

Comparison of Host Ranges of *Peronosclerospora philippinensis* and *P. sacchari*

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ABSTRACT

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Seventy-two plant species representing 22 genera within eight tribes of the Gramineae were tested for susceptibility to systemic colonization after conidial inoculation with two isolates of *Peronosclerospora philippinensis* from the Philippines. All susceptible species were members of the tribe Andropogoneae (genera—*Andropogon* [one species], *Bothriochloa* [10 species], *Eulalia* [one species], *Saccharum* [one species], *Schizachyrium* [three species], and *Sorghum* [three species]) or the tribe Maydeae

(genera—*Tripsacum* [one species] and *Zea* [three species]). Not all accessions susceptible to one isolate of the pathogen showed systemic symptoms when inoculated with the second isolate; in some instances, only a few plants of an accession developed systemic symptoms. The results were remarkably similar to our previous host range study with *P. sacchari* from Taiwan, and the information presented here indicates a very close phylogenetic relationship between *P. philippinensis* and *P. sacchari*.

Philippine downy mildew of maize, caused by *Peronosclerospora philippinensis* (Weston) C. G. Shaw, has not been reported in the western hemisphere, but it is a serious problem in the Philippines where disease losses in some fields have been 40–60% (7). Although maize varieties resistant to *P. philippinensis* have been developed in Asia, maize hybrids currently grown in the United States are highly susceptible to *P. philippinensis*, and American breeding lines that are highly resistant to *P. sorghi* (cause of sorghum downy mildew of maize) in the United States are highly susceptible to *P. philippinensis* (M. R. Bonde, unpublished).

Weeds and cultivated crops play a major role in the perpetuation of the pathogen in the absence of maize (6). Besides maize (13), *P. philippinensis* has been reported to infect *Avena sativa* L. (6), *Euchlaena mexicana* Schrad. (= *Zea mays* L. *mexicana*) (6), *E. mexicana* × *Zea mays* hybrids (6), *Miscanthus japonicus* Andress (14), *Saccharum officinarum* L. (6), *S. spontaneum* L. (14),

Sorghum arundinaceum (Willd.) Stapf (11), *S. bicolor* Moench (13), *S. halepense* (L.) Pers. (6), and *S. propinquum* (Kunth) Hitchc. (6).

As part of a program to determine the threat of specific foreign downy mildew pathogens to American agriculture should they spread to the United States, we conducted a study to determine whether *P. philippinensis* could infect additional alternative hosts that might allow the pathogen to overwinter and act as reservoirs of inoculum to infect maize. The information, besides having epidemiologic significance for maize production, also could help resolve the confusion over the taxonomy of *Peronosclerospora* spp. (2). For this latter purpose, we included plant species that, although not present in the United States, might be useful in differentiating species within the genus *Peronosclerospora*. The results obtained with *P. philippinensis* were remarkably similar to those we recently reported for an isolate of *P. sacchari* from Taiwan (4).

The purpose of this research was to compare the host ranges of the two pathogens by including recent data and data from the previous study of the susceptibility of various plant species to *P. sacchari*. As far as we are aware, this is the first report of host ranges

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of *P. philippinensis* and *P. sacchari* isolates from different countries being compared using the same techniques on the same plant accessions.

MATERIALS AND METHODS

Two cultures of *P. philippinensis* were obtained from the Philippines—one in 1975 and the other in 1979—and two cultures of *P. sacchari* were isolated in our laboratory in 1975 and 1977, respectively, from infected sugarcane sets sent from Taiwan. Seeds of test species were planted in pasteurized soil in 10-cm-diameter clay pots. Seedlings at the two- to three-leaf stage were sprayed with a suspension of conidia collected by the technique of Schmitt and Freytag (9) from infected *Zea mays* 'Pioneer 3369A' or 'DeKalb XL43.' The inoculum dosage used was 5.0×10^4 conidia per milliliter of suspension, 1 ml per pot of seedlings. The number of plants per pot depended on plant species. In a few instances, 20–40 plants were present in a pot; however, usually there were less than 10 per pot. A highly susceptible maize hybrid, either Pioneer 3369A or DeKalb XL43, was included as a control in each experiment. Recently planted sugarcane sets (with buds about to break) in 15-cm-diameter clay pots were sprayed with a suspension of conidia at 5.0×10^3 conidia per milliliter, 1 ml per set. All inoculated plants were incubated overnight in a dew chamber at

21–22 C and then placed in a greenhouse for disease development. The normal temperature fluctuation in the greenhouse was 21–28 C; however, on a few occasions during the summer months, it peaked as high as 34 C shortly after noon and returned to the normal temperature range within 3 hr. Plants were examined for at least 30 days, and usually for 6 wk, after inoculation and were compared with uninoculated controls.

To verify infection within a plant accession, a few plants displaying systemic symptoms were placed overnight in dew chambers, and their leaf surfaces were examined for development of conidia and conidiophores typical of *P. philippinensis* or *P. sacchari*. (In instances in which only one or a few plants had systemic symptoms, all were placed in the dew chambers). In addition, leaf pieces displaying systemic symptoms were placed in the whorls of highly susceptible maize seedlings in dew chambers and incubated overnight at an optimum temperature to induce sporulation and subsequent infection of maize. Susceptibility of a plant accession was based on the presence of sporulation and/or reinfection of maize, in addition to symptoms indicating systemic infection.

All plants lacking systemic symptoms also were placed overnight in dew chambers and examined for the absence of conidia formation to substantiate that they were not infected.

A few infected plants of each susceptible plant accession were

TABLE 1. Level of susceptibility of grass accessions susceptible to at least one isolate of *Peronosclerospora philippinensis*, and their susceptibility to *Peronosclerospora sacchari*

Plant species	P.I. number	Origin	Proportion of inoculated plants showing systemic symptoms ^a	
			<i>P. philippinensis</i>	<i>P. sacchari</i>
Tribe: Andropogoneae				
<i>Andropogon gerardii</i> Vitm.	315656	USA	3/10	2/20
<i>Bothriochloa ambigua</i> S. T. Blake	301264	Australia	7/11	... ^b
<i>B. barbinodis</i> (Lag.) Herter	216054	USA	1/7	... ^b
<i>B. decipiens</i> (Hack.) C. E. Hubb.	301290	Australia	10/54	... ^b
<i>B. edwardsiana</i> (Gould) Parodi	337509	Argentina	20/21	... ^b
<i>B. ischaemum</i> (L.) Keng var. <i>ischaemum</i>	302508	Hungary	48/59	33/89
<i>B. laguroides</i> (DC.) Pilger	404289	Brazil	14/205	0/110
<i>B. perforata</i> (Trin. ex Fourn.) Herter	228517	USA	36/79	7/84
<i>B. springfieldii</i> (Gould) Parodi	301727	USA	16/25	19/35
<i>B. woodrowii</i> (Hook f.) A. Camus	301732	India	14/67	9/25
<i>Eulalia fulva</i> (R. Br.) Ktze.	302078	Australia	3/11	3/54
<i>Saccharum officinarum</i> L. 'CP-44-101' ^c	...	USA	10/10	7/45
<i>Schizachyrium hirtiflorum</i> Nees	228507	USA	17/23	3/3
<i>S. microstachyum</i> (Desv. ex Hamilt.) Roseng., Arr. & Izog.	306269	Argentina	3/12	1/92
<i>S. scoparium</i> (Michx.) Nash	213875	USA	1/9	2/111
<i>Sorghum bicolor</i> (L.) Moench ^d [<i>drummondii</i>]	302141	Australia	1/32	5/47
<i>S. bicolor</i> [<i>gambicum</i>]	302150	Chad	2/102	0/30
<i>S. bicolor</i> [<i>hewisonii</i>]	302173	Sudan	8/113	13/118
<i>S. bicolor</i> [<i>japonicum</i>]	302174	Portugal	24/84	37/91
<i>S. bicolor</i> [<i>melaleucum</i>]	208708	Algeria	2/5	2/26
<i>S. bicolor</i> [<i>miliiforme</i>]	257293	Argentina	2/49	14/69
<i>S. bicolor</i> [<i>nigricans</i>]	302177	Portugal	1/39	0/12
<i>S. bicolor</i> [<i>niloticum</i>]	196890	Ethiopia	1/5	... ^b
<i>S. bicolor</i> [<i>saccharatum</i>]	302198	Argentina	6/39	12/63
<i>S. bicolor</i> [<i>sudanense</i>]	...	USA	1/98	1/61
<i>S. bicolor</i> [<i>technicum</i>]	...	USA	5/117	1/16
<i>S. halepense</i> (L.) Pers.	...	USA	2/26	... ^b
<i>S. plumosum</i> (R. Br.) Beauv. ^e	198999	Australia	4/26	... ^b
Tribe: Maydeae				
<i>Tripsacum dactyloides</i> (L.) L.	...	USA	16/34	20/23
<i>Zea diploperennis</i> Iltis, Doebley & Guzman	...	Mexico	9/11	2/14
<i>Z. mays</i> L. subsp. <i>mays</i> '3369A' and 'XL43'	...	USA	147/149	102/103
<i>Z. mays</i> subsp. <i>mexicana</i> (Schrad.) Iltis	384071	Mexico	72/79	49/59
<i>Z. perennis</i> (Hitche.) Reeves & Mangelsd.	...	Mexico	1/13	3/18

^aAt the two- to three-leaf stage seedlings of all accessions, except those of *Saccharum officinarum*, were sprayed with a conidial suspension of *P. philippinensis* or *P. sacchari* at 5.0×10^4 conidia per milliliter, 1 ml per pot of seedlings.

^bData were not obtained.

^cSugarcane sets (with buds about to break) were sprayed with a suspension of conidia at 5.0×10^3 conidia per milliliter, 1 ml per set.

^dThe taxonomic system described by J. M. J. DeWet (5) was used for *Sorghum bicolor*. This system combined 48 previously separate species with *S. bicolor*. The previous specific epithet is given in brackets.

^eAnother accession of *Sorghum plumosum* not tested against *P. philippinensis* was shown to be susceptible (5/85) to *P. sacchari*.

saved for later testing for the presence of oospores. Leaf pieces displaying systemic symptoms were collected from upper, middle, and lower leaves of plants with systemic symptoms at or near maturity and were fixed in a mixture of absolute ethanol and acetic acid (2:1, v/v). After at least 18 hr in the fixative, the pieces were cleared for 24 hr in lactophenol, stained 24–72 hr with Sudan III in lactophenol (time depending on the specific lot of commercial stain), mounted in lactophenol on glass slides, and observed microscopically.

RESULTS AND DISCUSSION

Results of tests for susceptibility of 72 plant species representing 22 genera within eight grass tribes to *P. philippinensis*, in addition to the susceptibility of many of the same plant accessions to *P. sacchari*, are summarized in Tables 1 and 2 and the text below. The data for each isolate per pathogen were bulked. In several

instances, several accessions of the same plant species were tested (Tables 1 and 2). Besides *Sorghum bicolor* 'Tx412' and *S. bicolor* accession 431392, 18 accessions of *S. bicolor* previously considered to belong to separate *Sorghum* species, and one sorghum-Sudan grass hybrid were tested. A major problem with several grass accessions was the poor germinability of the seed, which resulted in only limited numbers of plants.

The following plant species were not susceptible to *P. philippinensis*: *Agrostis stolonifera* and *Alopecurus aequalis* of the tribe Agrostideae; *Avena abyssinica*, *A. barbata*, *A. brevis*, *A. byzantina*, *A. fatua*, *A. longiglumis*, *A. nuda*, *A. eriantha*, *A. sativa*, *A. sterilis*, and *A. strigosa* of the tribe Aveneae; *Eleusine indica* of the tribe Chlorideae; *Bromus inermis*, *Festuca rubra* subsp. *rubra*, *Poa compressa*, and *P. nemoralis* of the tribe Festuceae; *Agropyron cristatum*, *A. repens*, and *Lolium multiflorum* of the tribe Hordeae; and *Panicum miliaceum*, *P. virgatum*, *Pennisetum americanum*, and *P. macrourum* of the tribe

TABLE 2. Plants of the tribes Andropogoneae and Maydeae not susceptible to *Peronosclerospora philippinensis*, and their corresponding susceptibilities to *Peronosclerospora sacchari*

Plant species	P.I. number	Origin	Proportion of inoculated plants showing systemic symptoms ^a	
			<i>P. philippinensis</i>	<i>P. sacchari</i>
Tribe: Andropogoneae				
<i>Andropogon distachyus</i> L.	300696	Hungary	0/19	0/24
<i>A. ternarius</i> Michx.	301216	USA	0/41	0/14
<i>Arthraxon hispidus</i> (Thunb.) Mak.	225986	Japan	0/213	0/62
<i>Bothriochloa alta</i> (Hitchc.) Henr.	337510	Argentina	0/26	0/13
<i>B. caucasica</i> (Trin.) C.E. Hubb.	300712	USA	0/38	2/16
<i>B. caucasica</i>	301737	Pakistan	0/81	0/20
<i>B. ewartiana</i> (Domin) C.E. Hubb.	301308	Australia	0/18	... ^b
<i>B. glabra</i> (Roxb.) A. Camus	300726	India	0/40	0/4
<i>B. grahamii</i> (Haines) Bor.	241498	New Guinea	0/15	0/15
<i>B. hybrida</i> (Gould) Gould	321437	USA	0/26	0/12
<i>B. insculpta</i> (Hochst.) A. Camus	300730	USA	0/91	0/13
<i>B. insculpta</i>	301436	S. Africa	0/41	0/26
<i>B. intermedia</i> (R. Br.) A. Camus	300806	USA	0/138	0/40
<i>B. intermedia</i>	300857	USA	0/58	0/28
<i>B. ischaemum</i> (L.) Keng var. <i>ischaemum</i>	301507	India	0/15	0/13
<i>B. odorata</i> (Lisboa) A. Camus	301632	India	0/68	0/9
<i>B. pertusa</i> (L.) A. Camus	301638	India	0/41	0/8
<i>B. pertusa</i>	301641	India	0/11	... ^b
<i>B. pertusa</i>	301645	...	0/12	... ^b
<i>B. radicans</i> (Lehm.) A. Camus	364353	Mozambique	0/145	0/13
<i>Capillipedium venustum</i> (Thw.) Bor.	301731	British Guiana	0/44	0/26
<i>Heteropogon contortus</i> (L.) Beauv. ex Roem. & Schult.	216429	USA	0/101	0/28
<i>H. contortus</i>	271174	India	0/172	0/26
<i>Schizachyrium cirratum</i> (Hack.) Woot & Standl.	216107	Mexico	0/8	... ^b
<i>S. condensatum</i> (H.B.K.) Nees	203835	Brazil	0/76	0/14
<i>Sorghum</i> × <i>almum</i> Parodi	207840	...	0/64	0/26
<i>S. bicolor</i> (L.) Moench 'TX412'	...	USA	0/216	0/64
<i>S. bicolor</i>	431392	India	0/46	... ^b
<i>S. bicolor</i> [<i>caffrorum</i>]	302135	India	0/60	4/64
<i>S. bicolor</i> [<i>caudatum</i>]	282834	Chad	0/51	1/45
<i>S. bicolor</i> [<i>cernuum</i>]	267126	USSR	0/58	0/12
<i>S. bicolor</i> [<i>durra</i>]	267105	USSR	0/45	5/44
<i>S. bicolor</i> [<i>guineense</i>]	282857	Chad	0/61	2/6
<i>S. bicolor</i> [<i>mellitum</i>]	267324	India	0/74	0/21
<i>S. bicolor</i> [<i>nervosum</i>]	208710	Algeria	0/19	0/17
<i>S. halepense</i> [<i>controversum</i>]	302268	Africa	0/29	0/63
<i>S. halepense</i> [<i>miliaceum</i>]	271615	India	0/24	... ^b
<i>S. plumosum</i> (R. Br.) Beauv.	220931	Australia	0/14	... ^b
<i>S. propinquum</i> (Kunth) Hitchc.	302191	Philippines	0/32	1/46
<i>S. pugionifolium</i> Snowden	271240	India	0/55	2/12
<i>S. versicolor</i> Anderss.	260273	Ethiopia	0/44	6/29
<i>S. verticilliflorum</i> (Steud.) Stapf	213901	Rhodesia	0/25	0/36
Tribe: Maydeae				
<i>Coix lacryma-jobi</i> L.	326342	Brazil	0/24	0/13

^aSeedlings of all accessions at the two- to three-leaf stage were sprayed with a conidial suspension of *P. philippinensis* or *P. sacchari* at 5.0×10^4 conidia per milliliter, 1 ml per pot of seedlings.

^bData were not obtained.

^cThe taxonomic system described by J. M. J. DeWet (5) was used for *Sorghum bicolor*. This system combined 48 previously recognized species with *S. bicolor*. The previous specific epithet is given in brackets.

Paniceae. No species of these tribes were susceptible to an isolate of *P. sacchari* (4).

The grass accessions that were susceptible to *P. philippinensis* (Table 1) represented 19 species in six genera in the tribe Andropogoneae (*Andropogon* [one species], *Bothriochloa* [10 species], *Eulalia* [one species], *Saccharum* [one species], *Schizachyrium* [three species], and *Sorghum* [three species]) or four species in two genera in the tribe Maydeae (*Tripsacum* [one species] and *Zea* [three species]). Not all accessions that developed symptoms of systemic infection in response to one isolate of *P. philippinensis* did so with the other.

Some grass accessions were very susceptible to *P. philippinensis* (Table 1). These include *Bothriochloa ambigua*, *B. edwardsiana*, one accession of *B. ischaemum* var. *ischaemum*, and *Saccharum officinarum* (sugarcane), all with 78% or higher rates of systemic infection at the inoculum dosage used.

Bothriochloa ischaemum var. *ischaemum* was represented by one accession that was not susceptible to *P. philippinensis* and *P. sacchari* (one pathogen isolate of each tested), and one accession that was susceptible to both isolates of each pathogen.

Eleven accessions of *S. bicolor* were susceptible to at least one isolate of *P. philippinensis*, and nine were not susceptible. This difference in susceptibility within *S. bicolor* probably is partly due to the heterogeneity in the plant species. However, the incidence, when present, was always low. *S. bicolor* (*japonicum*) P.I. 302174 was moderately susceptible to both isolates of *P. sacchari* and somewhat less susceptible to the isolates of *P. philippinensis*.

Exconde et al (6) reported that *Avena sativa* L. in the Philippines is susceptible to *P. philippinensis*; however, we were unable to infect any of 11 species of *Avena*, including four accessions of *A. sativa*. In a further test, *A. sativa* cultivar Clintland, besides being inoculated at 5×10^4 conidia per milliliter, was inoculated at the dosage 1.0×10^5 conidia per milliliter. None of 298 plants at the lower dosage or 261 at the higher dosage developed systemic symptoms, and the pathogen could not be recovered.

According to results presented here and previously (4), *P. philippinensis* and *P. sacchari* are both restricted to host species within the grass tribes Andropogoneae and Maydeae. Examination of host range results for the two pathogens on specific plant accessions within these two tribes indicates a remarkable similarity in their host ranges. Of 26 plant accessions in these tribes susceptible to at least one isolate of *P. philippinensis*, 23 also were susceptible to at least one isolate of *P. sacchari* (Table 1). Of 36 accessions in the Andropogoneae and Maydeae not susceptible to *P. philippinensis*, 28 also were not susceptible to *P. sacchari* (Table 2). The differences between pathogen species were similar to the differences between isolates within the same pathogen species. For example, of 21 accessions susceptible to at least one isolate of *P. philippinensis*, only 13 became infected by the other isolate. Of eight grass accessions susceptible to at least one isolate of *P. sacchari*, seven were susceptible when tested against the other isolate.

In a few instances where no infection occurred, the number of test plants was small; had more plants been available for testing, systemic disease might have developed in at least one or a few plants of a supposedly nonsusceptible combination.

Several species of *Andropogon*, *Bothriochloa*, and *Schizachyrium* that were susceptible in this study are common perennial forage and wild grasses in the United States (8). Big bluestem (*Andropogon gerardii*) and little bluestem (*Schizachyrium*

scoparium) are perhaps the most prevalent constituents of wild hay in the prairie states (8). These perennial grasses possibly could serve as reservoir hosts for *P. philippinensis* or *P. sacchari* if these pathogens entered the United States and if infected plants could survive the winter season.

Oospores were not detected in leaf tissue of any of the systemically infected plants, even when infected plants were held to maturity. However, the production of oospores by *P. sacchari* in sugarcane has been reported (12).

We believe there is a very close phylogenetic relationship between *P. philippinensis* and *P. sacchari*. Besides having essentially identical environmental requirements for optimum sporulation, conidial germination, and infection (1,3), and similar shapes of conidia and conidiophores (10), their host ranges are remarkably similar. Further studies may indicate the desirability of combining these two species. In fact, Weston (13) suggested in 1920 that all oriental forms infecting maize may be a single species. In a study of ours not reported here (M. R. Bonde, unpublished), one isolate of *P. sacchari* that we attempted to test from the Philippines was pathogenetically very different from the isolates of *P. philippinensis* from the Philippines or *P. sacchari* from Taiwan. It was only weakly pathogenic to maize to the extent that we could not collect enough conidia from maize to compare the isolate's host range against those of the other pathogen isolates. The species *P. sacchari* needs to be reexamined for homogeneity.

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