Host Range and Alternate Host of a *Puccinia coronata* Population from Smooth Brome Grass

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ABSTRACT

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A rust fungus was observed on smooth brome grass (*Bromus inermis* Leyss.) leaves growing in the fields of the University of Wisconsin (UW) Agricultural Research Station at Arlington, WI. The population (WPc-95A) was classified as *Puccinia coronata* Corda. Reports of *P. coronata* on *B. inermis* are rare, so a study of the pathogen host range, alternate host, and morphology of urediniospores and teliospores was undertaken. Fourteen grass species representing 10 genera were inoculated with *P. coronata* WPc-95A, which was maintained with repeated inoculations on *B. inermis* cv. PL-BDR1. Seventy-two 30-day-old seedlings of *B. inermis* were inoculated with urediniospores of the fungus. Infection type, pustule density, and disease incidence were recorded 15 days after inoculation. The same grass cultivars were also inoculated with aeciospores collected from *Rhannus cathartica* L. located on the UW campus. To test for host specificity, urediniospores produced on aeciospore-susceptible grass species were used to reinoculate plants of *B. inermis* and the host species from which the urediniospores were derived. *B. inermis*, *B. riparius* Rehm., *Festuca pratensis* Huds., and *Lolium perenne* L. were susceptible to *P. coronata* WPc-95A. The two *Bromus* spp. had the highest disease incidence. *R. cathartica* was found to be an alternate host of *P. coronata* WPc-95A, as it is for *P. coronata* isolates found on *F. pratensis*. However, cross-inoculations with urediniospores from *R. cathartica*-derived aeciospore infections indicated that only urediniospores of *B. inermis* origin were capable of infecting *B. inermis*. Thus, *P. coronata* WPc-95A appears to belong to a forma specialis previously undescribed in North America.

A rust fungus was intermittently observed in breeding nurseries of *Bromus inermis* Leyss. during the 1990s at Arlington, WI. Reports of rust on *B. inermis* include brown rust, *Puccinia recondita* Roberge ex Desmaz. (2,18), and crown rust, *P. coronata* Corda (4,8,13). An isolate of the rust fungus on *B. inermis*, WPc-95A, was established in a controlled environment and was classified as *P. coronata*, based on teliospore morphology.

P. coronata occurs on numerous *Bromus* spp. throughout much of North America, including both native and introduced species (4,6,9-12,14). Although *P. coronata* has numerous physiological forms (formae speciales), most descriptions of *P. coronata* on *Bromus* spp. do not identify the taxon beyond the species level and contain no morphological or physical description to allow any further taxonomic identification. *P. coronata* has been reported on *B. inermis* three times in North America, in a controlled-environment inoculation experiment with *P. coronata* var. *hordei* (11)

and unknown taxonomic forms in Alaska and South Dakota (1,4).

Fraser and Ledingham (8) described an isolate of *P. coronata* that produced uredinia and telia on *B. ciliatus*, *B. latiglumis*, and *B. porteri*, with aecia on the alternate host, rabbit berry (*Lepargyrea canadensis* L.). This isolate of *P. coronata* was common in northern Saskatchewan where both *B. ciliatus* and *L. canadensis* occur together. The relationship of aecial hosts and aecial morphology suggested that the *P. coronata* on *L. canadensis* was distinct from *P. coronata* on *Rhannus* spp. (8). These authors named this new isolate *P. coronata* f. sp. *bromi*, largely because of its predominance on several *Bromus* spp. Nevertheless, *B. inermis* was immune to *P. coronata* f. sp. *bromi* (8) as well as to *P. coronata* f. sp. *avenae* (2,8,12) and *P. coronata* f. sp. *holci* (12). *B. inermis*, *B. ciliatus*, *B. latiglumis*, and *B. porteri* are all members of the *Bromus* subgenus *Bromopsis*; therefore, there does not appear to be any relationship between *Bromus* taxonomy and *P. coronata* host range on *Bromus* spp.

P. coronata Corda is a complex species consisting of numerous formae speciales that form a telial state on one or more of many grass hosts. Alternate hosts include *Berchemia scandens* (Hill) K. Koch, *Condalia obovata* (Hook), *Elaeagnus commutata* Bernh. ex Rydb., *Lepargyrea canad-*

ensis (L.) Greene, and several species of *Rhannus* (16). In all, 290 plant species are reported as telial hosts of *P. coronata* in 72 genera distributed among 17 tribes in four subfamilies of the Poaceae (16). Genera within the subfamily Festucoideae are common hosts of *P. coronata* and, in nature, hosts outside this subfamily are rare (16). Physiological forms of *P. coronata* generally are restricted to one telial host, but may form the aecidial state on several alternate host species (7). The objective of this study was to determine the host range, alternate host, and morphology of urediniospores and teliospores of *P. coronata* WPc-95A.

MATERIALS AND METHODS

A rust collection from infected *Bromus inermis* leaves in fields of the University of Wisconsin (UW) Arlington Agricultural Station was classified as *P. coronata* and named WPc-95A. Measurements of 150 urediniospores and 150 teliospores were made to characterize the population in comparison with *P. coronata* f. sp. *bromi* and f. sp. *avenae* (8). Measurements were made on freshly collected spores. Urediniospores were measured along their greatest diameter as length and at right angles to this for width. For teliospores, the longitudinal measurement was taken from the point of attachment of the pedicel to the apex of the crown, as described by Fraser and Ledingham (8). Teliospore width was measured across the crown. Means and standard deviations were computed.

P. coronata WPc-95A was maintained with repeated inoculations of *B. inermis* PL-BDR1, a cultivar developed at the U.S. Regional Pasture Research Laboratory (University Park, PA) for resistance to *Pyrenophora bromi* (Died.) Drechs. (3). Urediniospores of *Puccinia coronata* were collected from *B. inermis* PL-BDR1 plants that had been infected with the original isolate of *P. coronata* WPc-95A. Urediniospores were harvested with a vacuum pump every 2 days until the fungus sporulation ceased. The inoculum was prepared by suspending 7- to 10-day-old spores (previously stored at about 4°C) in deionized water containing two drops of Tween 20 surfactant per 100 ml of water and agitated manually. The spore concentration used was approximately 2 to 4 × 10⁵ urediniospores/ml.

Seeds of 16 grass cultivars, representing 10 genera and 14 species (Table 1), were

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planted in 225-cm³ plastic pots filled with a 50:50 (vol/vol) mixture of peat moss and silt loam soil. One week after emergence, 72 plants per cultivar or population were transplanted to 30-cm³ plastic pots filled with the same soil medium. Each plant was fertilized 15 days after transplanting with 80 mg of N, 69 mg of P, and 56 mg of K. Inoculation was performed 4 weeks after transplanting. An air sprayer was used to uniformly apply 25 ml of inoculum suspension per flat (72 seedlings), after which flats were placed in a dew chamber for 48 h and returned to the greenhouse benches under fluorescent light supplementation (14-h day length) and a temperature range of 21 to 28°C. Pustules appeared approximately 12 to 15 days after inoculation.

The total number of pustules per leaf was determined for two leaves per cultivar using a microscope. The length and width of each leaf was determined, leaf area was computed according to the method of Casler and Carpenter (5), and the data were expressed as the number of pustules per square centimeter, or pustule density. Infection type (IT) was visually determined using a scale adapted from Roelfs (15), where 0 = no uredinia, 1 = chlorotic flecks (no sporulation), 2 = small uredinia sur-

rounded by necrosis with limited urediniospore production, 3 = medium-size uredinia with moderate sporulation, and 4 = large uredinia and abundant sporulation. IT was recorded for the two most heavily infected leaves per cultivar or population, which were sampled and preserved on paper towels covered with transparent tape. IT classifications were largely unambiguous, with individual plants rarely showing multiple IT classes. In these rare cases, IT scores were assigned based on the most advanced IT class. The frequency of plants with IT ≥ 2 was recorded to determine disease incidence for each cultivar.

Aeciospores were collected from *Rhamnus cathartica* bushes adjacent to fields of *B. inermis*. Collections were made from five adjacent bushes with a Pasteur pipette and bulked to form a single isolate. Twelve plants each of the 16 grass cultivars were inoculated with aeciospores to determine the primary host range of this *R. cathartica* metapopulation of *P. coronata*. The inoculation, post-inoculation, and data collection protocols followed were the same as described above for the urediniospore inoculations.

Urediniospores were collected with a vacuum pump from all plants that were

infected by aeciospores and separated according to grass species host. To test for primary host specificity of these urediniospore isolates (each deriving from the original *R. cathartica* metapopulation of *P. coronata*), they were reinoculated on two host species: *B. inermis* and the species from which the urediniospores were derived. The inoculation, post-inoculation, and data collection protocols followed were the same as described above for urediniospore inoculations, with one exception: cotton swabs covered with urediniospores were used instead of the sprayer-spore suspension. Earlier (unreported) experiments had shown similar effectiveness of the spray versus cotton swab inoculation techniques. The experimental design was a randomized complete block with three replicates. Experimental units consisted of 12 seedlings of one species. The experiment was repeated twice so that 72 plants per species were evaluated for their reaction to *P. coronata* from *R. cathartica*.

RESULTS AND DISCUSSION

Urediniospores of *P. coronata* WPC-95A were orange and only slightly longer than wide (Table 2). Black telia were covered by the host epidermis and produced on the host leaves in late October. Teliospores were two-celled, clavate-oblong, orange-brown, and darkest at the tip of the apical cell. Mean teliospore length was approximately 4.4 times the width. The range of teliospore size was 40 to 70 µm long and 10 to 15 µm wide. Urediniospore size was less variable than teliospore size. Urediniospores and teliospores of *P. coronata* WPC-95A were longer than those of *P. coronata* f. sp. *bromi* W. P. Fraser & Ledingham (8) (Table 2). Teliospores of *P. coronata* WPC-95A were longer than those of *P. coronata* f. sp. *avenae* W. P. Fraser & Ledingham (8). Thus, *P. coronata* WPC-95A appears to be morphologically different from both *P. coronata* f. sp. *avenae* W. P. Fraser & Ledingham and *P. coronata* f. sp. *bromi* W. P. Fraser & Ledingham. A dried and pressed sample of *B. inermis* including both teliospores and urediniospores has been deposited at the Arthur Herbarium, Purdue University (accession no. PUR N652).

Using urediniospores collected from *B. inermis* PL-BDR1, *P. coronata* WPC-95A caused infection in only 4 of the 16 grass cultivars (Table 3). The other 12 grass cultivars either showed no symptoms or developed only chlorotic or necrotic flecks. Four of these showed no visible reaction, suggesting that they are not hosts of *P. coronata* WPC-95A (Table 4). The other eight cultivars, with only chlorotic or necrotic flecks, may possess host resistance to *P. coronata* WPC-95A. Of these eight cultivars, three (*Lolium multiflorum* and both *Triticum aestivum* cultivars) have likely undergone human-directed selection

Table 1. Species of grasses used in the *Puccinia coronata* WPC-95A pathogenicity test

Species	Common name	Cultivar
<i>Arrhenatherum elatius</i> (L.) Nevski	Tall oat grass	Arone
<i>Avena sativa</i> L.	Oat	Gem
<i>Avena sativa</i> L.	Oat	Ogle
<i>Bromus riparius</i> Rehm.	Meadow brome grass	Fleet
<i>Bromus inermis</i> Leyss.	Smooth brome grass	PL-BDR1
<i>Dactylis glomerata</i> L.	Orchard grass	Justus
<i>Elytrigia × muctonata</i> (Opiz ex Bercht.) Prokud.	Hybrid wheat grass	WEm-ILR
<i>Elytrigia repens</i> (L.) Nevski	Quack grass	WEr-URS
<i>Festuca arundinacea</i> Schreb.	Tall fescue	KY-31
<i>Festuca pratensis</i> Huds.	Meadow fescue	Laura
<i>Lolium multiflorum</i> Lam.	Italian rye grass	Florida 80
<i>Lolium perenne</i> L.	Perennial rye grass	PR4
<i>Phalaris arundinacea</i> L.	Reed canary grass	Rival
<i>Phleum pratense</i> L.	Timothy	Climax
<i>Triticum aestivum</i> L.	Winter wheat	Menton
<i>Triticum aestivum</i> L.	Winter wheat	Glory

Table 2. Mean urediniospore and teliospore dimensions (µm) for three *Puccinia coronata* isolates

Organism ^a	Urediniospores		Teliospores	
	Length	Width	Length	Width
<i>P. coronata</i> f. sp. <i>avenae</i>	24.0 ± 0.06	20.4 ± 0.04	60.5 ± 0.32	17.0 ± 0.09
<i>P. coronata</i> f. sp. <i>bromi</i>	20.5 ± 0.05	17.7 ± 0.04	41.6 ± 0.18	15.3 ± 0.07
<i>P. coronata</i> WPC-95A	23.0 ± 0.61	19.8 ± 0.81	56.0 ± 1.05	12.8 ± 0.55

^a *P. coronata* f. sp. *avenae* and *P. coronata* f. sp. *bromi* are from Fraser and Ledingham (8).

Table 3. Mean values for disease incidence, infection type, and pustule density for all infected cultivars challenged with urediniospores of *Puccinia coronata* WPC-95A from *Bromis inermis*

Cultivar or population	Disease incidence (%)	Infection type ^a	Pustule density cm ^{-2b}
<i>B. inermis</i> cv. PL-BDR1	96	4	8.3
<i>B. riparius</i> cv. Fleet	51	3–4	8.1
<i>Festuca pratensis</i> cv. Laura	3	2	0.6
<i>Lolium perenne</i> cv. PR4	13	4	1.7

^a Range of values for susceptible plants (infection type ≥ 2).

^b Mean of values for susceptible plants (infection type ≥ 2).

for host resistance to some strains of *P. coronata*, whereas selection for host resistance in the others may have occurred by natural selection. *Phleum pratense* (nonhost in Table 4) and *Phalaris arundinacea* (resistant host in Table 4) were both reported to be susceptible to *Puccinia coronata* f. sp. *avenae* (8), further discriminating the host range of *P. coronata* f. sp. *avenae* and *P. coronata* WPC-95A.

The two *Bromus* spp. had higher disease incidence than *Festuca pratensis* and *L. perenne* (Table 3). Infection type was similar for *L. perenne* and the two *Bromus* spp., but pustule density was higher for the *Bromus* spp., indicating their greater susceptibility to *P. coronata* WPC-95A. These four host species belong to one subfamily (Festucoideae) and *P. coronata* f. sp. *lolii* has been reported to infect both *F. pratensis* and *L. perenne* (12), which are species of closely related genera (17). *P. coronata* f. sp. *lolii* has not been tested on *B. inermis*. However, *F. pratensis* and *L. perenne* both showed a nonhost reaction to *P. coronata* f. sp. *bromi* W. P. Fraser & Ledingham (8). Therefore, it is doubtful that *P. coronata* WPC-95A can be considered an isolate of *P. coronata* f. sp. *bromi* W. P. Fraser & Ledingham.

P. coronata f. sp. *bromi* and f. sp. *avenae* induced similar nonhost reactions on *B. inermis*, *F. pratensis*, and *L. perenne*, with the exception of a host-resistance reaction of *P. coronata* f. sp. *avenae* on *L. perenne* in one study (Table 5). Based on reaction to these three hosts, *P. coronata* WPC-95A appears most similar to *P. coronata* f. sp. *lolii*. However, this pattern breaks down when additional potential host species are examined. Melhus et al. (12) found *Avena sativa* L., *Dactylis glomerata* L., *Festuca arundinacea* Schreb., *F. pratensis* Huds., *Lolium multiflorum* Lam., *L. perenne* L., and *Phalaris arundinacea* L. to be highly susceptible to *Puccinia coronata* f. sp. *lolii*, whereas *Phleum pratense* showed a host-resistance reaction, and *A. elatius* and *E. repens* showed no visible reaction. Of the 10 grass species that were coincident between our study and that of Melhus et al. (12), only two (*F. pratensis* and *L. perenne*) showed similar host classification for *Puccinia coronata* f. sp. *lolii* (12) and *P. coronata* WPC-95A (Tables 3 and 4). Similarly, the reactions of *D. glomerata*, *Elytrigia repens*, *L. perenne*, and *Phalaris arundinacea* to *Puccinia coronata* var. *hordei* (11) were decidedly different than to *P. coronata* WPC-95A (Tables 3 and 4). Thus, it appears unlikely that *P. coronata* WPC-95A is an isolate of either *P. coronata* f. sp. *lolii* or *P. coronata* var. *hordei*.

B. inermis, *B. riparius*, *Elytrigia × muctonata*, *E. repens*, *F. pratensis*, and *A. sativa* cv. Ogle were susceptible to the population of *P. coronata* collected from *R. cathartica* (IT ≥ 2 for most plants). All other species and cultivars had IT < 2 for all plants inoculated. Thus, *R. cathartica* is

likely an alternate host of *P. coronata* WPC-95A. However, the host specificity of *P. coronata* WPC-95A is not clear from these results. When urediniospores collected from the aeciospore-infected cultivars were used to inoculate *B. inermis* plants and the hosts from which these urediniospores were derived, only urediniospores of *B. inermis* origin were able to infect *B. inermis*. A hypersensitive reaction (chlorotic flecking, IT = 1) was observed for the non-*B. inermis* urediniospore populations on *B. inermis*, whereas their respective host plants developed heavily sporulating pustules (Table 6).

The species *R. cathartica* is known to support *P. coronata* f. sp. *avenae*, f. sp. *lolii*, and f. sp. *hordei* (7,8,11,12) and, most likely, *P. coronata* WPC-95A. Aeciospores collected from only five adjacent *R. cathartica* bushes appeared to have supported several formae speciales of *P. coronata* in our study. Thus, individual plants or colonies of *R. cathartica* may be relatively insensitive to subtle differences in *P. coronata* taxonomy and appear to be capable of supporting large metapopulations of *P. coronata* genotypes. Within the *P. coronata* metapopulation collected on *R. cathartica*, the *P. coronata* aeciospores that infected *B.*

Table 4. Percentage of plants showing necrotic flecks, chlorotic flecks, or no visible reaction for all 12 cultivars with little or no symptoms following inoculation with *Puccinia coronata* WPC-95A^a

Species, cultivar	Reaction type ^b			Comments
	NF	CF	NR	
<i>Avena sativa</i> cv. Gem	0.0	0.0	100.0	No visible reaction
<i>A. sativa</i> cv. Ogle	0.0	0.0	100.0	No visible reaction
<i>Festuca arundinacea</i>	0.0	0.0	100.0	No visible reaction
<i>Phleum pratense</i>	0.0	0.0	100.0	No visible reaction
<i>Arrhenatherum elatius</i>	0.0	23.6	76.4	Large size, well-defined CF
<i>Dactylis glomerata</i>	12.9	25.7	61.4	Not well-defined flecks
<i>Elytrigia × muctonata</i>	27.5	29.0	43.5	Medium-size, well-defined CF
<i>E. repens</i>	16.1	54.8	25.0	Small size CF
<i>Lolium multiflorum</i>	0.0	8.3	91.7	Not well-defined flecks
<i>Phalaris arundinacea</i>	100.0	0.0	0.0	Large-size, well-defined NF
<i>Triticum aestivum</i> cv. Menton	0.0	100.0	0.0	Medium-size, well-defined CF
<i>T. aestivum</i> cv. Glory	0.0	94.3	6.7	Small-size CF

^a Inoculations were made using urediniospores from *Bromis inermis* PL-BDR1 plants.

^b NF = necrotic flecks, CF = chlorotic flecks, and NR = no visible reaction.

Table 5. Summary of reaction phenotypes from three experiments in which *Puccinia coronata* strains were tested against *Bromus inermis*, *Festuca pratensis*, and *Lolium perenne*^a

Host species, authors ^b	<i>P. coronata</i> form or isolate			
	f. sp. <i>avenae</i>	f. sp. <i>bromi</i>	f. sp. <i>lolii</i>	WPC-95A
<i>B. inermis</i>				
Other authors	0	0	NT	NT
Delgado, Grau, and Casler	NT	NT	NT	+
<i>F. pratensis</i>				
Other authors	0	0	+	NT
Delgado, Grau, and Casler	NT	NT	NT	+
<i>L. perenne</i>				
Other authors	0/1	0	+	NT
Delgado, Grau, and Casler	NT	NT	NT	+

^a NT = not tested, 0 = nonhost reaction, 1 = resistant host (weak, hypersensitive reaction), and + = susceptible host.

^b Other authors = data from Fraser and Ledingham (8) or Melhus et al. (12).

Table 6. Reaction of four grass species to urediniospores collected from pustules resulting from a *Rhamnus cathartica*-derived aeciospore challenge of each grass species^a

Urediniospore origin	Inoculated grass species	Number of days post-inoculation	
		10	12
<i>Avena sativa</i> cv. Ogle	<i>A. sativa</i> cv. Ogle	3–4	3–4
	<i>Bromus inermis</i>	0	1
<i>Elytrigia repens</i>	<i>E. repens</i>	3	3–4
	<i>B. inermis</i>	0	1
<i>Festuca pratensis</i>	<i>F. pratensis</i>	3–4	3–4
	<i>B. inermis</i>	0	1
<i>B. inermis</i>	<i>A. sativa</i> cv. Ogle	0	1
	<i>B. inermis</i>	0	3–4

^a Reaction was measured as pustule type: 0 = no visible reaction, 1 = chlorotic flecks without uredinia, 2 = small uredinia with limited necrosis and some urediniospore production, 3 = medium size uredinia with moderate sporulation, and 4 = large uredinia with abundant sporulation.

inermis showed differential pathogenicity to those that infected *A. sativa*, *F. pratensis*, or *E. repens* (Table 6).

Based on the alternate host, host range, and morphology of the urediniospores and teliospores, *P. coronata* WPC-95A is different from the population described in Canada (8) and may belong to *P. coronata* f. sp. *bromi* Mühlethaler described in Germany (13). *P. coronata* f. sp. *bromi* W. P. Fraser & Ledingham reported in Canada did not cause disease on *B. inermis*, *L. perenne*, or *F. pratensis*; its alternate host is different from *R. cathartica*; and its urediniospore and teliospore sizes are different from *P. coronata* WPC-95A. Furthermore, the German *P. coronata* f. sp. *bromi* Mühlethaler is known to infect *B. inermis* and *R. cathartica* is its alternate host (13).

Fraser and Ledingham (8) are the only authors to describe a *Bromus*-specific form of *P. coronata* in North America. They admitted that their use of the term "variety *bromi*" was one of convenience. This variety (or forma speciales) was most commonly observed on *B. ciliatus* and the alternate host *L. canadensis* in northern Saskatchewan. However, even their own data suggest that this subspecific designation was misleading. Mühlethaler (13) reported *B. inermis* to be highly susceptible to a *Bromus*-specific form of *P. coronata* (syn. *P. coronifera*), clearly distinguishable from Fraser and Ledingham's isolate based

on pathogenicity within the genus *Bromus*. We cannot rule out the possibility that *P. coronata* WPC-95A is a member of this German taxon; therefore, to avoid further confusion, we do not suggest a new variety taxon for *P. coronata* WPC-95A. We suggest *P. coronata* f. sp. *bromi* W. P. Fraser & Ledingham, which is widespread on *B. ciliatus* in northern Saskatchewan, should be renamed to reflect its different pathogenicity from the German isolate of *P. coronata* f. sp. *bromi* Mühlethaler.

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