Phytoprotection

Resistance to barley yellow dwarf virus, powdery mildew and leaf rust in wheat x Thinopyrum backcrosses
Résistance au virus de la jaunisse nanisante de l'orge, à l'oïdium et à la rouille des feuilles dans les rétrocroisements de blé x *Thinopyrum*

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Volume 85, numéro 1, avril 2004

URI : https://id.erudit.org/iderudit/008903ar
DOI : https://doi.org/10.7202/008903ar

Aller au sommaire du numéro

Éditeur(s)

Société de protection des plantes du Québec (SPPQ)

ISSN

0031-9511 (imprimé)
1710-1603 (numérique)

Découvrir la revue

Citer cet article

Sharma, H., Ohm, H. & Shaner, G. (2004). Resistance to barley yellow dwarf virus, powdery mildew and leaf rust in wheat x Thinopyrum backcrosses. *Phytoprotection*, *85*(1), 27–32. https://doi.org/10.7202/008903ar

Résumé de l'article

Les espèces proches du blé (*Triticumaestivum*) sont à l'origine de gènes utiles pour la résistance aux maladies. Les populations à ségrégation chromosomique d'hybrides intergénériques entre le blé et des espèces peu apparentées nous offrent la chance de procéder à l'étude et à l'introgression de la multirésistance aux maladies. Alors que nous introgressions la résistance au virus de la jaunisse nanisante de l'orge (BYDV) de *Thinopyrum* dans le blé, qui est sensible au BYDV, nous avons coté la résistance à l'oïdium (*Erysiphaegraminis*) et à la rouille des feuilles (*Pucciniatriticina*), et compté le nombre de chromosomes dans les deuxième et troisième rétrocroisements (BC2 et BC3) d'hybrides intergénériques entre le blé et le *Thinopyrum ponticum* ou le *Thinopyrumintermedium*. Le taux de multirésistance aux trois maladies était bas ou est devenu bas lorsqu'une sélection a été faite pour la résistance au BYDV et pour un faible nombre de chromosomes. La sélection pour un plus faible nombre de chromosomes étrangers tout en maintenant la résistance au BYDV a été plus efficace pour le croisement de blé x *T. intermedium* que pour celui de blé x *T. ponticum*. À la génération du BC3, pour les deux croisements, le nombre moyen de chromosomes était significativement différent entre les plantes résistantes et celles sensibles au BYDV. Des corrélations négatives significatives entre le nombre de chromosomes et les valeurs du test immunoenzymatique ELISA ont démontré qu'à mesure que le ou les chromosomes déterminants du *Thinopyrum* étaient éliminés, la sensibilité au BYDV augmentait. Les résultats montrent qu'il est peu probable que les gènes conférant une résistance complète aux trois maladies puissent être transférés simultanément du *Thinopyrum* au blé.

Resistance to barley yellow dwarf virus, powdery mildew and leaf rust in wheat x *Thinopyrum* backcrosses

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Received 2003-11-06; accepted 2004-06-03

PHYTOPROTECTION 85 : 27-32

Wheat (*Triticum aestivum*) relatives are sources of useful genes for disease resistance. Chromosomally segregating populations of intergeneric hybrids between wheat and its distantly related species provide opportunity to study and introgress multiple disease resistance. While introgressing resistance to barley yellow dwarf virus (BYDV) from *Thinopyrum* into wheat, which is susceptible to BYDV, we scored powdery mildew (*Erysiphae graminis*) and leaf rust (*Puccinia triticina*) resistance, and chromosome numbers in second and third backcrosses (BC2 and BC3) of intergeneric hybrids of wheat with *Thinopyrum ponticum* and *Thinopyrum intermedium*. The frequency of multiple resistance to all the three diseases was low or became low when selection was applied for BYDV resistance and low chromosome numbers. Selection for fewer alien chromosomes while maintaining BYDV resistance was more effective in wheat x *T. intermedium* than in the wheat x *T. ponticum* cross. Mean chromosome numbers were significantly different in BC3 generation between BYDV resistant and susceptible plants in both crosses. Significant negative correlations between chromosome numbers and enzyme-linked immunosorbent assay (ELISA) values showed that as the critical *Thinopyrum* chromosome(s) were eliminated, susceptibility to BYDV increased. Results indicated that it is unlikely that genes for full resistance to all three diseases can be transferred simultaneously from *Thinopyrum* to wheat.

[Résistance au virus de la jaunisse nanisante de l'orge, à l'oïdium et à la rouille des feuilles dans les rétrocroisements de blé x *Thinopyrum*]

Les espèces proches du blé (*Triticum aestivum*) sont à l'origine de gènes utiles pour la résistance aux maladies. Les populations à ségrégation chromosomique d'hybrides intergénériques entre le blé et des espèces peu apparentées nous offrent la chance de procéder à l'étude et à l'introgression de la multirésistance aux maladies. Alors que nous introgressions la résistance au virus de la jaunisse nanisante de l'orge (BYDV) de *Thinopyrum* dans le blé, qui est sensible au BYDV, nous avons coté la résistance à l'oïdium (*Erysiphae graminis*) et à la rouille des feuilles (*Puccinia triticina*), et compté le nombre de chromosomes dans les deuxième et troisième rétrocroisements (BC2 et BC3) d'hybrides intergénériques entre le blé et le *Thinopyrum ponticum* ou le *Thinopyrum intermedium*. Le taux de multirésistance aux trois maladies était bas ou est devenu bas lorsqu'une sélection a été faite pour la résistance au BYDV et pour un faible nombre de chromosomes. La sélection pour un plus faible nombre de chromosomes étrangers tout en maintenant la résistance au BYDV a été plus efficace pour le croisement de blé x *T. intermedium* que pour celui de blé x *T. ponticum*. À la génération du BC3, pour les deux croisements, le nombre moyen de chromosomes était significativement différent entre les plantes résistantes et celles sensibles au BYDV. Des corrélations négatives significatives entre le nombre de chromosomes et les valeurs du test immunoenzymatique ELISA ont démontré qu'à mesure que le ou les chromosomes déterminants du *Thinopyrum* étaient éliminés, la sensibilité au BYDV augmentait. Les résultats montrent qu'il est peu probable que les gènes conférant une résistance complète aux trois maladies puissent être transférés simultanément du *Thinopyrum* au blé.

INTRODUCTION

Wheat (*Triticum aestivum* L.) relatives are useful for wheat improvement for disease resistance and multiple resistance is not uncommon in them (Damania 1993; Fedak 1999; Friebe *et al.* 1996; Hegde *et al.* 2002; Sharma *et al.* 1984; Singh 1993; Wienhues 1963). Transfer of gene(s) for resistance from distantly related (alien) species to wheat through wide crosses may be associated with other desirable genes located in the alien donor species chromosomes. Transfer of multiple resistance in intergeneric crosses would be desirable. Backcrosses of intergeneric hybrids to wheat, in which alien chromosomes are eliminated at

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random and have wide variation for disease reaction and alien chromosome segregation, provide opportunity to investigate whether resistances to multiple diseases, present in the donor parent, are associated.

Barley yellow dwarf virus (BYDV), transmitted by *Rhopalosiphum* species of aphid [Homoptera: Aphididae], is one of the most serious viral diseases of wheat and no resistance genes have been found in *Triticum* species (Comeau and Plourde 1987; Sharma *et al.* 1997a). *Thinopyrum ponticum* (Podp.) Barkworth & Dewey (syn. *Agropyron elongatum* (Host) Beauv.) and *T. intermedium* (Host) Barkworth & Dewey (syn. *A. intermedium* (Host) Beauv.) are resistant to BYDV (Brettell *et al.* 1988; Comeau and Plourde 1987; Sharma *et al.* 1995), leaf rust (*Puccinia triticina* Erick.) (Cauderon *et al.* 1973; Franke *et al.* 1992; Knott 1978; Kochumadhavan *et al.* 1988; Wienhues 1963), and powdery mildew (*Erysiphe* (=*Blumeria*) *graminis* (DC.) E.O. Speer) (Franke *et al.* 1992; Sinigovets 1976). These diseases are important in soft red winter wheat production in Indiana (Patterson *et al.* 1990).

We produced backcross populations from the intergeneric hybrids of wheat (somatic chromosome number = 2n = 42) with *T. ponticum* (2n = 70) and *T. intermedium* (2n = 42) primarily to transfer resistance to BYDV from *Thinopyrum* into wheat (Sharma *et al.* 1989, 1995). During this introgression for resistance to BYDV, we also compiled data on the reaction of backcross populations to powdery mildew and leaf rust along with somatic chromosome numbers of individual plants. This paper reports the results of analysis of these four traits in the second and third backcross (BC2, BC3) populations.

MATERIALS AND METHODS

The backcross populations were developed from wheat x *T. ponticum* F1 hybrids, and wheat x *T. intermedium* F1 hybrids. We used soft red winter wheats in these hybrids and backcrosses (Sharma *et al.* 1989, 1995). The reaction of the F1 hybrids to the prevalent and virulent strain PAV of BYDV has been described earlier (Sharma *et al.* 1989). The backcross seedlings at two-three leaf stage were first inoculated with BYDV-PAV by feeding viruliferous aphids on them. Aphid survival was monitored and any plant without live aphids was reinfected (Sharma *et al.* 1989, 1995). The plants were inoculated with *Puccinia triticina* culture No. 901 collected in Indiana. For leaf rust, the seedlings were inoculated in a moisture chamber by applying spore suspension with an automizer and keeping the seedlings in the moisture chamber overnight (Shaner *et al.* 1997). Subsequently, natural infection by *Erysiphe graminis* was allowed to occur in a greenhouse where no fungicide was applied. The plants were grown under 20-25°C, 14 h light and natural humidity. Scoring was done 12-14 d after inoculation. We analysed 190 BC2 plants and 209 BC3 plants from the wheat x *T. ponticum* cross, and were able to score all four traits (BYDV, powdery mildew, leaf rust and chromosome number) on 28 BC2 plants and 49 BC3 plants, and all the three diseases on 63 BC2 plants and 146 BC3 plants. There were 92 BC2 plants and 60 BC3 plants from the wheat x *T. intermedium* cross, of which 29 and 26, respectively, had all the four traits scored, and 54 and 28, respectively, had all the three diseases scored. Checks for the ELISA were oat cultivar Clintland 64, wheat cultivars Abe, Caldwell and Cardinal, *T. ponticum* and *T. intermedium*. Additionally, P-PAV and healthy (uninfected) Clintland 64 were included to rule out variation due to the method. In the powdery mildew and leaf rust tests, the checks were wheat cultivar Morocco, *T. ponticum* and *T. intermedium*. The BC2 populations were random while the BC3 were the result of selection in BC2 for fewer alien chromosomes and lower enzyme-linked immunosorbent assay (ELISA) values (measure of level of BYDV resistance). Wheat was the recurrent parent. The *Thinopyrum* chromosomes do not pair meiotically with wheat chromosomes due to lack of homology and are thus randomly eliminated during backcrossing (Dvorak 1979; Johnson and Kimber 1967; Sharma and Gill 1983). The resistance to the diseases studied thus reflects the effect of the *Thinopyrum* chromosomes.

The procedure for testing BYDV resistance by ELISA is given in Sharma *et al.* (1989). No scoring was done on the basis of visual symptoms. Unlike oat, the concentration of virus in infected plants was not consistently correlated with symptom severity in wheat (Baltenberger *et al.* 1987, Sharma *et al.* 1989). The chromosome numbers were determined from root-tip cells of the germinated seeds by the Feulgen method (Metz *et al.* 1988). Plants for powdery mildew and leaf rust were scored as 1 for resistant, 2 for moderately resistant, 3 for moderately susceptible and 4 for susceptible (Hu *et al.* 1997; Shaner *et al.* 1997). Actual ELISA values were used for quantitative data analysis. For qualitative analysis, plants with ELISA values 0.3 or less were classified as resistant and those with higher than 0.3 were classified as susceptible (Sharma *et al.* 1995). Likewise, for qualitative analysis of powdery mildew and leaf rust, scores 1 and 2 were classified as resistant, and scores 3 and 4 as susceptible.

Data analyses were performed using SAS statistical software (SAS Inst. 1999).

RESULTS AND DISCUSSION

Results of our study showed that the possibility of having multiple resistance to all three diseases was low. Of the plants scored for all the four traits (three diseases and chromosome numbers), 53.6% and 6.9% were resistant to all the three diseases (powdery mildew, leaf rust and BYDV) in BC2 in wheat x *T. ponticum* cross and wheat x *T. intermedium* cross, respectively (Table 1). The proportion of plants in BC3 resistant to all the three diseases after selection for resistance to BYDV and fewer alien chromosomes in BC2 declined to 4.1% and 3.8%, respectively. The trend remained the same when larger population, scored for all the three diseases including those without chromosome counts, was analysed (Table 1). Taking two diseases at a time, the proportion of BYDV resistant plants with resistance to powdery mildew or leaf rust also decreased in the BC3 generation when compared to the BC2 generation in both crosses (Ta-

Table 1. Percentage of plants resistant to all three diseases (BYDV, powdery mildew and leaf rust) in BC2 and BC3 populations (values in parentheses are for the plants scored for all the three diseases but not all of them scored for chromosome numbers)

Cross	Generation	No. of plants	Percentage of plants resistant to all three diseases
Wheat x *T. ponticum*	BC2	28 (63)	53.6 (49.2)
	BC3	49 (146)	4.1 (3.4)
Wheat x *T. intermedium*	BC2	29 (54)	6.9 (3.7)
	BC3	26 (28)	3.8 (3.6)

ble 2). Only 9.8% and 6.8% of the BC2 plants resistant to powdery mildew and leaf rust, respectively, were resistant to BYDV in wheat x *T. intermedium* cross (data not shown). These percentages were higher (72.6% and 69.5%, respectively) in wheat x *T. ponticum* cross but were reduced drastically in BC3 to 8.3% and 7.7%, respectively, once selection was applied in the BC2 generation in favor of BYDV resistance and lower chromosome numbers (data not shown). The proportion of leaf rust resistant plants among powdery mildew resistant plants also decreased in going from BC2 to BC3 generation in both crosses (from 97.7% to 76.2% in wheat x *T. ponticum* cross and from 81.4% to 62.5% in wheat x *T. intermedium* cross) (data not shown). No selection was applied to leaf rust or powdery mildew and the decrease was probably due to random elimination of *Thinopyrum* chromosomes that carried resistance to these diseases.

In both crosses, mean values increased significantly (increased susceptibility) for powdery mildew, leaf rust and BYDV, and mean chromosome numbers decreased significantly, in the BC3 populations compared to the BC2 populations, except for BYDV and leaf rust in the wheat x *T. intermedium* cross, indicating increase in susceptibility with reduction in chromosome numbers (Table 3). Percentage of resistant plants decreased in both crosses for powdery mildew, leaf rust and BYDV, except for BYDV in wheat x *T. intermedium* cross. The resistance in BC2 generation of wheat x *T. ponticum* cross was relatively high but decreased in BC3. Barring sample size effect, comparison of percent resistant plants showed that selection for fewer chromosomes while maintaining BYDV resistance was more effective in the wheat x *T. intermedium* cross than in wheat x *T. ponticum* cross (Table 3). It appears that the genetic control for resistance to the three diseases studied is not on one chromosome.

T-test showed that the mean chromosome numbers were significantly different between BYDV resistant and susceptible plants in BC3 in both crosses, and in BC2 of wheat x *T. ponticum* cross (Table 4). Mean chromosome numbers between leaf rust resistant and susceptible plants in BC3 of wheat x *T. ponticum* cross, and between powdery mildew resistant and susceptible plants in BC2 of wheat x *T. intermedium* cross were also significantly different. In other cases, mean chromosome numbers were not statistically different. In all cases of significant differences, the chromosome numbers were significantly lower in susceptible plants, except for leaf rust in BC3 of wheat x *T. ponticum* cross (Table 4). *T*-test indicated that mean ELISA values were significantly different in both generations in wheat x *T. ponticum* cross between powdery mildew resistant and susceptible plants as well as between leaf rust resistant and susceptible plants (Table 5). The mean ELISA values were significantly higher in BC2 but significantly lower in BC3 for the plants susceptible to leaf rust or powdery mildew. The differences were not significant in the wheat x *T. intermedium* cross.

Correlation coefficients between chromosome numbers and ELISA values were negative for all the four populations (data not shown). They were highly significant ($P < 0.01$) for both BC3 polulations ($r = -0.296$ for wheat x *T. ponticum* cross and $r = -0.371$ for wheat x *T. intermedium* cross), and significant for BC2 of wheat x *T. ponticum* cross ($r = -0.172$, $P < 0.10$) and wheat x *T. intermedium* cross ($r = -0.330$, $P < 0.05$). These results showed that as the critical or major *Thinopyrum* chromosome(s) were eliminated, susceptibility increased.

Table 2. Percentage of barley yellow dwarf virus (BYDV) resistant plants (BYDV resistant plant numbers are given in parantheses) that were resistant to powdery mildew (PM) or leaf rust (LR) in BC2 and BC3 generations (data include whole populations with two or all three diseases scored)

Cross	Generation	% resistant to	
		PM	LR
Wheat x *T. ponticum*	BC2	72.6 (95)	95.3 (43)
	BC3	50.0 (18)	44.4 (18)
Wheat x *T. intermedium*	BC2	62.5 (8)	75.0 (4)
	BC3	50.0 (6)	66.7 (6)

Table 3. Ranges, means and standard deviations (SD) for powdery mildew (PM) scores, leaf rust (LR) scores, BYDV (ELISA) values and chromosome number (No. of plants and percent resistant plants are given in parantheses in each case; e = wheat x *T. ponticum* cross; i = wheat x *T. intermedium* cross)

	PM[a]			LR[a]			BYDV (ELISA)			Chromosome number		
Pop.	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
e BC2	1-4 (133, 71.4%)	1.84	1.28	1-4 (63, 93.6%)	1.21	0.70	0.008-2.000 (190, 74.7%)	0.283	0.385	43-73 (97)	48.40	5.71
e BC3	1-4 (184, 58.7%)	2.23 *	1.39	1-4 (148, 69.6%)	1.92 **	1.24	0.001-2.000 (209, 8.6%)	0.978 **	0.483	42-54 (97)	45.09 **	2.28
i BC2	1-4 (88, 58.0%)	2.30	1.29	1-4 (56, 78.6%)	1.64	1.09	0.074-2.000 (92, 8.7%)	1.109	0.621	42-56 (43)	48.77	2.88
i BC3	1-4 (42, 21.4%)	3.21 **	1.00	1-4 (29, 65.5%)	1.93	1.22	0.110-1.964 (59[b], 11.9%)	1.026	0.515	42-50 (55)	45.25 **	2.00

[a] For PM and LR, 1 = resistant, 2 = moderately resistant, 3 = moderately susceptible and 4 = susceptible, (1,2) = resistant, (3,4) = susceptible.
[b] Of the total 60 plants, one was not analyzed by ELISA.
*,** BC3 mean signifiantly different from BC2 mean at $P = 0.05$ and $P = 0.01$, respectively, for each of the four traits (PM, LR, ELISA and chromosome number) within each of the two crosses (e, i.).

Chi-square test by 2x2 contingency analysis of the three diseases showed that the patterns of resistance were significantly different for powdery mildew and leaf rust in BC2 and BC3, and for BYDV and leaf rust in BC3 in wheat x *T. ponticum* cross (Table 6). At 10% level of confidence, chi-square for BYDV and powdery mildew was significant in BC3 in the wheat x *T. intermedium* cross. Other chi-squares were non-significant i.e. the patterns of resistance or susceptibility were similar for any two diseases compared.

From progeny of a cross between wheat x *T. junceiforme* Love & Love (Love), Ellneskog (2002) obtained lines resistant to powdery mildew and leaf rust. Li *et al.* (1998) obtained wheat x *A. cristatum* (L.) Gaertner derivatives which were more resistant to both powdery mildew and BYDV compared to wheat. Such an association was not evident in the present intergeneric crosses. Larkin *et al.* (1995) reported that out of the disomic alien addition lines isolated from a partial amphiploid (2n = 56) of wheat x *T. intermedium*, one was resistant to BYDV, and one to leaf, stem and stripe rusts. In the study of Comeau *et al.* (1994), Agrotricum (*Agropyron* x *Triticum*) line OK211542 (2n = 56) was immune to BYDV. Through a selection for BYDV and threshable phenotype with wheat-like seed, F7-derived lines were obtained which were immune to BYDV with 44 somatic chromosomes. The low frequency of expression of immunity suggested that more than one gene was required for full expression of resistance (Comeau *et al.* 1994). Ander-

Table 4. *T*-test for chromosome numbers on BC2 and BC3 between resistant and susceptible plants for powdery mildew (PM), leaf rust (LR), or for BYDV

Cross	Generation	Disease	Resistant: Number of plants	Resistant: Mean chromosome number	Susceptible: Number of plants	Susceptible: Mean chromosome number	*t*-value
Wheat	BC2	LR	28	49.11	0	[a]	[a]
x *T. ponticum*	BC3		34	44.85	15	46.67	-2.46*
	BC2	BYDV	74	48.97	23	46.57	1.79[b]
	BC3		11	46.82	86	44.87	2.76**
	BC2	PM	28	49.36	12	49.08	1.04
	BC3		27	45.44	47	45.17	0.51
Wheat	BC2	LR	23	47.87	7	48.71	-0.84
x *T. intermedium*	BC3		17	45.88	10	45.50	0.40
	BC2	BYDV	8	48.38	35	48.46	-0.42
	BC3		6	47.33	48	45.00	2.84**
	BC2	PM	21	49.24	20	47.80	1.73[b]
	BC3		9	46.44	28	45.36	1.30

*, ** Significant at $P = 0.05$ and $P = 0.01$, respectively.
[a] All plants resistant (no susceptible plants with chromosome numbers).
[b] Significant at $P = 0.10$.

Table 5. *T*-test for ELISA on BC2 and BC3 between resistant and susceptible plants for powdery mildew (PM), or leaf rust (LR)

Cross	Generation	Disease	Resistant		Susceptible		*t*-value
			No. of plants	Mean ELISA	No. of plants	Mean ELISA	
Wheat	BC2	LR	59	0.312	4	1.092	-3.34**
x *T. ponticum*	BC3		104	0.988	44	0.777	2.38*
	BC2	PM	95	0.249	38	0.495	-3.02**
	BC3		108	1.025	76	0.880	1.99*
Wheat	BC2	LR	44	1.074	12	1.217	-0.73
x *T. intermedium*	BC3		19	0.999	9	0.777	0.90
	BC2	PM	51	1.106	37	1.110	-0.03
	BC3		9	0.874	32	1.088	-1.03

*, ** Significant at P = 0.05 and P = 0.01, respectively.

son *et al.* (1998) have shown that the full BYDV resistance of *T. intermedium* was not realized in the wheat-*T. intermedium* chromosome substitution line P29 for group 7 chromosome developed by Sharma *et al.* (1997b).

Sharma *et al.* (1997b) reported that substitution line P29 was resistant to BYDV but susceptible to four cultures of powdery mildew. Genes for resistance to Hessian fly (*Mayetiola destructor* Say) [Diptera: Cecidomyiidae] biotype L and BYDV were also found to be on different chromosomes of *T. intermedium* (Sharma *et al.* 1992, 1997b). This is consistent with the present finding that these resistances are not carried in a linkage block in *T. intermedium*. P29 showed resistance to leaf rust. It is not known whether this resistance was due to gene(s) in wheat or *T. intermedium*, or to BYDV reducing the resistance to leaf rust in the present study. BYDV infection increased the susceptibility of wheat to *Gibberella zeae* (Schwein.) Petch, *Alternaria* and *Cladosporium* (Smith 1962), *Cochliobolus sativus* (Ito & Kuribayashi) Drechs. ex Dastur (Scott 1968), and *Gaeumannomyces graminis* (Sacc.) Arx & D. Olivier (Price 1970). The present work did not include experiments to study synergetic effects. The results of our study indicated that whereas some gene(s) for resistance to leaf rust may be introgressed along with genes for resistance to BYDV, major genes for resistance to BYDV, powdery mildew and leaf rust cannot be bred simultaneously from *Thinopyrum* into wheat. Since we know little about the genetic control of resistance to these diseases, it is difficult to speculate the physical distribution and possible linkage.

Table 6. Frequency distribution by 2x2 contingency table for BC2 and BC3 plants for the three diseases, PM, LR and BYDV (resistant = R, susceptible = S)

Cross	Generation	Disease	R/S	BYDV R	BYDV S	BYDV Chi-square	LR R	LR S	LR Chi-square
Wheat x *T. ponticum*	BC2	PM	R	69	26	0.24	43	1	4.08*
			S	26	12		16	3	
	BC3		R	9	99	0.62	77	24	5.11*
			S	9	67		26	19	
Wheat x *T. intermedium*	BC2		R	5	46	0.08	22	6	0.02
			S	3	34		20	6	
	BC3		R	3	6	3.23[a]	5	3	0.04
			S	3	29		14	7	
Wheat x *T. ponticum*	BC2	LR	R	41	18	0.66			
			S	2	2				
	BC3		R	8	96	6.54*			
			S	10	34				
Wheat x *T. intermedium*	BC2		R	3	41	0.03			
			S	1	11				
	BC3		R	4	15	0.01			
			S	2	7				

* Significant at P = 0.05.
[a] Significant at P = 0.10.

ACKNOWLEDGEMENT

Purdue Agric. Res. Programs Journal No. 17245. Judy Santini's professional help in the statistical analysis is gratefully praised.

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