Erwinia chrysanthemi: Reaction of Eight Plant Species to Strains from Several Hosts and to Strains of Other *Erwinia* Species

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ABSTRACT

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Six plant species (*Chrysanthemum morifolium, Dieffenbachia amoena, D. maculata, Philodendron panduriforme, P. selloum,* and *Syngonium podophyllum*) were tested by standardized methods for reaction to 383 strains of *Erwinia chrysanthemi* from 35 plant species, subspecies, or cultivars, and 99 strains of other *Erwinia* species. All strains, except two strains of *E. cypripedii* and one of *E. rhapontici*, produced a positive reaction for *C. morifolium* and were separated into 10 plant reaction groups based on the reaction of the other five plant species. Two-hundred, thirty-nine strains of *E. chrysanthemi* and 93 strains of other *Erwinia* species failed to produce a positive reaction in any of the five plant species. Only strains of *E. chrysanthemi* originally isolated from dieffenbachia caused a positive reaction for *D. amoena* and *D. maculata.* Only strains isolated from syngonium and one strain of *E. carotovora* subsp. *carotovora* (*E. c.* subsp. *carotovora*) from caladium and one strain from banana produced positive reactions for *S. podophyllum*; some syngonium strains and the caladium strain of *E. c.* subsp. *carotovora* also were positive for *P. panduriforme* and/or *P. selloum.* Positive reactions were produced in philodendron plants by 126 strains of *E. chrysanthemi* and four strains of *E. c.* subsp. *carotovora* isolated from 22 hosts. Carnation plants (*Dianthus caryophyllus* 'Improved White Sim') were inoculated with 166 selected strains of *E. chrysanthemi* and 11 strains of other *Erwinia* spp. Symptoms were produced by 57 strains of *E. chrysanthemi* of which 48 of the strains originally had been isolated from *Dianthus* sp. Leaves of corn line NY3× D50 were tested for reaction to 225 strains of *E. chrysanthemi* from 29 hosts and 44 strains of other *Erwinia* spp. Seventy-three strains of *E. chrysanthemi* from 14 hosts caused positive or slightly positive reactions of the corn leaves. All eight plant species were tested for reactions to 108 of the 383 strains of *E. chrysanthemi.* Although all strains produced a positive reaction for chrysanthemum, 32 strains failed to produce a positive reaction for the other seven plant species. The remaining 76 strains were classified into 10 plant reaction groups.

Strains of *Erwinia chrysanthemi* Burkholder, McFadden, and Dimock have been tested for virulence or pathogenicity to plants or plant parts of 118 plant species or cultivars (2–6, 10–15, 17–29, 31–33, 35–39, 42). The tests were made with one or more strains isolated from 27 plant species or cultivars. Unfortunately, the diversity of inoculation methods, environmental parameters, plant species, and strains of the pathogen used, makes it difficult to utilize this wealth of information for the evaluation of the potential virulence and host range of strains isolated from a specific host.

The phenotypic characteristics of 352 strains of *E. chrysanthemi* from 28 hosts and the separation of the strains into six infrasubspecific subdivisions previously have been reported by Dickey (7) and Dickey and Victoria (8). The reaction of selected plant species to the strains of *E. chrysanthemi* were concurrently determined by standardized inoculation methods.

The purpose of the investigation was to determine whether any relationship could be found between the plant reactions, the phenotypic properties, and the original host of the strains.

MATERIALS AND METHODS

Bacterial strains. The host, strain number, source, and location of 352 strains of *E. chrysanthemi* have been given elsewhere (7,8). The following 31 strains also were included: five strains from *Allium cepa* L. (TA6, TA9, TA11, LA2, LA4, from Hsu, Taiwan); two from *Alocasia* sp. (078-255, 078-368, from Miller, Florida); 12 from *Ananas comosus* (L.) Merrill (G18-1 to G18-12 from Gonzalez, Costa Rica); one from *Iris ensata* Thunb. (EI1 from Goto, Japan); eight from *Oryza sativa* L. (ER1, ER4 to ER10; from Goto, Japan); two from *Solanum tuberosum* L. (LG19 from Gutarra, Peru, and SP1 from Hsu, Taiwan); and one from *Zea mays* L. (920, Otta, South Dakota). Strain SP1 from potato possessed the phenotypic characteristics of subdivision II, whereas the other 30 strains were identified as members of subdivision IV (7,8). The plant reactions for 77 strains of *E. carotovora* subsp. *carotovora,* 16 of *E. carotovora* subsp. *atroseptica,* two of *E. cypripedii*, one of *E. rhapontici*, and three of *Erwinia* sp. from sugar beet also were ascertained.

Inoculation tests. The bacteria were grown on yeast extract-dextrose-calcium carbonate agar (YDC) (1), or modified YDC (9) for 24 hr at 27 C unless otherwise noted. For the injection-infiltration of leaves (16), the bacteria were suspended in sterile distilled water and adjusted to OD of 0.30 at 620nm in a Spectronic 20 (Bausch & Lomb) spectrophotometer. The colony-forming units (CFU) for a random selection of suspensions ranged from 3.5 to 7.0 $\times 10^8$/ml. The suspensions or dilutions to required concentrations were used within 1 hr after preparation. All plants were grown in a steam-treated mixture of soil, perlite, and peat moss and a commercial soluble fertilizer was applied once each week.

Chrysanthemum morifolium 'Giant #4 Indianapolis White.' The inoculation of stems of whole plants that were held at 30 C and high relative humidity for 1–2 wk after inoculation was not satisfactory because the results were variable as noted by Burkholder et al (4). Several methods which utilized unrooted cuttings were tried and the following method was selected. Round, pointed toothpicks were sterilized by autoclaving them in water for 30 min, removed from the water, and dried in sterile petri dishes. Stems of unrooted cuttings were cut 40 mm below the apical expanding leaves. The tips of the toothpicks were infested by scraping cells from 24-hr YDC culture and were inserted about 2 mm into base of three cuttings for each strain; each strain was tested at least two times for a total of six or more cuttings. The inoculated cuttings were submerged as far as possible into a test tube (16 × 150 mm) filled with sterile distilled water. The tubes with cuttings were placed in a test tube rack and the rack was enclosed in a plastic bag. The rack was placed in the laboratory at 22 C with continuous overhead light (344 lx). After 5 days, the cuttings were examined for external and internal tissue breakdown and the amount of breakdown extending from the base of the cutting was measured.

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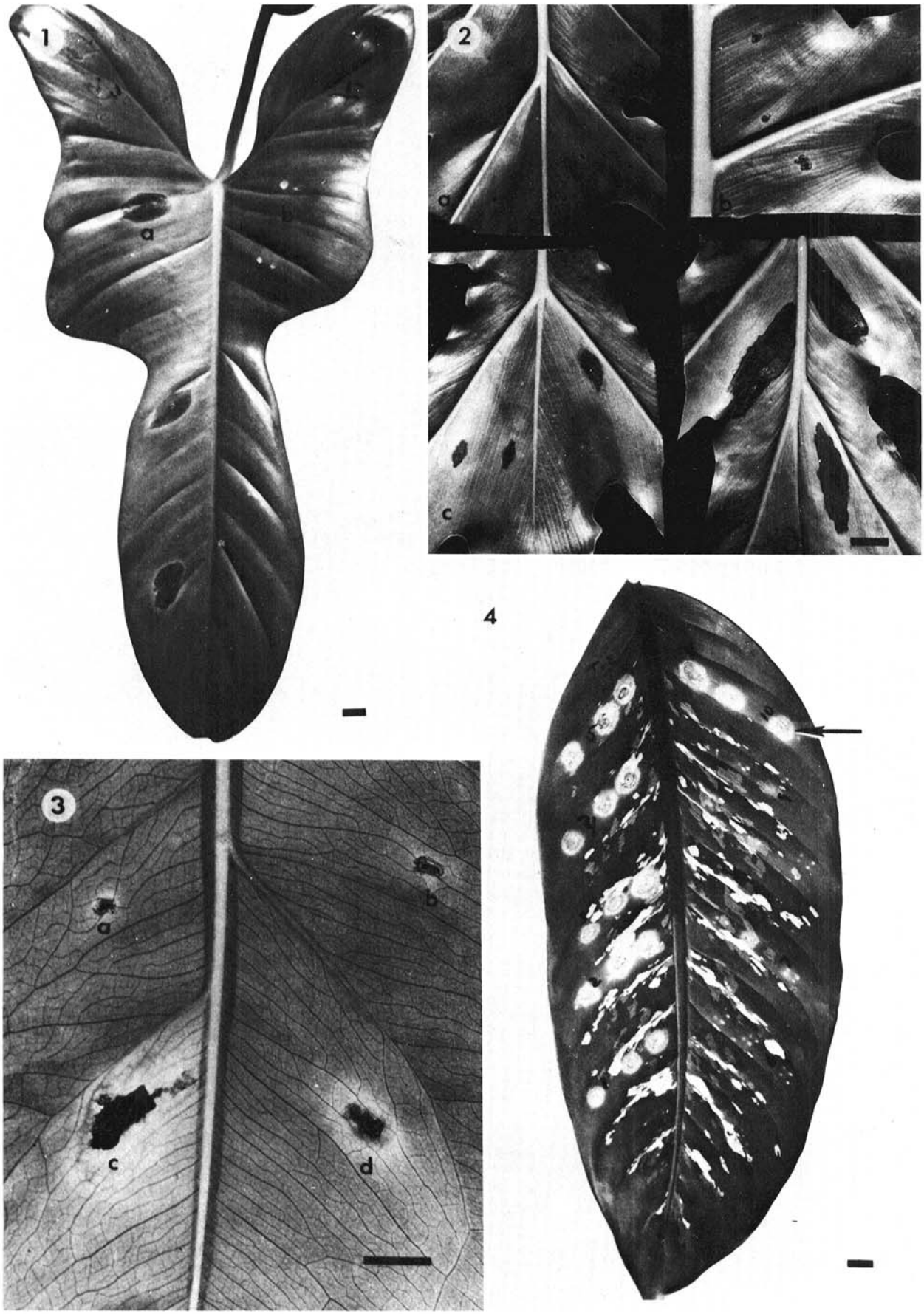

Figs. 1–4. Plant reactions to strains of *Erwinia chrysanthemi* and other *Erwinia* species. **1,** Positive (a) and negative (b) leaf reaction by *Philodendron panduriforme* 14 days after inoculation. **2,** Positive (c,d) and negative (a,b) leaf reaction by *Philodendron selloum* 7 days after inoculation. **3,** Positive (c,d) and negative (a,b) leaf reaction by *Syngonium podophyllum* 'Green Gold' 7 days after inoculation. **4,** Leaf reaction by *Dieffenbachia amoena* to five strains of *E. chrysanthemi*. Left side injected-infiltrated with suspensions containing ~10^8 CFU/ml; right side with ~10^6 CFU/ml. Only one strain (arrow) caused a positive reaction with 10^6 CFU/ml at 21 days after inoculation, whereas the other four strains were negative. Bars represent 1 cm.

Dieffenbachia maculata [*D. picta*], *Dieffenbachia amoena, and Philodendron panduriforme.* Plants with 5–8 expanded leaves were inoculated similar to the method described by Mazzucchi (24,25). Only the three leaves immediately below the expanding or recently expanded leaf were inoculated. The newly expanded leaves were not used because a positive reaction often was produced, whereas no reaction occurred in the three leaves immediately below. Each leaf was inoculated with 4–5 strains plus the positive check strain; a sterile distilled water control also was included. Each leaf received three inoculations of each strain for a total of nine inoculations per strain per plant. The inoculated plants were kept on the greenhouse bench and plant reactions were recorded 2, 5, 10, 14, and 21 days after inoculation. Each strain was tested during each of the following periods: January to April (average temperature = 24.4 C), May to August (24.3 C), and September to December (23.9 C) to reduce the effect of temperature, light intensity, and variability of plants. The initial inoculations were made by injection-infiltration (16) of suspensions containing ~10^8 CFU/ml. When plant reactions were not produced 2–21 days after inoculation by a strain, all subsequent inoculations of the strain were made with 10^8 CFU/ml. When a strain caused a plant reaction with 10^8 CFU/ml between 2–14 days (Fig. 1), subsequent inoculations of the strain were made with suspensions containing 10^8 and 10^6 CFU/ml. Only strains which produced plant reactions with 10^8 and 10^6 CFU/ml (Fig. 4, arrow) were rated as positive. The average size of the infiltrated leaf area was 1.0 × 1.25 cm for *D. maculata* and *D. amoena,* and 0.56 × 1.01 cm for *P. panduriforme.* Approximately 140 µl of suspension was used for each injection. Strain B-27 served as the positive check strain for the dieffenbachia plants and CU156 for *P. panduriforme.*

Philodendron selloum. Mature plants with 3–4 expanded leaves were kept on the greenhouse bench until inoculated. Only the two leaves immediately below the expanding or recently expanded leaf were inoculated. The plants were inoculated by removing a small loopful of cells from a 24-hr slant culture and placing them on the leaf surface. A sterile dissecting needle was punctured through the cells and leaf, and the bacterial cells were gently teased into the wound by the needle to assure intimate contact of cells with the leaf tissues beneath the epidermis. Each leaf was inoculated with seven strains and the check strain, plus a sterile needle puncture. The plants were immediately placed in a glass mist chamber which was located in the greenhouse and was maintained at 25.6 ± 2C with atomized mist for 30 sec/min and continuous supplemental light of 2,800 lx. Plant reactions were recorded 2, 5, and 7 days after inoculation. Strain 160 was used as the positive check. Leaf reactions usually were visible after 2 days. The spreading, water-soaked lesions (Fig. 2 c, d) were rated as positive, while the dry, negligible to small lesions (Fig. 2 a,b) were considered as negative.

Seedlings of *P. selloum* were compared with mature plants for reaction to 196 strains. The seedlings were transplanted to flats and kept on the greenhouse bench for 47–65 days when they were selected for uniformity of size and lack of contact with neighboring seedlings. The seedlings were inoculated by the needle puncture method described for mature plants. The flats of inoculated seedlings were immediately placed in the mist chamber and observed for plant reaction at 2 and 5 days after inoculation. The agreement of results for the seedlings and the mature plants was 94.9%; therefore, it was decided to discontinue the seedling test.

Syngonium podophyllum 'Green gold.' Stem cuttings were rooted under mist, transplanted into 10-cm diameter clay pots, staked, and grown in the greenhouse until 4–6 fully expanded leaves had developed. The first and third leaves below the expanding leaf of each plant were inoculated with a test strain and the second and fourth leaves were used for the check strain and the noninoculated control. The inoculated plants were placed in the mist chamber and observed for plant reaction at 3, 5, and 7 days after inoculation. The plants were inoculated by the needle puncture method described for *P. selloum* except that the leaf was gently punctured three times rather than only once. The check strain was B-73. Only lesions that developed and expanded beyond the point of inoculation (Fig. 3 c, d) and that had black to dark-brown centers and chlorotic margins were rated as positive plant reactions. The development of lesions restricted to the point of inoculation or the immediate surrounding area (Fig. 3 a,b) was recorded as negative plant reaction. The development of lesions usually was not as rapid and the lesions were not as large on the younger leaves as on the older leaves.

Dianthus caryophyllus 'Improved White Sim.' Only 166 strains of *E. chrysanthemi* and 11 of other *Erwinia* species were tested. The roots of the cuttings were inoculated with cells from 48-hr-old nutrient agar cultures as described by Nelson and Dickey (30). The plants were observed for at least 108 days after inoculation for the development of symptoms as previously illustrated (30).

Zea mays. The test was a modification of the leaf puncture inoculation method developed by Victoria (38). The two or three top leaves of corn line NY3×D50 (New York State Seed Improvement Cooperative, Inc., Cornell University, Ithaca, NY 14853) were removed from plants grown for approximately 30 days after seeding. The plants were grown in a chamber with 16-hr days at 26 C and a light intensity of approximately 13,000 lx and 8-hr nights at 21 C, or in the greenhouse. The center portions (about 10 cm long) of the leaves were excised and placed on sterile petri plates in a shallow glass baking dish which was lined with wet paper towels. An aqueous suspension of bacterial cells from 24-hr-old nutrient agar culture was prepared which contained approximately 10^8 CFU/ml. The adaxial surface was inoculated at 10 sites (one site/strain) by gently pressing the tip of an Eppendorf micropipet against the epidermal tissue to make a slight depression or wound and then depositing 5 µl of the suspension onto the depression. The glass dish was tightly covered with Glad Wrap® (Union Carbide Corp., 270 Park Ave., New York, NY 10017) and placed in a 32–33 C incubator without light for 24 hr. Each leaf was inoculated with the check strain 86. A water-soaked lesion ≤6 mm in length was rated as positive, 3–5 mm was slightly positive, and ≥2 mm was negative. The results for 225 strains of *E. chrysanthemi* from 29 hosts and 44 strains of other *Erwinia* species are reported herein.

RESULTS

All strains of *E. chrysanthemi* and the strains of other *Erwinia* species, except the two strains of *E. cypripedii* and one strain of *E. rhapontici,* produced a basal soft rot in cuttings of *Chrysanthemum*

TABLE 1. Groups of reactions by five plant species to 383 strains of *Erwinia chrysanthemi* and 99 strains of other *Erwinia* species (groups 1–10) and by seven plant species to 108 strains of *E. chrysanthemi* (groups 11–21)

Plant species	Plant reaction group																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Dieffenbachia amoena Hort.	–[a]	+	+	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–
Dieffenbachia maculata (Lodd.) G. Don [*D. picta* Schott]	–	–	+	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–
Philodendron panduriforme (HBK) Kunth.	–	–	–	+	+	+	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–
Philodendron selloum C. Koch	–	–	–	–	+	+	–	+	+	–	–	–	–	–	–	–	+	+	+	+	+
Syngonium podophyllum Schott	–	–	–	–	–	+	+	–	+	+	–	–	–	–	–	–	–	–	–	+	+
Dianthus caryophyllus L.	···	···	···	···	···	···	···	···	···	···	–	+	–	–	–	–	–	–	+	–	–
Zea mays L.	···	···	···	···	···	···	···	···	···	···	–	–	+	–	+	–	–	+	+	–	+

[a]Symbols: –, negative plant reaction; +, positive plant reaction; ···, no test.

morifolium. A correlation between the amount of breakdown and vascular discoloration from the base of the cuttings and the source or original host of the strains could not be established due to the variability of reaction between cuttings. Therefore, strains from various hosts could not be distinguished by this test because the results were based only on the qualitative development of basal soft rot.

The strains of *E. chrysanthemi* and other *Erwinia* species were assigned to a plant reaction group (hereafter referred to as 'group') based on the reactions of the five or seven plant species (Table 1). The infrasubspecific subdivision (7,8), original host, and number of strains of *E. chrysanthemi* in each group are shown in Table 2. A list of the strains for groups 2–10 and 12–21 that gives the subdivision, original host, and group is available from the author. A total of 239 strains (62.4%) of *E. chrysanthemi* failed to produce a positive reaction in any of the five plant species (group 1). Ninety-three of the 99 strains of other *Erwinia* species also belong in group 1. The following strains of *E. carotovora* subsp. *carotovora* were the exceptions: strains 191 and 192 from *Epipremnum aureum* (Linden & André) Bunt [*Scindapsus aureus* (Linden & André) Engl.] (Florida), B-56 from *Caladium* sp. (Florida), and 74-8 from *Allium cepa* L. (Barbados) in group 8; strain B-58 from *Caladium* sp. (Florida) in group 9; and strain 366 from rhizome of *Musa* sp. (Panama) in group 10.

Although 75 strains from 21 hosts of subdivisions I, IV, and V produced a reaction in *Dieffenbachia amoena* when the inoculum

TABLE 2. Subdivision, original host, and reaction of 383 strains of *Erwinia chrysanthemi* to five plant species (groups 1–10) and 108 strains to seven plant species (groups 11–21)[a]

Sub-division[b]	Original host	Number of strains per plant reaction group																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
I	*Dieffenbachia maculata* (Lodd.) G. Don [*D. picta* Schott]	5	...	3	...	...	...	...	...	...	...	2	...	1	...	...	...	...	...	...	...	...
	Dieffenbachia amoena Hort.	2	...	6	...	...	...	...	...	...	...	...	...	...	1	2	...	...	...	...	...	...
	Dieffenbachia sp.	1	1	2	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...
	Dieffenbachia 'Exotica'	2	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...
II	*Parthenium argentatum* A. Gray	3	...	...	...	...	...	...	...	...	...	1	...	1	...	...	...	...	...	...	...	...
	Solanum tuberosum L.	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
III	*Chrysanthemum morifolium* Ramat.	9	...	...	...	...	...	...	2	...	...	1	...	...	...	...	...	1	...	...	...	...
	Chrysanthemum superbum Bergmans ex J. Ingram [*C. maximum* Hort.]	2	...	...	...	...	...	...	1	...	...	1	...	...	...	...	...	1	...	...	...	...
	Dianthus caryophyllus L.	1	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...
	Euphorbia pulcherrima Willd.	8	...	...	...	...	...	...	2	...	...	3	...	1	...	...	...	...	...	...	...	...
IV	*Aglaonema commutatum* Schott 'Treubii'	1	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...
	Allium cepa L.	2	...	...	...	...	...	...	3	...	...	...	...	...	...	...	...	...	...	...	...	...
	Alocasia sp.	...	...	...	...	...	...	...	2	...	...	...	...	...	...	...	...	...	...	...	...	...
	Ananas comosus (L.) Merrill	5	...	...	...	...	...	...	8	...	...	1	...	...	...	...	...	...	...	...	...	...
	Chrysanthemum morifolium Ramat.	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
	Cyclamen sp.	...	...	...	...	...	...	...	2	...	...	...	...	...	...	...	...	2	...	...	...	...
	Dieffenbachia sp.	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...
	Dracaena marginata Hort.	...	...	...	...	...	...	...	3	...	...	...	...	...	...	...	...	2	...	...	...	...
	Ipomoea batatus (L.) Lam.	...	...	...	...	...	...	...	3	...	...	...	...	...	...	...	...	...	...	1	...	...
	Iris ensata Thunb.	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
	Musa sp. Cavendish cultivars	8	...	...	...	...	...	...	4	...	...	4	...	4	...	...	...	2	1	...	...	...
	Oryza sativa L.	8	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
	Pelargonium capitatum L'Her. ex Ait.	1	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...
	Philodendron selloum C. Koch	10	...	...	4	10	...	...	41	...	...	1	...	...	...	...	...	...	1	...	...	...
	Philodendron panduriforme (HBK) Kunth.	8	...	...	3	1	...	...	2	...	...	2	...	...	...	...	...	1	...	...	...	...
	Philodendron scandens C. Koch & Sello subsp. *oxycardium* (Schott) Bunt	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...
	Philodendron sp.	2	...	...	5	2	...	...	2	...	...	...	...	...	...	...	2	1	...	...	...	...
	Saintpaulia ionantha H. Wendl.	1	...	...	...	...	...	...	8	...	...	...	...	...	...	...	...	1	...	...	...	...
	Solanum tuberosum L.	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
	Syngonium podophyllum Schott	10	...	...	...	...	3	1	1	11	2	...	...	3	...	...	...	...	...	...	1	4
	Zea mays L.	36	...	...	...	...	...	...	2	...	...	1	...	6	...	...	...	...	...	...	...	...
	Zea mays L. var. *rugosa* Bonaf.	8	...	...	...	...	...	...	...	...	...	...	...	2	...	...	...	...	...	...	...	...
V	*Begonia intermedia* Hort. 'Bertinii'	1	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...
	Dahlia pinnata Cav. [*D. variabilis* (Willd.) Desf.]	9	...	...	...	...	...	...	...	...	...	3	4	...	...	...	...	...	...	...	...	...
	Daucus carota L. var. *sativus* Hoffm.	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	1	...	...	...	...
	Dianthus barbatus L.	2	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...
	Dianthus caryophyllus L.	55	...	...	...	...	...	...	...	...	...	5	24	...	...	...	...	...	...	...	...	...
	Dianthus sp.	3	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...
	Lycopersicon esculentum Mill.	1	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...
	Sedum spectabile Boreau	1	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...
VI	*Musa paradisiaca* L.	30	...	...	...	...	...	...	...	...	...	3	...	...	...	...	...	...	...	...	...	...

[a] The 108 strains were selected from plant reaction groups 1, 3, 8, and 9.
[b] See literature references 7 and 8 for phenotypic characteristics of strains included in each infrasubspecific subdivision.

concentration was approximately 10^8 CFU/ml, only 12 strains of subdivision I (Table 2) produced a typical reaction when approximately 10^6 CFU/ml were used (Fig. 4). The reactions produced by inocula containing 10^8 CFU/ml included water-soaked lesions followed by necrosis which developed between 2 and 5 days after inoculation, temporary water-soaking followed by a dry, light-brown necrosis of the infiltrated tissue, or a dry necrosis of the infiltrated tissue within 48 hr, similar to the results reported by Mazzucchi et al (25,26). Plant reaction to inocula containing 10^6 CFU/ml consisted of the development of water-soaked tissue followed by necrosis 5–10 days after infiltration and was rated as a positive reaction for the test; however, some strains caused only a slight chlorosis which was rated as a negative reaction. Similar reactions were observed for *D. maculata* (*D. picta*) and the same rating for positive results was used.

The reactions of seven plant species to 108 strains of *E. chrysanthemi* resulted in the formation of 11 groups (Table 1). Six of the groups (ie, 12, 13, 15, 18, 19, and 21) contained strains which produced positive reactions in *Dianthus caryophyllus* and/or *Zea mays*. The 108 strains were selected from strains included in groups 1, 3, 8, and 9, and included strains isolated from 28 hosts. Eighty-two of the strains had failed to produce a positive reaction in any of the five plant species listed in Table 1 (group 1), but only 32 of the 82 did not cause a positive reaction in any of the seven plant species (Table 2, group 11).

Positive reactions by *Dianthus caryophyllus* for 57 of the 166 selected strains of *E. chrysanthemi* were produced primarily by strains included in subdivision V (Table 3). All the positive strains of subdivision V had been isolated from *Dianthus* sp. except strain S204-107 from *Begonia intermedia* Hort. 'Bertinii,' strains NCPPB 1385, NCPPB 1955, NCPPB 1956, and t from *Dahlia pinnata* Cav. [*D. variabilis* (Willd.) Desf.], and strain 277-3 from *Lycopersicon esculentum* Mill. Eleven selected strains of other *Erwinia* species were tested and failed to produce symptoms.

Seventy-three of 225 strains of *E. chrysanthemi* caused a positive or slightly positive reaction in leaves from corn line NY3×D50. Positive or slightly positive reactions were produced by strains from subdivisions I–V, from 14 plant species, and from groups 1, 3–6, 8, and 9 (Table 4). Forty-two of the strains were from group 1, 27 of which had been isolated from corn. The 44 strains of other *Erwinia* species were unable to cause a positive or slightly positive reaction. Comparative tests were made with 72 strains of *E. chrysanthemi* or other *Erwinia* species for leaf segments from corn lines NY3×D50, W117^{Ht}, and cultivar Seneca Chief. Only 49 strains (68.0%) produced comparable reactions. The variation of reactions among corn lines by strains of *E. chrysanthemi* has been reported by Victoria (39).

DISCUSSION

It was assumed that each strain originally possessed the ability to incite a positive reaction in the host from which it was isolated, although many strains were received without any indication of their virulence. For seven plant species, only 28.6 to 85.5% of the strains produced a positive reaction in the artificially inoculated plant species from which they were originally isolated (Table 5). Although the loss of the ability to cause a positive reaction apparently had occurred while being maintained on an artificial medium or by lyophilization, the strains retained the phenotypic characteristics by which they were identified as strains of *Erwinia chrysanthemi* and were separated into infrasubspecific subdivisions (7,8). Two strains from *P. panduriforme*, four from *P. selloum*, one from *Syngonium podophyllum*, and two from *Z. mays* did not produce a positive reaction in the host from which they were originally isolated but did produce a positive reaction in one of the four other plant species (Table 2, plant reaction groups 1–10).

Only 144 (37.4%) of the 383 strains of *Erwinia chrysanthemi* from 37 hosts produced positive reactions when five plant species were used (groups 2–10, Table 2). When 189 strains of the 239 negative strains (group 1) were tested on *Dianthus caryophyllus* and/or *Zea mays*, 95 of the 189 strains produced a positive reaction in one or both of the plant species. This indicates that the number of strains that did not cause positive reactions could have been

TABLE 3. Reaction of *Dianthus caryophyllus* 'Improved White Sim' to 166 strains selected from the six subdivisions of *Erwinia chrysanthemi*[a]

Subdivision	Number of strains tested	Number of strains	
		Positive	Negative
I	8	...	8
II	2	...	2
III	11	...	11
IV	68	3[b]	65
V	72	54[c]	18
VI	5	...	5

[a] A portion of these results was supplied by P. E. Nelson, Department of Plant Pathology, Pennsylvania State University.
[b] Two strains (B-102 and B-107) from *Saintpaulia ionantha* and one (A-15) from *Ipomoea batatas*. These strains also produce a positive reaction in *Philodendron panduriforme* and are included in plant reaction group 8.
[c] One strain from *Begonia intermedia*; one from *Lycopersicon esculentum*; four from *Dahlia pinnata*; one from *Dianthus barbatus*; and 47 from *Dianthus caryophyllus*.

TABLE 4. Subdivision, original host, and plant reaction group of 73 strains of *Erwinia chrysanthemi* positive or slightly positive for leaf puncture inoculation of corn line NY3×D50

Subdivision	Original host	Number of strains	Plant reaction group
I	*Dieffenbachia maculata* [*D. picta*]	1	1
	Dieffenbachia amoena	3	3
	Dieffenbachia sp.	2	3
II	*Parthenium argentatum*	1	1
III	*Euphorbia pulcherrima*	4	1
		2	8
IV	*Ipomoea batatas*	1	8
	Musa sp.	4	1
		1	8
	Pelargonium capitatum	1	1
	Philodendron selloum	1	4
		4	5
		7	8
	Philodendron sp.	1	8
	Syngonium podophyllum	4	1
		3	6
		5	9
	Zea mays	22	1
	Zea mays var. *rugosa*	5	1
V	*Daucus carota* var. *sativus*	1	8

TABLE 5. Proportion of strains of *Erwinia chrysanthemi* which caused positive reactions by artificial inoculation in plant species from which they originally were isolated

Plant species	Total number of strains tested	Positive reactions	
		Number of strains	Percent of strains
Dieffenbachia amoena	8	6	75.0
Dieffenbachia maculata	8	3	37.5
Philodendron panduriforme	14	4	28.6
Philodendron selloum	65	51	78.5
Syngonium podophyllum	28	17	60.7
Dianthus caryophyllus	55	47	85.5
Zea mays	37	22	59.5

reduced by including all the hosts from which strains have been isolated. It also implies that the number of reaction groups would have been markedly increased because a limited selection of strains from four groups (groups 1, 3, 8, and 9) was increased to 11 groups (Tables 1, 2) when two additional plant species were included.

Preliminary tests of several inoculation methods were made for each plant species to determine which method would provide an appropriate rating of virulence by a distinguishable positive or negative reaction. Inoculation methods were eliminated if they produced inconsistent reactions or symptoms. The influence of moisture (4,27,28,35), temperature (4,6,12,13,15,27,28,35), concentration of inoculum (12,13,21,22), and plant part and age (5,11,13,14,22) also were considered when selecting a standardized inoculation method for each plant species. A high relative humidity and uniform temperature were necessary for the needle puncture or wound inoculation of *P. selloum, S. podophyllum,* and *Z. mays,* whereas concentration of inoculum and age of leaves were important factors in the injection-infiltration of leaves of *Dieffenbachia amoena, D. maculata,* and *P. panduriforme.* It is recognized that the inoculation methods are reflected in the results recorded for each strain and consequently the formation of the plant reaction groups.

The eight plant species used in these tests have been used by other investigators for artificial inoculation tests with strains of *E. chrysanthemi.* The published results are both similar and dissimilar to those reported herein. For example, the production of plant reactions or symptoms by strains from hosts other than the plant species being tested were: positive (15,17,18,28,32,35) and negative (4,11,27,29) for *Chrysanthemum morifolium*; positive (24–26) and negative (27,28) for *Dieffenbachia amoena;* only negative for *D. maculata* (*D. picta*) (5,15,28,35); negative for strains from *Euphorbia pulcherrima* (15) and *Dieffenbachia* sp. (27) for *Philodendron* sp.; positive (15,18) and negative (27,28) for *Syngonium podophyllum*; only negative (5,15,29) for *Dianthus caryophyllus*; and positive (11,12,19,21,39) or negative (11,12,19,21, 35,39) for *Zea mays.* The variability of results probably can be attributed primarily to the inoculation methods and strains used for the studies.

The occurrence of the diverse plant reaction groups (Tables 1 and 2) increases the credence that many strains of *E. chrysanthemi* often are not limited to causing disease only in plants from which they have been isolated. It seems likely that the plant from which a strain was isolated may not necessarily reflect the host in which the strain originally occurred. For example, strain 277-3 from *Lycopersicon esculentum* phenotypically belongs in subdivision V with strains from hosts of unrelated plant families (Table 2); furthermore, the relation of the strains in subdivision V is demonstrated by their ability to produce symptoms in *Dianthus caryophyllus* (Table 3). Several hosts of *E. chrysanthemi* often are grown in close proximity (eg, greenhouse) and it has been speculated (15,22,27) that dissemination of inoculum among plant species may occur within a production area. The cross inoculation of plant species in a production area could partially account for the diversity of hosts and plant reactions found for strains within a phenotypic subdivision.

A relationship, albeit sometimes tenuous, tends to exist between phenotypic subdivisions of the strains and the host from which the strains were isolated (7,8,34). This relationship suggests that the phenotypic studies reveal some of the characteristics which are inherent for strains after prolonged associations with specific plant hosts. However, a correlation between subdivisions and plant reaction groups (Tables 2, 3, and 4) is not strongly supported. Aside from the phenotypic characteristics used to separate the subdivisions, only one instance was found for a correlation between the strains of a subdivision which caused a positive reaction for specific plants and any phenotypic characteristic. All 12 strains of subdivision I which caused a positive reaction for *Dieffenbachia amoena* and/or *D. maculata* (groups 2 and 3 in Tables 1 and 2) failed to produce acid from D(+) melibiose whereas all strains included in groups 4 to 10 and those producing a positive reaction for *Dianthus caryophyllus* (Table 3) did produce acid from melibiose. However, this correlation was negated because only 5 of the 12 strains produced a slightly positive reaction in corn leaves. Therefore, it appears that the plant reaction group to which a strain belongs cannot be predicted by the phenotypic properties of the strain.

The infrasubspecific term pathovar has been proposed as a means to indicate the differences in pathogenic properties of phytopathogenic bacteria and any correlated phenotypic characteristics (40,41). Six pathovars of *E. chrysanthemi* have been proposed based primarily on the host of origin and a limited number of physiological or biochemical differences of the reference strains (7,8,40). If the plant reaction groups (Table 1) are considered as an indication of the host range or unique pathogenic properties of the strains of *E. chrysanthemi*, some problems can be foreseen. The proposed six pathovars (7,8,40) are woefully inadequate to designate the groups (host ranges) which were determined (Table 1) by the artificial inoculation of seven plant species. For example, positive pathogenic reactions for *Zea mays* have been demonstrated by strains originally isolated from hosts other than corn (19, 39, Table 4), that possessed different pathogenic capabilities (Table 1, groups 13, 15, 18, 19, and 21) and phenotypic characteristics (7,8). The numbers of groups undoubtedly will increase as the number of plant species is expanded to include the hosts from which strains of *E. chrysanthemi* have been isolated. This will inevitably result in a cumbersome or an unwieldy designation of pathovars which have limited or in some cases no distinguishing phenotypic characteristics. The available information suggests that it would be advisable to forgo the use of pathovar designations for strains of *E. chrysanthemi.* Perhaps a simple solution to this dilemma is to indicate the original host of the strain (eg, *E. chrysanthemi* [corn strain], *E. chrysanthemi* [carnation strain], etc.) until well defined biovars can be established that eventually may be shown to be correlated with pathogenic properties.

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