Theor Appl Genet (2008) 116:313–324
DOI 10.1007/s00122-007-0668-0

ORIGINAL PAPER

Mapping of adult plant stripe rust resistance genes in diploid A genome wheat species and their transfer to bread wheat

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Received: 10 July 2007 / Accepted: 20 October 2007 / Published online: 8 November 2007

Abstract Stripe rust, caused by *Puccinia striiformis* West. f.sp. *tritici*, is one of the most damaging diseases of wheat worldwide. Forty genes for stripe rust resistance have been catalogued so far, but the majority of them are not effective against emerging pathotypes. *Triticum monococcum* and *T. boeoticum* have excellent levels of resistance to rusts, but so far, no stripe rust resistance gene has been identified or transferred from these species. A set of 121 RILs generated from a cross involving *T. monococcum* (acc. pau14087) and *T. boeoticum* (acc. pau5088) was screened for 3 years against a mixture of pathotypes under field conditions. The parental accessions were susceptible to all the prevalent pathotypes at the seedling stage, but resistant at the adult plant stage. Genetic analysis of the RIL population revealed the presence of two genes for stripe rust resistance, with one gene each being contributed by each of the parental lines. A linkage map with 169 SSR and RFLP loci generated from a set of 93 RILs was used for mapping these resistance genes. Based on phenotypic data for 3 years and the pooled data, two QTLs, one each in *T. monococcum* acc. pau14087 and *T. boeoticum* acc. pau5088, were detected for resistance in the RIL population. The QTL in *T. monococcum* mapped on chromosome 2A in a 3.6 cM interval between *Xwmc407* and *Xwmc170*, whereas the QTL from *T. boeoticum* mapped on 5A in 8.9 cM interval between *Xbarc151* and *Xcfd12* and these were designated as *QYrtm.pau-2A* and *QYrtb.pau-5A*, respectively. Based on field data for 3 years, their R^2 values were 14 and 24%, respectively. *T. monococcum* acc. pau14087 and three resistant RILs were crossed to hexaploid

Communicated by B. Friebe.

Electronic supplementary material The online version of this article (doi:10.1007/s00122-007-0668-0) contains supplementary material, which is available to authorized users.

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wheat cvs WL711 and PBW343, using *T. durum* as a bridging species with the objective of transferring these genes into hexaploid wheat. The B genome of *T. durum* suppressed resistance in the F_1 plants, but with subsequent backcrossing one resistance gene could be transferred from one of the RILs to the hexaploid wheat background. This gene was derived from *T. boeoticum* acc. pau5088 as indicated by co-introgression of *T. boeoticum* sequences linked to stripe rust resistance QTL, *QYrtb.pau-5A*. Homozygous resistant progenies with 40–42 chromosomes have been identified.

Introduction

Stripe rust, caused by the fungal pathogen *Puccinia striiformis* West. f.sp. *tritici* (*Pst*), is one of the most damaging diseases of wheat. Worldwide, 43 million ha (46%) and in India about 9.4 million ha (>35%) area under wheat cultivation is prone to stripe rust (Singh et al. 2004). Stripe rust propagates in cool and moist environments and can infect the wheat crop in the early growth stages leading to yield losses as high as 50% (Roelfs et al. 1992). The development and deployment of cultivars with genetic resistance is the most economical and environment friendly approach to reduce yield losses due to rusts. For stripe rust, race specific seedling and adult plant resistance as well as race-non-specific adult plant resistance have been reported (Johnson 1988). In the long term, the major resistance genes have turned out to be non-durable as virulence in the pathogen population was selected or it rapidly evolved following the introduction of such resistance genes. Consequently, a constant search and transfer from novel and effective sources of resistance is necessary to counterbalance the continuous evolution of rust pathogens. So far, 40 stripe rust resistance (*Yr*) genes have been catalogued and designated and 11 of these have been transferred from alien species (McIntosh et al. 2005; Uauy et al. 2005; Marais et al. 2005a, 2005b, 2006; Kuraparthy et al. 2007). Except for *Yr28*, *Yr35* and *Yr36*, all other alien genes have been transferred from non-progenitor species. *Yr28* has been transferred from *Ae. tauschii* (Singh et al. 2000) and *Yr35* and *Yr36* have been transferred from *T. dicoccoides* (Marais et al. 2005b; Uauy et al. 2005). Most of the designated *Yr* genes confer a hypersensitive reaction and the majority of these are no longer effective due to evolution of new virulences in the pathogen (Ma et al. 1997). Genes *Yr5*, *Yr10*, *Yr15*, *Yr26* and *Yr40* are effective against the predominant *Pst* pathotypes in India, and all of them, except *Yr10*, are of alien origin and provide seedling resistance. *Yr27*, which had been the basis of resistance in the widely grown Indian cultivar PBW343 (an Attila sib), has now become ineffective against a new virulence designated as 78S84 (Prashar et al. 2007).

Many genes conferring resistance to rusts, powdery mildew and insect pests have been transferred from *Aegilops* species into cultivated wheat (Jiang et al. 1994; Friebe et al. 1996; Marais et al. 2005a, 2006). Some of the genes transferred from distantly related species have been exploited commercially, but others seem to be associated with yield penalty due to linkage drag (Friebe et al. 1996). The alien chromosome segments from distantly related species, once retained in early generations, are difficult to eliminate even after repeated backcrosses (Young and Tanksley 1989). The diploid "A" genome progenitor gene pool of wheat, comprising three closely related species *T. monococcum* ssp *monococcum* (*T. monococcum*), *T. monococcum* ssp *aegilopoides* (*T. boeoticum*) and *T. urartu*, harbours useful variability for many economically important genes, including resistance to diseases (Feldman and Sears 1981; Dhaliwal et al. 1993; Hussien et al. 1997). These species have served as a valuable source for leaf rust (Dyck and Bartos 1994; Kerber 1983; Valkoun et al. 1986; Hussien et al. 1997), stem rust (Kerber and Dyck 1973; McIntosh et al. 1984; The and Baker 1975; Valkoun et al. 1989; Ma et al. 1997) and powdery mildew resistance genes (Shi et al. 1998; Yao et al. 2007) for hexaploid wheat improvement. Their genomes share considerable homology with the A genomes of cultivated tetraploid and hexaploid wheat (Dvorak et al. 1993) enabling the transfer of desirable alleles from the "alien" A genome chromosomes into their "cultivated" homologues without any significant linkage drag. However, the transfers to hexaploid wheat generally require the use of *T. durum* as bridging species and the presence of suppressor loci on the A and/or B genome of *T. durum* may present a major hurdle in transferring useful variability from diploid to hexaploid wheats (Knott 2000; Ma et al. 1997; Qiu et al. 2005). Identification of DNA markers linked to the desirable genes at the diploid level can facilitate their transfer to hexaploid wheat (Yao et al. 2007). Some of the race-specific stripe rust resistance genes such as *Yr15* (Chague et al. 1999), *YrH52* (Peng et al. 1999), *Yr17* (Robert et al. 1999), *Yrns-B1* (Börner et al. 2000), *Yr28* (Singh et al. 2000) and *Yr40* (Kuraparthy et al. 2007) and race non-specific genes such as *Yr18-Lr34* complex (Bossolini et al. 2006) and *Yr39* (Lin and Chen 2007) have been tagged with DNA markers.

Genes for stripe rust resistance from the diploid A genome species, unlike genes for resistance to other diseases as mentioned above, have not been catalogued or transferred to hexaploid wheat. A large number of A genome germplasm accessions have been screened over many years at our institute. Most of the *T. monococcum* accessions showed moderate to complete resistance; most of the *T. boeoticum* accessions showed complete resistance and majority of the *T. urartu* accessions were highly susceptible. A spring type *T. monococcum* acc. pau14087 has

maintained a high level of resistance to a number of wheat diseases including stripe rust in Punjab (India) over years (Dhaliwal et al. 2003). In this accession, at the stage of infection initiation, compatible stripes developed at the tips of the leaves and the reaction could be categorized as susceptible. However, within a few days of infection, necrotic areas developed around stripe rust infection sites and the reaction was categorized as moderate resistant. The stripe rust reaction in this accession conforms to the criteria of slow rusting, as argued by Singh et al. (2005). This type of potentially durable resistance is less studied for stripe rust as compared to leaf rust. The identified *T. monococcum* accession was crossed with *T. boeoticum* acc. pau5088 to generate an RIL population, which besides stripe rust resistance showed segregation for leaf rust, powdery mildew, Karnal bunt and cereal cyst nematode (Dhaliwal et al. 2003; Singh et al. 2007a). This population was used for generating a linkage map of the diploid A genome of wheat (Singh et al. 2007b) and the mapping of several disease resistance genes. Here, we provide the first report of mapping of adult plant stripe rust resistance genes in *T. monococcum* and *T. boeoticum* and their transfer to hexaploid wheat using *T. durum* as a bridging species.

Materials and methods

Plant material

The plant material used for studying inheritance and mapping of the stripe rust resistance genes consisted of a set of 121 recombinant inbred lines (RILs) derived from the cross *T. boeoticum* acc. pau5088/*T. monococcum* acc. pau14087 (hereafter referred to as Tb5088 and Tm14087, respectively) through single seed descent. Detailed information on these accessions and a molecular linkage map generated using this population was described by Singh et al. (2007b) and is available at GrainGenes (http://wheat.pw.usda.gov/ggpages/map_summary.html). Of the 121 RILs, 93 were used for generating the linkage map, whereas all the RILs were screened against three stripe rust pathotypes at the seedling stage and against a mixture of three or four pathotypes at the adult plant stage under field conditions. For the transfer of resistance, *T. monococcum* and three RILs (designated as RIL86, RIL101and RIL130) were used as donors and two hexaploid spring wheat cultivars WL711 and PBW343 were used as the recipients. N59, a stripe rust susceptible *T. durum* cultivar served as a bridging cross parent.

Screening against stripe rust pathotypes

Four stripe rust pathotypes, 46S102, 47S103, 46S119 and 78S84 with known avirulence/virulence formula (Table 1), were used for screening parental accessions and the RIL population at the seedling stage. Screening at the seedling stage was done against individual pathotypes following the procedure of Nayar et al. (1997) in controlled conditions. Briefly, seedlings at the two-leaf stage were inoculated through atomization with rust urediospores immersed in light mineral oil (Pegasol). The inoculated material was placed in humid chambers at 10°C for 48 h. After incubation, the trays were shifted to a glass house maintained at 16 ± 2°C. Infection types (ITs) of seedlings were scored 14 days after inoculation, according to the modified scale of Stakman et al. (1962). Since the parents and the RIL population turned out to be susceptible to all pathotypes at the seedling stage, further screening was done against a mixture of these pathotypes at the adult plant stage under field conditions. The RIL population and the parents were screened for four consecutive crop seasons 2004, 2005, 2006 and 2007. For adult plant screening, the RILs were planted in 2 m rows, with a row-to-row distance of 70 cm. The RILs, being longer in duration, were planted in the last week of October, whereas the F_1 plants and the backcross populations were planted in the second fortnight of November. Spreader rows were planted all around the population to ensure an effective disease spread. Inoculations were done by spraying the mixture of pathotypes thrice a week, starting from the first week of January until second week of February when the crop was in Zadoks growth stages 23–33. The inoculum consisted of three stripe rust pathotypes, 46S102, 47S103 and 46S119, during 2004, 2005 and 2006 and a fourth pathotype, 78S84, which is virulent on *Yr27* (Prashar et al. 2007) was added to the

Table 1 Avirulence/virulence formulae of stripe rust (*Pst*) pathotypes used for screening of the Tb5088/Tm14087 RILs and the introgression lines

Pathotype	Avirulence[a]	Virulence[a]
46S102	*Yr1*[b], *Yr5*, *Yr9*, *Yr10*, *Yr15*, *Yr17*, *Yr24*, *Yr25*, *Yr26*, *Yr27*, *Yr40*	*Yr2*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr8*
47S103	*Yr5*, *Yr9*, *Yr10*, *Yr15*, *Yr17*, *Yr24*, *Yr25*, *Yr26*, *Yr27*, *Yr40*	*Yr1*, *Yr2*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr8*
46S119	*Yr1*,*Yr5*, *Yr10*, *Yr15*, *Yr24*, *Yr25*, *Yr26*, *Yr27*, *Yr40*	*Yr2*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr17*
78S84	*Yr1*,*Yr5*, *Yr10*, *Yr15*, *Yr17*, *Yr24*, *Yr25*, *Yr26*, *Yr40*	*Yr2*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr27*

[a] Determined at the seedling stage in a glasshouse under standard conditions (modified from Nayar et al. 1997)

[b] Most of the genes tested were in Avocet background except for *Yr3* (Vilmorin23), *Yr4* (Hybrid46), *Yr6*(Heines Kolben), *Yr7*(Lee), *Yr8* (Compair) *Yr10* (Moro) and *Yr40*(WL711)

mixture in 2007 as its field-testing was allowed only from 2007.

Disease reaction was recorded twice in the season at the adult plant stage (Zadoks stage 69–83), first when stripe rust reaction of the susceptible check reached 40–60S and the second when the disease reaction of the susceptible check reached 100S. The disease data was recorded following modified Cobb's scale (Peterson et al. 1948) that includes disease severity (percentage of leaf area covered with rust urediospores) as well as disease response (infection type). The infection types were recorded as zero (immune); TR (traces of severity); MR (moderately resistant), MS (moderately susceptible); S (susceptible) and disease severity was recorded as percent leaf area infected. Data recorded during second scoring was used for genetic analysis. The RILs were characterized as resistant or susceptible depending upon the maximum disease severity observed in the parental lines, Tm14087 and Tb5088, in a particular crop season. Chi square analysis was used to estimate the number of genes governing resistance in Tm14087 and Tb5088. Backcross populations and introgression lines were screened only at the adult plant stage and data were recorded as described above for RIL population.

QTL mapping

Disease severity recorded as percentage of leaf area covered with rust urediospores as well as coefficient of infection were used for detection and localization of QTL in the parental lines, Tm14087 and Tb5088. The coefficient of infection (CI), which weighs the modified Cobb scale rating by disease response (R, MR, MS, S), was calculated by multiplying the percentage infection with response values 0.2, 0.4, 0.8, and 1.0 assigned for the infection types TR, MR, MS and S, respectively as per Loegering (1959). Both the scores were used because the CI is probably more closely correlated with crop loss than is either scale from which it is calculated, but it does have a problem in that the two variables from which it is estimated are not independent (McIntosh et al. 1995). As the RIL population did not show a normal distribution, the data were transformed for making the distribution near normal, a prerequisite for QTL analysis using likelihood ratio statistics (Mao and Xu 2004; Yang et al. 2006). The data for stripe rust in a set of 93 RILs (for which genotypic data was available; Singh et al. 2007b) was used for detection and localization of QTLs for resistance in Tm14087 and Tb5088. QTL were detected and localized by single marker regression (SMA) and composite interval mapping (CIM) using MapManager QTXb20 (Manly et al. 2001). In this analysis, the data of the RILs for individual years and the pooled data were entered along with the genotypic data of the RILs. The "marker regression" function ($P = 0.01$) was used to detect possible single marker loci associated with the QTL. The locus with the highest likelihood ratio statistic (LRS) for each set of data was added to the background and composite interval mapping used for localization and estimation of effects of each QTL after correcting the effect of background loci. Significant ($P < 0.05$) and highly significant ($P < 0.01$) threshold levels were determined by the permutation test function of MapManager, which is based on the statistical methods developed by Churchill and Doerge (1994). A likelihood ratio statistic (LRS) value of 4.6 is equivalent to one logarithm of the odds (LOD). Phenotypic variance explained by each QTL (R^2) was estimated for each data set as difference between the total variance and the residual variance expressed as the percent of the total variance. The data was also analysed with software QTL-Network-2.0 (Yang et al. 2007) for detecting interactions between the QTL.

Transfer of stripe rust resistance to hexaploid wheat

Tm14087 was crossed as male with a stripe rust susceptible *T. durum* cultivar N59. The triploid F_1 (N59/Tm14087, $2n = 21$) plants were completely male sterile and susceptible to the stripe rust. The F_1 plants were backcrossed to durum parent N59. The BC_1F_1 and BC_1F_2 plants thus obtained were screened under field conditions at the adult plant stage against a mixture of three pathotypes 46S102, 47S103, and 46S119. The F_1 of N59/Tm14087 was also crossed to susceptible hexaploid wheat cultivars, WL711 and PBW343. WL711 was susceptible to all the four pathotypes, whereas PBW343 was resistant to pathotypes 47S103, 46S102, and 46S119, but susceptible to 78S84. The F_1 plants of the cross N59/Tm14087//WL711 were backcrossed to WL711 to generate BC_1F_1 progenies. These BC_1F_1 progenies were screened under field conditions at the adult plant stage against a mixture of three pathotypes 46S102, 47S103, and 46S119. Resistant plants obtained in the BC_1F_1 progenies of the cross N59/Tm14087//2*WL711 were either selfed or backcrossed to the recurrent hexaploid parent WL711. In addition to Tm14087, three resistant RILs, viz. RIL86, RIL101 and RIL130, were also crossed to WL711 and PBW343 using N59 as the bridging species and the crosses were followed as described above for Tm14087. Transfer of stripe rust resistance in PBW343 could not be followed in earlier generations because PBW343 was resistant to pathotypes 46S102, 47S103 and 46S119, and pathotype 78S84 became available for field evaluation in 2007. However, transfer of leaf rust resistance from Tm14087 and RIL101 to PBW343 was followed separately. The leaf rust resistant progenies were screened for stripe rust

during 2007. Screening against stripe rust and data recording were done as described in the preceding section.

Cytological analysis

Chromosome number was analysed in F_1 of N59/Tm14087 and N59/Tm14087//WL711 and BC_1F_1 and BC_2F_2 progenies of N59/Tm14087//n*WL711 and N59/Tm14087//n*PBW343. The chromosome number was analysed from pollen mother cells (PMCs) of individual plants using standard acetocarmine squashing technique. The spikes were fixed at the pre-booting stage in Carnoy's solution II (6 ethanol: 3 chloroform: 1 glacial acetic acid) and transferred to 70% ethanol after 48 h. Squash preparations were made in 2% acetocarmine.

Results

Inheritance of stripe rust resistance

At the seedling stage, Tm14087 showed susceptible reaction against all four stripe rust pathotypes. At maximum tillering stage under field conditions, it showed a susceptible reaction at the initiation of the disease with compatible stripes confined to the tips of the leaves. The terminal disease severity, however, was recorded as moderately resistant with necrotic areas developing around the rust stripes (Fig. 1), thus indicating the presence of adult plant resistance in Tm14087. Tb5088 was also susceptible to all the four pathotypes at the seedling stage, but at the adult plant stage, it showed complete resistance, displaying disease severity 0-TR. Tb5088, thus, also had adult plant resistance (APR) for stripe rust. The F_1 of Tm14087/Tb5088 showed stripe rust development similar to that of Tm14087, with small stripes at the tips of the leaves. The RIL population also showed susceptible reaction at the seedling stage to all the pathotypes.

At the adult plant stage, under field conditions, data was recorded for four consecutive years, but disease development during 2006 was poor and is not included for further discussions. At the initial stages of disease establishment in Tm14087, the first uredinia to appear induced susceptible reaction and disease severity of 10S, 20S and 10S was recorded during 2004, 2005 and 2007, respectively. Subsequent fungal mycelial growth, as is often observed in slow rusting, caused necrosis and the terminal disease severity recorded was 5MR-10MR (Fig. 1). Disease severity in the RIL population ranged from 0 to 80S (Fig. 1). As disease severity varied during 2004, 2005 and 2007 (Table 2), the stripe rust reaction of Tm14087 and Tb5088 in a particular year was taken into consideration for classifying a RIL as resistant or susceptible. During 2004 and 2007, Tb5088 showed complete resistance (0-TR), whereas Tm14087 developed stripe rust up to a maximum of 10S. Thus, the RILs with terminal stripe rust severity of 0–10S were classified as resistant and the ones with disease severity of 20S or more were classified as susceptible. In 2005, Tm14087

Fig. 1 Stripe rust reaction of Tm14087 (1–2), Tb5088 (3) and a set of RILs (4–9). Samples 1 and 2 show stripe rust reaction in Tm14087 at the initial stage of infection and a week later, respectively

Table 2 Distribution of Tb5088/Tm14087 RILs for rust severity against mixture of stripe rust pathotypes under field conditions

Stripe rust reaction	No. of RILs		
	2004	2005	2007
Tm14087	10S-10MR	20S-10MR	10S-5MR
Tb5088	–	0	TR
0	18	5	10
TR	18	16	18
5MR	17	17	26
5MS	25	3	11
10MR	0	6	8
10MS	11	12	17
10S	7	14	6
20S	15	23	13
40S	7	20	7
60S	2	4	1
80S	1	1	1
Total	121	121	118
χ^2 (3:1)	1.21 ($P < 0.27$)	1.21 ($P < 0.27$)	2.54 ($P < 0.11$)

showed stripe rust severity up to 20S; thus, RILs with stripe rust severity up to 20S were classified as resistant and ones with more than 20S were classified as susceptible. The segregation of RILs into resistant and susceptible fitted to a ratio of 3:1, expected for two-gene segregation (*P* values being <0.27 for 2004 and 2005 and <0.11 for 2007; Table 2). Thus, two genes, presumably one each from Tb5088 and Tm14087, conferred resistance in the Tb5088/Tm14087 RIL population.

Mapping of stripe rust resistance genes

Mapping the resistance genes as major genes, using software MAPMAKER, was not possible because both the parents had the same phenotype; hence, QTL mapping was used for identification of chromosomal regions harbouring these genes in Tb5088 and Tm14087. A framework linkage map, based on 169 SSR and RFLP loci (Singh et al. 2007b), was used for mapping the stripe rust resistance genes in a set of 93 RILs. The data for the individual years 2004, 2005 and 2007 and the average of 3 years was used for detection and mapping the QTLs for stripe rust resistance.

Based on SMA, one region each on chromosomes 2A and 5A were found to be significantly associated with resistance at the adult plant stage using both the disease severity as well as the CI. Composite interval mapping, using data for 2004, 2005 and 2007 and the pooled data also identified the same regions in chromosomes 2A and 5A to be associated with stripe rust resistance (Table 3). As per permutation test, the QTL located on 5A had significant LRS values for both disease severity and CI during the year 2004, 2005 and 2007 and the pooled data. For QTL located on 2A, LRS values based on CI were significant for all the 3 years and the pooled data, but for disease severity, significant LRS values were obtained for 2007 and the pooled data only. In addition, no significant interaction was detected between the two QTLs as revealed by the software QTLNetwork. The QTLs located on chromosomes 2A and 5A were contributed by Tm14087 and Tb5088, respectively. The QTL on 2A from Tm14087 mapped with an LRS value of 13.1, 14.9, 15.3 and 17.6 for the years 2004, 2005 and 2007 and for the pooled CI data, respectively (Table 3). This QTL in Tm14087, mapped to a 3.6 cM marker interval between *Xwmc407* and *Xwmc170* (Fig. 2a) with R^2 values of 11% for the year 2004, 12% for the year 2005, 13% for 2007 and 14% for the pooled data (Table 3). Similarly, the QTL on 5A from Tb5088 was detected at LRS values of 20.1, 23.3, 22.6 and 29.7 for the years 2004, 2005 and 2007 and for the pooled CI data (Table 3). This QTL mapped to a 8.9 cM marker interval between *Xbarc151* and *Xcfd12* (Fig. 2b) with an R^2 value of 18% for 2004, 20% for 2005, 20% for 2007 and 24% for the pooled data. The LRS values for both the QTLs for all the environments were higher than the threshold values estimated based on permutations (Table 3). Overall, the two QTLs explained 38.0% of the total phenotypic variation based on CI and 34.0% based on disease severity. The two QTLs detected on chromosomes 2A and 5A were designated as Q*Yrtm.pau-2A* and *QYrtb.pau-5A*, respectively. The LRS values of 17.6 and 29.7, at which Q*Yrtm.pau-2A* and Q*Yrtb.pau-5A* were detected, corresponded to LOD scores of 3.83 and 6.46, respectively.

Transfer of stripe rust resistance to hexaploid wheat background

Tm14087, RIL86, RIL101 and RIL130 were used for transferring stripe rust resistance to hexaploid wheat cultivars WL711 and PBW343 using *T. durum* cv. N59 as bridging species. Tm14087 and the three RILs were resistant under field conditions. The F_1 triploid plants were vigorous, but completely male sterile, despite a high level of chromosome pairing between the A genome of tetraploid wheat and the A genome of Tm14087. Up to six bivalents were observed in the F_1 (Fig. 3a). The F_1 plants were backcrossed to *T. durum* cv. N59 and hexaploid wheat cvs. WL711 and PBW343. More than 14,000 florets of F_1 triploid plants of various cross combinations were pollinated,

Table 3 Summary of the QTLs for stripe rust severity and coefficient of infection at adult plant stage, localized using composite interval mapping

Locus	Marker interval	2004		2005		2007		Pooled	
		LRS[a]	R^2 (%)	LRS	R^2 (%)	LRS	R^2 (%)	LRS	R^2 (%)
Disease severity									
QYrtm.pau-2A	*Xwmc407-Xwmc170*	9.3	8.0	7.8	7.0	13.2	11.0	14.5	12.0
QYrtb.pau-5A	*Xbarc151-Xcfd12*	19.3	18.0	21.3	19.0	19.1	17.0	25.2	22.0
Coefficient of infection									
QYrtm.pau-2A	*Xwmc407-Xwmc170*	13.1	11.0	14.9	12.0	15.3	13.0	17.6	14.0
QYrtb.pau-5A	*Xbarc151-Xcfd12*	20.1	18.0	23.3	20.0	22.6	20.0	29.7	24.0

[a] LRS values for declaring a QTL as significant (based on 1,000 permutations) for the years 2004, 2005 and 2007 and the pooled data were 12.3, 12.8, 12.2 and 12.1 for disease severity and 12.7, 12.5, 13.2 and 12.4 for CI, respectively

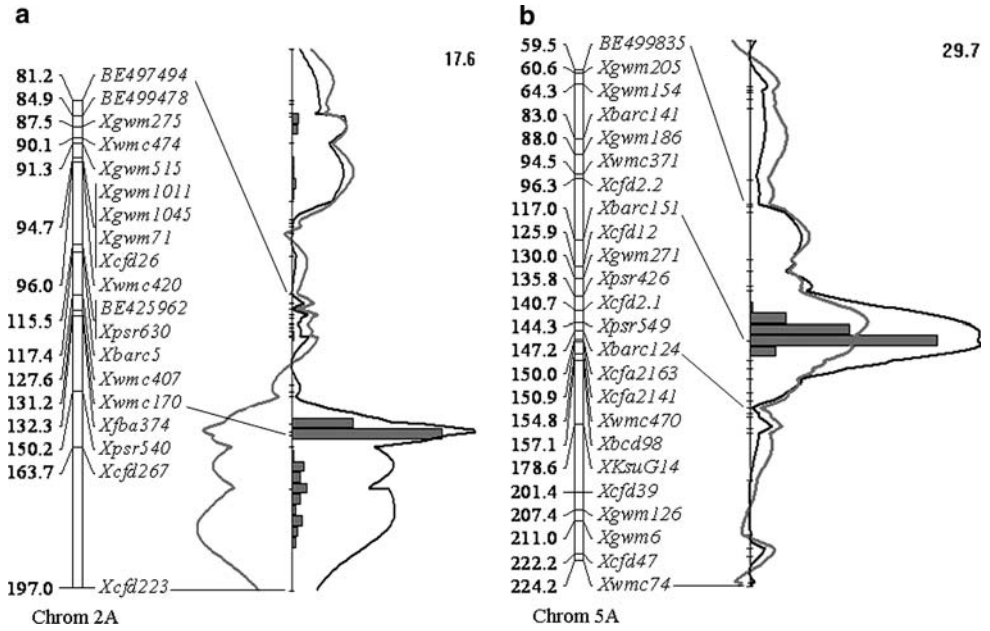

Fig. 2 Composite interval mapping based QTL for CI in the RIL population based on pooled data for 2004, 2005 and 2007 using Mapmanager QTXb20. A partial linkage map of chromosomes 2A and 5A (Singh et al. 2007b) is shown along a *vertical line*. *Curves* in *black* represent the LRS values for the markers and curves in *grey* represent the regression coefficients (additive effects). The *grey curves* on 2A map (**a**) represent the effect of the Tm14087 allele, and on 5A (**b**), it represents the effect of the Tb5088 allele. The *numerical values* on *top* of the figures are the highest LRS values for the detected QTLs. *Histograms* represent estimates of confidence interval by bootstrap resampling

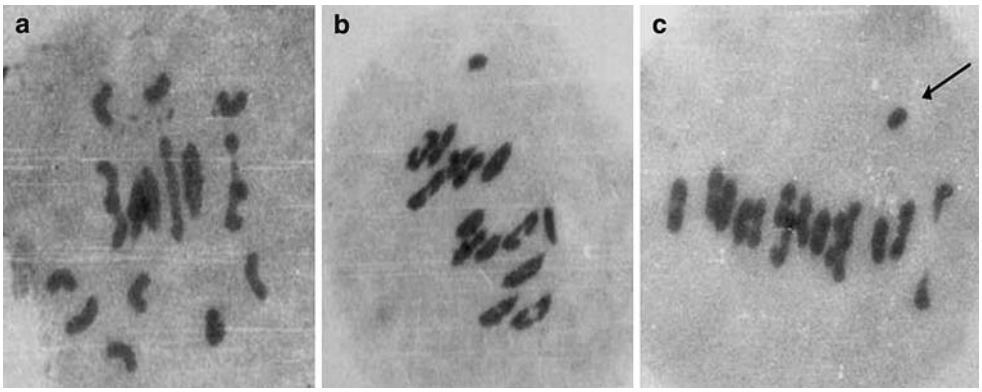

Fig. 3 Pollen mother cells showing chromosome number in F_1 of the cross N59/Tm14087 with $2n = 21$ (6″ + 9′) (**a**) and BC_1F_1 plants of the cross N59/Tm14087//N59 with $2n = 28$ (13″ + 2′) (**b**) and $2n = 29$ (14″ + 1′) (**c**)

and the seed set was only about 3.0% (Table S1). The germination of these seeds was less than 50%. The BC_1F_1 plants derived from the cross N59/Tm14087//N59 showed chromosome number ranging from $2n = 28$ to 29 (Fig. 3b, c), thus attaining a near-stable chromosomal constitution in one backcross.

T. durum cv N59 was highly susceptible both at the seedling as well as the adult plant stages. The F_1 plants from the crosses of N59 with Tm14087, RIL86, RIL101 and RIL130 were all susceptible, thereby indicating that the resistance was either recessive in nature or being suppressed by *T. durum* genome. In addition, all the BC_1F_1 plants of the cross N59/Tm14087//N59 and F_1 plants of the crosses N59/Tm14087//WL711, N59/RIL86//WL711, N59/RIL101//WL711 and N59/RIL130//Wl711 were susceptible at the adult plant stages. Similarly, BC_1F_2 plants of the crosses N59/Tm14087//N59, N59/RIL86//N59, N59/RIL101//N59 and N59/RIL130//N59 were also susceptible at the adult plant stage under field conditions (data not shown), thereby indicating that *T. durum* suppresses stripe rust resistance located on the A genome of Tm14087 and *T. boeoticum* when transferred into the tetraploid wheat background. To test whether only N59 had this suppressor locus or if it was present in other durum varieties as well,

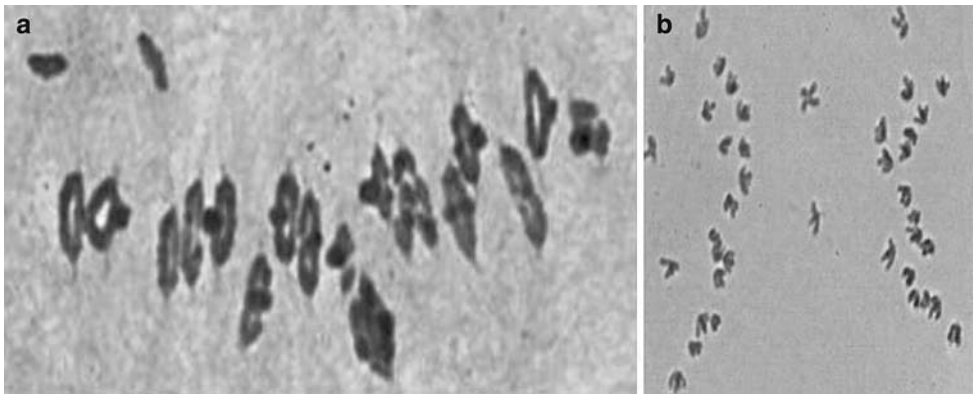

Fig. 4 Pollen mother cells of a stripe rust resistant BC_1F_4 plant showing chromosome number $2n = 40$ (19″ + 2′) at diakinesis (**a**) and 20–20 distribution at anaphase I (**b**)

Tm14087 was crossed with two other susceptible *T. durum* lines MACS 1967 and Malavi local. The F_1 plants of both crosses were susceptible, thereby suggesting that the suppression mechanism in *T. durum* may be widespread. Crosses with *T. durum* were not pursued further. The hexaploid wheat crosses N59/Tm14087//WL711, N59/RIL101//WL711 and N59/RIL130//WL711 were carried forward.

All the F_1 plants of the crosses N59/Tm14087//WL711 and N59/RIL101//WL711 were backcrossed with WL711. Out of 25 BC_1F_1 plants screened from the cross N59/Tm14087//2*WL711, only one resistant plant was recovered. However, from the cross N59/RIL101//2*WL711, out of 111 plants screened, 15 plants were resistant. Chromosome number of the BC_1F_1 plants ranged from 38 to 41. The resistant plants were selfed and backcrossed as well to generate BC_1F_2 and BC_2F_1 progenies. Of a total 136 BC_1F_2 plants obtained from crosses with Tm14087 and RIL101, only 58 were resistant. Two BC_1F_1 plants were advanced rapidly using off-season nurseries to generate BC_1F_3 progenies. Of the 18 BC_1F_3 progenies derived from two independent BC_1F_1 plants, three were homozygous resistant, eight segregating and seven homozygous susceptible. Chromosome numbers of some homozygous resistant introgression lines were also analysed. The chromosome number in these progenies varied from 40 to 42 (Fig. 4 a, b). A large number of BC_1F_2 progenies from stripe rust susceptible BC_1F_1 plants were also evaluated for resistance to test whether some of these progenies were still segregating for suppressors. Two progenies from the cross N59/Tm14087//2*WL711 and nine from N59/RIL101//2*WL711 were observed to segregate for stripe rust resistance. Of the 73 BC_1F_2 plants from these segregating progenies, 28 resistant plants were recovered, thus confirming the presence of suppressor gene(s) in *T. durum*.

Inheritance of stripe rust resistance in the introgression lines

A number of stripe rust resistant BC_1F_2 plants selected from crosses N59/Tm14087//2*WL711 (Fig. 5) and N59/RIL101//2*WL711 during 2006 were planted as plant-to-progeny rows in 2007. These progenies were screened under field conditions at the adult plant stage, against a mixture of four pathotypes. Disease severity of individual plants was recorded on agronomically desirable and segregating progenies to study the inheritance pattern of these genes in hexaploid wheat background. Results of one such progeny (#480) derived from the cross N59/RIL101//2*WL711 are presented in Table 4. The recipient parent WL711 showed stripe rust reaction of 80S and the progeny showed the disease reaction varying from 0 to 80S. Plants with disease reaction of 0–20 MS were classified as resistant. The progeny showed 3:1 segregation ($\chi^2 = 2.12$; Table 4), expected of a single gene segregation.

As described above, the transfer of stripe rust resistance from Tm14087 or RILs to the genetic background of PBW343 could not be monitored initially because the pathotypes that are virulent on this variety were not released for field-testing until the 2006–2007 crop season. However, leaf rust resistance was transferred from Tm14087 and

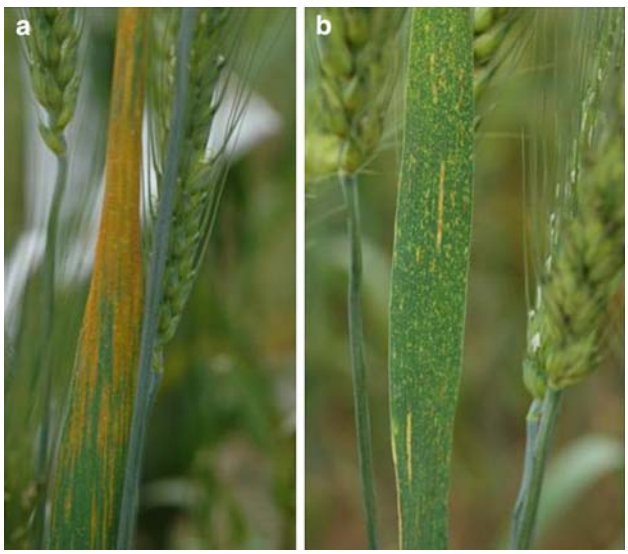

Fig. 5 Stripe rust reaction of WL711 (**a**) and a BC_1F_2 plant of the cross N59/Tm14087//2* WL711 (b)

Table 4 Stripe rust reaction of a set of segregating BC_1F_3 progenies against a mixture of four pathotypes during 2007

Disease reaction	Number of plants		
	Progeny # 480[a]	Progeny# T478	Progeny # T1065
0	152	05	07
TR	31	23	32
5MR-5MS	44	71	162
10MR-10MS	12	46	82
20MR-20MS	–	23	37
20S	10	26	41
40S	18	54	169
60S	25	43	23
80S	12	08	–
Total	304	299	553
χ^2	2.12 (3:1)	0.0 (9:7)	0.59 (9:7)

[a] Progeny # 480, T478 and T1065 were derived from the crosses N59/RIL101//2*WL711, N59/RIL101//2*PBW343 and N59/RIL130//2*PBW343, respectively

RILs in the genetic background of PBW343 (data not shown), and a large number of progenies were available. These progenies were evaluated against stripe rust pathotype 78S84 during 2006–2007. PBW343 showed a disease severity of up to 40S against this pathotype and some of the introgression lines showed segregation for stripe rust. Data for two such progenies are presented in Table 4. Progeny #T478 and #T1065 derived from the crosses N59/RIL101//2*PBW343 and N59/RIL130//2*PBW343 respectively, did not fit the expected monogenic (3:1) or digenic (15:1) segregation depending upon the donor RIL parent. The observed 9:7 segregation may not have regular genetic implications considering the nature of identified genes. Rather, it may signify distorted segregation.

Validation of markers linked to stripe rust resistance genes

Progenies from several generations such as BC_1F_3, BC_1F_4, BC_2F_2, etc. derived from the cross N59/RIL101//2*WL711 were available and these were screened against a mixture of four pathotypes under field conditions in 2007. A set of two susceptible and nine resistant introgression lines, originating from a common lineage (Table S2), were used for validating the SSR markers linked to two resistance genes mapped in Tb5088 and Tm14087. These lines were analysed for four 2A specific SSR markers and seven 5A specific SSR markers chosen from the region where the resistance QTL mapped in the RIL population. All the nine resistant introgression lines had Tb5088 allele at locus *Xbarc151–5A* (Fig. 6). Marker *Xbarc151* was closely linked to the adult plant resistance gene in Tb5088 (Fig. 2b). Six progenies, #464, 465, 466, 467, 468 and 477, also had the Tm14087 allele at the locus *Xwmc170-2A* (Fig. 6), which was linked to stripe rust resistance gene in Tm14087 (Fig. 2a). None of the susceptible lines showed any introgression at these loci.

Discussion

The adult plant stripe rust resistance genes identified from Tm14087 and Tb5088 in this study map on chromosomes

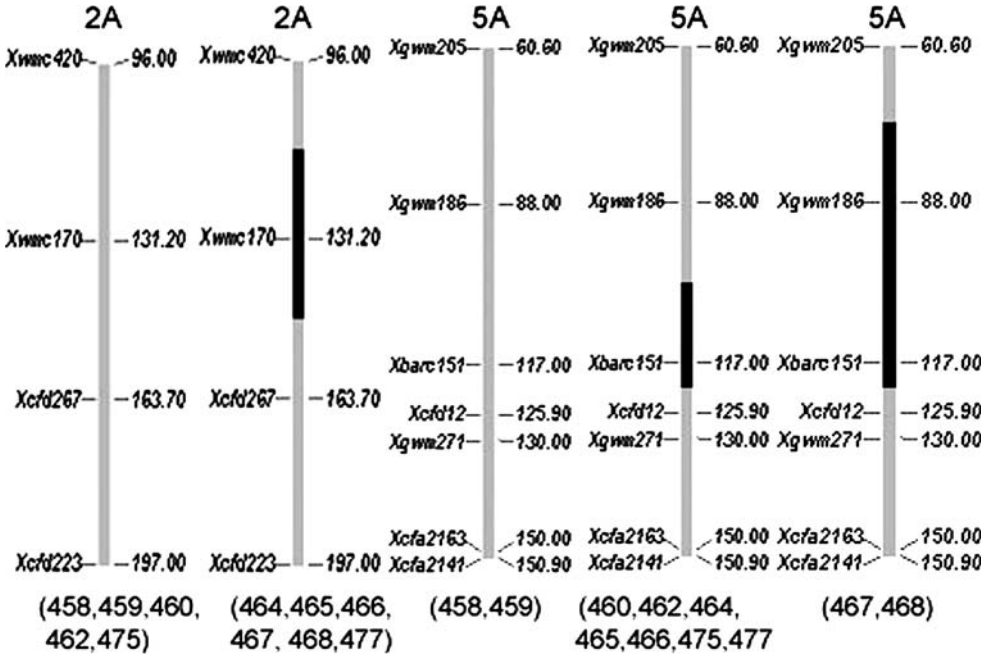

Fig. 6 Graphical genotypes of stripe rust susceptible (458, 459) and resistant (460, 462, 464, 465, 466, 467, 468, 475 and 477) introgression progenies analysed for SSR markers linked to *QYrtm.pau-2A* and *QYrtb.pau-5A* on chromosome 2A and 5A, respectively. The progeny number is same as given in Table S2. *Black regions* are the introgression from Tm14087 (2A) or Tb5088 (5A). *Numbers in the brackets* under each graph are the progeny numbers. Map distances on the *right side* of each graph are from Singh et al. (2007b)

2A and 5A, respectively. The two genes under discussion may be novel, as these do not correspond to any of the known *Yr* genes. Ten of the 40 characterized stripe rust resistance genes viz. *Yr11*, *Yr12*, *Yr13*, *Yr14*, *Yr16*, *Yr18*, *Yr29*, *Yr30*, *Yr36* and *Yr39* are effective at the adult plant stage and only *Yr16* is located on the homoeologous group 2 chromosomes i.e. 2DS (Worland and Law 1986). Although nine other genes (*Yr1*, *Yr5*, *Yr7*, *Yr8*, *Yr17*, *Yr27*, *Yr31*, *Yr32 and Yr37*) have been mapped on homoeologous group 2, but all these are race-specific seedling resistance genes. Genes *Yr1*, *Yr17* and *Yr32* map on 2A, the others map on either 2B or 2D. No APR gene for stripe rust resistance has been mapped on group 5 chromosomes so far, though, seedling resistance genes *Yr19*, *Yr34* and *Yr40* map on 5B, 5AL and 5DS, respectively (http://www.ars.usda.gov/main/docs.htm/docid=10342; Kuraparthy et al. 2007). Chromosomal location and effectiveness at the adult plant stage, both in diploid and hexaploid wheat background of the two genes establishes that these genes are novel. Hence, Tm14087 gene on 2AL and Tb5088 gene on 5AL are designated as Q*Yrtm.pau-2A* and Q*Yrtb.pau-5A*, respectively.

While transferring the stripe rust resistance genes from *T. monococcum* and *T. boeoticum* to hexaploid wheat, using *T. durum* as a bridging species, it became apparent that the B genome of *T. durum* suppressed the resistance of the A genome of diploid wheat. Since no resistant plants were recovered in the BC_1F_1 or BC_1F_2 generation of the cross N59/Tm14087//N59, it indicated that the resistance in diploid wheats was either recessive in nature or was being suppressed by the A and/or B genome of *T. durum*. The A genome of diploid wheat was expected to segregate in the BC_1F_1 generation of the cross N59/Tm14087//N59 as well as in the F_1 of the cross N59/Tm14087//WL711, but not the B genome, because in the F_1 triploid only those gametes are viable that have a full complement of A and B genomes (Gill et al. 1986). The B genome of *T. durum*, however, was expected to segregate in the BC_1F_1 generation of the cross N59/Tm14087//2*WL711. If the B genome suppressed the resistance, then resistant plants were expected in this generation. Recovery of resistant plants in BC_1F_1 generation established that the B genome of *T. durum* suppressed the stripe rust resistance transferred from the A genome of diploid wheats. Suppression of resistance seems to be widespread in *T. durum* as the F_1 plants derived from crosses of Tm14087 and Tb5088 with two other susceptible *T. durum* lines, Malavi local and MACS1967, were also susceptible. *T. durum* is known to suppress disease resistance located on D and the A genomes in amphiploids (Ma et al. 1997; Qiu et al. 2005) and some resistance genes present in the durum lines itself (Knott 2000). Kerber (1983) demonstrated that leaf rust resistance from durum wheat was inhibited by suppressors on the D genome of bread wheat and *Ae. tauschii* in their hybrids. The suppressors of stripe rust resistance were observed in both A and/or B genomes of *T. turgidum* and the D genome of *Ae. tauschii* (Kema et al. 1995; Ma et al. 1995). The observations described here on stripe rust and other reports for leaf and stem rust resistance (Bai and Knott 1992; Kerber 1983; Kerber and Green 1980) indicate that numerous suppressors for rust resistance exist in the genus *Triticum*, and that the suppression may be resistance gene-specific (Ma et al. 1995, 1997; Villareal et al. 1992). Aghaee et al. (2001) have also demonstrated the suppression of leaf and stripe rust resistance genes in amphiploids generated by crossing susceptible *T. durum* and several accessions of *Ae. umbellulata* and *Ae. caudata*.

After the resistant plants were recovered in segregating generations of the crosses with hexaploid wheat, our objective was also to study inheritance of these genes in a hexaploid background. Their inheritance in hexaploid wheat background indicated that these are major genes. Introgression lines in the background of WL711 showed monogenic inheritance, which was further confirmed with the co-introgression of linked SSR marker Xbarc151 in the homozygous resistant BC_1F_3 and BC_1F_4 progenies. Introgression lines in the background of PBW343 on the other hand showed a 9:7 segregation instead of an expected 3:1. The 9:7 segregation in PBW343 background may not be the complementary gene action, rather a segregation distortion due to chromosome number abnormalities, differential transmission of the gametes or the presence of some suppressor genes in PBW343. Differential transmission of male gametes has been well documented in wheat. In the *Lr19* translocation, for example, the genetic background of a heterozygote may strongly modify the degree of preferential inheritance of an alien segment (Prins and Marais 1999). The *Yr37* containing translocation from *Ae. kotschyii* showed 96% male transmission compared to 55% transmission of the resistance genes from the female (Marais et al. 2005a).

Most of the characterized APR stripe rust resistance genes do not confer adequate levels of resistance when present alone, but provide resistance only in combination with other genes. The APR gene mapped and transferred during this study provides a high level of stripe rust resistance in hexaploid wheat background, indicating its suitability for resistance breeding. The future identification of closely linked DNA markers for both the resistance genes will be useful for monitoring their transfer in breeding programmes.

Acknowledgments This work was carried under Indo-Swiss collaboration in Biotechnology. The financial support provided by the Department of Biotechnology (DBT), Ministry of Science and Technology, Government of India, Swiss Agency for Development and Cooperation (SDC; to KS and BK) and the Swiss National Science

Foundation (3100-105620 (BK) is gratefully acknowledged. We are thankful to the staff of the wheat breeding section of the department for the rust inoculum.

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