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Inheritance and linkage analysis of leaf rust resistance, node and leaf pubescence in interspecific derivative of *Triticum aestivum* L.

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Abstract

Genetic analysis was carried out in cytologically stable Selection (Sel.) T2836-1 (2n = 6x = 42), an interspecific derivative involving, bread wheat *Triticum aestivum*, a wheat progenitor *T. urartu* and *T. militinae,* a mutant of *T. timopheevi* to study the mode of inheritance of leaf rust resistance, leaf and node pubescence and glume hardness. Linkage between different traits was also investigated. The study revealed that Sel. T2836-1 carries a single dominant gene for resistance to Indian pathotypes, 77-1, 77-5 and 77-7 of *Puccinia triticina*. However, test of allelism revealed that the resistance is allelic to the gene *Lr*24. Further, molecular analysis also confirmed the presence of *Lr*24 in Sel. T2836-1. Study further indicated that pubescence of leaf was controlled by duplicate dominant genes, whereas node pubescence was governed by a single dominant gene. Monogenic dominant control was also indicated for glume hardness in Sel. T2836-1. The linkage analysis indicated that character node pubescence is linked with one of the duplicate dominant genes controlling leaf pubescence and the distance between these genes is 36.84 Kosambi unit.

Key words: Leaf rust resistance, interspecific gene transfer, leaf and node pubescence, glume hardness, inheritance , linkage, wheat

Introduction

Wheat rusts, particularly leaf rust (*Puccinia triticina* Syn. *Puccinia recondita tritici* Rob. Ex Desm.) occur world wide and is known to cause significant losses in wheat production. Leaf rust is highly variable and is known to have many physiological races or biotypes. Co-evolution of both host and parasite leads to appearance of new pathotypes, which renders resistant varieties susceptible in a short span of time. During the recent past, epidemics of leaf rust have occurred in some pockets of Northern India with a severity ranging between 60S to 80S in an estimated area of 4 million hectares [1]. Since leaf rust potentially causes a great damage, the sustained wheat production in India is ascribed largely to the strategic deployment of effective resistance genes singly or in combination against the regular occurrence of leaf rust. About 60 *Lr* genes providing resistance to a range of leaf rust pathotypes have been documented [2]. A large number of designated *Lr* genes have their origin in *Triticum aestivum* and most of them have become ineffective to virulent Indian pathotypes [3]. However, the resistance genes introgressed from progenitors and other alien species provide useful resistance to a broad spectrum of leaf rust pathotypes. In recent past the resistance conferred by the genes, *Lr*26 from *Secale cereale, Lr*9 (*Aegilops umbellulata*) and *Lr*19 (*Agropyron elongatum*) has been overcome by newly evolved Indian leaf rust biotypes of 77 race *viz*., 77-6, 77-8 and 77-1 respectively. The dynamism in evolution of new pathotypes necessitates the hunt for new sources of resistance continuously. Among wild species, *T. militinae*, a mutant of *T. timopheevi* (2n = 4x = 28, genome AAGG) offers an excellent source for disease resistance including leaf rust races prevailing in India [4]. Similarly, diploid progenitor of wheat *Triticum urartu* (2n = 2x = 14 genome AA) also possesses remarkable resistance to leaf rust under field conditions.

An interspecific derivative Selection (Sel.) T 2836-1 involving bread wheat, *Triticum urartu* and *T. militinae* in the pedigree was developed, which exhibited a high degree of leaf rust resistance. In addition, the leaf and the node of this derivative are pubescent. A study was conducted to understand the mode of inheritance of resistance, threshability, leaf and node pubescence and to determine the number of genes controlling these traits. The results of the investigation are communicated as under.

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Material and methods

Material comprised a leaf rust resistant genetic stock Selection (Sel.) T2836-1 derived from the cross *T. aestivum* cv. Chinese Spring/*T. urartu*//HD2012/C306//*T. militinae*, two susceptible stocks, Agra local and NI5439 and specific genetic stocks namely, HW 2003 (NI5439*[6]/TR380-14*[7]/3Ag#14), HD3007 (HW2002/CPAN2044//EC414149) and Sunstar*[6]/C80-1 carrying leaf rust resistance genes *Lr*24 and *Lr*19 respectively. In addition to leaf rust resistance, HD3007 also restores fertility in CMS lines having *T. timopheevi* and *T. araraticum* cytoplasms (unpublished data). The glume, leaf (ventral/upper side) and the node of Sel. T2836-1 are pubescent like that of *T. militinae* or *T.urartu* and the spike is club shaped at the top. Sel. 2836-1 was crossed with rust susceptible cultivars Agra Local and NI 5439 as well as resistant stocks and F_1 hybrids thus obtained were selfed as well as backcrossed to susceptible genotypes to generate F_2 and BC_1 generations. All the parents, F_1, F_2 and BC_1 generations were subjected to seedling tests with the leaf rust pathotypes *viz*., 77-1(109R63), 77-5(121R63-1) and 77-7(121R127) in green house conditions at 18 to 25°C. Fresh inoculum of leaf rust obtained from DWR Regional Station Flowerdale, Shimla was multiplied on Agra Local under greenhouse conditions at Delhi. Seedlings were inoculated as per the procedure described by Joshi *et al.* [5] and the infection type produced on the leaf was recorded 15 days after inoculation as per standard procedure [6]. Scored seedlings were transplanted in the field to take observation on pubescence on glumes, leaves and nodes and glume hardness in all the segregating generations. The segregation for individual trait was analysed by χ^2 test to determine the goodness of fit of the observed frequencies with the expected ratios. The linkage was detected by joint segregation analysis [7]. Once the linkage was proved, the recombination fraction was determined by the product ratio method. The Kosambi function was applied to convert non additive distances into additive distances.

Identification of gene *Lr*24 was done using SCAR marker $SCS1302_{609}$ and *Sr24*#12 (Mago *et al.*). DNA was isolated and purified from ten days old seedlings by CTAB method and quantified using gel assay method and then PCR was performed. 10µl PCR mixture was prepared for PCR analysis comprising 50ng template DNA, 10ng each of forward and reverse primers, 0.1mM dNTPs, 1X PCR buffer (10mMTris, pH 8.0, 50mM KCl and 50mM Ammonium sulphate), 1.8mM $MgCl_2$ and 0.25 unit Taq polymerase (MBI, Fermentas). The volume was made up to 10ml by autoclaved MQ H_2O. PCR was run for 39 cycles at 95°C for 2 min, 94°C for 1 min, 60°C for 1min, 72°C for 2 min and final extension step of 72°C for 7 min and final storage step at 4°C. Equal amount (10ml) of 1X gel loading dye was mixed with the PCR products. For gel analysis, 1.8% agarose gel was prepared and 8ml of PCR product +dye was run for 3 hours at 80Volt. Gel was visualized under UV light using Gel Documentation Equipment for scoring the bands.

Results and discussion

The seedling test with three leaf rust pathotypes, 77-1, 77-5 and 77-7 revealed a high level of seedling resistance in Sel. T2836-1 exhibiting infection type ";1" while the genotypes NI5439 and Agra Local exhibited infection type (IT) 3+, a susceptible reaction. The F_1 plants of Sel. T2836-1/NI 5439 exhibited resistance against tested pathotypes (77-1 & 77-7) while Sel.T2836-1/Agra Local showed resistant reaction to all the three pathotypes indicating that resistance in Sel. T2836-1 is dominant. The F_2 individuals from both the crosses, when tested with 77-1 and 77-7 segregated into expected ratio of 3 resistant (R) : 1 susceptible (S) showing that resistance in T2836-1 is determined by a single dominant gene. The BC_1F_1 progenies segregated into 1R:1S with acceptable χ^2 value confirming the F_2 hypothesis that the resistance in Sel. T2836-1 is determined by a single dominant gene against 77-1, 77-5 and 77-7. There are no reports available on transfer of resistance to leaf rust from *T. urartu* into wheat. However, derivatives of wheat and *T. militinae* imparting resistance to leaf rust determined by single dominant gene [8-10] have been isolated and tested. The selection exercised during introgression was based on morphological markers such as leaf and node pubescence along with field resistance to leaf rust. It is therefore, presumed that Sel T2836-1 carry diverse resistance. However, the data on test of allelism obtained from the crosses HW2003 (*Lr*24)/Sel. T2836-1 and Sunstar*6/C80-1(*Lr*19)/Sel.T2836-1 revealed that the resistance is not distinct from *Lr*24. The F_2 populations (more than 75 plants in each cross) tested with all the three pathotypes did not segregate and all plants exhibited seedling resistance. Molecular techniques can be precise in detecting the gene identity even in the absence of virulence. The molecular analysis using gene specific markers, $SCS1302_{609}$ [11] and *Sr24*#12 [12] confirmed the presence of *Lr*24 (Fig. 1). The original stock Sunstar*6/C80-1 supposed to carry *Lr*19 is in fact a carrier of *Lr*24 as reported by Prabhu *et al.* [13] and therefore, test of allelism also gave same results as

Table 1. Mode of segregation for resistance to leaf rust pathotypes of seedlings in the crosses of Sel.T 2836-1 with NI5439 and Agra Local

Parent/ Cross	Generation	No. of seedlings			Expected ratio	χ^2	P- value
		R	S	Total			
		Pathotype 77-1 (109R63)					
T2836-1	P1	24	0	24			
NI5439	P2	0	19	19			
Agra Local (AL)	P3	0	17	17			
T2836-1/NI5439	F_1	13	0	13			
T2836-1/NI5439	F_2	142	36	178	3R:1S	2.164	0.25-0.1
T2836-1/NI5439//NI5439	BC_1F_1	13	10	23	1R:1S	0.390	0.75-0.50
T2836-1/ AL	F_1	10	0	10			
T2836-1/ AL	F_2	139	41	180	3R:1S	0.473	0.50-0.25
T2836-1/ AL//AL	BC_1F_1	9	8	17	1R:1S	0.058	0.9-0.75
		Pathotype 77-5 (121R 63-1)					
T2836-1		21	0	21			
T2836-1/ AL	F_1	12	0	12			
T2836-1/ AL	F_2	134	44	176	3R:1S	0.051	0.90-0.75
T2836-1/ AL//AL	BC_1F_1	8	6	14	1R:1S	0.284	0.75-0.50
		Pathotype 77-7 (121R 127)					
T2836-1		17	0	17			
NI5439		0	14	14			
Agra local		0	8	8			
T2836-1/NI5439	F_1	17	0	17			
T2836-1/NI5439	F_2	114	42	186	3R:1S	0.580	0.50-0.25
T2836-1/NI5439//NI5439	BC_1F_1	11	8	19	1R:1S	0.472	0.5-0.25
T2836-1/ AL	F_1	11	0	11			
T2836-1/ AL	F_2	127	40	167	3R:1S	0.097	0.90-0.75
T2836-1/ AL// AL	BC_1F_1	7	5	12	1R:1S	0.343	0.75-0.50

R = Resistant, S = susceptible

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observed with HW2003 and HD3007 carrying *Lr*24. Further, Sel. T2836-1 when tested with the pathotype 77-8 virulent to *Lr*19, it exhibited resistance thereby ruling out the presence of *Lr*19 in Sel. T2836-1. Interspecific derivatives commonly show sterility during early generation of selection and it is likely that out crossing may occur if unstable selected plants are not covered to avoid foreign pollen. And it may be the case with Sel. 2836-1 that a selected plant with pubescence of node and leaf got out crossed with a line carrying the gene *Lr*24. This selction was maintained as a novel genetic stock based on morphological traits introgressed from wild species presuming that the resistance to leaf rust is also transferred from the donor. A sufficient care, therefore, should be taken during the introgression of genes through intergeneric and interspecific hybridization.

Inheritance of pubescence in leaf

Allelic variation for leaf pubescence in wheat has been reported earlier [14-15]. However, the present study indicates that there are two duplicate dominant genes governing leaf pubescence. The difference in intensity of leaf pubescence was noticed which suggested that they are independent of each other. The leaves of F_1 of Sel.T2836-1/NI5439 were pubescent indicating that leaf pubescence is a dominant trait. Out of 464 F_2 individuals; the leaves of 429 plants were pubescent while 35 plants produced non pubescent leaves. The observed data fit well into 15 pubescent:1 glaborous suggesting that leaf

pubescence is under digenic control. The BC_1F_1 population derived from the cross Sel. T2836-1/NI5439/ /NI5439, 48 plants showed pubescent leaves while 18 plants produced glabrous leaves. The observed frequency of plants in BC_1F_1 fits well into 3 pubescent:1 glabrous (Table 2). These results supported the hypothesis proposed from F_2 analysis that the leaf pubescence is controlled by two dominant genes. The knowledge of composition of external surface of leaf is vital to an interpretation of their response to the foliar pathogens and topically applied substances to control them. It is likely that epicuticular pubescence reduces water loss due to transpiration and may control gaseous exchange besides serving as morphological marker in genetic studies.

Inheritance of node pubescence

Node pubescence is normally not observed among hexaploid wheats. Some of the diploid species belonging to A genome, wild emmer and Timopheevi wheats carry pubescence on nodes. Inter specific derivatives involving either of the species mentioned above may receive the gene(s) through introgression. Kuspira *et al*. [15] suggested that only one major locus determines the node pubescence in *T. monococcum*. Wild emmer and Timopheevi wheat having received their A genomes either from *T. monococcum* or *T. urartu* also possess pubescence. The presence of hairy node character in Sel T2836-1 is indeed introgressed either from *T. militinae* or *T. uvartu*. Morphological characters though limited are useful in determining the significance, authenticity and varietal purity. They can also be used in genetic analysis and linkage studies.

To study the mode of inheritance of node pubescence, the data on F_1, F_2 and BC_1F_1 populations were analysed from the cross used for leaf pubescence. All the F_1 plants had pubescent nodes indicating the dominance of pubescence of node. In F_2 generation 359 plants showed pubescent node whereas 105 were glabrous. The observed frequency fits well into the expected ration of 3 pubescent and 1 glabrous node suggesting single dominant gene control of node pubescence. BC_1F_1 progenies segregated into 1 pubescent node vs. 1 non-pubescent node. This result demonstrated monogenic dominant control of node pubescence (Table 2)**.**

Inheritance of glume pubescence

The glumes in F_1 plants of the cross Sel. 2836-1 / NI5439 showed pubescence indicating that the trait glume

Table 2. Inheritance of leaf, node and glume pubescence and hardness

Cross	Characters	Generation	No. of plants			Expected ratio (P:G)	χ^2	P-value
			P	G	Total			
Sel.T2836-1		Leaf pub.	P_1	10	-	10	-	- -
	Node pub.	P_1	10	-	10	-	-	-
	Glume pub.	P_1	10	-	10			
	Glume hardness	P1	10	-	10			
Sel.T2836-1/	Leaf pub.	F_1	25	-	25	-	-	-
NI5439	Node pub.	F_1	25	-	25	-	-	-
	Glume pub.	F_1	25	-	25			
	Glume hardness	F_1	25	-	25			
	Leaf pub.	F_2	429	35	464	15:1	1.324	0.25-0.10
	Node pub.	F_2	359	105	464	3:1	1.394	0.25-0.10
	Glume pub.	F_2	433	31	464	15:1	1.147	0.25-0.10
	Glume hardness	F_2	352	112	464	3:1	0.184	0.75-0.50
F_1 /NI5439	Leaf pub.	BC_1F_1	48	18	66	3:1	0.181	0.70-0.50
	Node pub.	BC_1F_1	36	30	66	1:1	0.542	0.50-0.30
	Glume pub.	BC_1F_1	42	24	66	3:1	0.181	0.70-0.50
	Glume hardness	BC_1F_1	39	27	66	1:1	3.272	0.10-0.05

Pub. = pubescence; G = glabrous

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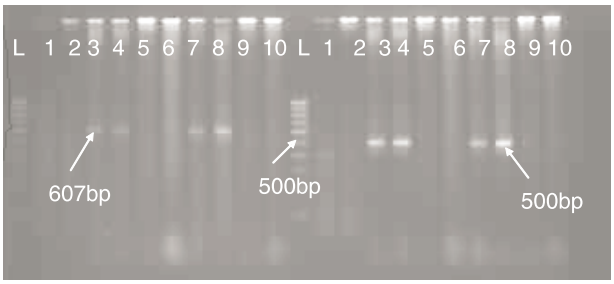
pubescence was dominant. In the F_2 generation out of 464 F_2 plants, 433 plants were pubescent while 31plants were found glabrous. The segregation pattern observed in the F_2 data fitted well to the expected ratio of 15 pubescent: 1 glabrous,which is evident from the non-significant χ^2 value of 0.147. The BC_1F_1 population derived from the cross F_1 x NI5439 segregated into 3 pubescent : 1 glabrous ratio. The calculated value of χ^2 (0.181) was non-significant. These results indicate that glume pubescence is governed by duplicated dominant genes in Sel. 2836-1. The trait glume pubescence has been reported under digenic [16-17] as well as monogenic control [18-19]. Kuspira *et al*. [15] found a multiple allelic series for a single major gene (*Hg*) locus. McIntosh and Bennet [20] localized the gene *Hg* on chromosome 1AS.

Inheritance of glume hardness

The trait threshability (de-husking of grain) of glumes has played a significant role in domestication of *T.durum* and *T. aestivum*. Since all the diploid progenitors involved in the evolution of free threshing wheat are having hard glume (tenacious glume), this trait must have been originated through mutation at very late stage in the evolution. The cultivation of *T. dicoccum*, which has hulled (very hard glumes) glumes got replaced by *T. durum* mainly because of easy threshability of these wheats. Sel. 2836-1 has medium hard glumes and the grains do not come out easily from the glumes. Therefore, genetic analysis was carried out to find out the nature and number of genes governing this trait. The F_1 plants of the cross Sel. 2836-1/NI5439 showed hard glumes, indicating that hardness of glumes is dominant over softness of glume. Out of 464 plants in F_2 generation, 352 plants were having hard glumes, while 112 plants showed easy threshability due to soft glumes. This data fitted well into expected ratio of 3 hard:1 easy threshability. The BC_1F_1 progenies also showed a segregation pattern with goodness of fit for the expected ratio of 1 hard:1 easy threshability. The value of χ^2 (3.272) was nonsignificant indicating a single dominant gene governing glume hardness. Rowland [21] proposed a gene *Tg* for tenacious glumes in hexaploid derivatives of wheat x *Ae. squarossa* which is located on chromosome 2D. Therefore the gene for hardness of glume present in Sel. 2836-1 is different. Waines [22] showed that the character hard glume (*Sg*) is monogenically inherited in *T. monococcum*.

Linkage between morphological markers

Joint segregation of leaf and node pubescence was carried out in the cross Sel. T2836-1 x NI5439 to detect linkage between the two traits. The gene symbols *Hl* and *Hn* have been used here for leaf and node pubescence respectively. The results showed a linkage between leaf and node pubescence (Table 3). The χ^2 value was significant at 5% level at 1 d.f. indicating the linkage between the genes *Hl* and *Hn* (χ^2_L= 19.37, P value < 0.01). The recombination fraction (R.F.) was observed as 31.36 $\pm$ 2.69 % which was converted into a linkage of 36.84 in terms of Kosambi units. Joint segregation of the traits hairy glumes and glume hardness was also carried out. The genetic analysis



Marker used, SCAR Marker: 1-10 (left) SCS1302, band size= 607bp
1-10 (right) *Sr*24#12, band size= 500bp

L= 100bp Ladder
1=HD2932
2= HD2877
3=Agent Lr24
4=HW1042
5= NI5439
6= S2427
7= T2836-1
8= HD3007
9=HD2687
10= WH147

Fig. 1. Identification of leaf rust resistance gene *Lr*24 with SCAR markers

Table 3. Joint segregation of genes *Hl* (leaf Pubescence) and *Hn* (node Pubescence)

Character	Phase	F_2 segregation					χ^2			P-value	R.F. (%)	S.E. (%)	Map distance (Kosambi unit)
		a	b	c	d	Total	Locus I (15:1)	Locus II (3:1)	Joint segregation				
Leaf Pub. and node Pub.	C	342	87	17	18	464	1.324	1.391	19.372	<0.01	31.36	2.69	36.84
Glume pubescence and glume hardness	C	332	101	20	11	464	0.147	0.184	2.403	0.25-0.10	-	-	-

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revealed non significant χ^2_L (χ^2_L= 2.403; P-value: 0.25-0.10) indicating the absence of linkage between the genes governing hairy glume and hard glume.

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