



Inheritance of *Triticum militinae* Zhuk. derived leaf rust and stem rust resistance in common wheat

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(Received: May 2002; Revised: February 2003; Accepted: February 2003)

Abstract

The rust resistant hexaploid stocks, Selection (Sel.) T 2600 and Sel. T 216-1 derived from *T. aestivum* × *T. militinae* cross were analysed to study the mode of inheritance and to establish the identity of genes conditioning seedling resistance to the leaf rust pathotype 77-5 and stem rust pathotype 40-1. The genetic analysis of different filial generations viz., P₁, P₂, F₁, F₂ and BC₁ F₁ of the crosses Agra Local × Sel. T 2600, Lal Bahadur × Sel. T 2600, Chinese Spring × Sel. T 2600, Agra Local × Sel. T 216-1, Kalyansona × Sel. T 216-1 and Chinese Spring × Sel. T 216-1 revealed that the resistance to leaf rust and stem rust was controlled by a single dominant gene. The test of allelism indicated that the gene governing leaf rust resistance in Sel. T 2600 was different from the known genes *Lr19*, *Lr24* and *Lr28* and that of Sel. T 216-1 from *Lr9*, *Lr19* and *Lr28*. The gene for leaf rust resistance in Sel. T 2600 and Sel. T 216-1 was allelic to *Lr9* and *Lr24*, respectively. The stem rust resistance present in Sel. T 216-1 was distinctly different than that of *Sr24* and *Sr26* as established through the test of allelism and the pattern of infection type.

Key words: *Triticum militinae*, rust resistance, seedling test, inheritance, test of allelism

Introduction

Wild progenitors of common wheat, *Triticum aestivum*, allied genera and related species constitute a vast reservoir of potentially useful genes for disease resistance, particularly rusts [1, 2]. Several useful genes have been transferred from these wild species to common wheat. Wild emmer and Timopheevi group of wheats have enormous genetic diversity with regards to many desirable characteristics. Amongst them, *T. timopheevi* and its free threshing mutant *T. militinae* Zhuk. Et. Migush. (2n = 4x = 28, genome AAGG) holds great potential for disease resistance, particularly rusts and powdery mildew [3]. *T. militinae* was isolated as a spontaneous mutant from collection plots of *T. timopheevi* by Zhukovskiy [4]. Selections derived from an interspecific hybrid between *T. aestivum* and *T. militinae* exhibited high resistance to leaf and stem rust races prevailing in the Nilgiri region, Tamil Nadu India [5]. The present paper reports the mode of inheritance

of resistance derived from *T. militinae* to leaf and stem rusts in selection Sel. T 2600 and Sel. T 216-1 of common wheat, and the identity of gene(s) in these selections in relation to other genetic stocks carrying different genes for resistance derived from alien sources.

Materials and methods

The experimental material comprised of Sel. T 2600 and Sel. T 216-1, which were selected from the crosses C 306 / *T. militinae* // C 306 and Sonalika / *T. militinae* // Sonalika respectively, followed by five generations of selfing. Both the selections showed resistance of high degree to leaf rust (5MR) and to stem rust (10MRMS).

In order to study the inheritance pattern of *T. militinae* derived stem rust and leaf rust resistance, the wheat cultivars viz., Agra Local (AL), Kalyansona (KS), Chinese Spring (CS) and Lal Bahadur (LB) were used as one of the rust susceptible parents. The near-isogenic lines (NILs) and stocks carrying known genes in use as differentials in India for pathotype analysis of leaf rust pathogen, *Puccinia recondita* f. sp. *tritici* [6] and stem rust pathogen, *P. graminis* f. sp. *tritici* [7] were considered in the present study. The initial inoculum of different pathotypes, 77-5 of leaf rust pathogen and 40-1 of stem rust pathogen was obtained from DWR, Regional Station, Flowerdale, Shimla and the same was used for genetic analysis of resistance gene(s) in Sel. T 2600 and Sel. T 216-1. Both Sel. T 2600 and Sel. T 216-1 were crossed to rust susceptible genotypes mentioned above. The resistant genotypes were also crossed with NILs carrying specific gene, *Lr9*, *Lr19*, *Lr24* and *Lr28* for leaf rust resistance and *Sr24*, *Sr25* and *Sr26* for stem rust resistance to test the identity of gene(s). The F₁, F₂ and BC₁ F₁ generations of the crosses along with parents were tested with pathotypes 77-5 of *P. recondita* and 40-1 of *P. graminis tritici*, while only F₂ generation of the crosses involving NILs were tested with above mentioned pathotypes at seedling stage. Seedling tests were conducted in glass house at mean temperature ranging

Table 1. Infection types (ITs) of selected pathotypes of *Puccinia recondita* and *P. graminis* f sp. *tritici* on Sel. T 2600, Sel. T 216-1 and different stocks at seedling stage

Genotypes	Pathotypes														
	Leaf rust								Stem rust						
	12A	12-1	12-2	77-2	77-5	77-6	104-2	106	11	40	40A	40-1	117A	117-3	117-6
Sel. T 2600	0	0	0	0	0	0	0	0	;1	;1+	;1	;1+	;1	;1	;1
<i>T. militinae</i>	0	0	0	0	0	0	0	0	0	0;	;	0	;	;	;
C 306	3+	3+	33+	3+	3+	3+	33+	3+	3+	3+	4	33+	3+	33+	3+
Agra local	3+	3+	33+	3+	3+	3+	33+	3+	3+	3+	4	33+	3+	33+	4
Lal Bahadur	3+	3+	33+	3+	3+	3+	3+	3+	3+	3+	3+	4	3+	4	33+
Sel. T 216-1	-	-	;	;1	;1N	;1	;1	-	-	;1	;1+	;1	-	-	;
Sonalika	;12+	X+	X+	3+	3+	3+	X+	-	;1	3+	4	3+	;12+	-	-
Chinese spring	33+	3+	33+	3+	3+	3+	33+	-	3+	3+	3+	3+	33+	4	3+
Kalyansona			3+	3+	3+	3+	33+	-		3+	3+	33+	3+	-	3+
Sunstar*6/C80-1	0;	;	;	0;	;	;	;	0	-	;1	;1	;1+	;	;1	;1
HW 2051	0	0	0;	0;	0	0	0	0	-	3+	3+	3+	;1	;1	-
HW 2033	;	0	0	;	0	;	0	0	3+	3+	3+	;12	3+	3+	-
Agent	;N	;1	;1	;1N	;1-N	;	;1+	;	;	0	;	3+	;	;	;1
DARF	;	;1	;1	;	;+	;	;1	;	;1	0	;	;1+	;1	;1	;

- = not tested

from 12°C to 30°C. Ten seeds were sown in each of ten rows in rectangular trays (27 × 10 × 7.5 cm) filled with soil. A week old seedlings were inoculated with uredospores of 77-5 and 40-1 according to the procedure described by Joshi *et al.* [8] and incubated in humidity chambers for 48h. Thereafter trays were shifted to the benches in glass house. Rust reactions were recorded according to the scale described by Stakman *et al.* [9] after ten days of inoculation. Seedlings were categorised on the basis of reaction pattern '1' to '2' as resistant (R) and '3' to '4' as susceptible (S). The chi-square (χ^2) test was used to establish validity of expected ratios in segregating generations.

Results and discussion

The results obtained in seedling tests on parental lines, F₁, F₂ and BC₁ F₁ generations are presented in Tables 1-4. The genetic analysis on resistance to leaf rust and stem rust is presented separately.

Leaf rust resistance

Genetic analysis on resistance in Sel. T 2600 to leaf rust pathotype 77-5 was carried out based on three crosses each involving a different susceptible parent viz., Agra Local, Lal Bahadur and Chinese Spring (Table 2). The resistant reaction in all F₁ plants tested and segregation of F₂ population into 3 resistant : 1 susceptible ratio in the cross Agra Local × Sel. T 2600 indicated the monogenic nature of resistance. The BC₁ F₁ progenies segregated into 1R : 1S ratio with good fit, which further validated the hypothesis. The same trend was observed in F₁, F₂ and BC₁ F₁ generations of the other two crosses Lal Bahadur × Sel. T 2600 and Chinese Spring × Sel. T 2600 indicating

monogenic dominant control for leaf rust resistance in Sel. T 2600. These results indicated that the parents in each cross differed at only one locus governing the resistance to the pathotype of *Puccinia recondita*.

Similarly, the genetics of resistance to leaf rust in Sel. T 216-1 was determined in the crosses, viz., Agra Local × Sel. T 216-1, Kalyansona × Sel. T 216-1 and Chinese Spring × Sel. T 216-1 (Table 2). The F₁, F₂ and BC₁ F₁ generations derived from the above mentioned crosses showed concordant segregation pattern across the crosses. The observations, where all F₁ plants with resistance indicated dominant nature of resistance and segregation in F₂ population with good fit to the expected ratio of 3R : 1S revealed monogenic control for resistance. Further segregation in BC₁ F₁ progenies fitting well to the expected 1R : 1S ratio again confirming the dominant monogenic control for resistance to 77-5 pathotype of leaf rust in Sel. T 216-1. Studies of similar nature on wheat × *T. militinae* derivatives have earlier been conducted [10-12] and single dominant gene imparting resistance to leaf rust pathotypes was reported. However, the plant material as well as the type of races of *Puccinia recondita* used were different in their studies.

Stem rust resistance

Both *T. militinae* derivatives, Sel. T 2600 and Sel. T 216-1 showed resistance to 40-1 pathotype of *Puccinia graminis tritici*. Genetic analysis was, therefore, carried out to find out the nature of inheritance and number of genes governing resistance to this particular pathotype 40-1 of stem rust. Table 3 indicate that all the F₁ plants of the crosses, Agra Local × Sel. T 2600, Lal Bahadur × Sel. T 2600 and Chinese Spring × Sel.

T 2600 showed resistant reaction in seedling stage indicating that the resistance to stem rust pathotype 40-1 in Sel. T 2600 is controlled by the dominant gene(s). The F_2 population in all the crosses segregated in good fit ratio of 3R : 1S demonstrating that the resistance is monogenically controlled. In the progeny of crosses of all F_1 with susceptible parent(s), an expected segregation ratio of 1R : 1S with non-significant Chi-square value was observed. Considering all these observations recorded in F_1 , F_2 and $BC_1 F_1$ generations it was confirmed that the resistance in Sel. T 2600 against stem rust pathotype 40-1 is determined by a single dominant gene.

In order to understand the inheritance of resistance in Sel. T 216-1 to stem rust pathotype 40-1, different generations derived from the crosses Agra Local \times Sel. T 216-1, Kalyansona \times Sel. T 216-1 and Chinese Spring Sel. \times T 216-1 and the test crosses were analysed genetically. The F_1 plants in all the three crosses exhibited resistance revealing dominance nature of resistance. The segregation pattern in F_2 population

fitted well to the expected ratio of 3R : 1S and the segregation in $BC_1 F_1$ progenies was also in agreement with the expected ratio of 1R : 1S. (Table 3). Based on the pattern of segregation in F_2 and $BC_1 F_1$ generations and the resistant reaction in F_1 plants it could be ascertained that the Sel. T 216-1 also carries a single dominant gene for resistance to 40-1 pathotype of stem rust. Most of the designated stem rust resistance genes in wheat are of dominant nature [13]. Sinha *et al.* [14] reported a similar genetic control for stem rust resistance in hexaploid derivatives of wheat \times *T. militinae*.

Inter-relationship among the rust resistant parents

Both Sel. T 2600, involving C-306 and Sel. 216-1 having Sonalika in the pedigree, confer resistance to leaf rust pathotype 77-5 and stem rust pathotype 40-1. The F_1 plants of the cross Sel. T 2600 \times Sel. 216-1 did not survive because of progressive hybrid necrosis genes Ne_1 and Ne_2 , which are reported from the cultivar C 306 and Sonalika respectively [14]. However, the

Table 2. Segregation of seedlings in F_2 and $BC_1 F_1$ generations of different crosses tested with the leaf rust pathotype 77-5

Parents/crosses	Generation	Number of seedlings			Expected ratio	χ^2	P value
		Resistant (IT : 0-2)	Susceptible (IT : 3-4)	Total			
Agra Local (AL)	P ₁	0	26	26			
Sel. T 2600	P ₂	31	0	31			
AL / Sel. T 2600	F ₁	12	0	12			
	F ₂	181	51	232	3R : 1S	1.126	0.50-0.25
AL / Sel. T 2600 // AL	$BC_1 F_1$	15	11	26	1R : 1S	0.615	0.50-0.25
Lal Bahadur (LB)	P ₁	0	25	25			
Sel. T 2600	P ₂	28	0	28			
LB / Sel. T 2600	F ₁	10	0	10			
	F ₂	176	59	235	3R : 1S	0.001	0.95-0.90
LB / Sel. T 2600 // LB	$BC_1 F_1$	20	15	35	1R : 1S	0.714	0.50-0.25
Chinese Spring (CS)	P ₁	0	21	21			
Sel. T 2600	P ₂	17	0	17			
CS / Sel. T 2600	F ₁	12	0	12			
	F ₂	86	33	119	3R : 1S	0.473	0.50-0.25
CS / Sel. T 2600 // CS	$BC_1 F_1$	14	17	31	1R : 1S	0.290	0.75-0.50
AL	P ₁	0	17	17			
Sel. T 216-1	P ₂	22	0	22			
AL / Sel. T 216-1	F ₁	10	0	10			
	F ₂	85	22	107	3R : 1S	1.125	0.50-0.25
AL / Sel. T 216-1 // AL	$BC_1 F_1$	20	13	33	1R : 1S	1.485	0.25-0.10
Kalyansona (KS)	P ₁	0	8	8			
Sel. T 216-1	P ₂	11	0	11			
KS / Sel. T 216-1	F ₁	7	0	7			
	F ₂	1	8	39	3R : 1S	0.419	0.75-0.50
KS / Sel. T 216-1 // KS	$BC_1 F_1$	15	21	36	1R : 1S	1.000	0.50-0.25
CS	P ₁	0	16	16			
Sel. T 216-1	P ₂	19	0	19			
CS / Sel. T 216-1	F ₁	10	0	10			
	F ₂	52	23	75	3R : 1S	1.284	0.50-0.25
CS / Sel. T 216-1 // CS	$BC_1 F_1$	24	17	41	1R : 1S	1.195	0.50-0.25

Table 3. F₂ and BC₁F₁ segregation for resistance in Sel. T 2600 and Sel. T 216-1 to stem rust pathotype 40-1 at seedling stage

Parent/Cross	Generation	Number of seedlings			Expected ratio	χ^2	P-value
		Resistant (IT : 0-2)	Susceptible (IT : 3-4)	Total			
Agra Local (AL)	P ₁	0	21	21			
Sel. T 2600	P ₂	31	0	31			
AL / Sel. T 2600	F ₁	9	0	9			
	F ₂	66	16	82	3R : 1S	1.317	0.50-0.25
AL / Sel. T 2600 // AL	BC ₁ F ₁	21	16	37	3R : 1S	0.675	0.50-0.25
Lal Bahadur (LB)	P ₁	0	23	23			
Sel. T 2600	P ₂	26	0	26			
LB / Sel. T 2600	F ₁	10	0	10			
	F ₂	110	30	140	3R : 1S	0.952	0.50-0.25
LB / Sel. T 2600 // LB	BC ₁ F ₁	20	14	34	1R : 1S	1.059	0.50-0.25
Chinese Spring (CS)	P ₁	18	0	18			
CS / Sel. T 2600	F ₁	18	0	18			
	F ₂	69	26	95	3R : 1S	0.284	0.75-0.50
CS / Sel. T 2600 // CS	BC ₁ F ₁	12	17	29	1R : 1S	0.862	0.50-0.25
AL	P ₁	0	19	19			
Sel. T 216-1	P ₂	11	0	11			
AL / Sel. T 216-1	F ₁	7	0	7			
	F ₂	26	5	31	3R : 1S	1.831	0.25-0.10
AL / Sel. T 216-1 // AL	BC ₁ F ₁	16	22	38	1R : 1S	0.947	0.50-0.25
Kalyansona (KS)	P ₁	0	15	15			
Sel. T 216-1	P ₂	12	0	12			
KS / Sel. T 216-1	F ₁	9	0	9			
	F ₂	26	5	31	3R : 1S	1.830	0.25-0.10
KS / Sel. T 216-1 // KS	BC ₁ F ₁	20	17	37	1R : 1S	0.243	0.75-0.50
CS	P ₁	0	14	14			
Sel. T 216-1	P ₂	18	0	18			
CS / Sel. T 216-1	F ₁	13	0	13			
	F ₂	48	20	68	3R : 1S	0.706	0.50-0.25
CS / Sel. T 216-1 // CS	BC ₁ F ₁	17	14	31	1R : 1S	0.290	0.75-0.50

infection types on Sel. T 2600 and Sel. 216-1 (Table 1) to selected pathotypes of leaf rust were different. Although both these belong to resistant category, the differential reaction pattern provides an indication of genetic diversity among the derivatives.

Test of allelism: The segregation frequency in F₂ population of the crosses Sunstar*6 / C80-1 (*Lr19*) // Sel. T 2600, Agent (*Lr24*) × Sel. T 2600 and HW 2033 (*Lr28*) × Sel. T 2600 had good fit to the expected ratio of 15R : 1S. The appearance of susceptible plants and segregation in F₂ into 15R : 1S ratio confirmed that the leaf rust resistance identified in Sel. T 2600 is conferred by genes different than *Lr19*, *Lr24* and *Lr28*. However, absence of susceptible seedlings in F₂ plants from the cross HW 2051 (*Lr9*) × Sel. T 2600 demonstrate that the resistance gene in Sel. T 2600 is allelic to *Lr9* present in HW 2051. The gene *Lr9* is derived from *Aegilops umbellulata* (2n = 2x = 14, genome UU), while the resistance identified in Sel. T 2600 is transferred from *T. militinae* (2n = 4x = 28,

genome AAGG), the possibility of both genes being identical is less. Although Enno *et al.* [12] reported that the resistance derived from *T. militinae* and *T. timopheevi* was identical with that of imparted by *Lr23* from emmer wheat. Testing of Sel. T 2600 with recently identified virulence, which has knocked down *Lr23*, *Lr26* and *Lr9* genes will help in establishing the correct identity of resistance in present stock. Techniques like chromosome banding, in situ hybridization or the use of molecular markers specific to *Lr9* gene can help establishing the correct identity of the gene.

The F₂ population of the crosses HW 2051 (*Lr9*) × Sel. T 216-1, Sunstar*6 / C80-1 (*Lr19*) × Sel. T 216-1 and HW 2033 (*Lr28*) × Sel. T 216-1 segregated into expected ratio of 15R : 1S indicating that the leaf rust resistance gene possessed by Sel. T 216-1 is different from *Lr9*, *Lr19* and *Lr28*. However, all 80 F₂ plants from Agent (*Lr24*) × Sel. T 216-1 showed resistance. The identity of resistance in Sel. T 216-1

Table 4. Segregation pattern in F₂ in the crosses of resistant parents to leaf rust and stem rust pathotypes 77-5 and 40-1, respectively

Cross	Number of seedlings			Expected ratio	χ^2	P-value
	Resistant (IT : 0-2)	Susceptible (IT : 3-4)	Total			
Seedling test with leaf rust pathotype 77-5						
HW 2051 (<i>Lr19</i>) // Sel. T 2600	161	0	161	15R : 1S	10.733	< 0.01
Sunstar*6 / C80-1 (<i>Lr19</i>) // Sel. T 2600	90	7	97	15R : 1S	0.155	0.75-0.50
Agent (<i>Lr24</i>) / Sel. T 2600	77	6	83	15R : 1S	0.136	0.75-0.50
HW 2033 (<i>Lr28</i>) / Sel. T 216-1	77	4	81	15R : 1S	0.297	0.75-0.50
HW 2051(<i>Lr9</i>) / Sel. T 216-1	84	7	91	15R : 1S	0.323	0.75-0.50
Sunstar*6 / C80-1 (<i>Lr19</i>) // Sel. T 216-1	61	6	67	15R : 1S	0.837	0.50-0.25
Agent (<i>Lr24</i>) / Sel. T 216-1	73	0	73	15R : 1S	4.867	< 0.01
HW 2033 (<i>Lr28</i>) / Sel. T 216-1	75	7	82	15R : 1S	0.732	0.50-0.25
Seedling test with stem rust pathotype 40-1						
Agent (<i>Sr24</i>)	0	10	10			
Agent/Sel. T 216-1	60	23	83	3R : 1S	0.325	0.75-0.50
DARF (<i>Lr24, Sr24, Sr26</i>) / Sel. T 216-1	93	8	101	15R : 1S	0.481	0.50-0.25

could be established based on the source of resistance as *Lr24* has been introgressed from *Agropyron elongatum* [15].

Diversity for stem rust resistance in Sel. T 2600 and Sel. T 216-1: Reference to Table 1 reveals that both Sel. T 2600 and Sel. T 216-1 exhibited resistance to five stem rust pathotypes. However, the infection types recorded in both these genotypes were different indicating genetic diversity among the derivatives. The F₂ population from the cross Agent (*Sr24*) × Sel. T 216-1 was subjected to seedling test with stem rust pathotype 40-1. The plants in F₂ generation segregated in a ratio of 3 resistant : 1 susceptible emanating that gene(s) present in both the parents are not identical. The gene *Sr24* has been reported ineffective [16] against stem rust pathotype 40-1 (62G29-1). The resistant reaction exhibited by Sel. T 216-1 and segregation in F₂ population of the cross Agent (*Sr24*) × Sel. T 216-1 suggest that Sel. T 216-1 carry a stem rust resistance gene different than *Sr24*. The Sel. T 216-1 was also crossed with DARF carrying rust resistance gene *Sr26* from *Agropyron elongatum*. The F₂ population segregated into 15R : 1S ratio revealing that the resistance gene present in Sel. T 216-1 is different than that of *Sr26*. Besides, Sel. T 216-1 exhibited resistance to selected pathotypes of stem rust, viz., 11, 40-1, 40A, 17-6 and 122. None of the wheat genes except those originated from allied and alien species showed resistance to all those above mentioned pathotypes [17-20].

The results of the present investigation showed that the resistance in Sel. T 2600 and Sel. T 216-1 to leaf rust pathotype 77-5 and stem rust pathotype 40-1 were imparted by an independent gene. The

tetraploid species, *T. militinae*, which shares one genome (AA) with *T. aestivum* and greater homology between B genome of *T. aestivum* and G genome of *T. militinae*, introduced additional genetic variability, which can be exploited in breeding for host plant resistance.

Conclusions

From the breeders' perspective, this study opens up the hcoice of diverse material for utilization in wheat improvement, particularly, for rust resistance. The study has also revealed that allied species *Triticum malitinae* is a potential donor for stem rust and leaf rust resistance genes. Genetic analysis and location of leaf rust and stem rust resistance gene(s) on chromosomes 6B and 1B respectively would stimulate interest in conventional breeding programmes. Partial genomic affinities between the B genome of wheat (*T. aestivum*) and G genome of *T. militinae* have been observed by earlier workers also [12, 21]. It is presumed that chromosome of B/G genomes are frequently involved in spontaneous translocations and have acquired natural polymorphism for translocations. The involvement of 1B/1G is also evident from the morphology as the colour of glumes in sel. T 2600 is black, which indeed is transferred from *T. militinae*. Similarly, the leaves of Sel. T 216-1 are pubescent like that of *T. militinae*. The study has illustrated that distant hybridization is an useful method for transferring desirable genes [22], which may be suitable for exploitation in wheat improvement and ultimately benefit the breeders.

Acknowledgement

Senior author acknowledges the IARI and CSIR for providing Merit Scholarship and Senior Research Fellowship, respectively.

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