A Bacterial Leaf Spot Caused in Yam Bean by *Pseudomonas syringae* pv. *phaseolicola*

Robert G. Birch, A. M. Alvarez, and Suresh S. Patil

Graduate student, assistant plant pathologist, and professor, respectively. Department of Plant Pathology, University of Hawaii, Honolulu 96822.

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This article reports the results of investigations on a bacterial leaf spot previously recognized by A. P. Martinez, A. C. Hayward, and I. W. Buddenhagen who kindly provided some of the original strains of the pathogen.

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ABSTRACT

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A bacterium causing leaf spot of yam bean, *Pachyrrhizus erosus*, in Hawaii was identified as *Pseudomonas syringae* pv. *phaseolicola* on the basis of in vitro biochemical properties; symptoms induced in yam bean, Red Kidney bean, and detached bean pods; remission of toxin-induced systemic symptoms at elevated temperatures and behavior in a microbial assay for antimetabolic toxins. It is distinct from *Pseudomonas syringae* pv. *syringae* and pv. *tabaci* in each of these aspects. Also, the phytotoxin produced by the yam bean pathogen in culture and in the plant strongly inhibits ornithine carbamoyltransferase activity, which is typical of pv. *phaseolicola*. Yam bean may be a significant alternative host for the bean halo-blight pathogen in tropical regions.

Additional key words: tropical legumes.

A bacterial leaf spot of yam bean, *Pachyrrhizus erosus* (L.) Urb., with symptoms consisting of small brown or water-soaked spots surrounded by a chlorotic or yellow area (Fig. 1), has been observed occasionally in Hawaii since 1969. However, no record of any bacterial disease of yam bean has been found in the literature. The observed symptoms are similar to those of halo blight of common bean (*Phaseolus vulgaris* L.) (8) caused by *P. syringae* pv. *phaseolicola* (ISPP List, 1980), syn. *Pseudomonas phaseolicola* (Burkh.) Dowson.

The recorded host range of pv. *phaseolicola* is restricted to *Phaseolus* spp. (1,3,17,23), *Macroptilium altropurpureum* (siratro) (9), *Glycine* spp. (9,23), *Pueraria thunbergiana* (kudzu vine) (1,3), and *Dolichos* sp. (potato weed, NCPPB 1647), and there is a doubtful record on *Vigna sinensis* (1). In Hawaii, pv. *phaseolicola* has been recorded only on *P. vulgaris*. Other bacterial nomenspecies which may incite similar symptoms on some bean species are *P. syringae* pv. *glycinea* (23), pv. *tabaci* (1,3,21), pv. *syringae*, and *Xanthomonas phaseoli* (1,3).

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The purpose of this study was to identify the yam bean (YB) pathogen by a combination of plant inoculations, biochemical tests, and toxin assays.

MATERIALS AND METHODS

Strains. Isolations of the yam bean pathogen were made from yam bean leaves showing symptoms of halo blight. Bacterial strains used in comparative experiments were *P. syringae* pv. *phaseolicola* HB-20, HB-33, HB-36 (supplied by M. N. Schroth, University of California, Berkeley), G50 and G50 tox$^-$ (19); pv. *glycinea* R-6 (supplied by N. T. Keen, University of California, Riverside), pv. *syringae* ATCC 19310, pv. *tabaci* ICPB PT5, pv. *tomato* ICPB PT111, pv. *lachrymans*, and *P. fluorescens*. *Escherichia coli* K-12 (N100) was supplied by N. J. Panopoulos, University of California, Berkeley.

Bacteriological characterization. Nutritional and biochemical tests (15) were performed on 18 strains that showed similar colony appearance on triphenyltetrazolium chloride medium (10) when isolated from yam bean. Three to five replicates of each test were carried out with each bacterial strain. Tests for fluorescent pigment production, presence of oxidase and arginine dihydrolase,

production of levan, and hydrolysis of aesculin were conducted according to Lelliott et al (13). For testing utilization of substrates, we employed the solid mineral base medium of Palleroni and Doudoroff (16). Filter-sterilized carbon sources were added to a final concentration of 0.1% before the plates were poured. Utilization of KNO_3 as sole nitrogen source was tested on the solid mineral base medium containing 0.2% glucose but no NH_4Cl.

Bacterial cell dimensions were determined on safranin and Gram-stained smears from 48-hr cultures on King's medium B (KMB) (11). Motility and presence of flagella were determined by the method of Mayfield and Inniss (14).

Pathogenicity. Strains were first screened for pathogenicity on yam bean and *Phaseolus vulgaris* 'Red Kidney' in the greenhouse (20–30 C) and later in a controlled environment chamber (20-22 C). Plants were inoculated by lightly spraying cell suspensions on young trifoliolate leaves, followed by a 4-hr period in a humid chamber. For comparative pathogenicity tests on yam bean, *P. vulgaris* cultivars Red Kidney and Red Mexican UI-3, inoculum was sprayed onto the undersides of recently unfolded primary leaves at 7–14 kPa to obtain uniform water-soaking, followed by 4 hr in a humid chamber at 24 C. Inocula consisted of cell suspensions (from 24-hr cultures) adjusted to approximately 10^8 cells per milliliter. Since YB strains differed somewhat in the severity of symptoms induced on yam bean and Red Kidney bean, three strains (A192-1, A192-2, and A192-4), which caused the entire range of pathogenic responses, were selected for further studies.

TABLE 1. Comparison of bacteriological properties of bacterial strains from yam bean with three pathovars of *Pseudomonas syringae*

Properties	Reactions[a] of strains or pathovars: Yam bean strains[b]	pv. *phaseolicola* HB-33	pv. *phaseolicola* HB-36	pv. *tabaci*	pv. *syringae*
Growth on					
L(+)-tartrate	−	−	−	+	−
D(−)-xylose	−	−	−	+	+
D-sorbitol	−	−	−	+	+
meso-erythritol	−	−	−	+	+
i-inositol	−	−	−	+	+
D-mannitol	+	−	−	+	+
Hydrolysis of aesculin	−	−	−	+	+
Use of 0.1% KNO_3 as sole N source	−	−	−	+	+
Pitting of sodium polypectate pH 5.0	+	+	+	−	−
pH 8.2	−	−	−	−	−
Action on litmus milk	Alk	Alk,R	Alk	D	D

[a] Alk = alkaline reaction, R = reduction, D = digestion (peptonization), + = positive reaction, and − = negative reaction.
[b] Yam bean strains A192-1, A192-2, and A192-4 (which reacted similarly).

Additional tests. Ability to cause pitting in polypectate gels at pH 5.0 and pH 8.2 was tested on the media of Hildebrand (7). Reaction of rehydrated Difco Bacto litmus milk was recorded after incubation at 28 C for 25 days.

Detached bean pods (cultivar Hawaiian Wonder) were surface sterilized by swabbing with 70% ethanol, then prick-inoculated with cells from 48-hr colonies on KMB. Inoculation sites were sealed with paraffin and the pods were incubated in a humid chamber at 24 C for 3 days before the results were recorded. Hypersensitive reaction on tobacco leaves (12) was tested on *Nicotiana glutinosa* and *N. tabacum* var. *xanthi*.

Selected YB strains, pv. *phaseolicola* HB-33 and HB-36, pv. *syringae*, and pv. *tabaci*, were tested for inhibition of *E. coli* K-12 in an agar overlayer (25). Cultures of the test strains on minimal agar were preincubated at 18 and 31 C for 13 hr before 10^7 cells per milliliter of *E. coli* K-12 were added in the overlayer. Diameter of inhibition of *E. coli* K-12 in the overlayer was measured after an additional 8 hr incubation at 37 C. Five replicates of each strain were tested at each preincubation temperature on three occasions. In addition, the assay included: pv. *glycinea*, pv. *tomato, pv. lachrymans, P. fluorescens,* and pv. *phaseolicola* strains G50, G50 tox^-, and HB-20, a naturally occurring nontoxigenic strain.

Leaves of yam bean and Red Kidney bean were detached 4 days after infiltration with bacterial suspensions of the YB strains or pv. *phaseolicola* strain G50, then extracted, diluted to 1:100 fresh leaf weight, and tested for ornithine carbamoyltransferase (OCT) inhibitory activity as described previously (6,26). Culture filtrates of YB strain A192-4 were prepared as described previously (20) and applied in 0.02 M ammonium bicarbonate to a 1.2×92-cm column of Sephadex G15 (also equilibrated with 0.02 M ammonium bicarbonate). Fractions were tested for OCT inhibitory activity (26).

RESULTS

The 18 YB strains reacted similarly in nutritional and biochemical tests and showed all characteristics of Group Ia in the determinative scheme of Lelliott et al (13) for phytopathogenic fluorescent pseudomonads. They resembled pv. *phaseolicola* in that they did not reduce nitrate, produce indole or H_2S, liquify gelatin, hydrolyze starch or aesculin. Acid was produced oxidatively within 4 days from fructose, galactose, glucose, and glycerol. No acid was produced in 20 days on lactose or maltose. Growth occurred in 2 and 3%, but not 4% NaCl medium. No lipolytic activity occurred on Tween-80 agar after 2 days. On litmus milk, all pv. *phaseolicola* and YB strains except two produced an alkaline reaction in 2 wk. Inhibition zones in antibiotic sensitivity tests were similar to known strains of pv. *phaseolicola* (19).

In further tests the three selected YB strains behaved uniformly, and differed from pv. *tabaci* and pv. *syringae* in substrate utilization, hydrolysis of aesculin, utilization, of KNO_3 as N source, ability to cause pitting of polypectate, and action on litmus

TABLE 2. Results of plant inoculations with bacterial strains from yam bean and three pathovars of *Pseudomonas syringae*

Plant	Plant reactions[a] to strains or pathovars: Yam bean strains A192-1	Yam bean strains A192-2	Yam bean strains A192-4	p.v. *phaseolicola* HB-33	p.v. *phaseolicola* HB-36	pv. *tabaci*	pv. *syringae*
Phaseolus vulgaris 'Red Kidney'	+	+	++	++	++	−	−
Phaseolus vulgaris 'Red Mexican UI-3'	−	−	−	−	+	−	−
Pachyrrhizus erosus (yam bean)	+	+	++	++	++	−	−
Detached pods							
P. vulgaris 'Hawaiian Wonder'	w	wn	w	W	W	*N*	N N

[a] Leaf reactions; + = water-soaking only, ++ = water-soaking and systemic chlorosis, and − = hypersensitive necrosis. Pod reactions: w = 50 to 90% sites water-soaked; wn = 90 to 100% sites water-soaked, some with a brownish necrotic surface layer; W = 100% sites water-soaked; and N = 90 to 100% sites necrotic.

milk (Table 1). The organism was indistinguishable from the tested pv. *phaseolicola* strains except for its ability to utilize D-mannitol as sole carbon source for growth.

A comparative study of pathogenicity of the three YB strains and strains of pv. *phaseolicola*, pv. *syringae*, and pv. *tabaci* revealed that only the YB strain A192-4 and the pv. *phaseolicola* strains produced systemic symptoms in inoculated yam bean and Red Kidney bean plants (Table 2). Water-soaked and brownish lesions surrounded by chlorotic halos occurred at primary infection sites on young trifoliolate leaves, with chlorosis and distortion of subsequently emerging trifoliolate leaves (Fig. 1). YB strains A192-1 and A192-2 caused persistent water-soaking of inoculated leaves of yam bean and Red Kidney bean but did not cause chlorosis or systemic symptoms. In yam bean, as in Red Kidney bean, primary and trifoliolate leaves became increasingly resistant as they became older. Plants recovered from chlorotic symptoms when maintained in the greenhouse at 25–30 C. At the cell concentration applied, pv. *syringae* and pv. *tabaci* caused hypersensitive necrosis in inoculated yam bean and Red Kidney bean plants. *Pseudomonas syringae* pv. *phaseolicola* strains HB-36, G50, and G50 tox⁻ caused water-soaking of inoculated primary leaves of bean cultivar Red Mexican UI-3, whereas strain HB-33, the three tested YB strains, and other phytopathogenic pseudomonads all caused hypersensitive necrosis.

Bean pods inoculated with pv. *phaseolicola* developed water-soaked lesions 2–5 mm in diameter after 3 days incubation. Necrotic, brownish lesions resulted at sites inoculated with pv. *tabaci* and pv. *syringae*. All YB isolates produced water-soaked lesions at most inoculation sites, but lesions often were less than 3 mm in diameter (Table 2).

In the *E. coli* microbial assay (Table 3), pv. *phaseolicola* strains HB-33, HB-36, and YB strain A192-4 produced large clear zones of inhibition of *E. coli* K-12 after preincubation at 18 C. In some replicates the inhibition zones were slightly turbid, but small, clear inner halos were apparent within the large zones around colonies of strains HB-33 and A192-4. With YB strains A192-1 and A192-2, some replicates produced only small halos while others caused no inhibition zones. *Pseudomonas syringae* ATCC 19310 produced turbid inhibition zones, and pv. *tabaci* PT5 produced a small clear zone (Fig. 2). After preincubation at 31 C, pv. *phaseolicola* and YB strains either produced no inhibition zones or only small halos (Fig. 3). Incubation at 31 C did not change results with pv. *syringae* whereas with pv. *tabaci* larger zones were produced at 31 C than at 18 C. In subsequent trials pv. *phaseolicola* strain G50 behaved similarly to other pv. *phaseolicola* strains and to YB strain A192-4, while G50 tox⁻ and HB-20 resembled A192-1 and A192-2. *Pseudomonas fluorescens* caused no inhibition zone, pv.

TABLE 3. Inhibition of *Escherichia coli* K-12 in overlaid plates by bacterial strains from yam bean (YB), *Pseudomonas syringae* pathovars, and *P. fluorescens* preincubated at 18 and 31 C on a minimal agar

Pathovar or strain	Preincubation temperature 18 C	31 C
Strains:		
YB A192-1	6.8 ± 0.8 d[y]	0.8 ± 0.8 e
YB A192-2	7.7 ± 1.0 d	1.4 ± 0.6 e
YB A192-4	21.0 ± 0.9 b	1.1 ± 0.7 e
Pathovars:		
phaseolicola HB-33	26.1 ± 0.4 a	4.1 ± 1.2 d
phaseolicola HB-36	26.9 ± 0.5 a	0.0 ± 0.0 e
phaseolicola G50	26.5 ± 0.0 a	1.7 ± 1.7 e
phaseolicola G50 tox⁻	3.7 ± 1.0 e	1.0 ± 0.6 e
phaseolicola HB-20	2.3 ±0.3 ef	1.7 ± 0.9 e
tabaci ICPB PT5	3.7 ± 0.7 e	7.7 ± 1.0 c
syringae ATCC 19310[z]	27.1 ± 0.4 a	28.8 ± 0.5 a
tomato ICPB PT111	20.5 ± 0.6 b	0.0 ± 0.0 e
glycinea R-6	26.2 ± 2.6 a	28.7 ± 0.7 a
lachrymans	11.3 ± 0.4 c	11.5 ± 0.8 b
P. fluorescens	0.0 ± 0.0 f	0.0 ± 0.0 e

[y]Mean diameter of inhibition in millimeters ± the standard error of the mean. Column means not followed by the same letter differ significantly, $P = 0.05$, as determined by Duncan's multiple range test.

[z]Inhibition zones produced by pv. *syringae* were more turbid than those caused by pv. *phaseolicola*.

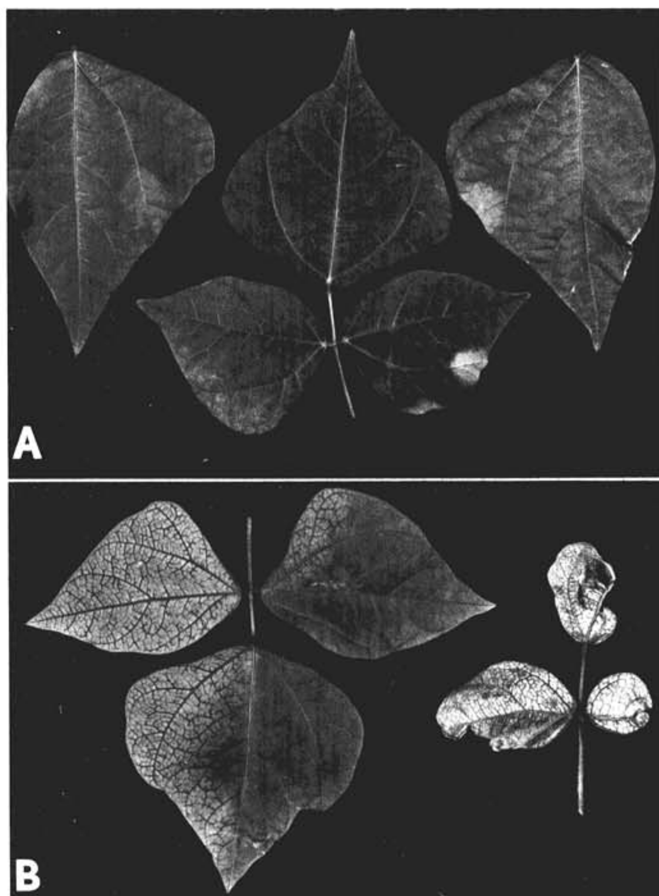

Fig. 1. Yam bean leaves showing chlorotic lesions at primary infection sites of **A,** strain A192-4 and **B,** systemic chlorosis and distortion following infection by strain A192-4.

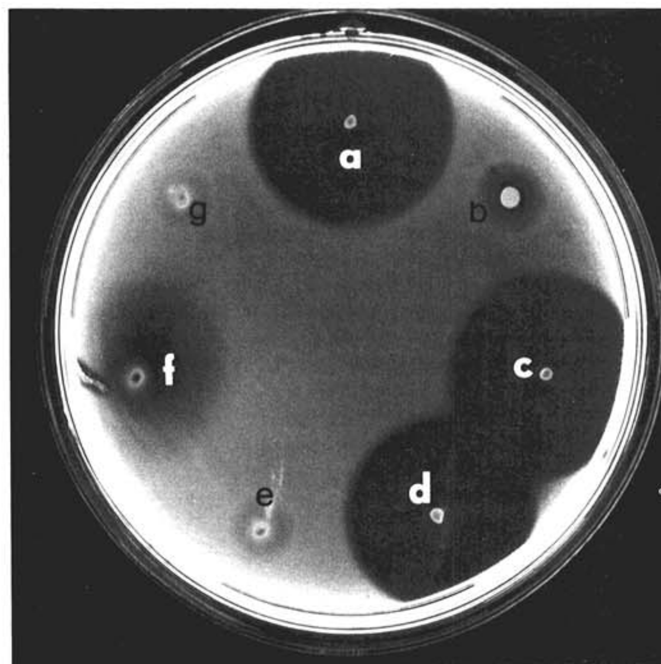

Fig. 2. Growth inhibition of *Escherichia coli* K-12 by yam bean (YB) strains and *Pseudomonas syringae* pathovars, preincubated at 18 C. Colonies a, pv. *phaseolicola* HB-33; b, pv. *tabaci*; c, pv. *phaseolicola* HB-36; d, YB strain A192-4; e, YB strain A191-2; f, pv. *syringae*; and g, YB strain A192-1.

lachrymans caused turbid zones at 18 and 31 C, pv. *tomato* caused inhibition zones like those of pv. *phaseolicola* or pv. *syringae* only at 18 C, and pv. *glycinea* produced similar zones at both 18 and 31 C (Table 3).

Extracts of yam bean and Red Kidney bean leaves inoculated with pv. *phaseolicola* strain G50 and YB strain A192-4 caused inhibition of bean OCT, whereas extracts of leaves inoculated with YB strains A192-1 and A192-2 caused no inhibition of OCT activity. Sensitivity of the enzymatic assay was similar for phaseotoxin from bean leaves and culture filtrates, in contrast with the *E. coli* assay, which required approximately 100-fold higher concentrations of toxin from inoculated plants than from culture.

After passage through a Sephadex G15 column, extracted culture filtrates of YB strain A192-4 yielded a single peak of OCT inhibitory activity at a K_{av} (0.25) corresponding to that of phaseotoxin from cultures of pv. *phaseolicola*. Toxin production by strain A192-4 declined during prolonged maintenance in culture, but was restored when the strain was reisolated from inoculated bean leaves.

DISCUSSION

The YB strains resembled pv. *phaseolicola* and were distinct from pv. *tabaci* and pv. *syringae* in biochemical and nutritional tests that distinguished these pathovars (2,7,13,15,22,23). Although YB strains differed from pv. *phaseolicola* strains used in the present study in D-mannitol utilization, several other strains of pv. *phaseolicola* are capable of utilizing mannitol (22,23).

Phytotoxin-producing and nonproducing strains of the YB pathogen occur, as they do in pv. *phaseolicola*. Toxigenic and nontoxigenic YB strains, and similar pv. *phaseolicola* strains, induce the same symptoms, including temperature dependence of chlorotic symptoms (8). The water-soaked lesions induced by YB strains in detached pods are typical of pv. *phaseolicola* (24). The smaller lesion size caused by YB strains relative to the pv. *phaseolicola* strains tested suggests that YB strains are less aggressive on the bean cultivar used.

The distinct phytotoxins produced by pv. *phaseolicola*, pv. *tabaci*, and pv. *syringae* (18) might be useful as determinative criteria for these bacteria, if simple, rapid, and specific tests for the phytotoxins were available. A rapid microbiological assay for toxin(s) produced by pv. *phaseolicola* has been described (25).

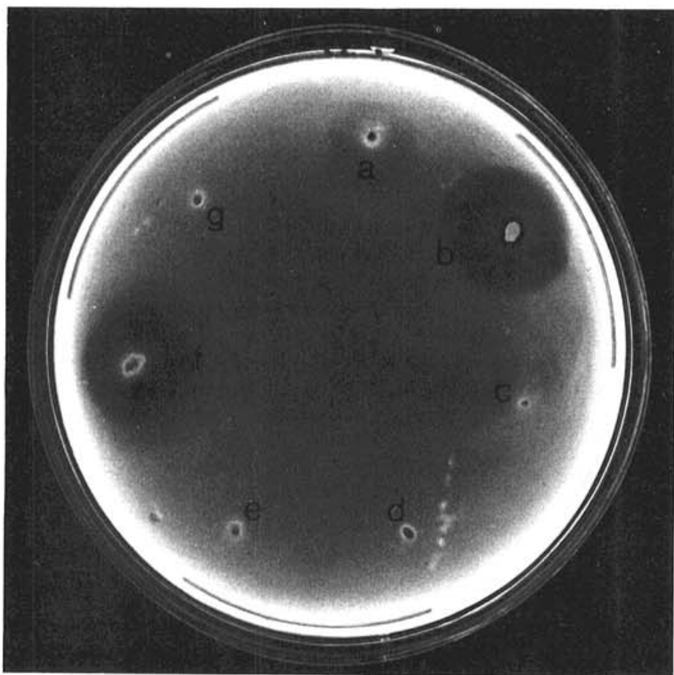

Fig. 3. Growth inhibition of *Escherichia coli* K-12 by yam bean (YB) strains and *Pseudomonas syringae* pathovars, preincubated at 31 C. Colonies a, pv. *phaseolicola* HB-33; b, pv. *tabaci*; c, pv. *phaseolicola* HB-36; d, YB strain A192-4; e, YB strain A192-2; f, pv. *syringae*; and g, YB strain A192-1.

In our investigation, YB strain A192-4 caused inhibition of *E. coli* K-12 similar to that caused by known toxigenic strains of pv. *phaseolicola*. The small inhibition zones produced by nontoxigenic pv. *phaseolicola* strains, and by some toxigenic strains at 31 C, suggest that diffusible products other than phytotoxins also inhibit *E. coli* in the assay. Moreover, inhibition zones caused by some other toxigenic pseudomonads resembled those of pv. *phaseolicola*. Gasson (4,5) also demonstrated that other toxin-producing phytopathogenic pseudomonads inhibit *E. coli*. Thus, caution is required in interpreting the results of the *E. coli* bioassay, especially as a determinative test. The mechanisms of inhibition of *E. coli* by dissimilar phytotoxins apparently differ, as evidenced by reversal of inhibition zones by different amino acids (5,25). It may, therefore, be possible to devise variations of the technique specific for particular phytotoxins, by altering the assay conditions.

Results of the microbial assay obtained by using overlaid cultures were consistent with those of the enzymatic bioassay on extracts from inoculated bean leaves, confirming phytotoxin production by YB strain A192-4 and no phytotoxin production by strains A192-1 and A192-2. The enzymatic bioassay demonstrated potent inhibition of OCT by the phytotoxin from the YB pathogen, which is characteristic of pv. *phaseolicola* (20). The nontoxigenic YB strains may represent variants selected in culture, since toxin production by strain A192-4 declined during maintenance in culture. We have observed similar decline in toxin production by some pv. *phaseolicola* strains (*unpublished*). Restored levels of toxin production in such strains reisolated from bean leaves suggests that selection in the host plant favors toxin-producing cells.

On the basis of biochemical features, plant reactions, and phytotoxin characteristics, we conclude that the pathogen causing leaf spot of yam bean is pv. *phaseolicola*. This is the first report of *Pachyrrhizus erosus* as a host of pv. *phaseolicola*. Yam bean may be significant as an alternative host for the bean halo-blight pathogen in tropical regions where this perennial vine is widely cultivated as a food crop.

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