Theor Appl Genet (1997) 95:950–953

X. Q. Huang · S. L. K. Hsam · F. J. Zeller

Chromosomal location of genes for resistance to powdery mildew in common wheat (*Triticum aestivum* L. em. Thell.) 4. Gene *Pm24* in Chinese landrace Chiyacao

Received: 12 May 1997 / Accepted: 23 May 1997

Abstract Chinese wheat landrace Chiyacao exhibited a response pattern different from that of the cultivars/lines possessing documented *Pm* genes after inoculation with 106 isolates of *Erysiphe graminis* f. sp. *tritici*. To characterize this resistance and to determine the chromosomal location of the gene or genes present, we crossed the landrace to susceptible cultivar 'Chinese Spring' and also to a set of 21 'Chinese Spring' monosomic lines. Monosomic F_1 plants were allowed to self-pollinate and to produce F_2 seeds. Seedlings of F_2 plants and their parents were inoculated with isolates nos. 5 and 12 of *Erysiphe graminis* f. sp. *tritici*. The results revealed that one major dominant gene is located on chromosome 6D of Chinese common wheat landrace Chiyacao. The new gene is designated *Pm24*.

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

Introduction

Powdery mildew, caused by *Erysiphe graminis* f. sp. *tritici*, constitutes one of the most serious foliar diseases of common wheat in China (Zhuang and Li 1993) and in many areas with a cool or maritime climate (Bennett 1984). The most economical and environmentally safe method for controlling powdery mildew is to develop resistant cultivars. Up to now, 23 gene loci for resistance to powdery mildew (*Pm1-Pm23*) have been assigned to specific chromosomes (McIntosh et al. 1993; Peusha et al. 1996; Yang and Ren 1996), of which some have been transferred from related species to *Triticum*. Genes *Pm4a* and *Pm5* from *Triticum dicoccum* (Briggle 1966; Law and Wolfe 1966) and *Pm4b* from *T. carthlicum* (The et al. 1979) were introduced into hexaploid common wheat. Genes *Pm6* and *Pm16* were derived from *T. timopheevii* (Jørgensen 1973) and *T. dicoccoides* (Reader and Miller 1991), respectively. Gene *Pm12* was transferred from *Aegilops speltoides* (Miller et al. 1988), *Pm13* from *Ae. longissima* (Zeller and Heun 1985; Ceoloni et al. 1992) and *Pm19* from *Ae. squarrosa* (Lutz et al. 1995). Four genes, *Pm7*, *Pm8*, *Pm17* and *Pm20,* originated from cultivated rye, *Secale cereale* (Driscoll and Anderson 1967; Zeller and Fuchs 1983; Heun et al. 1990; Friebe et al. 1994). Gene *Pm21* was introduced from *Haynaldia villosa* (Chen et al. 1995). However, most of the resistance genes, such as *Pm7*, *Pm12*, *Pm13*, *Pm16*, *Pm17* and *Pm19*, have not yet been utilized in commercial resistance breeding (Zeller et al. 1993b).

Si et al. (1987, 1992) and Sheng et al. (1992) found that several Chinese common wheat landraces are immune or highly resistant to powdery mildew. Chiyacao, a landrace from the Henan Province of China, was initially observed to be resistant to 11 mildew isolates used to differentiate documented genes (Huang et al. 1997). Additional tests with further isolates maintained in Weihenstephan indicated that Chiyacao possesses a new response pattern. The study presented here reports the characterization and chromosomal location of the resistance gene present in the landrace Chiyacao on the basis of disease response patterns, mode of inheritance and monosomic analysis.

Materials and methods

The near-isogenic lines of wheat cultivar 'Chancellor' with known powdery mildew resistance genes and TP114/2*Starke possessing gene *Pm6* were kindly supplied by R.A. McIntosh, Sydney, Australia. The wheat-*Haynaldia* 6VS/6AL translocation

Communicated by H. C. Becker

X. Q. Huang · S. L. K. Hsam · F. J. Zeller (✉)
Technische Universität München, Institut für Pflanzenbau und Pflanzenzüchtung, D-85350 Freising-Weihenstephan, Germany

line with gene *Pm21* (Chen et al. 1995) and line 81-7241 possessing gene *Pm23* (Yang and Ren 1996) were obtained from P.D. Chen, Nanjing Agricultural University, Nanjing and L.Y. Li, Southwest Agricultural University, Chongqing, respectively. Landrace Chiyacao was kindly provided by X.F. Wang, Institute of Plant Protection, Henan Academy of Agricultural Sciences, Zhengzhou. The 'Chinese Spring' monosomic and monotelosomic (MT) lines including MT 6D used for gene location were originally obtained from E.R. Sears, U.S.A. The *Erysiphe graminis 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 resistant landrace Chiyacao was 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. The mitotic chromosome numbers of all parental lines and F_1 plants of all cross combinations were determined using Feulgen staining procedures.

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 Zeller et al. (1993a). Three major classes of host reactions were distinguished: r = resistant, i = intermediate, and s = susceptible. Chi-square tests for goodness of fit were used to test for deviation of observed data from the theoretically expected segregation.

Results and discussion

Response of Chiyacao and wheat cultivars/lines to powdery mildew

The response patterns of 24 wheat cultivars/lines and the landrace Chiyacao inoculated with 14 differential *Egt* isolates are listed in Table 1. When these were compared with the response patterns of lines possessing known mildew resistance genes, Chiyacao was found to be resistant to 11 different *Egt* isolates and susceptible to isolates nos. 53, 72 and 117, and showed response patterns different from that of *Pm1*, *Pm2*, *Pm3* alleles, *Pm18*, *Pm22* and *Pm23*, which originate from *Triticum aestivum*. In addition, the disease response of Chiyacao was also different from that of *Pm4a*, *Pm4b*, *Pm5*, *Pm6*, *Pm8*, *Pm12*, *Pm16*, *Pm17*, *Pm19* and *Pm21*, which were derived from relatives of common wheat. After further tests with other isolates it was found that among 106 isolates tested Chiyacao is resistant to 85 isolates and shows an intermediate or resistant response to 11 isolates and susceptible response to 10 isolates (Table 1 and unpublished data).

Table 1 Differential reactions of 24 wheat cultivars/lines possessing powdery mildew resistance genes after inoculation with 14 isolates of *Erysiphe graminis* f. sp. *tritici*

Cultivar/line	*Erysiphe graminis tritici* isolates														*Pm* genes
	2	5	6	9	10	12	13	14	15	16	17	53	72	117	
Axminister/8*Cc[a]	r[g]	s	r	i, s	r	s	s	s	r	s	s	s	r, i	r	*1*
Ulka/8*Cc	s	r	r	s	r	s	s	s	s	s	s	s	s	r	2
Asosan/8*Cc	r	s	r	r	r	s	r	r	s	s	r	s	r	r	*3a*
Chul/8*Cc	r	s	s	r	r	r	r	r	s	r	i, s	r	r	s	*3b*
Sonora/8*Cc	r	s	s	i	r	s	r	i, s	s	s	s	r	r	s	*3c*
Kolibri	s	s	s	r	s	r	s	r	r	s	r	s	r	s	*3d*
W150	s	i, s	i, s	i	r	i, s	r	r, s	s	s	s	r	r	r	*3e*
Mich. Amb./8*Cc	r	s	s	i	r	s	r	i, s	s	s	s	s	s	s	*3f*
Khapli/8*Cc	s	r	s	r	i	r	s	s	i	s	i	s	s	s	*4a*
Armada	s	r	s	r	r	r	s	s	s	s	s	s	s	s	*4b*
Hope	s	s	s	s	r	s	s	r	s	s	s	s	i, r	s	*5*
TP114/2*Starke[b]	s	r, i	r, i	r	r, i	s	r, i	r, i	r, i	i	s	s	s	s	*6*
Disponent	r	s	s	r	s	r	s	s	s	s	r	i	s	r	*8*
Normandie	r	r	r	r	r	s	s	s	r	s	s	s	r	r	*1 + 2 + 9*
Maris Huntsman	s	r	r	r	r	s	r, i	r	r	i	s	–	–	–	*2 + 6*
6BS-6SS/6SL[c]	r	r	r	r	r	r	r	r	r	r	r	r	–	–	*12*
BRG 3N[d]	r	r	r	r	r	r	r	r	r	r	r	r	r	r	*16*
Amigo	i	i	i, s	i	i	i	r	s	i	r	r	i	r	i	*17*
M1N	r	r	r	r	r	r	r	r	r	r	r	r	s	r	*18*
XX 186[e]	s	s	r	i	r	r	i	i	s	i	r	s	r	s	*19*
6AL/6VS[f]	r	r	r	r	r	r	r	r	r	r	r	r	r	r	*21*
Virest	r	i	r	r	r	i	i, r	i	r	i, s	i, s	s	r	r	*22*
81–7241	i	r	s	r	r	r	s	i	i	s	i	s	s	s	*23*
Chiyacao	r	r	r	r	r	r	r	r	r	r	r	s	s	s	*24*

[a] Seven times backcrossed to 'Chancellor'
[b] Once backcrossed to 'Starke'
[c] Wheat-*Ae. speltoides* translocation line
[d] BRG 3N/76-F2-205, a *T. turgidum var* '*dicoccoides*' derivative
[e] XX 186, a *T. durum* × *Ae. squarrosa* hexaploid synthetic wheat line
[f] Wheat-*Haynaldia villosa* translocation line
[g] r, resistant; s, susceptible; i, intermediate; –, not tested

Chromosomal location of the resistance gene in Chiyacao and its mode of inheritance

F_1 progenies from crosses of euploid 'Chinese Spring' (CS) and 20 CS monosomics with Chiyacao were inoculated with *Egt* isolates nos. 5 and 12, which were both avirulent to Chiyacao. When euploid 'Chinese Spring'/Chiyacao was tested with isolate no. 5, the F_2 segregation ratio of 3 resistant to 1 susceptible (Table 2) indicated that Chiyacao has one dominant gene for resistance. The segregation of crosses of Chiyacao with all monosomic and monotelosomic lines (excluding mono 3A and MT6D) also fit a 3 : 1 ratio for resistance to susceptibility (Table 2), supporting further the hypothesis of one dominant gene for resistance. Segregation of the F_2 plants from crosses of Chiyacao with CS MT6D deviated from a 3 : 1 ratio ($P < 0.001$), indicating that chromosome 6D carries the gene for resistance. Monosomic line 3A was not included in the test because F_1 plants were not obtained. When tested with isolate no. 12, F_2 plants of the disomic cross and all monosomic crosses except 6D also segregated in a 3 : 1 ratio of resistant and susceptible plants, respectively (Table 2). Segregation of the cross with CS MT6D also deviated significantly ($P < 0.001$) from the 3 : 1 ratio. The results confirmed the location of the resistance gene in Chiyacao on chromosome 6D.

In the F_2 population of the critical cross, it was expected that disomics and monosomics would be resistant and that nullisomics lacking the chromosome pair with the resistance gene would be susceptible. In order to determine the association of mildew reaction with chromosomal status, the chromosome numbers of 19 F_2 plants from the cross of monotelosomic CS6D/Chiyacao were checked before inoculation with isolates nos. 5 and 12, respectively. One $2n = 42$ (disomic) and 17 $2n = 41$ (monosomic) plants were resistant and 1 $2n = 40$ (nullisomic) plant was susceptible, providing cytological evidence for the location of the resistance gene on chromosome 6D. Chiyacao showed a different response pattern from that of previously documented powdery mildew genes after inoculation with 14 differential isolates of *Egt* (Table 1). Thus the resistance gene on chromosome 6D in landrace Chiyacao, for which no mildew resistance gene has been documented so far, is designated *Pm24*.

It is known that gene *Pm21* is located on a translocated wheat-*Haynaldia* chromosome 6AL/6VS (Chen et al. 1995) and gene *Pm12* on a translocated wheat-*Ae. speltoides* chromosome 6BS-6SS/6SL (Jia et al. 1996).

Table 2 Segregation for seedling reaction to mildew isolates nos. 5 and 12 in progenies of monosomic F_1 plant from crosses of euploid 'Chinese Spring' (CS) and 20 CS monosomics with wheat landrace Chiyacao

Chromosome involved	Isolate no. 5 observed segregation		χ^2 (3 : 1)	Isolate no. 12 observed segregation		χ^2 (3 : 1)
	Resistant	Susceptible		Resistant	Susceptible	
CS × Chiyacao	136	45	0.00	134	47	0.09
1A	96	35	0.21	96	35	0.21
2A	95	39	1.20	94	40	1.68
3A[a]	–	–	–	–	–	–
4A	97	37	0.49	101	33	0.01
5A	95	38	0.90	95	38	0.90
6A	98	36	0.25	99	35	0.09
7A	105	30	0.56	108	27	1.80
1B	94	41	2.19	96	39	1.09
2B	100	32	0.04	102	30	0.36
3B	94	39	1.32	95	38	0.90
4B	97	34	0.30	102	29	0.57
5B	95	36	0.33	97	34	0.30
6B	98	26	1.08	95	29	0.17
7B	97	37	0.49	99	35	0.09
1D	102	27	1.13	96	33	0.02
2D	99	30	0.21	95	34	0.12
3D	94	34	0.17	93	35	0.37
4D	170	47	1.29	164	53	0.04
5D	100	35	0.06	101	34	0.00
6D	196	19	29.96***	197	18	31.70***
7D	99	36	0.20	98	37	0.42
Total (excluding 3A and 6D)	1925	669	0.86	1926	668	0.78

*** $P < 0.001$

[a] Not tested

Gene *Pm11* was found on the short arm of chromosome 6B in several wheat cultivars. However, this gene conferred resistance to *E. graminis* f. sp. *agropyri*, the goat grass powdery mildew pathogen (Tosa et al. 1988). *T. spelta duhamelianum*, which is known to possess *Pm11* (Tosa et al. 1988), was susceptible to 11 wheat *Egt* isolates (Peusha et al. 1996), indicating that *Pm11* does not confer resistance to *E. gramins* f. sp. *tritici*. It may be possible that genes *Pm12*, *Pm21* and *Pm24* are homoeoalleles on wheat chromosomes of group 6.

Acknowledgements We wish to thank Dr. F. Felsenstein for providing the mildew isolates, Ildiko Bellovics and Heidrun Glöckner for excellent technical help, and Prof. X.F. Wang for providing the wheat landrace. Financial support by Deutscher Akademischer Austauschdienst (DAAD) is gratefully acknowledged.

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