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Etiology

Bacterial Leaf Blight of *Syngonium* Caused by a Pathovar of *Xanthomonas campestris*

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We thank Herbert W. Israel and Susan J. Bucci for assistance with electron microscopy of bacterial cells and Robert E. Stall for identification of bacterial pigments.

Accepted for publication 20 March 1987 (submitted for electronic processing).

ABSTRACT

Dickey, R. S., and Zumoff, C. H. 1987. Bacterial leaf blight of *Syngonium* caused by a pathovar of *Xanthomonas campestris*. Phytopathology 77:1257-1262.

The bacterial leaf blight pathogen of *Syngonium podophyllum* was determined to be a xanthomonad. The pathogen was readily isolated from affected leaf surfaces, transferred on fingers from affected leaf surfaces to agar medium, and spread from infected to healthy leaves by overhead watering. It was not isolated from nodal and adjoining stem sections to which infected leaves were attached. Healthy plants were produced from stem cuttings removed from above the infected leaves of subirrigated plants. The strains of the *Syngonium* pathogen produced similar symptoms on leaves of three cultivars of *S. podophyllum* that were petiole- or spray-inoculated. The pathogen was identified as *Xanthomonas campestris* and was found to be phenotypically different from seven selected pathovar strains. Only three of the seven pathovar strains produced any reaction in *S. podophyllum*; the reactions, however, were distinctly different from those produced by the *Syngonium* strains. We propose that the pathogen be designated *Xanthomonas campestris* pv. *syngonii* pv. nov.

During the last 6 yr, *Syngonium podophyllum* Schott (nephthytis) plants affected by a leaf blight disease have been received for diagnosis. The symptoms are similar to or the same as those described by Wehlburg (19,20), who attributed the cause of the disease to a xanthomonad that was similar to *Xanthomonas campestris* pv. *vitians* (19). We have also isolated a xanthomonad from affected leaf tissues, but the strains isolated since 1980 have grown slower and been less pigmented than strains of *X. c.* pv. *vitians* from lettuce. Growers have estimated and we have confirmed that as much as one-third of a production crop can be affected by the disease. Therefore, an investigation was initiated concerning the identification and spread of the pathogen and the development of symptoms in selected cultivars of *Syngonium*.

MATERIALS AND METHODS

Bacterial strains. Six strains isolated from *Syngonium* plants between 1980 and 1984 were used. Strains LX 103, LX 105, and LX 106 were isolated from affected plants of the cultivar Cream, LX 114 was isolated from a leaf of a Cream plant artificially inoculated with LX 105, and L 212 and L 215 were isolated from plants of the cultivar White Butterfly. The following strains were included for the comparative studies: XV 29 (= NCPPB 2255 from the National Collection of Pathogenic Bacteria, Harpenden, Herts. AL5 2BD, England) isolated from *Syngonium* by Wehlburg in 1968; pathotype strain 19320 (= ATCC 19320 from the American Type Culture Collection, Rockville, MD 20852) and strain XL 6 (= NCPPB 969) of *X. c.* pv. *vitians* (Brown 1918) Dye 1978; B-24 of *X. c.* pv. *campestris* (Pammel 1895) Dowson 1939 isolated from broccoli by L. W. Moore, Oregon; pathotype strain XA-2 of *X. c.* pv. *aracearum* (Berniac 1974) Dye 1978 (= PDDCC 5381 from the Plant Diseases Division Culture Collection, Auckland, New Zealand); pathotype strain XD-3 of *X. c.* pv. *dieffenbachiae* (McCulloch & Pirone 1939) Dye 1978 (= PDDCC 5727); and pathotype strain XZ-1 of *X. c.* pv. *zantedeschiae* (Joubert & Truter 1972) Dye 1978 (= PDDCC 2372).

Isolation. Leaf pieces (about 3×4 mm) were aseptically removed from the outermost margins of water-soaked tissue, vortexed for 1 min in each of three rinses in sterile deionized water (SDW), and comminuted in 1.5 ml of sterile water. After 1–1.5 hr, the suspension was streaked onto nutrient broth-yeast extract (NBY) agar (14) and neutral potato-dextrose agar (PDA) prepared with fresh potatoes and 1% dextrose, incubated at 27 C, and observed for 7 days. Cells from separate yellow mucoid colonies were streaked on NBY and PDA agar to determine purity of the cultures.

Bacteria on leaf surfaces were isolated by placing 50–100 μl of SDW at discretionary locations on the surface of unwashed, nondisinfested leaves. After 15 min, 20 μl of the droplet was withdrawn with a pipet and discharged onto NBY agar in a plate and streaked over the agar surface with a sterile loop. The medium was incubated at room temperature and observed for growth at 3, 7, and 10 days. Cells were removed from characteristic colonies, streaked on NBY agar to determine purity, and tested for virulence. In addition, affected leaf areas were gently pressed between a washed thumb and forefinger that were immediately pressed onto the surface of NBY agar medium in a petri dish. The medium was incubated and observed for the development of characteristic colonies.

Morphological, cultural, physiological, and biochemical properties. The strains were stained by the Hucker modification of the Gram stain (16). Morphology and motility were determined by phase contrast microscopy of cells grown for 24 hr in yeast extract-salts (YS) broth (3). Selected strains were grown for 48 hr at 24 C on YS agar, fixed in a 1:1 mixture of uranyl acetate (0.5% aqueous) and 0.025% bacitracin solution, and examined with a Philips EM 200 transmission electron microscope. Colonial characteristics and pigment production were determined on NBY agar and PDA. Production of mucoid growth was observed on nutrient agar (Difco) plus 5% glucose (2), and growth on starch (SX) medium (5) was recorded at 7 days.

The methods of Dye (3) were used to test for the utilization of asparagine as sole source of carbon and nitrogen, nitrate reduction, acetoin production, hydrolysis of esculin and starch, H_2S production from peptone, urease activity, catalase production, and utilization of organic acids. Production of acid from carbohydrates initially was tested with medium C as recommended by Dye (3). When acid production was slight or questionable and growth on the medium with a carbohydrate was obviously greater than on the medium without the carbohydrate, the test was repeated with bromthymol blue (0.0016% w/v) as the indicator.

Several of the methods of Dye (3) were slightly modified for our tests. Growth at 33 or 35 C was determined in still YS broth cultures and by transferring a loopful of cultures with growth to a second tube of YS broth at the same temperature. Tolerance to NaCl (0.5–6.0% w/v NaCl) also was tested in still cultures. Gelatin hydrolysis was recorded after 28 days at 22 and 27 C for nutrient gelatin (Difco) and after 3 and 7 days at 27 C for the gelatin plate method (16). Kovac's indole reagent (4) was used as the indicator for indole production. Milk agar plates were prepared as described by Dye and incubated for 6 days, whereas Bacto litmus milk (Difco) was prepared according to the manufacturer's directions and proteolysis was recorded after 3, 7, 14, and 21 days.

Oxygen requirements and glucose metabolism were determined by the method of Hugh and Liefson (7) using OF basal medium (Difco) plus 1.0% glucose (w/v). Oxidase activity was tested by Patho Tec-CO test paper (General Diagnostics Division, Warner-Chilcott, Morris Plains, NJ 07950). The ability to hydrolyze Tween 80 was tested after 3, 7, and 14 days of growth on Sierra's medium (15). Growth factor requirements were determined for 14 days in shake culture tests by Starr's medium (17) containing 0.01% (w/v) DL-methionine, 0.1% L-glutamic acid, or no supplement. Tests for the presence of arginine dihydrolase (18) and detection of amino acid decarboxylases (4) with Decarboxylase Base Moeller (Difco) were observed for 14 days as recommended by Panagopoulos (12). Inhibition of growth by 2,3,5-triphenyltetrazolium chloride (TTC) in 0.01% increments from 0.01% to 0.1% (w/v) was tested with Kelman's TTC agar (10) supplemented with 0.2% yeast extract (13).

Inoculation tests. All plants were grown in a steam-treated mixture of soil, perlite, and peat moss (1:1:1, v/v), and a commercial soluble fertilizer was applied once each week. An automatic watering system or subirrigation was used to avoid splashing of water on the leaf surfaces. Inoculated plants were placed on a greenhouse bench without supplemental lighting or in a mist chamber with mist applied intermittently for 30 sec each minute. Ambient temperature was 21.1–26.4 C in the greenhouse and 21.1–23.0 C or 24.8–26.7 C in the mist chamber.

S. podophyllum 'Green Gold,' 'Cream,' and 'White Butterfly' plants were either spray-inoculated or petiole-inoculated. For spray-inoculation, a hand atomizer was used to thoroughly cover leaf surfaces with a SDW suspension of cells from 24-hr PDA slant cultures grown at 27 C. The cell suspensions were adjusted to OD of 0.30 at 620 nm in a Spectronic 20 (Bausch & Lomb) spectrophotometer and contained between 2.3 and 5.6×10^8 cfu/ml. Cell suspensions of strains L 212, XA-2, and XD-3 were diluted 1×10^2 and 1×10^4 with SDW. The petiole-inoculations were made by dipping the tip of a dissecting needle into a 48-hr PDA culture and gently puncturing the petiole about 2.5 cm from the petiole-leaf lamina junction. The plants had at least three or four unfolded, expanded leaves before inoculation. The two upper expanded leaves usually were inoculated unless noted for special studies.

Dieffenbachia maculata (*D. picta*), *D. amoena, Philodendron selloum*, and *P. panduriforme* plants were inoculated with all strains. Inoculated plants were maintained in a greenhouse at a mean ambient temperature of 22.8 C and observed for development of symptoms for 34 days. The youngest completely developed leaf and the leaf immediately below were inoculated. Plants were inoculated by 1) puncture of interveinal and intraveinal tissues with a needle containing cells from 48-hr PDA cultures, 2) injection-infiltration of leaves with a SDW cell suspension containing about 10^8 cfu/ml prepared from 24-hr PDA cultures, and 3) injection-infiltration of the latter suspensions diluted to about 10^6 cfu/ml with SDW.

Geranium (*Pelargonium* × *hortorum*) plants were inoculated with strains LX 103, LX 105, LX 106, LX 114, L 212, L 215, XV 29, and three strains of *X. c.* pv. *pelargonii*. A needle with cells from a 48-hr PDA culture was used to puncture a young stem at the base of a leaf. Plants were kept in the mist chamber before and after inoculation and observed for symptom development for 35 days.

RESULTS

Phenotypic characteristics. All strains were gram-negative, straight rods, nonsporing, motile with a single polar flagellum (Fig. 1), strictly aerobic, catalase-positive, and oxidase-negative. The strains produced yellow mucoid colonies on nutrient agar with 5%

glucose. The pigmentation of colonies of the *Syngonium* strains, however, was paler on nutrient agar with glucose, NBY agar, and PDA media than the pigmentation of the other strains. Three *Syngonium* strains—LX 103, LX 114, and L 215—were tested (8) and found to produce the xanthomonadin pigment (R. E. Stall, *personal communication*). All strains did not use asparagine as a sole source of carbon and nitrogen, produce acid in milk, reduce nitrate, or produce acid from L(+)-rhamnose, inulin, adonitol, dulcitol, sorbitol, salicin, or *meso*-inositol. The foregoing results have been listed by Dye (3) and Bradbury (2) as being characteristic for *Xanthomonas* species.

Evidence that all of the strains were *X. campestris* included the following results: positive for H_2S from peptone, hydrolysis of esculin, acid from L(+)-arabinose, D(+)-galactose, and utilization of acetate, citrate, malate, propionate, and succinate but negative for the Voges-Proskauer test, indole production, urease activity, arginine dihydrolase, lysine and ornithine decarboxylase, acid from α-methyl-D-glucoside, and utilization of tartrate.

Growth of the *Syngonium* strains was slower than that of the other strains. Colony size after 3 days at 27 C on NBY agar streaked with a dilution of the *Syngonium* strains was <1 mm, compared with 2–4.5 mm for other pathovar strains. Colonies of the *Syngonium* strains were not visible with the unaided eye on PDA medium after 3 days and were 1 mm or less after 7 days; colonies of other pathovar strains were between 2 and 5 mm at 3 days. Hydrolysis of starch was positive for all strains but was slow and weak for strain XL 6. Results for other tests are given in Table 1.

A comparison of results for 27 tests included in Table 1 showed that phenotypic characteristics of *Syngonium* strains obviously were different from those of other pathovar strains included in these tests. Strain XV 29 was the most similar to *Syngonium* strains, sharing 11 (41%) of the 27 characteristics.

Inoculation tests. The initial symptom on leaves of plants petiole-inoculated with the *Syngonium* strains occurred at the junction of the petiole and the leaf lamina as a dark water-soaked area that expanded predominantly along one or more veins toward

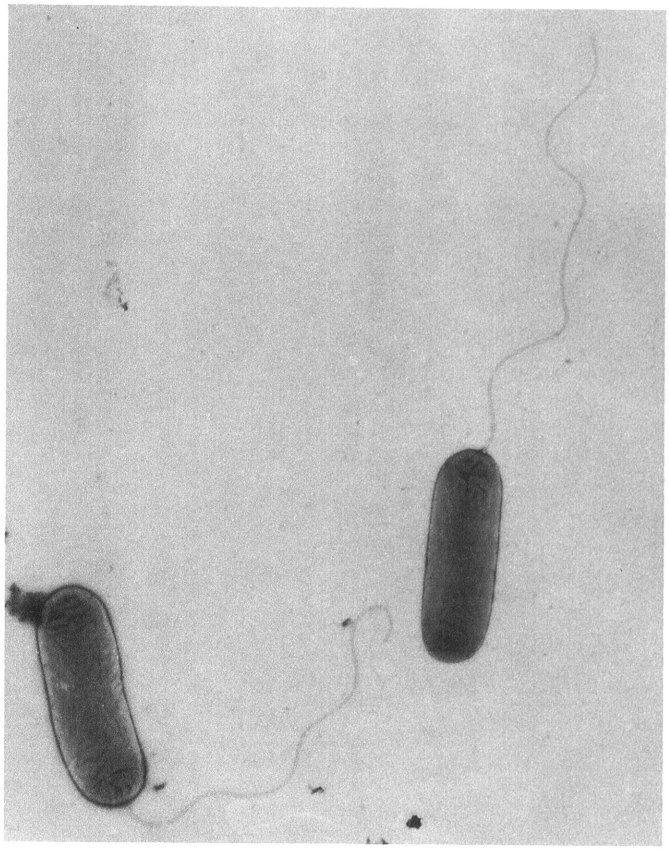

Fig. 1. Electron micrograph of *Syngonium* pathogen strain LX 103 showing single polar flagellum on cell fixed in 1:1 mixture of uranyl acetate (0.5%) and 0.025% bacitracin solution.

TABLE 1. Reactions of six *Syngonium* strains and seven pathovar strains of *Xanthomonas campestris* to physiological and biochemical tests

Test	*Syngonium* strains	*Xanthomonas campestris* pathovar strains[a]						
		XV 29	19320	XL 6	XA-2	XD-3	XZ-1	B-24
Growth on SX medium (7 days)	–[b]	sl	sl	sl	sl	+	+	+
Growth factor requirement:								
DL-Methionine	+	–	–	–	–	–	–	–
L-Glutamic acid	–	–	–	–	–	–	–	–
Growth at 35 C	–	+	+	+	+	+	+	+
Maximum NaCl tolerance (%)	2–3	3	4	4	5	5	5	5
Growth inhibition by TTC (%)	0.05	0.08	>0.1	0.09	0.1	>0.1	>0.1	>0.1
Hydrolysis of:								
Gelatin	–	+	+	+	+	+	+	+
Tween 80	slow	+	+	+	+	+	+	w+
Milk proteolysis	– or sl	+	+	+	+	+	+	+
Growth on benzoate medium	–	–	–	–	–	sl	sl	–
Acid production from (21 days):								
D(–)-Ribose	–	–	w+	w+	+	+	+	+
D(+)-Xylose, D(–)-fructose, D-glucose, D(+)-mannose, D(+)-cellobiose, sucrose, D(+)-trehalose	w+	+	+	+	+	+	+	+
D(+)-Lactose	–	+	+	+	+	+	+	–
D(+)-Maltose	–	–	+	w+	w+	+	+	+
D(+)-Melibiose	–	+	+	+	+	+	+	+
D(+)-Raffinose	–	–	–	+	+	+	+	+
D(+)-Melezitose	–	–	+	–	–	–	w+	–
Dextrin, glycogen	–	–	w+	–	–	+	+	+
Glycerol	–	+	+	–	–	+	+	+
Mannitol	–	–	–	–	–	–	+	–

[a] XV 29 = *X. c.* pv. *vitians* isolated from *Syngonium* in 1968 by Wehlburg; 19320 = *X. c.* pv. *vitians* pathotype strain; XL 6 = *X. c.* pv. *vitians* from lettuce; XA-2 = *X. c.* pv. *aracearum* pathotype strain; XD-3 = *X. c.* pv. *dieffenbachiae* pathotype strain; XZ-1 = *X. c.* pv. *zantedeschiae* pathotype strain; B-24 = *X. c.* pv. *campestris* from broccoli.

[b] + = Positive; – = negative; sl = slight reaction; slow = slow reaction; w+ = acid production weak but discernible when bromthymol blue substituted for bromcresol purple as indicator in medium C.

the "wing" of the lamina until it reached the margin (Fig. 2A). Although the symptom was most conspicuous on the upper surface of leaves of White Butterfly, it sometimes was almost colorless on Cream and occurred on Green Gold as limited areas of moist, dark to almost black, necrotic tissue. As water soaking continued to spread, older affected tissues became light brown, dark brown, obviously necrotic, and eventually dry and papery. When the spread of lesions subsided, a yellow border often developed between the necrotic and surrounding unaffected areas. Finally, unaffected areas became pale yellow and dry, and the entire leaf shriveled. The petiole curved downward as its tissue collapsed and became pale yellow and dry. The dried petiole and leaf remained attached to the stem (Fig. 2C) until disturbed or intentionally removed. The initial water-soaked symptom for spray-inoculated

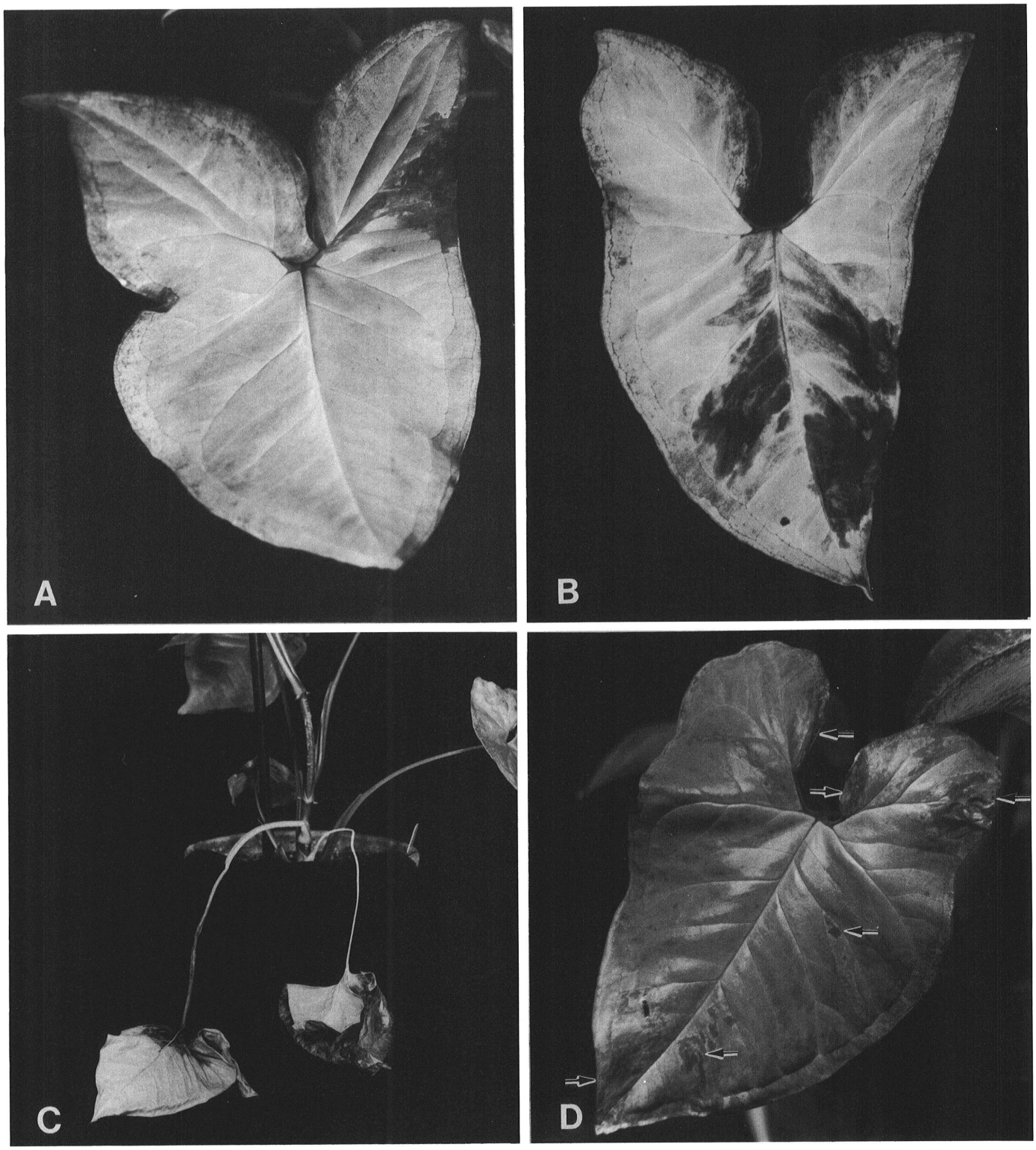

Fig. 2. Symptoms produced on *Syngonium podophyllum* by *Syngonium* strains LX 114 or L 212 and strain XA-2 of *Xanthomonas campestris* pv. *aracearum*. **A,** Water soaking and marginal necrosis of cultivar Cream leaf 35 days after petiole-inoculation with strain LX 114. **B,** Water soaking and necrosis of Cream leaf 25 days after spray-inoculation with a SDW suspension containing about 10^8 cfu/ml of strain L 212. **C,** Attached, pale yellow, dried, shriveled leaves and petioles of cultivar Green Gold 51 days after petiole-inoculation with strain LX 114. **D,** Limited lesions on Cream 34 days after spray-inoculation with a SDW suspension containing about 10^8 cfu/ml of cells of strain XA-2 (lesions indicated by arrows).

leaves occurred primarily at the margins and as separated areas of the leaf lamina (Fig. 2B). Individual lesions often coalesced to form large affected areas of the lamina. The development of symptoms after water soaking was the same as described for petiole-inoculated plants.

The progression of symptom development varied with the type of inoculation, environmental conditions, and cultivar (Table 2). Initial symptoms were slower to develop on petiole-inoculated leaves because the bacteria had to move about 2.5 cm from the point of inoculation to the leaf lamina, whereas spray-inoculation applied the bacteria directly onto the leaf lamina. The placement of plants in a mist chamber generally hastened development of symptoms for Cream and Green Gold. Discernible symptoms were slower to occur on Green Gold, possibly because water soaking was more difficult to determine in leaves of Green Gold than in leaves of the other cultivars. When spray-inoculated White Butterfly and Cream plants were kept at a lower ambient temperature (22.4 C) in the greenhouse, the mean number of days for occurrence of symptoms (White Butterfly = 16–19, Cream = 13) was similar to the results for the higher temperatures (Table 2). Severe necrosis, yellowing, and drying of the leaves (Fig. 2C) usually were evident about 45 days after inoculation for all tests. An exudate-like material occasionally was evident on the lower surface of affected leaf tissue.

Symptom development after spray-inoculation usually was faster on Cream than on White Butterfly and Green Gold plants (Table 2). When suspensions of about 10^8 cfu/ml of strain L 212 were spray-inoculated on the uppermost youngest leaf and the two older leaves immediately below, symptoms often developed faster in the youngest leaf than in the two older leaves, especially in the greenhouse. Production of symptoms was affected by the concentration of cells. Symptom development was delayed when the cell suspension was adjusted to about 10^6 cfu/ml, and symptoms did not develop on leaves spray-inoculated with suspensions of about 10^4 cfu/ml.

Strains XV 29 and XL 6 of *X. c.* pv. *vitians*, B-24 of *X. c.* pv. *campestris*, and XZ-1 of *X. c.* pv. *zantedeschiae* did not produce any symptoms in leaves of White Butterfly and Cream plants spray-inoculated with about 10^8 cfu/ml. Strain XA-2 of *X. c.* pv. *aracearum* and, to a lesser degree, strains XD-3 of *X. c.* pv. *dieffenbachiae* and 19320 of *X. c.* pv. *vitians* produced visible reactions that differed from the symptoms produced by the *Syngonium* strains. The reactions varied but were slightly more extensive on Cream than on White Butterfly plants. Strain XA-2 produced scattered, discrete lesions on Cream leaves that sometimes enlarged slowly for several days and eventually changed from light brown and water-soaked to medium brown with translucent areas and occasionally a slightly yellow border (Fig. 2D). The lesions varied in size but usually remained small and separated. Sometimes, however, several lesions coalesced to produce larger necrotic areas, and the leaf eventually died. The lesions produced by strains XD-3 and 19320 were light brown or yellow, tended not to enlarge, and were either smaller (XD-3) or very much smaller (19320) than those produced by XA-2. None of the strains produced any symptoms on the leaf lamina of petiole-inoculated plants, although the leaves sometimes collapsed and died between 29 and 43 days after inoculation with strain XA-2 or XD-3. The effect of concentration of cell suspension (i.e., 10^6 and 10^4) for spray-inoculation of strains XA-2, XD-3, and 19320 and the age of inoculated leaf was the same as described above for strain L 212.

When leaves of *Dieffenbachia* and *Philodendron* species were injected-infiltrated with SDW cell suspensions containing about 10^6 cfu/ml, only strains XD-3 and XZ-1 produced water soaking followed by necrosis of inoculated leaves of *D. maculata* and *D. amoena*. The *Syngonium* strains produced a slight yellowing of the injected-infiltrated areas of leaves of *D. amoena* plants but failed to produce any reaction in leaves of *D. maculata* plants. Strains L 212, L 215, XV 29, XA-2, XD-3, and XZ-1 produced small limited lesions immediately around the needle-puncture wound made in intraveinal leaf tissue of *D. maculata*. Although three strains of *X. c.* pv. *pelargonii* produced typical symptoms when inoculated into *Pelargonium* × *hortorum*, the *Syngonium* strains and XV 29 did not cause any reaction.

Isolations from leaf surfaces and plant parts. The *Syngonium* pathogen was isolated from the surface of lesions after initial water soaking was observed and at frequent intervals until the tests were terminated at 41 days (Table 3). Bacteria were more readily isolated from the edge of the lower surface of the lesions. The possibility that isolations included only cells of a residual epiphytic population established during spray-inoculation was nullified by results for petiole-inoculations that did not include the application of inoculum to the leaf surface.

The pathogen could be transferred on fingers from the surface of lesions, especially the lesion areas on the lower leaf surface, to an agar medium. Attempts to transfer bacteria on fingers from infected leaves to healthy leaves with the subsequent development of symptoms were not successful. However, the pathogen was readily spread from infected leaves to adjacent leaves of

TABLE 2. Occurrence of initial symptoms in cultivars of *Syngonium podophyllum* inoculated with strain L 212 of *Xanthomonas campestris* from *Syngonium*[a]

Cultivar	Petiole-inoculated		Spray-inoculated	
	Greenhouse	Mist chamber	Greenhouse	Mist chamber
White Butterfly	23	23	14–18	14
Cream	30	19	11–14	11
Green Gold	30	30	25–42	18–28

[a] Days after inoculation of occurrence of water soaking with or without slight necrosis; two figures represent differences for younger and older leaves on the plants. Mean ambient temperatures for greenhouse and mist chamber = 25.5 C.

TABLE 3. Isolation of *Syngonium* strains of *Xanthomonas campestris* from surfaces of lesions on leaves of *Syngonium podophyllum* 'White Butterfly'

Days after initial occurrence of lesion	Petiole-inoculated				Spray-inoculated			
	Upper leaf surface		Lower leaf surface		Upper leaf surface		Lower leaf surface	
	Lesion center	Lesion edge	Lesion center	Lesion edge	Lesion center	Lesion edge	Lesion center	Lesion edge
1–4	+[a]	···	+	···	+	···	+	···
5–7	+	···	···	+	−	−	+	+
8–10	−	+	−	+	+	+	+	+
11–13	−	···	+	+	···	···	···	···
14–16	−	−	+	+	−	−	−	+
17–20	···	···	···	···	−	+	−	+
21–24	−	···	−	···	−	···	−	···
25–28	−	−	−	+	···	···	···	···
29–32	−	−	−	+	−	−	−	−
35–38	−	−	−	−	−	−	−	+
39–41	−	+	−	+	···	···	···	···

[a] + = Pathogen isolated; − = pathogen not isolated; ··· = no isolations made.

noninoculated plants by normal overhead watering. Initial symptoms sometimes occurred within 20 days on leaves of noninoculated plants placed 2–3 cm from infected leaves of petiole-inoculated plants. The pathogen was not isolated from nodal and adjoining stem sections to which infected leaves were attached or from roots of Cream plants 69 days after development of symptoms on inoculated leaves immediately above the soil surface. Plants were healthy for at least 245 days after they were produced from stem cuttings taken from the five nodal areas above the infected leaf of subirrigated Green Gold and Cream plants.

DISCUSSION

The symptoms of the blight disease of *S. podophyllum* that we observed are the same as those described by Wehlburg in 1969 and 1970 (19,20), but his bacterial pathogen (XV 29 = NCPPB 2255) differed phenotypically from strains we have isolated (Table 1). Wehlburg demonstrated the pathogenicity of the bacterial strain by wound inoculation of leaves of *S. podophyllum*. Strain XV 29 failed to produce any symptoms during our inoculation tests, however. This discrepancy may be attributed to the loss of virulence during maintenance of the culture. The pathogen was described as a strain of *X. c.* pv. *vitians* with minor differences (19,20), and our comparative studies of strain XV 29 with two strains of *X. c.* pv. *vitians* (19320 and XL 6) tended to support his conclusion. Strain XL 6 failed to produce any reaction in leaves of *S. podophyllum*, and the lesions produced by strain 19320 were very small and markedly different from those of the *Syngonium* strains. Three additional strains, i.e., XA-2, XD-3, and XZ-1, were selected for inclusion in our studies because they were originally isolated from plants of the family Araceae (1,6,9,11), which also includes *S. podophyllum*, and have been designated as pathovars of *X. campestris*. The three strains differed phenotypically and pathologically from the *Syngonium* strains. The *Syngonium* pathogen had the phenotypic characteristics of *X. campestris*. Therefore, the name *Xanthomonas campestris* pv. *syngonii* pv. nov. is proposed for the pathogen. Strain L 212 (PDDCC 9154) is designated as the pathotype strain.

The results indicate that the pathogen probably egressed through stomata and possibly by the rupture of the epidermis during pathogenesis. Spread of the inoculum present for extended periods on lesion surfaces to adjacent leaves by overhead watering apparently constitutes the primary means of dispersal of the pathogen. This method of dispersal may account for the prevalence of infected leaves below rather than above the initially infected leaf on older plants. Although the pathogen could be transferred on fingers during handling of leaves, our results suggest that spread of the pathogen by this means probably is unlikely. The pathogen apparently does not move aggressively from infected leaves to other plant parts through vascular tissues (e.g., vessel elements) because it was not isolated from stem tissues and healthy plants were produced from nodal stem cuttings removed immediately above infected leaves on subirrigated plants. The best control measures seem to be removal of infected leaves at the junction of the petiole and stem as soon as symptoms occur and avoidance of overcrowding and overhead watering of stock plants.

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