Chromosomal location of genes for resistance to powdery mildew in Chinese wheat lines Jieyan 94-1-1 and Siyan 94-1-2

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Two Chinese wheat lines Jieyan 94-1-1 and Siyan 94-1-2 are resistant to all 120 isolates of *Blumeria graminis* f. sp. *tritici* maintained in Weihenstephan, Germany. Monosomic analyses employing the susceptible set of 21 Chinese Spring monosomic lines revealed that the line Jieyan 94-1-1 carries one dominant gene on translocated wheat/rye chromosome 1B/1R and one recessive gene on chromosome 7B, whereas line Siyan 94-1-2 possesses one recessive gene on chromosome 7B and one dominant gene on chromosome 5D. Allelism tests in combination with the use of specific isolates comfirmed that the dominant genes in Jieyan 94-1-1 and Siyan 94-1-2 are *Pm8* and *Pm2*, respectively. The recessive genes present in each of the two lines are shown to be new alleles located on chromosome 7B at the *pm5* locus. The two genes are tentatively designated *mljy* in Jieyan 94-1-1 and *mlsy* in Siyan 94-1-2, respectively.

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Powdery mildew, caused by *Blumeria graminis* (DC) E.O. Speer f. sp. *tritici* is an important leaf disease of common wheat (*Triticum aestivum* L.) in many regions of the world. Growing of resistant cultivars is the most economical and environmentally safe method for controlling this disease. Because of the co-evolution of the wheat host and the pathogen, the resistance of single genes is easy to be overcome by new races of the pathogen possessing corresponding virulence genes. However, gene combinations (gene pyramiding) can be used for enhancing powdery mildew resistance. Up to now, 27 gene loci for resistance to powdery mildew have been located on the different wheat chromosomes (HSAM and ZELLER 2002), of which the recessive resistance gene *pm5* was located on the long arm of chromosome 7B (LAW and WOLFE 1966), *Pm8* on the translocated wheat-rye chromosome T1BL·1RS (ZELLER 1973; MCINTOSH 1981) and *Pm2* on the chromosome 5D (MCINTOSH and BAKER 1970). Gene *pm5* is widely distributed in cultivars and landraces of China and Europe (HUANG et al. 1997; ZELLER et al. 1998). Four alleles and two alleles at the *pm5* locus have been recently reported by HSAM et al. (2001) and HUANG et al. (2000a), respectively.

HUANG et al. (1997) found that the two Chinese wheat lines Jieyan 94-1-1 and Siyan 94-1-2 were resistant to 11 differential mildew isolates used to classify documented powdery mildew resistance (*Pm*) genes. Further tests with 120 *Bgt* isolates maintained in Weihenstephan indicated that both lines showed resistant response patterns to all isolates. The objective of this study was to characterise the resistance genes involved in Jieyan 94-1-1 and Siyan 94-1-2 and to determine their chromosomal locations by monosomic analysis.

MATERIALS AND METHODS

The near-isogenic line Ulka/8 × Cc (*Pm2*) and the cultivar Disponent (*Pm8*) were kindly supplied by R.A. McIntoch, Sydney, Australia and Bayerische Pflanzenzuchtgesellschaft, Munich, Germany, respectively. The cultivar Hope carrying *pm5* was obtained from V. Chapman, Plant Breeding Institute, Cambridge, U.K. Chinese wheat lines Jieyan 94-1-1 and Siyan 94-1-2 provided by A.M. Zhang, China Agricultural University, Beijing, were selected for resistance to powdery mildew derived from wheat lines having *Aegilops tauschii*/wild oat (*Avena fatua*) and *T. spelta*/wild oat, respectively (A. M. Zhang, pers. comm.) in their pedigrees.

The Chinese Spring (CS) monosomic lines used for gene localization were originally obtained from E.R. Sears, U.S.A. The resistant lines Jieyan 94-1-1 and Siyan 94-1-2 were crossed with euploid Chinese Spring and its 21 monosomic lines. In all crosses, Chinese Spring and the 21 monosomic lines were used as the female parents. Cytologically confirmed monosomic F_1 plants were grown in the greenhouse

to obtain F_2 seeds. Mitotic chromosome numbers of all parental lines and F_1 plants of all cross combinations as well as F_2 plants of critical crosses were determined using Feulgen staining procedures. After knowledge of gene location in the F_2 populations, allelism at the *pm5* locus was tested between Hope carrying *pm5a* and the lines Jieyan 94-1-1 and Siyan 94-1-2, respectively. Furthermore, allelic tests at the *Pm8* locus between Disponent and Jieyan 94-1-1, and at the *Pm2* locus between Ulka/8 × Cc and Siyan 94-1-2 were also performed. All cross combinations were studied in the F_2 and F_3 populations.

After one dominant resistance gene was located on chromosome 1B in the line Jieyan 94-1-1 and was confirmed to be allelic to *Pm8*, this line was cytologically scored for the presence of satellited chromosome number in root tip mitosis using Feulgen standard staining procedure. Plants homozygous for the translocated chromosome pair T1BL·1RS was expected to have only two (6B) satellited chromosomes (ZELLER 1973). The line Jieyan 94-1-1 was also tested for the presence of secalin gene locus *Sec-R1* by acetic polyacrylamide gel electrophoresis (A-PAGE) according to the method of HSAM et al. (1993).

The *Blumeria graminis tritici* (*Bgt*) isolates used for the differentiation of the known major resistance genes were collected from different parts of Europe and selected from single spore progenies. The tests of mildew resistance were conducted on primary leaf segments cultured on 6 g/l agar and 35 mg/l benzimidazole in plastic boxes. The methods of inoculation, conditions of incubation and disease assessment were according to HUANG et al. (1997). Three major classes of host reactions were distinguished: r = resistant, i = intermediate, s = susceptible. Chi-square tests for goodness of fit were used to test for deviation of observed data from theoretically expected segregation.

RESULTS

Disease response patterns

The response patterns of the resistance wheat lines Jieyan 94-1-1 and Siyan 94-1-2, together with wheat lines Ulka/8 × Cc (*Pm2*), Hope (*pm5a*) and Disponent (*Pm8*) with known *Pm* genes were characterised with 15 differential *Bgt* isolates (Table 1). The lines Jieyan 94-1-1 and Siyan 94-1-2 were resistant to the 15 different *Egt* isolates tested and revealed a wide spectrum of resistances to the *Bgt* isolates in comparison to Ulka/8 × Cc, Hope and Disponent. Additional tests revealed that these two lines showed resistance responses to all 120 *Bgt* isolates maintained in Weihenstephan, Germany.

Chromosomal location of the resistance genes

Resistance tests of F_2 populations from crosses of CS and 21 CS monosomic lines with Jieyan 94-1-1 were made using *Bgt* isolate no. 9 and 10. The isolate no. 9 is avirulent for both resistance genes and isolate no. 10 is avirulent only for the recessive gene. The F_2 plants from the crosses CS/Jieyan 94-1-1 and 20 CS monosomic lines/Jieyan 94-1-1 tested with isolate no. 9, segregated in a 13:3 ratio (Table 2), indicating that Jieyan 94-1-1 carried two genes, one dominant and one recessive for resistance to *Bgt* isolate no. 9. The segregation of the F_2 plants from crosses of CS mono-1B and CS mono-7B with Jieyan 94-1-1, deviated significantly from the expected ratio of 13:3 ($P < 0.001$), revealing that chromosomes 1B and 7B each carried one resistance gene, respectively. Monosomic analysis using *Bgt* isolate no. 10 revealed a 1:3 segregation ratio in the F_1 progenies of crosses between CS, as well as 20 other CS monosomic lines and Jieyan 94-1-1. However, a significant deviation from this ratio was observed in the cross involving CS monos-7B (Table 2), indicating that the recessive

Table 1. *Differential reactions of five wheat cultivars/lines possessing powdery mildew resistance genes after inoculation with 15 isolates of Blumeria graminis f. sp. tritici*

Cultivar/line	*Blumeria graminis tritici* isolates															*Pm* gene
	2	5	6	9	10	12	13	14	15	16	17	71	100	117	E	
Ulka/8 × Cc[1]	s[2]	r	r	s	r	s	s	s	r	s	s	s	s	r	r	2
Hope	s	s	s	s	r	s	s	r	s	s	s	r,i	r,i	s	r	5a
Disponent	r	s	s	r	s	r	s	s	s	s	r	r	s,i	r	s	8
Jieyan 94-1-1	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	8+*mljy*
Siyan 94-1-2	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r	2+*mlsy*

[1] Seven times backcrossed to Chancellor.
[2] r = resistant, s = susceptible, i = intermediate.

Table 2. *Segregation for seedling reaction to Bgt isolate no. 9 and 10 in progenies of monosomic F_1 plants from crosses of Chinese Spring (CS) and 21 CS monosomic lines with wheat line Jieyan 94-1-1*

Chromosome involved	Isolate no. 9		χ^2 (13:3)	Isolate no. 10		χ^2 (1:3)
	Observed segregation			Observed segregation		
	Res.	Sus.		Res.	Sus.	
CS × Jieyan 94-1-1	140	30	0.14	49	121	1.32
1A	128	29	0.01	42	115	0.25
2A	111	26	0.00	38	99	0.55
3A	148	25	2.10	46	127	0.23
4A	110	30	0.66	35	105	0.00
5A	134	29	0.10	46	117	0.90
6A	219	50	0.00	72	197	0.45
7A	119	28	0.01	41	106	0.65
1B	**223**	**27**	**10.37****	74	176	2.82
2B	112	26	0.00	33	105	0.09
3B	131	19	3.64	45	105	2.0
4B	118	21	1.21	37	102	0.19
5B	128	32	0.16	40	120	0.00
6B	110	26	0.01	34	102	0.00
7B	**217**	**13**	**25.90*****	**215**	**15**	**575.21*****
1D	151	31	0.35	47	135	0.07
2D	129	32	0.13	45	116	0.75
3D	134	26	0.65	47	113	1.63
4D	143	36	0.10	53	126	2.03
5D	131	37	1.18	45	123	0.28
6D	136	33	0.07	48	121	1.04
7D	143	32	0.02	49	126	0.84

** $P<0.01$, *** $P<0.001$.

gene was located on chromosome 7B. Hence it could be inferred that the dominant gene was located on chromosome 1B.

Additional tests involving 27 and 22 F_3 families of resistant F_2 plants from the critical crosses of CS mono-1B and CS mono-7B with Jieyan 94-1-1 were also made to confirm the F_2 monosomic results. Forty plants from each F_3 families were tested again with *Bgt* isolate no. 9 and 10. No susceptible plant was observed in 20 F_3 families of CS mono-1B/Jieyan 94-1-1 with isolate no. 9 and also in 20 F_3 families of CS mono-7B/Jieyan 94-1-1 with isolate no. 9 and 10, confirming the location of the two resistance genes on chromosomes 1B and 7B, respectively. Very few susceptible plants were found in only seven and two F_3 families of the respective crosses. These plants were expected to be nullisomics ($2n = 40$) derived from monosomics F_2 plants.

F_2 monosomic analysis of CS monosomic crosses with the line Siyan 94-1-2 was carried out using *Bgt* isolate no. 10 and 14 (Table 3). The isolate no. 10 is avirulent to both resistance genes, whereas isolate no. 14 is avirulent only to the recessive gene in this line. In tests employing *Bgt* isolate no. 14, F_2 populations from the disomic cross CS/Siyan 94-1-2 and 19 out of the 20 aneuploid CS monosomics/Siyan 94-1-2 crosses segregated in a 1 resistant: 3 susceptible ratio indicating the presence of a recessive resistance gene in Siyan 94-1-2. The F_2 population from the cross involving CS mono-7B did not fit the 1:3 ratio. Only 23 out of 198 F_2 plants in the cross with 7B were susceptible (Table 3), inferring that the recessive gene was located on chromosome 7B.

When tested with *Bgt* isolate no. 10, F_2 populations from the crosses CS/Siyan 94-1-2 and 18 CS monosomic lines/Siyan 94-1-2 segregated in a 13 resistant:3 susceptible ratio, indicating that Siyan 94-1-2 had two resistance genes, one dominant and one recessive. The segregations of the crosses CS mono-7B/Siyan 94-1-2 and CS mono-5D/Siyan 94-1-2 deviated significantly from the expected ratio of 13:3 ($P < 0.001$). As a recessive gene was already found to be on chromosome 7B, it could now be inferred that the dominant gene in the line Siyan 94-1-2 was located on chromosome 5D.

Forty plants each from 23 and 22 F_3 families of resistant F_2 plants from the critical crosses CS mono-7B/Siyan 94-1-2 and CS mono-5D/Siyan 94-1-2 were tested further with *Bgt* isolates no. 10 and 14. A total of 22 F_3 families from the cross CS mono-7B/Siyan 94-1-2 inoculated with isolates no. 10 and 14 and 16 F_3 families of CS mono-5D/Siyan 94-1-2 tested with

Table 3. *Segregation for seedling reaction to Bgt isolate no. 10 and 14 in progenies of monosomic F_1 plants from crosses of Chinese Spring (CS) and 20 CS monosomic lines with wheat line Siyan 94-1-2*

Chromosome involved	Isolate no. 10		χ^2 (13:3)	Isolate no. 14		χ^2 (1:3)
	Observed segregation			Observed segregation		
	Res.	Sus.		Res.	Sus.	
CS × Siyan 94-1-2	97	20	0.21	31	86	0.13
1A	104	22	0.14	34	102	0.00
2A	–	–	–	–	–	–
3A	134	26	0.65	43	117	0.30
4A	130	25	0.70	39	116	0.00
5A	109	21	0.58	34	96	0.09
6A	101	27	0.46	37	91	1.04
7A	124	27	0.07	39	112	0.05
1B	131	25	0.76	42	114	0.31
2B	93	20	0.08	24	89	0.85
3B	128	24	0.87	45	107	1.72
4B	84	16	0.49	30	70	1.33
5B	32	5	0.67	13	24	2.03
6B	56	11	0.23	17	50	0.00
7B	**188**	**10**	**24.39*****	**175**	**23**	**424.25*****
1D	124	31	0.16	39	116	0.60
2D	134	31	0.00	42	123	0.02
3D	135	20	3.48	40	115	0.05
4D	99	20	0.29	31	88	0.07
5D	**228**	**10**	**33.07*****	63	175	0.74
6D	135	25	1.02	41	129	0.07
7D	134	22	2.21	43	113	0.55

*** $P < 0.001$, – not available for test.

isolate no. 10 produced no susceptible individuals. Very few susceptible plants were detected in only one and six F_3 families of the respective crosses. These susceptible plants were expected to be nullisomic ($2n = 40$) derived from monosomic F_2 plants. F_3 analyses confirmed that the two resistance genes in Siyan 94-1-2 were located on chromosomes 7B and 5D, respectively.

Allelism tests at the Pm2(5D), pm5(7B) and Pm8(T1BL·1RS) loci

The line Jieyan 94-1-1 was crossed to Disponent (*Pm8*) and Hope (*pm5a*) to test for allelism with known resistance genes located on the same chromosomes. Likewise, Siyan 94-1-2 was crossed to Ulka/8 × Cc (*Pm2*) and Hope respectively. No segregation was observed in the F_2 population from the cross Ulka/8 × Cc//Siyan 94-1-2 after inoculation with *Bgt* isolates no. 10 and 15 which were avirulent for both parents (Table 4). Similarly, 55 F_3 families from the same cross inoculated with the same *Bgt* isolates showed complete resistance. However, these same F_3 families tested with *Bgt* isolate no. 5, which was virulent to Ulka/8 × Cc but avirulent to Siyan 94-1-2,

Table 4. *Allelism tests between the resistance gene Pm2, pm5, Pm8 and other resistance genes in Jieyan 94-1-1 and Siyan 94-1-2 in the F_2 generations to various Bgt isolates*

Cross	Isolate no.[a]	Parent reaction		Observed segregation of F_2			Expected ratio	χ^2	P
		P_1[b]	P_2	Total	Res.	Sus.			
Ulka/8 × Cc(*Pm2*) × Siyan 94-1-2	10, 15	r	r	236	236	0	15:1	15.73	< 0.001
Hope (*pm5a*) × Siyan 94-1-2	10, 14	r	r	294	294	0	11:5	133.64	< 0.001
Hope (*pm5a*) × Jieyan 94-1-1	10, 14	r	r	221	221	0	11:5	100.45	< 0.001
Disponent (*Pm8*) × Jieyan 94-1-1	9, 12	r	r	250	250	0	15:1	16.67	< 0.001

[a] Avirulent isolates for both parents in each cross.
[b] P_1 = female parent, P_2 = male parent.

segregated into three groups, namely homozygous resistant, segregating for resistance and susceptibility, and homozygous susceptible, fitting a 1:2:1 ratios (Table 5). At present, no virulent *Bgt* isolate to Siyan 94-1-2 has been detected. Consequently, it was not possible to differentiate the dominant gene located on chromosome 5D in Siyan 94-1-2 and *Pm2* in Ulka/8 × Cc by their disease response patterns. It could only be inferred that the gene on chromosome 5D in Siyan 94-1-2 is either *Pm2* or allelic to this gene.

All F_2 plants from the crosses involving Hope/Jieyan 94-1-1 and Hope/Siyan 94-1-2 were resistant after inoculation with *Bgt* isolates no. 10 and 14 which were avirulent to both parents of each cross (Table 4), indicating that the recessive resistance genes in both the resistance lines studied are either allelic or very tightly linked to the *pm5* locus.

Forty-six and 59 F_3 families from the crosses Hope/Jieyan 94-1-1 and Hope/Siyan 94-1-2, inoculated with either *Bgt* isolates no. 16 or 9 (both virulent to Hope), segregated into three groups, namely homozygous resistant, segregating for resistance and susceptibility, and homozygous susceptible, fitting 1:2:1 ratios (Table 5). These same families when tested with *Bgt* isolates nos. 10 and 14 which were avirulent to both parents, showed homozygous resistance (Table 5), further supporting that the resistance genes in Jieyan 94-1-1 and Siyan 94-1-2 were each allelic to the *pm5* locus.

Similarly, no susceptible recombinant was found in the F_2 population from the cross Disponent/Jieyan 94-1-1 tested with *Bgt* isolates no. 9 and 12 (Table 4), indicating that the dominant gene on chromosome 1B in Jieyan 94-1-1 might be the gene *Pm8* on the T1BL·1RS wheat-rye translocated chromosome. Cytological and biochemical evidences further confirmed the identity of this gene. Root tips mitosis revealed only two satellited chromosomes indicating the absence of 1BS chromosome arm and the presence of the secalin *Sec-R1* locus from rye indicated that Jieyan 94-1-1 carried a T1BL·1RS wheat-rye translocated chromosome and that the dominant gene was probably *Pm8* located on the 1RS arm.

DISCUSSION

The line Jieyan 94-1-1 derived from wheat crosses involving originally a hybrid between *Aegilops tauschii* and wild oat *Avena fatua* (Zhang, A. M., pers. comm.), exhibited resistance to all the *Bgt* isolates used. Through monosomic analysis, one dominant gene and one recessive gene in this line were located on chromosomes 1B and 7B, respectively. It is documented that gene *Pm8* was on the wheat-rye translocated chromosome T1BL·1RS (McIntosh 1981), whereas the recessive gene *pm5a* in Hope was located on chromosome 7BL (Law and Wolfe 1966; Hsam et al. 2001). Results from monosomic analyses and allelism tests revealed that the resistance in Jieyan 94-1-1 was governed by two genes located on chromosomes 1B and 7B, respectively. This line possessed 42 chromosomes, including two instead of four satellited chromosomes. Moreover, the result from A-PAGE indicated the presence of the rye secalin gene *Sec-R1* on chromosome 1RS. Obviously a common wheat parent carrying a T1BL·1RS wheat-rye translocation must have contributed the *Pm8* gene which was located on the translocated chromosome. However, the source of the recessive gene on chromosome 7B could not be traced directly to the hybrid *Ae. tauschii*/*Avena fatua* which was originally involved in the cross, as *Ae. tauschii* (2n = 14) contributed the D genome of hexaploid wheat (Kihara 1944) and introgressions of *Avena fatua* (2n = 6x = 42) chromatin remains to be shown.

No segregation for resistance was observed in additional tests of F_2 population from the cross Disponent/Jieyan 94-1-1 with *Bgt* isolate no. 2, 17, 48, 52, 53, 71 and 72 (data not shown) which were avirulent to *Pm8* in Disponent, supporting further that the

Table 5. *Allelism tests between the powdery mildew resistance gene Pm2, pm5 and other resistance genes in Jieyan 94-1-1 and Siyan 94-1-2 analyzed in the F_3 populations of wheat crosses to various Bgt isolates*

Cross	Isolate no.	No. of F_3 families				Expected ratio	χ^2	P
		Total	Res.	Segr.	Sus.			
Hope (*pm5a*) × Jieyan 94-1-1	10, 14[a]	46	46	0	0	7:8:1	59.14	<0.001
	16[b]	46	12	20	14	1:2:1	0.96	0.50–0.70
Ulka/8 × Cc(*Pm2*) × Siyan 94-1-2	10, 15[a]	55	55	0	0	7:8:1	70.71	<0.001
	5[b]	55	11	30	14	1:2:1	0.78	0.50–0.70
Hope (*pm5a*) × Siyan 94-1-2	10, 14[a]	59	59	0	0	7:8:1	75.86	<0.001
	9[b]	59	21	31	7	1:2:1	6.80	0.02–0.05

[a] Avirulent for both parents in the cross.
[b] Virulent for Hope and Ulka/8 × Cc and avirulent for Jieyan 94-1-1 and Siyan 94-1-2.

dominant gene for resistance on the translocated T1BL·1RS chromosome of Jieyan 94-1-1 was the gene *Pm8*. Virulent *Bgt* isolates to the line Jieyan 94-1-1 were not found even after inoculation with 120 *Bgt* isolates from different regions of Europe and China. However, the combined reaction spectrum of the genes *pm5a* in Hope and *Pm8* in Disponent exhibited many susceptible responses (Table 1 and unpublished data). Therefore, the recessive gene in the line Jieyan 94-1-1 apparently possessed a different disease reaction pattern at the *pm5* locus. The new allele located on chromosome 7B at the *pm5* locus in Jieyan 94-1-1 is tentatively designated *mljy*.

The line Siyan 94-1-2 was developed from the hybrid *T. spelta*/*Avena fatua* (Zhang, A.M., pers. comm.) and was resistant to all 15 *Bgt* isolates used (Table 1). In this line, one dominant gene and one recessive gene were localized on chromosomes 7B and 5D, respectively, by mean of monosomic analysis. Allelism tests have shown that the dominant gene in Siyan 94-1-2 was allelic to the *Pm2* locus in Ulka/8 × Cc located on chromosome 5D (McIntosh and Baker 1970), whereas the recessive gene was located on chromosome 7B to the *pm5* locus (Tables 4 and 5).

No segregation was found in further resistance tests of F_2 population from the cross Ulka/8 × Cc// Siyan 94-1-2 with *Bgt* isolate nos. 6, 22, 23, 50, 56 and 64 which are all avirulent to *Pm2* in Ulka/8 × Cc. No virulent *Bgt* isolate was found after inoculation of the line Siyan 94-1-2 with 120 isolates from Europe and China. The complete resistant response pattern of the line Siyan 94-1-2 was different from the combined reaction spectrum of the genes *Pm2* in Ulka/ 8 × Cc and *pm5a* in Hope (Table 1 and unpublished data). Resistance tests of F_2 population from the cross CS/Siyan 94-1-2 with the first eleven isolates from Table 1 indicated a bi-factorial inheritance for one dominant gene and one recessive gene with three isolate no. 6, 10 and 15 avirulent to *Pm2*, but monogenic inheritance for one recessive gene with other eight isolates virulent to *Pm2* (data not shown). Thus it could be concluded that the dominant gene on chromosome 5D in line Siyan 94-1-2 is the gene *Pm2* and the recessive gene on chromosome 7B is one new allele at the *pm5* locus and hence is tentatively designated *mlsy*.

The origin of the genes *Pm2* and *mlsy* in the line Siyan 94-1-2 could not be directly determined as the wheat parents involved in the cross are no longer available. The *T. spelta* parent might be a source of powdery mildew resistance, as deduced from a report that a new gene *Pm1d* was derived from *T. spelta* var *duhamelianum* (Hsam et al. 1998). Recently, Tang et al. (1997) made tetrageneric crosses among *Triticum*, *Avena*, *Thinopyrum* and *Secale*, and developed one wheat line Yi 4155 which was resistant to powdery mildew, leaf rust, yellow rust and stem rust. The authors assumed that the resistance to powdery mildew might be on introgressed segments of *A. fatua* and (or) *S. cereale*. It was not known whether Jieyan 94-1-1 and Siyan 94-1-2 possessed introgressed alien chromatin. Apparently, they could be analysed further using molecular cytogenetical method such as genomic in situ hybridization (GISH).

The two lines Jieyan 94-1-1 and Siyan 94-1-2 showed very effective resistance to the various *Bgt* isolates collected from different parts of Europe and China. As the lines were developed from different germplasm sources it is most likely that they possessed different resistance genes and alleles and could play a significant role in resistance breeding to powdery mildew. In combining powdery mildew resistance genes to provide a more durable resistance in wheat cultivars conventional breeding are now being supplemented by the use of molecular markers. At present, molecular markers for the identification of alleles at the *Pm1*, *Pm3* and *Pm8* loci, as well as diagnostic marker for powdery mildew resistance gene *Pm24* are available (Hartl et al. 1993, 1999; Huang et al. 2000b; Mohler et al. 2001). Up to now, eight alleles at the *pm5* locus have been described (Huang et al. 2000a; Hsam et al. 2001; present study). Therefore, it would be beneficial to develop molecular markers for the differentiation of alleles at the *pm5* locus to aid in marker-assisted selection and gene pyramiding in future wheat resistance breeding programmes.

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