Inheritance of Resistance to *Leptosphaeria maculans* in *Brassica juncea*

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ABSTRACT

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The inheritance of resistance to *Leptosphaeria maculans*, the causal agent of black leg of crucifers, was studied in *Brassica juncea*. Three resistant accessions (UM3021, UM3043, and UM3323) and one susceptible accession (UM3132) of *B. juncea* were crossed in a complete diallel. Parents, F_1 , and F_2 progenies were evaluated for all crosses using both cotyledon and stem inoculation. Cotyledon reaction was evaluated with two isolates of *L. maculans*, but stem reaction was evaluated with one isolate. Disease reactions observed for individual plants were the same for both inoculation methods and for both isolates of the pathogen for cotyledon reaction. No segregation was observed for the crosses between resistant accessions (UM3043 $\times$ UM3323 and UM3021 $\times$ UM3323),

but a few susceptible plants were observed in the F_2 progeny of crosses between resistant parents (UM3021 $\times$ UM3043). This was probably due to heterozygosity in some parental plants of UM3021. For crosses between the susceptible parent and resistant parents, F_1 plants for two crosses were all resistant. For cross UM3132 $\times$ UM3021, some susceptible plants occurred, which was also suggestive of heterozygosity in UM3021. Although resistance in F_1 was dominant, for F_2 populations, segregation fit either 13:3, 3:1, or 1:3 ratios, indicating that resistance can be either a dominant or recessive trait. F_3 families derived from some susceptible F_2 plants from crosses UM3021 $\times$ UM3132 and UM3043 $\times$ UM3132 were evaluated using the cotyledon inoculation method only. Segregation of F_2 plants and F_3 families in crosses involving resistant and susceptible parents indicated that the resistance to *L. maculans* in *B. juncea* is controlled by two nuclear genes with dominant recessive epistatic gene action.

Black leg (stem canker), caused by *Leptosphaeria maculans* (Desmaz.) Ces. & de Not., is an important disease in many *Brassica* species and may cause serious seed yield losses in oilseed brassica crops in many parts of the world (6,10). The disease has been controlled primarily through the use of resistant cultivars. The genetics of resistance to *L. maculans* in *Brassica* spp. has been reviewed recently (11), but despite the importance of the disease, information on the number of genes involved in resistance and their effects and allelic relationships is rather limited. More knowledge concerning the genetics of resistance would be valuable for effective breeding for resistance to black leg in oilseed brassicas.

B. juncea (L.) Czern. (oilseed mustard) is more resistant to *L. maculans* at the seedling and adult plant stages than are *B. rapa* (turnip oilseed rape) and *B. napus* (oilseed rape), and this resistance is thought to be controlled by genes located on the b-genome (12,13). There is considerable interest in western Canada to develop canola-quality *B. juncea*, because of its resistance to black leg and its superior drought tolerance. Resistance in *B. juncea* has been transferred to *B. napus* through interspecific hybridization (12). Since no information on the inheritance of resistance in *B. juncea* is available, this study was undertaken to determine the genetic control of resistance to *L. maculans* in this species.

MATERIALS AND METHODS

Plant material. In preliminary experiments, 296 accessions of *B. juncea* (University of Manitoba collection, obtained primarily from P. F. Knowles, University of California, Davis, and R. K. Downey, Agriculture and Agri-food Canada, Saskatoon) were

evaluated for resistance to *L. maculans* (4), and four accessions (three resistant and one susceptible) were chosen to study the inheritance of resistance (Table 1). Single plants selected from the chosen accessions were inbred to the second generation selfed (S_2) level and crossed in a complete diallel. All plants that were used in crosses also were selfed to obtain third generation selfed (S_3) progeny. Racemes used for selfing or crossing were isolated in glycine bags to avoid pollen contamination. F_1 and F_2 populations were generated for all crosses, and F_3 families derived from randomly selected susceptible F_2 plants were generated for the crosses UM3021 $\times$ UM3132 and UM3132 $\times$ UM3043. To facilitate interpretation of the data presented in Tables 2, 3, 4, and 5, crosses between the susceptible parent UM3132 and the resistant parents were designated as follows: UM3323 $\times$ UM3132 as cross I and the reciprocal as cross IR; UM3132 $\times$ UM3043 as cross IIR; and UM3021 $\times$ UM3132 as cross III and the reciprocal as cross IIIR.

To evaluate the plants for disease reaction, seeds were planted separately in 5-cm jiffy pots (Koral flats; Koral Co., Bramalea, Ontario, Canada) filled with a soilless potting mixture (Metromix; W. R. Grace & Co. Canada Ltd., Ajax, Ontario, Canada) composed of the following as basic ingredients: vermiculite, perlite, sphagnum peat moss, and nutrients (NPK and trace elements). All plants were maintained in a growth chamber at 24/20°C day/night temperatures with a 16-h photoperiod. After 3 weeks, seedlings were transplanted into 20-cm fiber pots containing the soilless mixture. Plants were kept in a greenhouse with normal daylight, supplemented to 16 h with fluorescent light. Plants were fertilized regularly with a water-soluble formulation (20-20-20 NPK) containing micronutrients. Approximately 50 S_2 plants and 200 S_3 plants were evaluated for each accession, as well as 50 F_1 and several hundred F_2 plants of each cross. Six and 18 F_2 -derived F_3 families were evaluated for the crosses between UM3132 $\times$ UM3043 (cross IIR) and between UM3021 $\times$ UM3132 (cross IIIR), respectively.

Pathogen isolates. Two isolates of *L. maculans* (PI85-9 and PI86-14), obtained from widely separated regions of Manitoba,

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Canada, were used in this study. Both isolates belong to pathogenicity group 2, the predominant aggressive pathotype occurring in western Canada (7). To maintain pathogenicity, susceptible host plants were inoculated with the isolates using the cotyledon inoculation method (17). The infected cotyledons were surface-sterilized in 5% sodium hypochlorite for 2 to 3 min, rinsed twice in sterile distilled water, and transferred onto V8 juice agar plates

(800 ml of distilled water, 200 ml of V8 juice, 0.7 g of calcium carbonate, and 15 g of agar) containing streptomycin sulfate (100 mg liter⁻¹) and rose bengal (40 mg liter⁻¹). Plates were incubated under near-UV light or cool fluorescent light at room temperature to ensure high pycnidial production. After 5 to 7 days, plates were flooded with 5 to 10 ml of sterile distilled water and gently scraped with a sterile glass slide to release the pycnidiospores.

TABLE 1. Description of *Brassica juncea* accessions and interaction phenotype on second (S₂) and third (S₃) generation selfs following cotyledon inoculation with isolate PI86-14 of *Leptosphaeria maculans*

Accession	Country of origin	Name	Cotyledon rating ^z		General host reaction
			S ₂	S ₃	
UM3021	Pakistan	...	0.45 ± 0.14	0.25 ± 0.06	Resistant
UM3043	Pakistan	...	0.63 ± 0.14	0.25 ± 0.05	Resistant
UM3323	China	Ku	0.61 ± 0.11	0.30 ± 0.05	Resistant
UM3132	Bangladesh	Rai-5	8.48 ± 0.18	8.72 ± 0.07	Susceptible

^z Mean rating and standard deviation of interaction phenotype (0 to 9 scale) based on the cotyledon inoculation method (16).

TABLE 2. Observed segregation for host reaction, expected segregation ratios, chi-square values (χ^2), and probabilities (*P*) for goodness of fit for F₂ plants from crosses between accessions of *Brassica juncea* following cotyledon inoculation with isolate PI86-14 of *Leptosphaeria maculans*

Cross	Host reaction ^y		Total	χ^2			
	R	S		3:1 (R:S)	<i>P</i>	13:3 (R:S)	<i>P</i>
I (3323 × 3132)							
Total	152	23	175				
Pooled				13.122	<0.0001	3.603	0.05–0.10
Homogeneity (df = 5)				2.788	0.70–0.90	3.309	0.50–0.70
IR (3132 × 3323)							
1 Total	124	39	156				
Pooled				1.675	0.10–0.20	0.330	0.50–0.70
Homogeneity (df = 6)				1.832	0.10–0.20	2.244	0.10–0.20
2 Total	302	79	381				
Pooled				3.696	0.05–0.10	0.996	0.30–0.50
Homogeneity (df = 4)				1.377	0.70–0.90	1.684	0.70–0.90
3 Total	184	57	241				
Pooled				0.234	0.50–0.70	3.792	0.05–0.10
Homogeneity (df = 4)				1.063	0.70–0.90	1.305	0.70–0.90
4 Total	196	66	260				
Pooled				0.200	0.50–0.70	7.513	<0.01
Homogeneity (df = 4)				3.723	0.30–0.50	4.514	0.30–0.50
5 Total	181	70	251				
Pooled				1.117	0.20–0.30	13.706	<0.001
Homogeneity (df = 3)				6.283	0.10–0.20	7.356	0.10–0.20
IIR (3132 × 3043)							
Total	576	125	704				
Pooled				19.705	<0.001	0.456	0.50–0.70
Homogeneity (df = 6)				3.111	0.70–0.90	3.823	0.70–0.90
III (3021 × 3132)							
Total	2,056	433	2,489				
Pooled				76.744	<0.001	2.993	0.05–0.10
Homogeneity (df = 25)				20.079	0.70–0.90	24.852	0.30–0.50
IIIR (3132 × 3021)							
1	103	29	132	0.646	0.30–0.50	0.898	0.30–0.50
2	93	32	125	0.024	0.90–0.95	3.887	0.01–0.05
3	91	34	125	0.323	0.05–0.10	5.908	0.01–0.05
4	37	85	122	129.847	<0.001	207.314	<0.001
5	97	22	119	2.692	0.10–0.20	0.005	0.70–0.90
6	103	28	131	0.919	0.30–0.50	0.592	0.30–0.50
7	98	30	128	0.167	0.50–0.70	1.846	0.10–0.20
8	32	9	41	0.203	0.50–0.70	0.270	0.50–0.70
Total	654	269	923	134.820		220.720	
Pooled				8.454	<0.001	65.394	<0.001
Homogeneity (df = 7)				126.366	<0.001	155.326	<0.001
Total ^z	617	184	801	4.974		13.406	
Pooled ^z				1.758	<0.10–0.20	9.361	<0.001–0.01
Homogeneity (df = 6) ^z				3.216	<0.70–0.90	4.045	<0.20–0.30

^y Number of resistant (R) and susceptible (S) plants.

^z Cross IIIR 4 was excluded in pooling the data.

The spore suspension was filtered through four layers of sterilized cheesecloth and centrifuged for 30 min at 3,000 × g. The supernatant was decanted, and the pelleted spores were suspended in 5 ml of sterile distilled water and stored at -15°C. For inoculation, the spore suspensions were thawed and the inoculum concentration was adjusted to 10⁷ spores ml⁻¹. Using this method, the concentrated inoculum may be held frozen for 3 to 6 months without any noticeable loss in virulence of *L. maculans*.

Inoculation techniques. *Cotyledon inoculation.* Six days after seeding, cotyledons were wounded with a sterile needle and a 10-μl droplet of the pycnidiospore suspension was placed onto the wound. The two isolates, PI85-9 and PI86-14, were each applied to one cotyledon of each plant. Inoculated plants were allowed to dry overnight before transfer to a growth chamber. Ten days after inoculation, the disease reactions on the cotyledons (cotyledon interaction phenotype [IP]) were rated using a 0 to 9 scale (17). *B. napus* cv. Westar was included in all inoculation tests as a susceptible check.

Stem inoculation. Plants were inoculated at the early bolting growth stage (GS 3.0 to 3.2 [3]) with isolate PI86-14. A 10-μl droplet of the pycnidiospore suspension was injected into the stem of each plant (between the second and third node) with a hypodermic syringe (model 5602; Beckton Dickinson, Rutherford, NJ). Lesion length and amount of girdling were rated 38 days after inoculation. Lesion length was rated using a 0 to 5 scale in which 0 = no infection; 1 = lesion length <10 mm; 2 = lesion length 10 to 19 mm; 3 = lesion length 20 to 29 mm; 4 = lesion length >30 mm; and 5 = plant dead. Girdling was rated using a 0 to 5 scale as previously reported (9,16). Stem disease reaction (adult IP) was calculated as the sum of the ratings for girdling and lesion length. IPs accompanied by sporulation of the fungus on the host tissue were considered indicative of susceptibility. *B. napus* cv. Westar was included in all inoculation tests as a susceptible check.

Statistical analysis. The chi-square test was used to test the goodness of fit of segregation ratios for all data (15). The validity of pooling F₂ populations from the same cross was tested with the chi-square test for homogeneity.

RESULTS

Parents. Similar cotyledon IPs were observed with both isolates (PI85-9 and PI86-14) of *L. maculans*. Consequently, only data for isolate PI86-14 are presented. The mean IP of the three resistant accessions was less than 0.7 in the S₂ and S₃ generations (Table 1), and the mean cotyledon IP for the susceptible parent was greater than 8.4 in both the S₂ and S₃ generations. The cotyledon IP for the resistant accessions ranged from 0 to 3 and, for the susceptible accession, from 5 to 9. Following stem inoculation, the adult IP was less than 0.6 for resistant accessions and greater than 7.0 for the susceptible accessions. At the adult stage, IP ranged from 0 to 3 for resistant accessions and from 6 to 8 for the susceptible accession. No segregation was observed in the S₂ or S₃

TABLE 3. Interaction phenotype (IP), expected segregation ratio, chi-square values (χ²), and probabilities (P) for goodness of fit for F₃ families derived from susceptible F₂ plants of the cross UM3132 × UM3043 (cross II) following cotyledon inoculation with isolate PI86-14 of *Leptosphaeria maculans*

F ₃ family number	Host reaction ^z			Expected ratio (R:S)	χ ²	P
	R	S	Total			
1-1	1	47	48	0:1		
1-2	1	46	47	0:1		
1-3	16	31	47	1:3	2.050	0.10–0.25
6-1	11	36	47	1:3	0.064	0.75–0.90
7-1	16	32	48	1:3	1.778	0.10–0.25
7-2	1	44	45	0:1		

^z Number of resistant (R) and susceptible (S) plants.

progeny of any accession. Classification of cotyledon IP or adult IP of individual plants for subsequent F₁, F₂, and F₃ generations followed the same classifications as for the parental material. One exception to this is explicitly described below.

F₁ progeny. For crosses involving UM3323 × UM3132 (crosses I and IR) and UM3132 × UM3043 (cross IIR), the F₁ progeny were uniformly resistant with a mean cotyledon IP less than 0.43. Segregation for resistance and susceptibility was observed in the F₁ progeny for the cross UM3021 × UM3132 (cross III) (209 resistant:33 susceptible) and the reciprocal (cross IIIR) (449 resistant:41 susceptible), indicating heterozygosity in some parental plants of UM3021.

Following stem inoculation, adult IP ranged from 0 to 1 in the crosses between resistant accessions. For the crosses UM3323 × UM3132 (crosses I and IR) and UM3132 × UM3043 (cross IIR), adult IP ranged from 0 to 1. For the cross UM3021 × UM3132 (crosses III and IIIR), adult IP ranged from 0 to 5; most IPs were 0 to 1, as in the other crosses, and were classified as resistant. However, some plants were of adult IP 4 or 5. These were characterized by purple streaking that originated from the point of inoculation of stems; fungal sporulation occurred on stems of such plants 4 weeks after inoculation. Consequently, these plants, which also had a cotyledon IP of 5, were classified as susceptible.

F₂ progeny. With the cotyledon inoculation, F₂ progeny for the crosses between susceptible and resistant accessions fit both a 13:3 and 3:1 resistant/susceptible segregation ratio. Most F₂ progeny for the crosses of UM3132 with the resistant accessions were best fit to a 13 resistant:3 susceptible segregation ratio (Table 2). However, some progeny in the reciprocal crosses of UM3323 × UM3132 (cross IR) and UM3021 × UM3132 (cross IIIR) fit only a 3 resistant:1 susceptible segregation ratio. Chi-square tests for homogeneity on all families from the reciprocal cross of UM3021 × UM3132 (cross IIIR) were significant for both 13:3 (*P* < 0.001) and 3:1 (*P* < 0.001) resistant/susceptible segregation ratios. One family (cross IIIR 4, Table 2), which best fit a 1 resistant:3 susceptible segregation ratio (chi-square = 1.847), was then excluded in the tests for homogeneity; the pooled data for this cross was then homogeneous for a 3 resistant:1 susceptible segregation ratio. The chi-square test for homogeneity of the pooled F₂ data for the other crosses of UM3132 with resistant accessions was not significant for a 13:3 ratio of resistant/susceptible plants (Table 2). Thus, resistance in the *B. juncea* UM3323, UM3043, and UM3021

TABLE 4. Interaction phenotype (IP), expected segregation ratio, chi-square values (χ²), and probabilities (P) for goodness of fit for F₃ families derived from susceptible F₂ plants of the cross UM3132 × UM3021 (cross IIIR) following cotyledon inoculation with isolate PI86-14 of *Leptosphaeria maculans*

F ₃ family number	Interaction phenotype ^z			Expected ratio (R:S)	χ ²	P
	R	S	Total			
3-1	11	41	52	1:3	0.231	0.50–0.75
3-2	10	35	45	1:3	0.067	0.75–0.90
3-3	0	44	44	0:1		
3-4	29	15	44	3:1	1.939	0.10–0.25
3-5	21	23	44	1:3	2.735	0.05–0.10
3-6	11	34	45	1:3	0.007	0.90–0.95
4-1	1	44	45	0:1		
4-2	11	31	42	1:3	0.000	>0.95
4-3	16	32	48	1:3	1.361	0.25–0.50
4-4	14	26	40	1:3	1.633	0.20–0.50
4-5	13	33	46	1:3	0.116	0.75–0.90
4-6	10	32	42	1:3	0.000	>0.95
8-1	0	47	47	0:1		
8-2	30	16	46	3:1	2.348	0.10–0.25
8-3	12	34	46	1:3	0.000	>0.95
8-4	11	29	40	1:3	0.033	0.75–0.90
8-5	16	31	47	1:3	1.596	0.25–0.50
8-6	0	53	53	0:1		

^z Number of resistant (R) and susceptible (S) plants.

lines was controlled by two genes with dominant recessive epistatic interaction. A consequence of this model is that some susceptible F_2 genotypes, when selfed, will segregate for resistance in F_3 generation. A brief outline of this genetic model is presented at the beginning of the Discussion.

Following cotyledon inoculation, all plants in the F_2 populations of the crosses between the resistant parents, UM3323 $\times$ UM3043 and UM3323 $\times$ UM3021, and their reciprocals were resistant (data not shown). This indicates that the resistance genes in UM3323 are allelic to those in UM3043 and UM3021. The F_2 populations from the cross UM3021 $\times$ UM3043 and their reciprocal were predominantly resistant (1,452 resistant:74 susceptible). Sixty-three plants with IP 5 and 11 plants with IP 7, distributed over several families, were observed in this cross and its reciprocal; these plants could be due to the heterogeneous and heterozygous genetic make-up of UM3021.

Adult IP ranged from 0 to 1 in the crosses between resistant accessions following stem inoculation. In the crosses of resistant with the susceptible parent (crosses I, II, and III) and their reciprocals, adult IP ranged from 0 to 9. Plants with a rating 0 to 3 were classified as resistant, and plants with a rating from 4 to 9 were classified as susceptible. The classification for susceptibility was based on the fact that, with this range of adult IP, the pathogen was able to colonize and sporulate on the inoculated plants. The classification of individual plants as either susceptible or resistant, based on the IP ratings, was the same at the cotyledon and adult plant stages.

F_3 families. Although most F_2 populations derived from crosses between resistant and susceptible lines best fit a 13 resistant:3 susceptible segregation ratio, some populations in the reciprocal crosses of UM3323 $\times$ UM3132 (cross IR) and UM3021 $\times$ UM3132 (cross IIIR) best fit a 3 resistant:1 susceptible segregation ratio, and one population (cross IIIR 4) in the reciprocal cross of UM3021 $\times$ UM3132 (cross IIIR) best fit a 1 resistant:3 susceptible segregation ratio. The hypothesis of two genes with dominant recessive epistatic interaction was then tested further by evaluating F_3 families derived from susceptible F_2 plants from the populations of UM3021 $\times$ UM3132 (cross IIIR), which did not fit a 13 resistant:3 susceptible ratio. In addition, susceptible plants derived from some F_2 populations from the cross UM3132 $\times$ UM3043 (cross

IIR) and cross UM3021 $\times$ UM3132 (cross IIIR), which did fit a 13 resistant:3 susceptible ratio, were also evaluated in the F_3 generation. As predicted by the hypothesis, data from the F_3 families derived from susceptible F_2 plants of the crosses UM3132 $\times$ UM3043 (cross IIR) and UM3021 $\times$ UM3132 (cross IIIR) fit a 1:3 or 0:1 segregation ratio of resistant/susceptible plants (Tables 3 and 4, respectively). However, two F_3 families of the 24 tested fit a 3 resistant:1 susceptible ratio, a ratio not explainable by the dominant recessive epistatic hypothesis (Table 4). Overall, these results confirm that resistance to *L. maculans* in *B. juncea* lines UM3323, UM3043, and UM3021 is controlled by two nuclear genes with dominant recessive epistatic interaction.

DISCUSSION

Results from this study indicate that two gene pairs interact to determine both seedling and stem resistance to *L. maculans* in *B. juncea*. With dominant recessive epistasis, one gene (A/a) confers resistance in a dominant manner (i.e., A/A or A/a) and a second gene (B/b) in a recessive manner (i.e., b/b). Presence of the A-allele at the first locus or the b-allele in homozygous state on the second locus is required for the resistant IP. A 3:1, 1:3, or both resistant/susceptible segregation ratios were observed for some F_2 populations from resistant $\times$ susceptible crosses. This suggests that the resistant accessions were segregating for the first locus (A/a) only. Resistant genotypes heterozygous for at least one locus are AaBB, Aabb, AaBb, and the heterozygous susceptible genotype is aaBb. Only the genotypes AaBB and aaBb, upon selfing, will result in a 3:1 and 1:3 resistant/susceptible segregation ratio, respectively. The genotypes AaBB and aaBb may be obtained if the genotypes of the resistant parents used in crosses with the homozygous susceptible genotype (aaBB) are AABb and Aabb, respectively. Thus, the presence of families with 3:1, 1:3, or both resistant/susceptible segregation ratios indicate that the resistant accessions (UM3021, UM3043, and UM3323) used in the study were segregating for at least one locus.

That the two genes interact in a dominant recessive manner is supported by the segregation for resistance in F_3 families originating from single susceptible F_2 plants. Overall (22 of 24 families), F_3 families fit a 0:1 or 1:3 resistant/susceptible segregation

TABLE 5. Proposed genotypes of parent plants, F_1 plants, and F_2 plants from which F_3 families were derived, observed F_2 segregation model, and observed F_3 segregation for crosses between accessions UM3132 $\times$ UM3021 (cross IIIR) of *Brassica juncea* following cotyledon inoculation with *Leptosphaeria maculans* isolate P186-14

Cross IIIR families	Proposed genotype of resistant parent plants ^y	Expected F_1 genotypes	Proposed genotype of F_1 plant	Observed F_2 ratio (R:S)	Proposed genotype of F_2 plant to F_3 family	Observed F_3 ratio (R:S)
1	AABb	AaBb/AaBB	AaBb AaBB	13:3 3:1		
2	AaBB or AABb	AaBB/aaBB (only 1 plant selected)	AaBB	3:1		
3 ^z	AABb	AaBb/AaBB	AaBb AaBB	13:3 3:1	aaBb aaBB AaBB	1:3 0:1 3:1
4 ^z	Aabb	AaBb/aaBb	aaBb	1:3	aaBB aaBb	0:1 1:3
5	AABb	AaBB/AaBb	AaBb AaBB	13:3 3:1		
6	AABb	AaBB/AaBb	AaBb AaBB	13:3 3:1		
7	AABb	AaBB/AaBb	AaBb AaBB	13:3 3:1		
8 ^z		AaBB/AaBb	AaBb AaBB	13:3 3:1	aaBB aaBb AaBB	0:1 1:3 3:1

^y Resistant parent plants (accession UM3021). Genotype of susceptible parent (UM3132) is assumed to be aaBB.

^z F_3 plants tested and used.

ratio. The two families that fit a 3 resistant:1 susceptible segregation ratio were unexpected and not predicted by the dominant recessive model. It is very unlikely that these observations could be due to experimental error, such as the misclassification of IP scored. However, if F_2 plants with the genotype AaBB were scored as susceptible, a 3 resistant:1 susceptible segregation ratio would be observed in their F_3 families. Proposed genotypes for parents, F_1 , and F_2 progeny from which F_3 families were derived, and the obtained F_3 for UM3132 $\times$ UM3021 (cross IIIR) are presented in Table 5.

Using cotyledon inoculation, Mithen and Lewis (8) found that seedling resistance in *B. alboglabra* is controlled by dominant, epistatic genes (15 resistant:1 susceptible segregation ratio). Delwiche (2) found two linked, dominant genes in *B. napus*. Sawatsky (14) reported that seedling resistance was controlled by a single recessive gene in *B. napus* and, using stem inoculation, identified two dominant genes conferring stem resistance at the adult plant stage. In this study, we identified two epistatic genes in *B. juncea* that confer resistance at both the seedling and adult plant stages. To our knowledge, resistance inherited by dominant recessive epistasis is unusual. It has been reported for resistance in wheat to races of *Puccinia striiformis* (1). Virulence/avirulence in *Melampsora lini*, the flax rust pathogen, has also been reported to be controlled by dominant recessive interacting genes (5).

Previously, 296 *B. juncea* accessions were evaluated for disease reaction to *L. maculans* isolates. Most of the accessions tested were resistant to the *L. maculans* isolates used (4). UM3132, the susceptible parent used in this study, was one of only three accessions found to be susceptible to the two *L. maculans* isolates used (4). Thus, it appears that resistance to *L. maculans* is the norm in *B. juncea*. If this is the case and resistance is controlled by two genes with dominant recessive epistasis, then only certain genotypes of *B. juncea* are likely to be present for resistance to be homogeneous in the absence of selection pressure. Genotypes homozygous for at least one locus for resistance are AABB, AAbb, aabb, and the homozygous susceptible genotype is aaBB. Crosses between genotypes AABB and AAbb result only in resistant progeny (genotype AAbb). If the genotype aabb occurs among accessions of *B. juncea*, any crosses of this genotype with genotype AABB or AAbb will result in segregation for susceptibility and resistance only in crosses with genotype AABB. We chose three resistant accessions at random in this study, and segregation for susceptibility was not observed for UM3323 $\times$ UM3021 or UM3323 $\times$ UM3043. However, with UM3021 $\times$ UM3043, a small frequency of susceptible plants were observed (1,452 resistant:74 susceptible) in the F_2 populations with the susceptible plants occurring in a number of the families tested. The low number of susceptible plants occurring in this cross cannot simply be explained by the genotypes AABB, AAbb, or aabb above; we have no genetic explanation for this data, although it could be due to a variety of reasons including the heterogeneous and heterozygous genetic make-up of UM3021, other epistatic effects, or associative and dissociative effects of the genes.

The resistance of *B. juncea* to *L. maculans* is well known, and attempts have been made to transfer this resistance to *B. napus* (12,13). The inheritance of resistance has not been studied in resistant lines derived from interspecific crosses. Results from this study allow the evaluation of the efficiency of gene transfer using interspecific hybridization. The dominant recessive epistasis model suggests that both dominant and recessive control of resistance may occur in the *Brassica-L. maculans* pathosystem. The elucidation of the genetic control of resistance may depend on, or may be determined by, the genotype of the original parent used in a genetic study, and on the number of F_1 plants of a cross that were selected and used to generate F_2 populations. In this study, up to

eight F_1 plants were randomly selected and used to generate F_2 populations for crosses between resistant $\times$ susceptible accessions. With regard to transferring the resistance of *B. juncea* to *L. maculans* from *B. juncea* to the major brassicas (*B. napus*, *B. oleracea*, and *B. rapa*), this model suggests that if the *B. juncea* type of resistance is to be maintained, both genes may have to be transferred to susceptible cultivars, since the dominant gene has major effects on the expression of IP and the recessive gene has modifying effects on the expression of the dominant allele. However, it may be that the transfer of one of the two genes will result in expression of resistance in the recipient species as either a dominant or a recessive character. The possibility of the transfer of a single gene would be most desirable for plant breeding purposes.

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