GENETICS OF RUST RESISTANCE IN TETRAPLOID WHEATS. IV. GENETICS OF LEAF RUST RESISTANCE IN TWO DURUM WHEATS

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Abstract

The inheritance of resistance in C.I. 7809 *and P.I.* 109593 *to leaf rust of wheat,* Puccinia recondita tritici *was studied. It was found that resistance in C.I.* 7809 *to strain* 135*D was conditioned by a dominant gene* Lrt_1 *and two recessive genes* lrt_2 *and* lrt_3. *The gene* Lrt_1 *was epistatic to both the genes* Lrt_2 *and* Lrt_3. *The resistance to strain* 68*C was conditioned by gene* Lrt_1 *and to strain* 64*A by genes* Lrt_1 *and* lrt_2. *The physiologic resistance seemed to operate throughout the life of wheat plant.*

The resistance in P.I. 109593 *to strains* 135*D and* 64*A was found to be controlled by two recessive genes* lrt_4 *and* lrt_5. *It was further observed that these genes were different and independent of genes* Lrt_1, lrt_2 *and* lrt_3 *in C.I.* 7809.

Leaf rust caused by *Puccinia recondita* Rob. ex. Desm. f. sp *tritici* is a serious disease of wheat. It affects yield as well as quality of wheat grain. Mains (1930) observed that reduction in grain yield varied between 57.2 and 97.4 per cent, depending upon time, length and intensity of infection. The effect of leaf rust on the quality of wheat grain was studied by Phipps (1938) who found that severe infection reduced the nitrogen content from 2.869 to 2.673 per cent and leaf volume from 578 cc to 510 cc.

Efforts have been made to control this disease through the evolution of resistant varieties. The task of breeding such varieties is complex. This complexity is aggravated by the capacity of the rust organism to produce new virulent strains through hybridization and mutation. Samborski (1963) reported mutation in *Puccinia recondita* to virulence. The mutant culture 46-60 became virulent on Transfer, a derivative from the cross, *Triticum aestivum* var. Chinese Spring x *Aegilops umbellulata* Zhuk. New sources of resistance have therefore to be found in the host to combat new genes for virulence in the pathogen.

Tetraploid wheats have been found to possess a high potentiality for new sources of resistance to leaf rust (Watson & Stewart 1956, Watson & Luig 1958). The present paper describes the inheritance of resistance in two durum wheats to leaf rust of wheat.

Materials and Methods

The following durum wheats selected from International Rust Nursery of 1954 were studied:

(1) *C. I.* 7809: It is an Ethiopian durum wheat, with erect habit of growth, and short and solid straw. The spikes are awned and middense. The glumes are red and glabrous; and the kernels are short and purple. It is highly resistant to leaf rust strains 135D, 68C, 64A and 163A.

(2) *P. I.* 109593: It is a Turkish durum wheat. The shoots are semierect and the straws are short and hollow. Its ears are fully awned and dense. The glumes are white and glabrous. The grains are white, long and pointed. It is moderately resistant to leaf rust strains 135D and 64A.

A durum wheat P.I. 173401 was used as a susceptible parent which was fully susceptible to all the three strains, namely, 135D, 68C, 64A of leaf rust, *Puccinia recondita tritici.* The rust tests were performed by usual methods (Peterson *et al.* 1948, Stakman *et al.* 1944) and the Chi-square test was used to verify the genetical ratios.

Results and Discussion

C.I. 7809: The results from seedling tests in the green house on F_1, F_2 and F_3 generations (Tables 1 and 2) suggest that resistance in C.I. 7809 to leaf rust strain 135D is conditioned by three genes. All F_1 plants were highly resistant. The F_2 data could be fitted to the ratio, 3:1 or 49:15; but the F_3 results suggested that more than one gene was operating and the F_2 ratio 49: 15 appeared more likely. The F_3 segregation agreed to the expected ratio of 23 resistant, 34 segregating and 7 susceptible. These data show that, of the three genes, one is dominant and the other two recessive. They are designated Lrt_1, lrt_2 and lrt_3. The gene Lrt_1 is epistatic to both the genes Lrt_2 and Lrt_3. From the F_3 segregating lines it was possible to identify individual genes from the phenotypic rust reaction types. Among the progenies of resistant F_2 plants, there were 6 lines in which the resistant plants showed reaction type 1 and the proportions of resistant and susceptible plants were in the ratio of 3:1. From the progenies of susceptible F_2 plants, 5 lines segregated for a similar reaction (;1) and the proportions of resistant and susceptible plants were of the order of 1:3. There were another

6 lines which segregated for an x type reaction and proportions of resistant and susceptible plants approximated to the ratio of 1:3. These observations show that there is a dominant gene conditioning ;1 reaction, a recessive gene producing a similar reaction (;1) and another recessive gene controlling an x type. This indicates that the dominant gene is Lrt_1, the recessive gene responsible for a similar reaction of ;1 is lrt_2 and the recessive gene controlling an x type reaction is lrt_3.

The studies with strain 68C indicate that C.I. 7809 have one dominant gene for resistance to this strain. The F_2 and F_3 results (Tables 1 and 2) agree to one gene ratio and the resistant plants showed a ;1 reaction. In order to study the relationship between strains 135 D and 68C, 79F_3 lines of the cross, P.I. 173401 $\times$ C. I. 7809, were tested with both these strains. The results show that genes for resistance to strains 135D and 68C, are same or allelic. All the lines resistant to 135D were either resistant or segregating and none was susceptible to 68C. Similarly lines which were susceptible to 135D were also susceptible to 68C, except 2 lines which could be due to error in classification. The analysis of F_3 lines and the reaction types of resistant plants in the segregating lines indicated that gene Lrt_1 is effective against both the strains 135D and 68C.

The results from rust tests with strain 64A on F_3 lines (Table 2) suggest that resistance in C.I. 7809 to this strain is controlled by two genes. Of the 43 segregating lines, 11 segregated for a dominant gene conditioning high resistance (;1), 9 segregrated for recessive gene also conditioning high resistance (;1) and remaining 23 lines appeared to be segregating for both the genes. The results from cross C.I. 7809 x P.I. 173401 were similar. These data show that resistance to strain 64A is conditioned by two genes, one dominant and the other recessive.

The relationship studies between strains 135D and 64A show that lines which were resistant to 135D were either resistant or segregating and none was susceptible to 64A except one line (a case of misclassification). Five lines segregated for a dominant gene for resistance to both the strains. Another 5 lines segregated for a recessive gene for resistance to both the strains. Lines which segregated for a gene conditioning moderate resistance (type x) to 135 D were susceptible to 64A.

These observations suggest that genes Lrt_1 and lrt_2 which condition high resistance to 135D are also effective against 64A. The gene lrt_3 which conditions moderate resistance to 135D is not effective against 64A. On the basis of results presented so far, the probable genotypes of C.I. 7809 for seedling resistance to strains 135D, 68C and 64A are given below:

Strain of rust	*Probable genotype of C.I.* 7809
135D	$Lrt_1\ Lrt_1\ lrt_2\ lrt_2\ lrt_3\ lrt_3$
68C	$Lrt_1\ Lrt_1$
64A	$Lrt_1\ Lrt_1\ lrt_2\ lrt_2$

The results of the field tests on adult plants of F_1, F_2 and F_3 generations of reciprocal crosses of C.I. 7809 with P.I. 173401 (Tables 3 and 4) can be explained on the hypothesis of two dominant genes for resistance in C.I. 7809. The F_2 and F_3 data agreed with expected ratios of 15: 1 and 7:8:1 respectively. Strains of rust in the field were 135D, 68C and 64A.

The studies on the relationship of seedling and adult plant resistance were made on 79 F_3 lines from cross, P.I. 173401 x C.I. 7809. These were tested with strain 135 D in the green house, and then transplanted in the field where an artificial epidemic of rust strains 135D and 64A was produced. The results (Table 5) showed that, of 79 lines, 21 (26.58%) were resistant at both the stages of plant growth. No line which was resistant as seedling was susceptible in the field. On the other hand, of 10 susceptible lines, 4 became fully resistant as adult plants in the field. These data (Table 5) suggest that genes which confer seedling resistance on C.I. 7809 are either allelic or very closely linked to the genes conditioning adult plant resistance. In addition there are one or more minor genes operating only in the adult plant stage. Apparently these are responsible for conferring adult plant resistance to the plants which were susceptible as seedlings.

P.I. 109593: The results given in tables 1 and 2 suggest that the resistance of P.I. 109593 to leaf rust strain 135 D is conditioned by two recessive genes. All the F_1 plants were susceptible and the F_2 plants segregated into a ratio of 1 resistant to 15 susceptible. The F_3 results (Table 2) agree to the expected ratio of 1 resistant, 8 segregating and 7 susceptible. Of 48 segregating lines 11 segregated for a type 2 reaction, 10 segregated for an x reaction and the remaining 27 lines showed reactions ranging from type 1 to x. From the studies on both the strains 135 D and 64A it is indicated that genes which confer resistance to strain 135 D are also effective against strain 64A. They appear to be allelic or linked. Of the 65 F_3 lines tested, 24 lines were susceptible and 28 segregated to both the strains. The F_3 data for both the strains agree significantly to the expected ratio of 1:8:7, showing that resistance is controlled by two recessive genes. The genetic relationship between varieties C.I. 7809 and P.I. 109593 was studied. in crosses among them. The results of F_1 and F_2 seedling tests (Table 6) suggest that genes for resistance in C.I. 7809 are independent of genes for resistance in P.I. 109593. The F_2 segregation fits to a 5 factor ratio of 769 resistant to 255 susceptible. F_3 lines from susceptible F_2 plants were homozygous susceptible. This shows that genes in C.I. 7809 and P.I. 109593 are different. Therefore the recessive gene in P.I. 109593 which conditions a type 2 reaction is designated lrt_4 and the second recessive gene which produces an x type reaction is named lrt_5. On the basis of these results the probable genotype of P.I. 109593 is lrt_4 lrt_4 lrt_5 lrt_5 (Table 7).

The gene expression and reactions to leaf rust strains are shown in table 8. Genetics of leaf rust resistance in 8 differential wheat varieties studied by Soliman *et al.* (1964) revealed that Carina, Bretvit, Loros, Webster and Malakof each carried a dominant gene for resistance to race 15. Soliman (1964) in another study of monosomic analysis assigned this gene to chromosome 1B. The gene in Hussar for resistance to race 15B was placed on chromosome 2B; and the gene for resistance to race 9 in Mediterranean and Democrat belonged to chromosome 6B. Although the strains of leaf rust used in the present studies are different, yet the dominance of resistance in C.I. 7809 was similar to the observations by Soliman *et al.* (1964). Resistance was also found to be dominant by Anderson (1961) who postulated that a dominant gene Lr_L conditioned resistance in Lee, Gabo and Timstein to races 1a and 15a. Gabo and Timstein have received their resistance from tetraploid wheats Gaza and *Triticum timopheevi* respectively (Watson & Stewart 1956, Watson & Luig 1958).

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Table 1. Reactions of F_1 and F_2 seedlings of crosses of C.I. 7809 and P.I. 109593 with P.I. 173401 to strains 135D & 68C of *Puccinia recondita tritici*

Cross, generation & strain of rust	Number of plants				Ratio	P
	R*	Int	S	Total	(R+Int): S	
P.I. 173401 x						
C.I. 7809						
F_1 135D	17	—	—	17		
F_2 135D	300	22	92	414	3:1 or 49:15	0.10—.20
68C	226	—	85	311	3:1	0.30—.50
C.I. 7809 x						
P.I. 173401						
F_1 135D	11	—	—	11		
F_2 135D	231	—	72	303	49:15	0.80—.90
P.I. 109593 x						
P.I. 173401						
F_1 135D	—	—	21	21		
F_2 135D	13	17	483	513	1:15	0.70—.80

*R=Resistant (; to 2), Int=Intermediate (X), S=Susceptible (3 and 4).

Table 2. Reactions of F_3 seedlings of crosses of C.I. 7809 and P.I. 109593 with P.I. 173401, to strains 135D, 68C and 64A of *Puccinia recondita tritici*

Cross and strain of rust	Number of lines				Ratio R : Seg : S	P
	R	Seg	S	Total		
P.I. 173401 x C.I. 7809						
135D	42	64	11	117	23:34:7	0.80—.90
68C	28	60	22	110	1:2:1	0.50—.70
64A	43	43	6	92	7:8:1	0.80—.90
C. I. 7809 x P.I. 173401						
135D	39	46	10	95	23:34:7	0.50—.70
68C	18	37	14	69	1:2:1	0.50—.70
64A	36	38	6	80	7:8:1	0.80—.90
P.I. 109593 x P.I. 173401						
135D	6	48	51	105	1:8:7	0.50—.70

*R = Resistant, Seg = Segregating, S = Susceptible.

Table 3. Reactions of F_1 and F_2 adult plants of crosses of C.I. 7809 with P.I. 173401 to strains 135D and 64A

Cross and generation	Number of plants				Ratio (R+Int) : S	P
	R*	Int	S	Total		
P.I. 173401 x C. I. 7809						
F_1	11	—	—	11		
F_2	536	36	42	614	15:1	0.80—.90
C. I. 7809 x P.I. 173401						
F_1	7	—	—	7		
F_2	362	27	25	414	15:1	0.80—.90

*Resistant (R) = 0—25 %, Intermediate (Int) = 25-40 %,

Susceptible (S) = 65 to 100 % (Peterson *et al.* 1948).

Table 4. Reactions of adult plants of 117 F_3 lines of cross P.I. 173401 x C.I. 7809 to a mixture of strains 135D and 64A

Cross	Number of lines				Ratio	P
	R	Seg	S	Total	R: Seg.:S	
P.I. 173401 x C.I 7809	58	55	4	117	7:8:1	0.20—.30

Table 5. Reactions of seedlings and adult plants of 79 F_3 lines of cross P.I. 173401 x C. I. 7809 to strains, 135D & 64A

Seedling reaction to 135D	Adult plant reactions				Ratio for seedling resistance	P for seedling resistance
	R	Seg	S	Total		
Resistant (R)	21	5	—	26		
Segregating (Seg.)	19	24	—	43		
Susceptible (S)	4	4	2	10		
Total	44	33	2	79	23:34:7	0.80
Ratio for adult plant resistance		7:8:1				
"P" for adult plant resistance		0.10 -.05				

Table 6. Reactions of F_1 and F_2 seedlings of crosses between P.I. 109593 and C. I. 7809 to strain 135D

Cross and generation	No. of seedlings				Ratio (Int+R): S	P
	R	Int	S	Total		
P.I. 109593 x C.I. 7809						
F_1	22	—	—	22		
F_2	274	11	92	377	769:255	0.80—.90
C. I. 7809 x P.I. 109593						
F_1	16	—	—	16		
F_2	180	8	53	241	769:255	0.80—.90

Table 7. Pr

Variety

C.I. 7809

P.I. 109593

Table 8. G

triti

Gene symbol Gen exp

Lrt_1 Dor

lrt_2 Rec

lrt_3 Rec

lrt_4 Rec

lrt_5 Rec

*Suscep

**Susce

Table 7. Probable genotypes of two varieties of *Tritcum durum* for resistance to *Puccinia recondita tritici*

Variety	Genotype
C.I. 7809	Lrt_1 Lrt_1 lrt_2 lrt_2 lrt_3 lrt_3
P.I. 109593	lrt_4 lrt_4 lrt_5 lrt_5

Table 8. Gene expression and reactions of homozygotes to *Puccinia recondita tritici*

Gene symbol	Gene expression	Possessed by varieties	Reactions of homozygotes as seedlings to strains			Adult plant reactions to 135D, 64A & 68C in the field
			135D	64A	68C	
Lrt_1	Dominant	C.I. 7809	;1	;1	;1	Highly resistant
lrt_2	Recessive	C.I. 7809	;1	;1	3+	Resistant**
lrt_3	Recessive	C.I. 7809	X–	3+	3+	Moderately resistant*
lrt_4	Recessive	P.I. 109593	2	2	3+	Moderately resistant**
lrt_5	Recessive	P.I. 109593	X–	X	3+	Moderately resistant**

*Susceptible when strain 68 C or 64A is prevalent in the field.

**Susceptible when strain 68C is prevalent.