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RESISTANCE TO POWDERY MILDEW AND LEAF RUST IN WHEAT LINES DERIVED FROM A *Triticum aestivum*/*Aegilops variabilis* CROSS

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ABSTRACT

Lines with resistance to powdery mildew in adult plant stage have been selected from two groups of F_1 seeds produced by crossing *T. aestivum* with *Aegilops variabilis* (2n=28, UUSS). Two lines were derived from non-irradiated F_1 seeds and another five lines originated from irradiated hybrid seeds. Rusalka and Pliska bread wheat varieties were used as backcrossing parents. Two lines selected from the irradiated group, showed different resistance pattern in comparison to 18 wheat cultivars/lines possessing known powdery mildew resistance genes. Line 11-8 was previously identified with C-banding as a 1U(1B) substitution. It expressed a distinctive disease pattern, different from the parents and differential set of lines. It is suggested that the alien 1U chromosome is a carrier of resistance to powdery mildew, as evidenced by the disease pattern of doubled haploid lines derived from cv. Charodeika x line 11-8 cross. The DH lines expressed resistance to 8 from 11 isolates used. Additionally, the lines obtained from the original cross were subjected to a test for leaf rust resistance and compared to 11 cultivars possessing documented leaf rust resistance genes. At least four lines were postulated to carry unidentified genes that could not be resolved by the leaf rust isolates used.

Key words: *Aegilops variabilis*, 1U chromosome, Introgression, Leaf rust, Powdery mildew, *T. aestivum*

INTRODUCTION

Introgression of genetic variability into wheat from distantly or closely related species has been connected to economically important traits such as insect and disease resistance (Friebe et al., 1996; Hsam and Zeller, 2002; Xu et al., 2009). *Aegilops* species belong to the primary, secondary and tertiary gene pool of wheat and gene transfers into cultivated wheat can be achieved by direct hybridization, homologous and homoeologous recombination, irradiation, backcrossing and selection (Sears, 1956; Fedak, 1998; De Pace et al., 2001).

Aegilops variabilis Eig (syn. *Aegilops peregrina* 2n=28, genome UUSS) is an annual allotetraploid species inclusive in the tertiary gene pool of wheat. Genes for resistance to root knot and cereal cyst nematodes (Yu et al., 1990; Barloy et al., 2007), kernel bunt (Williams and Mujeeb-Kazi, 1996), eyespot (Thiele et al., 2002), powdery mildew (Spetsov et al., 1997), stripe rust (Liu et al., 2011) and leaf rust (Marais et al., 2008) from this species have been successfully transferred into common wheat. U genome is involved in diploid (*Ae. umbellulata*), tetraploid (*Ae. columnaris*, *biuncialis*, *geniculata*, *neglecta*, *triuncialis*, *kotschyi* and *peregrina*) and hexaploid (*Ae. neglecta* 6x and *Ae. juvenalis*) species of genus *Aegilops* (van Slageren, 1994). Several attempts succeeded in transferring genes for powdery mildew resistance from *Aegilops* species with U genome, *Ae. umbellulata* (Frauenstein and Hammer, 1985), *Ae. ovata* (syn. *geniculata*) (Zeller et al., 2002; Stoilova and Spetsov, 2006), and *Ae. triuncialis* (Harjit-Singh et al., 2000). Specifying the U chromosomes, Zhu et al. (2006) were the first to transfer powdery mildew resistance gene from *Ae. umbellulata* to wheat as selected and studied 2U(2B) substitution line. The new gene was temporarily designated *PmY39*.

Leaf rust resistance genes in wheat have been derived from species of *Triticum*, *Secale*, *Thinopyrum* and *Aegilops* (*Ae. ventricosa*, *kotschyi*, *sharonensis*, *peregrina*, *triuncialis*, *geniculata* and *neglecta*) (McIntosh et al., 2009). Chhuneja et al. (2008) indicated two new genes (*LrU1* and *LrU2*) that have been introgressed into wheat from *Ae. umbellulata*, but the alien chromosome/s was not identified. During backcrossing a chromosome segment containing a leaf rust resistance gene from *Ae. peregrina*, designated *Lr59*, was transferred and incorporated in wheat 1A chromosome (Marais et al., 2008). Thus, distantly related genera and species provide useful genetic resources of disease resistance for wheat breeding.

Following the aim to exploit the genes for powdery mildew resistance in *Aegilops* species through irradiation treatment, backcrossing and selection, we investigated the disease response of selected lines from a *T. aestivum*/*Ae. variabilis* cross with emphasis on their resistance to powdery mildew and leaf rust in seedlings, and possible donors of the transferred resistance in genotypes deriving from a group of hybrid seeds treated with gamma rays and backcrossing.

MATERIALS AND METHODS

Plant Materials

Lines with 2n=42 have been produced from a *T. aestivum* cv. Rusalka/*Ae. variabilis* cross. The alien species is an accession from the collection at the Dobroudja Agricultural Institute – General Toshevo. F_1 plants produced were divided into four groups depending on the variety of backcrossing and application of irradiation (Spetsov et al., 1997). Part of the hybrid seeds was irradiated with 100 Gy gamma rays of Co^{60}. Following one backcross to wheat and by 6 to 10 generations of selfing with selection for resistance in each generation, several hexaploid lines resistant to the mildew pathogen *Blumeria graminis* (DC.) E.O. Speer f.sp. *tritici* were isolated. All genotypes used in the study are presented in Table 1. Out of the seven hexaploid lines studied from the original cross, two lines, 28-1 and 28-7 were selected from the group of F_1 non-irradiated (normal) seeds and the hybrid plants were backcrossed once to another cultivar that resembling Rusalka. The remaining five lines (11-8, 37-3, 37-7, 104-4 and 104-5) were developed from the group of irradiated F_1 seeds and mixed pollen from Rusalka and Pliska varieties were used for obtaining BC_1 seeds. The selected substitution line 11-8 (1U/1B) was cross to common wheat cv. Charodeika to obtain several doubled haploid lines. Two of them, lines 51 and 131 did not possess 1U chromosome but were hexaploids and expressed resistance to powdery mildew.

Table 1. Pedigree and satellited chromosomes (sat) of genotypes (2n=42) derived from a *T. aestivum*/*Aegilops variabilis* cross

Line No.	Cross/grouping	Sat chromosomes
	Rusalka/*Ae. variabilis*	
28-1	F_1 backcrossed with Rusalka*	1B, 6B
28-7	-//- -//-	1B, 6B
11-8	Irradiated F_1 backcrossed with Rusalka-Pliska	1U, 6B
37-3	-//- -//-	1B, 6B
37-7	-//- -//-	1B, 6B
104-4	-//- -//-	1B, 6B
104-5	-//- -//-	1B, 6B
	Charodeika/line 11-8	
51	DH line	6B
131	-//- -//-	6B

Rusalka*, a wheat cultivar resembling Rusalka;
Rusalka-Pliska, mixed pollen from the two varieties;
DH line, doubled haploid line.

Powdery Mildew Test

The near-isogenic lines of Chancellor with known powdery mildew resistance genes and TP114/2*Starke possessing gene *Pm6* were supplied by R. A. McIntosh, Sydney, Australia. The eleven *Blumeria graminis* f.sp. *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 test for mildew resistance were conducted on primary leaf segments cultured on 0.6% w/v agar and 35mg/l benzimidazole in plastic boxes. The methods of inoculation, conditions of incubation and disease assessment were according to Hsam et al. (2003). Three major classes of host reactions were distinguished: r = resistant, i = intermediate, s = susceptible.

Leaf Rust Test

Resistance test was also conducted on primary leaf segments in petri dishes on 6 g/l agar and a final benzimidazole concentration of 35 mg/l following the method of Felsenstein et al. (1998). Uredospores of race specific *Puccinia triticina* (*Pt*) isolates were applied to leaf segments of the cultivars and assessed for disease response eleven days after inoculation using the 0 to 4 scale of Stakman et al. (1962). Infection types ; and 1 were regarded as resistant (R), types 2 and 3 as moderately resistant and moderately susceptible (MR and MS), respectively, and infection type 4 as susceptible (S). Most of the Pt isolates used were collected from Europe and Mediterranean regions and selected from single spore progenies. In the two experiments each line was tested in five replications. Pathological tests were carried out in Technical University of Munich, Institute of Plant Breeding, D-85350 Freising-Weihenstephan, Germany, with the isolates classified and maintained by F.J. Zeller's group.

Cytogenetical Analysis

Chromosome counts were made from squashes of root-tip cells pretreated with mono-bromonaphtalene and stained by the Feulgen method. 15 plants per line were checked for chromosome number and the presence of the satellited (sat) chromosome, starting from BC_1F_6 generation. The alien 1U chromosome is shorter than the wheat 1B and 6B chromosomes, with a secondary constriction that is visually differentiated in mitotic metaphases. In the course of 3 years (totally 45 plants per line used for chromosome counting) these plants were grown in greenhouse and estimated for plant morphology and resistance to powdery mildew.

RESULTS

Plant Morphology and Cytogenetical Analysis

Several hexaploid derivatives from a *T. aestivum* cv. Rusalka/*Ae. variabilis* cross with powdery mildew resistance in adult plant stage, were isolated. Only line 11-8 expressed different plant morphology compared to the wheat parent Rusalka and the other 6 lines by having short stem, short spike and brown coloured glumes. It was cytologically confirmed to have a 1U chromosome pair from *Ae. variabilis*, a carrier of genes for powdery mildew resistance and brown glumes in wheat (Spetsov, 1998). The variety Rusalka and *Ae. variabilis* exhibited two pairs of sat chromosomes, but differing in arm ratios, size and satellite expression. 1B and 6B chromosomes in common wheat have a secondary constriction, and can be visually differentiated in mitotic metaphases. Line 11-8 possessed 42 chromosomes with four sat chromosomes: one pair is 6B from the wheat Rusalka and the other is 1U chromosome pair from the alien species (Table 1). All the remaining lines had 42 chromosomes and exhibited the two sat chromosomes, 1B and 6B, a general characteristic for any cultivar of hexaploid wheat.

Line 11-8 was crossed to wheat variety Charodeika. From several doubled haploid lines produced with resistance to powdery mildew, two lines 51 and 131 were found not carrying the alien 1U chromosome. The analysis showed also that from the wheat sat chromosomes, only 6B chromosome pair was visualized.

Powdery Mildew Resistance

Five lines (28-1, 28-7, 37-3, 37-7 and 104-4) including Rusalka, showed susceptible response at seedlings stage to the eleven differential isolates of *Bgt*, while *Ae. variabilis* expressed a complete resistance response to all of them (Table 2). Line 104-5 expressed a little different pattern giving a resistant reaction to isolate 12 only, and the alien species showed the same reaction to this isolate too. The best interesting line is 11-8 expressing a unique resistant pattern, different from parents and lines with known pm resistance genes. Variety Pliska as a possible parent in five of the lines, including line 11-8, expressed a different response in comparison to Rusalka, *Ae. variabilis* and derivatives selected from the cross. Parents of Pliska are Rusalka and 5517-A-5-5-1P3, and the former variety is susceptible to wheat powdery mildew, when for the latter line originating from a complicate cross involving four cultivars, information is not available.

Table 2. Postulated powdery mildew resistance (pmr) genes of common wheat cultivars Rusalka, Pliska, Charodeika and their derivatives from crosses with *Ae. variabilis* in comparison with reactions after inoculation with 11 isolates of *Blumeria graminis* f.sp. *tritici* (Bgt)

Bgt isolates Cultivar/line	2	5	6	9	10	12	13	14	15	16	17	*Pm* gene
Aegilops variabilis	r	r	r	r	r	r	r	r	r	r	r	*u*
Rusalka	s	s	s	s	s	s	s	s	s	s	s	-
Pliska	s	i	r	s	r	s	i	r	i	i	i	*u*
11-8[1]	r	r	r	r	s	i	s	r	r	s	s	*u*
28-7, 28-1, 37-3, 37-7, 104-4[2]	s	s	s	s	s	s	s	s	s	s	s	-
104-5	s	s	s	s	s	r	s	s	s	s	s	*u*
Charodeika	s	s	i	s	r	s	s	r	s	s	s	*Pm5*
51, 131[3]	r	r	r	r	r	r	s	r	r	s	s	*u*
Axminister/8*Cc[4]	r	s	r	i,s	r	s	s	s	s	s	s	*Pm1*
Ulka/8*Cc	s	s	r	s	r	s	s	s	s	s	s	*Pm2*
Asosan/8*Cc	r	s	r	r	r	s	r	r	s	s	r	*Pm3a*
Chul/8*Cc	r	s	s	r	r	r	r	r	s	r	i,s	*Pm3b*
Sonora/8*Cc	r	s	s	i	r	s	r	i,s	s	s	s	*Pm3c*
Kolibri	s	s	s	r	s	r	s	r	r	s	r	*Pm3d*
W150	s	i,s	i,s	i	r	i,s	r	r,s	s	s	s	*Pm3e*
Michigan Amber/8*Cc	r	s	s	i	r	s	r	i,s	s	s	s	*Pm3f*
Khapli/8*Cc	s	r	s	r	i	r	s	s	i	s	i	*Pm4a*
Armada	s	r	s	r	r	r	s	s	s	s	s	*Pm4b*
Hope	s	s	s	s	r	s	s	r	s	s	s	*Pm5*
TP114/2*Starke[5]	s	r,i	r,i	r	r,i	s	r,i	r,i	r,i	i	s	*Pm 6*
Disponent	r	s	s	r	s	r	s	s	s	s	r	*Pm8*
BRG 3N[6]	r	r	r	r	r	r	r	r	r	r	r	*Pm16*
Amigo	i	i	i,s	i	i	i	r	s	i	r	r	*Pm17*
XX 186[7]	s	s	r	i	r	r	i	i	s	i	r	*Pm19*
Virest	r	i	r	r	r	i	i,r	i	r	i,s	i,s	*Pm22*
Chiyacao	r	r	r	r	r	r	r	r	r	r	r	*Pm24*

[1]Lines 11-8, 37-3, 37-7, 104-4 and 104-5, selected from irradiated F_1 (Rusalka/*Ae. variabilis*) and backcrossed with mixed pollen from Rusalka and Pliska

[2]Lines 28-7, 28-1, obtained from F_1 (Rusalka/*Ae. variabilis*) and backcrossed once to cultivar resembling Rusalka; [3]Lines 51 and 131, doubled haploids developed from Charodeika/line 11-8 cross

[4], Seven times backcrossed to Chancellor

[5], Once backcrossed to Starke; r-resistant, s-susceptible, i-intermediate; u-unknown

[6], BRG 3N/76-F_2-205, a wheat-*T. turgidum* var. *dicoccoides* derivative;

[7], XX 186, a *T. durum*/*Ae. tauschii* hexaploid synthetic wheat line;

The disease response of variety Charodeika fitted the expression of Hope from the differential set of lines, and postulated to carry a gene *Pm5*. The two DH lines, derived from a Charodeika/line 11-8 cross, exhibited resistance pattern different from all NILs used in this study. Both lines expressed resistance to 8 and susceptibility to 3 isolates, and in this term they surpassed Pliska, but stood between line 11-8 and *Ae. variabilis*. The resistance of all new derived lines were tentatively characterized as unknown (u) resistance, because their response patterns did not correspond to any of the lines possessing major single resistance genes.

Leaf Rust Resistance

Eight isolates of *Puccinia triticina* (*Pt*) were used to check the resistance of lines derived from the original cross in seedlings in comparison with a differential set of wheat lines possessing individual documented genes (NILs) resistant to leaf rust. Both parents, Rusalka and *Ae. variabilis*, showed different resistance responses to four isolates (S12, S16, S29 and S48) (Table 3). All the six lines possessed specific resistance patterns to the *Pt* isolates used. Their reactions were different from the parents as well as the NILs. Lines 28-1 and 28-7 were infected in higher extent giving susceptible reaction to all isolates, and thus differentiated from Rusalka. Lines 37-7 and 104-5 possessed a wide spectrum of resistance to the eight *Pt* isolates employed. Their reactions were distinguishable from the parents on at least five isolates (S12, S16, S47, S48 and S71). Lines 37-3 and 104-4 behaved also differently from parents (reactions to S28, S47, S48 and S71). As compared to other lines, they showed an intermediate response to at least three isolates, possibly indicating the presence of quantitatively inherited resistance genes. Results showed that at least four lines (37-3, 37-7, 104-4 and 104-5) are very different from Pliska regarding the resistance pattern, and the probability for this cultivar to donate some resistance genes in the selected lines during backcrossing remains very low. Non of the lines and parents fitted any of the 11 NILs with known resistance genes.

Table 3. Disease response patterns of six lines derived from a cv. Rusalka/*Ae. variabilis* cross and their parents in comparison to lines with documented resistance genes to isolates of the leaf rust pathogen

Parents	*Puccinia triticina* isolates								*Lr*
Lines	S12	S16	S27	S28	S29	S47	S48	S71	genes
Ae. variabilis	i	s	r	r	i	s	s	s	*u*
Rusalka	s	r	r	r	s	s	r	s	*u*
Pliska	r,s	i	i	i	s	r,s	i	r,s	*u*
28-1	s	s	i	s	s	s	s	s	*u*
28-7	s	s	s	s	s	s	s	s	-
37-3	r	r	i	s	i	s	s	r	*u*
37-7	r	r	r	r	i	r	r	r	*u*
104-4	i	i	r	r	i	r	r	r	*u*
104-5	r	r	r	r	s	r	r	r	*u*
Centenario	r	r	r	r	r	s	r	r	*Lr1*
Corina	s	s	r	s	r	s	r	i	*Lr2b*
Democrat	r	r	r	r	s	r	r	s	*Lr3*
Lee	i	r	r	s	i	s	r	i	*Lr10*
Kenya E19	r	r	r	r	s	s	i	s	*Lr15*
Kl. Lucero	i	i	s	i	s	s	i	r	*Lr17*
Ae. tauschii	s	s	s	s	s	i	s	s	*Lr21*
Ae. speltoides	r	r	r	r	r	s	i	s	*Lr28*
Terenzio	s	s	r	r	s	r	s	i	*Lr30*
PI58458	s	s	s	s	s	i	i	i	*Lr33*
T. spelta	i	i	s	s	s	i	s	s	*Lr44*

Lines 28-7 and 28-1 derived from F_1, backcrossed once to a cultivar resembling Rusalka;
Lines 37-3, 37-7, 104-4 and 104-5 were originated from irradiated F_1 and backcrossed once with mixed pollen from Rusalka and Pliska; r - resistant, i - intermediate, s – susceptible.

The variety Pliska, parents of which are Rusalka and line 5517-A-5-5-1P3, showed intermediate disease response as a whole. Rusalka expressed a disease pattern that is different from all lines used, and is characterized as unknown (u) resistance. The latter parent originated from a cross: Genesee/4/(54117A3)Genesee/3/Yorkwin/ /Brevor/Norin10 (T. Payne, personal information). Genesee was considered to be susceptible to both powdery mildew and leaf rust based on infection type following inoculation (Ellingboe, 1975), and the same information was published for Yokwin (Jensen and Kent, 1952). Norin 10 carried *Pm14* and *Pm15* genes for resistance to wheatgrass powdery mildew, but was highly susceptible to wheat mildew fungus (Tosa and Sakai, 1990).

DISCUSSION

Ionizing radiation and somaclonal variation have been recently utilised to induce wheat mutants resistant to powdery mildew and rusts (Duggal et al., 2000; Kinane and Jones, 2001; Rakszegi et al., 2010). Kinane and Jones (2001) reported thirteen mutants with increased resistance to powdery mildew and eleven from them exhibited grain yields at least as high as that of the wheat cv. Guardian, while one mutant line yielded significantly higher than the wheat parent. According to Brevis et al. (2008), wild *Triticeae* species have been extensively used to expand the pool of resistance genes in cultivated wheat and account for approximately half of the 55 named *Lr* resistance genes. One of the alien resistance gene *Lr47*, located on the short arm of *T. speltoides* chromosome 7S#1, has probably originated from a population obtained by irradiation of the hybrid CI15092/*T. speltoides*//Fletcher/3/5*Centurk with fast neutrons (Wells et al., 1982).

The wheat-*Aegilops* lines 37-7, 37-3, 104-4 and 104-5 in this experiment, originating from F_1 seeds irradiated with gamma rays, have showed increased resistance to powdery mildew and leaf rust in seedlings due to various wheat-alien chromosome rearrangements and/or mutations occurred during the selection process. This is supported by the waxy bloom character in these lines in contrast to lines 28-1 and 28-7, and cv. Rusalka. Additionally, lines 104-4 and 104-5 produced grain yield higher than Rusalka wheat (data not shown). Line 11-8 used in this study was reported as disomic substitution line with a 1U chromosome pair from *Ae. variabilis* substituted for 1B chromosome and causing brown glume character in maturity (Spetsov, 1998). All other lines selected from the Rusalka/*Ae. variabilis* cross possessed white glumes and absence of the alien 1U chromosome.

DHL 51 and 131 did not contain the 1U chromosome too, but were verified by checking to have only 6B satellited chromosomes. The introgression between 1B and 1U chromosomes might be occurred in these genotypes giving rise to resistance to 8 from the 11 pm isolates used. Noticeable the Charodeika itself has postulated *Pm5* gene which is widespread resistance gene in Russia (Zeller and Hsam, 1998) and Bulgaria (Petrova et al., 2000), , while Rusalka is susceptible. Two lines in this study, 28-1 and 28-7, that originated from a group of plants once backcrossed to variety resembling Rusalka, were morphologically similar to the wheat parent.

Among the 37 cultivars studied from Bulgaria, cv. Pliska was determined as intermediate in response, while Rusalka expressed resistance response pattern to nine isolates of the leaf rust pathogen (Petrova et al., 2000). Here, Rusalka showed four resistance reactions (to S16, 27, 28 and 48) and four susceptible patterns (to S12, 29, 47 and 71), and expressed better resistance than *Ae. variabilis* and Pliska. The resistance of parents and lines derived from a Rusalka/*Ae. variabilis* cross, except for line 28-7, was characterized as unknown (u) resistance, because their response patterns did not correspond to any of the lines possessing major single resistance genes.

CONCLUSION

The selected lines manifested different disease pattern from the parents and lines possessing known powdery mildew and leaf rust resistance genes. Line 11-8 as a 1U(1B) substitution and the two doubled haploid lines that are probably introgressed genotypes, exhibited different resistance to powdery mildew from any of the NILs and characterized tentatively as unknown resistance. Results showed that at least four lines (37-3, 37-7, 104-4 and 104-5) were very different from Pliska regarding the resistance to leaf rust, and these facts do not support this variety as a potential donor of resistance. Non of the lines derived from Rusalka/*Ae.variabilis* and Charodeika/11-8 crosses fitted any of the differential set possessing documented resistance genes to powdery mildew and leaf rust used in the study, and should be further investigated as promising genetic stocks in wheat breeding.

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