Broad-Spectrum Resistance to Crown Rust, *Puccinia coronata* f. sp. *avenae*, in Accessions of the Tetraploid Slender Oat, *Avena barbata*

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ABSTRACT

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The use of race-specific seedling genes for resistance has been the primary means of controlling crown rust of oat (*Puccinia coronata*). As resistance genes from hexaploid cultivated oat, *Avena sativa* and, later, the wild hexaploid animated oat, *A. sterilis*, were deployed in oat cultivars, corresponding virulence in the crown rust population increased rapidly, such that the effective lifespan of a resistant cultivar in the United States is now 5 years or less. Introgression of resistance genes from diploid and tetraploid *Avena* spp. into hexaploid oat has been difficult due to differences in ploidy levels and the lack of homology of chromosomes between the two species. The wild tetraploid slender oat, *A. barbata*, has been a source of powdery mildew and stem rust resistance in cultivated oat but has largely been unexploited for crown rust resistance. In total, 359 accessions of *A. barbata* from the National Small Grains Collection were evaluated in seedling greenhouse tests. Of these accessions, 39% were at least moderately resistant when inoculated with a crown rust race with low virulence (DBBC). When tested further with a highly diverse bulk inoculum from the 2006 and 2007 St. Paul buckthorn nursery, 48 accessions (approximately 13%) were resistant. Many of these accessions were heterogeneous in reaction, but two accessions (PI320588 from Israel and PI337893 from Italy) were highly resistant (immune) and two others (PI337886 from Italy and PI367293 from Spain) consistently produced resistant reactions (chlorotic flecks) in all tests. Resistant accessions were found from throughout much of the natural range of *A. barbata*. Crosses of some of the better accessions have been made to cultivated oat.

Crown rust, caused by *Puccinia coronata* Corda f. sp. *avenae* P. Syd. & Syd., is the most damaging fungal disease of domesticated oat, *Avena sativa* L., in the world (15). The disease is most damaging when heavy dews coincide with moderate temperatures during the growing season. In the United States, there are two major oat-production areas. Winter oat, sown in the fall and harvested in the spring, is grown in parts of the southern United States, often as a dual purpose (forage and grain) crop. Spring oat, sown in the early spring and harvested midsummer, is grown in the upper Midwest, mainly as a grain crop. In the winter-oat region, *P. coronata* successfully overwinters and crown rust epidemics can be severe because multiple infection cycles with urediniospores can occur over the long growing season. In the spring-oat region, the alternate host of *P. coronata*, common buckthorn (*Rhamnus cathartica* L.), is a widespread, pervasive, noxious weed in wooded areas and shelter belts adjacent to oat fields. Aeciospores from buckthorn as well as urediniospores from southern winter-oat production areas serve as abundant initial sources of inoculum in the spring-oat region.

Host resistance has been the primary means of controlling losses to crown rust in cultivated oat. The use of race-specific seedling genes for resistance to crown rust has a long history in the United States. Initially, cultivated hexaploid oat, *A. sativa*, was used as a source of crown rust resistance (*Pc*) genes. As cultivars with these genes were deployed, they rapidly succumbed to new virulent races of *P. coronata*. Virulence to *Pc* genes derived from *A. sativa* is now nearly fixed in the North American population of *P. coronata*. Subsequently, oat breeders turned to the wild hexaploid animated oat, *A. sterilis*, as a source of new *Pc* genes, but virulence to many of these genes was already present in the *P. coronata* population or increased rapidly as they were deployed in new cultivars. Virulence to all the reported *Pc* genes from *A. sterilis* is present in the U.S. crown rust population and the virulence complexity has continued to increase unabated (3). More recent efforts at finding new, effective *Pc* genes have centered on diploid or tetraploid *Avena* spp.. Crown rust resistance in the diploid black oat, *A. strigosa*, has been known and documented for quite some time but introgression of resistance into hexaploid oat is difficult due to differences in ploidy levels and the lack of homology of chromosomes between the two species (2,8,14). Cv. Leggett, recently released by the AAFC Winnipeg program, contains *Pc94* from the *A. strigosa* accession RL1697 (2). An effective crown rust resistance gene (*Pc91*) from the tetraploid species, *A. magna* CI 8330, was successfully transferred via the synthetic hexaploid Amagalon into oat cv. Hi-Fi, released by North Dakota State University in 2001 (12).

A. barbata Pott ex Link is a wild tetraploid ($2n = 28$) species that is widely distributed in the Mediterranean region, North Africa, the Middle East, South Asia, and much of Europe (9). It has also been introduced to Australia and the Americas. It is adapted to a range of natural and artificial habitats ranging from sea level to the snow line. In the United States, it is considered a restricted species because it is listed as a noxious weed by the state of Missouri and is considered a moderately invasive species of natural areas in California.

Genes for resistance to powdery mildew (*Eg-4*) and stem rust (*Pg-16*) have been successfully transferred from *A. barbata* into cultivated hexaploid oat (1,10,16). Resistance to crown rust in *A. barbata* has been reported in collections from Israel, Turkey, Portugal, and Australia; however, testing was done with a limited number of collections and races of *P. coronata* (5,6,11). In some cases, collections were resistant as seedlings but susceptible as adult plants and, in at least one instance, were susceptible as seedlings but resistant as adults (6).

MATERIALS AND METHODS

Available seed of *A. barbata* and *A. barbata* subsp. *barbata* was obtained from the United States Department of Agriculture (USDA) Agricultural Research Service National Small Grains Germplasm Collection in Aberdeen, ID. In all, 402 accessions were planted in vermiculite in 7-cm^2 pots with 10 to 20 seeds of each of four accessions planted in each corner of the pot. In every sixth pot, 10 to 15 seeds of the susceptible oat cv. Marvellous was planted in one corner to serve as a check for uniformity and viability of inoculum. Seven days after planting, primary leaves of seedlings were inoculated with a min-

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eral oil suspension of fresh urediniospores of a single-pustule-derived isolate of *P. coronata* f. sp. *avenae* with virulence on only 2 of 31 differential cultivars (06MN097), designated race DBBC according to the nomenclature of Chong et al (4). Inoculated plants were placed in a dew chamber overnight and moved to a greenhouse bench. Crown rust reactions were recorded 12 to 14 days after inoculation. A crown rust reaction of moderately large to large pustules with little or no chlorosis was scored as susceptible, those with moderately large pustules surrounded with extensive chlorosis were scored as moderately susceptible, those with small pustules surrounded by chlorosis or necrosis were scored as moderately resistant, those with chlorotic or necrotic flecks were scored as resistant, and those with no visible reaction were scored as highly resistant.

Seedlings of accessions of *A. barbata* that were scored at least moderately resistant in the initial test with race DBBC were fertilized with a solution of water-soluble fertilizer (Plantex 20-20-20, NPK; Plant Products Co. Ltd., Brampton, Ontario, Canada) and newly emerged leaves reinoculated as described above with a bulk population of *P. coronata* f. sp. *avenae* urediniospores collected in 2006 from the buckthorn nursery in St. Paul. The buckthorn and oat nursery at St. Paul, MN has been in existence since 1953 and supports an extremely diverse, sexually recombining population of *P. coronata*. In a given year, virulence to almost every described *Pc* gene in *Avena* spp. is detected in this population (Table 1). Crown rust reactions to the bulk population were recorded as described above.

Seed of accessions of *A. barbata* that were scored moderately resistant or better when tested with the 2006 bulk population of *P. coronata* f. sp. *avenae* were planted and inoculated with a bulk population of *P. coronata* f. sp. *avenae* from the 2007 St. Paul buckthorn nursery and scored as described above for the test with race DBBC. Seedlings of accessions that were scored moderately resistant or better were transplanted into a pasteurized soil mix in 12.5-cm-diameter plastic pots and grown on until they reached the stem elongation growth stage (Feekes 7 to 8) and were reinoculated with the 2007 buckthorn bulk population of *P. coronata* f. sp. *avenae*. In instances where the accession appeared to be heterogeneous in reaction, seedlings that were moderately resistant or better were chosen to be grown on and tested with the 2007 buckthorn bulk as adult plants. A few susceptible seedlings from heterogeneous accessions were also grown on and tested to confirm their susceptibility.

Table 1. Crown rust severities and reaction types on flag leaves of adult plants of oat differential lines in the St. Paul buckthorn nursery, 2006–08, and reactions of seedlings of those differentials to bulk urediniospore populations of *Puccinia coronata* from the buckthorn nursery (2007 and 2008) in greenhouse tests[a]

	Greenhouse		Nursery		
Differential	**2007Bulk**	**2008Bulk**	**2006**	**2007**	**2008**
Pc14	S	S	80S	80S	20S
Pc35	S	S	80S	80S	30S
Pc36	S	S	80S	80S	80S
Pc38	S	S	80S	Dead	40S
Pc39	S	S	80S	Dead	50S
Pc40	S	S	80S	80S	20S
Pc45	S	S	20MS	80S	10MR
Pc46	S	S	80S	80S	15MR/MS
Pc48	S	S	80S	80S	30S
Pc50	S	S	50S	60S	3S
Pc51	S	S	80S	80S	10S
Pc52	S	S	60S	50S	20S
Pc53	R	MS	TraceS	TraceS	TraceR/MR
Pc54	MS	MS	80S	25S	10S
Pc55	S	S	80S	80S	15S
Pc56	S	S	80S	80S	20S
Pc57	S	S	30MR/MS	80S	5S
Pc58[b]	MR/MS	MR/MS	80S	20S	5MS
Pc59	S	S	50S	80S	10MS/S
Pc60	S	MS	80S	60S	10S
Pc61	MS	S	30S	80S	20S
Pc62	MS	S	30S	5S	3S
Pc63	S	S	40S	80S	3MS/MR
Pc64	S	S	60S	10S	5S
Pc67	MR	MS	30MS/S	60S	25S
Pc68	S	S	30S	40S	10S
Pc70	S	S	40S	80S	10S
Pc71	S	S	80S	80S	Dead
Pc91	S	S	5MS/S	1S	1S
Pc94	HR	S	0	TraceS	0
Pc96	S	S	5S	10S	0
IAB605Xsel[c]	S	S	5S	80S	10S
WIX4361-9	S	S	20S	80S	1MS
TAM-O-405	S	S	10S	3S	1S

[a] Reaction phenotypes are HR = no visible reaction, R = chlorotic or necrotic flecking, MR = small pustule surrounded by chlorosis, MS = moderately large pustules surrounded by extensive chlorosis, and S = large to moderately large pustules with little or no chlorosis; Dead = plants died prematurely due to severe crown rust infection. When more than one reaction type is listed, the most frequent reaction type is listed first.

[b] *Pc58* in the differential TAM-O-301 has recently been shown to be a complex of three linked loci (7).

[c] IAB605X, WIX4361-9, and TAM-O-405 are widely used sources of crown resistance that have not been genetically characterized.

RESULTS

Of the 402 accessions of *A. barbata* received from the National Small Grains Germplasm Collection and planted, 359 actually germinated and were evaluated for crown rust resistance. When tested as seedlings with race DBBC of *P. coronata*, 140 accessions (39%) were rated at least moderately resistant. Of these, 48 were rated at least moderately resistant when tested as seedlings with bulk inocula from the 2006 and 2007 St. Paul buckthorn nursery (Table 2). Of the 48 accessions, 3 (PI320630, PI320727, and PI337737) were rated as moderately susceptible when evaluated as adult plants with bulk inoculum from the 2007 St. Paul buckthorn nursery.

Resistance reactions among the remaining 45 accessions ranged from moderately resistant to highly resistant (Table 2). Two accessions, PI320588 from Israel and PI337893 from Italy, were consistently highly resistant (no visible reaction) to all inocula used in the tests. Two other accessions, PI337886 from Italy and PI367293 from Spain, consistently produced resistant reactions (chlorotic flecks) to all inocula. With the remaining accessions, resistance reactions varied somewhat depending on the inoculum used or plant stage they were inoculated. Several accessions were clearly heterogeneous in reaction, either containing a mixture of both susceptible and resistant reactions or a mixture of resistant reaction types. When samples of resistant and susceptible seedlings from heterogeneous accessions were transplanted separately, grown on, and tested as adult plants with bulk inoculum from the 2007 St. Paul buckthorn nursery, they maintained their seedling reaction types, verifying their heterogeneity.

Broad-spectrum resistance (having at least a moderate resistant reaction to all inocula used) to *P. coronata* was found in accessions of *A. barbata* from a diversity of origins in its native range, including Israel, Italy, Greece, France (Corsica), Tunisia, Morocco, Algeria, Libya, Spain, Portugal, and Turkey (Fig. 1), as well as in three accessions from Canada, where it is an introduced species. No broad-spectrum resistance was found in accessions from Serbia, Bulgaria, the United Kingdom, Pakistan, India, Iran, Cyprus, Jordan, Egypt, Macedonia, or Brazil. These countries were only represented by one or two accessions of *A. barbata* each in the USDA germplasm collection.

DISCUSSION

The relatively high frequency of resistance (approximately 13%) in *A. barbata* to the highly diverse, widely virulent population of *P. coronata* in the St. Paul buckthorn nursery is surprising and encouraging. Every year, hundreds of oat lines from breeding programs across the United States and Canada, oat germplasm accessions, recombinant inbred and breeding populations of domesticated oat, selections of *A. strigosa* and *A. murphyii*, and oat lines with resistance genes introgressed from those wild relatives are evaluated for crown rust resistance in the buckthorn nursery in St. Paul. The only *A. sativa* cultivar or line that is totally resistant in the buckthorn nursery is AC Leggett (a combination of *Pc68* and *Pc94*). The only other *Avena* spp. completely resistant to the buckthorn population are a single accession of the diploid *A. strigosa* (PI258731) and a selection of the tetraploid *A. murphyii* (P12). It appears that *A. barbata* represents a previously untapped reservoir of new crown rust resistance genes for improvement of oat cultivars.

It is also likely that the resistance found in these accessions of *A. barbata* is diverse. First, their reaction to the bulk populations from the buckthorn nursery, ranging from highly to moderately resistant, is indicative of different resistance genes being expressed. Second, the resistant accessions come from geographically diverse regions from across the native range of *A. barbata* (Fig. 1) but also from an introduced population outside its native distribution. Thus, *A. barbata* appears to be a source of diverse and novel genes for resistance to a broad spectrum of virulence in *P. coronata* in the United States.

Many of the accessions of *A. barbata* exhibiting wide-spectrum resistance to *P. coronata* were from Israel (Table 1). Although it would be tempting to state that Israel is a particularly rich source of resistant accessions of *A. barbata*, this is more a reflection of the large number of accessions (165) from Israel in the collection. When the frequency of accessions with broad-spectrum resistance from different countries in the Mediterranean region is examined, Italy and Corsica appear to be richer sources of resistant accessions than Israel (Fig. 1). Given the relatively high frequency (approximately 13%) of accessions from throughout the natural range of *A. barbata* with effective resistance to crown rust, it would be desirable to make further collections from those areas that are underrepresented in the USDA germplasm collection.

Introgression of the resistance of the tetraploid *A. barbata* into hexaploid oat will be difficult. Sterility and the lack of homology between chromosomes between *A. barbata* and *A. sativa* represent significant barriers. Resistance to powdery mildew was successfully transferred from *A. barbata* to cultivated oat using two different approaches. First, a chromosomal addition line of *A. sativa* (42 + 2 chromosomes) with the *A. barbata* chromosome carrying the resistance gene was irradiated to induce a translocation between an *A. sativa* chromosome and the *A. barbata* chromosome, followed by selection in subsequent generations for resistant plants in families that segregated normally for resistance and susceptibility (1). The second method involved crossing a ditelocentric addition line of *A. sativa* cv. Sun II (42 *A. sativa* chromosomes plus a pair of telocentrics for the short arm of an *A. barbata* chromosome) with an 8x amphiploid between *A. sativa* cv. Pendek and *A. longiglumis* CW57 (16). CW57 carries a factor allowing recombination between

Table 2. Reactions of selected accessions of *Avena barbata* to race DBBC and bulk populations of *Puccinia coronata* from the St. Paul buckthorn nursery[a]

		Seedling[b]			Adult
Accession	Origin	DBBC	06Bulk	07Bulk	07Bulk
CIav8082	Israel	R	R	MR/R	HR/R
CIav9060	Canada	HR	R	HR/S	HR
CIav9067	Canada	MR	MR/MS	MR/MS/S	–
CIav9091	Libya	R	R	HR	MR
CIav9125	Canada	R	MR	MR	–
PI282710	Israel	R	HR	R	HR/R
PI282723	Israel	R	R/S	HR	R/MR/HR
PI287203	Israel	R	R	HR	HR/R
PI287205	Israel	MR	MR	S/R	MS/MR
PI295885	Israel	R	R	HR/S	HR
PI295891	Israel	HR	R	R/MR	HR/R
PI317945	Israel	HR	HR	HR	HR/R
PI317953	Israel	HR	HR	R/MR	HR
PI320588	Israel	HR	HR	HR	HR
PI320598	Israel	MS	R	MS/MR	MR/MS
PI320610	Israel	R/MR	R	MR/R	MR/R
PI320630	Israel	MR	–	HR	MS
PI320638	Israel	R	R/S	MR	MR
PI320659	Israel	R	MR	MS/MR	MR
PI320696	Israel	MR/MS	MR	HR/R	R
PI320727	Israel	MR	–	S/R	MS
PI337737	Italy	R/MR	MR/R	MS/MR	MS
PI337741	Italy	MR	R/MR	MR	R
PI337744	Italy	MR	MS/MR	MR	R
PI337763	France	R	R/MR	MR/R/S	MR/R
PI337795	Morocco	R	R	HR	R
PI337811	Turkey	MR	MR/MS	MR/MS	MR
PI337823	Greece	R	R	MR/R	MR
PI337863	Italy	R	MR	MS/MR	MR
PI337864	Italy	R	R/MR	R/MR	MR/R
PI337867	Italy	HR	MR	HR/R/MR	HR/R/MR
PI337868	Italy	R	R/MR	MR	MR
PI337877	Italy	R	MR	MR	MR/R
PI337878	Italy	R	MR	MR/R	R
PI337886	Italy	R	R	R	R
PI337893	Italy	HR	HR	HR	HR
PI337904	Italy	MR	R	MS/MR	MR
PI337945	Tunisia	R/MR	R/MR	MR	MR
PI337961	Italy	R	MR/S	MR/MS	MR
PI337962	Italy	R/MR	MR/MS	MR/R	MR/R
PI337966	France	R	R/MR/S	MR/R/MS	MR/R
PI337975	Algeria	R	R/MS	MR	MR
PI367293	Spain	R	R	R	R
PI367296	Spain	R	R	MR/R	R
PI367318	Portugal	R	R	R	HR
PI367319	Portugal	R	R	MR	HR/R
PI367338	Portugal	S	MR	R/MR	R/MR
PI411376	Turkey	R	R	MR/R	R/MR

[a] Reaction phenotypes are HR = no visible reaction, R = chlorotic or necrotic flecking, MR = small pustule surrounded by chlorosis, MS = moderately large pustules surrounded by extensive chlorosis, and S = large to moderately large pustules with little or no chlorosis – = accession not tested. When more than one reaction type is listed, this indicates that the accession was apparently heterogeneous. The more frequent reaction type is listed first.

[b] 06Bulk and 07Bulk populations represent random samples of urediniospores collected from the St. Paul buckthorn nursery in 2006 and 2007, respectively.

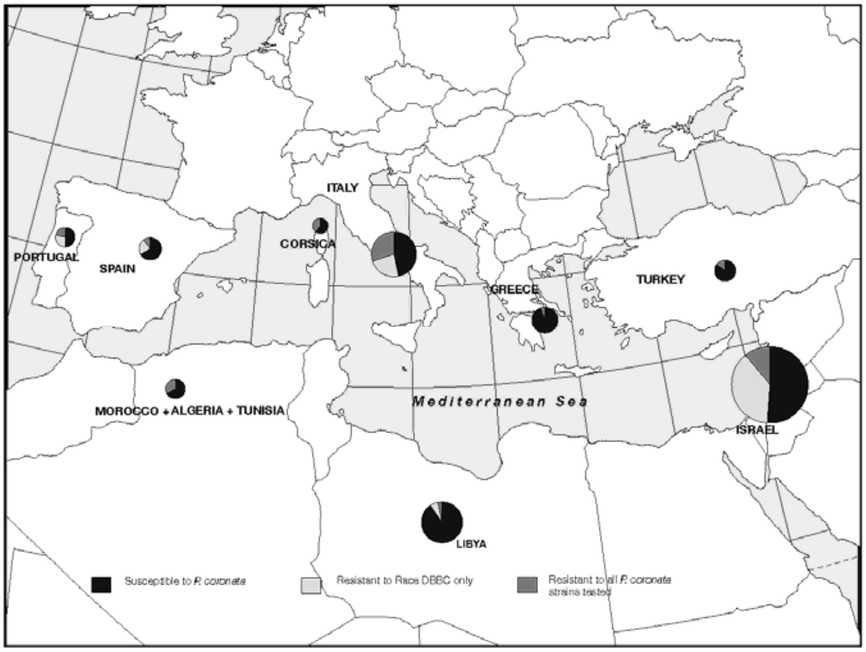

Fig. 1. Distribution of *Avena barbata* accessions with broad-spectrum resistance to *Puccinia coronata* in the world.

homologous chromosomes similar to what occurs when the *Ph-1* locus in wheat is suppressed or deleted. This initial cross was followed by selection in subsequent generations for fertile, resistant plants with 42 chromosomes. The stem rust resistance gene *Pg16* was also successfully transferred to *A. sativa* from *A. barbata* by backcrossing to *A. sativa* for several generations, selecting for resistance, followed by irradiation to facilitate chromosomal recombination followed by selection for resistance (10).

Initial crosses of some of the selected resistant accessions of *A. barbata* have been made with oat cvs. Otana and Ogle. Crossing was successful only when *A. barbata* was used as the female parent. A sampling of F_1 seedlings expressed resistance when inoculated with a bulk inoculum of *P. coronata,* indicating that resistance is not suppressed in interspecific crosses with *A. barbata* as has been reported in crosses of *A. strigosa* and *A. murphyii* with *A. sativa* (13).

Although *A. barbata* appears to be a promising source of new, broad-spectrum crown rust resistance in oat, there is no reason to expect that this resistance will be any more durable than seedling resistance derived from other wild *Avena* spp. such as *A. sterilis* or *A. strigosa* if not used wisely. However, it is likely that the *A. barbata* germplasm pool contains a diversity of resistance genes. This raises the possibility of extending the useful life of this resistance by increasing the diversity of highly resistant cultivars deployed in a given region by using different resistant genes from *A. barbata* in different cultivars, rather than breeding programs relying on a single new effective resistance gene in all new cultivars. This would reduce the likelihood of a new race or races virulent on any one of these new resistance genes predominating in the *P. coronata* population and causing widespread damage. Different effective resistance genes from *A. barbata* could also be pyramided into cultivars, theoretically increasing their effective lifespan.

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