

Etiology

Etiology of Bacterial Leaf Streak of Wild Rice

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ABSTRACT

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Bacterial leaf streak of wild rice (*Zizania aquatica*) is characterized by narrow, translucent, water-soaked lesions that eventually become brown or black and dry. Isolations from diseased plants collected in northern Minnesota from 1976 to 1980 yielded 167 cultures of *Pseudomonas syringae* and 21 cultures of *Xanthomonas campestris*. Strains from both species were

pathogenic to wild rice. Three *X. campestris* strains were similar to pv. *cerealis* and one to pv. *translucens*. Strains of *P. syringae* were biochemically similar to pv. *striaefaciens*, but were pathogenic only to wild rice. The name *P. syringae* pv. *zizaniae* pv. nov. is proposed.

Wild rice (*Zizania aquatica* L.) is a native, semiaquatic, annual grass that has been utilized as a food source in the Upper Great Lakes Region for centuries (4). Since about 1960, wild rice has been grown in paddies as a commercial field crop. By 1980, approximately 6,400 ha were in production in Minnesota and these fields produced 1,090,000 kg of processed wild rice with a retail value of \$9.6 million (1). Minnesota's natural lake and river stands of wild rice produced a total of ~1,135,000 kg, worth \$10 million in 1980.

Bacterial leaf streak (BLS) of wild rice is characterized by translucent, water-soaked spots and streaks that are usually 1–3 mm wide. Lesions may expand lengthwise along the leaf blade for up to 25 cm, but lateral expansion is restricted by the leaf veins.

Water-soaked tissues become necrotic after 1–7 days, giving leaves a brown or black-striped appearance (Fig. 1). Frequently, white flakes or yellow droplets of exudate are present on lesion surfaces.

BLS was first observed in fields near Aitkin, MN, in 1975, and it affected up to 80% of the leaf area of some plants (12). A yellow bacterium was isolated that produced "typical but mild symptoms" in artificial inoculation. Apparently, no attempt was made to characterize the organism and the cultures were subsequently lost.

The objective of this study was to ascertain the organisms causing BLS of wild rice, and if there were multiple causes to determine which was most important in Minnesota. Preliminary reports of this research have been published (2,3).

MATERIALS AND METHODS

Isolations. Isolations were made from diseased leaves collected in 1976 and 1978 from paddies in northern Minnesota, and preserved at –25 C. Isolations were also made from fresh material

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collected in 1979 and 1980 from four University of Minnesota experiment stations, 13 commercial fields, and six natural wild rice stands. Leaves with lesions were cut into sections 1 mm square and immediately placed in a drop of sterile distilled water (SDW). After 5–10 min, the drop was diluted 10- to 1,000-fold in SDW and a loopful was streaked on King's medium B (KMB) (13). Cultures were incubated at 24 C in the dark and were examined after 2 and 4 days. Single colonies were streaked on KMB, and single colonies from the second plate were subsequently transferred to slants of Difco nutrient agar (Difco, Detroit, MI 48232) for temporary storage at 5 C. Cultures were stored for up to 2 yr by pipetting 1 ml of a heavy suspension (10^6 – 10^9 colony-forming units [cfu] per milliliter) into tubes of moistened, sterile, sandy-loam soil; capping tightly; then maintaining at 5 C.

Pathogenicity tests. Smooth brome grass (*Bromus inermis* Leysser), quack grass (*Agropyron repens* (L.) Beauv.), yellow foxtail (*Setaria glauca* (L.) Beauv.), timothy (*Phleum pratense* L. 'Toro'), barnyard grass (*Echinochloa crus-galli* (L.) Beauv.), reed canarygrass (*Phalaris arundinacea* L. 'Rise'), crabgrass (*Digitaria sanguinalis* (L.) Scop.), oats (*Avena sativa* L. 'Lodi'), barley (*Hordeum vulgare* L. 'Morex'), wheat (*Triticum aestivum* L. 'Angus'), rye (*Secale cereale* L. 'Von Lochow'), sweet corn (*Zea mays* L. 'Golden Cross Bantam'), sorghum (*Sorghum bicolor* (L.) Michx. 'Bugoff'), rice (*Oryza sativa* L. 'Starbonnet'), southern wild rice (*Zizaniopsis miliacea* (Michx.) Doll and Aschers), Manchurian wild rice (*Zizania latifolia* Stapf.), and wild rice (*Zizania aquatica* L. 'Netum') were grown in 16.5-cm-diameter plastic pots filled with approximately 1 L of a greenhouse potting mixture of soil, coarse sand, and peat (1:1:1, v/v). Three grams of 10-10-10 fertilizer per pot were incorporated into the soil, and each pot was topped with 1 cm of sand. Plants were grown from seed except for *Zizania latifolia* and *Zizaniopsis miliacea*, which were grown from rhizomes. Plants were grown on the greenhouse bench at 20–25 C in ambient light supplemented with fluorescent light to obtain a 16-hr photoperiod. *Zizania aquatica*, *Z. latifolia*, *Zizaniopsis miliacea*, and *Oryza sativa* seedlings were placed in wooden boxes lined with plastic sheeting. The boxes were filled with water and the level was maintained at 1–2 cm above the surface of the sand.

White and yellow bacterial strains were grown on nutrient agar plates and incubated at 24 C for 48 and 96 hr, respectively. Cells were washed from plates with 20 ml of SDW and the resulting suspension was adjusted spectrophotometrically to the desired concentration according to a previously determined calibration curve at a wavelength of 600 nm. Unless noted otherwise, approximately 10^6 cfu/ml were used. Suspensions were pressure-infiltrated into leaves by using a 3-ml plastic disposable syringe

fitted with a 2.5 cm section of rubber tubing (I.D. = 8 mm, O.D. = 14 mm) at the tip. Some plants were infiltrated with SDW as controls. Plants were kept on the greenhouse bench approximately 1 hr to allow visible water-soaking from inoculation to disappear, and were then incubated for up to 7 days in a mist chamber at 18–25 C, 90–100% relative humidity, and a 12-hr photoperiod. Isolates

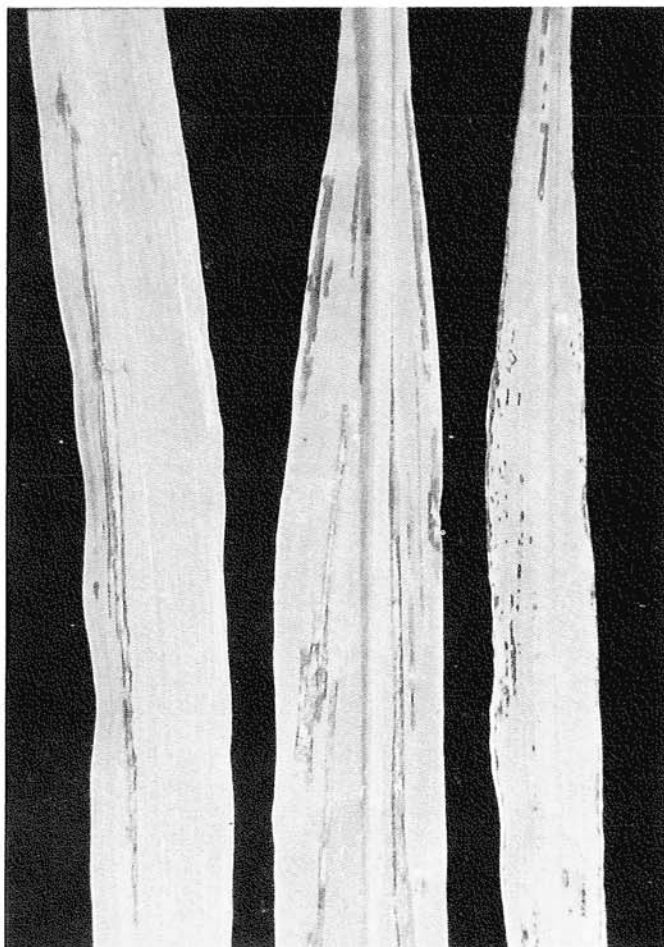


Fig. 1. Symptoms of bacterial leaf streak caused in wild rice by *Pseudomonas syringae* pv. *zizaniae* (X2).

TABLE 1. List of reference cultures used to study the etiology of bacterial leaf streak of wild rice

Strain ^a	Original source	Source ^b	Designation
<i>Pseudomonas syringae</i> pv. <i>coronafaciens</i>	Rye (<i>Secale cereale</i>)	1	C-107, C-122
<i>P. syringae</i> pv. <i>coronafaciens</i>	Corn (<i>Zea mays</i>)	1	C-163
<i>P. syringae</i> pv. <i>atropurpurea</i>	Italian ryegrass (<i>Lolium multiflorum</i>)	1	C-159, C-160, C-161
<i>P. syringae</i> pv. <i>syringae</i>	Lilac (<i>Syringa vulgaris</i>)	2	ATCC 19310
<i>P. fluorescens</i>		2	ATCC 13525
<i>P. aeruginosa</i>		2	ATCC 10145
<i>P. syringae</i> pv. <i>glycinea</i> , race 2	Soybean (<i>Glycine max</i>)	3	PSGL
<i>P. syringae</i> pv. <i>phaseolicola</i>	Bean (<i>Phaseolus vulgaris</i>)	3	PSPH
<i>P. syringae</i> pv. <i>pisi</i>	Pea (<i>Pisum sativum</i>)	3	PSPI
<i>P. syringae</i> pv. <i>syringae</i>	Adzuki bean (<i>Phaseolus angularis</i>)	3	PSS-A
<i>P. syringae</i> pv. <i>syringae</i>	Bean	3	PSS-B
<i>P. syringae</i> pv. <i>syringae</i>	Wheat (<i>Triticum aestivum</i>)	4	C-1
<i>P. syringae</i> pv. <i>tagetis</i>	Sunflower (<i>Helianthus annuus</i>)	4	PSTA
<i>P. syringae</i> pv. <i>syringae</i>	Corn	5	Holcus-1
<i>P. syringae</i> pv. <i>syringae</i>	Fall panicum (<i>Panicum dichotomiflorum</i>)	6	1448
<i>P. syringae</i> pv. <i>striaefaciens</i>	Oats	6	1514, 1515, 1516, 1517
<i>Xanthomonas campestris</i> pv. <i>cerealis</i>	Quack grass (<i>Agropyron repens</i>)	6	Xt-2, XT-25
<i>X. campestris</i> pv. <i>phaseoli</i>	Bean	3	XCP

^a Pathovar names sensu ISPP List, 1980 (6).

^b Cultures received from: 1, B. Cunfer, University of Georgia, Experiment; 2, American Type Culture Collection, Rockville, MD 20852; 3, B. W. Kennedy, University of Minnesota, St. Paul; 4, J. S. Baumer, University of Minnesota, St. Paul; 5, E. L. Stromberg, University of Minnesota, St. Paul; and 6, isolations by the author.

that produced visible water-soaking of tissues within 7 days were scored as pathogenic, and reisolations were made to verify that cultures resembled the original isolates with respect to colony morphology, color, fluorescence, and oxidase reaction (see below).

Field tests were made at the University of Minnesota's Grand Rapids experiment station by inoculating plants of wild rice cultivar K2 at the mid-tillering stage. Plants were sprayed with approximately 30 ml of bacterial suspension per meter of a single row planting using a specially designed backpack CO₂ pressurized sprayer system. Inoculum concentrations of approximately 0, 10², 10⁴, 10⁶, and 10⁸ cfu/ml with 0.01% (v/v) Tween-40 wetting agent were applied at night after dew formation.

Characterization of strains. Colony color, shape, production of fluorescent pigments, Gram reaction, and cell shape were determined on plates of KMB. Oxidase production was tested according to Kovacs' method (14). Oxygen requirements were determined in deep tubes of Difco phenol red agar with 1% (w/v) dextrose. Liquefaction of gelatin and tests for catalase, tyrosinase, and tobacco hypersensitivity were performed according to the methods of Lelliot et al (15). Dye's (5) method was used for esculin hydrolysis. White and yellow strains were treated separately for further characterization.

White cultures were tested for arginine dihydrolase activity, potato soft rotting ability, production of levan and 2-ketogluconate, nitrate reduction, and growth at 37 C according to the methods of Misaghi and Grogan (16). Carbon source utilization was tested at 0.1% (w/v) concentrations using the basal medium of Palleroni and Doudoroff (17). Production of syringomycin was bioassayed with the fungus *Geotrichum candidum* Link ex Pers. on Difco potato-dextrose agar according to the procedures of Gross and DeVay (9). The medium of Woolley et al (21) was used to assay for chlorosis-inducing toxins. Cultures were centrifuged at 1,800 g for 10 min, filtered through a sterile 0.22- μ m Millipore filter, then injected into wild rice leaves with the modified syringe. *Pseudomonas syringae* pv. *coronafaciens* (ISPP List, 1980 [6]) strains C-161 and C-163 were used as toxin-producing controls.

Yellow cultures were tested for color and slime formation, growth at 36 C, and acid production from carbohydrates by the methods of Dye (5). Starch hydrolysis was determined on plates of the following medium: Difco Bacto peptone, 5 g; Difco yeast extract, 3 g; Mann soluble starch, 2 g; agar, 15 g; and distilled water, 1 L. Plates were flooded with Gram's iodine solution and hydrolysis was assumed if clear zones appeared around the colonies. Casein hydrolysis was indicated by clear zones around colonies grown on Difco nutrient agar amended with 1% (w/v) Difco dehydrated skim milk. Production of hydrogen sulfide was detected in tubes containing 5 ml of the following medium: Difco yeast extract, 5 g; Difco Bacto peptone, 5 g; NaCl, 5 g; cysteine hydrochloride, 0.1 g; agar, 15 g; and distilled water, 1 L. Lead acetate paper was suspended above the medium and H₂S production was indicated by blackening of the paper.

Reference cultures. Reference cultures used in biochemical and host range tests are listed in Table 1. All pathovar names are sensu the ISPP List, 1980 (6).

RESULTS

Isolation and pathogenicity. Two hundred three cultures were obtained from fresh or frozen infected wild rice leaves. Fifteen strains were not pathogenic in greenhouse tests and were not studied further. One hundred sixty-seven of the pathogenic strains produced white colonies; of these, 152 were from commercial fields, nine were from experiment station paddies, and six were from natural stands. Twenty-one pathogenic strains were yellow; seven were isolated from commercial fields, 12 from experiment stations, and two from natural stands.

Both white and yellow pathogenic strains from BLS of wild rice produced narrow, water-soaked, expanding lesions on wild rice leaves artificially inoculated in moist chambers or in the field. Infection was produced by pressure-infiltration with inoculum concentrations as low as approximately 10² cfu/ml, but about 10⁶ cfu/ml were required to obtain consistent infection of all plants

with the method used. In outdoor spray inoculations consistent infection resulted from 10⁶ cfu/ml or higher. Both white and yellow strains were reisolated from the margin of young, expanding lesions.

Symptoms caused by the two species were almost indistinguishable except that lesions caused by yellow strains sometimes produced bright yellow droplets of exudate while lesions caused by white strains produced shiny white scales of exudate. Also, the former tended to remain water-soaked longer under the same conditions.

Characterization of strains. All the 167 pathogenic white strains were oxidase-negative, and 162 produced a fluorescent green pigment on KMB. Most colonies were circular, raised, and finely granular with a slightly undulate margin, but two produced slightly domed, smooth colonies with entire margins. A subset of twenty-five white strains including one nonfluorescent strain was compared to the proposed neotype strains of *P. aeruginosa* (Schroet.) Migula 1900 and *P. fluorescens* Migula 1895 as well as the suggested working type of *P. syringae* Van Hall 1902. The 25 white strains from wild rice were Gram-negative, rod-shaped, catalase-positive, arginine dihydrolase-negative, and strictly aerobic. All 25 strains produced levan and 24 produced the tobacco hypersensitive reaction. None produced 2-ketogluconate, reduced nitrate, grew at 37 C, or rotted potato slices. White wild rice strains were identified as *P. syringae* and were distinguished from *P. fluorescens* and *P. aeruginosa* on the basis of the oxidase, arginine dihydrolase, tobacco hypersensitive, and 2-ketogluconate tests (16,18).

Eleven strains of *P. syringae* from wild rice were compared with six pathovars of *P. syringae* (Table 2). Wild rice pseudomonads were distinguishable from *P. syringae* pv. *syringae*, pv. *phaseolicola*, pv. *pisi*, pv. *glycinea*, and pv. *tagetis* on the basis of four or more tests. However, they could not be distinguished biochemically from pv. *striaefaciens*.

The 21 yellow strains from BLS were Gram-negative and oxidase-negative, and produced convex, mucoid, slow-growing colonies. Six strains were compared to two strains of *Xanthomonas campestris* pv. *cerealis* and one strain of *X. campestris* pv. *phaseoli*. Wild rice isolates were aerobic, rod-shaped, catalase-positive, produced hydrogen sulfide, grew at 36 C, hydrolyzed esculin, casein, and gelatin, but not starch, and produced acid from D-glucose, D(+)-mannose, D(+)-cellobiose, L(+)-arabinose, and D(+)-galactose. Reactions of reference cultures were identical except pv. *phaseoli* hydrolyzed starch. Based on these results, the yellow strains from wild rice were identified as *X. campestris* (5).

Host range. Results of host range trials for *P. syringae* are given in Table 3. Isolates PSZ-1363 and PSZ-1364 were from a natural stand and the rest were from commercial paddies. All strains were pathogenic on wild rice and caused very weak water-soaking or necrosis on quackgrass and Southern wild rice. Some also weakly attacked rye, smooth brome grass, or timothy. The reaction of these other grasses was less consistent than that of wild rice, and these plants were not considered true hosts for these strains.

The *X. campestris* strains exhibited a variety of pathogenicity patterns on the test hosts (Table 4). Strain Xt-12 was pathogenic only to wild rice and barley. The other three strains attacked wild rice, wheat, and either smooth brome grass, quack grass, barley, or a combination of these hosts. These three had host ranges similar or identical to the two pv. strains of *cerealis* from quack grass.

DISCUSSION

Bacterial leaf streak of wild rice is caused by at least two different species of bacteria. Both *P. syringae* and *X. campestris* were associated with BLS lesions, were isolated in pure culture, reproduced symptoms of the disease by artificial inoculation, and were reisolated from artificially infected plants. Thus, Koch's postulates were fulfilled for both species.

The pseudomonad was isolated about 20 times more frequently than the xanthomonad from commercial fields and therefore seemed to be the more important species. However, *X. campestris*

TABLE 2. Comparison of *Pseudomonas syringae* strains from wild rice with reference strains of *P. syringae*

	Number of strains positive						
	Wild rice ^a strains	Pathovar ^b <i>strifaciens</i>	Pathovar ^c <i>syringae</i>	Pathovar <i>phaseolicola</i>	Pathovar <i>pisi</i>	Pathovar <i>glycinea</i>	Pathovar <i>tagetis</i>
No. of strains tested	11	4	6	1	1	1	1
Characters							
Levan production	11	4	6	1	1	1	0
Tyrosine hydrolysis	11	4	0	0	0	1	1
Esculin hydrolysis	10	4	6	0	0	0	1
Gelatin hydrolysis	9	ND ^d	6	0	1	0	1
Syringomycin production	0	0	5	0	0	0	0
Chlorosis-inducing toxin	0	0	ND	ND	ND	ND	ND
Utilization of:							
D-glucose	11	ND	6	1	1	1	1
Sucrose	11	4	6	1	1	1	0
L(+)-arabinose	11	4	6	1	1	1	1
D(+)-galactose	11	4	6	1	1	1	1
Fructose	11	ND	6	1	1	1	1
D(+)-mannose	11	4	5	1	1	1	1
D(+)-trehalose	0	ND	1	0	0	0	0
D(+)-cellobiose	0	ND	0	0	0	0	0
Citrate	11	4	6	1	1	1	1
L(+)-tartrate	0	0	0	0	0	0	1
D(-)-tartrate	0	0	0	0	0	0	0
D(-)-quininate	11	4	5	1	1	1	1
L(+)-lactate	0	0	6	0	0	0	0
Anthranilate	0	0	0	0	0	0	0
Succinate	11	4	5	1	1	1	1
Acetate	11	ND	5	1	1	0	1
DL-homoserine	0	0	0	0	1	0	0
I-erythritol	10	4	6	0	0	0	1
D-mannitol	11	4	6	0	1	1	0
D-sorbitol	11	4	6	0	1	0	0
I-inositol	9	4	6	0	1	1	1
Trigonelline	0	0	6	1	1	1	1
Betaine	11	4	6	0	1	0	1
L-serine	11	ND	6	1	1	0	1
DL-ornithine	0	ND	0	0	0	0	0
DL-β-hydroxybutyrate	0	0	1	0	0	0	0

^aStrains PSZ-2, PSZ-6, PSZ-1079, PSZ-1347, PSZ-1351, PSZ-1363, PSZ-1364, PSZ-1368, PSZ-1405, PSZ-1433, and PSZ-1457.

^bStrains 1514, 1515, 1516, and 1517.

^cStrains ATCC 19310, PSS-A, C-1, Holcus-1, PSS-B, and 1448.

^dNot done.

was isolated slightly more frequently than *P. syringae* from experiment station paddies. Both species were extremely rare in natural stands.

The symptoms of infection by the two bacteria are very similar and consequently differentiation is difficult. In some cases, the xanthomonad can be distinguished from the pseudomonad on the basis of exudate color or subtle differences in symptoms. In general, however, the only reliable method of diagnosis is by isolation.

In host-range studies, wild rice strains Xt-8 and Xt-22 were identical to *X. campestris* pv. *cerealis* strains Xt-25 and Xt-2, respectively. Xt-26 from wild rice was similar, but was pathogenic to smooth brome grass rather than quack grass. All three wild rice strains conform to pv. *cerealis* sensu Fang et al (8).

Isolate Xt-12 from wild rice was pathogenic to barley but not quack grass, wheat or smooth brome grass. The ISPP List (6) includes the names pv. *hordei* (10) Dye 1978 and pv. *translucens* (11) Dye 1978 as pathogens of barley. However, Hagborg (10) clearly indicated the objective synonymy of these two names. Therefore, we propose that these names be combined under pv. *translucens* according to Appendix 1, Parts 13 and 29 of the Standards and that the neopathotype for pv. *translucens* be retained (6). Wild rice strain Xt-12 should therefore be designated *X. campestris* pv. *translucens*.

In the single instance of collection of the xanthomonad in the wild, the infected plants were growing on a lake shore next to several species of wild grasses. Although these grasses did not exhibit obvious symptoms of infection, they may have harbored populations of the pathogen. In one of the two instances when *X.*

TABLE 3. Host range of *Pseudomonas syringae* strains from wild rice

Host	Reaction to strains:				
	PSZ-2	PSZ-1351	PSZ-1363	PSZ-1364	PSZ-1457
Smooth brome grass	- ^a	-	-	+/-	-
Quackgrass	+/-	+/-	+/-	+/-	+/-
Yellow foxtail	-	-	-	-	-
Timothy	-	-	-	-	+/-
Barnyard grass	-	-	-	-	-
Reed canarygrass	-	-	-	-	-
Crabgrass	-	-	-	-	-
Oats	-	-	-	-	-
Barley	-	-	-	-	-
Wheat	-	-	-	-	-
Rye	-	+/-	+/-	-	-
Maize	-	-	-	-	-
Sorghum	-	-	-	-	-
Rice	-	-	-	-	-
Southern wild rice	+/-	+/-	+/-	+/-	+/-
Manchurian wild rice	-	-	-	-	-
Wild rice	+	+	+	+	+

^aSymbols: - = no reaction or chlorosis only; +/- = weak water-soaking or necrosis; and + = strong water-soaking and expanding lesions with delayed necrosis.

campestris was found in commercial fields, infected quack grass was found on the paddy dike <5 m from infected rice plants. Isolates from the quack grass and adjacent wild rice were identical in all characters tested. It appears, therefore, that wild rice isolates of *X. campestris* originated on hosts other than wild rice. Whether these strains overwinter in association with wild rice is unknown.

TABLE 4. Host range of *Xanthomonas campestris* strains from wild rice and quack grass

Host	Reaction to indicated strains					
	Wild rice strains				Quackgrass strains	
	Xt-8	Xt-12	Xt-22	Xt-26	Xt-2	Xt-25
Wheat	+ ^a	—	+	+	+	+
Smooth brome grass	—	—	—	—	—	—
Quack grass	+	—	+	—	+	+
Barley	+	++	—	+	—	+
Rice	—	—	—	—	—	—
Rye	—	—	—	—	—	—
Timothy	—	—	—	—	—	—
Wild rice	+	++	+	+	++	+

^aSymbols: — = no reaction or chlorosis only; + = weak to moderate water-soaking of tissues; and ++ = strong water-soaking and expanding lesions with delayed necrosis.

P. syringae isolates from wild rice could not be differentiated biochemically from *pv. striafaciens*, which causes oat stripe blight. They are also very similar culturally and symptomologically (7). Despite these similarities, oats were not susceptible to five wild rice strains tested (Table 3) and wild rice was not attacked by four *pv. striafaciens* isolates (*unpublished*).

Elliott (7) noted the close cultural and biochemical relationship between *pv. striafaciens* and *pv. coronafaciens*, which causes oat halo blight. She differentiated these strains based on the slightly larger cell size of *pv. coronafaciens* and the difference in symptoms on oats. Tessi (20) studied Argentinian isolates of *pv. striafaciens* and *pv. coronafaciens* and confirmed their cultural, morphological, physiological, biochemical, and serological similarity. He also noted the continuum of symptoms between typical halo blight and typical stripe blight observed in the field. However, he asserted that isolates from intermediate lesions invariably produced symptoms typical of either *pv. striafaciens* or *pv. coronafaciens* in artificial inoculations. In addition, he showed that *pv. coronafaciens*, but not *pv. striafaciens*, produced a chlorosis-inducing toxin that was believed to account for the difference in symptoms.

Sands et al (18) reported that the biochemical characteristics of *pv. striafaciens* and *pv. coronafaciens* were identical except that *pv. coronafaciens* utilized quinate whereas *pv. striafaciens* did not. In the present study, strains of *pv. striafaciens* did utilize quinate (Table 2).

Schaad and Cunfer (19) compared *pv. coronafaciens*, *pv. atropurpurea*, and *pv. striafaciens* with respect to serology and 41 biochemical and physiological tests, and found no significant differences. In host range tests with oats, rye, wheat, barley, corn, timothy, quack grass, and four *Bromus* spp., all strains exhibited considerable cross-pathogenicity except *pv. striafaciens*, which attacked only oats. Chlorosis-inducing toxins were detected in all strains except *pv. striafaciens* and three isolates of *pv. atropurpurea*. Based on these similarities, Schaad and Cunfer concluded that the names *P. coronafaciens*, *P. coronafaciens* subsp. *atropurpurea*, *P. coronafaciens* *pv. zaeae*, and *P. striafaciens* were subjective synonyms, with the name *P. coronafaciens* having nomenclatural priority over the others.

The ISPP List (6) of valid pathovars of phytopathogenic bacteria retained the names *P. syringae* *pv. coronafaciens*, *pv. striafaciens* and *pv. atropurpurea*. It is possible that the authors did not have access to Schaad and Cunfer's (19) data. Nevertheless, the synonymy of these strains has not been validly published.

Schaad and Cunfer's (19) concept of the *P. coronafaciens* seems to include the wild rice *P. syringae* strains. As mentioned above, the wild rice isolates are culturally and biochemically identical to *pv. coronafaciens* and *pv. striafaciens*. Like *pv. striafaciens*, wild rice strains produce a stripe blight lesion with (usually) no halo, produce no detectable toxin, and have a very narrow host range. In cross-inoculation studies *pv. striafaciens* did not infect wild rice but *pv. coronafaciens* strains from oats, corn and Italian ryegrass were able to cause some water-soaking and chlorosis (*unpublished*). However, since wild rice isolates did not infect any hosts of either *pv. coronafaciens* or *pv. striafaciens*, they must be considered

distinct strains and merit recognition at the pathovar level. Accordingly, the name *P. syringae* *pv. zizaniae* *pv. nov.* is proposed and PSZ-2 is designated as the pathotype. The close relationship that is recognized between wild rice strains and *pv. coronafaciens* and *pv. striafaciens* would probably be most appropriately recognized at the level of subspecies. However, the erection of subspecies within the species *P. syringae* will require more extensive studies.

Although common in commercial fields, *pv. zizaniae* was found only once in natural stands of wild rice and then only on a few plants growing near the shore of a lake. No infected wild grasses could be found growing nearby and the source of inoculum is unknown. Nevertheless, the near absence of *pv. zizaniae* in natural stands suggests that it is not native to wild rice. Strains in commercial wild rice fields may originate on an as yet undiscovered alternative host(s) or may have evolved recently to fill a niche in this new agro-ecosystem.

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