Strains of Pseudomonas solanacearum from Central and South America: A Comparative Study

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ABSTRACT

Forty-two isolates of *Pseudomonas solanacearum* from solanaceous and musaceous hosts in both North and South America, including 11 isolates from the Amazon River basin, were compared with respect to colony morphology, melanin formation, and pathogenicity under greenhouse conditions.

Size, shape, coloration and slime deposition in colonies of isolates grown on a tetrazolium medium, and melanin formation in a tyrosine medium, were useful in the classification of isolates into races and strains. Differential hosts were *Musa balbisiana*, susceptible to race 2 isolates only, and eggplant (*Solanum melongena*), susceptible to all race 1 isolates. Peruvian race 2 isolates from the Amazon River basin were similar to race 2 isolates from Colombia in pathogenicity, colony characteristics, and host range. Both groups of isolates reportedly are insect-transmitted, causing Moko disease on plantains (*Musa* Groups AAB and ABB). The present Moko disease epiphytotic in Peru is advancing upstream along the Amazon River at about 22 km/year, and it is suggested that the disease has spread from Colombia into Peru. All Peruvian Amazon basin race 2 isolates had identical pathogenic potential on various hosts, and could be distinguished from the Central American insect-transmitted strain (SFR) on the basis of colony morphology. Because the Amazon isolates appeared to belong to a distinct, stable group, they have been designated as race 2, strain A. An Amazon isolate of race 1 was not pathogenic to tobacco, a characteristic shared by only a few isolates from the North American continent. Phytopathology 60:506-512.

The recent epiphytotic of bacterial wilt of plantains (*Musa* groups AAB and ABB) and bananas (*Musa* Group AAA) in small plantings along the Peruvian headwaters of the Amazon river (6, 7, 16) seriously threatens the wellbeing of thousands, since bananas and plantains constitute one of the major sources of carbohydrates in the native diet. It seemed important to determine whether isolates of *Pseudomonas solanacearum* E.F. Sm. from that area were akin to other strains previously described or belonged to an entirely different group. Strain determination in this species, however, is difficult. The numerous hosts affected by this pathogen, its wide geographic distribution, the intrinsic complexities of strain differentiation in this variable species, and the lack of communication among researchers, have resulted in the development of several methods of classification at the subspecific level, including races, strains, and pathotypes, on the basis of widely different criteria.

Natural host range, reaction of differential hosts (including tobacco and banana), and colony appearance on a tetrazolium (TZC) medium, were used by Buddenhagen et al. (5) to classify several hundred *P. solanacearum* isolates obtained from a wide range of hosts in Central and South America into 3 races, characterized as follows: race 1 affects tobacco (*Nicotiana tabacum*) and other solanaceous hosts; race 2 causes wilt of bananas, *Heliconia* spp., and other musaceous hosts; race 3 affects potato (*Solanum tuberosum*), but has limited pathogenicity to tobacco. Although several races and strains occur naturally in the same area, they usually attack different hosts. Sequeira & Averre (17) and Buddenhagen (1) distinguished race 1 from race 2 isolates by the intense brown pigment produced by the former when grown on a tyrosine-containing medium. Race 3 isolates produce small amounts of this pigment, however (18).

Based on various physiological characteristics, Hayward (8) classified 95 isolates of *P. solanacearum* into four major biochemical types. These types were not related to natural distribution or host range of the majority of isolates tested, although biochemical type II corresponded to race 3 under the scheme of Buddenhagen et al. (5).

In most classification schemes, colony morphology is used to distinguish not only the three major races but also certain strains within these races (4). The virulence of different isolates on artificially inoculated hosts has been useful to determine strains within each race, although such studies may be poor indices of pathogenic potential in nature. Okabe & Goto (14) found that pathotypes for hosts such as tomato, tobacco, eggplant, sesame, and peanut rarely coincided with the grouping of isolates based upon biochemical or other laboratory determined properties. More recently, Lozano & Sequeira (13) showed that virulent race 2 isolates can be differentiated from those of race 1 and 3 by a hypersensitive reaction induced on tobacco leaves.

Differentiation of strains within race 2 were made by Sequeira & Averre (17), Buddenhagen (1, 2), and Buddenhagen & Elsasser (3): B, causing fast wilting of banana plants; D, isolated from *Heliconia* and causing leaf distortion and slow wilting of bananas (1); R, of similar origin as D but not virulent to bananas, and characterized by rapid red pigment formation on TZC medium (17); SFR, an insect-disseminated strain from Honduras, Venezuela, and Colombia (3, 12) with dis-

tinct (small, fluidal, round) colony characteristics; and a strain from Costa Rica affecting plantains (*Musa* Group AAB) but not bananas, designated here as H.

The purpose of these investigations, therefore, was to determine if isolates of *P. solanacearum* collected from musaceous hosts in the Peruvian Amazon basin were similar to the strains of race 2 as described above. Since the methods for control of the pathogen differ in accordance with the particular strain involved, such information is essential in developing a rational program to prevent further spread of the pathogen.

MATERIALS AND METHODS.—Isolates of *Pseudomonas solanacearum* utilized to determine differences in colony morphology form part of the world collection of this pathogen maintained at the Department of Plant Pathology, University of Wisconsin, Madison. The source, race, and strain designation of these isolates are listed in Table 1.

The isolates were kept in sterile distilled water in screw-cap tubes at room temperature. The wild type was maintained by periodic streaking on TZC medium followed by selection of fluidal colonies (10) that were transferred to tubes containing 5 ml of sterile distilled water.

Colony characteristics were observed on TZC medium after incubation at 32 ± 0.5 C for 40-44 hr or 64-68 hr. Colonies on plates were viewed from the underside under oblique transmitted light from a lamp provided with a blue filter (10).

Melanin formation was estimated visually as high, low, or intermediate, based on the degree of brown pigment formation after 64-68 hr growth of *P. solanacearum* at 32 C on a modified TZC medium containing 0.1% L-tyrosine, but without tetrazolium salts.

Host plants used were: potato (*Solanum tuberosum* L. 'Russet Burbank'); pepper (*Capsicum annuum* L. 'Sweet Yellow'); eggplant (*Solanum melongena* L. 'Black Beauty'); tomato (*Lycopersicon esculentum* Mill. 'Bonny Best'); tobacco (*Nicotiana tabacum* L. 'Bottom Special'); and *Musa balbisiana* Colla. Potato plants were grown in the greenhouse at temperatures ranging from 10 to 22 C from small tubers planted one

TABLE 1. Description of isolates of *Pseudomonas solanacearum* used for comparative studies of colony morphology

No.	Race	Strain	Host	Location	Year isolated
2	2	B	Banana	Costa Rica, Coto	1959
5	2	D	*Heliconia*	Costa Rica, Coto	1959
6	2	R	*Heliconia*	Costa Rica, Coto	1959
7	2	R	*Heliconia*	Costa Rica, Coto	1959
11	2	D	*Heliconia*	Costa Rica, Coto	1959
18	2	SFR	Plantain (Chato)	Honduras, Montana	1964
20 (41)	2	SFR	Banana (Dwarf Cavendish)	Venezuela	1960
21	2	SFR	Banana	Honduras	1960
25 (K 60)	1	T	Tomato	USA, North Carolina	1953
26	1	T	Tomato	USA, Georgia	1954
30	1	T	Tomato	B.W.I., Trinidad	1957
70	2	SFR	Plantain	Colombia, Ibague	1965
71	2	SFR	Plantain	Colombia, Ibague	1965
127	2		Plantain (French[a])	Peru, Timicuro[b]	1966
128	2		Plantain (Chato)	Peru, Timicuro	1966
129	2		Plantain (French)	Peru, San Pablo	1966
130	1		Tomato	Peru, Lupuna	1966
131	2		Plantain (Chato)	Peru, Taperillo	1966
135	2	B	Banana (Valery)	Honduras, Buena Vista	1964
138	2	H	Plantain (Chato)	Costa Rica, San Isidro	1967
155	2	H	Plantain (Chato)	Costa Rica, Acosta	1966
156	2		Plantain (French)	Peru, Panguana	1966
157	2		Plantain (French)	Peru, Panguana	1966
158	2		Banana (Gros Michel)	Peru, Ramon Castilla	1966
159	2		Plantain (French)	Peru, Caballococha	1966
160	2		Plantain (French)	Peru, Isla Padre	1966
162	2		Plantain (French)	Peru, Iquitos	1967
163	2		Plantain (French)	Peru, Nauta	1967
164	2	SFR	Plantain	Colombia, Villavicencio	1966
166	2	B	Plantain	Costa Rica	1958
167	2	B	Banana	Costa Rica, Coto	1958
169	2	D	*Heliconia*	Colombia	1961
170	2	D	*Heliconia*	Colombia	1961
171	2	D	*Heliconia*	Colombia	1961
172	2	D	*Heliconia*	Colombia	1961
173	2	D	*Heliconia*	Colombia	1961
175	2	SFR	Plantain (Chato)	Colombia	1961
176	2	SFR	Plantain (Chato)	Colombia	1961
177	2	SFR	Plantain (Chato)	Colombia	1961
178	2	SFR	Plantain (Chato)	Colombia	1961
179	2	SFR	Plantain (Chato)	Colombia	1961
180	2	SFR	Plantain (Chato)	Colombia	1961

[a] French plaintain, known as Inguiri in Peru, is *Musa paradisiaca* (AAB Group).
[b] All Peruvian isolates are from sites along the Amazon river or tributaries, Department of Loreto.

to a 10-cm pot in muck soil; only one stem was allowed to develop to a height of about 50 cm for inoculation. Pepper, eggplant, tomato, and tobacco were seeded in vermiculite and transplanted after about 30 days, one to a 10-cm pot containing a soil-sand-muck mixture, then grown for about 30 days before inoculation. *M. balbisiana* germinated best at 28 C in vermiculite, and seedlings were transplanted when about 6 cm tall, one to a 10-cm pot containing muck soil, and were inoculated when 15 cm tall. All plants were irrigated daily with Hoagland's nutrient solution. With the exception of potatoes, all plants were grown in a greenhouse with a minimum temperature of 15 C at night and a maximum of 30 C during the day.

Inoculum was obtained from the 48-hr growth of each isolate on TZC medium without tetrazolium salts to avoid pigment formation. Suspensions were made in distilled water and adjusted to OD 0.5 (10^9 cells/ml) with a Bausch & Lomb "Spectronic 20" colorimeter.

Inoculations were made by the stem puncture technique (19). A drop of the standardized suspension was placed on the axil of the third fully expanded leaf from the top, and the stem was pierced by thrusting a scalpel-tipped dissecting needle downward through the inoculum drop. In the case of *M. balbisiana,* the pseudostem was held horizontally and pierced 2-3 cm above the soil line. Inoculated plants were held in a greenhouse at temperatures ranging from 30-33 C at night and from 30-40 C in the daytime.

Host reactions were recorded on the 4th, 8th, and 12th days after inoculation according to the following index: 1 = healthy; 2 = epinasty, distortion, or browning of inoculated leaves; 3 = wilting of one or two leaves; 4 = wilting of one half the total number of leaves; and 5 = complete wilting.

RESULTS.—*Characteristics of isolates of P. solanacearum.*—Morphological features of individual colonies of all isolates were recorded at intervals during a 48-hr growth period on TZC medium at 32 C. Determinations were made on colonies growing in three separate plates. Colony diam of the four largest isolated colonies were measured by superimposing a ruled scale upon the longest axis of each colony.

On TZC medium, all isolates were smooth and somewhat translucent under transmitted light, but there were differences in size, fluidity, shape, formazan pigmentation patterns, slime deposition, and melanin formation in the presence of 1% L-tyrosine. After 44-48 hr growth, isolates could be differentiated into five different categories (Table 2, Fig. 1).

Isolates of race 1 (category I) could be easily differentiated on a morphological basis from most other isolates; all mechanically-transmitted isolates of race 2 from musaceous hosts (4) belonged to a single category (II), but the insect-transmitted isolates belonged to three distinct categories (III, IV, V). Category III and IV isolates had distinct colony characteristics. The latter's colonies were generally faster growing and more fluidal, and formazan formation in a helical pattern developed rapidly during the 3rd day. Colony morphology was notably constant within these recently isolated Peruvian Amazon isolates of race 2. In contrast, considerable variation occurred in cultures of Colombian race 2 plantain isolates (Category V), subcultures of which resembled isolates of both categories III and IV. A subculture of isolate 70 was strikingly similar to category IV isolate 163. Subcultures remained constant after subculturing five times in 10 days.

In three separate tests, all race 1 isolates produced melanin on a tyrosine medium and presumably had high tyrosinase activity, whereas most race 2 isolates had none. A few race 2 isolates, such as Nos. 5, 18, 21, and 164, had low activity, and only one (No. 20) had high activity. The production of tyrosinase by these isolates did not conform to previous observations (1, 17) that isolates from musaceous hosts (race 2) do not produce tyrosinase. Since no isolates of race 2 had tyrosinase activity when freshly isolated, it appears that

TABLE 2. Classification of colony types of *P. solanacearum* obtained on a tetrazolium medium (10) after 44-48 hr incubation at 32 C

Category	Colony shape and texture	Formazan formation	Colony size mm	Race	Strain	Melanin formation[a]	Isolate No.
I	Elliptical, smooth slime deposition	Intense toward center	2.0-4.0	1	T	High	25, 26, 30, 130
				2	H	Low	138, 155
II	Elliptical, lacelike slime deposition	Slight toward center	1.6-3.3	2	B	Low	2, 135, 166, 167
				2	D		5, 11, 169, 170, 171, 172, 173
				2	R		6, 7
III	Near round, slight slime deposition, smooth	Absent or slight	0.7-2.3	2	SFR	Low	18, 20, 21, 164, 176, 180
IV	Near round, fluidal, faint lacelike slime deposition	Absent or faint-pink in a helical pattern	1.3-2.6	2	Amazon	Low	127, 128, 129, 131, 156, 157, 158, 159, 160, 162, 163
V	Variable, with characteristics of both categories III and IV	Absent or slight	0.7-2.6	2	SFR	Low	70, 71, 175, 177, 178, 179

[a] 0.1% (w/v) L-tyrosine present in medium.

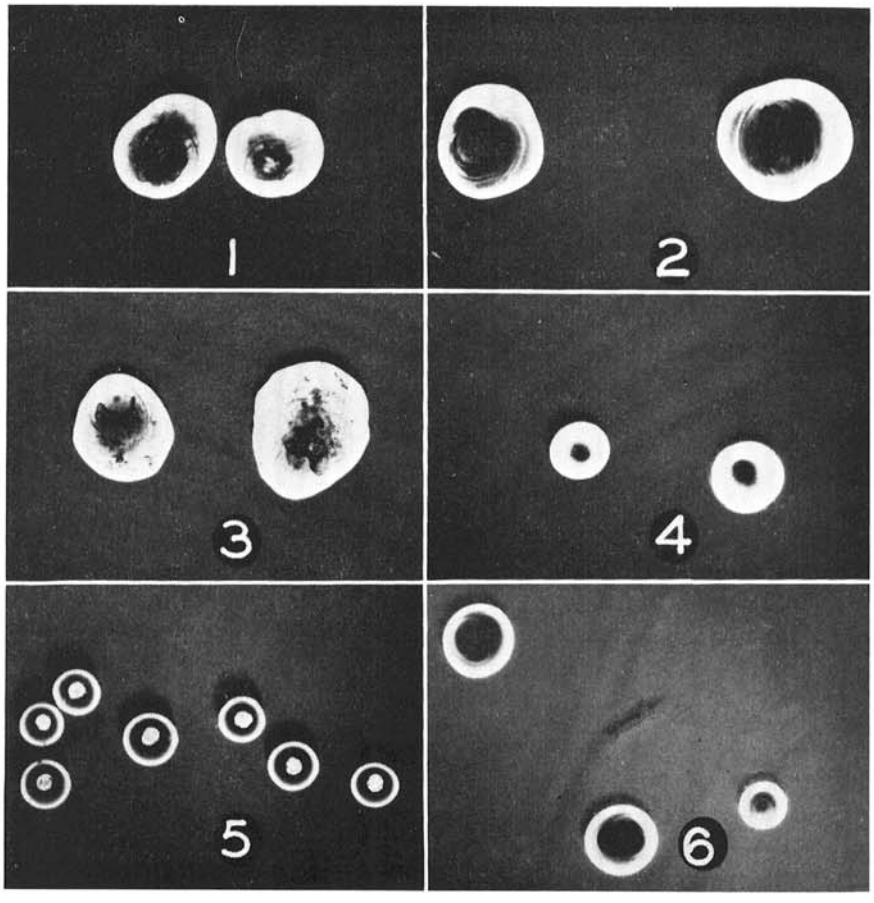

Fig. 1. Typical colony morphology on TZC agar of selected isolates of *Pseudomonas solanacearum* after 60-hr incubation at 32 C. **1)** Isolate 25, race 1, strain T. **2)** Isolate 2, race 2, strain B. **3)** Isolate 6, race 2, strain R. **4)** Isolate 21, race 2, strain SFR. **5)** Isolate 160, race 2, strain from Peruvian Amazon. **6)** Isolate 128, race 2 strain from Peruvian Amazon (×10).

this characteristic may be acquired in vitro over long periods of storage. Two cultures of isolate 20(41), for instance, were originally tyrosinase-negative, but, after storage for 6 years, one culture exhibited high tyrosinase activity while the other had only low activity. The cultures also differed in pigmentation pattern and intensity on TZC medium.

Pathogenicity tests.—Isolates representative of each of the five categories listed above were selected for inoculation experiments, as follows: I) 25, 130, 138; II) 11 and 135; III) 21; IV) 163; and V) 70. Five of each of the test plants were inoculated with each isolate in three separate tests. Symptoms began to develop on the 2nd and 3rd day after inoculation. *Musa balbisiana* plants wilted and died within 4 to 8 days when inoculated with all race 2 isolates except Nos. 138 and 11 (Table 3). The former isolate gave inconsistent results, since about half the plants always escaped infection while the latter produced initial symptoms including tipburn, leaf distortion, and slight wilting, followed by stunted growth and occasional death.

Eggplant wilted rapidly when inoculated with race 1 isolates, particularly with isolate 130. All plants died within 4 to 12 days after inoculation. During the same period, all race-2 isolates caused only mild symptoms characterized by distortion of new leaves that grew unevenly and became sickle-shaped.

Tobacco plants developed symptoms slowly when inoculated with race 1 isolates. Isolate 25 caused leaf distortion within 4 days, wilting within 8, and death of plants within 12. Of the race 2 isolates, only Nos. 70 and 163 caused slight wilting initially, but the tobacco plants subsequently recovered; no remaining isolates caused wilt, although some caused slight stunting.

Pepper was consistently susceptible only to isolates 70, 163, and 130. Most plants died within 6-12 days. Other isolates caused wilting only of the inoculated leaf or slight inhibition of internode elongation. Most pepper varieties have been considered moderately or highly resistant to race 1 isolates in the past (9).

Potato was highly susceptible to isolates 25, 130, 70, and 163, most plants dying within 4-12 days. Most plants were affected by isolate 11, but a few showed no symptoms. Isolates 135, 21, and 138 gave highly variable results on potato.

Tomato was susceptible to all race 1 and race 2 isolates tested. Symptoms of epinasty developed to varying degrees in response to all isolates within 3 days.

TABLE 3. Susceptibility of test plants to selected isolates of *Pseudomonas solanacearum*, based on disease indices 12 days after inoculation.

Isolate no.	Race	Pathogenicity ratings[a] on hosts					
		Musa balbisiana	Eggplant	Tobacco	Pepper	Potato	Tomato
25	1	L	H	M	M	H	H
130	1	L	H	L	H	H	H
135	2	H	M	L	L	M	M
21	2	H	M	L	L	M	M
70	2	H	M	L-M	H	H	H
163	2	H	L	L-M	H	H	H
11	2	M-H	L	L	L	H	M
138	2	L-H	L	L	L	M	M
CK		0	0	0	0	0	0

[a] H = high (index 4.1-5.0); M = medium (index 2.6-4.0); L = low (index 1.1-2.5); 0 = none (index 1.0). Paired rating indicates inconsistent results covering the greater index range.

Isolates 70, 130, and 163 caused rapid wilt, plants collapsing in 4-8 days, but isolates 11 and 135 killed only a small number of plants, and isolates 21 and 138 rarely caused death in 12 days.

Characteristic symptoms obtained after inoculation with six of the isolates used are shown in Fig. 2. A summary of the interactions is given in Table 3.

The high virulence to tobacco of plantain isolates, 163 from Peru and 70 from Colombia, and the report that a Peruvian plantain isolate was pathogenic to tobacco (15), led to a comparative study of three isolates (No. 158, 159, 163) from the upper, middle, and lower Peruvian Amazon basin, and a typical race 1 isolate (No. 25). Tobacco was affected inconsistently by the three Peruvian isolates. Occasional plants had unilateral wilting affecting part of a leaf or up to three entire leaves, but most plants recovered. Race 1 isolate 25, however, was consistently more virulent to tobacco. This isolate has been used extensively for inoculations on tobacco for many years. *M. balbisiana*, on the other hand, was consistently killed by all race 2 isolates, but was immune to isolate 25, confirming all previous tests with race 1 isolates.

Because eggplant was highly susceptible to race 1 isolates 25 and 130, and is susceptible to several race 1 isolates (11), it seemed possible that this plant might be a better differential for this race than tobacco. Eggplant was the only solanaceous host consistently killed by all race 1 isolates 8 days after inoculation (Table 4).

DISCUSSION.—Colony morphology on a tetrazolium medium appears to be useful in differentiating certain races and strains of *P. solanacearum*. After 48-hr incubation the faster-growing, elliptical, fluidal colonies (categories I and II) were typical of all race 1 isolates and of strains B, D, R, or H of race 2. Since colonies of race 2 isolates, with the exception of strain H, had a typical lacelike growth pattern, as compared with the uniform, solid colony appearance of race 1, differentiation of the two races was possible. Slow-growing, round to elliptical, slightly fluidal colonies generally belong to the SFR strain of race 2. Race 3 isolates, not included in this report, grew even more slowly in this medium. The Peruvian isolates from musaceous hosts could be distinguished from the SFR strain (4) from Central America in that they were more fluidal, larger, and developed red formazan pigmentation in a characteristic helical pattern.

Melanin formation on a tyrosine medium was a useful complement to colony appearance in determining races. Race 1 isolates turned the medium brown very rapidly, and presumably had high tyrosinase activity. Fresh race 2 isolates had no tyrosinase activity, and race 3 isolates have been reported to have low tyrosinase activity (18).

The results of test plant inoculations indicated that *M. balbisiana* is a reliable differential host for race 2, whereas eggplant is the best differential for race 1 isolates. *M. balbisiana* was highly susceptible to the

TABLE 4. Susceptibility of test plants to race 1 isolates of *Pseudomonas solanacearum*, based on disease indices 8 days after inoculation

Isolate no.	Host	Site	Pathogenicity ratings[a] on hosts			
			Eggplant	Tobacco	Pepper	Tomato
25	Tomato	North Carolina, USA	H	L	M	M
130	Tomato	Peru	H	L	H	H
26	Tomato	Georgia, USA	H	L	M	M
30	Tomato	Trinidad	H	L	M	H
118	Tomato	Costa Rica	H	L	M	H
143	Tomato	Queensland, Australia	H	M	H	H
8	*Eupatorium*	Costa Rica	H	M	H	H
154	Tobacco	Colombia	H	M	L	H
27	Tobacco	Florida, USA	H	M	M	M
147	Tobacco	Queensland, Australia	H	L	H	H
CK			0	0	0	0

[a] H = high (index 4.1-5.0); M = medium (index 2.6-4.0); L = low (index 1.1-2.5); 0 = none (index 1.0).

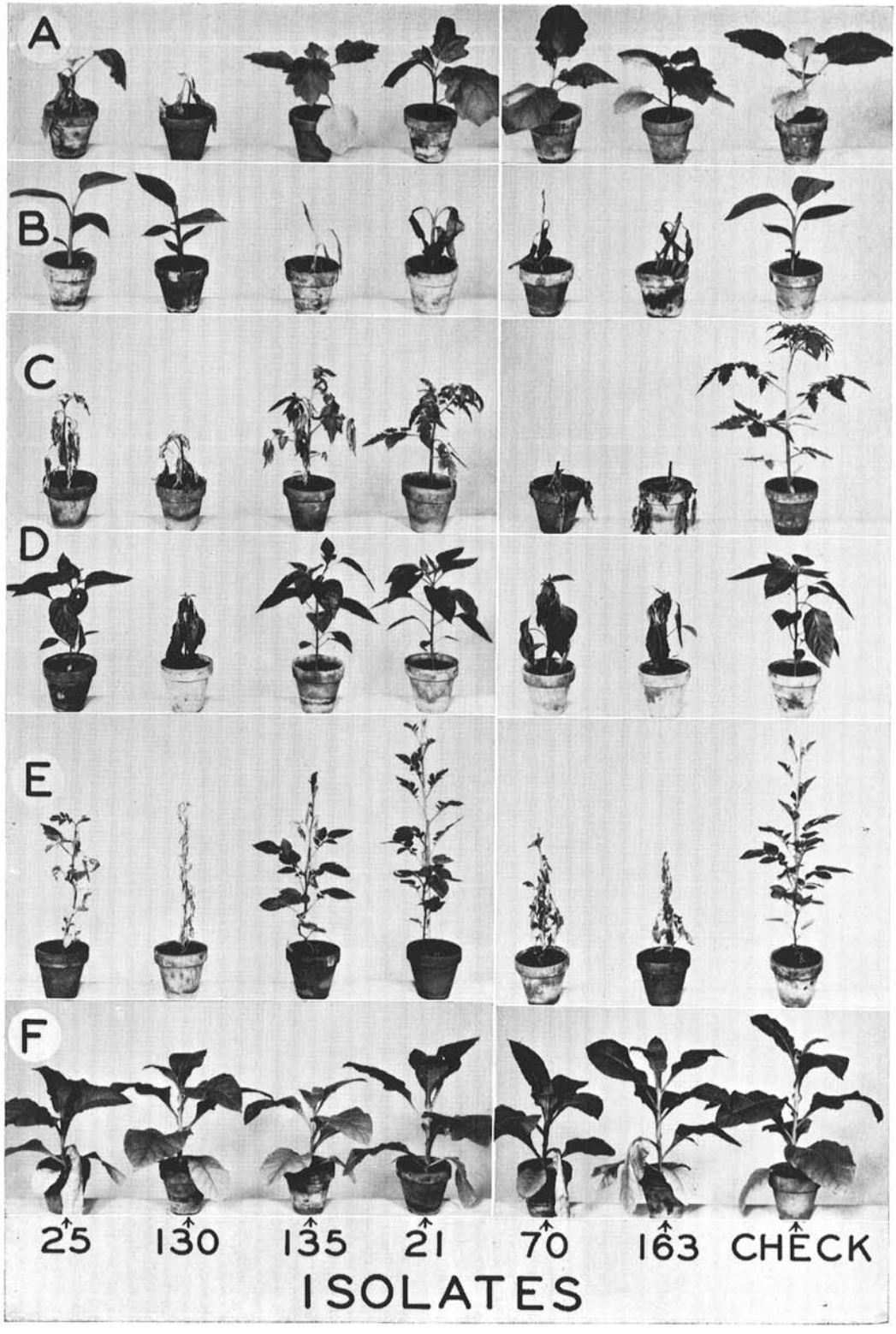

Fig. 2. Typical symptoms obtained on **A)** eggplant; **B)** *Musa balbisiana*; **C)** tomato; **D)** pepper; **E)** potato; and **F)** tobacco, 8 days after inoculation with different isolates of *Pseudomonas solanacearum*. Origin of isolates as follows: 25 (tomato, U.S.A.), 130 (tomato, Peru), 135 (banana, Honduras), 21 (banana, Honduras), 70 (plantain, Colombia), and 163 (plantain, Peru); classification as indicated on Table 1.

D strain from Heliconias and to the H strain that affects plantain but not bananas. On the other hand, *M. balbisiana* was immune to all race 1 isolates. Eggplant was consistently and highly susceptible to all race 1 isolates from both North and South America (Fig. 2, Tables 3, 4). Tobacco, the differential host for race 1 used successfully for many years in North America, was not susceptible to a race 1 isolate from the Peruvian Amazon basin, and was susceptible to race 2 isolates from the same region (Table 3).

There was a remarkable similarity in the reaction of test plants to race 2 isolates from plantains in Colombia and Peru. Isolates from both regions killed tomato, potato, and pepper plants rapidly (Fig. 2), and were pathogenic to tobacco, as already noted. The similarity in pathogenicity of these isolates, and the remarkable similarity in appearance of a subculture from isolate 70 (Colombia) to Peruvian isolates as previously noted, suggest that these may have a common origin. Since the Peruvian epiphytotic of Moko disease on plantains appears to be more recent than the Colombian, and these two countries have a common boundary in the Amazon basin, it seems possible that the disease has spread from Colombia into Peru. The recent origin of the Peruvian epiphytotic is further substantiated by our recent observation that the disease is spreading upstream along the Amazon tributaries at a rate of about 22 km each year, having reached the Marañon River in 1966 and the Ucayali River in 1968. The striking similarity in colony appearance of the 11 isolates obtained along the entire length of the Amazon basin in Peru, and the similar reaction of *M. balbisiana* and tobacco to three of these isolates, suggests a single source for the epiphytotic that has been developing for approximately 10 years. Little genetic diversity appears to have developed in that short a period.

The Peruvian isolates of *P. solanacearum* from musaceous hosts resemble the SFR strains from Central America, and are also insect-disseminated, but differ in pathogenicity to certain hosts. They can be readily distinguished from the SFR strains in culture. These isolates from the Peruvian Amazon basin constitute a separate strain, for which the letter A is proposed to reflect the presence of this strain in the Amazon River basin.

It should be pointed out that isolates of *P. solanacearum* stored for long periods do undergo change in colony morphology and in physiological characteristics such as tyrosinase activity. For instance, category V isolates, originally uniform, had two preponderant types of colonies after several years' storage in vitro, some types corresponding to categories III and others resembling those of category IV. These findings stress the problems of any classification scheme based on isolates which have been stored as water suspensions. It is hoped that the studies with isolates maintained by lyophilization will give clearer answers.

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