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Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em Thell.).
5. Alleles at the *Pm1* locus

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Abstract The chromosomal location and genetic characterization of powdery mildew resistance genes were determined in the common wheat lines MocZlatka, Weihenstephan Stamm M1N and in a resistant line of *Triticum aestivum* ssp. *spelta* var. *duhamelianum*. Monosomic analyses revealed that one major dominant gene is located on chromosome 7A in each of the lines tested. Allelism tests with *Pm1* in the backcross-derived line Axminster/8*Cc on 7A indicated that the resistance genes are alleles at the *Pm1* locus. These alleles are now designated *Pm1a* in line Axminster/8*Cc, *Pm1b* in MocZlatka, *Pm1c* in Weihenstephan Stamm M1N, and *Pm1d* in *T. spelta* var. *duhamelianum*, respectively.

Key words *Triticum aestivum* · Powdery mildew resistance · Monosomic analysis · Gene location · Allelism

Introduction

Powdery mildew, caused by *Erysiphe graminis* (*Blumeria graminis*) DC. f. sp. *tritici*, is a widespread disease of common wheat in areas with cool or maritime climates. Twenty four gene loci for resistance to this disease (*Pm1–Pm24*) have been assigned to specific chromosomes (Huang et al. 1997). Most of these loci were located on individual wheat chromosomes by means of monosomic analyses. The resistance gene *Pm1* was located on the long arm of chromosome 7A (Sears and Briggle 1969). This gene was identified in the Canadian wheat cv Axminster by Pugsley and Carter (1953) and was transferred by backcrossing to cv Chancellor by Briggle (1969).

Diploid einkorn wheat *Triticum monococcum* (AA, 2n = 14) is a source of disease and pest resistance for commercial bread wheat. Valkoun and Mamluk (1993) introduced powdery mildew resistance from *T. monococcum* into a susceptible common wheat cultivar Zlatka. The resistance gene in a derivative line, referred to as MocZlatka in the present study, was tentatively designated *PmTm1*. A common wheat strain, Weihenstephan Stamm M1 (M1), used by many workers as a differential standard (Nover 1957; McIntosh and Baker 1966), is known to possess the resistance gene *Pm4b* (Wolfe 1967). In 1986, a M1 seed sample was obtained from Bayerische Landesanstalt für Bodenkultur und Pflanzenbau (LBP), Weihenstephan. This line proved not to be the differential line with *Pm4b*, but gave a distinctive pattern of disease response to a differential set of *E. graminis* f. sp. *tritici* isolates. This new line, designated Weihenstephan Stamm M1N (M1N), was earlier reported to carry the resistance gene *Pm18* (Zeller et al. 1993).

The present study describes the location and characterization of genes for resistance to powdery mildew on chromosome 7A in three lines of common wheat, namely MocZlatka, M1N and a resistant line of *Triticum spelta* var. *duhamelianum* (TSD), and demonstrates that the genes are either alleles at the *Pm1* locus or else a closely linked cluster of genes.

Materials and methods

The backcross-derived line Axminster/8*Chancellor (Axminster seven times backcrossed to Chancellor), possessing powdery mildew gene *Pm1*, was kindly supplied by R. A. McIntosh, University of

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Sydney, Australia. The common wheat line MocZlatka, selected from the cross of a diploid *T. monococcum* line ATRI 1509/SLK and a *T. durum* line ATRI 3310/SLK and subsequently backcrossed to the Czech wheat cultivar Zlatka (Valkoun and Mamluk 1993), was provided by P. Bartoš, Prague-Ruzyne, Czech Republic. Wheat strain M1N was obtained from G. Zimmerman (LBP), Weihenstephan. The blue-grained wheat line Blaukorn Weihenstephan, six other blue-grained wheat lines previously described by Zeller et al. (1991), and *T. spelta* var. *duhamelianum* TRI 2258 originating from Cluj, Romania, were provided by C. Lehmann, Gene Bank Gatersleben, Germany.

The Chinese Spring monosomic series and Zlatka monosomic lines 1A, 2A, 3A, 4A and 7A, used for locating the resistance genes, were originally obtained from E. R. Sears, USA, and J. Košner, Prague, Czech Republic, respectively. All 21 Chinese Spring (CS) monosomic lines were used as the female parents in crosses with M1N and TSD, whereas only A-genome CS and Zlatka monosomics were used in crosses with MocZlatka, as the resistance in this line originated from *T. monococcum*. 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 were determined using standard Feulgen staining procedures. After the determination of gene location in the F_2 populations from monosomic F_1 plants, allelic tests were made among Axminster/8*Cc and the wheat lines MocZlatka, M1N and TSD. In addition, allelic tests between Normandie possessing genes *Pm1*, *Pm2* and *Pm9* and MocZlatka and M1N lines, as well as allelic tests between TSD and M1N, were also carried out. All cross combinations were studied as F_2 populations; those crosses involving Axminster/8*Cc and the three tested lines, as well as the cross Normandie/M1N, were further tested as F_3 lines.

The *E. graminis* f. sp. *tritici* (*Egt*) isolates used for the differentiation of the known major resistance genes were collected from different parts of Europe and selected from single-spore progenies (Felsenstein et al. 1991). The *Egt* isolates are classified under Weihenstephan accession numbers and maintained at the Institut für Pflanzenbau und Pflanzenzüchtung, Weihenstephan. The tests for mildew resistance were conducted on primary leaf segments cultured on 6 g/l of agar and 35 mg/l of benzimidazole in plastic boxes. The methods of inoculation and the conditions of incubation and disease assessment were according to Hsam and Zeller (1997). Three main classes of host reactions were distinguished: r = resistant (0–20% infection relative to cv Kanzler), i = intermediate (30–50% infection), s = susceptible (> 50% infection). In some cases, due to larger variation of disease reactions, the creation of combined classes (r,i ; i,s) was necessary. Chi- square tests for goodness of fit were used to test for deviation of the observed data from the theoretically expected segregation. In the tests of allelism, the method of Giese et al. (1981) was followed to estimate recombination.

Results

Disease responses of wheat cultivars/lines to *E. graminis tritici*

A set of 14 *Egt* isolates was used to characterize the disease response patterns of the resistant lines MocZlatka, M1N and TSD in comparison with lines possessing known resistance genes (Table 1). The line Axminster/8*Cc carrying the resistance gene *Pm1* showed a distinctive pattern of response to the *Egt* isolates employed. The cultivar Normandie possesing genes *Pm1*, *Pm2* and *Pm9* (McIntosh 1983) showed the combined response spectra of the lines Axminster/8*Cc, Ulka (*Pm2*) and N14 (*Pm9*), a derivative line of Normandie/Ares. The MocZlatka, M1N and TSD lines exhibited different patterns of response from one another and from lines with the documented resistance genes. The different disease response patterns of M1N and the original M1 were also apparent. A further search for the source of the M1N resistance led to a blue-grained wheat line known as Blaukorn Weihenstephan, which exhibited the same response pattern to the 14 differential *Egt* isolates. Additional tests with 90 *Egt* isolates, maintained at Weihenstephan, revealed that the two lines were identical in disease response. M1N and Blaukorn Weihenstephan showed susceptible disease responses to isolates no. 71, 72, 90, 94, 95 and 99, intermediate responses to isolates no. 22, 24, 47, 70 and 93 and resistant reactions to all other isolates. The six blue-grained wheat lines W70a86, Blue Chinese Spring, Blaukorn Tschermak, Blaukorn Berlin,

Table 1 Differential response patterns of nine wheat cultivars/lines possessing powdery mildew resistance genes after inoculation with 14 isolates of *E. graminis* f. sp. *tritici*

Cultivar/line	*E. graminis tritici* isolates														Current *Pm*-genes	Proposed *Pm*-genes
	2	5	6	9	10	12	13	14	15	16	17	21	24	90		
Axminister/8*Cc[b]	r[a]	s	r	i,s	r	s	s	s	r	s	s	s	s	r	*1*	*1a*
MocZlatka	r	r	r	r	r	i	r,i	r	r	s	s	r	r	r	–	*1b*
M1 N	r	r	r	r	r	r	r	r	r	r	r	r	r	s	*18*	*1c*
Weihenstephan M1	s	r	s	r	r	r	s	s	r	s	s	s	r	r	*4b*	–
Blaukorn Weihenstephan	r	r	r	r	r	r	r	r	r	r	r	r	r	s	–	*1c*
T. spelta var. *duhamelianum*	r	r	r	r	r	i	r	r,i	r	r,i	s	r	r	r	–	*1d*
Normandie	r	r	r	r	r	s	s	s	r	s	s	r	r	r	*1 + 2 + 9*	*1a + 2 + 9*
Ulka	s	r	r	s	r	s	s	s	r	s	s	s	r	s	*2*	–
N14[c]	s	s	i	r	s	s	s	s	i	s	s	r	s	s	–	*9*

[a] r = resistant, s = susceptible, i = intermediate

[b] Seven times backcrossed to 'Chancellor'

[c] A derivative line of Normandie/Ares

Blaukorn Moskau and Blaukorn Probstdorf, previously described by Zeller et al. (1991), were all susceptible.

Chromosomal location of resistance genes in wheat lines MocZlatka, M1N and TSD

F_2 populations from crosses of the A-genome monosomic lines of powdery mildew-susceptible Chinese Spring and Zlatka and the mildew-resistant line MocZlatka were tested with *Egt* isolate no. 2. Six of the F_2 populations segregated in ratios of 3 resistant : 1 susceptible conforming to a dominant monogenic inheritance (Table 2). The segregation of the cross Zlatka mono-7A/MocZlatka deviated significantly ($P \leq 0.001$) from the expected ratio of 3 : 1, indicating the location of the resistance gene on chromosome 7A.

With the exception of CS mono-7A/M1N, the F_2 segregation ratios for all 21 Chinese Spring monosomics/M1N crosses indicated that a single dominant gene was responsible for the resistance. The frequency of resistant and susceptible individuals satisfactorily fitted 3 resistant:1 susceptible ratios. Only the cross combination involving CS mono-7A/M1N deviated significantly ($P \leq 0.001$) from the expected ratio, indicating the location of the resistance gene on chromosome 7A (Table 2).

Table 2 F_2 segregation for seedling reaction to *E. graminis tritici* isolates in progenies of A-genome monosomic F_1 plants from crosses involving lines MocZlatka, M1N and *T. spelta* var. *duhamelianum*

Monosomic hybrids	Isolate no.	Observed segregation		χ^2 (3 : 1)
		Resistant	Susecptible	
[a]1A/MocZlatka	2	128	44	0.03
[a]2A/MocZlatka		111	36	0.07
[a]3A/MocZlatka		91	36	0.76
[a]4A/MocZlatka		52	18	0.02
[b]5A/MocZlatka		64	21	0.01
[b]6A/MocZlatka		84	26	0.11
[a]7A/MocZlatka		131	13	19.60**
[b]1A/M1N	10	69	17	1.26
[b]2A/M1N		73	16	2.34
[b]3A/M1N		65	22	0.01
[b]4A/M1N		25	6	0.53
[b]5A/M1N		50	12	1.05
[b]6A/M1N		53	16	0.12
[b]7A/M1N		93	9	14.24**
[b]1A/TSD	2	105	33	0.09
[b]2A/TSD		105	27	1.85
[b]3A/TSD		91	41	2.17
[b]4A/TSD		107	29	0.99
[b]5A/TSD		83	27	0.08
[b]6A/TSD		98	34	0.03
[b]7A/TSD		257	10	64.33**

[a] Zlatka monosomic lines
[b] Chinese Spring monosomic lines
** $P < 0.001$

Similarly, the resistance gene in TSD was also found to be located on chromosome 7A. In the cross CS mono-7A/TSD, more resistant individuals were obtained than expected for a ratio of 3 resistant : 1 susceptible ($P \leq 0.001$). Although all crosses between the 21 CS monosomics and M1N and TSD were made, only results for crosses involving A-genome monosomics are shown in Table 2.

Powdery mildew resistance alleles at the *Pm1 locus*

Allelism tests between the resistant genes in the lines MocZlatka, M1N and TSD, and the gene *Pm1* found in the backcross-derived line Axminster/8*Cc, were performed. No susceptible plant was detected among 540 plants in the cross between Axminster/8*Cc and MocZlatka ($\chi^2{}_{15:1} = 32.8$, $P \leq 0.001$), indicating that the resistance gene in MocZlatka was very tightly linked ($r = 0 \pm 0.028$) to *Pm1* or else is an allele at that locus (Table 3). In testing segregation in the F_2 population from MocZlatka/Normandie, *Egt* isolates nos. 2 and 6, which were avirulent for *Pm1* and virulent for *Pm2* and *Pm9,* were used to discriminate between the loci. The F_2 plants tested were all resistant. Similarly, F_2 segregations in crosses involving Axminster/8*Cc//M1N and Normandie/M1N produced no susceptible progeny, indicating that the resistance gene in M1N was allelic, or else very closely linked, to the *Pm1* locus in Axminster/8*Cc and Normandie (Table 3). Furthermore, the results of allelic tests of the F_2 populations of the crosses between Axminster/8*Cc and TSD and M1N/TSD, indicated that the resistance gene in TSD was again very closely linked to the gene *Pm1* in Axminster/8*Cc, and also to the resistance gene in M1N, or else to an allele at the same locus in the respective lines (Table 3).

Random F_2 plants from crosses tested for allelism with *Pm1* in Axminster/8*Cc were grown to maturity. The F_3 families from crosses between Axminster/8*Cc and MocZlatka, Axminster/8*Cc and M1N, Axminster/8*Cc and TSD and Normandie/M1N, inoculated with *Egt* isolates avirulent to both parents of each cross, produced no susceptible individuals (Table 4). The same families segregated into three groups, homozygous resistant, homozygous susceptible and segregating for resistance and susceptibility, when tested with *Egt* isolates virulent to one of the parents in each cross. The segregation ratios of the F_3 families in crosses between Axminster/8*Cc and MocZlatka and between Axminster/8*Cc and TSD fitted 1 : 2 : 1 ratios, as expected. In crosses between Axminster/8*Cc//M1N ($\chi^2_{3.57:1} = 0.02$) and Normandie/M1N ($\chi^2_{1:3.57} = 0.07$), the resistance gene of M1N was preferentially transmitted. This transmission rate was similar to the results of F_2 pooled data from non-critical Chinese Spring monosomics/M1N (1155 resistant : 324 susceptible) which corresponded to a ratio of 3.57 : 1.

Table 3 Tests between the powdery mildew resistance gene *Pm1* and other alleles at the *Pm1* locus in the F_2 generation of hybrids between cultivars and lines

Hybrid	*Egt* isol. no.[a]	Observed segregation		χ^2 (15:1)	Recombination %	
		Resistant	Susceptible		Estimated	95% confidence limit
Axminister/8*Cc// MocZlatka	2 and 6	540	0	32.8**	0	< 0.28
Normandie/ MocZlatka	2 and 6	331	0	22.1**	0	< 0.45
Axminister/8*Cc// M1N	6 and 10	223	0	14.9**	0	< 0.67
Normandie/ M1N	2 and 15	243	0	16.2**	0	< 0.62
Axminister/8*Cc// TSD	2 and 6	267	0	17.8**	0	< 0.56
M1N/TSD	2 and 6	178	0	11.8**	0	< 0.84

[a] Avirulent *Egt* isolates for both parents in each cross
** $P < 0.001$

Table 4 Allelism tests between the powdery mildew resistance gene *Pm1* and other alleles at the *Pm1* locus analysed in the F_3 populations of wheat hybrids

Hybrid	*Egt* isol. no.	No. of F_3 families		
		Resistant	Segregating	Susceptible
Axminister/8*Cc//MocZlatka	2[a]	47	0	0
	10[a]	47	0	0
	24[b]	12	25	10
Axminister/8*Cc//M1N	6[a]	56	0	0
	10[a]	56	0	0
	12[c]	26	16	14
Normandie/M1N	2[a]	54	0	0
	10[a]	54	0	0
	90[d]	11	14	29
Axminister/8*Cc//TSD	2[a]	58	0	0
	10[a]	58	0	0
	9[e]	6	12	4

[a] Avirulent for both *Pm*1 alleles in the cross
[b] Virulent for Axminister/8*Cc and avirulent for MocZlatka
[c] Virulent for Axminister/8*Cc and avirulent for M1N
[d] Virulent for M1N and avirulent for Nomandie
[e] Virulent for Axminister/8*Cc and avirulent for TSD

Thus the available evidence obtained from the F_2 and F_3 populations indicated that the lines MocZlatka, M1N and TSD possess resistance genes which are allelic to *Pm1*. In addition, these genes exhibited differential disease responses to a set of *Egt* isolates and could be distinguished from one another. It is proposed that the powdery mildew resistance alleles at or near the *Pm1* locus be designated *Pm1a* in Axminster/8*Cc and cv Normandie, *Pm1b* in line MocZlatka, *Pm1c* in Weihenstephan Stamm M1N and Blaukorn Weihenstephan, and *Pm1d* in *T. spelta* var. *duhumelianum* accession TRI 2258. The gene symbol *Pm1c* is recommended to replace the earlier designation *Pm18* in M1N (Zeller et al. 1993).

Discussion

Favret and Vallega (1949) first reported a single dominant gene in the common wheat cultivar Axminster, which was developed by S. Larcombe at Winnipeg, Canada, and was believed to be a natural cross between wheat cv Marquis and an unknown cultivar (Pugsley and Carter 1953). This gene, known to occur also in several other common wheat cultivars, was designated *Pm1* and was localized on chromosome 7AL (Sears and Briggle 1969). The resistance allele from *T. monococcum* in the MocZlatka line, characterized in the present study, demonstrates the successful transfer of a powdery mildew resistance gene from diploid einkorn to hexaploid wheat. Normal chromosome pairing facilitates the transfer of genes from diploid to hexaploid wheat because, with the exception of chromosome 4A (Dvořák et al. 1990; Zeller et al. 1991), the chromosomes of *T. monococcum* pair readily with those of the A genome of *Triticum aestivum* (The and Baker 1975).

It appears that the resistance allele *Pm1c* in M1N and Blaukorn Weihenstephan also traces back to a *T. monococcum* strain. Zeller et al. (1991) found that Blaukorn Weihenstephan possessed a chromosome 4A from *T. monococcum* or *T. boeoticum.* Due to chromosomal rearrangements in chromosome 4A (Dvorak et al. 1990) two unpaired univalent chromosomes occurred in the meiosis of hybrids of Blaukorn Weihenstephan and common wheat. As the postulated A-genome donor of common wheat, *T. urartu*, was unknown at the beginning of the 20th century (Jakubziner 1958), and was unlikely to have been used for wide crosses in that period (Tschermak 1914), it appears that *T. monococcum* or *T. boeoticum* was the donor of the structurally altered chromosome found in Blaukorn Weihenstephan. As seen in the present study, M1N and Blaukorn Weihenstephan possess the same disease response pattern to 104 *Egt* isolates. In addition, the assumption that M1N and Blaukorn Weihenstephan carry the same *Pm1* allele is supported by a recent finding (Hartl, unpublished) that an AFLP marker closely linked to the resistance allele was detected only in these two lines among 35 tested. It may be further postulated that Blaukorn Weihenstephan was the donor of the resistance allele *Pm1c* to Weihenstephan Stamm M1N. The occurrence of blue-grained wheat lines or 'Blaukorn' had been described in Weihenstephan as early as the 1930s (Katterman 1932). Aufhammer (1953) also reported on the resistance of Weihenstephan Blaukornwinterweizen (blue-grained winter wheat) to several *E. graminis* f. sp. *tritici* pathotypes. It is most probable that an undocumented outcrossing event had occurred from the mildew-resistant line Blaukorn Weihenstephan to a common wheat line. Further unconcious selection for normal grain colour, may have given rise to the line Weihenstephan Stamm M1N. However, the chance of a spontaneous mutation cannot be ruled out.

Nover and Lehmann (1964) first described powdery mildew resistance in the accession TRI2258 of *T. spelta* var. *duhamelianum* from the Gatersleben Gene Bank. Zeller et al. (1994) screened 20 cultivars of *T. aestivum* ssp. *spelta* grown in Germany, but observed that, with the exception of Bauländer Spelz, all cultivars, were susceptible to the *Egt* isolates employed. A strain of *T. spelta* var. *duhamelianum* possessing *Pm11* that confers resistance to *E. graminis agropyri* (Tosa et al. 1987) did not show resistance to *E. graminis tritici* (Peusha et al. 1996). However, it may still be worthwhile to transfer resistance from *T. monococcum* since successful transfers for resistance to diseases, pests and other traits have already been reported (The 1973; McIntosh et al. 1984; Valkoun et al. 1986, 1989; Potgieter et al. 1991; Dyck and Bartoš 1994). In addition, *T. aestivum* ssp. *spelta* should also be seriously considered as a source of resistance for diseases (Zeller et al. 1994).

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