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Suppression of powdery mildew resistance gene *Pm8* in *Triticum aestivum* L. (common wheat) cultivars carrying wheat–rye translocation T1BL·1RS

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Disease response pattern of 127 T1B·1RS translocation and substitution wheat cultivars, possessing powdery mildew resistance gene *Pm8* and leaf rust resistance gene *Lr26* located on rye chromosome arm 1RS, revealed that sixteen of these cultivars express *Lr26*, but not concomitant *Pm8* resistance. The mode of inheritance studied in the F_1, F_2 and F_3 generations, and involving hybrids of cultivars Agra, Florida, Olymp, Sabina and Tjelvar not expressing *Pm8* resistance indicated inhibition of resistance gene *Pm8* by a dominant suppressor.

Keywords: *Pm8* suppressor gene, powdery mildew resistance, *Secale cereale*, *Triticum aestivum*, wheat–rye translocation.

Introduction

The transfer of resistance genes from related species to common wheat (*Triticum aestivum* L.) has been successfully exploited in the past decades. Species that share one or two genomes with wheat such as *T. monococcum*, *Aegilops squarrosa*, *T. timopheevii* or *T. turgidum* and relatives such as *Secale cereale*, *Haynaldia villosa* and *Agropyron* that are crossable with wheat have been widely used for this purpose. However, numerous studies in *Triticum* have revealed that the expression of resistance is reduced when genes are transferred from lower to higher ploidy levels. This phenomenon of a 'dilution' of the resistance was reported by Kerber & Dyck (1969, 1979) for leaf rust, Trottet *et al.* (1982) for leaf and stripe rust, mildew and glume blotch, Gill *et al.* (1986) for leaf rust, mildew, greenbug and Hessian fly, Chevre *et al.* (1989) for leaf and stripe rusts, Valkoun *et al.* (1990) for mildew and leaf rust, Siedler *et al.* (1994) for tan spot and Lutz *et al.* (1994) for powdery mildew. Moreover, there are also examples of complete suppression of resistance genes transferred from alien species to common wheat (Kerber, 1983). Rye chromosome arm 1RS widely used in wheat breeding (Villareal *et al.*, 1991) confers resistance to various diseases. The resistance genes for leaf rust, stem rust, stripe rust and powdery mildew attributed to this chromosome are designated *Lr26*, *Sr31*, *Yr9* and *Pm8* (Singh *et al.*, 1990; McIntosh *et al.*, 1993).

In *T. aestivum* it was presumed that the expression of mildew resistance gene *Pm8* transferred from *Secale cereale* (Zeller, 1973), and located on the T1BL·1RS wheat–rye interchanged chromosome was suppressed (Friebe *et al.*, 1989, Jönsson, 1991; Hanušová, 1992; Lutz *et al.*, 1992, 1995). The present study provides evidence of a suppressor gene of *Pm8*, and describes its mode of inheritance.

Materials and methods

A total of 127 wheat cultivars and lines possessing a T1BL·1RS translocation or substitution were tested for their disease response at the seedling stage. The presence of resistance genes *Pm8* and *Lr26* was scored after inoculation with their respective pathogenic isolates. Two single-pustule-derived *Erysiphe graminis tritici (Egt)* isolates Nos 47 and 58, avirulent to *Pm8*, and one *Puccinia recondita tritici (Prt)* isolate, No. 243, avirulent to *Lr26*, maintained at Prague-Ruzyně, were initially used to verify the presence of genes *Pm8* and *Lr26*, respectively. The virulence of these isolates to other resistance genes of the standard differential cultivars and the method used have been described previously by Hanušová (1992).

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After the initial crosses between selected cultivars, seeds of the various filial generations were tested at one of two locations either at Prague-Ruzyně, or in Weihenstephan. Tests for resistance in Weihenstephan were carried out on segments of primary leaves of host plants. The leaf detachment method employed was described previously by Zeller *et al.* (1993) using leaf segments cultured in petri dishes on 6 g L^{-1} agar and 35 mg L^{-1} benzimidazole. *Egt* isolates Nos 2 and 17 are avirulent to *Pm8*, but possessing differential virulences to other *Pm* genes present in the standard set of test cultivars (Lutz *et al.*, 1992). *Prt* isolate No. L-13 is avirulent to leaf rust resistance gene *Lr26*. Somatic chromosomes of the 127 wheat cultivars and lines were also studied by the standard Feulgen method for detection of the number of satellited chromosome pairs (1B, 6B).

Five cultivars, Agra, Florida, Olymp, Sabina and Tjelvar, which possess the T1BL·1RS translocated chromosome and express *Lr26*, but not *Pm8* resistance were crossed to cultivars Vala, Hana and Viginta lacking both *Pm8* and *Lr26*. The hybrids Agra/Vala, Florida/Hana, Sabina/Hana, Tjelvar/Hana and Olymp/Viginta were studied in the F_1, F_2 and F_3 generations. Fifty to sixty F_2 plants randomly selected from each hybrid combination were propagated to form F_3 populations. However, several F_3 families did not produce sufficient amount of seeds and were excluded. The hybrid combinations Disponent/Olymp, Disponent/Florida and Disponent/Sabina were studied for the disease resistance to *Pm8* and *Lr26* in the F_1 and F_2 generations. The hybrid combinations Agra/Sabina, Florida/Sabina, Agra/Olymp, Olymp/Sabina, Tjelvar/Sabina and Tjelvar/Olymp, all presumably possessing suppressors, were evaluated in the F_1 and F_2 generations for *Pm8* resistance to assess the identity of the suppressing factor.

The different *Egt* and *Prt* isolates used in the present study were selected for their abilities to differentiate the reponse patterns of the parental cultivars for resistance to *Pm8* and *Lr26*. Disponent showed resistance response to the various *Egt* and *Prt* isolates used. Cultivars Agra, Florida, Olymp, Sabina and Tjelvar were resistant to both *Prt* isolates, but susceptible to all *Egt* isolates. Cultivars Hana, Vala and Viginta exhibited susceptible reactions to all *Egt* and *Prt* isolates used.

Results and discussion

The 127 common wheat cultivars and lines which were assumed to carry a T1BL·1RS wheat–rye translocation or substitution, were found to possess only two satellited chromosomes by mitotic analysis. This infers that the short arm of one satellited chromosome pair, presumably 1B, had been replaced by the 1RS rye chromosome arm.

From the set of cultivars tested against *Egt* isolates Nos 47 and 58, and a *Prt* isolate No. 243, avirulent to *Lr26*, 111 cultivars were resistant to *Egt* and *Prt* isolates inferring that *Pm8* and *Lr26* are located on chromosome arm 1RS, as all resistant individuals carry this translocation. Sixteen T1Bl·1RS carriers showed the presence of resistance gene *Lr26*, but did not express *Pm8* resistance, suggesting that a suppression mechanism is in operation (Table 1). Five of the cultivars which show *Lr26* resistance but lack *Pm8* resistance, Agra, Florida, Sabina, Tjelvar and Olymp, were crossed with *Pm8* susceptible cultivars Vala, Hana and Viginta. Hence both parents in each cross combination showed susceptibility to powdery mildew pathogens. As seen in Table 2 all the F_1 generations also revealed susceptible response to *Pm8* avirulent isolates Nos 2, 47 and 203, respectively. However, the F_2 generation derived from susceptible F_1 hybrids segregated resistant and susceptible plants in the crosses Agra/Vala, Florida/Hana, Tjelvar/Hana which conformed to a ratio of 3 resistant:13 susceptible. The results showed that the resistance gene *Pm8* was not expressed in the presence of a suppressor gene in the F_1 generation. However, segregants in the F_2 generation, possessing the *Pm8* gene in the absence of the dominant suppressor segregated into the 3 resistant class, whereas those carrying *Pm8* in combination with the suppressor, as well as the homozygous recessive individuals lacking both *Pm8* and the suppressor were susceptible and segregated as the 13 susceptible class. The F_2 mode of inheritance from hybrid combinations between mildew susceptible cultivars possessing the T1BL·1RS translocation and other susceptible parents indicated the presence of the *Pm8* gene that was suppressed in the parents, but the resistance was again detected in the F_2 segregants. The F_2 segregation from the hybrids Sabina/Hana and Olymp/Viginta deviated from the 3:13 genetic ratio (Table 2). In these cross combinations more susceptible individuals were observed than the expected numbers. It had been previously reported that gametic transfer of the T1BL·1RS translocated chromosome may vary between different hybrid combinations (Mettin *et al.*, 1973), resulting in more susceptible F_2 individuals when the resistance gene in question is on the 1RS chromosome arm (Wienhues, 1965; Bartoš & Bareš, 1971; Bartoš, 1993).

The F_3 lines derived from F_2 plants segregated

Table 1 Genealogies of 16 wheat cultivars carrying wheat–rye translocation T1BL·1RS which possess *Lr26* leaf rust resistance, but not expressing *Pm8* powdery mildew resistance

Cultivar/line	Country	Pedigree†
Agra	Czech Republic	Avrora/S985//Purdue 66278
Druzba	CIS	Winnetou/Heine//Leone
Feldkrone	Germany	Heines VII/Taca//Rieti/3/Taca/4/Zorba
Florida	Germany	Caribo/Disponent
Ikarus	Austria	Caribo/Weihenstephan Stamm 623-65
Istra	Czech Republic	S958/Avrora
Kalojan	Bulgaria	Snem/Avrora//Rusalka
Lovrin 10	Romania	Abbondanza/Triumph//Bezostaya 1
Lovrin 24	Romania	Lovrin 10/Lovrin 62
Olymp	Germany	Mex./ Götz//Kronjuwel(Götz: Tenor/2xJubilar//Benno)
Palur	Germany	Hadm.05792-71/Hadm.03924-63/ 2x//Suwon/3/2xAlmus
Riebesel 47/51‡	Germany	Criewener 104/Petkus rye
Sabina	Czech Republic	Weihenstephan Stamm 378-57 132b/Caribo
Skorospelka 35	CIS	Erythrospermum 315-N-60/Bezostaya 1
Tjelvar	Sweden	WW 20999/Benno
Yugoslavija	Former Yugoslavia	NS 646/Bezostaya 1//Avrora

†Information partly obtained from Zeven & Zeven-Hissink (1976).
‡(1R/1B) wheat–rye substitution line (Zeller, 1973).

Table 2 Genetic analyses of wheat cultivars Agra, Florida, Sabina, Tjelvar and Olymp carrying wheat–rye translocation T1BL·1RS but not expressing powdery mildew resistance in crosses with *Pm8* susceptible cultivars

Hybrid and generation	Isolate no.	Numbers of plants/lines				Expected ratio	χ^2	*P*
		Res.	Susc.	Segr.	Total			
Agra/Vala								
F_1	47	0	5	0	5			
F_2	47	24	87	0	111	3:13	0.61	0.5–0.2
F_3	47	3	19	26	48	1:7:8	0.34	0.9–0.8
Florida/Hana								
F_1	203	0	9	0	9			
F_2	2	17	79	0	96	3:13	0.07	0.8–0.7
F_3	203	2	24	24	50	1:7:8	0.66	0.8–0.7
Sabina/Hana								
F_1	2	0	5	0	5			
F_2	2	16	288	0	304	3:13	36.3	0.01
F_3	203	0	20	10	30	1:7:8	7.14	0.05–0.02
Tjelvar/Hana								
F_1	2	0	4	0	4			
F_2	2	43	205	0	248	3:13	0.32	0.7–0.5
F_3	2	1	9	12	22	1:7:8	2.57	0.3–0.2
Olymp/Viginta								
F_1	2	0	5	0	5			
F_2	2	4	161	0	165	3:13	23.5	0.01
F_3	2	0	11	17	28	1:7:8	2.46	0.3–0.2

Res., resistant; Susc., susceptible; Segr., segregating.

into three groups: resistant, susceptible and segregating families. The F_3 lines derived from the crosses of Agra/Vala, Florida/Hana and Tjelvar/Hana corresponded to a ratio of 1res:7sus:8seg. However, complete resistance families in the F_3 lines were not detected in the crosses between Sabina/Hana and Olymp/Viginta. It is likely that during the random propagation of limited numbers of F_2 plants for

derivation of F_3 families, homozygous resistant plants were not included. Nevertheless, the segregation ratio in the F_3 generation in these crosses provided further evidence of a suppressor gene that inhibited the expression of mildew resistance gene *Pm8*.

The F_2 generation derived from crosses involving cultivars Olymp, Florida and Sabina expressing *Lr26*, but not *Pm8* resistance, and Disponent with both *Lr26* and *Pm8* resistances were tested against *Prt* isolate No. L-13, avirulent to *Lr26*, and *Egt* isolate No. 17, avirulent to *Pm8*. Segments from primary leaves of each individual were inoculated with either *Egt* or *Prt* isolates. As expected, all F_2 plants were resistant to *Prt* isolate L-13 confirming that cultivars Olymp, Florida and Sabina possess the same *Lr26* gene as Disponent. However, the same plants simultaneously tested for *Pm8* segregated into mildew resistant and mildew susceptible individuals corresponding to a ratio of 1res:3sus (Table 3). This ratio revealed that the suppressor segregated as a dominant gene and that *Pm8*, inherited from both parents, was expressed only in the absence of the suppressor. The concomitant test for two genes, namely *Pm8* and *Lr26* located on the same translocated chromosome arm served as useful genetic markers, and revealed that in these cross combinations gametic transfer of *Lr26* was normal as expected. Because of the location of these two genes, aberrant gametic transfer of T1BL·1RS could be ruled out for the nonexpression of resistance, hence segregation for *Pm8* resistance resulted from the action of the suppressor gene.

No mildew-resistant plants were found in crosses Agra/Sabina (5 F_1; 335 F_2 plants), Florida/Sabina (10 F_1; 320 F_2 plants), Agra/Olymp (7 F_1; 79 F_2 plants), Olymp/Sabina (8 F_1; 87 F_2 plants), Tjelvar/Sabina (8 F_1; 91 F_2 plants) or Tjelvar/Olymp (8 F_1; 95 F_2 plants). This indicates that these cultivars possess the same suppressor gene. The presence of a suppressor gene for *Pm8* was also detected in Australia in derivative lines possessing a T1BL·1RS translocation. The suppressor gene was designated *SuPm8* (R. A. McIntosh, personal communication).

The powdery mildew resistance gene *Pm8* located on rye chromosome 1RS was introduced into common wheat by hybridization of *T. aestivum* with *S. cereale*, developed independently in Salzmünde and Weihenstephan, Germany (Zeller, 1973). Nonexpression of *Pm8* resistance has been described by Friebe *et al.* (1989), Jönsson (1991), Hanušová (1992) and Lutz *et al.* (1992, 1995). In the transfer of leaf rust, stem rust and stripe rust resistance genes from alien species (e.g. *Aegilops squar-rosa, Triticum dicoccoides)* to common wheat Kerber & Green (1980), Bai & Knott (1992), Kema *et al.* (1995) and Ma *et al.* (1995) have also provided evidence that incorporated resistance genes can be suppressed by gene(s) located in the wheat genome. In spite of the existence of suppressors of resistance that may limit the potential use of tranferred alien genes, several studies advocate that alien genetic variation could be successfully exploited. Thus germplasm resources from remote relatives of wheat may still serve as a vast genetic reservoir for future wheat improvement.

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Table 3 Genetic analysis of wheat cultivars Olymp, Florida and Sabina carrying wheat–rye translocation T1BL·1RS which express *Lr26*, but lacking *Pm8* powdery mildew resistance in hybrids with *Pm8* and *Lr26* resistant cultivar Disponent

Hybrids	Generation	No. of plants	*Pm/Lr* isolate	Reaction†		Plants		Ratio R:S	χ^2
				P_1	P_2	Res.	Susc.		
Disponent (*Pm8*, *Lr26*)	F_1	5	17	r	s	0	5		
× Olymp (*Pm8*, *SuPm8*,	F_2	135	17	r	s	41	94	1:3	2.08
Lr26)			L-13	r	r	135	0		
Disponent (*Pm8*, *Lr26*)	F_1	12	17	r	s	0	12		
× Florida (*Pm8*,	F_2	327	17	r	s	94	233	1:3	2.45
SuPm8, *Lr26*)			L-13	r	r	327	0		
Disponent (*Pm8*, *Lr26*)	F_1	15	17	r	s	0	15		
× Sabina (*Pm8*, *SuPm8*,	F_2	386	17	r	s	109	277	1:3	2.16
Lr26)			L-13	r	r	386	0		

†r, resistant; s, susceptible.

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