed from those of the HR.

Pathogenicity. Typical bacterial wilt symptoms (10) were observed on potato, tomato, eggplant, bean, and tobacco. Atypical symptoms consisting of "considerable decay of the pith surrounding the point of inoculation, but no systemic symptoms," previously described by He et al (22) and by Digat and Escudié (12), were observed on pepper and peanut. Such plants were rated 1 on the disease scale. All strains except MA4 caused a rapid wilting of potato and tomato. Most strains were highly pathogenic to eggplant, whereas GT5 and S247 produced moderate disease after 21 days. Most (80%) of the new strains were pathogenic to peanut, but reference strains, except K136 and S225, were not. Strain MA4 was pathogenic only to eggplant (Table 1).

The strains differed in capacity to cause disease on pepper, peanut, bean, and tobacco. On the basis of host reaction, strains were divided into five groups (Table 1): group 1—strains pathogenic on all hosts, including reference strains K136 from Trinidad and S225 from Peru; group 2—strains pathogenic on pepper but not on peanut; group 3—strain GP1, not pathogenic on pepper or peanut; group 4—strain MA4, a slightly pathogenic strain from eggplant; and group 5—strain GT5, not pathogenic on peanut or tobacco. All reference and new strains with broad host ranges were considered race 1, except GT5, which was included in race 3 because it was highly pathogenic only on potato and tomato.

DISCUSSION

Strains of *P. solanacearum* from the FWI were basically similar to each other in terms of cultural, biochemical, and physiological characteristics. Some variation occurred among strains (e.g., gas from nitrate, levan production, cellulolytic activity), but these differences did not seem to have taxonomic significance.

The strains differed according to Hayward's (21) biovar classification. Previously, only strains of biovar I and III were found (10), whereas the majority (70%) of the strains tested in our study were typed as biovar III. Biovar II was detected in Martinique but not in Guadeloupe. In earlier reports (17,28), biovars I and II appeared to be the most widespread in the Americas and biovar III was rare. Our collection of *P. solanacearum* did not have a representative of biovar IV, which has not been found in the Americas. At present in the FWI, strains collected from potato are biovar I. All biovar I representatives were negative for Tween esterase and arabinose oxidation but positive for malonate utilization. Strains in biovar I, including reference strains, were not able to induce HR on tobacco. This may be complementary to Hayward's biovar I classification (21).

According to the host range (22), most strains from the FWI belong to race 1. However, one strain, MA4, was pathogenic only to eggplant. This strain may be an exception to the race classification system, although we placed it in race 1 because of its pathogenicity to eggplant, a universal suscept for race 1 (18).

Representatives of race 2 that originated from the Caribbean area (2,18) were not found among the strains from the FWI. This is consistent with the absence of true Moko disease in the FWI (12). Recently, Moko disease was

Table 2. Characteristics of strains of *Pseudomonas solanacearum* from the French West Indies compared with those of reference strains

	Test[a]											
									NaCl tolerance			
Strain	Gas from nitrate[b]	Esculin hydrolysis[c]	Levan production[b]	Tween 80 hydrolysis[b]	Cellulase	DNase[d]	Tartrate oxidation	Malonate oxidation	1.0%	1.4%	1.7%	2.0%
Martinique												
MT1	+	−	−	+	−	−	+	−	+	+	+	−
MT2	+	−	+	+	−	−	+	−	+	+	+	−
MT3	+	−	−	+	−	−	+	−	+	+	+	−
MT4	−	−	−	+	−	−	+	−	+	+	+	−
MT5	+	−	+	−	+	+	+	+	+	+	−	−
MA1	+	−	+	+	−	−	+	−	+	+	+	−
MA2	−	−	+	+	−	−	+	−	+	+	+	−
MA3	+	−	−	+	−	−	+	−	+	+	+	−
MA4	+	+	−	+	−	+	+	−	+	+	−	−
MPT1	+	−	−	−	−	+	−	+	+	+	−	−
MPT2	+	−	−	+	−	+	+	−	+	+	+	−
MPT3	+	−	−	−	+	+	+	+	+	+	+	−
MP1	+	−	−	+	−	−	+	−	+	+	+	−
MB1	+	−	−	+	+	+	+	−	+	+	+	+
Guadeloupe												
GT1	+	−	−	−	+	−	+	+	+	+	−	−
GT4	+	−	−	+	−	−	+	−	+	+	−	−
GT5	−	−	−	−	+	−	+	+	+	+	−	−
GA1	+	−	+	+	−	−	+	−	+	+	+	−
GA2	+	−	−	+	−	−	+	−	+	+	+	−
GA3	+	−	+	+	+	−	+	−	+	+	+	−
GA4	+	−	+	+	−	−	+	−	+	+	+	+
GA5	+	+	−	+	−	−	+	−	+	+	+	−
GPT1	+	−	+	−	+	+	−	+	+	+	−	−
GP1	+	+	−	+	−	−	+	−	+	+	−	−
Reference												
1000	+	+	+	+	+	+	+	−	+	+	+	−
K60	+	+	−	+	+	+	+	−	+	+	+	−
K105	+	+	−	−	+	+	−	−	+	+	−	−
K136	−	−	+	+	+	−	−	−	+	+	+	−
S225	+	−	−	+	+	−	+	−	+	+	+	−
S236	+	−	+	−	+	+	+	−	+	+	+	−
S247	+	−	+	−	−	+	+	+	+	+	+	−

[a] + = Positive reaction or growth, − = negative reaction or no growth.
[b] Method described in Fahy and Hayward (14).
[c] Method described in Cassagne (7).
[d] Method described in bioMérieux (1).

observed in Grenada (8). Care should be taken to prevent the introduction of this race into Martinique and Guadeloupe. Surveys must be intensified. Recent sporadic cases of bacterial wilt of ornamental banana were apparently caused by strains belonging to race 1. Although this plant species has not been previously listed as a host of race 1, convergent reports from the Philippines (33,37) and Honduras (3) are consistent with the concept that race 1 can induce wilting in certain diploid *Musa* species under field conditions (4).

One strain, GT5, was classified as race 3, biovar I. It was isolated from the cooler area of Guadeloupe (elevation, 900 m; average temperature, 20 C). This strain may not be indigenous to this location and may have been introduced on infected potato tubers used for seed (16). The biovar I typing does not correspond to the normal biovar relationship for strains in race 3 (21); most race 3 strains are typed as biovar II. Moreover, we detected a biovar II strain that belonged to race 1 rather than to race 3. We therefore believe that the host range of an unknown strain, rather than the results of physiological and biochemical tests, is the most practical way of classifying *P. solanacearum* strains for disease management.

Most strains in the FWI belong to race 1, and on the basis of pathogenicity groups, it appears that 80% of these strains belong to group 1, with a homogeneous distribution. In contrast, most reference strains were typed as group 2 (not pathogenic to peanut). Heavy losses of eggplant to bacterial wilt in Martinique were not associated with a new or particular specialized strain of the bacterium. Since the 1970s, strains of *P. solanacearum* may have evolved or may have been introduced. For example, previously, biovar II was not found, strains isolated from tomato were not pathogenic to tobacco, and all strains had the same antibiotic sensitivity (10). Knowledge of the variation is essential to epidemiological studies of disease. We cannot state with certainty that other races of *P. solanacearum* are absent from the FWI because they may exist in undetectable populations. Knowledge about the variation among strains of *P. solanacearum* in the FWI will be helpful in making decisions about crop rotations and in selecting strains of different pathogenicity groups for use in breeding programs for resistance to bacterial wilt.

Table 3. Biovar determination of strains of *Pseudomonas solanacearum* from the French West Indies

	Carbohydrate[a]							
Strain	**Arabinose**	**Maltose**	**Lactose**	**Cellobiose**	**Mannitol**	**Sorbitol**	**Dulcitol**	**Biovar**
MT5	−	−	−	−	−	−	−	I
MPT1	−	−	−	−	−	−	−	I
MPT3	−	−	−	−	−	−	−	I
GT1	−	−	−	−	−	−	−	I
GT5	−	−	−	−	−	−	−	I
GPT1	−	−	−	−	−	−	−	I
MA4	+	+	+	+	−	−	−	II
MT1	+	+	+	+	+	+	+	III
MT2	+	+	+	+	+	+	+	III
MT3	+	+	+	+	+	+	+	III
MT4	+	+	+	+	+	+	+	III
MA1	+	+	+	+	+	+	+	III
MA2	+	+	+	+	+	+	+	III
MA3	+	+	+	+	+	+	+	III
MPT2	+	+	+	+	+	+	+	III
MP1	+	+	+	+	+	+	+	III
MB1	+	+	+	+	+	+	+	III
GT4	+	+	+	+	+	+	+	III
GA1	+	+	+	+	+	+	+	III
GA2	+	+	+	+	+	+	+	III
GA3	+	+	+	+	+	+	+	III
GA4	+	+	+	+	+	+	+	III
GA5	+	+	+	+	+	+	+	III
GP1	+	+	+	+	+	+	+	III

[a] + = Positive and − = negative for carbohydrate utilization.

Table 4. Sensitivity of French West Indies and reference strains of *Pseudomonas solanacearum* to selected antibiotics

		Strains[a]						
Antibiotic	**Concentration (μg/ml)**	**MT4, MT5, S225**	**MA1, MPT3, MB1, GT1, GA5**	**MA2**	**MA4, GA1**	**GT5**	**MP1, GA3, MT2, K60**	**Others[b]**
Colistin	10	R	R	R	R	R	R	S
Penicillin G	10	R	R	R	S-WS	WS	S-WS	S
Ampicillin	10	S	R	R	S	WS	S	S
Erythromycin	15	S	S	R	R	WS	S	S
Chloramphenicol	30	S	S	WS	R	WS	WS	S-WS
Rifampicin	30	S	S	S	S	R	S	S

[a] R = resistant, no inhibition zone; S = sensitive, diameter of inhibition zone more than 20 mm; WS = weakly sensitive, diameter of inhibition zone less than 20 mm.
[b] MT1, MT3, MA3, MPT1, MPT3, GA2, GA4, GPT1, GP1, 1000, K105, K136, S236, and S247.

Table 5. Hypersensitivity in tobacco cultivar Xanthi of French West Indies and reference strains of *Pseudomonas solanacearum*[a]

	Hours after infiltration[b]			
Strains	**24**	**48**	**72**	**96**
MT5, MPT1, MPT3, GT1, GPT1, GP1, 1000, K60, S247	−	N	N	N
MT1, MT2, MT3, MA1, MA3, GA1, K105, S236	−	HR	HR	HR
MT4, MA2, MPT2, MP1, MB1, GT4, GA2, GA3, GA4, GA5, K136, S225	HR	HR	HR	HR
GT5	−	C	C	N
MA4	−	−	−	C
Check	−	−	−	−

[a] Panels of leaves were infiltrated with 10^8 cfu/ml.
[b] − = No reaction, N = infiltrated area necrotic with chlorotic margins, HR = hypersensitive reaction, C = infiltrated area chlorotic.

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