

Moko Disease: Atypical Symptoms Induced by Afluidal Variants of *Pseudomonas solanacearum* in Banana Plants

A. C. Woods

Associate pathologist, Plant Pathology Department, Vining C. Dunlap Laboratories, United Fruit Co., La Lima, Honduras, Central America.

The author gratefully acknowledges the technical assistance of Leonidas Navarro and Ramón L. Suazo.

Accepted for publication 4 February 1984.

ABSTRACT

Woods, A. C. 1984. Moko disease: Atypical symptoms induced by afluidal variants of *Pseudomonas solanacearum* in banana plants. *Phytopathology* 74: 972-976.

Isolations were made from 1,476 moko-diseased banana plants in Honduras, and the bacteria obtained were classified according to colony morphology. Large fluidal (F) colony types were found in 73% and small fluidal round (SFR) colony types in 10% of the cases. Small afluidal variant (AFV) colony types were associated with either F or SFR colony types in 41% of the cases and occurred alone in 17% of the cases. AFV isolates were morphologically indistinguishable from spontaneous afluidal mutants produced after prolonged still broth culture or storage in water. When inoculated into potted or mature field plants by methods simulating wound infection during routine cultivation, all three colony types incited disease, AFV being the least aggressive. Symptoms typical of moko disease developed in field plants inoculated with F or SFR bacteria. AFV bacteria

never caused external symptoms in mature wound-inoculated plants, but suckers arising from the same corms often became stunted and showed discoloration and necrotic areas. Other plants remained symptomless even though invasion by AFV bacteria into corm tissue was evident. Streptomycin-resistant AFV types occurred in 78% of diseased corms from suckers of banana plants inoculated 28 wk previously with a streptomycin-resistant F strain. An average of 18.1% of colony-forming units recovered was of the AFV type. Ten AFV isolates selected from F-inoculated mats were injected into small banana plantlets. All developed wilt and necrosis, although at a reduced rate compared to the F parent. Results suggest that AFV colony types of *P. solanacearum* have a previously unrecognized potential for causing disease in banana plants.

Additional key words: bacterial wilt, virulence.

Loss of fluidity or of the ability to produce copious extracellular polysaccharide has been correlated with loss of virulence in many phytopathogenic bacteria (2-5,9,13). In these studies, afluidal variants formed spontaneously after prolonged storage of parent fluidal cultures or after manipulation of conditions in artificial culture. The recovery of naturally occurring afluidal variants from diseased tissue has received less attention. Ark (1) found that afluidal colonies of *Erwinia amylovora* could be isolated from old fire blight cankers and sometimes from oozing cankers of apple and pear trees. These variants were always found in mixed populations with the fluidal type. Virulence of the variant type was severely reduced relative to the fluidal type when artificially inoculated into test plants. Buddenhagen and Kelman (7) reported the isolation of butyrous (afluidal) mutants of *Pseudomonas solanacearum*

directly from diseased plants (species unreported) but only in small numbers and always associated with the fluidal type.

Bacterial wilt of bananas (moko disease) is caused by *P. solanacearum* (race 2) which occurs predominantly as two strains differentiated on the basis of colony morphology on tetrazolium chloride agar (TZC) (6). At the Tropical Research Laboratories of United Fruit Company in Honduras, isolations from moko-diseased commercial banana plants are made routinely to determine the relative proportions of the two strains. Close inspection of cultures revealed the frequent occurrence of afluidal variants (18). The variants often occurred in mixtures with either strain, but occasionally samples yielded pure cultures of afluidal variant. When eradication of plants that had yielded only afluidal variant (AFV) could be delayed, subsequent isolation from all diseased plant parts yielded only the afluidal variant type.

The banana plant regenerates by constant production of new suckers from an underground corm (15). Several shoots arising from a single corm form a mat, with the oldest shoot referred to as the mother plant. Maintenance of mats is done by cyclic pruning of unwanted suckers and leaves. Due to a large underground corm and constant sucker production, a moko-diseased banana mat may have some shoots free of bacteria. To ensure eradication of the

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. § 1734 solely to indicate this fact.

causal organism, the entire mat is destroyed by methyl bromide fumigation or by the injection of systemic herbicides. Since plants are routinely destroyed before samples of diseased tissue arrive at the laboratory, complete inspection of infected mats is not practical. Therefore, this study was initiated to determine the frequency of the afluidal variant in moko-diseased commercial bananas and whether pure cultures of afluidal variant types can incite the disease and to compare symptoms that develop following infection by the afluidal variant and the fluidal colony types of *P. solanacearum*.

MATERIALS AND METHODS

Samples. Between December 1982 and April 1983, bacteria were isolated from moko-diseased samples and classified according to colony type. The banana-growing area encompassed ~11,000 ha in four districts in the Sula Valley of northern Honduras. Bananas were of the Cavendish type (*Musa acuminata* AAA) cultivars Valery or Grand Nain. Samples from commercial plants usually consisted of portions of corm tissue from which isolations were made within 1 wk after field eradication of the diseased mat.

Samples of the inner corm tissue were obtained from experimental mats by using a borer tube (160 mm long by 3 mm in diameter). This technique permitted sampling of bacteria without sacrificing the plant.

Analysis of field samples. Pieces (~4 g) of diseased tissue were removed aseptically from samples received from commercial field operations, placed in 10 ml of sterile distilled water, and left to stand 15–30 min with intermittent shaking. Aliquots of diffusates were streaked with a sterile loop on TZC (13) or TZC amended with 0.5 ppm crystal violet, 100 ppm tyrothricin, 100 ppm polymyxin B sulfate, and 50 ppm cycloheximide. The selective isolation medium, similar to that of Granada and Sequeira (11), significantly reduced the growth of contaminants while permitting the development of characteristic morphology necessary to distinguish among colony types of the banana race of *P. solanacearum*. All plates were incubated at 32 C (\pm 0.5) for 48 hr.

Strains were identified according to colony morphology based on the characteristics for classification outlined by French and Sequeira (10). Colonies containing diffuse formazan pigmentation, elliptical to irregular borders, and diameters $>$ 2.5 mm were designated as fluidal (F) (corresponding to the "B" of French and Sequeira). Round, F colonies containing concentrated formazan pigmentation and with diameters between 1.5 and 2.5 mm were classified small, fluidal, round (SFR). Round colonies usually $<$ 1.5 mm in diameter with narrow clear borders surrounding intensely concentrated formazan pigmentation were classified as AFV. The colony morphology of AFV strains was indistinguishable from spontaneous afluidal mutants of F produced after prolonged still broth culture or after extended storage in distilled water (14). Cultures containing both F and AFV colonies were called mixed (MIX) (Fig. 1).

Strains were confirmed as *P. solanacearum* if they were aerobic, Gram-negative rods, catalase- and oxidase-positive, and accumulated poly- β -hydroxybutyrate.

Inoculation and disease evaluation. Bacterial strains used in these experiments were originally isolated from diseased commercial banana plants in the Sula Valley of Honduras. J3667 is an F type (colony diameter, 2.8 mm) collected in 1980. A38 is an AFV type (colony diameter, 1.0 mm) isolated in 1981 from one of a group of seven mats infected with AFV. W153, an SFR type (colony diameter, 2.0 mm) collected and identified in 1964, was kindly provided by L. Sequeira, University of Wisconsin-Madison.

Strains were purified by subculture on TZC, after which single colonies were selected and grown on TZC minus tetrazolium chloride at 32 C for 48 hr. Cells were suspended in 14% sucrose-14% peptone solution and lyophilized for permanent storage at -5 C. During the experiments, strains were maintained in distilled water and renewed periodically from lyophilized stocks. Strains were grown on TZC minus tetrazolium chloride at 32 C for 24 hr in preparation for artificial inoculation. Bacteria were suspended in sterile distilled water and adjusted to $A = 0.40$ at 600

nm ($\sim 10^9$ colony-forming units [CFU] per milliliter) with a Bausch and Lomb Spectronic 20 colorimeter. Culture purity and cell counts were checked during each experiment by dilution plating.

Artificial inoculations were made using laboratory-selected mutants resistant to streptomycin. Samples from artificially inoculated plants were plated on TZC amended with 500 ppm of streptomycin and 50 ppm of cycloheximide. The antibiotics allowed virtually contaminant-free isolations from experimental plants, thereby permitting accurate determination of populations and colony characteristics. Streptomycin-resistant mutants did not differ in virulence from parent cultures when tested on greenhouse-grown banana plants.

Infection and symptom development induced by the three colony types were compared by inoculation techniques simulating tool transmission of the pathogen under normal cultivation practices. Potted banana plants ~1.0 m high were inoculated by severing the fourth newest leaf at the junction with the pseudostem and applying 1.0 ml of inoculum evenly over the exposed surface. Mature field plants were inoculated through the cut surface of freshly pruned suckers. After the suckers were severed at the base, 1.0 ml of inoculum was applied evenly over the cut surface. Ten plants were inoculated with each strain in both experiments, and symptom evaluations were made weekly. Corm samples were collected at regular intervals from sucker-inoculated plants in the field. Virulence of AFV strains was determined using meristem-propagated potted banana plantlets (cultivar Grand Nain) (17). When plantlets had five to six expanded leaves (~15 cm high) $\sim 5 \times 10^4$ CFU were injected into the base of the pseudostem by using a hypodermic needle fitted to a 1.0-ml syringe. The experiment was replicated three times, using four plants per strain in each replication. Symptom evaluations were made every 2 days.

RESULTS

Distribution of colony types. Isolations were made from 1,476 moko-diseased plants from commercial plantations. Colony types were distributed similarly among the four districts (Table 1). The F type was predominant, occurring in 73% of samples. However, 56% of F type were isolated as mixtures with AFV. Pure cultures of AFV were obtained from 17% of the samples, and SFR was isolated from 10%.

Pathogenicity and symptom development. The pathogenic potential of the AFV type after leaf stub inoculation was demonstrated in potted plants. Typical symptoms of leaf yellowing

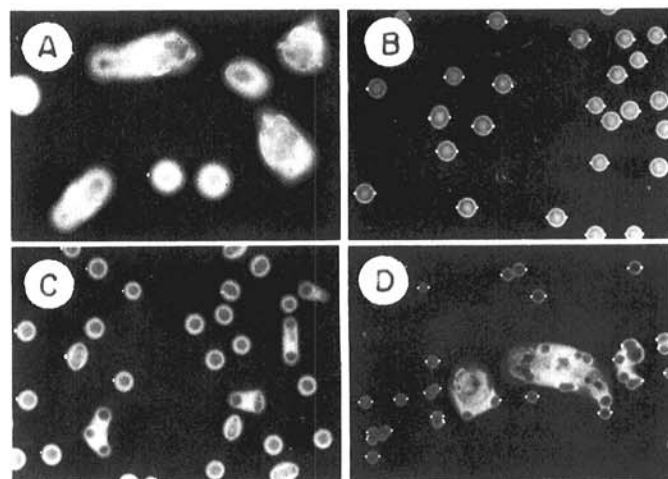


Fig. 1. Colony characteristics of isolates of *Pseudomonas solanacearum* obtained from diseased banana plants ($\times 2$). **A**, Highly fluidal with diffuse formazan pigmentation (F type). **B**, Afluidal with concentrated formazan pigmentation surrounded by narrow clear border (AFV type). **C**, Small, fluidal, round with centralized formazan pigmentation (SFR type). **D**, Mixture of F and AFV colony types from a single diseased plant (MIX). Characteristics determined after 48 hr at 32 C on modified or plain tetrazolium chloride medium.

and wilt developed in plants infected with A38, as well as with J3667 and W153. Reduced virulence of A38 was characterized by fewer plants becoming diseased and a slower rate of disease development (Fig. 2). Twenty-four weeks following inoculation, only two of 10 plants inoculated with A38 had visible symptoms, whereas six and five each of the groups inoculated with J3667 and W153, respectively, had visible symptoms.

TABLE 1. Distribution of colony types^a of *Pseudomonas solanacearum* race 2 among moko-diseased plants in commercial banana plantations of northern Honduras

District	Total samples	Percent of total			
		F	SFR	AFV	MIX
Progreso	978	30.3	8.7	18.3	42.7
Guanacastales	71	33.8	9.9	12.7	43.7
La Lima	264	42.0	7.2	14.8	36.0
Ulua	163	24.5	14.1	20.9	40.5
All districts					
Mean		32.7	10.0	16.7	40.7
SD±		7.3	3.0	3.6	3.4

^aDesignation of colony types: F = fluidal, elliptical to irregular margins with diffuse formazan center; SFR = small, fluidal, round with concentrated formazan center; AFV = afluidal variant, small round colonies with narrow clear borders and an intensely pigmented formazan center; MIX = mixed cultures with colonies of AFV and F or SFR.

TABLE 2. Afluidal variants (AFV) of *Pseudomonas solanacearum* isolated from suckers of banana plants 28 wk after inoculation with fluidal (F) colony type^a

Mat no.	Sucker no.	Total population ^b	AFV (%)
10	1	1.2×10^7	11.7
	2	1.0×10^9	2.6
	3	5.0×10^9	50.0
	4	4.9×10^9	43.0
15	1	6.7×10^8	0.7
	2	9.2×10^6	5.2
	3	6.5×10^6	3.8
25	1	3.0×10^9	11.3
	2	3.0×10^5	0.0
	3	2.0×10^8	40.0
	4	1.5×10^9	5.0
30	1	4.0×10^6	5.0
	2	5.3×10^8	17.0
35	1	3.7×10^7	30.0
	2	0.0	0.0
	3	7.5×10^6	28.0
	4	1.0×10^7	0.0
40	1	6.0×10^5	0.0
	2	2.6×10^6	1.6
	3	3.5×10^6	17.0
	4	1.3×10^7	13.0
	5	3.0×10^6	0.0
	6	1.5×10^7	62.0
45	1	0.0	0.0
	2	1.0×10^5	0.0
	3	1.0×10^5	0.0
50	1	2.7×10^9	21.5
	2	2.1×10^9	1.4
	3	4.6×10^6	9.8

^aMats were inoculated through cut sucker surface with 10^9 cells of fluidal isolate J3667. Samples were obtained from sucker corms contiguous to, but not including, the original inoculated sucker.

^bTotal numbers of F and AFVs determined by dilution plate technique. Each sample contained ~ 10 g corm tissue. Numbers represent colony-forming units recovered per gram.

Inoculated field plants showed similar trends. Analysis of corm samples taken every 4 wk showed more rapid establishment of W153 and J3667 than A38 (Fig. 3). Eight weeks after inoculation, W153 and J3667 were becoming established in the corms of mother plants, whereas A38 was not detected in this region. By 16 wk, bacteria were isolated from 30% of mother plant corms sucker-inoculated with A38, from 90% of those inoculated with J3667, and from 100% of those inoculated with W153. Twenty weeks following inoculation, A38 had invaded the main sucker adjacent to the mother plant in 10% of mats, while J3667 and W153 were found in main suckers of 70 and 80% of mats, respectively. By 36 wk, bacteria were recovered from main suckers of 100, 90, and 80% of W153-, J3667-, and A38-inoculated mats, respectively. Although AFV colony types were often recovered from plants inoculated with J3667 and W153, F types were never recovered from plants inoculated with A38.

Symptom development in field plants infected with J3667 or W153 was characteristic of moko disease. Newer leaves became pale or yellowish, often with necrotic areas. As disease progressed, leaves became flaccid and more necrotic. Mother plants were destroyed after 24 wk at which time symptoms were apparent in 45% of suckers.

Symptoms in suckers of mother plants infected with J3667 or W153 were characterized initially by marginal necrosis along the border of the older leaves. As the disease progressed, the newest leaves collapsed followed by death of the entire plant. Yellow to brown discoloration was visible in scattered vascular bundles in the corms.

Typical symptoms never developed in mother plants inoculated with A38. Plants remained green and produced normal fruit. Symptoms of disease were apparent first on the suckers of A38-infected plants and began developing 28 wk following inoculation of the mother plant. Initial marginal necrosis in the oldest leaves of suckers was similar to that produced by J3667 and W153. However, even though plants often became weak and stunted, they did not die. The suckers matured and produced fruit that was often small and somewhat deformed. Some plants infected with A38 developed healthy new leaves and appeared symptomless except for marginal necrosis in the oldest leaves. The corms of these plants, as well as

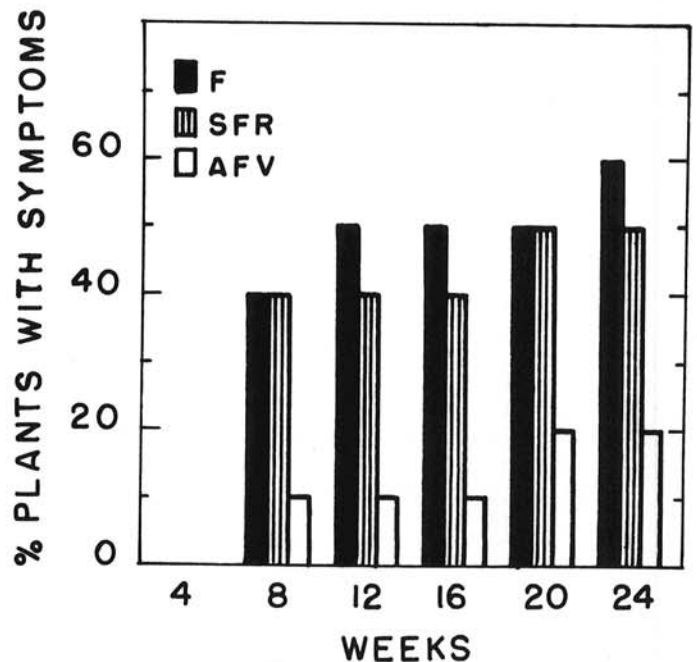


Fig. 2. Symptom development in potted banana plants inoculated with three colony types of *Pseudomonas solanacearum* race 2. Approximately 10^9 cells were applied to the exposed cut stub of the fourth newest leaf of plants 1 m in height. Ten plants were inoculated for each colony type: F = fluidal isolate J3667; SFR = small, fluidal, round isolate W153; and AFV = afluidal variant isolate A38.

those of many apparently healthy suckers, were intensely discolored throughout the vascular region. Wilt was never observed in suckers of A38-inoculated field plants.

Development of AFV in situ. Development of AFV types in situ was determined in a separate field experiment in which 10 plants (cultivar Valery) were inoculated with the streptomycin-resistant F strain J3667 by using sucker pruning techniques. Corm samples removed from diseased mother plants 10 wk after inoculation contained AFV mixed with the original F in 40% of mats. AFV colonies were indistinguishable from those obtained from moko-diseased commercial plants or from spontaneous AFV induced in still broth culture. Isolations made on streptomycin-amended TZC indicated that recovered AFV was derived from the streptomycin-resistant parent F strain. At 10 wk, a mean of 1.5% of total bacteria in MIX populations was AFV. Subsequent biweekly sampling yielded AFV from 20 to 50% of mother plant corms. The proportion of AFV in MIX populations ranged from 0.02 to 61.9% up to 20 wk when the mother plant corms were severely decayed. Two mats with no living suckers were eradicated at this time.

Suckers that appeared during disease development in the mother plant were tested for the presence of bacteria 28 wk after inoculation. Although mother plants and inoculated suckers had completely decayed by this time, there was an average of 3.6 living suckers per mat. Of these, 93% had moko disease, and 78% of diseased suckers contained AFV colony types (Table 2). The relative proportion of the AFV type varied, ranging from 0.7 to 62% of recovered bacteria, with an average of 18.1%.

Ten AFV colonies were randomly selected from cultures of diseased suckers described above and tested for virulence on banana plantlets. The development of disease was compared with that of the parent F strain. All AFV strains incited disease, although virulence was lower than that of the parent strain (Table 3). Plants injected with water never developed symptoms. Wilt in AFV-infected plants commenced approximately 16 days following inoculation. By day 26, almost all AFV-infected plants were completely wilted, whereas the F-inoculated plants were completely necrotic. A mean of 36.5 days was required for complete necrosis of AFV-infected plants. Similar levels of virulence were observed when strains isolated from diseased commercial plants were tested.

DISCUSSION

AFV colony types of *P. solanacearum* were frequently isolated from moko-diseased commercial banana plants in northern Honduras with up to 17% of diseased plants yielding only the AFV type. This is in contrast to previous reports of the occurrence of AFV types only in the presence of F types in diseased tissue (1,7,12).

TABLE 3. Levels of disease incited in banana plantlets inoculated with afluvidal variants (AFV) of *Pseudomonas solanacearum*

Strain ^a	Disease level ^b at day:	
	16	26
AFV-1	2.0	4.0
AFV-2	2.0	4.0
AFV-3	1.8	3.8
AFV-4	2.3	3.7
AFV-5	1.5	3.0
AFV-6	2.0	4.0
AFV-7	1.3	2.8
AFV-8	2.5	4.5
AFV-9	1.3	3.0
AFV-10	2.0	4.0
Mean	1.9	3.7
J3667 (F)	3.3	5.0

^aAFV inocula were obtained from field plants 28 wk after artificial inoculation with the fluidal (F) strain J3667.

^bDisease level rated as: 1 = no symptoms; 2 = leaves flaccid or deformed; 3 = all leaves wilted; 4 = discoloration and necrosis beginning; 5 = all leaves necrotic. Control plantlets injected with water did not develop symptoms.

The incidence of AFV was similar among four districts comprising 11,000 ha of commercial bananas, suggesting a broad existence. It is likely that due to morphological similarity to the SFR colony type, AFV has been confused with SFR. Although no physiological tests have been found that distinguish SFR from F (8) and therefore, presumably, from the AFV of F, SFR is more virulent than AFV. Colony size, intensity of pigmentation on TZC, and margin characteristics can help to distinguish these strains under laboratory conditions.

Recovery of only AFV from diseased commercial mats suggests infection by AFV alone occurs. That AFV can incite disease in commercial banana plants is further supported by colonization and symptom development in plants inoculated with AFV by methods simulating cultivation practices. Although AFV was less virulent than F or SFR, bacteria in AFV-diseased plants invaded systemically and spread eventually into new sucker growth.

Pathogenicity was also demonstrated when AFV isolates were inoculated into small banana plantlets. Although only 5×10^4 cells per plant were used as inoculum, AFV became established and plantlets eventually died. This is in contrast to reports that plants artificially inoculated with AFV types did not develop disease (3) or developed only localized deformity or necrosis (5,9,12). Recently the limited invasive ability of an AFV of *P. solanacearum* strain K60 was demonstrated in potato (4). Only the parent F and not the AFV strain was found beyond 1 cm from the inoculation point 12 days after introducing 8×10^6 bacterial cells into the stem.

Symptom development was comparatively mild in AFV-infected field plants even though extensive invasion was detected in the corms. Leaf distortion, discoloration, and stunting were typical symptoms of AFV infection in mat suckers. Husain and Kelman (12) reported similar symptoms of leaf epinasty and stunting in tomatoes inoculated with an AFV of *P. solanacearum* (race 1), whereas plants inoculated with wild F types wilted dramatically and died within 2 wk. Permanent wilt never developed in the

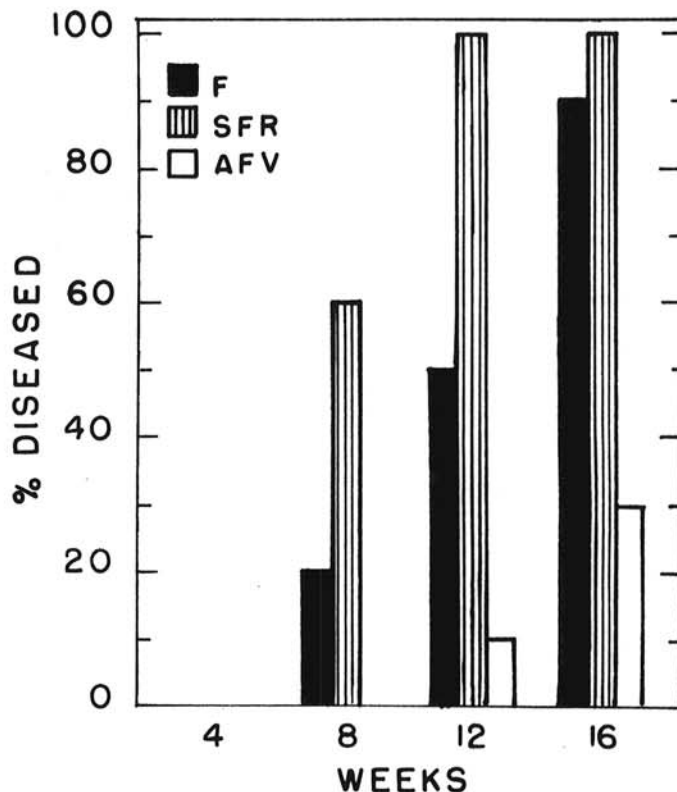


Fig. 3. Infection rate of mature, field-grown banana plants inoculated with three colony types of *Pseudomonas solanacearum* race 2. Approximately 10^9 cells were applied to the exposed surface of a freshly pruned sucker. Samples from the corm stela of mother plants were plated on tetrazolium chloride agar for determination of the presence of bacteria. Ten plants were inoculated for each colony type: F = fluidal isolate J3667; SFR = small, fluidal, round isolate W153; and AFV = afluvidal variant isolate A38.

AFV-inoculated tomato plants. In contrast, AFV-inoculated young banana plantlets wilted and died after infection became established. Wilt has also been noted occasionally in young suckers infected with AFV in commercial plantings. Since AFV apparently does not produce copious quantities of extracellular polysaccharide, as evidenced by colony morphology, other factors may contribute to the development of wilt in moko disease.

Leaf and sucker pruning are daily operations in commercial banana plantations and are a major means of disseminating moko disease bacteria (16). Apparently, pruning wounds are favorable infection courts for the less virulent AFV that in the absence of such wounds would probably not gain entry to the plant. Evidence of root or insect transmission of AFV has not been observed.

Reduced rate of symptom development combined with mild symptom expression render AFV infections in large banana plants difficult to detect, thus providing a persistent reservoir of bacteria for tool transmission. Since early eradication of diseased plants is a key strategy in moko disease control, the existence of symptomless infections by AFV poses a special problem for commercial banana growers.

Although AFVs have been recovered from diseased plants before, they have always occurred in low numbers mixed with F types and have never been considered to play a primary role in disease development. Banana pruning operations combined with perpetual vegetative sucker production from a large underground corm apparently provide a favorable environment for the establishment of AFV and for its dispersal. Banana mats infected with a virulent strain of *P. solanacearum* can survive many months by the constant production of new suckers. This investigation has shown that AFV types readily evolve under these conditions.

Since reversion to the F type has never been observed, the evolutionary advantage of changing to a less aggressive pathogen is unclear. Under less intensive cultivation such a weak pathogen probably would not compete successfully. The existence of AFV in bananas offers opportunity for the study of the ecological and pathological significance of these forms.

LITERATURE CITED

1. Ark, P. A. 1937. Variability in the fire-blight organism, *Erwinia amylovora*. *Phytopathology* 27:1-28.
2. Ayres, A. R., Ayres, S. B., and Goodman, R. N. 1979. Extracellular polysaccharide of *Erwinia amylovora*: A correlation with virulence. *Appl. Environ. Microbiol.* 38:659-666.
3. Bennett, R. A., and Billing, E. 1978. Capsulation and virulence in *Erwinia amylovora*. *Ann. Appl. Biol.* 89:41-45.
4. Bowman, J. E., and Sequeira, L. 1982. Resistance to *Pseudomonas solanacearum* in potato: Infectivity titrations in relation to multiplication and spread of the pathogen. *Am. Potato J.* 59:155-164.
5. Bradshaw-Rouse, J. J., Whatley, M. H., Coplin, D. L., Woods, A., Sequeira, L., and Kelman, A. 1981. Agglutination of *Erwinia stewartii* strains with a corn agglutinin: Correlation with extracellular polysaccharide production and pathogenicity. *Appl. Environ. Microbiol.* 42:344-350.
6. Buddenhagen, I. W., and Elsasser, T. A. 1962. An insect-spread bacterial wilt epiphytotic of Blugoe banana. *Nature* 194:164-165.
7. Buddenhagen, I. W., and Kelman, A. 1964. Biological and physiological aspects of bacterial wilt caused by *Pseudomonas solanacearum*. *Annu. Rev. Phytopathol.* 2:203-230.
8. Buddenhagen, I. W., Kennedy, K. R., and Wang, C. H. 1966. Comparative carbohydrate catabolism in three different pathogenic strains of *Pseudomonas solanacearum*. *Phytopathology* 56:999-1002.
9. Corey, R. R., and Starr, M. P. 1957. Colony types of *Xanthomonas phaseoli*. *J. Bacteriol.* 74:137-140.
10. French, E. R., and Sequeira, L. 1970. Strains of *Pseudomonas solanacearum* from Central and South America: A comparative study. *Phytopathology* 60:506-512.
11. Granada, G. A., and Sequeira, L. 1983. A new selective medium for *Pseudomonas solanacearum*. *Plant Dis.* 67:1084-1088.
12. Husain, A., and Kelman, A. 1958. Relation of slime production to mechanism of wilting and pathogenicity of *Pseudomonas solanacearum*. *Phytopathology* 48:155-165.
13. Kelman, A. 1954. The relationship of pathogenicity in *Pseudomonas solanacearum* to colony appearance on a tetrazolium chloride medium. *Phytopathology* 44:693-695.
14. Kelman, A., and Hruschka, J. 1973. The role of motility and aerotaxis in the selective increase of avirulent bacteria in still broth cultures of *Pseudomonas solanacearum*. *J. Gen. Microbiol.* 76:177-188.
15. Pursglove, J. W. 1972. *Tropical Crops: Monocotyledons* 2. Wiley Inc., New York. 356 pp.
16. Sequeira, L. 1958. Bacterial wilt of bananas: Dissemination of the pathogen and control of the disease. *Phytopathology* 48:64-69.
17. Vessey, J. C., and Rivera, J. A. 1980. Meristem culture of bananas. *Turrialba* 31:162-163.
18. Woods, A. C. 1982. Frequency and pathogenicity of afluoid variants of *Pseudomonas solanacearum* from moko-diseased bananas. (Abstr.) *Phytopathology* 72:991.