Additional Sources of Broad-Spectrum Resistance to *Puccinia coronata* f. sp. *avenae* from Canadian Accessions of *Avena barbata*

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ABSTRACT

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Crown rust (*Puccinia coronata* f. sp. *avenae*) is considered the most damaging disease of oat and the use of race-specific seedling (*Pc*) genes for resistance has been the primary means of control. As these resistance genes from cultivated oat, *Avena sativa*, and the wild hexaploid animated oat, *A. sterilis*, were deployed in oat cultivars, corresponding virulence in the U.S. 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 from diploid and tetraploid *Avena* spp. into hexaploid oat has been difficult due to the difference in ploidy levels and the lack of pairing of homeologous chromosomes between 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. A relatively high percentage of *A. barbata* accessions from the United States Department of Agriculture (USDA) National Small Grains Collection were resistant to a highly diverse crown rust population in recent tests. Tests of 1,099 *A. barbata* accessions from the Canadian Plant Gene Resources Center not represented in the USDA collection revealed that a similar percentage (11.4%) were at least moderately resistant at the seedling and adult plant stage when tested with a highly diverse bulk inoculum derived from the St. Paul buckthorn nursery. Eighteen accessions were rated as highly resistant or a mix of highly resistant and resistant plants in both seedling and adult plant tests. Three accessions (CN21531 from Italy and CN26271 and CN26305 from Spain) displayed a unique "blotchy" resistant reaction as adult plants. Resistant accessions were found from throughout much of the natural range of *A. barbata* but the Western Mediterranean and Lebanon had the highest frequency of accessions with broad-spectrum resistance.

Crown rust, caused by the heterecious macrocyclic fungus *Puccinia coronata* Corda f. sp. *avenae* Eriks., is the most widespread and damaging fungal disease of domesticated oat, *Avena sativa* L., in the world (20). Crown rust is most damaging when moderate temperatures are accompanied by heavy dews or rain during the growing season. In the United States, there are two major oat-production areas with differing crown rust epidemiology. In the southern United States, winter oat crops are sown in the fall and harvested in the spring, often as a dual-purpose (forage and grain) crop. In this region, there is no known alternate host of *P. coronata* but the fungus successfully overwinters as urediniospores on cultivated oat, *A. sativa*, and common wild oat, *A. fatua*. Multiple infection cycles with urediniospores can occur throughout the long growing season, resulting in severe epidemics in the winter oat region. In the upper Midwest, spring oat crops are sown from late March to mid-May and harvested in midsummer, mainly as a grain crop. Common buckthorn (*Rhamnus cathartica* L., the alternate or aecial host of *P. coronata*) is a widespread, pervasive, noxious weed in woods and shelterbelts throughout the spring oat region. Aeciospores arising from buckthorn in the spring as well as urediniospores from southern winter oat production areas serve as abundant initial sources of inoculum in this region.

The use of race-specific, seedling (*Pc*) genes for resistance has been the primary means of reducing losses to crown rust in cultivated oat in the United States. Initially, *Pc* genes were introgressed from cultivated hexaploid oat, *A. sativa*, and later from the wild hexaploid animated oat, *A. sterilis*. As cultivars with these genes were deployed, they have 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*, such that it is now difficult to find races avirulent on these genes. Virulence to all the described *Pc* genes from *A. sterilis* is present in the U.S. crown rust population, and its virulence complexity has continued to increase unabated (6). Diploid and tetraploid *Avena* spp. have been the focus of more recent efforts at identifying new, effective *Pc* genes. Resistance in the diploid black oat, *A. strigosa*, has been well documented for some time but introgression of this resistance into cultivated hexaploid oat is hampered by differences in ploidy levels and the lack of chromosome homology between the two species (1,11,19). The University of Wisconsin–Madison and the Agriculture Agri-Foods Canada–Winnipeg (AAFC-Winnipeg) oat breeding programs have released cultivars with crown rust resistance genes derived from *A. strigosa.* The AAFC-Winnipeg program recently released Leggett, a cultivar that contains *Pc94* from the *A. strigosa* accession RL1697 (1) that is effective against most of the North American crown rust population. The tetraploid species, *A. magna* CI 8330, was the source of an effective crown rust resistance gene (*Pc91*) in the oat cv. Hi-Fi released by North Dakota State University in 2001 (15).

Slender oat, *A. barbata* Pott ex Link, is a wild tetraploid ($2n$ = 28) species, widely distributed throughout the Mediterranean region, including North Africa, the Middle East, South Asia, and much of Europe (3,12). *A. barbata* is the second most frequently occurring species following *A. sterilis*, and is adapted to a wide range of habitats ranging from sea level to the snow line. Slender oat is considered to be a weed of poor, shallow soils in cultivated fields, roadsides, and waste sites and along walls and excavation sites (3). Additionally, it is a widely distributed introduced species in Australia and the Americas. *A. barbata* is considered a restricted species in the United States, and is listed as a noxious weed in seed lots by the state of Missouri and a "moderately invasive" species of natural areas in California (5).

A. barbata has been a source of genes for resistance to powdery mildew (*Eg-4*) and stem rust (*Pg-16*) that have been successfully transferred from *A. barbata* into cultivated hexaploid oat (2,13,21). Resistance to crown rust in *A. barbata* has been known for some time but testing was confined to a limited number of collections of *A. barbata* and races of *P. coronata* (9,10,14). Recently, the United States Department of Agriculture (USDA) collection of *A. barbata* was systematically evaluated for resistance to a highly diverse

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sexual population of *P. coronata* (7). Of the 359 accessions tested in the greenhouse for both seedling and adult plant resistance, 13% were resistant to all isolates and at both growth stages. Resistance was detected in accessions from throughout much of the natural range of *A. barbata*.

The objective of this research was to identify additional sources of resistance to a diverse North American population of *P. coronata* within the broader Canadian collection of *A. barbata.*

Table 1. Reactions of seedling and adult plants of selected Canadian accessions of *Avena barbata* to race DBBC (06MN097) and a bulk population of *Puccinia coronata* f. sp. *avenae* from the St. Paul, MN buckthorn nursery[a]

			Seedling reaction to buckthorn bulk population		Adult reaction to buckthorn bulk population	
Accession	**Origin**	**Seedling reaction 06MN097**	**Greenhouse**	**Growth cabinet**	**Greenhouse**	**Growth cabinet**
CN 19719	Algeria	R	R	R	R	R
CN 19726	Algeria	R	R	R	R	R
CN 19728	Algeria	R	R	R	R/HR	HR
CN 19729	Algeria	R	R/HR	R	R/HR	R/HR
CN 19735	Algeria	R/S	MR/S[b]	MR	MR	R/MR
CN 19736	Algeria	R	R	R	R/MR	R/MR
CN 19768	Algeria	R	R/HR	R/MR	R/HR	R/HR
CN 19777	Algeria	R	HR/R	R/MR	R/MR	R
CN 23631	Algeria	R	R/S[a]	R	R	R
CN 23638	Algeria	HR	HR	R	HR	HR
CN 23714	Algeria	R	R	R	R/MR	R
CN 23720	Algeria	R	R	R/MR	R/MR	R/MR
CN 23775	Algeria	HR	HR	R/MR	R/MR	R
CN 23804	Algeria	R	R/MS[b]	R/MR	R/MR	R
CN 23805	Algeria	R	R	R	R/MR	R/MR
CN 23807	Algeria	R	R	R	HR	R/HR
CN 23813	Algeria	–	R	HR	R/MR	HR
CN 23899	Algeria	MR	HR	R	R/HR	HR
CN 23904	Algeria	MR/R[b]	HR	R	HR	HR
CN 23905	Algeria	R	HR	MR	HR	R/HR
CN 23906	Algeria	S/R	R	R/MR	R/HR	R/HR
CN 23908	Algeria	R	R	R/MR	R/HR	HR
CN 23911	Algeria	R	MR	MR	HR	R
CN 23917	Algeria	R	R	R/MR	R/MR	R
CN 24012	Algeria	R	R	R	R	HR
CN 3450	Australia	HR	HR	R	R	HR
CN 3674	Australia	R/HR	HR	R/HR	HR/R	HR/R
CN 21485	Greece	R/S	R/S[b]	R	R	R
CN 24369	Israel	R	R	R	R/MR	R
CN 25081	Israel	HR	HR	R	HR	HR
CN 21531	Italy	R	R	R	R[c]	R[c]
CN 21547	Italy	MR	MR/S[b]	R/MR	R/MR	R/MR
CN 21556	Italy	R	R	R	R/HR	HR
CN 21646	Italy	HR	HR	HR	HR	HR
CN 19468	Lebanon	HR	HR	HR	HR	HR
CN 19469	Lebanon	HR	HR	HR	HR	HR
CN 19470	Lebanon	HR	HR/R	R/HR	HR	HR
CN 19472	Lebanon	R/HR	HR	R	HR	HR/R
CN 19473	Lebanon	HR	HR	R	R	HR
CN 19474	Lebanon	R/HR	R/HR[b]	R	HR	HR
CN 19476	Lebanon	HR	HR	R	HR	HR
CN 19477	Lebanon	HR/R	R/HR	R	R/MR	R
CN 19478	Lebanon	MR/MS	MR/MS[b]	R/MR	R/MR	R/MR
CN 19479	Lebanon	R	R	R/MR	R/MR	R/MR
CN 19481	Lebanon	HR	R/HR	R	HR/R	HR/R
CN 19482	Lebanon	R/HR	R	MR	R/MR	R
CN 19484	Lebanon	R	R	MR	R	R
CN 21710	Morocco	HR	HR	HR	HR	HR
CN 23086	Morocco	R/HR	R/HR	HR	HR	HR
CN 23087	Morocco	R/HR	R/HR	R/HR	R/MR	R
CN 23326	Morocco	MR	R/MR	R/MR	R/MR	R/MR
CN 25651	Portugal	R	R/S[b]	R	R/HR	R/HR
CN 25667	Portugal	R	MR	MR	R	R
CN 25701	Portugal	R	R	R	R	R
CN 25801	Portugal	HR	HR	HR	HR	HR
CN 26013	Portugal	HR	R	R	R/HR	HR
CN 26053	Portugal	R	R	R	R/MR	R
CN 26064	Portugal	MR	MR	MR	MR	MR
CN 26065	Portugal	R	R	R	R	R

(*continued on next page*)

[a] Crown rust reactions of moderately large to large pustules with little or no chlorosis were scored as susceptible (S), those with moderately large pustules surrounded by extensive chlorosis were scored as moderately susceptible (MS), those with small pustules surrounded by chlorosis or necrosis were scored as moderately resistant (MR), those with chlorotic or necrotic flecks were scored as resistant (R), and those with no visible reaction were scored as highly resistant (HR); – = accession not tested with that inoculum.

[b] Indicates reaction of accession was heterogeneous; only resistant plants were advanced to the next stage of testing.

[c] Accession exhibited a “blotchy” type of resistant reaction.

MATERIALS AND METHODS

Available seed of *A. barbata* accessions, not duplicated in the USDA Agricultural Research Service National Small Grains Collection, were obtained from the AAFC-Plant Genetic Resources of Canada, Saskatoon, SK. In total, 1,143 accessions from 17 countries were planted in vermiculite in 7-cm^2 pots with approximately 10 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 were planted in one corner to serve as a check for uniformity and viability of inoculum. Seven days after planting, pri-

Table 1. (*continued from previous page*)

Accession	Origin	Seedling reaction 06MN097	Seedling reaction to buckthorn bulk population		Adult reaction to buckthorn bulk population	
			Greenhouse	Growth cabinet	Greenhouse	Growth cabinet
CN 26069	Portugal	R	R	R	R	HR
CN 26269	Portugal	MR	R	MR	R	R
CN 26270	Portugal	R	R	HR	HR	HR
CN 26482	Portugal	R	MR	MR	MR	R
CN 22972	Spain	R	R	R	R/MR	R
CN 22983	Spain	R	R	R/MR	R	R
CN 22993	Spain	R/HR	R/HR	HR	HR/MS[b]	HR
CN 25518	Spain	R	R	R	R/MR	R
CN 25524	Spain	R	R	R	MR	R
CN 25598	Spain	R	R	R	R	R
CN 26071	Spain	R	R	R	R	R
CN 26077	Spain	R	R	R	R	R
CN 26083	Spain	R	R	R	R	R
CN 26094	Spain	MR	MR	MR	R/HR	R/HR
CN 26128	Spain	R	R	R	R	R
CN 26136	Spain	R	R	R	R	R
CN 26152	Spain	R	R	R	R	R
CN 26161	Spain	R	R	R	R	R
CN 26205	Spain	R	R	R	R	R
CN 26206	Spain	R	R	R	R	R
CN 26224	Spain	R	R	R	R	HR/R
CN 26225	Spain	R	R	R	R	HR/R
CN 26271	Spain	R	R	R	R[c]	R[c]
CN 26275	Spain	R	R	R	R/HR	R/HR
CN 26285	Spain	R	R	R	R	R
CN 26304	Spain	R	R	R	R	R
CN 26305	Spain	R	R	R	R[c]	R[c]
CN 26310	Spain	MR	R	R	R	R
CN 26312	Spain	HR	R	R	R/HR	HR
CN 26313	Spain	HR	R	R	HR	HR
CN 26314	Spain	R	R	R	R	R
CN 26319	Spain	R	R	R/MR	R	R
CN 26325	Spain	R	R	R	R	R
CN 26353	Spain	R	R	R	R	R
CN 26372	Spain	HR	HR	HR	HR	HR
CN 26373	Spain	HR	R	R	HR/R	HR/R
CN 26400	Spain	R	R	R	R/MR	R
CN 26448	Spain	MR	R	R	R	R
CN 19455	Syria	R	HR	R	R/MR	R/HR
CN 19368	Tunisia	HR	HR/R[b]	MR	R/MR	R
CN 19659	Tunisia	R	R/MR	R	R/MR	R
CN 19669	Tunisia	R/S	MR/S[b]	MR	MR	R/MR
CN 19671	Tunisia	R	MR	MR	MR/S	R
CN 19693	Tunisia	HR	HR	R	R/HR	HR
CN 19712	Tunisia	R	MR/HR[b]	R	HR	HR
CN 19713	Tunisia	HR	HR/R	HR/R	HR	HR
CN 21641	Tunisia	R	R	R	R/HR	HR
CN 21642	Tunisia	R	R	R	MR/MS	MR
CN 22619	Tunisia	HR/MS[b]	R	R/MR	R/MR	R
CN 22623	Tunisia	R	R	R	R/MR	R
CN 22628	Tunisia	HR	HR	HR	HR	HR
CN 22635	Tunisia	MR	MR	–	MR/MS	–
CN 22645	Tunisia	R/HR	R/HR	R	R/MR	R
CN 22919	Tunisia	R/HR	R	R	R/MR	R
CN 22930	Tunisia	R	R	R	R/MR	HR
CN 22941	Tunisia	R/S	R/MR	R	HR	HR
CN 22950	Tunisia	–	R	R	R	R
CN 22953	Tunisia	MR	R	MR	R/MR	R
CN 22955	Tunisia	MR	MR	MR	R/MR	R
CN 23582	Tunisia	R	R	MR/R	R/MR	R
CN 19551	Turkey	R	R	R	R/S	HR
CN 19552	Turkey	R	R	R	R	HR
CN 19573	Turkey	R/HR	HR	HR	R	HR
CN 25113	Turkey	R	MR	MR	MR	R
CN 25117	Turkey	R	MR	MR	R	R
CN 25123	Turkey	R	MR	MR	MR	R

mary leaves of seedlings were inoculated until covered with a mineral oil (Soltrol 70; Phillips-Conoco, Tulsa, OK) suspension of approximately 1×10^2 fresh urediniospores of a single-pustule-derived isolate of *P. coronata* f. sp. *avenae* (06MN097), designated race DBBC according to the nomenclature of Chong et al (8). Methods used to obtain single-uredinial cultures of *P. coronata* have been described previously (6). This race is virulent upon only 2 of the 36 differential cultivars used in our annual crown rust survey. Cultures of *P. coronata* were kept at –50°C (if not used within 2 weeks of collection) or at 4°C at 20% relative humidity (if used within 2 weeks). Inoculated plants were placed in a dew chamber overnight (16 h) and moved to a greenhouse bench maintained at 20 to 25°C with supplemental lighting to insure a 14-h day length. Crown rust reactions were recorded 12 to 14 days post inoculation. Crown rust reactions of moderately large to large pustules with little or no chlorosis were scored as susceptible, those with moderately large pustules surrounded by 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 *A. barbata* accessions that were scored at least moderately resistant in the initial test with race DBBC were fertilized with solution of water-soluble fertilizer (Plantex 20-20-20; 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 2008 from the buckthorn nursery in St. Paul, MN. The buckthorn/oat nursery at St. Paul 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 the genus *Avena* is detected in this population (7). Seedling crown rust reactions to the 2008 bulk population were recorded as described above. 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 until they reached the stem elongation growth stage (Feekes 7-8) and were reinoculated with the 2008 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 selected for growing on and tested with the 2008 buckthorn bulk as adult plants. Adult plants that exhibited any susceptible or moderately susceptible reactions were considered susceptible, even if the majority of reactions were resistant.

The 125 accessions found to be resistant in both seedling and adult plant greenhouse tests using the bulk inoculum from the St, Paul buckthorn nursery were retested in growth cabinet tests. The growth cabinet was set at 18 and 16°C (day and night, respectively) with an 18-h photoperiod. Seedling tests were planted, inoculated, incubated, and scored as described for the greenhouse tests. For the adult plant test, a seedling of each accession was transplanted to pasteurized soil mix in "cone-tainers" in trays (21 cm deep by 3.8 cm in diameter; Stuewe and Sons, Corvallis, OR) and grown on to the stem elongation growth stage (Feekes 7-8) in the growth cabinet. Inoculation with a bulk population of *P. coronata* from the St. Paul buckthorn nursery and incubation was as described previously. Plants were evaluated for disease reaction as described previously 15 days later.

RESULTS

Of the 1,099 accessions that germinated, 337 (30.7%) were at least moderately resistant to race DBBC at the seedling growth stage. In total, 212 (19.3%) and 125 (11.4%) accessions were resistant to the bulk population of *P. coronata* f. sp. *avenae* from the buckthorn nursery at the seedling and adult plant stages, respectively. Resistant reactions ranged from moderately resistant to highly resistant. Eighteen accessions originating from eight different countries (Algeria, Australia, Israel, Italy, Morocco, Portugal, Spain, and Tunisia) were rated as highly resistant or a mix of highly resistant and resistant plants in all tests (Table 1). Three accessions (CN21531 from Italy and CN26271 and CN26305 from Spain) displayed a unique "blotchy" resistant reaction as adults (Fig. 1). Rather than being the restricted small chlorotic or necrotic spots typical of the resistant reaction, these reactions continued to grow, consisting of larger, irregular, chlorotic changing to necrotic spots with distinct water-soaked margins.

Repetition of the testing of the 125 accessions deemed resistant in greenhouse tests under the more controlled conditions of a growth cabinet confirmed their resistance (Table 1). In no case was an accession found to be susceptible in the growth-cabinet tests. As a general rule, plants expressed resistance reactions in the growth cabinet equal to or higher than that expressed under greenhouse conditions. Lower temperatures such as those in the growth cabinet have been shown to increase the resistance expressed by several known *Pc* genes in *A. sativa* (4).

When data from this and a previous study of the USDA collection of *A. barbata* (7) were combined (excluding countries from which fewer than 15 accessions were tested), accessions with apparent broad-spectrum resistance to crown rust were identified in accessions of *A. barbata* from 11 countries (Fig. 2). No broad-spectrum resistance was detected among accessions from Iran, Iraq, or Syria. The frequency of resistance was higher in accessions from the western Mediterranean (Portugal, Spain, Morocco, Algeria, Tunisia, and Italy) and Lebanon.

DISCUSSION

These data support the previous report of the relatively high frequency of resistance to a broad spectrum of races of *P. coronata* in *A. barbata* (7). Given the diversity of resistant reactions and the wide geographic distribution of *A. barbata* ac-

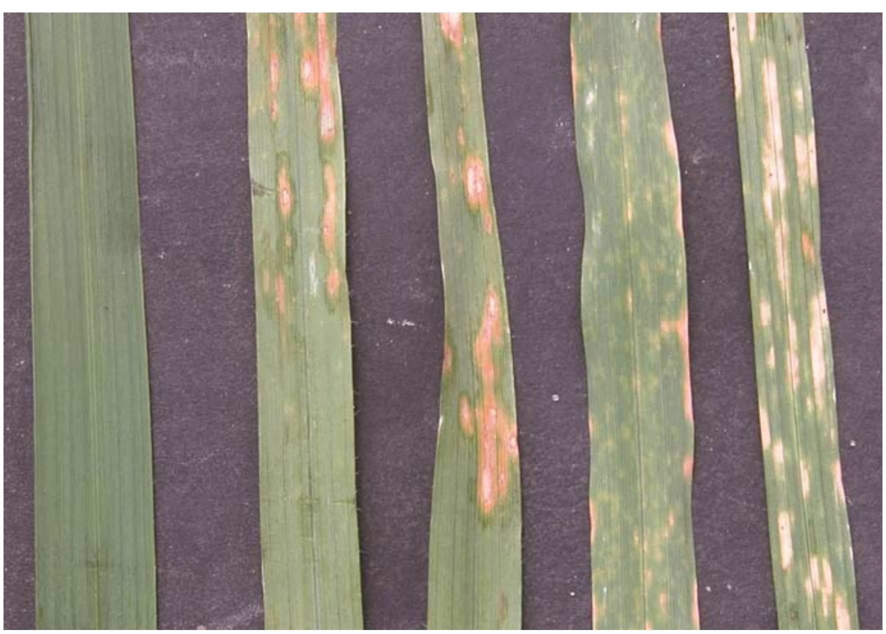

Fig. 1. Adult oat leaves showing (from left to right) highly resistant, "blotchy" resistance (leaves 2 and 3), chlorotic resistant, and necrotic reactions to oat crown rust, *Puccinia coronata* f. sp. *avenae*.

cessions that display this broad-spectrum resistance, it seems likely that at least some of the genes involved in the resistant accessions differ from one another. Of particular interest is the so-called blotchy resistance reaction observed in three accessions. This type of reaction has not been reported previously in crown rust of oat (or any other cereal rust, for that matter). The frequency of resistance is particularly high from the western Mediterranean and Lebanon, where higher precipitation levels tend to occur in the winter season when *A. barbata* is actively growing. Further exploration and collection of *A. barbata* from these areas for additional crown rust resistance is warranted.

The introgression of crown rust resistance from *A. barbata* into cultivated hexaploid oat will be a daunting but not impossible task. Resistance to powdery mildew and stem rust have been successfully transferred from *A. barbata* to cultivated oat via backcrossing to develop a chromosome addition line (21 + 1 pair of chromosomes), followed by either irradiation (2,13) or crossing with *A. longiglumis* CW57 (21) to induce recombination between the additional *A. barbata* chromosome carrying the resistance gene and its homologue in *A. sativa*. Initial crosses of resistant *A. barbata* accessions from the USDA collection with cultivated oat were easily made if *A. barbata* was used as the female parent (*unpublished data*). When the resulting crosses were treated with colchicine, the resulting plants (presumably decaploids) were reasonably fertile. Unlike crown rust resistance derived from *A. strigosa* or *A. murphyii* (16,17), resistance from *A. barbata* is not suppressed in crosses with *A. sativa*, at least in the crosses made to date. A more direct method to introgress crown rust resistance from *A. barbata* is to cross it with *A. longiglumis* CW57 (a diploid), followed by colchicine doubling to produce a synthetic hexaploid which would then be the donor parent in a backcrossing program with *A. sativa*. Presumably, the factor in *A. longiglumis* CW57 that allows pairing between homologous chromosomes (21) would allow introgression of the alien chromosome segment carrying the resistance gene into the *A. sativa* genome early in the backcrossing procedure, bypassing the need to first create an alien chromosome addition line. A similar method was used to transfer *Pc91* crown rust resistance from the tetraploid *A. magna* into *A. sativa* using the synthetic hexaploid 'Amagalon' as the donor parent in backcrossing with cultivated oat (18).

Despite the promise of *A. barbata* as a source of new, broad-spectrum crown rust resistance genes, there is no reason to expect that this resistance will be any more durable than seedling resistance derived from other wild *Avena* spp. Given the diversity of resistant reactions observed, the wide geographic origins, and the large number of *A. barbata* accessions with broad-spectrum resistance, it is likely that a diversity of new resistance genes exists in the species. The useful lifespan of these new crown rust resistance genes could be enhanced if different oat breeding programs used different effective genes from *A. barbata*, thus increasing the diversity of highly resistant cultivars deployed in a given region rather than breeding programs relying on the same new effective resistance gene in all new cultivars. New races virulent on any one of these new resistance genes would not predominate in the *P. coronata* population and cause widespread damage. Pyramiding various combinations of effective resistance genes into oat cultivars could also enhance the durability of those genes from *A. barbata*. A concerted effort will be required to introgress this resistance from numerous accessions into oat cultivars adapted to the various spring and winter oat-production areas of North America.

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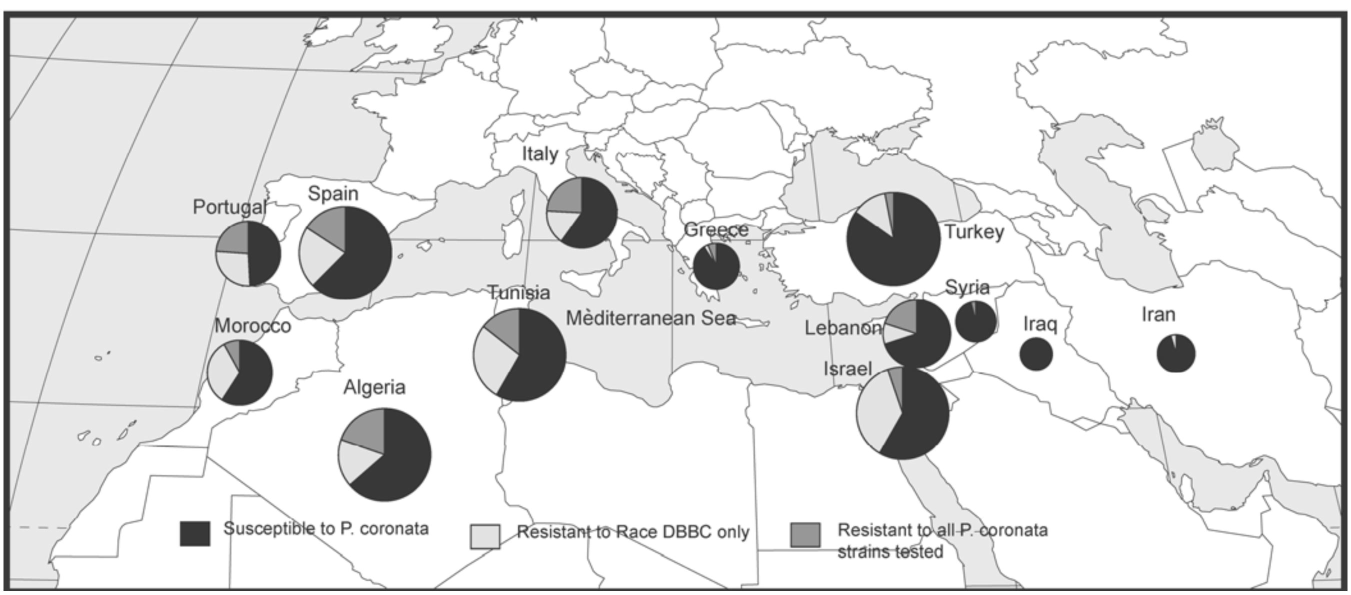

Fig. 2. Origin and frequency of accessions of *Avena barbata* from the United States Department of Agriculture (7) and Canadian germplasm systems susceptible to all tested isolates of *Puccinia coronata*, resistant to race DBBC only, or resistant to all isolates tested. Relative numbers of accessions from each country is indicated by the size of the corresponding pie chart. Countries with fewer than 15 accessions were not included in the figure.

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