Development of Monogenic Lines for Resistance to *Albugo candida* from a Canadian *Brassica napus* Cultivar

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ABSTRACT

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Resistance to *Albugo candida* race 7 in the Canadian *Brassica napus* cultivar Regent is conditioned by three dominant genes, designated $Ac7_1$, $Ac7_2$, and $Ac7_3$. Gene $Ac7_3$ is present in a heterozygous condition. Homozygous resistant BC_1F_3 lines carrying $Ac7_1$ or $Ac7_2$ were developed from a BC_1F_1 family in which segregation for white rust resistance fitted a 3 resistant (R):1 susceptible (S) ratio. To isolate the resistance genes, one BC_1F_3 line was assumed to have genotype $Ac7_1Ac7_1ac7_2ac7_2$ and was used as a tester to cross with other selected BC_1F_3 lines. Progenies from test crosses were self-pollinated and backcrossed to susceptible line 2282-9. Thus, two monogenic lines possessing $Ac7_1$ or $Ac7_2$ were developed as F_2 and backcross populations produced from four test crosses segregated to fit 15 R:1 S and 3 R:1 S ratios, respectively, whereas the other four lines were homozygous resistant. The two single-gene lines were used as testers to develop a monogenic line with $Ac7_3$ from a BC_1F_1 family that segregated in a 7 R:1 S ratio. These single genes are being incorporated into rapid-cycling *B. napus* lines susceptible to several pathotypes of *A. candida* to develop isogenic differential lines. The monogenic lines will be used to study the mechanism(s) of resistance response conditioned by the individual genes. These lines also should facilitate molecular mapping of the loci in *B. napus* for resistance to *A. candida* race 7.

Additional keywords: inheritance of resistance, oilseed rape.

White rust, caused by *Albugo candida* (Pers.) Kunze, is one of the most important diseases of *Brassica* species in Canada and other parts of the world. In western Canada, average yield losses due to white rust on turnip rape, *Brassica rapa* L. (synamorph *Brassica campestris* L.), were between 1.2 and 9.0% in some years (1,7,11). In heavily infected fields, yield losses ranging from 30 to 60% have been reported (2). White rust has been controlled by incorporation of resistance into widely grown cultivars such as Tobin. However, new pathotypes of *A. candida* virulent to the resistance utilized in Tobin can now be found in western Canada. Some recently released cultivars (e.g., Colt, Eldorado, Horizon, and Klondike) are highly susceptible to the pathotypes of *A. candida* commonly found on *B. rapa*. Commercial cultivars of *B. napus* are resistant to all pathotypes of *A. candida* present in North America (12,13,18) but are susceptible to some Ethiopian isolates originally collected from *B. carinata* (9) as well as European isolates from *B. oleracea* (S. R. Rimmer, *unpublished data*).

To date, at least 10 physiologic "races" of *A. candida* have been identified and classified based on specificity to different crucifer species (8,15). However, races of *A. candida* do not exhibit an absolute adaptation to a particular host species, because most races also can infect some genotypes of related *Brassica* species (heterologous hosts), especially those sharing genomes with the *Brassica* species from which they were originally collected (homologous hosts). Several studies have suggested that *Brassica-Albugo* specificity occurs at the levels of genus, species within a genus (4,8, 13–15,18), and cultivars within a species (S. R. Rimmer, *unpublished data*). The predominant races of *A. candida* in western Canada are race 2 on *B. juncea* and race 7 on *B. rapa* (9,13,14).

The genetic control of resistance to *A. candida* has been studied in *B. napus*. Monogenic dominant resistance to a *B. carinata* pathotype of *A. candida* from Ethiopia was reported by Liu and Rimmer (9), using F_2 progenies of crosses between resistant Chinese *B. napus* line 2282-9 and a susceptible doubled haploid line derived from the Canadian cultivar Stellar (16). A single dominant gene for resistance to a *B. carinata* pathotype in *B. napus* also was found by Ferreira et al. (6). Verma and Bhowmik (19) demonstrated that resistance in *B. napus* to a *B. juncea* pathotype of *A. candida* from India was governed by duplicate dominant genes. The inheritance of resistance in *B. napus* to a *B. rapa* pathotype of *A. candida* (race 7) was studied by Fan et al. (5) in resistant Canadian cultivar Regent in crosses to two susceptible Chinese lines, 2282-9 and Green Cup Leaf (GCL). Resistance in Regent was conditioned by three dominant genes, designated *Ac7-1*, *Ac7-2*, and *Ac7-3*, with gene *Ac7-3* present in a heterozygous condition.

The objective of the current study was to develop monogenic lines with the three resistance genes from cultivar Regent, so their mode of action could be studied independently of each other. These genes are designated $Ac7_1$, $Ac7_2$, and $Ac7_3$ in the following text. This work forms part of a research program designed to develop near isogenic lines with differential resistance to races of *A. candida* and to study the host-pathogen relationship between *Brassica* species and *A. candida*.

MATERIALS AND METHODS

Genetic analysis. Several BC_1F_1 families from the cross of cultivar Regent (University of Manitoba [UM] accession 2025) with susceptible Chinese line 2282-9 (UM 2243) or GLC (UM

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2229), obtained from a previous study (5), were tested again with race 7 in the cotyledon stage to ascertain the number of resistance genes involved. In the first experiment, one BC_1F_1 family whose segregation for white rust resistance gave a good fit to a two-gene ratio (3 resistant [R]:1 susceptible [S], $\chi^2 = 0.0032$, $P = 0.95$ to 0.99) was selected and used as a source for the development of two lines, each carrying a single dominant gene for resistance to race 7. After disease evaluation, 30 resistant BC_1F_1 plants were selected and grown in the greenhouse. At the onset of anthesis, the main raceme of each selected plant was self-pollinated, and one or two secondary racemes were backcrossed to susceptible line 2282-9. BC_1F_2 and BC_2F_1 families produced from single BC_1F_1 plants were tested with race 7. Nine BC_1F_2 families that segregated to fit a single-gene ratio were selected. Within each family, at least 15 plants were self-pollinated to produce BC_1F_3 lines. To assist the selection of homozygous resistant BC_1F_3 lines, the selected BC_1F_2 plants also were backcrossed with 2282-9.

Two homozygous resistant BC_1F_3 lines from each of the selected BC_1F_2 families were maintained and grown to flower. To separate the two resistance genes, one homozygous resistant BC_1F_3 line was assumed to have genotype $Ac7_1Ac7_1ac7_2ac7_2$ and was used as a tester to cross with the other selected BC_1F_3 lines. Progenies from test crosses were self-pollinated and backcrossed to 2282-9. Genotypes of the selected homozygous resistant BC_1F_3 lines were determined by evaluating test cross-derived lines for white rust resistance. Seeds were increased for two BC_1F_3 selections carrying homozygous resistance genes $Ac7_1$ and $Ac7_2$, respectively. In the following experiment, they were used as testers to isolate the third resistance gene ($Ac7_3$) from cultivar Regent.

In the second experiment, 60 resistant plants were selected from one BC_1F_1 family with observed segregation giving a good fit to a three-gene ratio (7 R:1 S; $\chi^2 = 0.441$, $P = 0.50$ to 0.75). The selected plants were grown to flower in the greenhouse. At anthesis, the selected BC_1F_1 plants were self-pollinated and backcrossed to susceptible line GCL. Homozygous resistant lines were developed by selfing resistant plants selected from BC_1F_2 families in which segregation for white rust resistance fit a 3 R:1 S ratio. To isolate gene $Ac7_3$, homozygous resistant BC_1F_3 lines were crossed with the two tester lines developed in the first experiment, followed by selfing and backcrossing to GCL. Monogenic BC_1F_3 lines possessing gene $Ac7_3$ were differentiated from those possessing gene $Ac7_1$ or $Ac7_2$ based on segregation for white rust resistance in test cross-derived lines.

Plant growth and disease evaluation. Seeds of test materials were sown in Jiffy pots containing Metro mix (W.R. Grace & Co., Canada Ltd., Ajax, ON) and kept in a growth room at day/night temperatures of 22/16°C, with a 16 photoperiod. Seven days after sowing, plants were tested for white rust resistance by inoculating cotyledons with a zoospore suspension (10^4 zoospores per ml). Mature zoosporangia of race 7 used in this study were originally collected from naturally occurring infections on susceptible cultivar Torch (*B. rapa*) grown in Manitoba. They were stored in gelatin capsules (T. V. B. Enterprises, North Augusta, Ontario, Canada, size 00) in glass screw-cap vials at about –10°C. Inoculum preparation, inoculation method, and incubation conditions were as described by Williams (20). Briefly, zoosporangia were germinated in a small volume of distilled water at 12°C, zoospore concentration was adjusted, inoculum (10 µl) was applied to the cotyledons of seedlings, and inoculated seedlings were incubated in a misting chamber in the dark for 24 to 36 h. After incubation, seedlings were returned to the growth room.

Seven days after inoculation, interaction phenotypes (IP) were observed and scored using a rating scale of 0 to 9 (20). Cotyledons that showed no symptoms or small necrotic flecks on the adaxial surface without sporulation were scored as 0 or 1 and were considered resistant, whereas those showing scattered or coalescing

TABLE 1. Segregation for reaction to *Albugo candida* race 7 in selected BC_1F_2 and BC_2F_1 lines derived from a cross of susceptible *Brassica napus* line 2282-9 with resistant cultivar Regent

Line[a]	Reaction[b] R	Reaction[b] S	$\chi^2_{3:1}$	P
BC_1F_2				
3	20	6	0.051	0.75–0.90
8	69	20	0.303	0.50–0.75
13	44	11	0.733	0.25–0.50
14	52	9	3.415	0.05–0.10
16	65	15	1.667	0.10–0.25
20	30	9	0.077	0.75–0.90
23	41	12	0.157	0.50–0.75
27	16	4	0.267	0.50–0.75
29	25	5	1.111	0.25–0.50
Total	362	91	7.781	
Deviation χ^2			5.829	0.01–0.03
Heterogeneity χ^2			1.952	0.95–0.99
BC_2F_1			$\chi^2_{1:1}$	
3	19	19	0.000	0.99–1.00
8	17	17	0.000	0.99–1.00
13	15	16	0.032	0.75–0.90
14	19	15	0.735	0.25–0.50
16	22	22	0.000	0.99–1.00
20	19	18	0.027	0.75–0.90
23	26	20	0.783	0.25–0.50
27	17	25	1.524	0.10–0.25
29	16	11	0.926	0.25–0.50
Total	170	163	4.315	
Deviation χ^2			0.147	0.50–0.70
Heterogeneity χ^2			4.168	0.75–0.90

[a] BC_1F_2 and BC_2F_1 lines were derived from single BC_1F_1 plants. The line numbers for BC_1F_2 and BC_2F_1 populations correspond to each other, indicating that both populations were derived from the same BC_1F_1 parent.
[b] R = resistant; S = susceptible.

TABLE 2. Segregation for reaction to *Albugo candida* race 7 in some F_2 and backcross populations from crosses of tester line A (line 8-2) with homozygous resistant BC_1F_3 lines derived from a cross of susceptible *Brassica napus* line 2282-9 with resistant cultivar Regent

BC_1F_3 line[a]	Reaction[b] R	Reaction[b] S	$\chi^2_{15:1}$	P
F_2 (BC_1F_3 × tester line A)				
3-1 A	94	5	0.244	0.50–0.75
3-1 B	140	10	0.044	0.75–0.90
13-3 A	276	19	0.018	0.75–0.90
13-3 B	272	16	0.237	0.50–0.75
14-4 A	208	10	1.031	0.25–0.50
14-4 B	210	11	0.610	0.25–0.50
16-5 A	83	5	0.048	0.75–0.90
16-5 B	142	8	0.217	0.50–0.75
Total	1,425	84	2.449	
Deviation χ^2			1.202	0.25–0.50
Heterogeneity χ^2			1.247	0.95–0.99
(BC_1F_3 × tester line A) × 2282-9			$\chi^2_{3:1}$	
3-1 A	26	4	2.718	0.10–0.25
3-1 B	25	7	0.044	0.75–0.90
13-3 A	40	10	0.667	0.25–0.50
13-3 B	31	8	0.419	0.50–0.75
14-4 A	43	11	0.617	0.25–0.50
14-4 B	28	6	0.980	0.25–0.50
16-5 A	47	14	0.137	0.70–0.75
16-5 B	64	19	0.197	0.50–0.75
Total	304	79	5.239	
Deviation χ^2			3.907	0.03–0.05
Heterogeneity χ^2			1.332	0.95–0.99

[a] Lines A and B following the same serial number were derived from the same BC_1F_2 line.
[b] R = resistant; S = susceptible.

pustules on the abaxial or adaxial surface were scored as 7 or 9 and were considered susceptible. Intermediate IPs (3 and 5) rarely were observed.

After disease evaluation, selected resistant plants were vernalized at about 4°C for 3 weeks and transplanted to 15-cm peat pots containing a 1:2:1 (vol/vol/vol) mixture of peat, soil, and sand. The plants were grown to flower in the greenhouse at about 22°C. Susceptible line 2282-9 was planted 4 weeks earlier than selected lines to synchronize flowering times.

Statistical analysis. Chi-square tests for goodness-of-fit and heterogeneity (17) were applied to analyze data from segregating populations. The level of significance used to test the fit of the data was $P = 0.05$.

RESULTS

Isolation of genes $Ac7_1$ and $Ac7_2$. The resistant plants selected from the BC_1F_1 family of (2282-9 × Regent) × 2282-9, which had segregated to fit a 3 R:1 S ratio, were considered to have genotypes $Ac7_1ac7_1Ac7_2ac7_2$, $Ac7_1ac7_1ac7_2ac7_2$, and $ac7_1ac7_1Ac7_2ac7_2$. When the resistant BC_1F_1 plants were self-pollinated and backcrossed to susceptible line 2282-9, some resulting progenies segregated to fit 15 R:1 S and 3 R:1 S ratios respectively, and others segregated to fit 3 R:1 S and 1 R:1 S ratios, respectively. This can be explained by assuming that the former were derived from the BC_1F_1 plants of genotype $Ac7_1ac7_1Ac7_2ac7_2$, and the latter were derived from the BC_1F_1 plants of genotype $Ac7_1ac7_1ac7_2ac7_2$ or $ac7_1ac7_1Ac7_2ac7_2$. Resistant plants were selected from nine BC_1F_2 families in which segregation fit a 3 R:1 S ratio (Table 1) and advanced to the BC_1F_3 generation. Data from the corresponding backcross progenies (F_1BC_2) were used to assist selection. Approximately one-third of the BC_1F_3 lines originating from single BC_1F_2 plants were homozygous resistant to race 7 (data not shown). These lines were considered to have genotype $Ac7_1Ac7_1ac7_2ac7_2$ or $ac7_1ac7_1Ac7_2Ac7_2$.

To determine the genotypes of the selected BC_1F_3 lines, one BC_1F_3 line (8-2) was assumed to have genotype $Ac7_1Ac7_1ac7_2ac7_2$ and was used as a tester to cross with the other selected BC_1F_3 lines. Progenies from test crosses were all resistant to race 7. F_2 populations from crosses of line 8-2 (tester line A) with homozygous resistant BC_1F_3 lines 3-1, 13-3, 14-4, and 16-5 segregated to fit a 15 R:1 S ratio. The results were a good fit ($P > 0.05$) to the ratio expected for segregation of two independent dominant genes (Table 2). The data indicated that resistance in these four BC_1F_3 lines was conferred by a pair of dominant alleles at the second locus ($ac7_1ac7_1Ac7_2Ac7_2$). Progenies from the corresponding backcrosses segregated to fit the 3 R:1 S ratio expected of a single dominant gene (Table 2). This confirmed that genes $Ac7_1$ and $Ac7_2$ are not allelic. F_2 populations from crosses of tester line A with homozygous resistant BC_1F_3 lines 20-6, 23-7, 27-8, and 29-9 were all resistant (Table 3), indicating that resistance in these four lines is conditioned by a pair of dominant alleles at the first locus ($Ac7_1Ac7_1ac7_2ac7_2$). Thus, these lines have the same genotype as tester line A. This result was confirmed by the data from the backcross populations (Table 3).

Isolation of gene $Ac7_3$. BC_1F_2 families derived from single resistant BC_1F_1 plants of (GCL × Regent) × GCL segregated to fit a 63 R:1 S, 15 R:1 S, or 3 R:1 S ratio (data not shown). Resistant plants were selected from 14 BC_1F_2 families in which segregation fit a 3 R:1 S ratio (Table 4). These plants were assumed to carry a single resistance gene or allele at the $Ac7_1$, $Ac7_2$, or $Ac7_3$ locus. Forty-nine BC_1F_3 families homozygous resistant to race 7 were crossed with tester line A and line 23-7 (tester line B). The resulting progenies were all resistant to race 7. The segregation for white rust resistance in F_2 populations from crosses of the selected BC_1F_3 lines with tester lines A and B is shown in Table 5.

F_2 populations from crosses of homozygous resistant lines 9-1, 23-3, 25-1, 32-9, and 34-1 with tester line A were all resistant, whereas those from crosses with tester line B segregated to fit a two-gene ratio. Therefore, these five BC_1F_3 lines must have genotype $Ac7_1Ac7_1ac7_2ac7_2ac7_3ac7_3$. F_2 populations from crosses of lines 6-7, 8-3, 40-1, 43-5, and 46-6 with tester line A segregated to fit a two-gene ratio, whereas those from crosses with tester line B were all resistant. This indicated that these five BC_1F_3 lines have genotype $ac7_1ac7_1Ac7_2Ac7_2ac7_3ac7_3$. Segregation of F_2 families from crosses of lines 11-1, 18-3, 24-10, and 42-4 with tester lines A and B gave a good fit to a two-gene ratio, indicating that these four BC_1F_3 lines carry a resistance gene that is nonallelic to either $Ac7_1$ or $Ac7_2$ and, thus, were assigned genotype $ac7_1ac7_1ac7_2ac7_2Ac7_3Ac7_3$.

The genotypes of the selected BC_1F_3 lines were confirmed by testing backcross populations from (BC_1F_3 × tester line A or B) × GCL (Table 6). All backcross populations segregated to fit a 3 R:1 S ratio ($P > 0.05$), except for three families derived from crosses of the tester lines with BC_1F_3 lines 6-7, 18-3, and 40-1. The deviation from a 3 R:1 S segregation ratio for these backcross families could be due to disease escape or seed contamination, because the segregation of the corresponding F_2 populations gave a good fit to a 15 R:1 S ratio (Table 5).

To confirm the presence of gene $Ac7_3$, two more F_2 families derived from the cross of BC_1F_3 line 42-4 with tester lines A and B and their corresponding backcross families were tested for white rust resistance. F_2 and backcross populations from both test crosses fit 15 R:1 S and 3 R:1 S ratios, respectively (Table 7).

TABLE 3. Reaction to *Albugo candida* race 7 in some F_2 and backcross populations from crosses of tester line A (line 8-2) with homozygous resistant BC_1F_3 lines derived from a cross of susceptible *Brassica napus* line 2282-9 with resistant cultivar Regent

	Reaction[b]			
	F_2 (BC_1F_3 × tester line A)		(BC_1F_3 × tester line A) × 2282-9	
BC_1F_3 line[a]	R	S	R	S
20-6 A	140	0	30	0
20-6 B	138	0	55	0
23-7 A	145	0	34	0
23-7 B	128	0	35	0
27-8 A	191	0	45	0
27-8 B	152	0	39	0
29-9 A	149	0	35	0
29-9 B	141	0	35	0

[a] Lines A and B following the same serial number were derived from the same BC_1F_2 line.
[b] R = resistant; S = susceptible.

TABLE 4. Segregation for reaction to *Albugo candida* race 7 in selected BC_1F_2 lines derived from a cross of susceptible *Brassica napus* line Green Cup Leaf with resistant cultivar Regent

	Reaction[b]			
BC_1F_2 line[a]	R	S	$\chi^2_{3:1}$	P
6	125	41	0.000	0.99–1.00
8	113	46	1.109	0.25–0.50
9	108	34	0.038	0.50–0.75
11	137	40	0.424	0.50–0.75
18	130	47	0.153	0.50–0.75
23	148	48	0.007	0.90–0.95
24	129	44	0.002	0.95–0.99
25	132	40	0.194	0.50–0.75
32	145	44	0.213	0.50–0.75
34	122	52	1.962	0.10–0.25
40	125	48	0.557	0.25–0.50
42	136	37	1.019	0.25–0.50
43	148	45	0.209	0.50–0.75
46	129	33	1.613	0.10–0.25
Total	1,827	599	7.500	
Deviation χ^2			0.124	0.50–0.75
Heterogeneity χ^2			7.376	0.75–0.90

[a] BC_1F_2 lines were derived from single BC_1F_1 plants.
[b] R = resistant; S = susceptible.

DISCUSSION

The genetic model with dominant resistance to *A. candida* race 7 in cultivar Regent postulated by Fan et al. (5) was confirmed, and three monogenic lines carrying different homozygous resistance genes were successfully developed. We propose that the resistance genes described in this work be designated $Ac7_1$, $Ac7_2$, and $Ac7_3$ (22) for resistance to white rust caused by race 7 of *A. candida*. The monogenic lines should permit detailed studies on the mechanism(s) of resistance response conditioned by the individual genes. Furthermore, the lines should facilitate molecular mapping of the loci in *B. napus* for resistance to *A. candida* race 7. A dominant gene at a single locus, *ACA*1, for resistance to a *B. carinata* pathotype of *A. candida* has been mapped with restriction fragment length polymorphism markers in *B. napus* (6). Crute et al. (3) mapped a single major gene, which they termed *RAc*1, that conditions resistance to *A. candida* in *Arabidopsis thaliana*. Knowledge of the number and location of genes governing white rust resistance would be useful in understanding the genetics and evolution of host-pathogen interactions and in the development of resistant cultivars.

The general acceptance of the gene-for-gene theory in host-pathogen interactions has focused attention on interactions between individual genes in the host and pathogen. An incompatible interaction phenotype is usually considered to be the result of the interaction of a gene conferring resistance in the host and the corresponding gene in the pathogen for avirulence. Near isogenic lines (NILs) carrying single genes for resistance to plant-pathogenic fungi are widely used to differentiate isolates of the pathogen and to characterize genetic variation for pathogenicity in pathogen populations. To elucidate the genetic relationship between *Brassica* species and isolates of *A. candida*, it is desirable to develop sets of NILs that can differentiate *A. candida* isolates by species and cultivar specificity. The genes for resistance to race 7 isolated from cultivar Regent are being transferred and incorporated into rapid-cycling *B. napus* lines (21) susceptible to several pathotypes of *A. candida*. This approach also will be used for resistance genes identified in *B. napus* to *B. juncea* (19) and *B. carinata* pathotypes of *A. candida* (9). When sufficient numbers of isogenic lines are developed with a common genetic background, they could be used as differential hosts to identify *A. candida* races and to detect virulence changes in the pathogen population. NILs with specific resistance and corresponding isolates of

TABLE 5. Segregation for reaction to *Albugo candida* race 7 in F_2 families from crosses of tester lines A (line 8-2, $R_1R_1r_2r_2r_3r_3$) and B (line 23-7, $r_1r_1R_2R_2r_3r_3$) with homozygous resistant BC_1F_3 lines derived from a cross of susceptible *Brassica napus* line Green Cup Leaf with resistant cultivar Regent

BC_1F_3 line[a]	Putative genotype[b]	F_2 (BC_1F_3 × tester line A) Reaction[c] R	S	Expected ratio	χ^2	*P*	F_2 (BC_1F_3 × tester line B) Reaction R	S	Expected ratio	χ^2	*P*
6-7	$r_1r_1R_2R_2r_3r_3$	79	1	15:1	2.613	0.10–0.25	80	0	1:0	...	...
8-3	$r_1r_1R_2R_2r_3r_3$	74	6	15:1	0.053	0.75–0.90	80	0	1:0	...	...
9-1	$R_1R_1r_2r_2r_3r_3$	77	0	1:0	...	...	76	4	15:1	0.053	0.75–0.90
11-1	$r_1r_1r_2r_2R_3R_3$	75	5	15:1	0.000	0.99–1.00	77	1	15:1	2.492	0.10–0.25
18-3	$r_1r_1r_2r_2R_3R_3$	79	1	15:1	2.613	0.10–0.25	76	4	15:1	0.053	0.75–0.90
23-3	$R_1R_1r_2r_2r_3r_3$	80	0	1:0	...	...	78	1	15:1	2.555	0.10–0.25
24-10	$r_1r_1r_2r_2R_3R_3$	78	1	15:1	2.555	0.10–0.25	78	2	15:1	1.333	0.10–0.25
25-1	$R_1R_1r_2r_2r_3r_3$	80	0	1:0	...	...	72	6	15:1	0.085	0.75–0.90
32-9	$R_1R_1r_2r_2r_3r_3$	80	0	1:0	...	...	79	1	15:1	2.613	0.10–0.25
34-1	$R_1R_1r_2r_2r_3r_3$	80	0	1:0	...	...	74	2	15:1	1.137	0.25–0.50
40-1	$r_1r_1R_2R_2r_3r_3$	76	4	15:1	0.053	0.75–0.90	80	0	1:0	...	...
42-4	$r_1r_1r_2r_2R_3R_3$	75	5	15:1	0.000	0.99–1.00	76	4	15:1	0.053	0.75–0.90
43-5	$r_1r_1R_2R_2r_3r_3$	76	4	15:1	0.053	0.75–0.90	80	0	1:0	...	...
46-6	$r_1r_1R_2R_2r_3r_3$	74	4	15:1	0.031	0.75–0.90	80	0	1:0	...	...

[a] Homozygous resistant BC_1F_3 lines were derived from different BC_1F_2 lines that segregated for white rust resistance in a single-gene ratio.
[b] $R_1 = Ac7_1$; $r_1 = ac7_1$; $R_2 = Ac7_2$; $r_2 = ac7_2$; $R_3 = Ac7_3$; and $r_3 = ac7_3$.
[c] R = resistant; S = susceptible.

TABLE 6. Segregation for reaction to *Albugo candida* race 7 in backcross families from crosses of tester lines A (line 8-2, $R_1R_1r_2r_2r_3r_3$) and B (line 23-7, $r_1r_1R_2R_2r_3r_3$) with homozygous resistant BC_1F_3 lines derived from a cross of susceptible *Brassica napus* line Green Cup Leaf (GCL) with resistant cultivar Regent

BC_1F_3 line[a]	Putative genotype[b]	(BC_1F_3 × tester line A) × GCL Reaction[c] R	S	Expected ratio	χ^2	*P*	(BC_1F_3 × tester line B) × GCL Reaction R	S	Expected ratio	χ^2	*P*
6-7	$r_1r_1R_2R_2r_3r_3$	20	0	3:1	5.400	0.01–0.05	20	0	1:0	...	...
8-3	$r_1r_1R_2R_2r_3r_3$	15	5	3:1	0.000	0.99–1.00	20	0	1:0	...	...
9-1	$R_1R_1r_2r_2r_3r_3$	19	1	1:0	...	...	12	8	3:1	1.667	0.10–0.25
11-1	$r_1r_1r_2r_2R_3R_3$	16	4	3:1	0.667	0.25–0.50	18	1	3:1	2.961	0.05–0.10
18-3	$r_1r_1r_2r_2R_3R_3$	12	8	3:1	1.667	0.10–0.25	19	0	3:1	5.070	0.01–0.05
23-3	$R_1R_1r_2r_2r_3r_3$	20	0	1:0	...	...	17	3	3:1	0.600	0.25–0.50
24-10	$r_1r_1r_2r_2R_3R_3$	18	2	3:1	1.667	0.10–0.25	17	3	3:1	0.600	0.25–0.50
25-1	$R_1R_1r_2r_2r_3r_3$	20	0	1:0	...	...	16	4	3:1	0.667	0.25–0.50
32-9	$R_1R_1r_2r_2r_3r_3$	20	0	1:0	...	...	17	3	3:1	0.600	0.25–0.50
34-1	$R_1R_1r_2r_2r_3r_3$	20	0	1:0	...	...	18	2	3:1	1.667	0.10–0.25
40-1	$r_1r_1R_2R_2r_3r_3$	10	10	3:1	5.400	0.01–0.05	20	0	1:0	...	...
42-4	$r_1r_1r_2r_2R_3R_3$	11	9	3:1	3.267	0.05–0.10	15	5	3:1	0.000	0.99–1.00
43-5	$r_1r_1R_2R_2r_3r_3$	16	4	3:1	0.667	0.25–0.50	20	0	1:0	...	...
46-6	$r_1r_1R_2R_2r_3r_3$	14	6	3:1	0.667	0.25–0.50	20	0	1:0	...	...

[a] Homozygous resistant BC_1F_3 lines were derived from different BC_1F_2 lines that segregated for white rust resistance in a single-gene ratio.
[b] $R_1 = Ac7_1$; $r_1 = ac7_1$; $R_2 = Ac7_2$; $r_2 = ac7_2$; $R_3 = Ac7_3$; and $r_3 = ac7_3$.
[c] R = resistant; S = susceptible.

TABLE 7. Segregation for reaction to *Albugo candida* race 7 in F_2 and backcross populations from crosses of tester lines A (line 8-2, $R_1R_1r_2r_2r_3r_3$) and B (line 23-7, $r_1r_1R_2R_2r_3r_3$) with homozygous resistant BC_1F_3 line 42-4 derived from a cross of susceptible *Brassica napus* line Green Cup Leaf with resistant cultivar Regent

Plant number	Reaction[a] R	Reaction[a] S	Expected ratio	χ^2	*P*
F_2 (BC_1F_3 × tester line A)					
42-4-1-1	75	5	15:1	0.000	0.99–1.00
42-4-2-1	77	3	15:1	0.480	0.50–0.75
42-4-3-1	78	2	15:1	1.333	0.10–0.25
Total	230	10	15:1	1.813	
Deviation χ^2				1.440	0.10–0.25
Heterogeneity χ^2				0.373	0.75–0.90
F_2 (BC_1F_3 × tester line B)					
42-4-1-1	76	4	15:1	0.053	0.75–0.90
42-4-2-1	75	9	15:1	2.146	0.10–0.25
42-4-3-1	81	3	15:1	0.622	0.25–0.50
Total	232	16	15:1	2.821	
Deviation χ^2				0.017	0.75–0.90
Heterogeneity χ^2				2.804	0.10–0.25
(BC_1F_3 × tester line A) × GCL					
42-4-1-1	11	9	3:1	3.267	0.05–0.10
42-4-2-1	14	4	3:1	0.000	0.99–1.00
42-4-3-1	16	2	3:1	1.185	0.25–0.50
Total	41	15	3:1	4.452	
Deviation χ^2				0.024	0.75–0.90
Heterogeneity χ^2				4.428	0.10–0.25
(BC_1F_3 × tester line B) × GCL					
42-4-1-1	15	5	3:1	0.000	0.99–1.00
42-4-2-1	15	3	3:1	0.296	0.50–0.75
42-4-3-1	14	4	3:1	0.000	0.99–1.00
Total	44	12	3:1	0.296	
Deviation χ^2				0.214	0.50–0.75
Heterogeneity χ^2				0.082	0.95–1.00

[a] R = resistant; S = susceptible.

the pathogen with specific avirulence genes should provide the basic materials for parallel studies on the genetics of host-pathogen interactions between genotypes of *Brassica* species and isolates of *A. candida* from *Brassica* species.

In Canada, resistance in *B. napus* cultivars to *A. candida* appears to be durable in that it has remained effective for over 50 years of exposure to the isolates of *A. candida* that can attack *B. rapa* and *B. juncea*. This can be attributed to the number of resistance genes carried by *B. napus* cultivars and the low capacity of the pathogen to adapt to this resistance. In England, white rust has become a widespread and destructive disease of cruciferous vegetables, e.g., Brussels sprout (*B. oleracea*) (I. R. Crute, *personal communication*). The *B. oleracea* pathotypes of *A. candida* from Europe and some *B. carinata* pathotypes from East Africa are pathogenic to commercial *B. napus* cultivars grown in western Canada (S. R. Rimmer, *unpublished data*). White rust oospores are frequent contaminants of Brassica seed lots (12), and there is no restriction on importation of Brassica seed lots into Canada. Thus, the potential for this disease to become a problem on *B. napus* in western Canada exists if these isolates are introduced inadvertently from abroad. Moreover, races 2 and 7, the two predominant pathotypes of *A. candida* in Canada, are interfertile on common susceptible hosts (10), and new pathotypes could develop through sexual recombination. Therefore, oilseed rape breeders and pathologists should be on the alert against the appearance of isolates of *A. candida* that can attack *B. napus* cultivars and be cautious not to introduce susceptibility through interspecific crosses between *Brassica* species.

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