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A study of modified forms of the *Lr19* translocation of common wheat

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Abstract Following the induction of allosyndetic pairing between the *Thinopyrum*-derived *Lr19* translocation in 'Indis' wheat and homoeologous wheat chromatin, eight suspected recombinants for the *Lr19* region were recovered. These selections were characterised for marker loci that were previously used to construct a physical map of the *Lr19* segment. At the same time near-isogenic lines were developed for some of the selected segments and tested for seedling leaf-rust resistance in order to confirm the presence of *Lr19*. It appeared that three of the four white-endosperm selections do not possess *Lr19* and only one, 88M22-149, is a true *Lr19* recombinant. The resistance gene in the three non-*Lr19* selections resides on chromosome 6B, appears to derive from 'Indis', and was selected unintentionally during backcrossing. The pedigree of 'Indis' is suspect and it is believed that the *Lr19* translocation in 'Indis' is in reality the *Th. ponticum*-derived (T4) segment rather than being of *Th. distichum* origin as was believed earlier. The white-endosperm recombinant, 88M22-149, retained the complete *Lr19* resistance and was apparently re-located to chromosome arm 7BL in a double-crossover event. 88M22-149 has lost the *Sd1* gene and often shows strong self-elimination in translocation heterozygotes. This effect may result from additional gametocidal loci or from an altered chromosome structure following re-location of the segment. 88M22-149 in fact contains a duplicated region involving the *Wsp-B*1 locus. Three selections had partially white endosperms and expressed *Lr19* and other *Thinopyrum* marker alleles. Polymorphisms for the available markers confirmed that the translocated segment in at least one of them had been shortened through recombination with chromosome arm 7DL. Further markers need to be studied in order to determine whether the translocation in the remaining two partially white recombinants had also undergone recombination with wheat. The eighth selection has yellow endosperm and appears to self-eliminate in certain translocation heterozygotes. No evidence of recombination could be found with the markers used. If the latter selections are in fact recombinants they may prove useful in attempts to unravel the complex segregation distortion mechanism.

Key words *Lr19* translocation · *Thinopyrum* · *Ph*-induced recombinants · Physical mapping

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Introduction

The *Lr19* leaf-rust resistance gene occurs on the T4 translocated segment originally transferred to common wheat from *Thinopyrum-ponticum* by Sharma and Knott in 1966. The wheat 'Indis' was found to carry a translocation that showed identical polymorphisms to the T4 translocation at various loci. 'Indis' was selected by Pienaar (Marais et al. 1988) among the B_2F_3 progeny of the cross 'Inia 66' *3/*Thinopyrum distichum* and it was believed that its translocated segment is homoeologous to the T4 segment (Marais 1992 a). Both translocations express *Lr19*, *Sr25*

(stem-rust resistance), *Sd1* (segregation distortion), *Wsp-D1c* (water-soluble protein), *Y* (yellow-endosperm pigmentation) and null alleles for *Ep-D1* and *α-Amy-D2*. Prins et al. (1996) compared polymorphisms at three RFLP (restriction fragment length polymorphism) loci in 'Indis', *Th. distichum*, A2558 (a T4 homozygote) and W743 (a $7el_1$ ditelosomic addition line having the *Th. ponticum* chromosome arm that carries *Lr19*). They concluded that the translocation in 'Indis' does not derive from *Th. distichum* and that it probably is the T4 segment.

The *Lr19* translocated segment does not pair with the homoeologous chromosome 7DL arm during meiosis in heterozygotes, with the result that its genes are transmitted as a single large linkage block (Knott 1980; Marais and Marais 1990). This precludes mapping studies based on recombination and also renders the resistance useless in countries where the yellow-endosperm trait is regarded as undesirable. Following gamma-irradiation, Marais (1992 a) derived 29 deletion mutants, each homozygous for a different deletion of the *Lr19* translocated segment in 'Indis'. Through deletion mapping, the relative positions of a number of marker loci on the *Thinopyrum* segment were determined as: centromere, *Sd1*, *Xpsr165*, *Xpsr105*, *Xpsr129*, *Lr19*, *Wsp-D1*, Sr25/*Y* (Marais 1992 a; Prins et al. 1996). Bournival et al. (1994) deduced the gene order on the T4 translocation as being: *Lr19-Sr25-Y* (yellow pigment).

In an attempt to break the linkage between *Lr19* and *Y*, Marais (1992 c) made use of the *ph1b* and *ph2b* mutants of 'Chinese Spring' to induce allosyndetic pairing and crossovers between the 'Indis' *Lr19* segment and homoeologous areas of the wheat genome. Resistant suspected-recombinants giving white endosperm (four), partially white endosperm (three) and one producing yellow endosperm but sometimes showing self-elimination, were recovered. The white-endosperm selections were thought to be the result of double-crossover events and were apparently relocated to different chromosomes (Marais 1993). Marais (1993) attempted to determine the new chromosome locations of the segments, but the results were ambiguous due to segregation distortion, and some of the preliminary allocations proved to be incorrect (unpublished data).

Lr19 is often transmitted preferentially in heterozygotes (Kibirige-Sebunya and Knott 1983; Marais 1990; Zhang and Dvořák 1990) due to the presence of *Sd1*. The degree of segregation distortion appears to be determined by the hybrid genotype. In 'Chinese Spring'/'Indis' hybrids only mild distortion was seen, whereas in crosses of 'Indis' with 'Morocco' or 'Inia 66' very strong preferential transmission was evident. According to Sibikeev (1994) no evidence of segregation distortion was found when 'Saratovskaya 29' with *Lr19* was crossed with 'Saratovskaya 46-, -55, 58' or 'Chinese Spring'. The selective abortion of gametophytes which receive a normal chromosome 7D is triggered by the absence of the translocated segment rather than by the presence of the normal chromosome 7D (Marais 1992 b). The severity of the gametocidal response elicited by *Sd1* is determined by several genes located on a number of wheat chromosomes. The individual responder loci may act as suppressors or promoters of the response, yet their effects are generally small (Marais 1992 b). Unlike the original *Lr19* segment some of the suspected recombinants often showed mild-to-strong self-elimination in heterozygotes depending on the genetic background (Marais 1990).

In the present paper, we describe the results of an attempt to verify and determine the relative sizes and location of the *Thinopyrum* segments that are retained in the various suspected recombinants derived by Marais (1992 c). We also wished to confirm the tendency of some of the selections to self-eliminate in heterozygotes with certain genetic backgrounds.

Materials and methods

Plant material for RFLP analyses

Eight suspected recombined translocation lines (Marais 1992 c) were tested for the presence of various marker loci (see Table 3). Two of them were selected from the cross 'Chinese Spring monosomic 3D'/'Indis'//'Chinese Spring *ph2b*'/3/'Inia 66' (= 87M70), and the remainder from the cross 'Chinese Spring monosomic 5B'/'Indis'//'Chinese Spring *ph1b*'/3/'Inia 66' (= 88M22).

Plant and pathotype material for leaf-rust resistance tests and segregation analyses

Near-isogenic lines differing with regard to the *Lr19* segment they contain were developed in the varieties 'Inia 66', 'SST 66', 'Chinese Spring', and in the breeding line 'W84-17'. The unmodified *Lr19* segment associated with yellow endosperm, and the four white-endosperm selections, namely 87M70-63, 88M22-149, 88M22-157 and 88M22-184, as well as a yellow-endosperm selection showing self-elimination (87M70-348) (Marais 1992 c), were used for this purpose. Mostly, five to six backcrosses were made; however, in a few instances backcrossing had only progressed for two to four cycles. Pathotype UVPrt8 of *Puccinia recondita* Rob. ex. Desm. f. sp. *tritici* was used to test for the presence of the translocation during backcrossing. This pathotype is virulent on the recurrent parents but is avirulent on *Lr19*. Segregation of the leaf-rust resistance was studied in the F_2 of the last backcross of the near-isogenic lines.

Leaf-rust resistance conferred by the original and 'recombined' forms of the *Lr19* translocation was studied in homozygous selections (which were selected from F_2-derived F_3 populations) of the various near-isogenic lines using the pathotypes UVPrt2, UVPrt3, UVPrt9, UVPrt13 and UVPrt16. UVPrt13 was used as representative of the related UVPrt6, UVPrt8 and UVPrt12 pathotypes. The recurrent parents of the various near-isogenic lines were included as controls. The avirulence/virulence characteristics of the pathotypes were described by Marais and Pretorius (1996). Primary leaf-infection types were recorded on the 0 to 4 scale described by Roelfs et al. (1992).

The three partially white recombinants (88M22-42, 88M22-98 and 88M22-103) were crossed with the wheat cultivars 'Inia 66', 'Chinese Spring', 'Condor', 'SST3', and a breeding line, 'W84-17'. The F_1-derived F_2 families were tested with UVPrt8 to study the

segregation of leaf-rust resistance as an indicator for the presence of a segregation distortion gene(s).

cDNA clones

Three anonymous cDNA clones specific for chromosome 7, i.e. PSR105, PSR165 and PSR129 (Sharp et al. 1989; Chao et al. 1989), were utilized. Each clone detects a locus on the segment containing *Lr19* ('Indis'), which was previously physically mapped with the use of deletion mutants (Prins et al. 1996). The putative recombinants were screened for the presence of the wheat 7DL fragment, or the *Thinopyrum*-derived fragment, using RFLP analyses.

RFLP procedures

The procedures used for RFLP analyses are as described in Prins et al. (1996).

Results and discussion

Lr19 near-isogenic lines

The original translocation and four apparently modified *Lr19* segments which are associated with white-endosperm colour were incorporated through backcrossing into four common wheat backgrounds. A further, suspectedly modified *Lr19* translocation, which has retained the yellow-pigment genes yet has an altered segregation distortion effect, was used to develop near-isogenic lines in the cultivars 'Inia 66' and 'Chinese Spring' only. Segregation of leaf-rust resistance was studied in the F_2 of the most-advanced backcrosses (Table 1) and the various near-isogenic lines were compared for their resistance to five leaf-rust pathotypes (Table 2).

Segregation distortion in the F_2 generations

The segregation-distortion effect appeared to vary depending on the modified segment and recurrent parent that were involved (Table 1). In keeping with earlier data (Marais 1990), the complete alien segment (unmodified) showed mild preferential transmission in the 'Chinese Spring' and 'SST66' backgrounds, but very strong preferential transmission in the 'Inia 66' and 'W84-17, backgrounds. Recombinant 87M70-348 was selected by Marais (1992 c) because of its tendency to self-eliminate in certain genetic backgrounds. This

Table 1 Segregation of the original and apparently modified forms of the *Lr19* translocation in backcross F_2 families (tested with pathotype UVPrt18)

Lr19 segment used		Recurrent parent Inia 66	W84-17	SST 66	C Spring
Original[a]	Doses[c]	5/6	6/7	6	6
	Plants[d]	338	555	209	149
	Ratio[e]	96:4	96:4	89:11	87:13
	χ^2[f]	77.2**	131.4*	21.5**	3.3
87M70-348[a]	Doses	5/6	–	–	3/4
	Plants	60	–	–	144
	Ratio	86:14			67:33
	χ^2	4.4*	–	–	5.3*
88M22-149[b]	Doses	5	7	7	6
	Plants	159	176	205	119
	Ratio	56:44	50:50	58:42	65:35
	χ^2	30.1**	58.7**	31.9**	6.4**
87M70-63[b,g]	Doses	4/5	3	3	3
	Plants	147	160	172	130
	Ratio	76:24	72:28	73:27	68:32
	χ^2	0.1	0.8	0.3	4.1*
88M22-157[b,g]	Doses	7	7	7	6
	Plants	1782	240	255	145
	Ratio	75:25	60:40	78:22	57:43
	χ^2	0.0	28.8**	1.5	24.9**
88M22-184[b,g]	Doses	7	7	7	6
	Plants	2148	252	244	144
	Ratio	76:24	69:31	68:32	63:37
	χ^2	1.1	4.8*	6.3*	10.7**

[a,b] Produce yellow and white endosperm, respectively
[c] Number of doses of the recurrent parent
[d] Number of plants tested for seedling resistance
[e] Ratio of resistant : susceptible progeny
[f] χ^2 = chi-square for correspondence to a 3:1 ratio (** significant at the 99% confidence level, * significant at the 95% confidence level)
[g] Unknown resistance gene

Table 2 Infection types produced following the inoculation of near-isogenic lines with five leaf-rust pathotypes

Recurrent parent	Leaf-rust pathotype	Resistance contained in near-isogenic lines						Recurrent parent
		Lr19			Unknown gene (*Lr?*)			
		Original	87M70-348	88M22-149	87M70-63	88M22-157	88M22-184	
Inia 66	UVPrt2	0;	0;	;1^{c}	;1^{c}	;–;$1^{=cn}$	;^{n}	;^{cn}
	UVPrt3	0;	0;	;	0;	;	0;	;1^{c}
	UVPrt9	0;	0;	;	0;–;1	0;	;	;–;1
	UVPrt13	0;	0;	0;	0;	0;	0;	3^{++}
	UVPrt16	0;	0;	;	;	0;	;	;
SST66	UVPrt2	0;	–	0;	1^{cn}	1^{cn}	1^{cn}	;1^{cn}
	UVPrt3	0;	–	;	;	;	;	;^{cn}
	UVPrt9	0;	–	0;	$2^{=cn}$	2	2_{cn}	2
	UVPrt13	0;	–	0;	0;	0;	0;	3^{+}
	UVPrt16	0;	–	0;	;	;	;^{n}	;^{n}
W84-17	UVPrt2	0;	–	;	;	;	;	;
	UVPrt3	;	–	;	;	;	;	1^{c}
	UVPrt9	0;	–	;	3^{+}	$2^{+}3$	3	3
	UVPrt13	0;	–	0;	0;	0;	0;	3^{+}
	UVPrt16	0;	–	;	;1	;	;1	;
Chinese Spring	UVPrt2	;	;	;	3^{-},3	$3^{+}3^{++}$	3^{+},3^{++}	3^{++}
	UVPrt3	;	;1	;–;1	;, ;1^{cn}, ;$1^{=c}$,X	;, ;1,;1^{+},$X^{=}$,3^{++}	;$1^{=}$, X,3^{++}	3^{++}
	UVPrt9	;	;	;	X,3^{++}	X,3^{+},3^{++}	3^{++}	3^{++}
	UVPrt13	0;	;–;1	;	0;	;	;	3^{++}
	UVPrt16	;	;	;–1	;, $X^{=}$, X, X^{+}, 3^{+}	X, X^{++}, 3^{+}, 3^{++}	3^{+}, 3^{++}	3^{++}
	UVPrt8	;	;	;	;	;	;	3^{++}

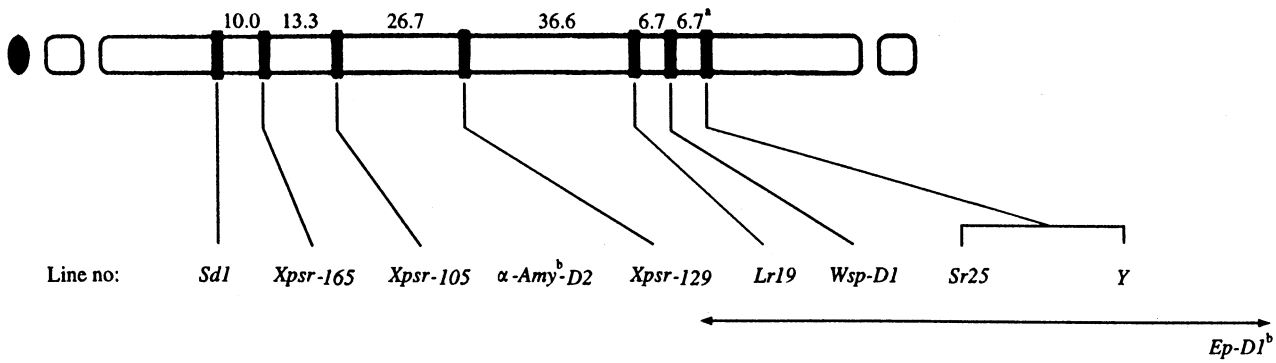
tendency is reflected in its backcrosses to 'Chinese Spring' and may imply the loss of a part of the *Sd*-function. Recombinant 87M70-348, however, does express the *Thinopyrum* polymorphisms with all the markers and genes that were used to map the initial translocation (Table 3). As will be discussed, the *Lr19* segment in the white-endosperm recombinant 88M22-149 has lost *Sd1*, but has apparently acquired a strong tendency to self-eliminate. Thus, it seems possible that segregation distortion may be caused by more than one *Sd* gene. A second, distally located segregation distortion gene was also implicated in another study of 29 *Lr19* deletion lines (Prins et al. 1996). However, an alternative explanation of the self-elimination effect of 88M22-149 may be that it is due to modifications (structural and/or genetical) that occurred following recombination. As a group, selections 87M70-63, 88M22-157 and 88M22-184 have near-normal transmission in the 'Inia 66' and "SST66' genetic backgrounds, but show mild self-elimination in the 'W84-17' and 'Chinese Spring' backgrounds. Indeed, as will be shown, these lines might have lost the *Lr19* gene, with their resistance to UVPrt8 (here referred to as *Lr?*) not being derived from *Thinopyrum*.

Leaf-rust resistance of the *Lr19* and *Lr?* near-isogenic lines

The leaf-rust resistance data (Table 2) show that whereas all five pathotypes are avirulent on *Lr19*, three of them UVPrt2, UVPrt3 and UVPrt16, are also avirulent on 'Inia 66', 'SST66' and 'W84-17'; UVPrt9 is avirulent on 'Inia 66' and 'SST66', and UVPrt13 is virulent on all four wheat backgrounds. 'Chinese Spring' is susceptible to the five pathotypes.

The near-isogenic lines were obtained by testing F_2-derived F_3 families from the final backcrosses with UVPrt8 (pathogenicity similar to UVPrt13, except for virulence to *Lr26*), and making separate bulks of homozygous-resistant and homozygous-susceptible progenies. When tested with the different pathotypes the susceptible bulks derived following backcrossing to 'Inia 66', 'W84-17' and 'SST66' produced the infection types expected for the specific recurrent parents, thus confirming that the desired backgrounds have been established. However, the corresponding susceptible bulks obtained following backcrossing of the resistance to UVPrt8 in 87M70-63, 88M22-157 and 88M22-184 to 'Chinese Spring' revealed segregation of background resistance genes to UVPrt3, UVPrt9 and UVPrt16. The data of Table 2 show two types of resistance, one conferred by *Lr19*, the other conditioned by an unknown (*Lr?*) gene. The original translocation, 87M70-348, and 88M22-149 produce infection types and resistance to all races characteristic of *Lr19*. The *Lr?* gene in selections 87M70-63, 88M22-157 and 88M22-184 appears to have different race specificity as compared to *Lr19*. Resistant homozygotes from the latter group develop a 0;-infection type upon inoculation with UVPrt8 and UVPrt13 but turn out to be susceptible when tested with UVPrt2 and produce variable results, with

Table 3 Polymorphisms for marker loci in selections suspected to have recombined *Lr19* translocated segments (T: the *Thinopyrum* allele; W: the common wheat allele; -: the alternative form which is a null condition or an allele that could not be positively identified; ?: unknown



Translocation on chromosome arm 7DL: yellow and partially white endosperm										
87M70-348	?	T	T	–	T	T	T	T	T	–
88M22-42	?	W	W	W	T	T	T	T	T[c]	–
88M22-98	?	T	T	–	T	T	T	T	T[c]	–
88M22-103	?	T	T	–	T	T	T	T	T	–
Unmodified	T	T	T	–	T	T	T	T	T	–
Resistance not associated with chromosome 7D: white endosperm										
87M70-63	–	W	W	W	W	*Lr*[f]	W	–	–	W
88M22-157	–	W	W	W	W	*Lr*[f]	W	–	–	W
88M22-184	–	W	W	W	W	*Lr*[f]	W	–	–	W
88M22-149	–	W	W	W	T[d,e]	T	T[d]	–	–	W

[a] Physical deletion map constructed by Prins et al. (1996)
[b] Mapped within this region by Chao et al. (1989)
[c] Partially white recombinants (see text)
[d] Retained the *Thinopyrum* locus and regained the wheat 7DL locus
[e] Lost the wheat 7BL locus
[f] Unknown reistance gene (*Lr?*)

infection types ranging from highly resistant to susceptible when tested with pathotypes UVPrt3, UVPrt9 and UVPrt16. As a similar range of infection types was observed in the corresponding UVPrt8 susceptible bulks, this would suggest the presence of background resistance genes. Such genes may derive from the 'Inia 66' and 'Indis' parents that were involved in the original crosses made to induce allosyndetic pairing. It would therefore appear as though *Lr?* has the resistance/susceptibility formula: UVPrt8, UVPrt13/UVPrt2, UVPrt3, UVPrt9, UVPrt16.

Characterization of the recombinants

Prins et al. (1996) constructed a physical map of the *Lr19* translocated segment. Their data have been integrated with the present results to construct rough physical maps of the apparently recombined *Lr19* segments (Table 3). The selections were found to fall into two groups: (1) those that retained large *Thinopyrum* segments are still located on chromosome 7D as the original segment, and produce yellow or partially white endosperms; and (2) those that occur on different chromosomes, and are not associated with yellow flour pigments.

As to the former group, the three partially white selections (Table 3) are similar to the partially white deletion mutants encountered by Marais (1992 a) and thought to be due to the presence of only one of two possible *Y* loci or to the modified expression of a single locus (Prins et al. 1996). If two *Y* loci are assumed, the partially white selections 88M22-98 and 88M22-103 could have resulted from single crossovers which replaced terminal portion of 7DL with wheat chromatin. Recombinant 88M22-42 could have resulted from a double crossover that occurred in the interval *Xpsr105–Xpsr129* and the *Y* region. This recombinant expresses the *α-Amy-D2a* allele, whose locus is located close to the centromere, in the region between *XPsr105* and *Xpsr129* (Chao et al. 1989). However, further distally located markers will need to be studied to determine if the distal parts of these three selections have indeed been exchanged with wheat chromatin. A comparison of the segregation distortion of the resistance phenotype observed in the progeny of the three partially white recombinants is given in Fig. 1. These putative recombinants are segregates from cross 88M22, which can be calculated to contain on average 50% 'Inia 66', 37.5% 'Chinese Spring' and 12.5% 'Indis' genes. The genetic backgrounds (and thus the

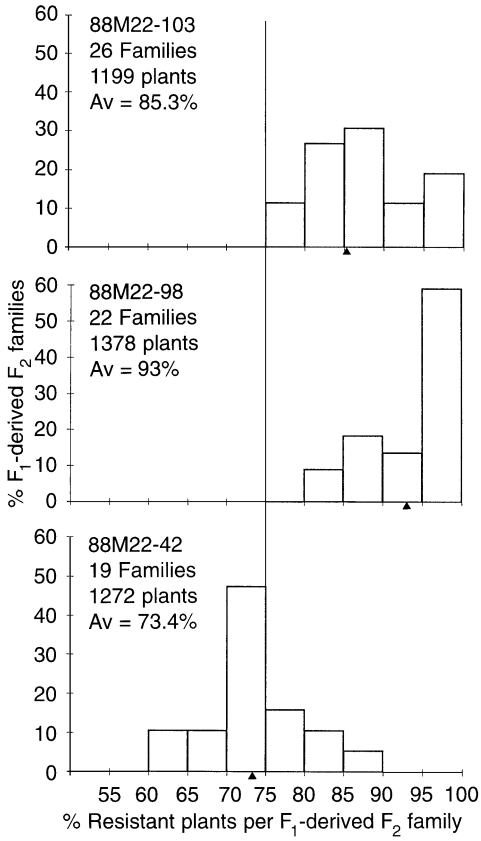


Fig. 1 Segregation distortion of the resistance phenotype observed in the F_2 progeny of each of three partially white recombinants (88M22-103, 88M22-98 and 88M22-42) crossed with the wheats Inia 66, Chinese Spring, Condor, SST3 and W84-17. Average (Av) = ▲

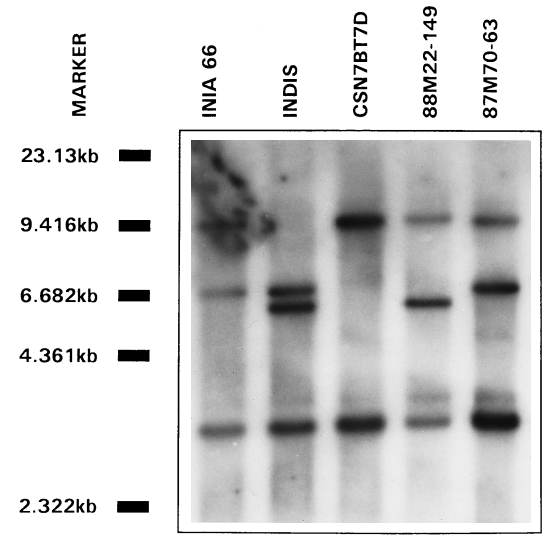


Fig. 2 Hybridization pattern for PSR129 on control genotypes ('Inia 66', 'Indis', CSN7BT7D = Chinese Spring Nullisomic 7B Tetrasomic 7D) and 'recombinants' (88M22-149, 87M70-63). The DNA was digested with *Hin*dIII. The size marker was lambda DNA digested with *Hin*dIII

wheat segregation-distortion responder genes) were highly heterogeneous in the three selections. The data obtained in crosses with four wheats are depicted in Fig. 1. It is evident that 88M22-98 and 88M22-103 always had mild to strong preferential transmission and have probably retained *Sd1*. The 88M22-42 effect, on the other hand, varied from mild self-elimination to mild preferential transmission. Recombinant 88M22-42 has apparently lost the *Sd1* locus. Recombinant 87M70-348 has probably retained *Sd1* but may have lost/exchanged an unidentified part of the translocation causing it to have reduced transmission in certain genetic backgrounds.

Concerning the white-endosperm recombinant lines, 88M22-149 appears to be the product of a double crossover (Table 3). It has retained a considerably reduced *Thinopyrum* segment yet including the complete *Lr19* resistance. During recombination the *Xpsr129-7B* locus has been replaced with the *Thinopyrum*-derived *Xpsr129* locus (Fig. 2). This confirms the relocation of this segment to chromosome 7B as suggested by the data of Marais (1993). Both the *Wsp-B1* and *Thinopyrum*-derived *Wsp-D1* loci are expressed in 88M22-149. This would suggest that an unequal crossover occurred which created a duplicated region. The recombination event did not replace the α-*Amy-B2* or *Ep-B1* loci on chromosome 7B, which would suggest that these loci do not occur within the recombined segment. According to Chao et al. (1989), *Ep-B1* is located distally with respect to *Xpsr129*. The data of Table 3 would therefore imply that *Ep-B1* is situated in the vicinity of, or distal to, *Wsp-B1*. According to Kim et al. (1993), the physical distance from the centromere to the T4 translocation break point amounts to about half the length of chromosome 7DL of wheat. The physical map constructed by Prins et al. (1996) does not depict the physical distance of the translocation from the centromere and telomere. It is not known exactly where the break occurred between *Xpsr105* and *Xpsr129* in recombinant 88M22-149. At least 23.3% of the original translocation has been replaced with wheat chromatin in the centromeric region (Table 2). Due to the duplication, it is difficult to deduce the amount of reduction in the *Wsp-D1–Sr25/Y* interval. 88M22-149 has probably lost *Sd1* and has a very consistent tendency to self-eliminate when it occurs in the heterozygous condition (Table 1). The self-elimination response of 88M22-149 is extremely severe and appears to be stronger than that produced by 88M22-42 (Fig. 1). When the 88M22-149 segment was transferred to 'W84-17', 78 resistant B_6F_2-derived F_3 populations were tested for resistance to leaf rust. Only two populations were homogyzous-resistant while 76 segregated. Similarly, when 88M22-149 was backcrossed into 'SST66', 47 B_6F_2-derived F_3 populations all segregated for resistance. If these data are combined, it appears that instead of the 41 resistant homozygotes expected from normal segregation, only two were obtained. When integrated with the data obtained in the F_2 of the

same crosses (Table 2), it can be calculated that the F_2 contained the genotypic frequencies: 0.01 RR: 0.53 RR: 0.46 rr. It is not clear whether the strong self-elimination in the translocation heterozygotes stems from the disruption of a complex of *Sd* genes or whether it is due to (or enchanced by) a disruptive chromosome duplication that occurred during recombination. If the latter is true, it may not be an impediment to the utilisation of the resistance since homozygotes for the 88M22-149 segment have a perfectly normal phenotype and fertility.

The selections 87M70-63, 88M22-157 and 88M22-184 do not exhibit any of the marker phenotypes except for having strong leaf-rust resistance (*Lr?*) against UVPrt8 and UVPrt13 (Table 2). Monosomic analyses have shown that this resistance is associated with chromosome 6B (unpublished results). Even hypothesizing that the *Lr19* translocation carries an intercalary region that bears homoeology to a group-6 chromosome arm, it nonetheless seems extremely unlikely that pairing of such a region with a group-6 chromosome arm would have taken place frequently enough to produce three double-crossover recombination products. Known leaf-rust resistance genes that occur on chromosome 6B are *Lr3* (three alleles, i.e. *Lr3a, Lr3ka* and *Lr3bg*), *Lr9* (from *Ae. umbellulatum*) and *Lr36* (from *Ae. speltoides*) (McIntosh et al. 1995). At present, however, the identity of the unknown gene remains unclear.

The origin of the *Lr19* translocation in the germplasm line 'Indis' is somewhat doubtful (Prins et al. 1996). Initially it was believed to be a near-isogenic line of 'Inia 66' carrying a homoeolocus of *Lr19* that was derived from *Th. distichum* (Marais et al. 1988). Recently, we have come to believe that 'Indis' contains the T4 *Lr19* translocation in an unknown background (Prins et al. 1996). Thus, it is possible that the observed resistance in selections 87M70-63, 88M22-157 and 88M22-184 is due to a wheat gene that was introduced together with *Lr19* in the course of the breeding process. Transmission of *Lr?* is mostly normal, yet mild self-elimination of preferential transmission is sometimes observed (Table 1, Marais 1992 c, 1993). Luig (1964) reported that distorted segregation ratios were associated with the 'Mentana'-type of resistance to wheat leaf rust, i.e. *Lr3a* (McIntosh et al. 1995). The white-endosperm recombinant 88M22-149 retained the *Thinopyrum* alleles of the *Xpsr129* and *Wsp-D1* loci, each of which can serve as a marker of its presence. Should the *Lr19* resistance in 88M22-149 prove to be stable and not to be associated with any negative agronomical effects, it will be the only useful white-endosperm recombinant that has been obtained (Marais 1992 a) following the use of the *Ph* mutants.

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References

Bournival B, Obanni M, Abad A, Ohm H, Mackenzie S (1994) Isolation of a new species-specific repetitive sequence from *Thinopyrum elongatum* and its use in the studies of alien translocations. Genome 37 : 97–104

Chao S, Sharp PJ, Worland AJ, Warham EJ, Koebner, RMD, Gale MD (1989) RFLP-based genetic maps of wheat homoeologous group-7 chromosomes. Theor Appl Genet 78 : 495–504

Kibirige-Sebunya I, Knott DR (1983) Transfer of stem-rust resistance to wheat from an *Agropyron* chromosome having a gametocidal effect. Can J Genet Cytol 25 : 215–221

Kim NS, Amstrong K, Knott DR (1993) Molecular detection of *Lophopyrum* chromatin in wheat-*Lophopyrum* recombinants and their use in the physical mapping of chromosome 7D. Theor Appl Genet 85 : 561–567

Knott DR (1980) Mutation of a gene for yellow pigment linked to *Lr19* in wheat. Can J Genet Cytol 22 : 651–654

Luig NH (1964) Heterogeneity in segregation data from wheat crosses. Nature 204 : 260–261

Marais GF (1990) Preferential transmission in bread wheat of a chromosome segment derived from *Thinopyrum distichum* (Thunb.) Löve. Plant Breed 104 : 152–159

Marais GF (1992 a) Gamma irradiation-induced deletions in an alien chromosome segment of the wheat 'Indis' and their use in gene mapping. Genome 35 : 225–229

Marais GF (1992 b) Genetic control of a response to the segregation-distortion allele, *Sd-1d*, in the common wheat line 'Indis'. Euphytica 60 : 89–95

Marais GF (1992 c) The modification of a common wheat-*Thinopyrum distichum* translocated chromosome with a locus homoeoallelic to *Lr19*. Theor Appl Genet 85 : 73–78

Marais GF (1993) Characterization of modified forms of a *Lr19* translocation. In: Li ZS, Xin ZY (eds) Proc 8th Int Wheat Genet Symp, Beijing, China, pp 937–941

Marais GF, Marais AS (1990) The assignment of a *Thinopyrum distichum* (Thunb.) Löve-derived translocation to the long arm of wheat chromosome 7D using endopeptidase polymorphisms. Theor Appl Genet 79 : 182–186

Marais GF, Pretorius, ZA (1996) Gametocidal effects and resistance to wheat leaf rust and stem rust in derivatives of a *Triticum turgidum* ssp. *durum*/*Aegilops speltoides* hybrid. Euphytica 88 : 117–124

Marais GF, Roux HS, Pretorius ZA, Pienar R de V (1988) Resistance to leaf rust of wheat derived from *Thinopyrum distichum* (Thunb.) Löve. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp, pp 369–849

McIntosh RA, Wellings CR, Park RF (1995) Wheat rusts: an atlas of resistance genes. Jeans K, Cloud-Guest A (eds) CSIRO Publications, East-Melbourne, Australia, pp 53–54

Prins R, Marais GF, Janse BJH, Pretorius ZA, Marais AS (1996) A physical map of the *Thinopyrum*-drived *Lr19* translocation. Genome 39 : 1013–1019

Roelfs AP, Singh RP, Saari EE (1992) Rust diseases of wheat: concepts and methods of disease management. Mexico, D.F. Cimmyt, p 81

Sharma D, Knott DR (1966) The transfer of leaf rust resistance from *Agropyron* to *Triticum* by irradiation. Can J Genet Cytol 8 : 137–143

Sharp PJ, Chao S, Desai S, Gale MD (1989) The isolation and characterization and application in the *Triticeae* of a set of wheat RFLP probes identifying each homoeologous chromosome arm. Theor Appl Genet 78 : 342–348

Sibikeev SN (1994) Personal communication. Laboratory of Genetics and Cytology, Agricultural Research Institute for South Eastern Regions, Tulaikov St. 7, Saratov, Russia

Zhang HB, Dvořák J (1990) Characterization and distribution of an interspersed repeated nucleotide sequence from *Lophopyrum elongatum* and mapping of a segregation distortion factor with it. Genome 33 : 927–936