Variation in the Pathogenicity and Aggressiveness of Strains of *Erwinia carotovora* subsp. *carotovora* Isolated from Different Hosts

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ABSTRACT

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Thirty-seven strains of soft-rot erwinias isolated from lesions on different hosts in Florida varied in their physiological and pathological phenotype. Based on the production of phosphatase, acid from methyl-α-D-glucopyranoside, reducing substances from sucrose and growth at 36 C, 35 strains were typical or atypical members of *Erwinia carotovora* subsp. *carotovora*, and two strains were typical of *E. chrysanthemi*. All strains caused lesions in pepper and tomato fruit, potato tubers, and young tomato plants but varied in pathogenicity in the pseudostem of corn and in the stems of chrysanthemum, potato, and tobacco. Significant differences were found ($P = 0.05$) among the strains for aggressiveness in the tubers and fruit, but the relative aggressiveness in one host was not always associated with aggressiveness or pathogenicity in the other hosts. Strains isolated from a particular host were not always more aggressive than the others when inoculated to that host. Thus, certain strains of *E. c. carotovora* may exhibit a host specificity that is not related to their original host or to their relative aggressiveness in common hosts (such as potato tuber or tomato fruit).

Host specificity is not recognized among strains of *Erwinia carotovora* subsp. *carotovora* (Jones) Bergey et al (27). These bacteria are pathogenic in succulent tissue of most plants; only certain fruits are immune (18,27). In contrast, strains within *E. chrysanthemi* Burkholder et al differ in host range (11,27). Dickey (11) assigned 383 strains to plant reaction groups based on pathogenicity in a series of hosts and proposed six different phenotypic subdivisions based on physiological and biochemical tests on 322 strains (10). A relationship was noted between phenotype and source plant of the strains. Schaad and Brenner (28) observed that strains of *E. chrysanthemi* isolated from lesions on sweet potato caused disease in chrysanthemum, corn, pepper, tomato, tobacco, sweet potato, and petunia, whereas strains obtained from various culture collections appeared nonpathogenic in one or more of these plants.

Two other taxons of soft-rot erwinias appear to have restricted host ranges; strains of *E. c.* subsp. *atroseptica* (van Hall) Dye are found in potatoes grown in temperate climates (27), and strains of *E. c.* subsp. *betavasculorum* Thomson et al occur only on sugar beet (29). However, strains of *E. c. atroseptica* have been isolated from tomato in France and from Chinese cabbage in Japan (9).

Certain differences in pathogenicity have been observed among strains of *E. c. carotovora* (14,17,19,22,23). Strains isolated from tobacco with hollow stalk caused similar symptoms in inoculated plants, whereas most strains from a culture collection did not (23). A strain of *E. c. carotovora* from onion caused a more rapid soft rot when inoculated to that host than did a strain from potato (17). Jones (19) found three levels of aggressiveness (quantity of host tissue rotted) among 45 strains of soft-rot bacteria. A strain obtained by Jones (19) from Townsend (from calla lily) was in the most aggressive group, whereas the type strain of the *E. c. carotovora* isolated by Jones from carrot was typical of strains in the least aggressive group. Massey (22) noted that the carrot strain of *E. c. carotovora* obtained from Jones was nonpathogenic in beet root, cauliflower, kohlrabi, sweet potato, tobacco stems and suckers, common calla lily, and golden or yellow cultivated calla lily, whereas a strain obtained from E. F. Smith (isolated from calla lily) was pathogenic. However, the former was pathogenic and the latter nonpathogenic in leaves of cultivated and wild iris. Subsequently, Gregg (14) suggested that the quantitative pathogenic superiority in potato tuber of a strain of *E. c. carotovora* (referred to as *Bacillus aroideae*), as compared with two other strains (referred to as *B. carotovorus*), was associated with a more rapid growth rate in culture, production of a greater quantity of pectolytic enzymes, and a reduction in the rate of acidification of the growth media.

In this study, we explored the quantitative and qualitative differences in the pathogenicity of 37 strains of soft-rot erwinias selected randomly from collections of strains in Florida. Our purpose was to determine whether host specificity could be detected among strains of *E. c. carotovora* and, if it existed, whether it was correlated with aggressiveness in common hosts for soft-rot erwinias in Florida (e.g., potato tubers and fruit of tomato and pepper).

MATERIALS AND METHODS

Strains. All strains were isolated from soft-rot lesions; 26 came from our collection, and the rest were obtained from J. W. Miller, Florida Division of Plant Industry. The host of origin included five strains from tomato fruit (*Lycopersicon esculentum* Mill.; Tom-1 to -5) (1); seven from bell pepper fruit (*Capsicum annuum* L.; Pep-1 to -7); nine from potato tubers (*Solanum tuberosum* L.; Pot-1 to -9); three each from caladium (*Caladium* × *hortulanum* Birdsey; Cal-1 to -3), fern (*Nephrolepis exaltata* L.; Fer-1 to -3), and lettuce (*Lactuca sativa* L.; Let-1 to -3); two each from cabbage (*Brassica oleracea* var. *capitata* L.; Cab-1 to -2) and cantaloupe (*Cucumis melo* L.; Mel-1 to -2); and one strain each from carrot (*Daucus carota* L.; Car-1), chrysanthemum (*Chrysanthemum* × *morifolium* L.; Chr-1), and sunflower (*Helianthus annuus* L.; Sun-1). A strain of *E. c. atroseptica* and five strains of the corn (*Zea mays* L.) pathotype of *E. chrysanthemi* obtained from the collection of Arthur Kelman, University of Wisconsin, Madison, were included as reference strains for production of disease in potato and corn, respectively. These strains were also used for positive controls for production of reducing substances from sucrose and production of phosphatase, respectively.

Some strains were stored on nutrient agar in petri plates at 4 C and transferred to fresh media every 2–5 wk. Others were stored in distilled water in screw-capped vials at room temperature for up to 6 mo. Inocula were prepared from nutrient broth shake cultures that were centrifuged and the pellets diluted in sterile distilled water based on turbidity of the stock suspension measured at 600 nm with a spectrophotometer (3).

Presumptive identification of the strains. All strains tested were presumed to be soft-rot erwinias because each pro-

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duced deep pits in crystal violet pectate medium (6), a cross-hatched colony type on crystal violet pectate medium (12), soft rot in tomato fruit and potato tuber, and an anaerobic fermentation of glucose in the Hugh-Leifson test (12). The strains were tested for growth at 36 C, production of acid from methyl-α-D-glucopyranoside (α-methylglucoside), production of reducing substances from sucrose, production of phosphatase, utilization of melibiose and cellobiose, and sensitivity to erythromycin (12). Some strains that produced reducing substances from sucrose were tested for utilization of palatinose.

Aggressiveness tests in common hosts. Mature green fruit of pepper (one fruit each of the cultivars Delray Bell, Pip, and Big Bell and two fruit of the cultivar Early Calwonder) and tomato (cv. Flora-Dade) were inoculated by a modification of the technique of Bartz and Crill (3). A cork was mounted on a metal rod and punctured with five straight pins that were spaced 10 mm apart. The pins, which protruded through the cork by about 1.5 mm, were dipped briefly in an aqueous cell suspension of bacteria and then pressed against the fruit. The experimental design included 37 strains, two concentrations of inoculum (10^8 or 10^9 colony forming units [cfu] per milliliter), 10 punctures per inoculum concentration per fruit, and three five-fruit replicates for each strain. The inoculated fruit were incubated at 30 C and >85% relative humidity (RH) for about 45 hr. The tests were repeated with the pepper Early Calwonder and the tomato cultivar Walter.

Potato tubers were inoculated by a modification of the technique of DeBoer and Kelman (8). Freshly harvested tubers (cv. Red LaRouge) were immersed in 0.5% aqueous solution of NaOCl for 10 min, rinsed with deionized water, and air dried. A cylinder of tissue, 4 mm in diameter × 5 mm in length, was removed with a flamed cork borer (No. 1) from a site midway between the stem and bud ends of each tuber. Ten microliters of water containing 10^6 cfu of bacteria was deposited in each hole, the cylinder was replaced, and the wound was covered with cellophane tape. The inoculated tubers were wrapped in wet paper towels, placed in polyethylene bags, and incubated at 30 C for 4 days. The macerated tissues at each wound site were weighed. There were six single-tuber replications for each strain. The test was repeated with tubers of the cultivar Red LaSoda. The results reported were the average of both tests.

Pathogenicity tests in a series of hosts. Potato, tobacco, and tomato plants were inoculated by a modification of the technique of DeBoer et al (7). A drop of an aqueous cell suspension containing 1×10^8 cfu/ml was applied with a Pasteur pipet to the lowest leaf axil of each plant, and a flamed straight pin was inserted through the drop and into the center of the stem and then withdrawn. The inoculated plants were incubated in a growth chamber for 7 days with a 12-hr photoperiod under 1,000 lux illumination measured at the top of the plants. For potato, six to eight stems of 5-wk-old plants of Red LaSoda were inoculated with each strain, covered with a plastic bag, and incubated at 19 C for 7 days. The test was repeated with Sebago. Symptoms of disease caused by the test strains were compared with those induced by an authentic strain of *E. c. atroseptica*. For tobacco (*Nicotiana tabacum* L. 'Havana 425'), three to four 8-wk-old plants were inoculated with each strain, covered with plastic bags, and incubated at 28 C for 7 days. The test was repeated. For tomato, three 6-wk-old plants (cv. Manalucie) were inoculated with each strain and then incubated uncovered at 29 C under high humidity (>85% RH). The test was repeated.

Six-week-old corn plants (cv. Iobelle) were inoculated by a modification of a technique originally described by Hartman and Kelman (15). One milliliter of an aqueous cell suspension of 2×10^8 cfu/ml of sterilized tap water containing 0.9% w/v Tween 20 (polyoxyethylene sorbitan monolaurate) (Chemicals Division, Atlas Chemical Industries, Inc. Wilmington, DE) was added to the whorl of plants that had been grown in 20-cm pots in a greenhouse. Five plants were inoculated with each strain and incubated uncovered in a growth chamber for 3 days at 28 C and >85% RH. Control plants were inoculated with strains of five known corn pathotypes of *E. chrysanthemi* or treated with tap water plus Tween 20.

For chrysanthemum (cv. May Shoesmith), cuttings were rooted and grown to a height of about 20 cm in a greenhouse and then were inoculated in a leaf axil near the growing tip of the stem in the same manner as were potato stems. Three plants were inoculated with each strain and then incubated uncovered in a growth chamber at 28 C as described in the corn experiment. The number of plants with visible stem lesions was recorded after 48 and 72 hr. After 7 days, stems were cut longitudinally to reveal the extent of tissue maceration and necrosis.

Statistical analyses. The percentage of wounds on fruit that became diseased was transformed by the arcsin method and analyzed with the analysis of variance test for a split-plot design. Tests were main plot factors. If the interaction of test with strain was not significant, the data for the tests were pooled and analyzed by Duncan's new multiple range test. Differences among strains for maceration of potato tubers were evaluated similarly. All analyses were done with the Statistical Analysis System (SAS Institute Inc., Box 8000, Cary, NC).

RESULTS

Identity of the strains. Two strains, Tom-3 and Tom-4, produced phosphatase and were sensitive to erythromycin; presumptively, they were *E. chrysanthemi*. All strains utilized melibiose and cellobiose; therefore, none were *E. c. betavasculorum* (12,21,29). Fifteen strains were typical of *E. c. carotovora*; they grew at 36 C but did not utilize α-methylglucoside, produce reducing substances from sucrose, or produce phosphatase. The remaining strains did not produce typical responses of *E. c. carotovora*, but none were typical of *E. c. atroseptica* (12, 21). Three grew at 36 C but produced reducing substances from sucrose, produced acid from α-methylglucoside, and utilized palatinose. Two produced acid from α-methylglucoside and grew at 36 C but did not produce reducing substances from sucrose. Eleven grew at 36 C and produced reducing substances from sucrose but did not produce acid from α-methylglucoside. Five strains did not grow at 36 C but did not produce either acid from α-methylglucoside or reducing substances from sucrose.

Host range and relative aggressiveness. Each strain caused bacterial soft-rot lesions in tomato and pepper fruits, potato tubers, and stems of tomato plants (Table 1). However, significant differences in quantity of tuber macerated and incidence of lesions in the fruit were observed. As expected, more lesions developed in the fruit when the higher inoculum concentration was used (data not shown). In the analysis of variance for these tests, the independent variables "strains" and "inoculum concentration" did not interact. Thus, the concentration did not affect the evaluation of strains for production of lesions. Also, the variable "test" did not interact with "strains"; thus, the difference in the production of lesions by the different strains was comparable between the two tests. Similarly, in the test with potato tubers, the variables "strains" and "test" did not interact; thus, differences among the strains for quantity of tuber rotted was consistent between the two tests.

In the two tests with tomato plants, every strain caused a darkening at the point of inoculation, water-soaking, and maceration of stems (Table 1). As the maceration progressed, the upper portion of the plants toppled. Within each set of plants inoculated with a given strain, the rate of symptom development was similar. Eighteen strains caused the toppling of plants within 24 hr in each of the two tests, whereas 14 strains caused symptoms between 24 and 48 hr. Thus, most of the strains produced a consistent disease response over both tests and plants.

The strains varied in pathogenicity in the four remaining test hosts (Table 1). In plants of chrysanthemum, corn, and tobacco, lesions appeared within 1–3 days or not at all. Plants of chrysanthemum or tobacco, free of symptoms at 48 or 72 hr after inoculation, respectively, remained healthy for the rest of the incubation period. In potato plants, the disease caused by the pathogenic test strains within the 7-day incubation period was similar to that caused by a reference strain of *E. c. atroseptica*. Water-soaking began at the point of inoculation and progressed in both directions. Tissue behind the margin of water-soaking became macerated, and the entire diseased portion of the stem darkened. Only two strains, Pep-6 and Let-1, failed to produce the same host response in the first as compared with the second test, whereas all strains produced the same response in each of the six to eight stems into which they were inoculated. In tobacco, water-soaking developed about the point of inoculation and spread both upward and downward. The interior of the stem became macerated and dark brown. Only three strains, Tom-5, Pep-6, and Fer-1, produced symptoms within a different period in the first test than the second test. The strains produced the same response in each of the three to four stems into which they were inoculated. In stems of chrysanthemum, a water-soaking and tissue maceration spread downward from the point of inoculation. The upper portion of the plants toppled. When the stems of the diseased plants were cut open at the end of the test, vascular discoloration was observed several centimeters below the margin of the tissue maceration. Plants of sweet corn inoculated with 23 strains developed a darkening and water-soaking of the lower pseudostem that was associated with a wilting of the leaf emerging from the whorl. The meristem and other internal tissues rotted, and many of the plants toppled, or the whorl could be easily separated from the rest of the plant. The five reference strains of *E. chrysanthemi* from corn caused similar symptoms. In some sets of plants inoculated with a strain that caused disease, one or two of the plants remained healthy. These were considered escapes associated with whorl morphology (15).

Differences in aggressiveness in the common hosts. In general, strains that

Table 1. Pathogenicity of 37 strains of soft-rot erwinias from Florida to various hosts[s,t]

Strains	Days to disease[u] after stem inoculation				Disease after 7 days in Potato	% Wounds diseased		Weight of diseased tissue in potato tubers (g)[v]
	Chrysanthemum	Tobacco	Corn	Tomato		Tomato fruit	Pepper fruit	
Tom-1	2	...[w]	...	2	−	42 d–l[x]	64 e–g	24de
Tom-2	...	...	...	2	−	24 l	42 i–m	NT[y]
Tom-3	...	3	2	1	+	60 a–c	80 b–d	19 f–h
Tom-4	...	...	3	1	−	59 a–d	90 ab	33 b
Tom-5	1	2/3[z]	2	1	+	52 b–h	94 a	20 fg
Pot-1	...	...	...	2	+	44 c–k	46 h–l	10 k–m
Pot-2	1	2	2	1	+	38 e–l	86 bc	17 gh
Pot-3	2	...	...	1	+	28 kl	26 m	7 m–o
Pot-4	1	2	3	2	+	46 c–j	52 g–i	6 m–o
Pot-5	...	...	...	2	−	30 i–l	30 lm	22 ef
Pot-6	2	...	...	1	−	35 h–l	44 i–m	15 gh
Pot-7	2	3	3	1	−	36 gl	50 g–k	12 i–k
Pot-8	2	2	3	1	+	30 i–l	32 k–m	11 j–l
Pot-9	1	2	3	1/2	−	48 b–i	46 h–l	16 gh
Pep-1	...	...	...	2	−	24 l	28 lm	3 o
Pep-2	1	2	3	1	+	37 f–l	78 c–e	22 ef
Pep-3	1	2	2	1/2	−	56 b–e	70 d–f	19 f–h
Pep-4	...	...	...	2	+	30 i–l	28 lm	15 h–j
Pep-5	...	...	3	1	−	41 e–l	28 lm	7 l–o
Pep-6	1	2/3	3	2	+/−	54 b–f	74 c–e	25 de
Pep-7	...	...	3	1	−	38 e–l	38 i–m	19 f–h
Cal-1	...	...	...	1/2	−	52 b–h	74 c–e	8 k–n
Cal-2	...	...	...	2	−	53 b–g	76 c–e	6 m–o
Cal-3	...	...	...	2	−	72 a	90 ab	6 m–o
Fer-1	1	3/2	2	1	+	44 c–k	60 f–h	40 a
Fer-2	...	...	...	2	−	38 e–l	88 a–c	9 k–n
Fer-3	1	2	3	1	−	64 ab	86 a–c	28 cd
Let-1	1	2	3	1	+/−	56 b–f	84 b–d	29 c
Let-2	2	...	...	2	−	26 kl	34 j–m	7 m–o
Let-3	2	3	...	2	−	29 i–l	40 i–m	5 no
Cab-1	2	3	3	1	+	40 e–l	88 a–c	17 gh
Cab-2	1	...	3	1	+	41 e–l	78 c–e	17 gh
Mel-1	2	3	3	1	+	43 d–k	80 b–d	29 c
Mel-2	1	...	...	2	−	51 b–h	80 b–d	15 h–j
Car-1	2	2	3	2/1	−	44 c–k	52 g–i	12 i–k
Chr-1	2	...	3	1	−	28 j–l	38 i–m	6 no
Sun-1	1	2	3	1	+	40 e–l	76 c–e	26 c–e

[s] For all plants except corn, a drop of 1×10^8 cfu/ml was placed in a leaf axil and a straight pin was inserted through the droplet to a point halfway through the stem and then removed. For corn, 1 ml of 2×10^8 cfu/ml with 0.9% Tween 20 was added to each whorl. All plants were incubated under high humidity and at 27–29 C except for potato (19 C). The tests with potato, tobacco, and tomato were repeated.

[t] Each fruit was punctured 10 times with pins previously dipped in 1×10^8 cfu/ml and then incubated at 30 C for 45 hr. There were two five-fruit replicates in each of two separate tests.

[u] Stem collapse.

[v] A cylinder of tissue (4 mm in diameter and 5 mm long) was removed with a cork borer, 10 µl containing 1×10^6 cfu was added, the tissue was replaced, and the wound was sealed with wax. The entire tuber was wrapped with a wet paper towel, enclosed in a polyethylene bag, and stored at 30 C for 4 days. There were six single-tuber replicates in each of two separate tests.

[w] No disease at the end of the 7-day incubation period.

[x] Values within each column not followed by the same letter were statistically different at $P = 0.05$ in the Duncan's new multiple range test.

[y] Not tested.

[z] Disease in first/second tests.

produced higher incidences of disease in the fruit also macerated larger amounts of the potato tubers. For example, the average of all strains for weight of tissue rotted during the 4-day incubation period was 15.9 g per tuber, whereas the averages for the strains that ranked among the upper quarter for aggressiveness in pepper or tomato fruit were 19.0 and 20.5 g per tuber, respectively. In contrast, Fer-1, the most aggressive strain in the tubers, was ranked in a tie for 13th place for tomato fruit (incidence = 44%) and 20th place among pepper fruit (incidence = 60%). The most aggressive strain in tomato, Cal-3, caused an incidence of 72% in that host and 90% in pepper fruit (tied for the second highest ranking) but only macerated an average of 6 g per tuber. Thus, the capacity of the strains to produce lesions in wounded pepper or tomato fruit was not necessarily indicative of their ability to rapidly macerate potato tubers. The reverse statement could also be made, that is, the ability of a strain to macerate tubers was not always correlated with its ability to produce lesions in the fruit.

Differences in pathogenicity in the series of hosts. Many of the strains failed to produce lesions in each of the host plants incubated under ideal conditions for disease, that is, high humidity and temperatures of 28 C for corn, chrysanthemum, tomato, and tobacco or 19 C for the blackleg disease of potato. This failure appeared to be complete as several individual plants were inoculated with each strain within each test, but none became diseased. In contrast, strains that were pathogenic caused lesions in each plant. Strains that appeared highly aggressive in potato tubers or fruit were not always pathogenic in each of the hosts in the series. For example, Tom-4 macerated 33 g per tuber and ranked second for aggressiveness in tubers but failed to initiate lesions in stems of chrysanthemum, tobacco, or potato. Conversely, Pot-4 macerated only 6 g per tuber but produced lesions in each of the hosts.

Strains isolated from lesions on a particular host were not the most aggressive ones in that host. In tomato fruit, the average incidence caused by strains from tomato, fern, or caladium was 47, 49, or 59%, respectively. However, the highest incidence was caused by a strain that had been isolated from a rotted caladium corn. In pepper fruit, the average incidence caused by strains isolated from soft-rotted pepper, fern, or caladium was 49, 78, or 80%, respectively. The most aggressive strain originated from a soft-rot lesion on a tomato fruit. In contrast, the most aggressive strain from pepper was ranked below 11 strains from other hosts. Strains isolated from diseased potato tubers macerated an average of 14.5 g per tuber, whereas those from fern, tomato, and caladium averaged 25.7, 24.0, and 6.7 g per tuber, respectively.

DISCUSSION

The 35 strains of *E. c. carotovora* and the two strains of *E. chrysanthemi* that we tested clearly differed in aggressiveness in common hosts (e.g., tomato fruit, pepper fruit, and potato tuber) and differed in pathogenicity in a series of hosts (e.g., plants of chrysanthemum, corn, potato, tobacco, and tomato). There have been previous reports of differences among strains of *E. c. carotovora* for aggressiveness (14,17,19) and for pathogenicity in certain hosts (22,23) as outlined above, but these reports were focused primarily on etiology or taxonomy and have not been accepted as evidence for host specificity among strains of *E. c. carotovora*.

In our tests, the most aggressive strains in the fruit produced an average incidence three or more times that produced by the least aggressive strain. Previously, such differences have been associated with resistance in tomato fruit (3) and with 10- to 10,000-fold differences in the inoculum concentration used to inoculate fruit (2,4). In our tests, the average weight of potato tuber macerated by the most aggressive strain was more than 10 times that macerated by the least aggressive strain. Lapwood et al (20) reported a four- to sixfold difference for weight of tuber macerated between the highest and lowest ranking entries in the test of 21 cultivars for resistance to tuber rot caused by *E. c. atroseptica*. The lowest-ranking cultivars were considered to possess resistance to the disease. Thus, the differences in disease produced in common hosts by the strains tested here were consistent with those associated in other reports with resistance and susceptibility or major differences in inoculum concentration.

Some differences in aggressiveness among strains of *E. c. carotovora* may be caused by subculturing. Freshly isolated strains are more likely to have retained pathogenicity and aggressiveness than strains obtained from culture collections (5,26). However, in our tests, the aggressiveness of certain strains differed with host and varied among strains that were isolated at the same time (e.g., Tom-1 to -5) (1). Thus, the lack of aggressiveness or failure to cause disease did not appear to have resulted from subculturing or other laboratory practices (26).

We suggest that the failure of certain strains to cause disease in one or more of the test hosts is evidence for host specificity among strains of *E. c. carotovora*. Whether every strain would have caused disease in every host if the postinoculation environment, host susceptibility, or pathogen population had been more conducive is subject to speculation. Whitney and Mackey (30) suggested that the aggressiveness in sugar beet expressed by strains of *E. c. betavasculorum* varied with cultivar and environment. A strain that was highly aggressive in plants grown in the greenhouse was not so aggressive when the same lines were planted in the field. In our tests, inoculated plants were incubated under ideal conditions (humidity and temperature) for disease. The relative humidity was near saturation in most tests. Except for the potato stem test, the temperatures used were optimal for the growth of the organism and the development of disease (27,31). In the potato stem test, the temperature (19 C) was ideal for blackleg. Since this temperature is nearly 10 degrees C below the optimum for pathogenicity by *E. c.* subsp. *carotovora*, it is possible that some of the nonpathogenic strains would have been able to cause an aerial soft rot or blackleg if the temperature had been 28–30 C. However, each of the plant species we used was grown in a greenhouse and inoculated while still young and succulent, a situation widely known to enhance the susceptibility of plants to disease. The inoculum concentration used led to the introduction of about 10^5 to 10^6 cfu into freshly wounded tissues (2). Larger populations would not be introduced into potential infection courts in nature except where inoculation occurs from direct contact with diseased tissue. Therefore, strains that were not pathogenic in certain hosts in our tests would not be likely to initiate disease in those hosts in nature.

The physiological phenotype of the strains tested here was not associated with a particular plant response. Certain differences in pathogenicity and aggressiveness among the taxons of the soft-rot erwinias have been related to the optimum growth temperature (26,27). For example, strains of *E. c. atroseptica* have a lower optimum growth temperature (27 C) than strains of *E. c. carotovora* (28–30 C) (27). Compared to strains of the latter, strains of *E. c. atroseptica* are more aggressive in potato tubers at 15 C (20) and cause blackleg at lower soil temperatures 19–22 C (13,24,25). In contrast, strains of *E. c. carotovora* may cause blackleg symptoms in potatoes grown at temperatures above 24 C (13), in warmer soils (24), and at 30 C (25). However, in the tests reported here, the strains that did not grow at 36 C (Pot-5, Pot-8, Pep-4, Pep-5, and Pep-7) were not very aggressive in the common hosts. Two of these strains did not cause a blackleg or soft rot in potato stems incubated at 19 C. Thus, their weak aggressiveness in the common hosts would not appear to be caused by the incubation temperature. In contrast, strains that produced other responses in the physiological tests, such as reducing substances from sucrose, were as likely to be highly aggressive in one or more of the hosts as were strains that did not produce other responses (data not shown).

The failure of many strains to be highly aggressive toward the host of origin is

not easily explained. Dickey (11) observed that certain strains of *E. chrysanthemi* were not pathogenic on their host of origin and suggested that such strains may not have initiated the lesions from which they were isolated. Alternatively, weakly aggressive strains may have been the only ones to be introduced or present in infection courts when the host was predisposed.

Several of the test strains caused a rapid stalk rot of sweet corn. In general, *E. c. carotovora* is not considered to be a pathogen of corn (16). The Tween 20 component of the inoculum appears to have predisposed the plants to disease. Visible phytotoxicity was not observed in control plants treated with the solution of Tween. However, in several subsequent tests, when surfactant was omitted from the inoculum, strains of *E. c. carotovora* failed to cause a stalk rot (Bartz, unpublished). Thus, we cannot conclude that some of our strains of *E. c. carotovora* have the ability to be natural pathogens of corn although they did vary in their ability to cause stalk rot when Tween-amended inoculum was used.

The physiological phenotypes of strains of the soft-rot erwinias are in a continuum over the major taxons of the group. Thus, it would appear likely that the pathogenic phenotypes also would be in a continuum. Strains of *E. chrysanthemi* have host specificity (10); therefore, strains of *E. carotovora* might also be expected to be host specific. Indeed, two subspecies, *E. c.* subsp. *atroseptica* and *E. c.* subsp. *betavasculorum*, have highly restricted host ranges (11,25,27). Now, we report that certain strains within *E. c.* subsp. *carotovora* also show host specificity and suggest that plant reaction groups can be set up for strains of *E. c.* subsp. *carotovora*, just as it has been done for those of *E. chrysanthemi* (10).

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