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Puccinia coronata var. *hordei* var. nov.: morphology and pathogenicity

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Abstract: A new variety of *Puccinia coronata* causing a disease on barley and other gramineous species is described. The fungus is different from other reported forms of *P. coronata* in both morphology and pathogenicity. Its most prominent characters are the elongated teliospore appendages with dichotomous branching and wide pathogenicity on species in the tribe Triticeae, particularly the genus *Hordeum*. The name of *P. coronata* var. *hordei* is proposed for the rust fungus. The common name 'crown rust of barley' is proposed for the disease of barley caused by this rust fungus. Results of inoculation indicated that *P. coronata* var. *hordei* is pathogenic on species of *Aegilops, Agropyron, Elymus, Elytrigia, Leymus, Pascopyrum, Psathyrostachys, Secale,* and *Triticum* in the tribe Triticeae, and some species of *Brachypodium, Bromus, Festuca,* and *Lolium* in the tribe Poeae, and *Phalaris* in the tribe Aveneae. In the northern Great Plains of the USA, the following native and introduced gramineous species were found naturally infected by *P. coronata* var. *hordei*: *Bromus tectorum, Elymus canadensis, E. trachycaulus, E. virginicus, Elytrigia intermedia, E. repens, Hordeum jubatum, H. vulgare, Leymus angustus, L. cinerius, L. dahuricus, L. racemosus, Pascopyrum smithii, Psathyrostachys juncea,* and *Secale cereale.*

Key Words: barley, crown rust, *Rhamnus,* Uredinales

INTRODUCTION

In 1991, a rust fungus, tentatively identified as *Puccinia coronata,* was found on barley (*Hordeum vulgare*) in a breeding nursery near Clay Center, Nebraska. The disease caused by this pathogen was severe at that location (Jin et al 1992) as some barley lines exhibited up to 90% rust severity (percent leaf tissue covered by uredinia). In 1992, uredinial and telial states of this rust were found on many native and introduced gramineous species in Minnesota, North Dakota and South Dakota. The aecial state also was isolated from common buckthorn (*Rhamnus cathartica*) in the region. The development of the disease on barley and grasses in the northern Great Plains has been monitored since 1992. Epidemics on barley and several forage grasses have been observed in some localities where *R. cathartica* is abundant. The rust severity frequently reached more than 60% in some fields and nurseries. Based on disease surveys conducted between 1992 and 1997, this rust has increased markedly in its incidence on barley in the region. Studies were conducted to investigate the morphology of the rust, its pathogenicity on gramineous and rhamnaceous species, and distribution.

MATERIALS AND METHODS

The description of the rust fungus was based on the uredinial and telial states on *H. vulgare.* Uredinial and telial states for the type specimen were obtained from barley plants (CV 'Aim') inoculated in the greenhouse with a uredinial culture originally isolated from barley plants from Clay Center county, Nebraska. The description of pycnial and aecial states was based on samples from *R. cathartica* collected near Absaraka, North Dakota, which were later verified to be the same rust by inoculation experiments. Measurements of spore dimensions were based on 100–120 spores for each spore state. Photomicrographs were made using a scanning electron microscope (SEM) and a compound microscope.

Seeds of most gramineous species used in this study were provided by the USDA-ARS National Small Grains Germplasm Research Facility at Aberdeen, Idaho, and the USDA-ARS Western Regional Plant Introduction Station at Pullman, Washington. Up to 10 accessions of each species were tested when multiple accessions were available. Five to 20 seeds per accession, depending on the species, were planted in plastic cones (3.8 cm diameter and 21 cm depth) filled with a peat moss:perlite (3:1) potting mix (#1 Sunshine Mix from Fisons Horticulture, Inc., Vancouver, Canada). Plants were grown in a greenhouse or growth chamber with a photoperiod ranging from 14–16 h and daily average temperatures of 20–24 C. Plants were inoculated at the two to three leaf stage. Ten to 20 accessions of the cultivated cereals, barley, oat (*Avena sativa*), rye (*Secale cereale*), and common wheat (*Triticum aestivum*) were tested at the adult

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plant stage. Plants were grown in a greenhouse and inoculated after heading. Seeds of *Rhamnus* spp. were obtained from the North Dakota State University arboretum located near Absaraka, North Dakota, and from the United States National Arboretum, Washington, DC. These seeds were air-dried, scarified with a scalpel, and planted in pots filled with clay loam soil. Plants were trimmed to induce new leaf growth 1 wk prior to inoculations for determining the aecial hosts of the rust in the greenhouse.

Three single uredinial isolates of the pathogen, originating from different locations/hosts, were used to test the pathogenicity on gramineous species. Isolate JIN91–36 was the type culture isolated from infected barley near Clay Center, Nebraska, in 1991. Isolate Hv-8 was a culture isolated from barley at Casselton, North Dakota, in 1992. Isolate AE-1-B was originally derived from a mass collection of aeciospores collected from *R. cathartica* near Absaraka, North Dakota, in 1992. An isolate (AE-1-O) of *P. coronata* var. *avenae,* also derived from aeciospores collected from *R. cathartica* in 1992, was used for comparison.

Evaluation of pathogenicity on gramineous species.—Urediniospores of the rust isolates described above were used to inoculate plants of gramineous species following the procedures used for other cereal rusts (Steffenson et al 1993). Urediniospores suspended in a lightweight mineral oil (3 mg spores/0.5 mL of oil) were applied using an atomizer at a rate of 10 μg spores/plant. Plants were placed in chambers maintained near saturation by intermittent mistings from ultrasonic humidifiers. Plants were incubated for 16 h at 20–21 C in the dark, and allowed to dry slowly. Then, the inoculated plants were incubated in a greenhouse or growth chamber with a photoperiod ranging from 14–16 h and daily average temperatures of 20–24 C. Infection types were assessed 14–20 d after inoculation, depending upon rust development. Host infection types were evaluated in two different greenhouse experiments from Oct 1992 to Apr 1993. A 0–4 qualitative scale for evaluating infection types was adapted from the system developed by Stakman et al (1962) for stem rust, where 0 = no visible infection; ';' = necrotic or chlorotic infection sites (flecks) without sporulation; 1 = minute uredinia, often surrounded by necrosis; 2 = small uredinia surrounded by extensive chlorosis; 3 = medium sized uredinia with or without chlorosis; 4 = large uredinia with or without chlorosis; and X = a mesothetic reaction [presence of low (e.g., ;, 1, or 2) and high (3 or 4) infection types on the same plant]. Infection types 3 and 4 were indicative of a susceptible host response, whereas infection types ;, 1, 2, or X were indicative of a resistant host response.

Evaluation of pathogenicity on rhamnaceous species.—Telia of the rust on leaves and leaf sheaths were conditioned to germinate by overwintering (Oct to Apr) outside at Fargo, North Dakota. Tissue pieces bearing overwintered telia were rinsed in running tap water for 24 h and suspended on a polyester screen in inoculation chambers. The chambers were maintained near saturation by intermittent mistings from ultrasonic humidifiers at temperatures ranging from 15–17 C. Glass slides coated with a thin layer of water agar were placed under the telia and examined daily with a microscope to monitor the release of basidiospores. Once basidiospores were detected, rhamnaceous plants (with new leaf growth) were placed under the telia. After an incubation period of 48 h in the dark, plants were removed from the chambers and new plants were placed under the telia. The inoculated plants were incubated in a greenhouse at daily average temperatures of 20–24 C.

RESULTS

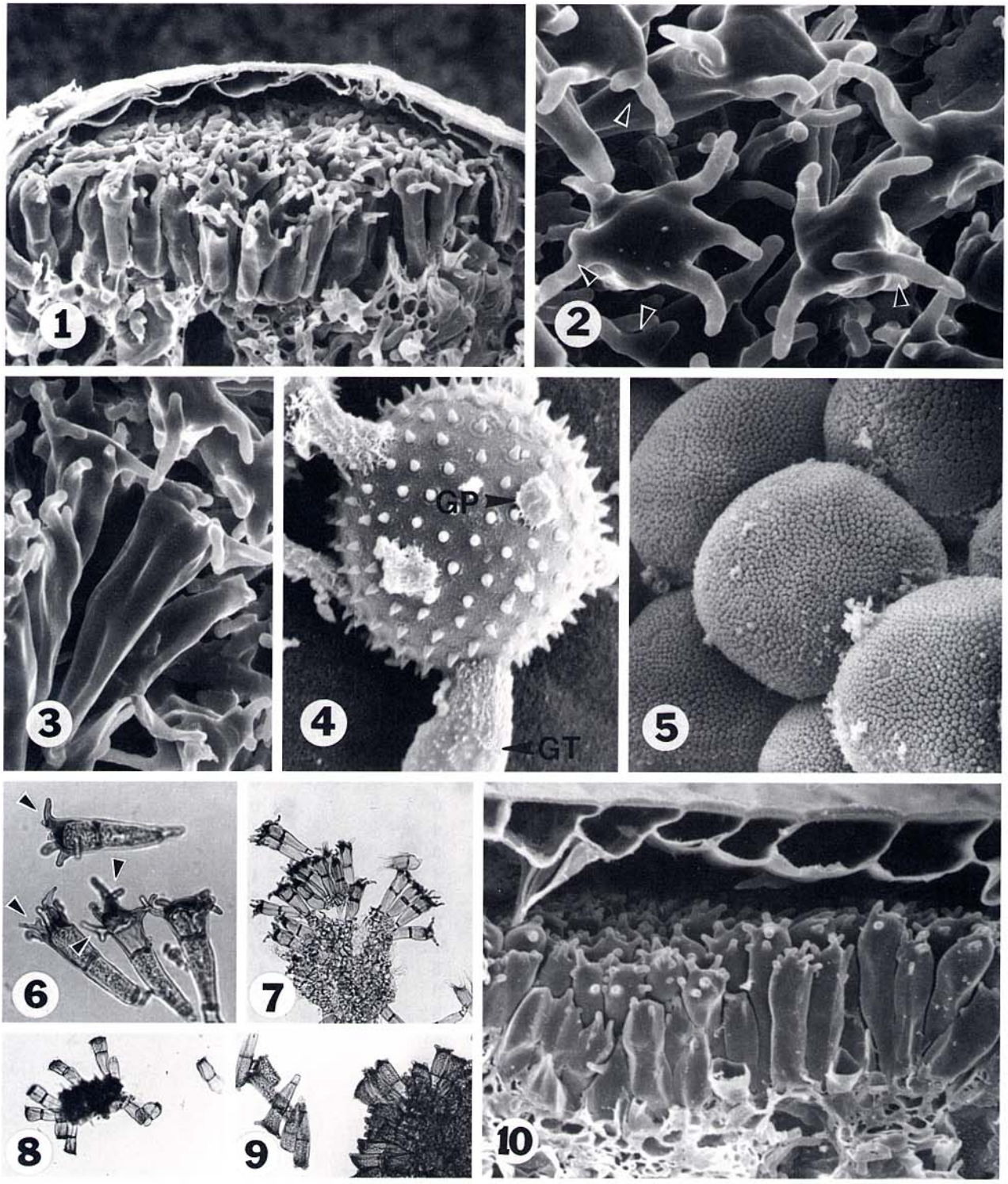
Puccinia coronata Corda var. hordei Jin & Steff. var. nov. FIGS. 1–7

Teliis nigris, plerumque linearibus, epidermide pertinaciter tectis. Teliosporis magnitudine (34–)39–56(–58) × (10–)11–13(–14) μm, pallide brunneis, apendicibus apicalibus 4–6, (7–)9–17(–18) μm longis, frequenter dichotomice clavatis. Urediniis plerumgue linearibus, pallide aurantiacis. Urediniosporis echinulatis magnitudine (18–)19–24(–27) × (16–)17–20(–22) μm, poris germinationis obscuris, usque invisibilis 5–8, dispersis, echinulis 0.4–0.5 μm in diametro, 0.7–0.8 μm altis, 1.0–2.5 μm distantibus, circulo basali prominente circumcinctis. Pycnia in *Rhamnus cathartica* emersa. Aeciis plerumque abaxialibus plerumque in foliis interdum etiam in fructibus et petioliis, aurantiaco-fulvis, poculatis. Aeciosporis magnitudine (22–)24–27(–32) × (16–)22–24(–27) μm, membrana 1 μm, poris germinationis 7–10, obscuris, verrucis 0.3–0.4 μm in diametro, regulariter dispersis.

Telia black, mostly linear, persistently covered by host tissue. *Teliospores* (34–)39–56(–58) × (10–)11–13(–14) μm, light brown, apical appendages 4–6, (7–)9–17(–18) μm long, with frequent dichotomous branching. *Uredinia* mostly linear, light orange. *Urediniospores* echinulate, (18–)19–24(–27) × (16–)17–20(–22) μm, germ pores obscure to invisible, 5–8, scattered, echinulae 0.4–0.5 μm diameter, 0.7–0.8 μm high, 1.0–2.5 μm between centers, surrounded by a prominent basal ridged ring. *Pycnia* on *Rhamnus cathartica,* emersed. *Aecia* mainly abaxial, mainly on leaves, also on fruits and flowers, orange yellow, cupulate. *Aeciospores* (22–)24–27(–32) × (16–)22–24(–27) μm, wall 1 μm, germpores 7–10, obscure, verrucae 0.3–0.4 μm diameter, uniformly distributed.

Specimens examined. UNITED STATES. NORTH DAKOTA: Fargo, 46°52′30″N/96°47′30″W, on inoculated *Hordeum vulgare* plants, *Y. Jin JIN91-36,* 29 March 1992, (HOLOTYPE: PUR 89857). JAPAN. IWATE: Morioka. *Puccinia rangiferina* on *Calamagrostis arundinacea* var. *sciuroides, Yamada.* CANADA. ONTARIO: Ottawa, *Puccinia coronata* on *Agropyron repens, Peturson,* (DAOM 35203).

Pathogenicity on gramineous species. We evaluated 140 gramineous species, belonging to 34 genera in the Poaceae, with isolates JIN91-36, Hv-8, and AE-1-B of *P. coronata* var. *hordei* and an isolate (AE-1-0) of *P. coronata* var. *avenae.* Species susceptible (exhibiting compatible infection types) to either or both *P. coronata* var. *hordei* and *P. coronata* var. *avenae* are



FIGS. 1–10. *Puccinia coronata*. 1–5. Scanning electron micrographs of *P. coronata* var. *hordei*. 1. A cross section of a telium (× 490). 2. The orientation and morphology of apical appendages on teliospores (× 1470), showing some with dichotomous branching (arrows). 3. Detached teliospores (× 980). 4. Germinating urediniospores (× 2940), revealing scattered germpores (GP) and a germtube (GT). 5. Aeciospores with uniformly distributed verrucae (× 2350). 6. Light photomicrograph (× 390) of teliospores of *P. coronata* var. *hordei*, showing dichotomous branching (arrows) of apical appendages. 7. Light photomicrograph of teliospores (× 157) of *P. coronata* var. *hordei*. 8. Teliospores (× 157) of *P. coronata* on *Calamagrostis canadensis* in comparison with *P. coronata* var. *hordei*. 9. Teliospores (× 157) of *P. coronata* var. *avenae* in comparison with *P. coronata* var. *hordei*. 10. Scanning electron micrograph of a cross section of a telium (× 490) of *P. coronata* var. *avenae* in comparison with *P. coronata* var. *hordei*.

TABLE I. Infection types of *Puccinia coronata* var. *avenae* and *P. c.* var. *avenae* on seedlings of cultivated and wild grass species

Grass species	*P. c.* var. *hordei*			*P. c.* var. *avenae*
	JIN91-36	Hv-8	AE-1-B	AE-1-O,
Aegilops cylindrica	;/4[a]	;,1	;	;
A. juvenalis	4	4	3	;
A. ovata	3	3	3	0
A. triuncialis	4	3	3	0
A. ventricosa	3	3	3	;
Agropyron cristatum	3	3/;	3/;	;
A. desertorum	3	3	4	;
Avena abyssinica	0	0	0	4
A. barbata	0	0	0	;,1
A. brevis	0	0	0	X
A. byzantina var. *anopla*	;	;	;	4
A. fatua	0	0	0	4
A. hybrid	0	0	0	X
A. longiglumis	0	0	0	4
A. maroccana	0	0	0	2
A. nuda	0	0	0	4
A. sativa CV 'Otana'	0	0	0	4
A. vaviloviana	0	0	;	4
A. wiestii	0	;	0	4
Brachypodium distachyon	4	4	3	;
Bromus commutatus	4	3	3	0
B. inermis	0/1	;	0	0
B. japonicus	3	3	3	;
B. secalinus	3	3	4	0
B. tectorum	3	3	3	;
B. unioloides	3	3	3	0
Calamagrostis arundinacea	0	0	0	2
Dactylis glomerata	0	0	0	;/3
Deschampsia cespitosa	0	0	0	;/2
Elymus caninus	4	4	4	3
E. trachycaulus	3	3	3	0
E. t. subsp. *subsecundus*	4	4	4	;,1
E. virginicus	3	3	3	;
Elytrigia elongata	3	3	3/;	;
E. intermedia	—[b]	3/;	3/;	;
E. i. subsp. *barbulata*	4	3	3/;	0
E. juncea	3	3	3	;
E. repens	4	3	3	;
Festuca arizonica	;,1	;/3	;/2	X
F. idahoensis	;,1	—	—	—
F. mairei	2	3	2	3
F. pratensis	2/;	2/;	2/;	0
F. thurberi	2	—	—	—
Holcus lanatus	;	;/2	;	;
Hordeum arizonicum	4	—	—	—
H. bogdanii	4	4	4	4
H. brachyantherum	4	4	4	;,1
H. brevisubulatum	4	4	—	0
H. b. subsp. *violaceum*	4	3	4	0
H. bulbosum	3	4	3	;,1
H. californicum	3	3	4	;
H. capense	4	4	4	0
H. chilense	3	4	—	;
H. comosum	4	—	—	—

TABLE I. Continued

Grass species	*P. c.* var. *hordei* JIN91-36	Hv-8	AE-1-B	*P. c.* var. *avenae* AE-1-O
H. euclaston	3	4	c—	—,
H. hybrid	3	3	3	;
H. jubatum	4	4	4	;
H. lechleri	4	4	4	;
H. marinum	3	3	3	;
H. m. subsp. *gussoneanum*	4	3	3	;,1
H. m. subsp. *glaucum*	3	4	3	2
H. m. subsp. *leporinum*	4	3	3	;,1
H. muticum	3	3	3	;,1
H. parodii	4	4	4	;
H. patagonicum	4	4	4	;
H. procerum	4	4	4	;
H. roshevitzii	3	;,1	;/2	;
H. secalinum	X	;,1	;,1	0
H. setifolium	3	3	3	;
H. spontaneum	3	3	3	0
H. stenostachys	3	;/2	3	—
H. vulgare CV 'Aim'	3	3	3	0
Lolium perenne	0/2	0/;	0/1	0
L. temulentum	3/;	2	3	0
Pascopyrum smithii	4	4	4	;
Phalaris arundinacea	;/3	;/3	;/3	;/1
Phleum subulatum	0	0	0	;/3
Psathyrostachys juncea	4/;	4	4	2/;
Secale ancestrale	;/3	3	3	0
S. cereale CV 'Dacold'	3	3	3/;	0
S. montanum	;/2	X	;,1	;
S. m. subsp. *anatolicum*	;,1	2/;	3/;	;
S. segetale	2/;	3/;	3	0
S. vavilovii	3	3	3	;
Triticum aestivum	3/0	3/0	3/0	;
T. boeoticum	2/;	;,1	;	;
T. hybrid	;	;,1	;,1	0

[a] Infection types were: "0" = immune; ";" = necrotic flecking without sporulation; "4" = the most susceptible (compatible) infection type; and "1", "2" and "3" denote intermediate types based on uredinium size and degree of associated necrosis and chlorosis. "X" denotes a mesothetic (mixed) reaction on the same plant. "/" indicates mixture of plants in reaction within or among accessions. The plant type with the most prevalent infection types is given first.

[b] Not tested or missing data.

given in TABLE I. Species susceptible to *P. coronata* var. *hordei* were mostly in the genera *Aegilops, Agropyron, Elymus, Elytrigia, Hordeum, Pascopyrum, Psathyrostachys,* and *Secale* of the tribe Triticeae. Nearly all of the species (23 of 24) evaluated in *Hordeum* were susceptible. *Triticum* spp. were highly resistant; however, some accessions in *T. aestivum* were susceptible at the seedling stage. Compatible infection types also were found in the genera *Brachypodium, Bromus, Festuca,* and *Lolium* of the tribe Poeae, and *Phalaris* of the tribe Aveneae. Species in *Avena* generally were immune to *P. coronata* var. *hordei.* In contrast, *Avena* spp. were very susceptible to *P. coronata* var. *avenae.*

Reactions of adult plants of cultivated cereals to *P. coronata* var. *hordei* were evaluated by inoculating plants after heading. Barley was highly susceptible as abundant compatible uredinia developed on leaf blades, leaf sheaths, awns, and peduncles. Telia formed readily on leaf blades and leaf sheaths of barley plants. Rye was moderately susceptible, and uredinia were observed on leaf blades only and were restricted in number and size. Wheat was highly resistant, exhibiting minute chlorotic flecks on leaf blades. Wheat accessions that were susceptible at the seedling stage showed a resistant reaction at the adult plant stage. No visible symptom was observed on oat plants, indicating that oat is immune to *P. coronata* var. *hordei.*

In surveys of the northern Great Plains region of Minnesota, North Dakota, and South Dakota from 1992 to 1997, the following native and introduced gramineous species were found naturally infected by *P. coronata* var. *hordei: Bromus tectorum, Elymus canadensis, E. trachycaulus, E. virginicus, Elytrigia intermedia, E. repens, H. jubatum, H. vulgare, Leymus angustus, L. cinerius, L. dahuricus, L. racemosus, Pascopyrum smithii, Psathyrostachys juncea,* and *S. cereale.* Among these grasses, *E. trachycaulus, E. repens, H. jubatum,* and *P. smithii* were frequently observed with a high level of infection throughout the region.

Pathogenicity on Rhamnus *species.* Natural infections by *P. coronata* var. *hordei* have not been observed on *R. crenata, R. davurica, R. frangula, R. japonica,* and *R. pallasii,* which were growing adjacent to heavily infected *R. cathartica* plants at the North Dakota State University arboretum near Absaraka, North Dakota. Greenhouse inoculations failed to produce any infection on *R. crenata, R. davurica, R. frangula,* and *R. japonica.* The same inoculum, however, resulted in severe infections on *R. cathartica.* These results suggest that *R. cathartica* is the primary aecial host for the fungus in this region.

Life cycle. The pycnial state was produced on *R. cathartica* 7 d after inoculation with basidiospores from germinating teliospores on barley leaf tissue in greenhouse experiments. Two wk after inoculation, mature aeciospores were obtained and inoculated onto *Bromus tectorum* (PI 219992), *H. vulgare* (CV 'Aim'), *S. cereale* (CV 'Dacold'), and *T. aestivum* (PI 350005), which were all found to be susceptible to *P. coronata* var. *hordei* in previous experiments, and *A. sativa* (CV 'Otana'), which was immune to *P. coronata* var. *hordei.* Uredinia were produced on all species, except *A. sativa* 9–12 d after the plants were inoculated. Telia formed readily on the inoculated *H. vulgare* and *S. cereale* plants, but not on *T. aestivum* and *B. tectorum.*

Distribution. Minnesota (on hosts 1, 3, 6, 7, 8, 13, 16); Nebraska (on host 8); North Dakota (on hosts 1 to 16); South Dakota (on hosts 1, 3, 6, 7, 8, 13, 15, 16); and Wisconsin (on host 16) of USA, and Manitoba (on hosts 6, 7, 8, 16) and Saskatchewan (on hosts 3, 6, 7, 16) of Canada. Hosts are indexed as follows: 1 = *Bromus tectorum,* 2 = *Elymus canadensis,* 3 = *E. trachycaulus,* 4 = *E. virginicus,* 5 = *Elytrigia intermedia,* 6 = *E. repens,* 7 = *H. jubatum,* 8 = *H. vulgare,* 9 = *Leymus angustus,* 10 = *L. cinerius,* 11 = *L. dahuricus,* 12 = *L. racemosus,* 13 = *Pascopyrum smithii,* 14 = *Psathyrostachys juncea,* 15 = *S. cereale,* and 16 = *R. cathartica.*

DISCUSSION

Typical visible signs of the pathogen on barley are linear, light orange uredinia (Plate 63, Jin and Steffenson 1997) and black telia (Plate 64, Jin and Steffenson 1997). Uredinia are usually associated with chlorosis. An evaluation of 30 barley cultivars indicated that the rust fungus can infect plants at all growth stages up to maturity. Infections occurred mostly on leaves, but also on leaf sheaths, peduncles (which represents true stem tissue), and awns of adult barley plants. The common name 'crown rust of barley' is proposed for the disease of barley caused by *P. coronata* var. *hordei.*

Although the rust pathogen was found in many parts of the northern Great Plains region on *R. cathartica,* barley, and other grasses and in the central Great Plains on barley, the highest incidence occurred in the central part of the Red River Valley region where *R. cathartica* is abundant in shelterbelts and riparian areas. Infection on barley is established early from local inoculum on *R. cathartica.* Sexual reproduction of the pathogen on the alternate host may contribute to a high degree of pathogenic variation in the fungal population. Thus, the pathogenic potential of the rust on barley and forage grasses is high in the region. Weedy grasses, such as quackgrass (*E. repens*) and foxtail barley (*H. jubatum*), and native forage grasses such as slender wheatgrass (*E. trachycaulus*) and western wheatgrass (*P. smithii*) may play an important role in the survival and multiplication of the rust pathogen when barley is absent, because these species are widely distributed and well established in the region. Our investigation showed that these grasses can harbor the uredinial state of *P. coronata* var. *hordei* from early summer until late autumn. Abundant telia are produced on these species, which in turn serve as the source of inoculum for the infection of *R. cathartica* during the following spring.

Variation in Puccinia coronata.—*Puccinia coronata* is known to vary greatly in host specialization. Based on the alternate hosts, Klebahn (1892) divided *P. coronata* into two separate species: *P. coronata* with *R. frangula* as the aecial host, and *P. coronifera* with *R. cathartica* as the aecial host. Melthus et al (1922) did not find marked differences between *P. coronata* and *P. coronifera* with respect to infection on *R. frangula* and *R. cathartica* and concluded that Klebahn's division of crown rust into two species was not applicable in North America. Dietz (1926) used teliospores from *A. sativa, Calamagrostis canadensis,* and *Festuca pratensis* to inoculate *R. frangula, R. cathartica,* and 12 other species of *Rhamnus,* and observed that these three forms overlapped in aecial host ranges, suggesting that the division of *P. coronata* and *P. coronifera* was not justified. Studies by Brown (1938) in Great Britain showed that rusts on *A. sativa, Lolium perenne,* and other grasses (representing forms

of the *P. coronifera* group) infected only *R. cathartica,* whereas the rust from *C. lanceolata* (representing the *P. coronata* group) infected only *R. frangula,* thus supporting Klebahn's conclusion in the specialization of aecial hosts. Brown (1938) did not, however, support the separation of these rusts into two different species based solely on aecial hosts in light of lacking morphological differences.

Eriksson and Henning (1894) used formae speciales (f. sp.) to designate crown rusts from different grasses and considered the host range of a f. sp. to be restricted to species within a genus. Six f. sp.: *avenae* (on *A. sativa*), *alopecuri* (on *Alopecurus pratensis*), *calamagrostis* (on *C. lanceolata*), *festucae* (on *F. pratensis*), *lolii* (on *L. perenne*), and *melicae* (on *Melica nutans*) were designated by these workers. Further research led to the designation of additional f. sp., including *agropyri, agrostis, bromi, glycereae, holci, phalaridis,* and *secalis* (Brown 1937, Eriksson 1908, Melhus et al 1922, Peturson 1954), although it became apparent that some f. sp. could attack different species from a number of genera and the host ranges of f. sp. overlapped. Eshed and Dinoor (1980, 1981) studied 8 f. sp. from Israel on 106 gramineous species belonging to 43 genera. They found an overlap in host range among f. sp. with species of the same genus, with genera of the same tribe, and with different tribes. The isolate of oat crown rust used in our study infected not only *Avena* spp. of tribe Aveneae, but also *F. mairei* of tribe Poeae, and *E. caninus* and *H. bogdanii* of tribe Triticeae (TABLE I). In addition, the host ranges of *P. coronata* f. sp. *festucae* and f. sp. *lolii* in our study were nearly identical, except for the primary hosts *F. arundinacea* and *L. perenne,* respectively (Jin and Steffenson unpubl). These findings place considerable doubts on the usefulness of the forma specialis concept for the intraspecific classification of *P. coronata.*

Morphological differences were not recognized in the aforementioned f. sp. with the exception of f. sp. *secalis.* Peturson (1954) isolated this rust from *R. cathartica* and found it was pathogenic on *Hordeum, Secale,* and several other gramineous species in artificial inoculation experiments. The fungus described by Peturson (1954) appears to fit our description of *P. c.* var. *hordei.* However, we regard the combination of morphologically distinct teliospores and a unique host range to warrant recognition at the variety level rather than merely as a new forma specialis. A form of crown rust on *Elytrigia* (=*Agropyron repens*) was reported in North Dakota (Schwinghamer 1955) and in eastern Canada (Sampson and Watson 1985). According to these workers, the crown rust on quackgrass resembled *P. c.* f. sp. *secalis* as described by Peturson (1954). Based on their descriptions, we believe that this fungus is the same as *P. c.* var. *hordei.* Natural crown rust infections were reported on *Hordeum* in the USA (Lutey and Covey 1959). The species *P. rangiferina* reported in Japan (Ito 1909) and China (Cummins 1951) on *Calamagrostis* spp., has a teliospore morphology similar to that of *P. c.* var. *hordei,* and was later named var. *rangiferina* (Cummins 1971). *Puccinia c.* var. *hordei* was, however, not pathogenic on *C. arundinecea* (TABLE I), *C. canadensis* or *C. epigeios* in our tests (data not shown). The urediniospores of *P. c.* var. *rangiferina* were not available from the type specimen we examined. Moreover, the distribution, aecial host, and telial hosts other than *Calamagrostis* spp. for this rust are unknown.

Fraser and Ledingham (1933) proposed 4 varieties of *P. coronata* based on aecial hosts, and to a lesser degree, on the morphology of aecia. These are var. *avenae* (on *R. cathartica*), *calamagrostis* (on *R. alnifolia*), *bromi* (on *Lepargyraea canadensis*) and *elaeagni* (on *Elaeagnus commutata*). Differences in teliospore sizes were recognized, but were not used as criteria to separate the varieties. In a more recent taxonomic review, Cummins (1971) recognized 5 varieties in *P. coronata*: *avenae, coronata, himalensis, gibberosa,* and *rangiferina* based on morphology as well as aecial and telial hosts. In the course of our studies, we detected morphological differences in various forms of *P. coronata.* For example, a crown rust collection from *C. canadensis* in Wisconsin had a teliospore morphology (FIG. 8) that was markedly different from var. *hordei* (FIG. 7) or var. *avenae* (FIG. 9), and resembled closely var. *bromi* of Fraser and Ledingham (1933). Thus morphological differences do exist in *P. coronata,* and these differences should be considered important in taxonomy.

The parallel usage of both f. sp. and var. in the intraspecific classification of *P. coronata* is confusing. It is apparent that the f. sp. based classification has little value in the delineation of the *P. coronata* complex and should be abandoned. The description of *P. coronata* var. *hordei* in this report, as well as descriptions of various varieties by Cummins (1971) and Fraser and Ledingham (1933), indicate that distinct morphological variations are present in telial, uredinial, as well as aecial states in *P. coronata.* One or more of these morphological traits is frequently associated with one or several crown rust forms that have unique aecial, and in some cases telial, host specificity. Thus, varieties should be considered as the primary intraspecific taxa in *P. coronata,* and morphological differences, in combination with aecial and telial host specificity, should be used as the primary criteria for the classification of varieties.

Invalidation of previous published name.—Although the name "*Puccinia coronata* Corda var. *hordei* Jin &

Steff." was used in Vorträge für Pflanzenzüchtung (Jin and Steffenson 1992), it was not validly published because a Latin diagnosis was not given and a holotype specimen was not designated. Thus, we declare the previous name "*Puccinia coronata* Corda var. *hordei* Jin & Steff." to be invalid.

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