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Inheritance of Resistance to Two Races of *Puccinia coronata* Cda. var. *avenae* Fraser and Led.¹

By M. D. SIMONS AND H. C. MURPHY

Oats rank third in importance among the cereal crops of the United States and represent the most important small grain crop in many states. Crown rust (*Puccinia coronata* Cda. var. *avenae* Fraser & Led.) usually has been the most destructive disease of oats in the United States and throughout the world. The most effective means of controlling this disease has been the development and distribution of varieties resistant to the common races of the fungus. Before a resistant variety can be used effectively and efficiently as a source of resistance in breeding, it is essential that the genetic factors controlling the resistance to specific races be identified and their mode of inheritance determined.

REVIEW OF LITERATURE

V. C. Finker (in press) reviewed the literature concerning earlier studies of the inheritance of resistance to crown rust and also found that the variety Landhafer possessed a single gene controlling resistance to race 57. He concluded that the variety Santa Fe was heterogeneous for resistance to this race; some plants carried a single gene while others carried two genes probably linked with about 23 percent crossing over. The variety Trispernia was also heterogeneous, individual plants carrying one, two, or three factor pairs for resistance, one of which was allelic with one of the genes carried by Santa Fe.

An investigation (R. E. Finkner, 1953) of the inheritance of resistance of Santa Fe, Trispernia, and Landhafer to races 57 and 109 of crown rust indicated that the resistance of Santa Fe was conditioned by two genes linked with about 29 percent crossing over. Trispernia possessed two independent factor pairs for resistance to these races. The resistance of Landhafer was attributed to a single partly dominant gene.

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The resistance of Santa Fe has also been attributed (Osler and Hayes, 1953) to three factor pairs. Two of these were dominant and complementary, conditioning resistance when together. The third was also dominant and conditioned resistance, either alone, or in the presence of the other two. These three genes were inherited independently of each other.

MATERIALS AND METHODS

The parents and F_2 progenies of six oat crosses were tested in the seedling stage with races 45 or 101 of crown rust (table 1). The varieties Landhafer, Santa Fe, and Trispermia contributed the three sources of resistance present in the parents of the crosses studied in this investigation. The inoculation techniques and classification of reaction were the same as those described by Murphy (4).

(SAC x HAJIRA-JOANETTE) x (LANDHAFER x (MINDO x HAJIRA-JOANETTE))

When tested for reaction to race 101, the Sac x Hajira-Joanette parent was completely susceptible, while the Landhafer x (Mindo x Hajira-Joanette) parent exhibited a uniform highly resistant 0 type reaction. The reactions of 194 F_2 plants from a cross of these two selections fell into three classes (table 1). Forty-six were as resistant as the Landhafer x (Mindo x Hajira-Joanette) parent; 92 were intermediate between 2 and 3 types; while 56 were susceptible like the Sac x Hajira-Joanette parent.

The Landhafer x (Mindo x Hajira-Joanette) parent apparently contributed a single gene, lacking dominance, for resistance to race 101, giving a ratio of 1:2:1 of resistance, intermediate and susceptible segregates. A chi-square test for goodness of fit supported this hypothesis.

LANDHAFER x RESELECT CLINTON

Under the conditions of this experiment Landhafer exhibited a uniform, highly resistant 0 type reaction to race 101, while Reselect Clinton showed a completely susceptible 4 type reaction. Approximately one-fourth of the 196 F_2 plants from a cross of these two varieties were as resistant as the Landhafer parent. With the exception of four moderately resistant plants the remaining F_2 's were moderately or completely susceptible. This suggested a 3:1 ratio characteristic of single gene inheritance, and examination of the data showed that the numbers observed in each class were very close to those expected under the assumption that Land-

Table 1.
Seedling reaction of parents and F₂ progenies
of six oat crosses to crown rust.

Cross	Race	Parental reaction		I	0	No. of F ₂ plants in each phenotypic class				4 ¹
		Female	Male			1	2	2-3	3	
(Sac x Hajira-Joanette), C.I. 5927, x (Landhafer x (Mindó x Hajira-Joanette)), C.I. 5935	101	4	0	-	46	-	-	92	-	56
Landhafer, C. I. 3522, x Reselect Clinton, C.I. 4969	101	0	4	-	47	-	4	-	78	67
Landhafer, C.I. 3522, x Santa Fe-Clinton, C.I. 5400	101	0	0	21	101	12	23	-	-	9
Landhafer, C.I. 3522, x Trispernia, C.I. 4009	101	0	0	52	63	4	32	-	3	15
Early Santa Fe, C.I. 4518-1, x Trispernia, C.I. 4009	101	0-1	0	-	71	21	25	-	-	56
Cherokee, C.I. 3846, x Early Santa Fe, C.I. 4518-1	45	4	0	-	60	5	28	-	65	30

¹ Types of reaction described by Murphy, 1935.

hafer carried a single gene recessive to its allele in Reselect Clinton for resistance to race 101.

The dominance of the gene in Reselect Clinton was not complete, however, as many of the F_2 segregates assumed to be heterozygous (including the four moderately resistant plants) were not as fully susceptible as the Reselect Clinton parent. The dominance of the Reselect Clinton gene was, nevertheless, sufficiently strong to preclude accurate separation of a phenotypic class corresponding to the genotypically heterozygous plants.

These results substantiate the conclusion drawn with regard to the (Sac x Hajira-Joanette) x (Landhafer x (Mindoo x Hajira-Joanette)) cross. The two crosses differed somewhat in that the Landhafer gene in the Landhafer x Reselect Clinton cross was apparently recessive, with the heterozygotes exhibiting 3 or 4 type reactions. In the other cross the expressivity of the "recessive" gene was more pronounced as the heterozygotes showed 2 or 3 type reactions. It appeared that the same gene was involved, but the difference in the F_2 progenies indicated that the degree of dominance exhibited by this gene was dependent upon the genic background upon which it functioned.

LANDHAFER X SANTA FE-CLINTON

Landhafer and Santa Fe-Clinton both showed a 0 type reaction to race 101. The interpretation of the segregation obtained in the F_2 progeny of this cross was based upon the assumption that Landhafer possessed a single gene for resistance while Santa Fe-Clinton carried two linked genes having a recombination value of approximately 23 percent, as had been suggested by Finkner, (in press). Apparently the three genes were additive in effect, each allele contributing an increment of resistance.

The presence of F_2 plants showing an immune type reaction (more resistant than either parent) indicated transgressive segregation for resistance. The reaction of immune plants could be explained by assuming that they carried all six or any five of the alleles for resistance contributed by the parental varieties. Plants showing 0 to 1 type reactions presumably carried from two to four of the parental alleles, while plants with a single allele showed a 2 type reaction. No 3 type reactions were observed, and plants showing 4 type reactions were presumably those carrying no alleles for resistance.

When the numbers of F_2 plants of each of the observed phenotypic classes were tested against the numbers that would be expected under the hypothesis, a satisfactory fit was obtained.

LANDHAFER X TRISPERNIA

Both parents of the Landhafer x Trispernia cross exhibited a 0 type reaction to race 101. The segregation of the F_2 progeny suggested that each parent carried a single, incompletely dominant gene for resistance. The large class of F_2 segregates exhibiting an immune type reaction is especially interesting. These plants had a higher degree of resistance than either parent, which presumably was due to their possessing some combination of genes for resistance from both parents. The data indicated that all four or any three alleles conferred the immune type resistance. Any two alleles, regardless of their source, apparently conditioned a uniform 0 type reaction, with the exception of occasional plants showing a few very small uredia. A single allele of either gene permitted a 2 type reaction to develop, while plants possessing neither of the parental genes showed a 4 type reaction.

When the numbers of F_2 segregates observed in the different F_2 classes were tested against the numbers expected under the foregoing hypothesis, the chi-square value was 7.93. This figure is barely significant at the .05 level of probability.

EARLY SANTA FE X TRISPERNIA

When the parents of the cross Early Santa Fe x Trispernia were tested for reaction to race 101, Trispernia exhibited a uniform 0 type reaction. Early Santa Fe was not quite as resistant, showing a few very small uredia .

A large proportion of the F_2 plants tested were completely susceptible to race 101, indicating that the parental plants did not carry allelic genes. Neither did the mode of inheritance follow the pattern of the Landhafer x Santa Fe-Clinton cross discussed above, as there was no evidence of transgressive segregation for resistance and the proportion of susceptible segregates was much higher. This large number of susceptible segregates was difficult to explain on a simple, factorial basis without resorting to unusual assumptions of gene interaction.

CHEROKEE X EARLY SANTA FE

The Cherokee parent was completely susceptible to race 45, while Early Santa Fe exhibited a uniform 0 type reaction. The frequency of different infection types among the F_2 progeny of the cross of these two varieties indicated that the resistance of Early Santa Fe might be conditioned by the presence of a single gene. Under this assumption it was not possible to assign the moderately

resistant and the susceptible types to specific genotypes due to overlapping of 2 and 3 types. Consequently these phenotypic classes were combined, and when the data were thus tested for goodness of fit to a 3:1 ratio a chi-square value of 4.80 was obtained. This value was significant at the .05 level but not at the .01 level of probability.

The data were also tested against a hypothesis which assumed that the resistance of Early Santa Fe was conditioned by two genes linked with a recombination value of approximately 23 percent. It appeared that at least three alleles for resistance were required to condition a 0 type reaction. The classes comprised of 1 and 2 types could not be separated from the class made up of 3 types. They were combined to form a single intermediate class representing those genotypes possessing either one or two alleles for resistance. The phenotypic class composed of plants exhibiting a 4 type reaction corresponded to the genotype of the susceptible parent. The observed numbers of each of these classes corresponded very closely to the numbers expected.

DISCUSSION

Finkner (in press) has suggested the desirability of combining genes for resistance found at different loci among the various sources of resistance into a single variety. He also mentioned the technical difficulties involved in carrying out such a plan. The problem would be greatly simplified if progenies with combinations of genes for resistance could be distinguished phenotypically from parental types.

Under the conditions of this experiment, parents carrying resistant genes from Landhafer, Santa Fe, and *Trispermia* reacted to the particular races of crown rust used by exhibiting a strong flecking reaction. In crosses of Landhafer x Santa Fe and Landhafer x *Trispermia*, however, certain individuals of the F_2 population were macroscopically immune, thus showing greater resistance than either parent. The relative proportions of these individuals in their respective F_2 populations indicated that the effects of the genes involved were additive, and that true-breeding lines possessing a combined type of resistance higher than that found in either parent might be obtained by direct visual selection under the proper conditions.

SUMMARY

F_2 progenies of six crosses of oats involving three sources of resistance to crown rust (Landhafer, Santa Fe, and *Trispermia*)

were studied. Data from four crosses indicated the resistance of Landhafer to race 101 was conditioned by a single partly dominant gene. Data from two crosses indicated the resistance of Santa Fe to races 45 and 101 could be satisfactorily explained by assuming Santa Fe carried two genes for resistance, which were linked with a recombination value of about 23 percent. In one cross, the resistance of Trispermia to race 101 was attributed to the action of a single gene.

In crosses involving Landhafer and Santa Fe, and Landhafer and Trispermia, certain segregates appeared that were more highly resistant than the parental types. The proportions of these segregates in the F_2 populations indicated the effects of the different genes in conferring resistance were cumulative.

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