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INHERITANCE OF SPRING OAT RESISTANCE TO *Puccinia coronata avenae*

Mirjana D. Staletic[1], Milivoje S. Milovanović[1], Aca I. Marković[2] and Gorica T. Đelić[2]

[1]*Small Grains Research Centre Kragujevac, Save Kovačevića 31, 34000 Kragujevac, Republic of Serbia*
e-mail: staleticm@kg.ac.rs

[2]*Faculty of Science, University of Kragujevac, Radoja Domanovića 12, 34000 Kragujevac, Republic of Serbia*

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ABSTRACT: The qualitative inheritance of resistance to *Puccinia coronata avenae* in spring oats was governed by a single or two major genes. The most frequent segregation ratios in the F_2 generation of hybrids were determined to be 3:1 and 9:7, which indicated that the resistance was conditioned by a single dominant major gene or two interacting major genes (duplicate negative recessive epistasis).The segregation ratios in certain crosses were found not to be consistent across all prevalent pathotypes, which confirmed that they differed genetically. In hybrids of some combinations, with respect to prevalent pathogen pathotypes, the 2:1 segregation ratios were obtained, indicating the assumption of heterozygosity or inhomogeneity of some parents regarding the major genes for resistance to them.

Key words: *Puccinia coronata avenae*, oats, qualitative inheritance, major genes, oat hybridisation method

INTRODUCTION

Study on the inheritance of oat resistance to *P. coronata avenae* refers primarily to the determination of the mode of inheritance of resistance as well as of the number of genes governing it. As regards the inheritance of oats resistance to pathogens in general and hence to the leaf rust agent, it primarily refers to meiotic inheritance, i.e. to nuclear resistance genes.

The inheritance of oat resistance to *P. coronata avenae* can be dominant (complete or incomplete), recessive or intermediate. Resistance can be governed by a single gene (monogenic), several genes (oligogenic) or a series of genes (polygenic). In the majority of cases resistance can be inherited dominantly (completely or incompletely). Conventional breeding methods and analysis of the F_1, F_2, B_1 and B_2 generations of hybrids resulted in different ratios of resistant (R) to susceptible (S) plants, based on which conclusions are made about the inheritance of resistance and the number of genes conditioning it (STOJANOVIĆ *et al.,* 1998; STOJANOVIĆ, 2004).

Concerning the degree of effectiveness, resistance genes can be classified as those with great effects (major genes or oligogenes) and those with small effects (minor genes or polygenes). The major genes have a race-specific nature, while the minor ones usually have additive effects and ensure horizontal resistance (BOROJEVIĆ, 1981). HOWEVER, NELSON (1978) considers this classification as inadequate, because vertical and horizontal resistance genes are identical differing only in the expression mode and effectiveness in different genotypes.

The classification of traits into qualitative and quantitative ones is not biologically based, it is rather only a reflection of man's desire to systematise phenomena in order to gain a better understanding and knowledge of them (BOROJEVIĆ and BOROJEVIĆ, 1971). BOROJEVIĆ (1992) underlines that quantitative traits are not governed by minor genes only, but that major genes are also present in some of them. VAN DER PLANK (1963) and CALDWELL (1968) have come to the conclusion that the horizontal resistance conditioned by minor genes is more superior to the vertical resistance resulting from the major genes effect. NELSON (1978) has pointed out that vertical and horizontal resistance genes are identical, or in other words, that major and minor genes according to this theory do not exist but that there are only resistance genes which can be differentiated according to the mode of expression and effectiveness.

Qualitative or alternative traits include all the traits whose development is governed by the the highly effective genes or the so-called major genes. As such traits, in a number of cases, resistance to pathogenic organisms were considered (BOROJEVIĆ, 1992). Many researchers across the world have studied the qualitative inheritance of resistance to *P. coronata avenae* in oats (BAKER and UPADHYAYA, 1967; FLEISCHMANN and MCKENZIE, 1968; FLEISCHMANN *et al*., 1971; KIEHN *et al*., 1976; ŠEBESTA, 1976, 1977, 1979, 1983; HARDER *et al*., 1984, 1990; ŠEBESTA and KUHN, 1990; MARSHALL and SHANER, 1992; GONG-XIN YU *et al*., 2001).

The aim of these investigations was to broaden knowledge in the field of qualitative inheritance of resistance to *P. coronata avenae* in oats with a specific pathogen population structure present in Serbia.

MATERIAL AND METHOD

From 1999 to 2003 an investigation was conducted on the *P. coronata avenae* pathogen population in Serbia, on 67 samples following the method (STAKMAN *et al.,* 1962). Determination of the pathogen virulence spectrum was performed on a set of isogenic oat lines with known major resistance genes (*Pc* 38, *Pc* 39, *Pc* 48, *Pc* 50, *Pc* 50-2, *Pc* 54-1, *Pc* 54-2, *Pc* 55, *Pc* 56, *Pc* 58, *Pc* 59, *Pc* 60, *Pc* 61, *Pc* 62, *Pc* 63, *Pc* 64, *Pc* 67 and *Pc* 68) after GREEN (1965) and ŠEBESTA and HARDER (1983) method. Prevalent (the most widely distributed) pathogen pathotypes having different virulence formulas were used in further research. The pathotype having the (V/A) formula 50, 50-2, 54-2, 61, 62, 64, 67 / 38, 39, 48, 54-1, 55, 56, 58, 59, 60, 63 and 68 was designated as a prevalent pathotype I, the one with the formula (V/A) 38, 39, 48, 50, 50-2, 54-2, 56, 60, 63, 64, 67 / 54-1, 55, 58, 59, 61, 62 and 68 was designated as a prevalent pathotype II and that with the formula (V/A) 38, 39, 48, 50, 50-2, 54-2, 56, 60, 63, 64, 67 / 54-1, 55, 58, 59, 61, 62 and 68 as a prevalent pathotype III. Their multiplication was carried out on the susceptible cultivar Pan for the obtainment of sufficient inoculum amounts for the artificial infection of plants under laboratory conditions.

The inheritance of resistance of spring oat to *P. coronata avenae* was examined by crossing resistant and susceptible genotypes, investigating the resistance of parents and their F_1, F_2 hybrids and determining the number of genes governing it.

For the purpose of parent selection for crossings laboratory, examinations were performed in 1999/2000 on 47 lines and cultivars at the seedling stage from the European Oat Disease Nursery (EODN), which had expressed good resistance in field conditions for a number of years. Based on the results obtained, parent pairs were selected for crossings. The resistant

genotypes *Pc* 39, *Pc* 58, *Pc* 59, *Pc* 68, *Avenae fatua* CS1, *Avenae sterilis* CAV 2648, *A. sterilis* 2648 x KR 396 x PAN 2010/ 2-8-2-57, *A. sterilis* WYR 343-1 and *A. sterilis* WYR 343-2 were selected as resistance donors and the susceptible cultivar Zlatak as a recipient (Tab. 1).

The origin and the genetic constitution of the resistance of some donors is known and of others unknown. The origin of this trait in all resistance sources is more or less complex. However, of high importance is the original resistance derived from other species, as was the case with many donors. As seen from the very names of resistant parents, their pedigree includes resistance genes primarily from wild species of *A. sterilis* and *A. fatua*, but also from their other parents. FLEISCHMAN and MCKENZIE (1968) in Israel managed to transfer the resistance from the wild species *A. sterilis* and the Pendek and F-366 cultivars and create the isogenic line *Pc* 39. The resistance of the *Pc* 58 isogenic line originates from *A. sterilis* and P. I. 295919 (C. I. 8387) and TAM-0-301 cultivars, and that of the *Pc* 59 line from *A. sterilis* and P. I. 296244 (C. I. 8393) and TAM-0-312 (SIMONS *et al*., 1978). The *Pc* 68 line resistance derives from a wild relative *A. sterilis* and CAV 4274 and Fraser cultivars (HARDER *et al.*, 1980).

Oat hybridisation method: Single-cross breeding method was used to obtain the F_1 and F_2 progeny. The hybridisation was made between maternal and paternal plants in laboratory conditions using a modified method after MAKSIMOVIĆ (1999) and MILOVANOVIĆ (2000). The maternal plant panicles sampled at the end of the stage of their emergence from the sheaths were brought into laboratory for flower emasculation by anther removal from all panicle flowers. The paternal plant panicles sampled in the phase just before or immediately after anther dehiscence were prepared by cutting the upper third of the glumae so that pollen grains could be more easily released onto the maternal plant stigma. Three maternal and two paternal panicles were put into each 0.5-l glass bottle containing a previously prepared nutrition solution (10 l of water, 5 % of sugar and 0.5 % Cineb S-65). The parental plants were inclosed in parchment insulated bags and pollination was achieved by occasional "shaking" of the paternal panicles for the first seven days upon hybridisation. The bottle solution was changed every seven days until the grain matured. The plants were kept at room temperature, near a daylight source. The hybrid seed obtained was stored in paper bags at a temperature of +5°C until planting. Hybridisation for obtaining the F_1 generation was done in 2001.

The planting of all oat genotypes was performed in the spring of 2001. at the experimental field of the Small Grains Research Centre in Kragujevac employing spaced row planting, with the row length of 1 m, a row spacing of 25 cm and plant spacing of 10 cm. The single cross method used in 2001 resulted in zygote obtaining of grains of $9F_1$ combinations. In the F_1 hybrid plants self-pollination was permitted in 2002 for producing seed for the F_2 generation. The investigation of the resistance of seedlings of the F_2 hybrid progenies was conducted following the methods (STAKMAN *et al.,* 1962 and PETERSON *et al.,* 1948) for examination of the resistance of oat genotypes during 2002 under controlled conditions. 200 F_2 plants were analysed at each cross. The plants were classified into four replications according to a completely randomised design. Based on the F_2 generation analysis, different ratios of resistant (R-infection types 0, 1 and 2) to susceptible (S-infection types 3 and 4) plants were obtained. This analysis and the assessment of the infection intensity in each plant tested were used to gain an understanding of the resistance of tested hybrids, resistance inheritance and the number of genes governing it.

The qualitative interpretation of the obtained resistant to sensitive (R:S) segregation ratios in the F_2 generation plants in single crossings was made using the χ^2 test MEAD *et al*. (1996), for a comparison with corresponding theoretical ratios.

RESULTS AND DISCUSSION

The data obtained on segregation ratios in the F_2 generation, by determining infection types in spring oat hybrid seedlings, indicate the presence of a single or two major genes in the qualitative oat resistance of inheritance, depending on the mating combination and *P. coronata avenae* pathotype.

Table 1. presents crossing parent pairs and their reaction to prevalent pathotypes (I, II and III) and *P. coronata avenae* pathogen population at the seedling stage and in the phase of adult plants in the field. Immune (infection type 0), moderately resistant (infection type 2) and susceptible (infection type 4) parents were selected for crossing. Some of them have known *Pc* genes for the resistance to this pathogen and were obtained owing to the kindness of Prof. dr Josef Šebeste from the Czech Republic in 1999.

The isogenic lines with the genes *Pc* 39, *Pc* 58, *Pc* 59, *Pc* 68 and genotypes *A. fatua* CS1, *A. sterilis* CAV 2648, *A. sterilis* 2648 x KR 396 x Pan 2010/2-8-2-57, *A. sterilis* WYR 343-1 and *A. sterilise* WYR 343-2 were selected as resistance donors. Most resistance donors responded by the infection type 0 and expressed immunity. It was only the *A. sterilis* 2648 x KR 396 x Pan 2010/2-8-2-57 genotype that reacted with the infection type 2 but it also expressed high resistance. The donor reaction indicated that each of them had minimum one resistance major gene complementary to avirulence genes in the prevalent pathotypes I, II and III. All these genotypes were used as maternal parents.

The Zlatak genotype used as a paternal parent was chosen as a recipient and it was susceptible both at the seedling stage and in the phase of adult plants in the field because it reacted with the infection type 4. The selection of this genotype as a resistance receiver was made in order to gain the broadest possible genetic hybrid variability for easier definition of the modes of inheritance and genes effects and select the best genotypes by breeding. The control cultivar Pan which was not used in the crossing was highly susceptible and it reacted with the infection type 4.

Table 1. - Reaction and infection types in parental genotypes of spring oats against prevalent pathotypes I, II and III and *P. coronata avenae* pathogen population at the seedling stage and in the phase of adult plants in the field (Kragujevac, 2001).

Genotype	Seedlings						Adult plants	
	Prevalent pathotypes						Pathogen population	
	I		II		III			
	Reaction /Infection type							
Pc 39	R	0	R	0	R	0	R	0
Pc 58	R	0	R	0	R	0	R	0
Pc 59	R	0	R	0	R	0	R	0
Pc 68	R	0	R	0	R	0	R	0
Avena fatua CS1	R	0	R	0	R	0	R	0
Avena sterilis CAV 2648	R	0	R	0	R	0	R	0
Avena sterilis 2648 x KR 396 x Pan 2010/2-8-2-57	R	2	R	2	R	2	R	2
Avena sterilis WYR 343-1	R	0	R	0	R	0	R	0
Avena sterilis WYR 343-2	R	0	R	0	R	0	R	0
Susceptible parent								
Zlatak	S	4	S	4	S	4	S	4
Control cultivar								
Pan	S	4	S	4	S	4	S	4

R-resistant infection type (0,2)
S-susceptible infection type (4)

The investigation of the type of infection of F_2 hybrid seedlings of spring oats in terms of I, II and III pathotypes resulted in segregation ratio (tab.2) data indicating the presence of a single or two major genes in the qualitative inheritance of oat resistance, depending on the parental combination and the *P. coronata avenae* pathotypes.

In single-cross combinations against all pathotypes in the *Pc* 39 x Zlatak, *Pc* 59 x Zlatak and *A. fatua* CS1 x Zlatak hybrids, the segregation ratio established was 3:1, indicating that the resistance of the *Pc 39* and *Pc 59* genotypes was conditioned by a single known (*Pc 39* and *Pc 59*) dominant major gene, which was also the case with the *A. fatua* CS1 genotype, but the gene governing its resistance was still unknown.

The resistance of the *A. sterilise* WYR 343-1 genotype was controlled by two major interacting genes (duplicate negative recessive epistasis [(a = b) > B, A]), because the segregation ratio in the F_2 generation against all prevalent pathotypes was 9:7. The segregation ratio obtained against all pathotypes in the *A. sterilis* 2648 x KR 396 x Pan 2010/2-8-5-57 x Zlatak hybrid was 7:9, indicating that the resistance of the *A. sterilis* 2648 x KR 396 x Pan 2010/2-8-5-57 genotype was conditioned by two major interacting genes (duplicate positive recessive epistasis).

In the *Pc* 58 x Zlatak hybrid the obtained 3:1 segregation ratio in the F_2 generation indicated that the *Pc* 58 genotype had a single dominant major gene for resistance against the pathotype I, while the ratio against other pathotypes was 2:1. In the *Pc* 68 x Zlatak hybrid the obtained ratio in F_2 against the pathotype I was 9:7, indicating that the resistance to this pathotype was caused by two interacting genes (duplicate negative recessive epistasis). The 3:1 ratio against the pathotype III showed the difference in one dominant major gene. The 2:1 ratio determined against the pathotype II indicated the assumption of heterozigosity or inhomogeneity in parents.

The resistance of the *A. sterilis* WYR 343-2 x Zlatak hybrid to the pathotypes II and III was found to be controlled by a single dominant major gene due to the F_2 3:1 ratio obtained. However, the ratio obtained against the prevalent pathotype I was 2:1, again indicating parental inhomogeneity. The type of reaction and the segregation ratio for the F_2 *A. sterilis* CAV 2648 x Zlatak hybrid showed that the resistance of the *A. sterilis* CAV 2648 genotype was governed by a single dominant major gene. The segregation ratio obtained against the genotypes I and II was 3:1, being the difference in a single dominant major gene. The ratio against the pathotype III was 2:1.

The most frequently obtained segregation ratio in hybrid single-cross combinations was 3:1, indicating that the resistance to the prevalent pathotypes I, II and III was governed by a single dominant major gene. The role of two dominant major genes (duplicate negative recessive epistasis) in the inheritance of resistance to all prevalent pathotypes was indicated by the 9:7 segregation ratio obtained in the F_2 generation in several combinations. In hybrids of one combination the segregation ratio obtained was 7:9 indicating that the resistance was governed by two major interacting genes (duplicate positive recessive epistasis).

In investigations on the F_2 segregation ratios in oats, against the races (216, 265, 240, 239, 231 and 234) of *P. coronata avenae*, ŠEBESTA (1977, 1979, 1983) also obtained resistant and susceptible hybrids whose segregation ratio corresponded to theoretical ratios of 3:1 and 9:7, respectively, indicating that the resistance was conditioned by a single dominant or two recessive major genes and by the 0.70 to 0.95 probability that this would be the case in the F_2 generation as well, which was in accordance with the results obtained. The inheritance of wheat resistance to leaf rust and powdery mildew agents was investigated by FITZGERALD *et al*. (1957), RAO *et al*. (1964), STOJANOVIĆ (1983), MOMČILOVIĆ and JERKOVIĆ (1985), JERKOVIĆ (1988), BOŠKOVIĆ (1992) etc. The F_2 segregation ratios obtained were 3:1, 9:7 and 7:9, which was also in accordance with the F_2 segregation ratios obtained in this research.

Segregation ratios in certain crosses were observed not to coincide across all prevalent pathotypes, confirming that they differed genetically. In the hybrids of some combinations, in terms of the prevalent pathogen pathotypes, the segregation ratios obtained were 2:1, indicating the assumption of heterozigosity or inhomogeneity of some parents concerning major genes for resistance to them (*Pc* 58 x *Pc* 68). In these investigations, it did not significantly affect the accuracy of conclusions, but pointed to the need to use completely stable and homogeneous (pure) lines (dihaploids) in future investigations on resistance for the obtainment of most reliable results.

With the probability of $P \leq 0.05$, the difference obtained is statistically significant and is considered not to be due to random chance but to specific reasons, and if $P > 0.05$ than the differences between experimental and theoretical values are not significant and the difference obtained occurres due to random samples (KRALJEVIĆ-BALALIĆ *et al*., 1991). The probabilities (P) for the χ^2 values determined were satisfactory for the obtained and corresponding theoretical segregation ratios, because of $P > 0.05$ in all cross combinations. The highest probability (over 90%) that the segregation ratio obtained would reoccur in the F_2 generation against the prevalent pathotype I of *P. coronata avenae* was established in the combinations of *A. sterilis* WYR 343-2 x Zlatak and *Pc* 68 x Zlatak, against the prevalent pathotype II in the *Pc* 68 x Zlatak combination and against the prevalent pathotype III in the *A. sterilis* CAV 2648 x Zlatak and *Pc* 58 x Zlatak combinations.

CONCLUSION

The qualitative inheritance of resistance to *Puccinia coronata avenae* in spring oats was governed by a single or two major genes.

-The most frequent segregation ratios in the F_2 generation of hybrids were determined to be 3:1 and 9:7, which indicated that the resistance was conditioned by a single dominant major gene or two interacting major genes (duplicate negative recessive epistasis).

-The segregation ratios in certain crosses were found not to be consistent across all prevalent pathotypes, which confirmed that they differed genetically.

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Table 2. - Segregation ratios in the F_2 generation of single crossings in spring oat against the prevalent *Puccinia coronata avenae* pathotypes (I, II and III)

Combinations (single crossings)	Pathotype I						Pathotype II						Pathotype III					
	n	R	S	Theoretical ratio	χ^2	P	n	R	S	Theoretical ratio	χ^2	P	n	R	S	Theoretical ratio	χ^2	P
Pc 39 x Zlatak	197	149	48	3 : 1	0.0423	0.86	198	150	48	3 : 1	0.0606	0.82	197	150	47	3 : 1	0.1371	0.72
Pc 58 x Zlatak	122	85	37	3 : 1	1.8470	0.19	108	71	37	2 : 1	0.0417	0.86	106	70	36	2 : 1	0.0189	0.90
Pc 59 x Zlatak	130	94	36	3 : 1	0..5026	0.49	158	123	35	3 : 1	0.6835	0.43	137	97	40	3 : 1	1.2871	0.26
Pc 68 x Zlatak	134	76	58	9 : 7	0.0119	0.92	173	115	58	2 : 1	0.0029	0.95	167	117	50	3 : 1	2.1737	0.17
Avena fatua CS 1 x Zlatak	167	121	46	3 : 1	0.5768	0.48	149	104	45	3 : 1	2.1499	0.16	157	112	45	3 : 1	1.1231	0.31
Avena sterilis CAV 2648 x Zlatak	145	103	42	3 : 1	1.2161	0.28	141	96	45	3 : 1	3.5957	0.06	156	104	52	2 : 1	0.0000	0.99
Avena sterilis 2648 x KR 396 x Pan 2010/2-8-5-57 x Zlatak	115	45	70	7 : 9	0.9972	0.35	109	45	64	7 : 9	0.2692	0.63	111	46	65	7 : 9	0.2403	0.68
Avena sterilis WYR 343-1 x Zlatak	137	78	59	9 : 7	0.0261	0.89	157	84	73	9 : 7	0.4813	0.49	143	77	66	9 : 7	0.3358	0.55
Avena sterilis WYR 343-2 x Zlatak	184	123	61	2 : 1	0.0027	0.95	193	135	58	3 : 1	2.6269	0.11	184	131	53	3 : 1	1.4202	0.24