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ABSTRACT

In comparative studies, isolates of *Pseudomonas solanacearum* which were obtained from eight different host plants in the Philippines differed in virulence to inoculated tobacco, ginger, pepper, and peanut plants. All isolates, however, were highly virulent to potato and eggplant. Isolates obtained from diseased ginger plants were more virulent to ginger but less virulent to tomato than were isolates obtained from other hosts. All Philippine isolates were of low virulence to diploid banana; and they appeared to be race 1 despite the relatively low virulence of many isolates to tobacco. Philippine isolates were of greater virulence to eggplant than was North Carolina isolate K-60 (race 1) or Colombia isolate S-208 (race 3).

Some isolates induced wilt symptoms at 27-32 C but not at 23-24 C. Potato plants that were inoculated at cooler temperatures (18-24 C) did not wilt when moved to warmer temperatures (27-32 C). Apparently plant resistance to the pathogen was not affected by this practice. Temperature was an important factor for wilt development in inoculated tobacco plants. Symptoms in Bottom Special tobacco plants were more effected by temperature changes than were symptoms in Reax tobacco plants. A change of the inoculum concentration from 1×10^6 to 6×10^8 cells/ml had little effect on disease severity at 27-32 C.

Pseudomonas solanacearum E. F. Smith, the causal agent of bacterial wilt of tomato (*Lycopersicon esculentum* Mill.) and other plants, is a pathogen of great diversity, and that many strains are known to differ in host range (Buddenhagen and Kelman, 1964; Buddenhagen, Sequeira, and Kelman, 1962; Harrison, 1961; Kelman and Person, Okabe and Goto, 1961; Quiñon, Aragaki, and Ishii, 1964; Thurston, 1963) Strains are numerous in relatively limited geographical regions (Okabe and Goto, 1961), but some-

times their number differ qualitatively in different parts of the world. Strains that are virulent to banana (*Musa* sp.) in some parts of Central and South America for example, have not been reported in many other banana-growing countries (Buddenhagen, 1961; Buddenhagen and Kelman, 1964). In Hawaii, there are 3 known strains of *P. solanacearum* attacking tomato, ginger (*Zingiber officinale* Roscoe), and bird-of-paradise (*Strelitzia reginae* Banks), respectively (Quiñon, Aragaki, and Ishii, 1964).

A review of extensive investigation on the influence of temperature in wilt development has been published by Kelman in 1953. Most investigators have concluded that relatively high temperatures (above 21 C) favor wilt development. Thurston (1963), however, demonstrated that certain strains from high mountain elevations in Colombia can induce wilt at relatively low temperatures. He observed an epiphytotic of bacterial wilt of potatoes (*Solanum tuberosum* L.) at elevations with mean temperature of 13.1 C. Strains that cause wilt at low temperatures also have been reported in Portugal (Moraes, 1947) and in Kenya (Robinson, 1967).

In the Philippines, *P. solanacearum* has been recognized as a pathogen causing wilt of tomato, tobacco (*Nicotiana tabacum* L.), eggplant (*Solanum melongena* L.), pepper (*Capsicum annuum* L.), and potato since 1919 (Reinking, 1919). Bacterial wilt of ginger was recently reported (Zehr, 1970b), and abaca (*Musa textilis* Nee) is affected by the wilt organism in some localities of the Philippines (Zehr, 1970c). Infection of bananas (*Musa* spp.) has occurred under certain conditions in the Philippines, but strains that are highly virulent to bananas and abaca have not been encountered (Zehr, 1970c). Very little information is available concerning the occurrence of pathogenic strains of *P. solanacearum* in the Philippines; therefore, isolates collected from various plants were compared for virulence to selected host species. Also, the influence by temperature on the development of wilt symptoms in potato and tobacco plants inoculated with Philippine strains of the pathogen was investigated.

Materials and Methods

Thirty-five isolates of *P. solanacearum* were obtained from tomato, potato, eggplant, pepper, tobacco, ginger, abaca, and banana. Isolates K-60 from North Carolina and S-208 from Colombia were kindly supplied by Dr. Arthur Kelman, University of Wisconsin and used for comparison. Diseased specimens were collected and the presence of *P. solanacearum* was determined by aseptically transferring a small portion of diseased vascular tissue to 10 ml sterile distilled water. The resulting suspension was subsequently streaked on tetrazolium medium (TTC) (Kelman, 1954). After 48 hr of incubation at 32 C, a single, discrete and fluidal colony was transferred with a 2-mm wire loop to another 10 ml sterile distilled water. The

suspension was again streaked on TTC medium, incubated, and a single, discrete colony transferred to sterile distilled water. After repeating the above procedure for at least 3 times, stock cultures were prepared by transferring two loopfuls from a single, discrete bacterial colony to 10 ml sterile distilled water, and kept at room temperature (23-32 C). Virulence of each isolate was confirmed by the development of symptoms in the inoculated susceptible hosts.

Suscepts inoculated. — Eight different plant species, including tomato (cv. 'Marglobe'), tobacco (cv. 'Reax'), pepper (cv. 'Pimiento'), eggplant (cv. 'Black Beauty'), potato (cv. 'Katahdin'), banana (*Musa balbisiana* Colla 'Butuhan'), ginger, and peanut (*Arachis hypogaea* L. 'UPCA 101') were used as test plants for inoculation experiments. These were inoculated with each isolate. Ginger rhizomes purchased from Philippine local markets were used because certified propagative material was not available. Seed of tomato, tobacco, pepper, eggplant, banana and peanut were germinated in flats with heat-sterilized soil (1/3 day loam, 1/3 river-bottom sand; and 1/3 compost). The germinated seedlings were transplanted in 6-inch day pots with sterilized soil when they were 3.5 cm tall. Seed pieces of ginger and potatoes were separately planted directly in clay pots. Vigor of the test plants was maintained by frequent watering and fertilization.

Method of inoculation. — Bacterial suspension from stock cultures were streaked on TTC medium and incubated at 32 C for 48 hr. A single discrete fluidal colony was then transferred to 10 ml sterile distilled water and diluted to 1×10^7 cells/ml (1×10^6 cells/ml for potatoes) (Breed and Brew, 1916.) Test pants were inoculated using the stem-puncture method of Winstead and Kelman (1952).

At least 12 seedling plants of each species were inoculated with each isolate, except that 6 to 8 plants of *M. balbisiana* and 5 to 6 of ginger were used. Five to 20 isolates were compared simultaneously.

Environmental conditions. — All experiments, except those with Katahdin potatoes, were conducted in a tropical environment of high temperatures (night-time minima of 20-25 C, and daytime maxima of 29-36 C) and high relative humidity, under a glass roof with open sides. Potatoes were inoculated in the greenhouse (23-29 C) at Ithaca, New York. Controlled environment experiments were made in Cornell plant growth chambers.

Disease evaluation. — Symptom development was evaluated at weekly intervals for 3 consecutive weeks. The following disease rating system, a modification of that described by Winstead and Kelman (1952), was used: 0 = symptoms; 1 = limited necrosis or vascular browning at the point of inoculation; 2 = vascular browning extending 1 inch or more from the point of inoculation with no external symptoms, or with 1 leaf partially wilted; 3 = 1 or more leaves entirely wilted; 4 = all leaves

wilted; and 5 = plant dead. Disease ratings were made at weekly intervals for three consecutive weeks and were converted to a disease index (Winstead and Kelman, 1952). Isolates inducing little or no external symptoms (a disease index of 40 or less) in a given host are herein described as a low virulence, those inducing severe wilt or death in at least half of the replicates (an index of 70 or more) are of high virulence; and those with an index between 40 and 70 are of moderate virulence.

RESULTS

Response of host plants to inoculation. — Philippine isolates of *P. solanacearum* differed considerably in virulence to some of the inoculated host plants (Table 1). Differences in virulence were especially noticeable in

TABLE 1. Relative virulence of certain isolates of *Pseudomonas solanacearum* to eight selected host plants[a]

Isolate	Host	Province	Relative virulence to: Potato	Tomato	Eggplant	Tobacco	Pepper	Banana	Peanut	Ginger
1 — BC-1[b]	tomato	Benguet	H[c]	H	H	L	H	L	L	L-M
2 — Ce-1[d]	pepper	Cebu	H	H	H	M	H	L	L	L-M
3 — 1-3	tomato	Isabela	H	H	H	L	H	L	M	L
4 — La-2	pepper	Camarines Sur	H	H	H	L	H	L	M	L
5 — Ba-1	tomato	Nueva Ecija	H	H	H	L	H	L	M	M
6 — 1.4	eggplant	Isabela	H	H	H	M	H	L	M	L
7 — LB-5	pepper	Laguna	H	H	H	M	H	L	M	L
8 — Li-1	eggplant	Cebu	H	H	H	M	H	L	M	L
9 — Ki-1	eggplant	Leyte	H	H	H	M	H	L	M	M
10 — V-1	pepper	Neg. Oriental	H	H	H	M	H	L	M	M
11 — [illegible].C-1	tomato	Batangas	H	H	H	H	H	L	L	L
12 — LB-6	potato	Laguna	H	H	H	H	H	L	M	L
13 — 1-2	tobacco	Isabela	H	H	H	H	M	L	L	L
14 — A-2	tobacco	La Union	H	H	H	H	M	L	L	M
15 — A-3	tomato	La Union	H	H	H	L	M	L	L	L
16 — Sl-1	ginger	Batangas	H	M	H	L	M	L	L	H
17 — Ta-1	ginger	Batangas	H	M	H	L	M	L	L	H
18 — K-60	tomato	———[e]	H	H	M	M	M	L	L	L
	potato	———[e]	H	H	M	M	M	L	L	L

[a] Relative virulence based on disease index obtained from 12 plants each for potato, tomato, eggplant, tobacco, pepper, and peanut; 6 or 8 plants for banana (*Musa balbisiana* Colla); and 5 or 6 plants for ginger.

[b] Representative of 12 isolates from tomato, pepper, eggplant, and banana that were alike in host range.

[c] High virulence (H) = disease index of 70-100; moderate virulence (M) = disease index of 41-69; low virulence (L) = disease index of 40 or less 3 weeks after inoculation.

[d] Representative of 8 isolates from tomato, pepper, eggplant, and abaca that were alike in host range.

[e] Isolates K-60 and S-208, from North Carolina and Bogota, Colombia, respectively, were supplied by Arthur Kelman, University of Wisconsin.

tobacco and ginger, and also were apparent in inoculated tomato, pepper, and peanut plants. Although all Philippine isolates were highly virulent to potato and eggplant, none of them caused wilt of bananas. When diploid bananas were used in the present study, representative isolates did not induce wilt of various cultivars of triploid bananas (Zehr, 1970c). Only isolates from diseased ginger plants were highly virulent to ginger; these isolates were less virulent to tomatoes than the isolates from other hosts. Following inoculation with ginger isolates, wilt of eggplant developed slower than those inoculated with isolates from other hosts. Ginger isolates killed almost all the inoculated eggplants during the three-week test period. Many highly virulent isolates from other hosts killed inoculated eggplants within 10 days.

Differences between highly virulent and less virulent isolates usually were apparent within 1 week. Moderately virulent isolates induced partial wilting, distortion, and stunted growth in 1 week (Fig. 1), and such symptoms intensified thereafter without recovery or death of the diseased plants. Most isolates were highly virulent to the hosts from which they had been originally isolated; but those from abaca and banana were of relatively low virulence to their hosts (Zehr, 1970c).

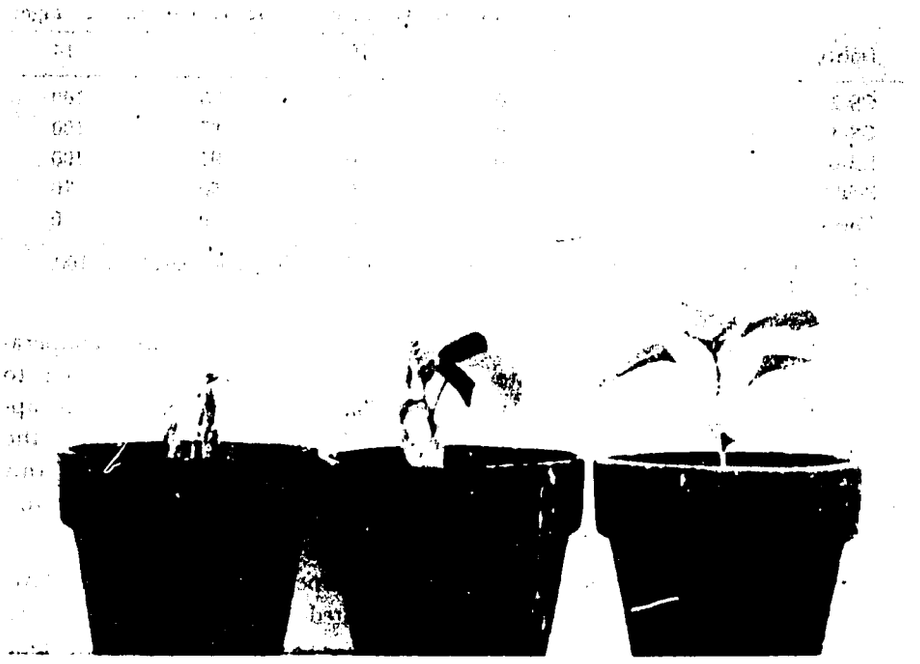

Fig. 1. Pimiento pepper plants 7 days after stem-inoculation with *Pseudomonas solanacearum*. Plant inoculated with isolate LB-5 wilted completely (left), while inoculation with isolate 1-2 (center) resulted in only partial wilt, reduced growth, and downward curl of shoot. A noninoculated check plant is at right.

Relation of temperature to disease development in potatoes. — In inoculation experiments, 17 of the 34 isolates did not induce wilt symptoms on Katahdin potatoes at greenhouse temperatures of 23-29 C. However, many of these isolates had caused severe disease symptoms in various potato cultivars in the Philippines at temperatures higher than those in the greenhouse. Several experiments were made with controlled temperature conditions to determine whether temperature might account for the differences observed. Greenhouse-grown plants of certified Katahdin potato (15-30 cm in height) were placed in Cornell growth chambers (21 C day, 16 C night; or 32 C day, 27 C night; 2000 ft-c, 14 hr/day). After 24 hr, 6 plants for each isolate GS-2, GS-4, LB-6, and S-208 (1 x 10^6 cells/ml) were inoculated. Two plants were injected with sterile, distilled water and placed at each temperature to serve as checks.

Differences in disease development became apparent within 7 days after inoculation (Table 2). After two weeks, most of the inoculated plants at the higher temperature range died, while those at the lower range produced

TABLE 2. Symptom development in Katahdin potatoes stem-inoculated with *Pseudomonas solanacearum* at two different temperature ranges (2000 ft-c, 14 hr/day)

	Disease Index[a]			
	21 C day, 16 C night		32 C day, 27 C night	
Isolate	7[b]	10	7	14
GS-2	0	0	73	100
GS-4	0	0	87	100
LB-6	0	0	97	100
S-208	0	0	50	70
Check	0	0	0	0

[a] Disease index after Winstead and Kelman (1952). All plants dead = 100.
[b] Day after inoculation.

no symptoms. None of the inoculated plants growing at lower temperature developed symptoms even after 3 weeks. When these were moved to the greenhouse with temperature range of 23-29 C, still no symptoms appeared within 3 weeks. Wilt symptoms also did not develop when the temperature was 24 C day and 18 C night. However, 2 of the 24 plants inoculated at this temperature range wilted 3 weeks after they were transferred to another growth chamber (32 C day, 27 C night).

These experiments indicated that higher temperature favored the development of bacterial wilt symptoms in inoculated Katahdin potato plants. Therefore, young Katahdin potato plants in a growth chamber with temperature of 32 C day and 27 C nights, were inoculated separately with 13 isolates (A-3, Li-1, Sl-1, Ab-1, La-2, Da-1, DC-1, LB-4, Ce-1, DC-7, Ba-1, and 1-4) that did not induce symptoms in the greenhouse. All the inocu-

lated plants in the growth chamber developed wilt symptoms and died or were dying 1 week after inoculation.

To determine whether potatoes inoculated with bacterial wilt organism might develop resistance at relatively cool temperatures, the following experiment was made. Thirty-five young greenhouse-grown Katahdin potato plants (5-10 cm tall) were placed in a growth chamber (24 C day, 18 C night; 2000 ft-c, 14 hr/day). When the plants were 10-15 cm tall (8 days after), 20 were inoculated with isolate LB-6 (1 x 10^6 cells/ml), employing the procedure used in other experiments. Fifteen plants were provided as control. Twelve days after inoculation, none of the plants developed symptoms; they were then moved to another growth chamber (32 C day, 27 C night; 2000 ft-c, 14 hr/day). Ten of the inoculated plants were reinoculated 4-6 cm above the previous inoculation site with isolate LB-6. Ten of the 15 non-inoculated check plants were also inoculated. All remaining plants that received the first inoculation and control were injected with sterile, distilled water.

One week after the second inoculation, all the inoculated plants wilted (Table 3). The check plants and those that were not reinoculated showed no symptoms. After 2 weeks, all the plants that were reinoculated died. All unaffected plants that received first inoculation were removed and dis-

TABLE 3. Influence of temperature and reinoculation on symptom development of Katahdin potatoes stem-inoculated with *Pseudomonas solanacearum*

Treatment	Disease Index[a]	
	7[b]	14
Inoculated[c]	0	0
Inoculated[d]	80	100
Reinoculated[e]	80	100
Noninoculated[f]	0	0

[a] Disease index after Winstead and Kelman (1952). All plants dead = 100.
[b] Days after last inoculation.
[c] Ten plants inoculated, kept at 24 C day, 18 C night for 12 days, moved to 32 C day, 27 C night without reinoculation.
[d] Ten plants inoculated only after moving to 32 C day, 27 C night
[f] Five noninoculated checks.

sected. Those that were kept at the cooler temperature showed a small, darkened, hydrotic lesion at the site of inoculation, but no vascular browning was apparent. The pathogen was successfully re-isolated from the hydrotic tissue of 4 randomly selected plants. All colonies of the reisolated bacteria on TTC medium were virulent (fluidal). Young potato plants rapidly developed typical wilt symptoms after inoculation from these bacterial colonies.

Relation of cultivar, temperature, and inoculum concentration to disease development in tobacco. – Relatively few Philippine isolates were found

to be highly virulent to tobacco (Table 1). However, tobacco plants inoculated with North Carolina isolate K-60 which has been reported by other investigators (Kelman and Person, 1961; Sequeira, 1964) to be highly virulent to tobacco did not wilt severely in the present study. Tobacco cultivar, temperature, and inoculum concentration were studied to determine whether these factors contribute to these apparently conflicting results.

Tobacco cultivars 'Reax' and 'Bottom Special' were comparatively studied. Seedlings of each cultivar were grown in Vermiculite until they were 2 cm tall and then transplanted in 4-inch clay pots with sterilized soil. These 5-leaf seedling (5-7 cm height) were inoculated using procedures described previously, except that the inoculum concentration was 1×10^6 cells/ml. Four to 5 plants of each cultivar were inoculated with each isolate.

In the greenhouse (23-29 C) no difference was observed between the cultivars inoculated separately with 6 isolates. Isolates LB-6 and A-2 killed the inoculated plants of both cultivars. Isolates K-60 and Li-1 induced mild wilt symptoms but did not kill the plants. Isolates Sl-1 and A-3 induced no wilt symptoms. In the growth chamber (32 C day, 27 C night; 2000 ft-c, 11 hr/day), however, marked differences occurred between cultivars inoculated with K-60. All the inoculated Bottom Special tobacco plants were killed. Some of the inocuated Reax plants wilted, but remained alive.

Two inoculum concentrations (6×10^8 cells/ml and 1×10^6 cells/ml) were compared in the growth chamber, using 6 plants of Bottom Special tobacco for each isolate. Results indicated that inoculum concentration at these levels did not influence evaluation of susceptibility. Bottom Special plants inoculated with 3 Philippine isolates wilted less severely than those inoculated with isolate K-60, regardless of the inoculum level.

Discussion

All isolates of *P. solanacearum* used in this study were highly virulent to Katahdin potatoes, but certain isolates required a relatively high temperature before disease symptoms appeared. Optimum disease development occurred when maximum temperatures were near the optimum temperature for the pathogen in vitro, which was approximately 33 C for most isolates (Zehr, 1970d). For Katahdin potatoes, however, factors other than optimum growth for the pathogen appeared to be involved in the apparent resistance of the plants at greenhouse temperatures, because tobacco and tomato plants wilted rapidly under the same conditions. Philippine potato cultivars also wilted rapidly when they were inoculated under tropical climatic conditions where the average maximum temperature was about 32 C. The reaction of Philippine cultivars to inoculation under cooler conditions was not determined. If Philippine cultivars are resistant at cooler tempera-

tures, then temperature may explain the apparent absence of the disease in potatoes at higher mountain elevations in the Philippines (Zehr, 1970a).

Reax tobacco did not demonstrate a resistance factor conditioned by temperature. Reax tobacco, however, demonstrated resistance to isolate K-60 under tropical climatic conditions, warm growth chamber conditions, and in the greenhouse. Philippine isolates that were highly virulent to Reax tobacco under tropical conditions killed the plants in the greenhouse, although the rate of wilt development was slower. The response of Bottom Special tobacco to K-60 was similar to Reax tobacco in the greenhouse. At warmer temperatures in the growth chamber, however, the former was more susceptible to K-60 than the latter. Bottom Special tobacco was resistant to certain Philippine isolates even in the growth chamber.

Isolates of high virulence to ginger were obtained only from diseased ginger plants. Ginger isolates, however, were highly virulent to potatoes and eggplants. It is not clear whether the Philippines ginger strain attacks only ginger in nature, or its absence in other hosts is due to its limited distribution. In general, isolates were highly virulent to the hosts from which they were originally isolated, except those isolates from abaca and banana (Zehr, 1970c).

The role of inoculum concentration in determining symptom expression was not thoroughly investigated in this study. Increasing the inoculum concentration from 1×10^6 cells/ml to 6×10^8 cells/ml did not substantially affect disease severity, although the rate of disease development was slightly faster at higher concentration. However, more dilute inoculum concentrations might have different effects on symptom development.

In the Philippines, *P. solanacearum* apparently consists of a number of strains that differ considerably in relative virulence to different plants. The most common isolates used in these studies were of low virulence to tobacco, peanuts, and *M. balbisiana*, low or moderate virulence to ginger, and high virulence to tomatoes, potatoes, eggplants, and peppers. Surprisingly, few isolates that were highly virulent to tobacco were collected, and even in areas of the country where tobacco is commonly grown, strains of low virulence to tobacco were found. Indications are that different strains might occur simultaneously in a single field. Isolates LB-4 and LB-5, from eggplant and pepper, respectively, were collected in the same field, but they differed in virulence to tobacco and peanut. Isolate LB-6, collected from a potato field located 1 km away from the above field, was of much higher virulence to tobacco than either LB-4 or LB-5 even though tobacco has not been grown in the area for many years. Although isolates I-2 and I-3 were collected within 300 m away from one another in adjoining fields, they differed greatly in relative virulence to tobacco, peppers, and peanuts. In Japan, 2 or more strains of *P. solanacearum* are not uncommon in a given field (Okabe and Goto, 1961).

Presumably, all Philippine isolates of *P. solanacearum* tested are race 1, because they are virulent to tomato, eggplants, pepper, and potato. North Carolina isolate K-60, also race 1, was less virulent to eggplant than the Philippine isolates, and was somewhat less virulent to pepper than most of the other isolates. The Colombian potato isolate (S-208) was typical of race 3, except for its high virulence to *M. balbisiana*. This isolate, however, was not virulent to triploid bananas (Zehr, 1970c).

The isolation of virulent cells of *P. solanacearum* from artificially-inoculated potatoes with no visible symptoms was surprisingly an interesting development. Digat (1966) isolated virulent cells from inoculated tomatoes that had no apparent symptoms of wilt; his studies indicated that a form of induced resistance might occur in inoculated tomatoes under certain conditions. The results herein presented, however, gave no evidence of generalized induced resistance in potatoes under cool temperature conditions, but a form of localized, induced resistance might have been stimulated.

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