Confirmation of a Digenic Model of Inheritance of Resistance to Albugo candida Race 7 in Brassica napus

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INTRODUCTION

White rust, caused by Albugo candida (Pers. ex Lev.) Ktze., is a major hazard to the production of turnip rape (Brassica campestris L.) and of brown mustard (B. juncea L.) in western Canada and other regions of the world. Average yield losses of turnip rape in Alberta and Saskatchewan due to white rust were reported to be between 1.2 and 9.0% (Berkenkamp, 1971; Petrie, 1973). In Manitoba, yield reduction ranging from 30 to 60% occurred in heavily infected fields (Bernier, 1972).

In western Canada, commercial varieties of summer rape (B. napus) are highly resistant to A. candida. Moreover, resistance in B. napus has remained effective over 40 years of continuous cultivation. In central and eastern China, however, some cultivars are quite susceptible. In a field survey of the Shanghai region in 1973, more than 70% of the plants had systemically infected inflorescences (stagheads) causing yield losses between 20 and 30%.

A model of inheritance of resistance to white rust in B. napus has been proposed by Fan et al. (1983). In this model resistance is conditioned by three independent dominant genes designated Ac7-1 (R_1), Ac7-2 (R_2), and Ac7-3. The first two genes are homozygous in cultivar Regent. As a single dominant allele at any one of the three loci is sufficient to confer resistance, the heterozygosity or heterogeneity of the third locus tends to be masked.

In the present study, F_1BC_1 plants from 2282-9 (susceptible) x Regent (resistant) x 2282-9 were developed and tested to confirm the digenic model with dominant resistance conferred by Ac7-1 and Ac7-2.

MATERIALS AND METHODS

The experiment was conducted in the growth cabinet and greenhouse during 1985-1986. Seedlings from the backcross (2282-9 x Regent) x 2282-9 were tested for resistance to A. candida race 7 by inoculating cotyledons with zoospores. Resistant F_1BC_1 plants were selected and grown to flower. While one inflorescence of each selected plant was self-pollinated, another was backcrossed to the susceptible line 2282-9.

The genotype of each resistant F_1BC_1 plant was determined by inoculating the cotyledons of F_2BC_1 and F_1BC_2 plants with race 7. Resistant plants were selected from the F_2BC_1 progenies which had

segregated in the ratio of 3 resistant to 1 susceptible. They were self-pollinated and backcrossed to 2282-9. Plants of genotype $R_1R_1r_2r_2$ and $r_1r_1R_2R_2$ could be obtained when F_3BC_1 and F_2BC_2 populations were tested for white rust resistance. Non-segregating resistant progenies were considered to be derived from the F_2BC_1 parent of homozygous dominance, and segregating progenies were assumed to be derived from the F_2BC_1 parent of heterozygous dominance.

To determine the genotype of each F_3BC_1 accession, one established accession was assumed to be $R_1R_1r_2r_2$ and used as a tester to cross with the others. Each accession was divided into two subunits. As they were derived from same F_3BC_1 plant, paired subunits were similar genetically and expected to give identical results when crossed with the tester. Also, when paired subunits were sib-mated and then self-pollinated, subsequent progenies should not segregate unless mutation had occurred. The objective of employing two subunits for each F_3BC_1 accession was to check the validity of experimental results.

F_1 progenies from the crosses (Accession 1, 2, ...8 x tester) were self-pollinated and backcrossed to 2282-9 once more. The genotype of each accession was then determined according to the segregation ratios of the F_2 progenies and verified by the corresponding backcross data. The digenic model could be confirmed if some of the progenies segregated into 15:1 (F_2) ratio and 3:1 (BC_1) ratio. The Chi-square test was used for analysis of the data from the segregating progenies.

RESULTS AND DISCUSSION

Progeny from the backcross (2282-9 x Regent) x 2282-9 segregated with the ratio of 3 resistant to 1 susceptible. The genotypes of the F_1BC_1 plants were considered as $R_1r_1R_2r_2$, $R_1r_1r_2r_2$, $r_1r_1R_2r_2$ and $r_1r_1r_2r_2$. When the resistant F_1BC_1 plants were self-pollinated and backcrossed to the susceptible line 2282-9, some resulting progenies segregated into 15:1 and 3:1 ratios respectively, while others segregated into 3:1 and 1:1 ratios. This can be explained by assuming that the former were derived from the F_1BC_1 parent of genotype $R_1r_1R_2r_2$, whereas the latter were derived from the F_1BC_1 parent of genotype $R_1r_1r_2r_2$ or $r_1r_1R_2r_2$. Resistant plants were selected from F_2BC_1 progenies (Accession numbers 1 to 9) which segregated for white rust resistance in the ratio of 3 resistant to 1 susceptible and advanced to the F_3BC_1. The observed segregations and Chi-square tests for these nine accessions (F_2BC_1) are shown in Table 1. The data from the corresponding backcross progenies (F_2BC_1) are given in Table 2. Approximately, one third of the resistant plants in each selected F_2BC_1 progeny were homozygous dominant at either of the two loci ($R_1R_1r_2r_2$ or $r_1r_1R_2R_2$) involved in white rust resistance. Accessions of these two genotypes were obtained by inoculating F_3BC_1 and F_2BC_2 plants.

One F_3BC_1 was assumed to be $R_1R_1r_2r_2$ and used as parent for test crosses with the other accessions. The resulting F_1 progenies from the crosses (Accession 1, 2, 3, ... 8 x Tester) were all resistant to white rust. So were the progenies from the sib-mating between paired subunits (F_3BC_1).

The F_2 progenies from the crosses of the tester with Accession 1, 2, 3 and 4 segregated for white rust resistance in the ratio of 15 resistant to 1 susceptible. The results are a good fit ($P>0.05$) to the ratio expected for a segregation of two independent dominant genes

(Table 3). These data indicate that resistance in the four accessions was conferred by a pair of homozygous dominant alleles at the second locus ($r_1r_1R_2R_2$). We have, therefore, conclusive evidence that R_1 and R_2 are two non-allelic resistance genes at two discrete loci.

Progenies from the backcross (Accession 1, 2, 3 and 4 x Tester) x 2282-9 segregated with the ratio of 3 resistant to 1 susceptible ($P>0.05$) (Table 4), thus confirming the non-allelism of gene R_1 and R_2.

The F_2 progenies from the crosses of the tester with Accession 5, 6, 7 and 8 were all resistant (Table 9), indicating that resistance in these four accessions was conditioned by a pair of homozygous dominant alleles at the first locus ($R_1R_1r_2r_2$). In other words, these accessions had the same genotype as the tester. This was confirmed by the data from the backcross (Accession 5, 6, 7 and 8 x Tester) x 2282-9 (Table 5).

From these data, the digenic model with dominant resistance conferred by R_1 and R_2 has been confirmed. Presence of a dominant allele at either of the two loci will confer resistance to a plant, whereas homozygous recessives at both loci will result in a susceptible phenotypical expression.

In Canada, resistance in B. napus cultivars to A. candida appears to be so durable that it has remained effective over 40 years of exposure to the isolates of A. candida which can attack B. campestris and B. juncea. This can be ascribed to the number of resistance genes carried by B. napus cultivars and/or the low capacity of the pathogen to adapt to the resistance genes in B. napus. Even so, rapeseed breeders should be cautious not to introduce susceptibility from Oriental cultivars or through interspecific crosses between B. napus and B. campestris.

REFERENCES

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Table 1. Observed segregations and Chi-square tests for F_2BC_1 data from 2282-9 x Regent involving resistance (R) and susceptibility (S) to A. candida race 7.[@]

Accession	Reaction R	Reaction S	Ratio	χ^2	P
1	20	6	3:1	0.051	.75-.90
2	44	11	3:1	0.733	.25-.50
3	52	9	3:1	3.415	.05-.10
4	65	15	3:1	1.667	.10-.25
5	30	9	3:1	0.077	.75-.90
6	41	12	3:1	0.157	.50-.75
7	16	4	3:1	0.267	.50-.75
8	25	5	3:1	1.111	.25-.50
9	69	20	3:1	0.303	.50-.75
Total	362	91	3:1	7.781	
Deviation χ^2				5.829	.01-.03
Heterogeneity χ^2				1.952	.97-.99

[@]Each F_2BC_1 population was derived from a single identified F_1BC_1 plant.

Table 2. Observed segregations and Chi-square tests for F_1BC_2 data from [(2282-9 x Regent) x 2282-9] x 2282-9 involving resistance (R) and susceptibility (S) to A. candida race 7.

Accession[@]	Reaction R	Reaction S	Ratio	χ^2	P
1	19	19	1:1	0.000	>.99
2	15	16	1:1	0.032	.75-.90
3	19	15	1:1	0.735	.25-.50
4	22	22	1:1	0.000	>.99
5	19	18	1:1	0.027	.75-.90
6	26	20	1:1	0.783	.25-.50
7	17	25	1:1	1.524	.10-.25
8	16	11	1:1	0.926	.25-.50
9	17	17	1:1	0.000	>.99
Total	170	163	1:1	4.315	
Deviation χ^2				0.147	.50-.70
Heterogeneity χ^2				4.168	.75-.90

[@]The accession numbers correspond to those in F_2BC_1, indicating that both populations were derived from the same maternal parent.

Table 3. Observed segregations and Chi-square tests for F_2 data from crosses F_3BC_1 x Tester involving resistance (R) and susceptibility (S) to A. candida race 7.

Accession[@]	Reaction R	Reaction S	Ratio	χ^2	P
1 (A)	94	5	15:1	0.244	.50-.75
1 (B)	140	10	15:1	0.044	.75-.90
2 (A)	276	19	15:1	0.018	.75-.90
2 (B)	272	16	15:1	0.237	.50-.75
3 (A)	208	10	15:1	1.031	.25-.50
3 (B)	210	11	15:1	0.610	.25-.50
4 (A)	83	5	15:1	0.048	.75-.90
4 (B)	142	8	15:1	0.217	.50-.75
Total	1425	84	15:1	2.449	
Derivation	χ^2_2			1.202	.25-.50
Heterogeneity	χ^2			1.247	.95-.99

[@]The accession numbers correspond to those in F_2, indicating that both populations were derived from the same maternal parent.

Table 4. Observed segregations and Chi-square tests for backcross data from (F_3BC_1 x Tester) x 2282-9 involving resistance (R) and susceptibility (S) to A. candida race 7.

Accession[@]	Reaction R	Reaction S	Ratio	χ^2	P
1 (A)	26	4	3:1	2.178	.10-.25
1 (B)	25	7	3:1	0.044	.75-.90
2 (A)	40	10	3:1	0.667	.25-.50
2 (B)	31	8	3:1	0.419	.50-.75
3 (A)	43	11	3:1	0.617	.25-.50
3 (B)	28	6	3:1	0.980	.25-.50
4 (A)	47	14	3:1	0.137	.50-.75
4 (B)	64	19	3:1	0.197	.50-.75
Total	304	79	3:1	5.239	
Deviation	χ^2_2			3.907	.03-.05
Heterogeneity	χ^2			1.332	.95-.99

[@]The accession numbers correspond to those in F_2, indicating that both populations were derived from the same maternal parent.

Table 5. Reaction of F_2 and F_1BC_1 from the crosses F_3BC_1 x Tester to *A. candida* race 7

	Reaction			
	F_2		F_1BC_1	
Accession	R	S	R	S
5 (A)	140	0	30	0
5 (B)	138	0	55	0
6 (A)	145	0	34	0
6 (B)	128	0	35	0
7 (A)	191	0	45	0
7 (B)	152	0	39	0
8 (A)	149	0	35	0
8 (B)	141	0	35	0