Chromosomal location of powdery mildew resistance genes in *Triticum aestivum* L. (common wheat). 2. Genes *Pm2* and *Pm19* from *Aegilops squarrosa* L.

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Two mildew resistant accessions of diploid *Aegilops squarrosa* and their hexaploid synthetics derived from crosses with mildew susceptible *Triticum durum* cultivars were tested with differential isolates of *Erysiphe graminis* f. sp. *tritici* and their responses were compared with the response patterns of 16 wheat cultivars or lines possessing known mildew resistance genes. Resistance in the *A. squarrosa* accession 'Braunschweig BGRC 1458' was conditioned by the dominant gene *Pm2*. This gene confers the same response pattern with a set of mildew isolates when present at the diploid species level or in a hexaploid synthetic with *T. durum*. It was located on wheat chromosome 5D. The resistance gene in the *A. squarrosa* accession 'Gatersleben AE 457/78' showed a different response pattern in the hexaploid synthetic line 'XX 186' tested with mildew isolates compared with that of the diploid. Its response pattern was also different from all other wheats with named genes for resistance to powdery mildew. The gene, localized on chromosome 7D in the synthetic 'XX 186', was designated *Pm19*.

Keywords: *Aegilops squarrosa*, powdery mildew, resistance genes, synthetic amphiploid wheats, *Triticum aestivum*.

Introduction

Several examples of successful transfers of genes for resistance to powdery mildew caused by *Erysiphe graminis* f. sp. *tritici* from cultivated and wild relatives of *Triticum* to commercial bread wheat have been reported. Genes *Pm4a* and *Pm5* from *Triticum dicoccum* (Briggle, 1966; Law & Wolfe, 1966) and *Pm4b* from *T. carthlicum* were transferred from the tetraploid level to hexaploid common wheat (The *et al.*, 1979). Gene *Pm6* in several bread wheat cultivars traces to *Triticum timopheevii* (Jørgensen & Jensen, 1972) and gene *Pm16* to *T. dicoccoides* (Reader & Miller, 1991). Gene *Pm12* originated from *Aegilops speltoides* (Miller *et al.*, 1988) and *Pm13* from *A. longissima* (Zeller & Heun, 1985; Ceoloni *et al.*, 1992). In addition, four designated genes, *Pm7*, *Pm8*, *Pm17* and *Pm20*, in common wheat, were derived from cultivated rye, *Secale cereale* (Driscoll & Anderson, 1967; Zeller, 1973; Zeller & Fuchs, 1983; Heun & Friebe, 1990; Friebe *et al.*, 1994). Finally, gene *Pm21* traced to

Dasypyrum villosum (Qi *et al.*, in press; P. D. Chen, personal communication). Thus several genes from relatives of wheat are presently being utilized in commercial resistance breeding. Furthermore, there is a tremendous potential in many other perennial species of the Triticeae resistant to powdery mildew waiting to be used for the improvement of disease resistance in common wheat (Wang *et al.*, 1993).

Aegilops squarrosa ($2n = 14$) which shares the D genome with *Triticum aestivum* is also a potential donor of numerous beneficial genes to cultivated wheat (Lutz *et al.*, 1994). The transfer of genes into hexaploid wheat is relatively easy as the chromosomes of the diploid species pair readily with those of the D genome of *Triticum aestivum*. Mains (1933) first reported on the resistance of *A. squarrosa* to wheat powdery mildew. Later Pasquini (1980), Frauenstein & Hammer (1985), Gill *et al.*, (1986), Valkoun *et al.* (1985, 1990) and Cox *et al.* (1992) confirmed *A. squarrosa* as a potential source of mildew resistance. Tosa & Sakai (1991) found that *A. squarrosa* also possesses resistance genes (*Pm10* and *Pm15*) to *Erysiphe graminis* f. sp. *agropyri*, the wheatgrass mildew fungus. Recently, Lutz

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et al. (1994) described several mildew resistances that were transferred from *A. squarrosa* to common wheat. The present study reports on the chromosomal location of two resistance genes *Pm2* and *Pm19* in synthetic wheat lines by monosomic analysis and allelism tests.

Materials and methods

The *Aegilops squarrosa* accession 'BGRC 1458' was obtained from the gene bank at Braunschweig, Germany, and accession 'AE 457/78' from the gene bank at Gatersleben, Germany. The latter was originally from Georgia (former USSR). The mildew susceptible *Triticum durum* cultivars 'Moroccos 182' and 'Santa Marta' were provided by A. Zeven, The Netherlands. The *A. squarrosa* accessions were crossed as male parents to *T. durum* cultivars 'Moroccos 182' and 'Santa Marta'. Embryos of the F_1 hybrids were rescued and the plantlets treated with colchicine. The synthetic wheat lines 'XX 186' (*T. durum* 'Santa Marta' $\times$ *A. squarrosa* 'BGRC 1458') and 'XX 194' (*T. durum* 'Moroccos 183' $\times$ *A. squarrosa* 'AE 457/78') were selected on the basis of their response pattern from the synthetic wheat lines described by Lutz *et al.* (1994). The 'Chinese Spring' monosomic lines used for gene location were originally obtained from E. R. Sears, USA. Mildew isolate no. 10 known to be avirulent to synthetic lines 'XX 186' and 'XX 194' (Table 1; Lutz *et al.*, 1994) was used to test segregating F_2 populations. Segments of primary leaves of host plants were placed in Petri dishes on agar (6 g/L) and 35 μ g/g benzimidazole. The detailed methods for inoculation of leaf segments and disease assessments were described in Zeller *et al.* (1993).

Results

Response of synthetic wheat lines 'XX 186' and 'XX 194' and other wheat cultivars/lines to mildew

The response pattern of 15 wheat cultivars/lines together with the synthetic wheat lines 'XX 186' and 'XX 194' inoculated with 12 different powdery mildew isolates are listed in Table 1. Line 'XX 186' was resistant to six isolates, gave an r, i-response to one and was intermediate to susceptible in response to four isolates, thus differing from all other wheats tested (Table 1). However, its diploid *A. squarrosa* parent was resistant to all tested mildew isolates (Lutz *et al.*, 1994). In comparison with the reaction of cultivars or lines possessing known mildew resistance genes, synthetic 'XX 194' developed by hybridization with a mildew susceptible *T. durum* cultivar showed an identical pattern to that of 'Ulka/8*Cc'.

Chromosomal location of the resistance genes in synthetic lines 'XX 186' and 'XX 194'

F_2 populations from crosses of the D genome monosomics (1D-7D) with 'XX 186' and 'XX 194' were inoculated with mildew isolate no. 10 avirulent to both host lines. Most of the populations of each combination segregated in a ratio of three resistant to one susceptible (Table 2). In line 'XX 186' the results from monosomic 7D and in line 'XX 194' from monosomic 5D deviated significantly ($P < 0.01$) from the expected ratio. Although crosses involving mono-4D and mono-7D $\times$ 'XX 194' gave an unexpected high number of susceptible plants, the data indicated that the resistance genes in lines 'XX 186' and 'XX 194' are located on chromosomes 7D and 5D, respectively. The locus on chromosome 7D, for which no mildew resistance gene is known so far, was designated *Pm19*.

*Allelism tests with synthetic line 'XX 194' and near-isogenic line 'Ulka/8*Cc'*

For allelism tests, 'XX 194' was crossed to the near-isogenic line 'Ulka/8*Cc' which possesses gene *Pm2*. All 193 F_2 plants tested with isolates no. 5, 6, 10 and 15 were resistant confirming that both 'XX 194' and line 'Ulka/8*Cc' have the same resistance gene.

Discussion

The data presented indicate that the gene responsible for mildew resistance in synthetic 'XX 194' is *Pm2*. Firstly, the response pattern with several mildew isolates was identical with that of the near-isogenic line 'Ulka/8*Cc' (Table 1) known to possess *Pm2* (Briggle, 1969). Secondly, the monosomic analysis with 'XX 194' clearly showed the location of the resistance gene on chromosome 5D which is in accordance with the results of McIntosh & Baker (1970) concerning *Pm2*. Thirdly, the F_1 progenies from the hybrid between 'XX 194' and line 'Ulka/8*Cc' were uniformly resistant to a *Pm2*-avirulent isolate indicating identical resistance genes.

Nyquist (1963) found in the *T. timopheevii* derivative 'C.I. 12633' a dominant mildew resistance gene, designated *MI_x* which was effective in the early seedling stage. Allard & Shands (1954) suggested that the resistance gene from *T. timopheevii* has been transferred to 'C.I. 12633'. Furthermore, Pugsley & Carter (1953) described 'Ulka' as a mildew resistant cultivar that was introduced by a farmer from Russia into the USA. In the F_1 progeny of test crosses between 'Ulka' and 'C.I. 12632', a sister line of 'C.I. 12633', inoculated with two mildew isolates, no susceptible segregate was observed (Briggle, 1969). As the near-isogenic lines

Table 1 Differential reactions of 16 wheat cultivars/lines possessing powdery mildew resistance genes inoculated with 12 isolates of *Erysiphe graminis* f. sp. *tritici*

Cultivar/Line	Res. gene (<i>Pm</i>)	<i>Erysiphe graminis tritici</i> isolate no.											
		2	5	6	9	10	12	13	14	15	16	17	20
Axminster/8* <i>Cc</i> †	1	r	s	r	i,s	r	s	s	s	r	s	s	s
Ulka/8* <i>Cc</i> †	2	s	r	r	s	r	s	s	s	r	s	s	s
Asosan/8* <i>Cc</i> †	3a	r	s	r	r	r	s	r	r	s	s	i	r
Chul/8* <i>Cc</i> †	3b	r	s	s	r	r	r	r	s	r	s	i,s	r
Sonora/8* <i>Cc</i> †	3c	r	s	s	i	r	s	r	i,s	s	s	s	s
Kolibri†	3d	s	s	s	r	s	r	s	r	r	s	r	s
Khapli/8* <i>Cc</i> †	4a	s	r	s	r	i	r	s	s	i	s	i	s
Armada	4b	s	r	s	r	r	r	s	s	r	s	s	s
Hope	5	s	s	s	s	r	s	s	r	s	s	s	s
TP 114/St.2§	6	s	r,i	r,i	r	r,i	s	r,i	r,i	r,i	i	s	s
Disponent	8	r	s	s	r	s	r	s	s	s	s	r	s
Normandie	1 + 2 + 9	r	r	r	r	r	s	s	s	r	s	s	r
BRG 3N§§	16	r	r	r	r	r	r	r	r	r	r	r	/
Amigo	17	i	i	i,s	i	i	i	r	s	i	r	r,i	/
XX 194	2	s	r	r	s	r	s	s	s	r	s	s	s
XX 186	19	s	s	r	r	r	r	i,s	r	s	r,i	r	/

r: resistant; s: susceptible; i: intermediate; /: not tested.

†Eight times backcrossed to 'Chancellor'.

‡Data after Zeller *et al.* (1993).

§Twice backcrossed to 'Starke'.

§§BRG 3N/76-F₂-205', a *T. turgidum* var. *dicoccoides* derivative.

Table 2 Segregation for seedling reaction to mildew isolate no. 10 in monosomic F₂ populations from crosses of seven 'Chinese Spring' monosomics (mono-1D to mono-7D) with the synthetic wheat lines 'XX 194' and 'XX 186'

Chromosome involved	Observed segregation (resistant:susceptible)	χ^2 3:1
1D × XX 194	86:26	0.19
2D × XX 194	106:37	0.06
3D × XX 194	138:47	0.02
4D × XX 194	32:23	8.30**
5D × XX 194	92:4	22.22**
6D × XX 194	51:19	0.17
7D × XX 194	37:22	4.75*
Total excluding mono-5D hybrids	450:174	2.77
1D × XX 186	11:3	0.10
2D × XX 186	33:9	0.29
3D × XX 186	113:40	0.11
4D × XX 186	27:11	0.32
5D × XX 186	53:13	0.99
6D × XX 186	87:26	0.24
7D × XX 186	53:5	8.30**
Total excluding mono-7D hybrids	324:102	0.25

The synthetic lines 'XX 186' and 'XX 194' were resistant and cultivar 'Chinese Spring' susceptible.

* $P < 0.05$, ** $P < 0.01$.

'Ulka/*8Cc' and 'C.I. 12632/*8Cc' show identical response patterns, Briggie (1969) concluded that *Pm2* and *ML_x* are allelic. McIntosh & Baker (1970) located *Pm2* in 'Ulka' on the short arm of wheat chromosome 5D. The species *T. timopheevii* (genome formula: AAGG, $2n=14$) does not share genome D with common wheat (AABBDD, $2n=6x=42$). Therefore it is unlikely that *Pm2* was derived from this tetraploid species. Already Pugsley (1961) had found *ML_x* (*Pm2*) in the Australian wheat selection 'Javelin-325' which received its resistance from Sears' 6x synthetic wheat, *T. durum* cv. 'Iumillo' $\times$ *A. squarrosa*. 'Iumillo' is susceptible to mildew isolates not attacking the synthetic amphiploid (McIntosh & Baker, 1970). *A. squarrosa* ssp. *stragulata* is proposed to be the D genome donor of hexaploid wheat (Jaaska, 1981; Lagudah & Halloran, 1988). However, as *Pm2* is widespread in diploid *A. squarrosa* accessions other than ssp. *stragulata* (Lutz *et al.*, 1994) it is suggested that its presence in hexaploid wheats could have originated from other *squarrosa* subspecies. However, an independent occurrence of a spontaneous mutation which may have led to the *Pm2* gene in cultivar 'Ulka' cannot be ruled out.

With regard to *Pm19*, so far no other powdery mildew resistance gene has been described that is located on chromosome 7D. It is known that *Pm1* and *Pm9* are located on chromosome 7AL (Sears & Briggie, 1969; McIntosh, in press) and *Pm5* on chromosome 7BL (Law & Wolfe, 1966). Therefore it is possible that some of these genes are homoeo-alleles on wheat chromosomes of group 7.

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