Characteristics of Resistance to *Puccinia coronata* f. sp. *avenae* in *Avena fatua*

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Abstract

Crown rust, caused by *Puccinia coronata* f. sp. *avenae*, is the most widespread and harmful fungal disease of oat. The best defense against the pathogen is use of cultivars with genetic resistance, which is effective, economic, and an environmentally friendly alternative to chemical control. However, the continuous evolution of the pathogen can rapidly overcome major gene resistance, creating an urgent need to identify new sources. Wild oat accessions have already proven to be valuable donors of many resistance genes, but the weed species *Avena fatua* remains underexploited. Its abundance across multiple environments and the frequent occurrence of herbicide-resistant populations demonstrate its ready ability to adapt to biotic and abiotic stresses; yet, surprisingly, there are no extensive studies which describe crown rust resistance occurrence in gene bank stocks of *A. fatua*. In this study, 204 accessions of *A. fatua* maintained in the collections of the United States Department of Agriculture (USDA) and Polish National Centre for Plant Genetic Resources were evaluated at the seedling stage for

crown rust reaction using host–pathogen tests with five highly diverse and virulent races of *P. coronata*. Of tested genotypes, 85% showed a heterogeneous infection pattern, while 61% were susceptible or moderately susceptible to all races. Of the 79 resistant *A. fatua* accessions, seedling resistance to at least two *P. coronata* isolates was recognized within 19 accessions, with 13 displaying a homogeneously resistant phenotype to one or two races. Accessions showing multiple single seedling resistance to three or four isolates were observed. Based on the seedling reaction to isolates used in the study, 18 infection profiles (IP) were determined. Using UPGMA clustering, resistant accessions were divided into six main clusters encompassing samples with similar IPs. Twelve of 18 patterns allowed us to postulate the likely presence of novel crown rust resistance genes, whose origin was predominantly from Kenya or Egypt. Future work will clarify the genetic basis of the resistances observed here, as well as confirm their potential utility in breeding resistant oat cultivars.

Crown rust, caused by *Puccinia coronata* Cda. f. sp. *avenae*, is considered the most damaging disease of oat, and the use of race-specific (*Pc*) genes for resistance has been the primary means of control (Gnanesh et al. 2014). In the *Avena* genus, over 100 *Pc* genes have been discovered (Chong et al. 2011; Gnanesh et al. 2013). Many of these genes originated from hexaploids *A. sativa* L. (*Pc3c*, *Pc4c*, *Pc6c*, *Pc6d*, *Pc9*, *Pc13*, *Pc22*, *Pc95*, *Pc96*) and *A. byzantina* Koch. (*Pc1-Pc8*, *Pc9c*, *Pc10-Pc12*, *Pc14*, *Pc21*), but the main sources of crown rust resistance were accessions of wild hexaploid *A. sterilis* L. collected in the 1960s and 1970s from Israel and other Mediterranean countries (Cabral and Park 2014; CDL 2017; Gnanesh et al. 2014; Šebesta et al. 2003; Simons et al. 1978). Diploid and tetraploid *Avena* species have also been broadly investigated as a potential source of new, effective *Pc* genes. Resistant genotypes were identified in diploids: *A. atlantica* Baum et Fedak, *A. damascena* Rajhathy et Baum, *A. hirtula* Lag., *A. longiglumis* Dur., *A. strigosa* Schreb., and *A. wiestii* Steud, as well as tetraploids: *A. agadiriana* Baum et Fedak, *A. barbata* Pott ex Link, *A. magna* Murphy et Terrell, and *A. murphyi* Ladiz (Aung et al. 2010; Cabral and Park 2014; Cabral et al. 2011; Carson 2009a, 2010; CDL 2017; Mitchell Fetch et al. 2007; Nazareno et al. 2017; Rines et al. 2018; Sowa et al. 2016; Tan and Carson 2013). Resistance appears to be particularly common in the diploid *A. strigosa* (AsAs)

(*Pc15*, *Pc16*, *Pc17*, *Pc19*, *Pc23*, *Pc30*, *Pc37*, *Pc81*, *Pc82*, *Pc83*, *Pc84*, *Pc85*, *Pc86*, *Pc87*, *Pc88*, *Pc89*, *Pc90*, *Pc94*) (Cabral et al. 2014; CDL 2017) and the tetraploid *A. barbata* (AABB) (Carson 2009a, 2010). However, all diploid and tetraploid *Avena* species belong to the tertiary gene pool. Problems arise during introgression of resistance from these species into cultivated hexaploid oat as a result of differences in the ploidy level and reduced chromosome homology, which prevents pairing of homologous chromosomes (Jellen and Leggett 2006). Exploitation of resistance from these species is consequently laborious, and despite the large number of known resistance genes within the tertiary germplasm, only *Pc23* and *Pc94* derived from *A. strigosa* have been incorporated into *A. sativa*, although *Pc94* has been widely used in resistance breeding (Aung et al. 1996; Dyck and Zillinsky 1963). Despite the large number of resistance genes identified within the tertiary *Avena* pool, due to barriers in the integration of resistance, *Pc* genes introduced from hexaploid oats: *A. sativa*, *A. byzantina*, and *A. sterilis*, were mainly used in breeding programs in North America, Europe, and Australia (*Pc38*, *Pc39*, *Pc48*, *Pc50*, *Pc58*, *Pc59*, *Pc60*, *Pc61*, *Pc68*) (Cabral and Park 2014; Gnanesh et al. 2014; Šebesta et al. 2003).

The primary gene pool of *Avena* contains a number of hexaploid species besides the *A. byzantina*, *A. sativa*, and *A. sterilis* mentioned above. These include *A. fatua* L., *A. ludoviciana* Durieu, and *A. occidentalis* Durieu. *A. fatua* is the most widely distributed of all of these and is considered one of the 10 worst annual weeds of cereal crops globally (Holm et al. 1991; Loskutov and Rines 2011). Its abundance across multiple environments, and the frequent occurrence of herbicide-resistant populations (Adamczewski et al. 2013; Owen and Powles 2009; Thill et al. 1994), demonstrate its ready ability to adapt to biotic and abiotic stresses; yet, surprisingly, no extensive studies have been reported of *A. fatua* potential as a source of crown rust resistance. The large collections of *A. fatua* held in gene banks across the world, running to thousands of accessions, could be a very rich resource, which could be easily deployed in breeding for crown rust resistance. The objective of this research was to identify and characterize resistance to *P. coronata* within a representative selection of *A. fatua* accessions maintained in United States Department

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Fig. 1. Distribution of *Avena fatua* genotypes used in the study for searching new sources of resistance to crown rust in oat.

of Agriculture (USDA) and Polish National Centre for Plant Genetic Resources collections.

Materials and Methods

A set of 204 accessions of *A. fatua* from different parts of the world was chosen proportionally to the availability of accessions in the gene banks. Examined plant material came originally from 29 countries located in North and South America, Asia, Europe, and Africa (Fig. 1, Table 1, Supplementary Table S1). Seeds of *A. fatua* accessions were obtained from the USDA National Small Grains Collection Aberdeen, Idaho, USA (186 accessions) and the National Centre for Plant Genetic Resources, Radzików, Poland (18 accessions). Crown rust resistance of each of the genotypes was tested using five highly virulent *P. coronata* isolates (Pca) by means of host–pathogen test (Hsam et al. 1997). Crown rust pathogen races CR230, CR241, and CR257 were kindly supplied by Dr. J. Menzies from Morden Research and Development Centre, AAFC, Canada along with their virulence characterization in relation to 18 *Pc* genes (Table 2). Pca isolates 94U(63) and 51U(22) were selected from a wide collection of single-pustule pathotypes derived from populations collected in Poland in the years 2010–2014 according to the method described by Sowa et al. (2016).

Before the main experiment, the virulence of each isolate was tested on a set of 34 differential oat lines with single resistance genes as well as control cultivar Kasztan. Differentials for genes *Pc58*, *Pc59*, *Pc60*, and *Pc61* were represented by cultivars TAM-O-301, TAM-O-312, Coker227, and Coker234, respectively (Simons et al. 1978). The near-isogenic lines with genes *Pc35*, *Pc38*, *Pc39*, *Pc40*, *Pc45*, *Pc46*, *Pc48*, *Pc50*, *Pc54*, *Pc55*, *Pc56*, *Pc57*, *Pc62*, *Pc63*, *Pc64*, *Pc68*, *Pc91*, *Pc94*, *Pc96*, *Pc97*, *Pc98*, *Pc101*, *Pc103-1*, *Pc104* were developed at the Cereal Research Centre AAFC, Winnipeg, Canada; and the differentials representing *Pc14*, *Pc36*, *Pc51*, *Pc52*, *Pc70*, *Pc71* genes were created at Iowa State University (Carson 2011; Chong et al. 2011; Menzies et al. 2015). For subsequent inoculation, microfuge tubes filled with urediniospores were heat-shocked for 4 min at 42°C and multiplied on leaf fragments of 10-day-old seedlings of susceptible cultivar Kasztan using the host–pathogen test procedure. Leaves were placed into petri dishes filled with agar (0.6%) with the addition of benzimidazole

(3.4 mM) and inoculated in a settling tower by applying 500–700 spores of *P. coronata* per square centimeter. The dishes were incubated for 10 days in a phytotron at about 18°C with 70% humidity and light intensity of approximately 4 kLx. In order to define virulence of the fungal samples, each of the isolates was examined on a set of reference oat lines. Seeds of *Pc* lines were placed on plug trays filled with a universal substrate mixed with peat. Seedlings were grown for 10 days and used to perform host–pathogen tests according to the methodology described above. Leaves were placed onto 12-well culture plates filled with agar using Kasztan as an infection control in each well. Disease symptoms were assessed on three leaf fragments, each from a different seedling of one reference oat line. A crown rust reaction of medium-sized to large colonies with little or no chlorosis was considered to be susceptible, whereas lines with no visible symptoms as well as small or no colonies with necrotic and chlorotic changes were scored as resistant.

To screen the susceptibility of the gene bank accessions, *A. fatua* grains were seeded onto plug trays filled with a universal substrate with peat, and allowed to germinate. After 10 days, six leaf fragments, each from a different seedling of the *A. fatua* accessions, were placed on 12-well culture plates with agar and benzimidazole medium. Control cultivar leaf was put into each well of a plate. The plates were inoculated with the selected *P. coronata* isolates as detailed and incubated in a growth chamber for 10 days according to the methodology described above. Crown rust disease symptoms were evaluated using the qualitative scale of S, MS, MR, R, and HR, where S = susceptible – large to moderately large pustules with little or no chlorosis; MS = moderately susceptible – moderately large pustules surrounded by extensive chlorosis; MR = moderately resistant – small pustule surrounded by chlorosis; R = resistant – chlorotic or necrotic flecking; and 0 = HR = highly resistant – no visible reaction (Carson 2009a; Sowa et al. 2016).

Reactions to the isolate infections were grouped into two classes: phenotypes described as S and MS were considered as susceptible, and the remainder as resistant. In order to select genotypes with crown rust resistance conditioned by genes not described so far, the infection profiles (IP) of differential lines were compared with the infection profiles assigned to analyzed *A. fatua* accessions. Scores of infection were transformed into a binary matrix to perform

hierarchical analysis. Susceptibility or resistance to each *P. coronata* pathotype was considered as 1 and 0, respectively. Accessions with uniform susceptibility reaction were excluded from the analysis, remaining data were used to conduct clustering and construct a similarity dendrogram based on the unweighted pair-group method (UPGMA) in PAST 3.19 software (Hammer et al. 2001). Groups and subgroups were determined using Dice similarity coefficients (Dice 1945) with 1,000 bootstraps.

Results

The *P. coronata* isolates used in this research were selected to overcome immunity of resistance genes in the selected reference lines and thus exclude the presence of these genes in screened genotypes. The most aggressive, inducing susceptible response in 18 of 34 evaluated *Pc* genes, was pathotype 94U(63). CR230 and 51U(22) isolates overcame the resistance of 15 reference lines, whereas CR241 and CR257 were virulent toward 13 and 11 *Pc* lines, respectively (Table 2).

All *P. coronata* isolates were used to perform the host–pathogen tests on the 204 *A. fatua* accessions. Resistance reactions ranged from susceptible (S) to highly resistant (HR) (Table 1). Most of the tested *A. fatua* accessions (173; 85%) displayed heterogeneous phenotypes,

and the response of single seedlings within accessions to specific *Pca* inoculation could vary even from susceptible to highly resistant. Nevertheless, 125 accessions were completely susceptible for all tested races of *P. coronata*. For 33 accessions, only single seedlings were rated as resistant or moderately resistant to one crown rust race, whereas in 20 accessions more than one of six screened seedlings displayed a variable level of resistance to one or two *Pca* pathotypes, most of which were resistant to 51(22), CR257, or CR230 (Table 1). For 13 accessions, more than one seedling was resistant, but each plant responded to one to three different *Pca* pathotypes. The remaining 13 accessions (6.4%) displayed a consistent resistant phenotype. Four of these accessions were immune to race CR257 (PI 411458, PI 411491) or CR230 (PI 362374, PI 411476), and eight were assessed as resistant simultaneously to 94U(63) and CR257 strains. Distinct, but also homogenous and comparably effective patterns of resistance on races CR230 and 51(22) were presented by the Egyptian PI365611 accession. In some of the accessions described above, multiple resistance of single seedlings was observed. Single plants of PL 502694, PI 411458, PI 411465, and PI 411469 were resistant to three *P. coronata* isolates, and two seedlings of PI 365611 from Egypt showed resistance to four isolates.

Table 1. Characteristics of resistant *Avena fatua* accessions reactions on inoculation with 5 *Puccinia coronata* isolates

Plant ID	GenBank ^b	Origin	<i>P. coronata</i> race ^a					Infection profile (number of resistant seedlings) ^c
			51(22)	94(63)	CR230	CR241	CR257	
PI 269358	NSGC	Afghanistan, Kandahar	S,MS,MR	S	S,MS	S,MS	S,MS	1 (1)
PI 269870	NSGC	Pakistan, North-West Frontier	MS,MR	S,MS	S	S	MS	1 (1)
PI 287310	NSGC	Greece, Peloponnese	MS,R	MS	MS	MS	MS	1 (1)
PI 365602	NSGC	Iraq	MS,R	S,MS	MS	S	MS	1 (1)
PI 365603	NSGC	Iraq	S,MS,R	MS	MS	S,MS	S,MS	1 (1)
PI 432465	NSGC	United States, Montana	S,MS,R	S,MS	MS	MS	MS	1 (1)
PI 538801	NSGC	Russian Federation, Altay	MS,R	MS	MS	MS	S	1 (1)
PI 545392	NSGC	United States, Utah	MS,R	S	S	S	S	1 (1)
PI 545393	NSGC	United States, Utah	MS,R	S	S	S	S	1 (1)
PL 51532	IHAR	Peru	S,MS,R	S	MS	S	S	1 (1)
PL 51702	IHAR	Poland	S,MS,R	S,MS	MS	S	MS	1 (1)
PI 287309	NSGC	Greece, Peloponnese	MS,MR	MS	MS	MS	MS	1 (1)
PI 366424	NSGC	Afghanistan, Parwan	MS,R	MS	S	MS	S	1 (2)
PI 374393	NSGC	Serbia	MS,R	MS	S,MS	S,MS	S	1 (2)
PI 545394	NSGC	United States, Utah	MS,R	S	S	S	S,MS	1 (2)
PI 388760	NSGC	Morocco, Taroudannt	MS,R	S,MS	S,MS	S	S	1 (3)
PI 411494	NSGC	Turkey, Erzurum	MS,R	MS	MS	MS	S	1 (3)
PI 210998	NSGC	Afghanistan, Bamian	S,MS	S,MS,R	S	S	S,MS	2 (1)
PI 545371	NSGC	United States, Minnesota	S,MS	MS,MR	S,MS	S	S	2 (1)
PI 545377	NSGC	United States, Montana	S,MS	MS,MR	S,MS	S	S	2 (2)
PI 228338	NSGC	Iran, East Azerbaijan	S,MS	MS	MS,R	MS	MS	3 (1)
CIav 2526	NSGC	United Kingdom, Wales	S,MS	S	MS,MR	MS	MS	3 (1)
PI 269360	NSGC	Afghanistan, Bamian	MS	S,MS	S,MS,MR	S,MS	MS	3 (1)
PI 344854	NSGC	Serbia	S,MS	S,MS	MS,R	S,MS	MS	3 (1)
PI 544414	NSGC	United States, Idaho	MS	MS	MS,MR	MS	S,MS	3 (1)
CIav 3213	NSGC	United States, New York	S,MS	S,MS	MS,MR	S	S	3 (1)
PI 287312	NSGC	Greece	MS	S,MS	MS,R	S,MS	MS	3 (2)
PI 639335	NSGC	Tajikistan, Badakhshoni Kuhi	S	S	S,MS,MR	S,MS	S	3 (2)
PI 411470	NSGC	Turkey, Erzurum	S	MS	MS,MR,R	MS	S	3 (3)
PI 165601	NSGC	India, Uttar Pradesh	S,MS	MS	MS,R	S,MS	S,MS	3 (4)
PI 365600	NSGC	Iraq	S	S,MS	MS,R	MS	MS	3 (5)
PI 411476	NSGC	Turkey, Van	S	S	R	MS	MS	3 (6)
PI 266828	NSGC	United Kingdom, England	MS	S,MS	MS	S,MR	MS	4 (1)
PI 447299	NSGC	China, Gansu	MS	MS	MS	MS,R	S	4 (1)
PI 544372	NSGC	United States, North Dakota	MS	MS	MS	MS,R	S,MS	4 (1)
PI 544697	NSGC	United States, Wyoming	MS	MS	S,MS	MS,R	MS	4 (1)
PI 545352	NSGC	United States, Arizona	MS	S,MS	MS	MS,MR	S,MS	4 (1)

(Continued on next page)

^a Resistance phenotype: S = susceptible, large to moderately large pustules with little or no chlorosis; MS = moderately susceptible, moderately large pustules surrounded by extensive chlorosis; MR = moderately resistant, small pustule surrounded by chlorosis; R = resistant, chlorotic or necrotic flecking; and HR = highly resistant, no visible reaction.

^b IHAR – National Centre For Plant Genetic Resources, The Plant Breeding and Acclimatization Institute – NRI, Radzików, Poland; NSGC – National Small Grains Collection, Aberdeen, Idaho, USA.

^c IP – infection profile – infection pattern determined for five tested isolates; number of resistant seedlings in brackets.

Based on the seedling reactions to the five *P. coronata* isolate inoculations, 18 infection profiles (IPs) of screened *A. fatua* accessions were determined (Table 3). IP 0 corresponded to highly virulent reactions to all of the crown rust races. Resistance to one of five pathotypes was assigned as IP 1 – IP 5, while resistance to two *P. coronata* isolates was described as IP 6 – IP 11. IP 12 – 16 indicated a combination of resistance to three crown rust races. Resistance to four pathotypes: 51(22), CR230, CR241, CR257, was reported only once (PI 365611 Minya, Egypt), and was assigned as IP 17 (Table 1). Next, the infection profiles of the *A. fatua* accessions were compared with IPs of differential *Pc* lines. The infection pattern of reference lines containing genes *Pc36*, *Pc39*, *Pc55*, *Pc61*, *Pc70*, and *Pc71* were identical to IP 1. *Pc38* and *Pc63* lines corresponded to IP 6, as observed for PI 221435 (Afghanistan) and PI 411453 (Iran). IP 10 was one of the most frequently appearing profiles, characterizing almost all accessions from Kenya as well as two accessions from the United States (PI 545361, PI 545479). This infection scheme fitted the phenotype of the oat differential line containing *Pc14*. Resistance to 51(22), CR230, and CR240 was characteristic of the differential line for *Pc94*. This pattern was assigned as IP 13 and observed for

accession PI 365611 from Egypt. IP 14 was observed for lines *Pc48*, *Pc103-1*, and accession 502694 from Iran. IP 16 corresponded to resistance to crown rust isolates 94(63), CR241, CR257, and was seen in seedlings of two accessions from the Rift Valley in Kenya (PI 411458, PI 411465) as well as the oat differential line for *Pc35*.

The virulence level of the crown rust isolates used in the study was very high and relatively similar, ranging from 84 to 93%, taking into account single seedling response (Table 1). Pathotypes CR241 and 94(63) were found to be the most virulent, infecting single seedlings of 190 and 186 accessions, respectively. No cases of consistent resistance to isolate CR241 were reported. Out of 204 analyzed accessions, only eight displayed simultaneous homogenous resistance to isolates 94U(63) and CR257, whereas only one equal and highly resistant reaction to both isolates 51U(22) and CR230 was ascertained.

Using UPGMA clustering based on the Dice coefficient calculated on infection data, we separated the 79 accessions which were characterized by at least moderate resistance of single seedling to crown rust into six main divisions (Fig. 2). The first and the sixth divisions were represented by single accessions, each characterized by a distinctive and complex resistance profile. All six seedlings of the Egyptian

Table 1. (Continued from previous page)

Plant ID	GenBank ^b	Origin	<i>P. coronata</i> race ^a					Infection profile (number of resistant seedlings) ^c
			51(22)	94(63)	CR230	CR241	CR257	
PI 544373	NSGC	United States, North Dakota	S	MS	S,MS	MS,MR	MS	4 (2)
PI 227353	NSGC	Iran, Esfahan	S,MS	S	S	S	S,MS,R	5 (1)
PI 344859	NSGC	Macedonia	MS	S	MS	S	MS,MR	5 (1)
PI 411440	NSGC	Ethiopia, Gonder	S	S	MS	MS	MS,R	5 (1)
PI 411462	NSGC	Kenya, Rift Valley	S,MS	S	MS	S,MS	MS,MR	5 (1)
PI 542090	NSGC	Nepal	S	MS	MS	S,MS	S,MS,R	5 (1)
PL 51633	IHAR	Poland	S	MS	S,MS	MS	MS,R	5 (1)
PL 52107	IHAR	Poland	S	S,MS	S	S	S,MS,R	5 (1)
PL 52366	IHAR	Poland	S,MS	S	S,MS	S,MS	S,MS,R	5 (1)
PI 432464	NSGC	United States, Montana	S,MS	MS	MS	MS	MS,MR,R	2 (2)
PI 411454	NSGC	Iran, East Azerbaijan	S,MS	S	S,MS	MS	S,MS,R	5 (3)
PI 411483	NSGC	Turkey, Kars	S	S,MS	S,MS	S	MS,MR	5 (4)
PI 411491	NSGC	Turkey, Kayseri	S	MS	MS	S	R	5 (4)
PI 365601	NSGC	Iraq	MS	S,MS	MS	S	MS,MR,R	5 (5)
PI 411484	NSGC	Turkey, Kars	S	S,MS	MS	S	S,MR	5 (5)
PI 436009	NSGC	Chile, La Araucania	MS	S,MS	S,MS	S	MS,MR,R	5 (5)
PI 221435	NSGC	Afghanistan, Bamian	MS,R	S,MR	MS	S,MS	S,MS	6 (1)
PI 411453	NSGC	Iran, East Azerbaijan	S	S,R	MS	MS	MS,R	6 (1)
PI 411460	NSGC	Kenya, Rift Valley	S,MS	R	MS	MS	R	10 (6)
PI 411463	NSGC	Kenya, Rift Valley	S,MS	R	MS	MS	HR	10 (6)
PI 411466	NSGC	Kenya, Rift Valley	S,MS	R	MS	S,MS	HR	10 (6)
PI 411468	NSGC	Kenya, Central	MS	R	MS	MS	HR	10 (6)
PI 545361	NSGC	United States, Texas	S	HR	S,MS	S	HR	10 (6)
PI 545479	NSGC	United States, Oklahoma	S	R	S,MS	S	HR	10 (6)
PI 365608	NSGC	Egypt, Daqahliya	MS,MR,R	S,MS,R	S,MS	MS	MS	1 (2); 2 (1)
CIav 4644	NSGC	Argentina	MS, MR	S,MS	MS,R	S	MS	1 (1); 3 (1)
PI 344855	NSGC	Serbia	MS,R	MS	S,MS,MR	S	MS	1 (1); 3 (1)
PI 344857	NSGC	Serbia	S,MS,MR	MS	MS,MR	S,MS	S,MS	1 (1); 3 (1)
PI 436023	NSGC	Chile, Los Lagos	MS,R	MS	MS	MS,MR,R	S,MS	1 (1); 4 (3)
PI 151083	NSGC	Uruguay	S	S,MS,R	MS,MR,R	S,MS	MS	2 (1); 3 (2)
PI 349888	NSGC	Serbia	MS	S,MS	MS,R	S	MS,R	3 (1); 5 (1)
CIav 4643	NSGC	Argentina	MS,S	MS,MR	MR,R	S	MS	3 (4); 9 (2)
PI 362374	NSGC	Serbia	S	S	MR,R	S	S,MS,R	3 (5); 11 (1)
PI 411464	NSGC	Kenya, Rift Valley	S,MS,R	S,MS	MS	MS,MR	S,MS,R	1 (1); 4 (1); 8 (1)
PL 502694	IHAR	Iran	MS,MR,R	S,MS	S,MS,R,HR	S,MS,R	S,MS,R	1 (1); 4 (1); 7 (1); 14 (1)
PI 411485	NSGC	Turkey, Kars	S,MS,R	MS	MS	MS,MR,R	MS,R	4 (2); 8 (1)
PI 411461	NSGC	Kenya, Rift Valley	S,MS	MS,R	S,MS	MS,MR	MS,R	4 (1); 10 (5)
PI 411459	NSGC	Kenya, Rift Valley	S	S,MS,R	S,MS	S,MS	MS,R	5 (1); 10 (3)
PI 411458	NSGC	Kenya, Rift Valley	S,MS	MS,R	MS	MS,R	MR,R	5 (2); 10 (2); 16 (2)
PI 365611	NSGC	Egypt, Minya	R	MS	R	S,MS,R	MS,R	7 (2); 13 (3); 17 (2)
PI 411465	NSGC	Kenya, Rift Valley	MS	R	MS	MS,MR	R	10 (2); 16 (4)
PI 411469	NSGC	Kenya, Central	MS,R	R	MS,MR	MS	HR	10 (3); 12 (1); 15 (2)

accession PI 365611 belonging to the first cluster displayed resistance to two to four *P. coronata* pathotypes (51U(22), CR230, CR241, and CR257). Resistance was seen in four of six seedlings from the Iranian accession 502694, from the sixth division; each seedling showed a different IP. The second division was composed of nine accessions from Kenya and two from the United States, mostly of IP 10, with crown rust resistance against 94U(63) and CR257 races. The fourth cluster contained six accessions of IP 5, resistant toward CR257, whereas the fifth one encompassed four accessions mostly of IP 3 with resistance to CR230 race. The third cluster contained the 56 remaining *A. fatua* accessions, which displayed a relatively low level of resistance to the crown rust isolates used in this study.

With regard to the geographical origin of analyzed materials, *A. fatua* accessions from Egypt and Kenya exhibited a higher percentage of crown rust resistant seedlings within each genotype in comparison with other countries (Fig. 3). About 15% of accessions from Argentina, Chile, and Turkey as well as 10% from Morocco, Uruguay, Iraq, India, Serbia, Iran, and the United States were assessed as fully or partially resistant to a particular Pca race. No resistant forms were identified within *A. fatua* collected in Mexico or Kazakhstan. The single accessions from Hungary, Slovakia, and South Africa were also crown rust susceptible.

Discussion

Studies conducted worldwide confirm the extremely virulent dynamics and phenotypic diversity of *P. coronata* f. sp. *avenae* as a causative agent of crown rust in oats (Carson 2009b, 2011; Chong et al. 2011; Jiráková and Hanzalová 2008; Menzies et al. 2015). The emergence of new rust pathotypes differing in virulence and aggressiveness is linked to the life cycle of the pathogen, involving sexual and asexual reproduction. In the absence of an alternate host on which the sexual part of the cycle and meiotic recombination events take part, new pathotypes arise by mutation and somatic recombination (Chaves et al. 2008; Fetch et al. 2011). Due to the continuous evolution of the pathogen, current sources of resistance to crown rust rapidly lose their effectiveness, so that new ones are urgently needed. Wild oat genotypes have already been proven to be donors of many resistance genes (Gnanesh et al. 2014; Loskutov and Rines 2011); however, *A. fatua* still remains unexploited.

Previous studies of crown rust resistance genes in *A. fatua* were limited in terms of number or geographical origin of tested materials. Briggie (1974) identified resistant genotypes in a small collection of *A. fatua* from California after a test performed with one Pc race. Simons and Briggie (1984) screened about 400 U.S. accessions of *A.*

Table 2. Virulence profile of *Puccinia coronata* f. sp. *avenae* isolates used for testing resistance of *Avena fatua* accessions

Isolate number	Phenotype code ^a	Virulence to standard differentials ^b	Virulence to supplemental differentials ^c	Avirulence to differentials
51U(22)	SBLP	<i>Pc40, Pc45, Pc46, Pc51, Pc54, Pc62, Pc64</i>	<i>Pc14, Pc35, Pc57, Pc96, Pc97, Pc98, Pc101, Pc104</i>	<i>Pc36, Pc38, Pc39, Pc48, Pc50, Pc52, Pc56, Pc58, Pc59, Pc60, Pc61, Pc63, Pc68, Pc70, Pc71, Pc91, Pc94, Pc103-1</i>
94U(63)	NJBP	<i>Pc39, Pc40, Pc46, Pc48, Pc54, Pc62, Pc64</i>	<i>Pc36, Pc55, Pc57, Pc61, Pc70, Pc71, Pc94, Pc96, Pc97, Pc98, Pc103-1</i>	<i>Pc14, Pc35, Pc38, Pc45, Pc50, Pc51, Pc52, Pc56, Pc58, Pc59, Pc60, Pc63, Pc68, Pc91, Pc101, Pc104</i>
CR230	LQCB	<i>Pc38, Pc39, Pc40, Pc59</i>	<i>Pc14, Pc35, Pc36, Pc55, Pc57, Pc60, Pc61, Pc63, Pc70, Pc71, Pc91</i>	<i>Pc45, Pc46, Pc48, Pc50, Pc51, Pc52, Pc54, Pc56, Pc58, Pc62, Pc64, Pc68, Pc94, Pc96, Pc97, Pc98, Pc101, Pc103-1, Pc104</i>
CR241	DSGB	<i>Pc38, Pc39, Pc46, Pc48, Pc52</i>	<i>Pc14, Pc36, Pc55, Pc61, Pc63, Pc70, Pc71, Pc103-1</i>	<i>Pc35, Pc40, Pc45, Pc50, Pc51, Pc54, Pc56, Pc57, Pc58, Pc59, Pc60, Pc62, Pc64, Pc68, Pc91, Pc94, Pc96, Pc97, Pc98, Pc101, Pc104</i>
CR257	BRBG	<i>Pc38, Pc39, Pc56, Pc68</i>	<i>Pc36, Pc55, Pc61, Pc63, Pc70, Pc71, Pc94</i>	<i>Pc14, Pc35, Pc40, Pc45, Pc46, Pc48, Pc50, Pc51, Pc52, Pc54, Pc57, Pc58, Pc59, Pc60, Pc62, Pc64, Pc68, Pc91, Pc94, Pc96, Pc97, Pc98, Pc101, Pc103-1, Pc104</i>

^a Phenotype code based on the standard differentials set Chong et al. (2000).

^b Chong et al. (2000).

^c Chong et al. (2011).

Table 3. Infection profiles (IP) of screened *Avena fatua* accessions based on the reaction to *Puccinia coronata* race infection

IP	<i>P. coronata</i> race					Oat differential line with a corresponding phenotype
	51(22)	94(63)	CR230	CR241	CR257	
0	H ^a	H	H	H	H	-
1	L	H	H	H	H	<i>Pc36, Pc39, Pc55, Pc61, Pc70, Pc71</i>
2	H	L	H	H	H	-
3	H	H	L	H	H	-
4	H	H	H	L	H	-
5	H	H	H	H	L	-
6	L	L	H	H	H	<i>Pc38, Pc63</i>
7	L	H	L	H	H	-
8	L	H	H	L	H	-
9	H	L	L	H	H	-
10	H	L	H	H	L	<i>Pc14</i>
11	H	H	L	H	L	-
12	L	L	H	H	L	-
13	L	H	L	L	H	<i>Pc94</i>
14	L	H	L	H	L	<i>Pc48, Pc103-1</i>
15	H	L	L	H	L	-
16	H	L	H	L	L	<i>Pc35</i>
17	L	H	L	L	L	-

^a H = high infection (virulent reaction); L = low infection (avirulent reaction).

fatua, but all were susceptible to five races of *P. coronata* as seedlings, and to common races as adult plants in the field. Brouwer et al. (1982) as well as Burdon et al. (1983) analyzed Australian populations of *A. fatua* and described them as a mixture of resistant and susceptible individuals. Šebesta and Kühn (1990) identified a wide range of crown rust resistance in an *A. fatua* population collected in Czechoslovakia in 1971. Out of 40 selections, one homozygous line described as *A. fatua* CS1 was chosen for analysis. Based on the reaction with a single Pc race, the authors stated that its resistance was conditioned by

one recessive gene, which was in interaction with one partially dominant gene. The same genotype, *A. fatua* CS1, was tested by Staletic et al. (2009) using three different races. In this second study, the segregation ratio indicated that resistance was conditioned by a major dominant gene. The current work presents the characteristic of resistance to *P. coronata* in a set of 204 *A. fatua* accessions coming originally from 29 countries located in North and South America, Asia, Europe, and Africa, and confirms the species potential as a donor of effective resistance genes.

Fig. 2. UPGMA dendrogram of 79 *Avena fatua* accessions based on the similarity of infection obtained by five *Puccinia coronata* isolates inoculation.

Five highly virulent *P. coronata* isolates were used to carry out the host–pathogen test to assess the susceptibility of the studied genotypes. The use of races derived from diverse populations collected in North America and Europe has allowed us to expand the number of defeated genes screened, and in consequence to detect resistance with the greatest potential benefit for current breeding programs. Of studied accessions, 85% showed a heterogeneous infection pattern, in some cases showing a full range from S to HR. Of tested genotypes, 61% could be unambiguously described as susceptible or moderately susceptible to all *P. coronata* races, however. Other studies on wild oat resistance have also revealed variable response to the rust inoculation within single accessions (Carson 2009a, 2010; Sowa et al. 2016; Tan and Carson 2013). Carson (2009a) screened 359 accessions of the tetraploid slender oat, *A. barbata*, and stated that 39% were at least moderately resistant to crown rust, some of which displayed variable phenotypes. In a further study encompassing 1,143 *A. barbata* accessions, 11.4% of genotypes showed at least a moderately resistant response to *P. coronata* at the seedling and adult plant stage, with only a small number of the tested materials being variable in reaction (Carson 2010). Tan and Carson (2013) in a study involving 332 accessions of 11 different, mainly diploid and tetraploid, wild oat species from Morocco, assessed 49% of materials as moderately resistant to resistant in a seedling stage and 55% as moderately resistant to highly resistant in the adult plant stage. A significant proportion of the accessions (25%) displayed heterogeneous phenotypes. Among the 92 tetraploids, *A. magna*, *A. murphyi*, and *A. insularis* tested by Sowa et al. (2016),

58.7% were resistant to at least one crown rust race, and 37% of accessions were characterized by nonuniform reaction.

The level of phenotype variability within the *A. fatua* accessions analyzed in this research was significantly higher in comparison with previously studied species, and ranged 85% of tested genotypes. In case of *A. fatua*, the tendency to develop populations which are diverse in the infection response may result from the maintenance of assorted set of resistance gene alleles. This phenomenon, called balancing selection, occurs in natural ecosystems, in which natural selection favors different alleles in distinct host populations specialized to specific environments (Möller and Stukenbrock 2017; Mundt and Browning 1985). Genetic variation at the genomic and population levels in both plants and pathogens are the effect of antagonistic interaction between plants and their pathogens (Van der Hoorn et al. 2002). Oates et al. (1983) concluded that in environments where pathogens are widespread and variable, there is a tendency for heterogeneous resistance to arise. The predominance of host genotypes with low or intermediate level of resistance conditioned by various combinations of weak genes or alleles may be beneficial for the host population in a long-term perspective.

Crown rust, as the most widespread and harmful oat disease, appears in almost every region of oat cultivation (Chong 2003). Loskutov (2007) claims that the most resistant genotypes should be expected in the center of origin of the genus *Avena*, believed to be located in the Mediterranean region. This thesis works in the case of *Pc* genes derived from animated oat *A. sterilis* (Gnanesh et al.

Fig. 3. Percentage of resistance reaction within *Avena fatua* accessions from different countries to crown rust isolates used in host–pathogen tests.

2014; Šebesta et al. 2003). *A. fatua* is one of the most common and obnoxious cereal weeds worldwide, and so may be subjected to different disease dynamics (Briggle and Youngs 1975; Holm et al. 1991). In our research, *A. fatua* genotypes from a given country were represented proportionally to their availability in the gene banks. The distribution of resistant accessions varied and was not concentrated in one particular area. The largest number of accessions tested was from the United States (36), and as many as 15 exhibited resistance. However, this resistance was mostly on a very low level, occurring in single seedlings within accessions. Only in the cases of PI 545361 from Texas and PI 545479 from Oklahoma with IP 10, every screened seedling was found to be resistant to 94(63) and CR257. This phenotype corresponded to reference line Pc14 and was also observed in 9 highly resistant accessions from Kenya, which composed the second cluster of the UPGMA dendrogram. IP 10 was the most common profile for Kenyan accessions, where each of the 11 screened genotypes showed exceptionally high and homogenous levels of resistance. Genotype 502694 from Iran and Egyptian accession PI 365611, characterized by distinctive and complex profiles of resistance, were strikingly different from the remaining accessions. Within the first mentioned genotype, four of six seedlings were resistant, each showing different IP based on the resistance to three crown rust pathotypes: 51(22), CR230, and CR241. Similar variability was observed in PI 365611. In this case, all six tested seedlings displayed variable resistance to two to four *P. coronata* pathotypes (51U(22), CR230, CR241, and CR257). Within this accession, two plants were resistant to all four crown rust races (IP 17) and presented the highest level of resistance of all tested materials. Overall, five profiles of infection corresponding to resistance to three of five analyzed crown rust pathotypes were identified. Two of them, PI 12, indicating resistance to 51(22); 94(63) and CR257 as well as PI 15 (94(63); CR230, and CR257) were unique and appeared within accession PI 411469 from Kenya. Overall, 12 of 18 determined infection profiles did not correspond to the phenotype of any of the reference Pc lines used in the research. This suggests they result from the presence of the new sources of resistance to crown rust, which in the cases of PI 365611 and PI 411469 should be highly effective against current pathogens.

Currently, one of the major challenges of the oat breeding programs is the durability of genetic resistance. New genes identified in the study may be valuable as components in the resistance gene pyramids, even where their levels of resistance are equivalent to existing *Pc* genes. Pyramiding is considered one of the most promising strategies of plant resistance breeding (Joshi and Nayak 2010). In recent years, quantitative resistance has also gained a great interest, and due to the development of molecular biology, improved tools are becoming available to better integrate this type of resistance into breeding strategies (Pilet-Nayel et al. 2017). Combinations of partial resistance are expected to result in much more durable polygenic resistance than can be obtained through use of single major genes. Future work will clarify the genetic basis of the resistances observed here, as well as confirm their potential utility in the field, where resistance may be affected by the plant development stage as well as other factors such as temperature (Niks et al. 2015). There remains considerable scope to investigate *A. fatua* as a model for selection of durable disease resistance under agricultural conditions.

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