Transfer of rust resistance genes from *Triticum* species to common wheat

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A programme aiming to transfer leaf rust resistance genes identified in a collection of wild *Triticum* species was initiated in 1993. In 2000, 25 promising backcross populations were available, 19 of which bred true for resistance. Seedlings of the above lines were tested with nine leaf rust, four stem rust and two stripe rust pathotypes endemic to South Africa. A subset of five lines in which resistance (derived from *T. dicoccoides*, *T. sharonense*, *T. speltoides* and *T. peregrinum*) appeared to be integrated on wheat chromosomes and six addition lines with added chromosomes from *T. kotschyi*, *T. peregrinum*, *T. umbellulatum*, *T. macrochaetum* and *T. neglectum* appeared to have wide spectrum resistances, and were retained. In several instances promising stem rust and/or stripe rust resistance genes were co-transferred with leaf rust resistance. The stripe rust resistance was also effective to four Australian pathotypes and appeared to be novel. Temporary gene designations were assigned to the resistance genes in four euploid derivatives.

Keywords: *Puccinia triticina*, *P. graminis tritici*, *P. striiformis tritici*, wide hybridisation

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Introduction

The wild relatives of common wheat (*Triticum aestivum* L.) have provided valuable sources of genetic diversity for rust resistance (Kerber & Dyck, 1990). The accessibility of these genes for crop improvement is determined by the degree of relatedness to wheat of the donor species, which can be grouped into the primary, secondary and tertiary gene pools (Bothmer, von Seberg & Jacobsen, 1992). Numerous genes have been introgressed from wild Triticeae species and assigned gene symbols (McIntosh *et al.*, 1998). Fourteen, 13 and three genes for resistance to leaf rust (*Lr*), stem rust (*Sr*) and stripe rust (*Yr*), respectively, were derived from the primary gene pool (*Triticum*) species *monococcum*, *tauschii*, *turgidum* and *timopheevii*. Four *Lr* and two *Sr* genes were derived from the secondary gene pool species *T. speltoides*, whereas eight *Lr*, seven *Sr* and two *Yr* genes were transferred to wheat from the tertiary gene pool (*T. umbellulatum*, *T. comosum*, *Thinopyrum intermedium*, *Th. elongatum*, *Th. ponticum* and *Secale cereale*). The linked genes *Lr37*, *Sr38* and *Yr17* were introgressed from *T. ventricosum* that has both a primary gene pool genome (D) and a tertiary gene pool genome (Un). Further examples of genes that were present in the same transferred alien chromosome segment are *Lr19* and *Sr25* (*Th. ponticum*), *Lr24* and *Sr24* (*Th. ponticum*), *Lr26*, *Sr31* and *Yr9* (*S. cereale*), *Sr34* and *Yr8* (*T. comosum*) (Anonymous, 2001).

Two hundred and six *Triticum* accessions were found to be resistant in the seedling stage to mixed inoculum of five South African leaf rust pathotypes (Antonov & Marais, 1996). Of these, 127 (from 19 species) were successfully crossed with the common spring wheat variety, 'Chinese Spring' ('CS'). Resistance was expressed in 83 F_1 hybrids. Backcrosses to 'CS' were attempted with the resistant group. Backcrosses involving the primary gene pool species and some of the secondary gene pool species were undertaken without prior doubling of the F_1 chromosome numbers. In the case of certain secondary gene pool species as well as all the tertiary gene pool species, colchicine treatment to double the F_1 chromosome numbers was attempted. Many of the backcross attempts eventually failed because of the formation of embryo-less or non-viable seeds, inability to effect chromosome doubling, seedling inviability or infertility. This study reports the performance of germplasm that carried leaf rust resistance derived from alien species when evaluated for seedling resistance to a wider spectrum of pathotypes. In view of the fact that resistance genes are often clustered in the same chromosomal region, the material was also tested for resistance to stem rust and stripe rust.

Materials and methods

Germplasm and its screening

Antonov & Marais (1996) produced viable F_1 hybrids of 70 *Triticum* accessions with 'CS' wheat and initiated backcrosses to the wheat parent. For various reasons including low fertility, poor viability, reduced expression of resistance and segregation of more than one gene, the potentially useful combinations were reduced to 25 by year 2000, derived from twelve species (Table 1). Eighteen lines appeared to have resistance genes integrated on wheat chromosomes, five occurred as addition chromosomes and the status of two genes were not determined. Resistant backcross-derived homozygotes or disomic additions were available for 19 sources. These, as well as the remaining three segregating stocks and three monosomic additions, were tested for seedling reaction to *Puccinia triticina* pathotypes UVPrt 2, 3, 4, 5, 8, 9,10, 13, 14 and 17; *P. graminis* f. sp. *tritici* pathotypes UVPgt 50, 51, 53 and 54 and *P. striiformis* f. sp. *tritici* pathotypes 6E16A- and 6E22A-. The three monosomic additions were tested with an inoculum mix of either leaf rust or stem rust, rather than the individual pathotypes. Genotypes were grown in a sterilized soil-peat mixture in 10-cm diameter plastic pots. Four lines (five to 10 seeds per line) were sown in clumps per pot. Primary leaves of 7-day-old seedlings were

inoculated with freshly collected urediniospores of each pathotype suspended in light mineral oil (1 mg spores ml^{-1} oil). Inoculated seedlings were allowed to dry for 1 h before placement in a dew chamber overnight. Upon removal from the chamber, seedlings were placed at 20-23°C in a greenhouse. Infection types (0-4 scale, Roelfs, Singh & Saari, 1992) were scored when pustules on susceptible entries appeared fully developed. A subset of three disomic and three addition lines were also tested against four Australian pathotypes of *P. striiformis* f. sp. *Tritici*, following inoculation procedures described by Wellings, McIntosh & Hussain (1988). The latter pathotypes were selected to allow for identification of resistance genes *YrA*, *Yr1*, *Yr6*, *Yr7* and *Yr9* that represent common resistance genes among international spring wheats.

Table 1 Donor *Triticum* species and estimated numbers of leaf rust resistance genes retained in selected derivatives by the end of 2000

Donor species[1]	Donor species genomes[1]	Gene pool[2]	Estimated number of leaf rust resistance genes in derivatives
T. turgidum L. var. *dicoccoides*	AB	P	6
T. turgidum L. var. *durum*	AB	P	1
T. timopheevii (Zhuk.) Zhuk.	AG	P	2
T. cylindricum (Host.) Ces., Pass. & Gibelli	CD	T/P	2
T. sharonense (Eig) Feldman & Sears	S^1	S	1
T. speltoides (Tausch) Gren. *ex* K. Richter	S	S	3
T. kotschyi (Boiss.) Bowden	US	T/S	1
T. peregrinum Hackel *in* J. Fraser	US	T/S	2
T. columnare (Zhuk.) Morris & Sears	UM	T	1
T. macrochaetum (Shuttlew. & A. Huet ex Duval-Jouve) K. Richter	UM	T	2
T. neglectum (Req. *ex* Bertol.) Greuter	UM	T	1
T. triunciale (L.) Raspail	UC	T	2
T. umbellulatum (Zhuk.) Bowden	U	T	1

[1] Nomenclature and genome symbols are according to Morris and Sears (1967) as modified by Kimber and Feldman (1987).

[2] P, S & T = primary, secondary and tertiary gene pools, respectively.

On the basis of the results a subset of lines, showing promise for use in local breeding programmes, were identified. Two such lines were tested with a new South African *P. graminis* f. sp. *tritici* pathotype, 2SA88, obtained from W.H.P. Boshoff (Small Grain Institute, Bethlehem, South Africa).

DNA extraction and RFLP analyses

DNA was extracted from each of six disomic addition lines using the protocol of Doyle and Doyle (1990). Approximately 10 µg of DNA was digested with the restriction endonuclease *Hind*III, separated on a 0.8% agarose gel in 1 X TBE buffer, and alkaline blotted overnight onto positively charged nylon membrane (Roche), following the recommendations of the manufacturer. The hybridisation probes were DIG labelled, hybridised to the membranes and detected using the methodology outlined in the DIG Application Manual for Filter Hybridisation (Roche Diagnostics GmbH, Roche Molecular Biochemicals, 68298 Mannheim, Germany). RFLP probes diagnostic for sets of wheat homoeologues were obtained from the John Innes Centre, UK. The probes used were as follows: PSR949 (group 1), PSR666 (group 2), PSR931 (group 3), PSR914 (group 4), PSR628 (group 5), PSR154 and PSR167 (group 6), PSR129 and PSR160 (group 7).

Results

Sources with resistance to all local pathotypes of a disease are listed in Table 2. Among these are five sources that appear to occur on wheat chromosomes and five that appear to occur on addition chromosomes.

Resistance from *Triticum dicoccoides*

A *T. dicoccoides* accession (479 obtained from Israel in 1983) and its F_1 hybrid with 'CS' were tested by Antonov & Marais (1996) for seedling resistance to mixed inoculum of five leaf rust pathotypes. The infection types ranged from 0; to ;1^- in both cases. Leaf rust (UVPrt8) resistant F_1 and BF_1 plants were selected for backcrossing (six times) to 'CS'. A B_6F_2 plant (98M71) with 2n = 42 that proved to be a resistant homozygote was isolated. Chromosome counts on four resistant seedlings from a cross of this plant with the breeding line W84-17 showed 2n=42.

Testing of the 98M71 plants for resistance against a wider range of leaf rust, stem rust and stripe rust pathotypes (Table 2) showed that the gene provides highly effective resistance to the local leaf rust isolates. The introgressed region is clearly not associated with stem rust resistance, but does seem to contain a useful gene for stripe rust resistance. The latter gene was effective against the four Australian *P. striiformis* pathotypes (Table 3), although the low infection type was similar to that of *Yr15*, also derived from *T. dicoccoides*. However, *Yr15* is not known to be associated with leaf rust resistance. The genes were designated with the temporary symbols *LrS8* and *YrS8*, respectively. A total of 127 testcross progeny were tested for seedling response to both diseases. *LrS8* and *YrS8* co-segregated, confirming close linkage. Plants with the resistance had normal vigour and seed set.

Table 2 Infection types produced by eleven *Triticum* species-derived resistance sources inoculated with isolates of common South African rust pathotypes

Triticum donor species, accession number and source code	Leaf rust, UVPrt:									Stem rust, UVPgt:				Stripe rust, 6E:	
	2	3	4	5	9	10	13	14	17	50	52	53	54	16	22
Resistance appearing to be integrated into wheat chromosomes:															
dicoccoides (479: S8)	;1$^{=}$	0;	0;	0;	0;	0;	;	;	0;	3	3	3	3	;^{cn}	;1
sharonense (174: S12)	0;	0;	0	0;	0;	0;	0;	0;	0;	3^{++}	3^{++}	3^{++}	3	;^{cn}	;1^{c}
speltoides (691: S13)	;^{c}	;^{c}	0	;^{c}	;^{c}	;^{c}	;^{c}	;^{c}	;^{c}	;1$^{=}$	1	1^{+}	1	0	;^{cn}
speltoides (150: S24)	3^{+}	2^{+}3	3	3^{++}	XX^{+}(Y)	33^{+}	3^{+}	3	;3-(X)	;^{c}	;	;1^{cn}	;^{cn}	-	3^{++}
peregrinum (680: S15)	;	0;1	-	-	0;1	;1	;1^{+}	-	;1$^{=}$	-	-	-	-	-	-
Genes occurring on addition chromosomes															
kotschyi (617: S14)	;	0;1	0	;	0;	0;	;1	;1	;	3	3^{-}	3^{-}	33^{+}	;^{cn}	1
peregrinum (673: S16)	;	0;1	0	0;	0;	0;	;1	;1	0;	4	4	4	3^{+}4	;^{cn}	;1^{cn}
macrochaetum (683: S19)	1	2^{-}	1	1^{+}2	;1	;1	;1^{++}	;1	;1	33^{+c}	1^{+}2	;1	1^{+}2	0;	0;
umbellulatum (740: S23)	;1	2^{+}	;	;-1$^{=c}$	;1$^{=c}$	;	2^{+}3	;1	;1	3^{++}	3^{++}	33^{+}	33^{+}	;	;1
macrochaetum (763: S18)[1]	Tested with mixed inoculum - produced infection types ;, ;1$^{=}$, 2$^{=}$, 4													-	33^{+}
neglectum (155: S20)[1]	Tested with mixed inoculum - produced infection types ;, ;1$^{=}$, 2$^{=}$2, 4													-	4
Controls															
'Chinese Spring '	3^{++}4	3^{++}4	3^{++}4	3^{++}4	3^{++}4	3^{++}4	3^{++}4	3^{++}4	3^{++}4	3^{++}	3^{++}4	3^{++}4	3^{++}4		
'Morocco'	3^{++}	3^{++}4	3^{++}4	3^{++}4	3^{++}4	4	3^{++}4	4	4	4	4	4	4		4

[1] Monosomic additions, disomic additions were subsequently recovered from the resistant progeny.

Table 3 Seedling results of six alien transfers tested with four Australian *P. striiformis* pathotypes

Test line	Source	Stripe rust pathotype			
		104 E137 A+	110 E143 A+	238 E143 A+	111 E143 A-
S8	*T. turgidum*	;^{c}	;1^{c}	;1$^{=c}$	;;^{c}1^{-}
S12	*T. sharonense*	;;^{c}	;^{c}	;^{c}	;
S13	*T. speltoides*	0;	0;	0;	0;
S14	*T. kotschyii*	;^{c}1^{-}	;^{c}	;;^{c}	;;^{c}
S16	*T. peregrinum*	;;^{c}	;^{c}1^{-}	;^{c}	;^{c}
S19	*T. macrochaetum*	0;	;;^{c}	0;;	0;

Resistance from *Triticum sharonense*

Accession 174 was obtained from Israel in 1979. When tested for resistance to a composite of five pathotypes (Antonov & Marais, 1996) it produced IT 0; to ;. It was crossed with 'CS' and the F_1 produced IT ; to 1$^{=}$ with UVPrt8. Leaf rust resistant F_1s were then backcrossed eight times to 'CS'. Testing of cross 8028: *T. sharonense*/6* 'CS' homozygotes for seedling response to a wide range of leaf rust, stem rust and stripe rust pathotypes (Tables 2 and 3) confirmed high levels of leaf rust (IT 0; to ;1) and stripe rust resistance. The plants were, however, stem rust susceptible. The resistances showed strong preferential transmission in the 'CS' background that may have been due to the presence of a gametocidal (Gc) gene. An attempt was made to determine the chromosome location by crossing resistant B_5-derived plants to the 'CS' B-genome monosomics. However, the F_2 derived from all monosomic F_1 combinations showed pronounced preferential transmission with all populations containing 98% to 100% resistant plants. Thus, it was not possible to discern monosomic segregation. Backcrosses were initiated to transfer the genes into W84-17, since this background does not appear to induce a gametocidal response and may be more amenable to monosomic analysis. Chromosome counts on resistant F_1 plants from the cross: *T. sharonense*/9* 'CS'//3* W84-17 revealed that 10 plants had 42 chromosomes whereas two plants had 41 chromosomes. While the aneuploidy may result from the introgressed region it is also possible that the two wheat genomes may differ by a translocation(s). The resistant plants appear to have normal vigour and fertility. The useful genes in the homozygous resistant stock 8028 were designated *LrS12* and *YrS12*, respectively.

Resistance from *Triticum speltoides ssp. ligustica*

Both the species parent (accession 691, obtained from Israel) and its F_1 hybrid with 'CS' produced IT ; to ;1= when seedlings were infected with a mixture of spores from five leaf

rust pathotypes (Antonov & Marais, 1996). Resistant progeny were backcrossed six times to 'CS'. In the B_4, homozygous resistant progeny were obtained (population 8029) and tested for response to leaf rust, stem rust and stripe rust (Table 2). The resistance phenotype showed preferential transmission. When 31 F_1: *T. speltoides*/ 5* 'CS'// W84-17 seedlings were infected with UVPrt8, only resistant progeny was found. Root tip chromosome counts on 14 plants indicated 12 seedlings had 2n=42, whereas two had 2n=43, confirming that the foreign chromatin has been integrated into a wheat chromosome. Apart from strong leaf rust resistance (IT 0 to ;^{c}), the introgressed region appears to also carry genes for stem rust (IT ;1$^{=}$ to 1) and stripe rust (IT ;^{cn}) resistances. Further testing of the source with a recent South African stem rust pathotype, 2SA88, produced a 1^{-} infection type. The stripe rust resistance gene also proved to be effective against the four Australian pathotypes. The temporary symbols *LrS13*, *SrS13* and *YrS13* are proposed to designate the respective genes. Unfortunately, the resistance appears to be associated with a Gc gene. Carriers have strongly reduced fertility and show seed shrivelling, hybrid necrosis and impaired plant development.

Resistance from *Triticum speltoides ssp ligustica*

Marais & Pretorius (1996) reported the transfer of non-linked leaf rust and stem rust resistance genes from accession 150 (obtained from the University of California in 1977) to wheat. However, it was subsequently found that the leaf rust resistance was not effective against the local leaf rust pathotypes UVPrt4 and UVPrt5 (unpublished data) and it was not pursued further. The material also harbours a gametocidal gene(s) with adverse effects on both fertility and seed quality and it has not been possible to separate the resistance from these undesirable traits. Although the stem rust and *Gc* loci are not completely linked, the strong expression of the *Gc* locus has thus far made it impossible to select resistant progeny without *Gc*. Attempts to obtain resistant recombinant progeny lacking the *Gc* gene(s), are being continued. As is apparent from Table 2 the stem rust resistance gene is highly effective against local pathotypes, including 2SA88 (IT ; to ;1$^{=}$). This gene was designated *SrS24*.

Leaf rust resistance from *Triticum peregrinum*

Accession 680 (Israel) and its F_1 hybrid with 'CS' produced IT ; to ;1^{-} when inoculated with five leaf rust pathotypes (Antonov & Marais, 1996). The chromosome number of the F_1 was doubled through colchicine treatment and the C_1 backcrossed to 'CS'. Root tip chromosome counts on resistant plants of the B_3F_1: *T. peregrinum*/4* 'CS' and the B_2F_1: *T. peregrinum*/2* 'CS'//2* W84-17 ranged from 2n = 42 to 45, suggesting that further backcrosses are required to restore a balanced chromosome complement. The gene also needs to be tested against a wider range of leaf rust pathotypes to confirm its usefulness (Table 2, source S15).

Resistance from *T. kotschyi*

Accession 617 (Israel) and its hybrid with 'CS' produced IT ; upon inoculation with an inoculum mix of leaf rust (Antonov & Marais, 1996). Backcrosses were made to 'CS' and disomic addition plants were selected from the F_2: *T. kotschyi*/4* 'CS'. Backcrosses to both 'CS' (five completed) and W84-17 (two completed) were continued. From Tables 2 and 3 (source S14) it appears that promising leaf and stripe rust resistance genes occur in the material.

Leaf and stripe rust resistance from *T. peregrinum*

Accession 673 (USA) and its F_1 with CS produced IT ;-1^{-} following seedling inoculation (Antonov & Marais, 1996). The hybrid was backcrossed to 'CS' for six cycles before a disomic addition line was derived. The added chromosome is telocentric and carries useful leaf and stripe rust resistance genes (source S16 in Tables 2 and 3).

Leaf and stripe rust resistances from *T. macrochaetum*, accession 683 (Israel)

A disomic addition line was selected from the F_2: *T. macrochaetum*/8* 'CS'. From Tables 2 and 3 it appears that the added chromosome in S19 carries effective leaf and stripe rust resistance genes. Although the resistance occurs on an addition chromosome it has relatively high transmission and the latter F_2 (derived from a monosomic addition) consisted of 66% resistant plants. However, the disomic addition plants are poorly developed with strong hybrid necrosis. Probe PSR931 that hybridises to homoeoloci on the group 3L arms of wheat detected an additional fragment (approximately 3.2 kb in size) to those normally produced by 'CS'. Thus, the resistance probably occurs on a group 3 homoeologue of the U or M genomes.

Resistance from *Triticum umbellulatum* accession 740 (Bulgaria)

This source was originally selected on the basis of leaf rust resistance and a disomic addition line *T. umbellulatum*/4* 'CS' was selected. Although the leaf rust resistance proved less useful (Table 2, S23), the stripe rust resistance is being pursued.

Resistance from *T. macrochaetum* accession 763 (Bulgaria) and *T. neglectum* accession 155 (USA)

Monosomic addition chromosomes segregated in progeny derived from both sources. The resistances appeared to be effective against the entire array of pathotypes. Resistant plants were selected from both populations and from these disomic additions should be derived. In the case of the *T. macrochaetum*-derived (S18) resistance five backcrosses to 'CS' have been completed. For the *T. neglectum* source (S20) seven backcrosses have been completed. Comparison of the RFLP profile generated on the *T. neclectum* addition line using probe PSR931 (detects 3L arms) with the 'CS' profile revealed two extra fragments (approximate sizes 3.0 and 3.3 kb). Thus, the leaf rust resistance probably occurs on a group 3 homoeologue (U or M genome).

Discussion

Overall, the transfer attempt had a low success rate. Of the 206 resistant accessions originally identified by Antonov and Marais (1996), genes from only ten are still being pursued. However, it must be noted that the large numbers involved were difficult to manage during the initial stages of transfer so effort was concentrated on those derivatives that survived and produced viable seeds. If failed combinations were

repeated, a larger number of successes would have resulted. The tetraploid progenitors of wheat also produced disappointingly few successes. Antonov and Marais (1996) reported that only eight of 24 resistant *T. turgidum* accessions showed useful levels of resistance in F_1 hybrids with 'CS'. Genes from seven of these were retained through subsequent backcrosses and were tested more extensively at the end of 2000. Only one of the *T. turgidum* sources had resistance to all the pathotypes in the extended seedling tests. Generally, the more distant relatives contributed more genes with a wide spectrum of resistance. Another interesting feature of the results was the relatively frequent co-transfer of stem and/or stripe rust resistance genes. This is, however, not totally unexpected as at least five instances of linked transfers can be found among the designated species-derived genes in the wheat gene catalogue (Anonymous, 2001).

The leaf and stripe rust resistance genes *LrS8*, *YrS8*, *LrS12* and *YrS12* appear to be free of obvious linked deleterious effects. In 'CS' background, *LrS12* and *YrS12* were associated with strong preferential transmission. However, when crosses were made to W84-17, normal segregation resulted. At least two of the resistance sources (S13 and S24) appear to be associated with gametocidal (*Gc*) genes. Gametocidal genes of wheat were mostly introduced through interspecific hybridisation and originated from species such as *Thinopyrum ponticum* (Knott, 1961; Sharma & Knott, 1966; Kibirige-Sebunya & Knott, 1983), *T. timopheevii* (Nyquist, 1962), *T. dichasians*, *T. triunciale* and *T. cylindricum* (Endo, 1979), *T. longissimum* (Maan, 1976), *T. sharonense* (Miller, Hutchinson & Chapman, 1982) and *T. speltoides* (Tsujimoto & Tsunewaki, 1988). In most *Gc* heterozygotes a percentage of non-carrier gametes survive, however, in some instances elimination appears to be complete. A *Gc* gene with apparently complete penetrance was co-transferred with *SrS24* (Marais & Pretorius, 1996). For this gene, F_1 heterozygote fertility did not exceed 50% and was strongly skewed towards the 0-5% interval. A small proportion of F_2 progeny were susceptible, suggesting that the *Gc* and *Sr* genes are closely linked on the same chromosome. Fertility of homozygotes ranged from 0-100% and the more fertile plants generally produced higher proportions of shrivelled, often sprouted, seeds. *Gc* homozygotes also showed signs of hybrid necrosis and had an inferior phenotype. Thus, the *Gc* gene(s) in S24 behaves like a 'molecular parasite' that cannot be removed by hybridisation and crossing over, rendering the resistance seemingly impossible to use commercially. Despite extensive attempts to disrupt the *Gc* system through irradiation and treatment with the mutagen, N-nitroso-N-methyl-urea (Marais & Pretorius, 1996), segregates that had lost the *Gc* gene could not be recovered. When crosses were made to the CS nulli-tetrasomics, some of the F_1 plants having CS nulli 3A tetra 3D or CS nulli 6A tetra 6D as one parent, had fertility higher than 60%. The respective F_1s were pollinated with diverse stem rust susceptible genotypes and the testcross F_1s are being screened for possible recombinants without the *Gc* gene. The S13 genes (*T. speltoides*) also have strong preferential transmission and are associated with inferior plant type, low fertility and poorly developed seeds. It is likely that a *Gc* gene is also involved in this case. Attempts will be made to find a genotypic background that will reduce the *Gc* effect and allow for the survival of recombinants without the detrimental effects.

Testing of the six disomic additions with RFLP probes that are diagnostic for the different chromosome arms of wheat detected variation for fragment size in only two lines. A *T. macrochaetum* addition chromosome with both leaf rust and stripe rust resistance genes appears to be a group 3 (U- or M-genome) homoeologue. Similarly, a group 3U or 3M homoeologue from *T. neglectum* carrying leaf rust resistance appears to be present in another addition. Further markers and restriction enzymes will need to be used in an attempt to determine the homoeologies of the remaining additions. Since the chromosomes are from the tertiary gene pool, allosyndetic pairing induction will be required to translocate the resistance to wheat homoeologues. Some of the addition lines show poor plant type and strong hybrid necrosis. Such effects may persist after translocation of the target areas onto wheat chromosomes. Due to the more distant relationships involved, correction of defects are likely to require the continued use of laborious homoeologous pairing induction procedures.

Despite the potential difficulties in the exploitation of these resistances in the short term, the results reported indicate that there is a useful source of novel resistances to the rust diseases among wheat relatives. Further cytogenetic manipulations and future refinement in molecular technologies, especially gene cloning and transformation, may allow opportunities to capitalise on the material generated from these studies.

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