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RFLP markers associated with *Sr22* and recombination between chromosome 7A of bread wheat and the diploid species *Triticum boeoticum*

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Abstract Analysis of the bread wheat variety Schomburgk, and related lines in its pedigree, identified RFLP markers associated with the segment of chromosome 7A carrying the *Sr22* gene derived from the diploid species *T. boeoticum*. The distribution of the RFLP markers indicated that at least 50% of 7AS and 80% of 7AL in Schomburgk is of *T. boeoticum* origin. Evaluation of five sets of near-isogenic lines, backcross lines in 20 different genetic backgrounds and an F_2 population segregating for *Sr22* demonstrated a very low level of recombination between the 7A chromosomes of *T. boeoticum* and *T. aestivum*. Several recombinants carrying *Sr22* but with a much reduced segment of *T. boeoticum* were identified and these may prove useful in the breeding of further varieties with *Sr22*.

Key words RFLP · *Sr22* · *Triticum aestivum* *T. boeoticum* · Recombination

Introduction

The *Sr22* gene conditioning resistance to stem rust caused by *Puccinia graminis* Pers. f. sp. *tritici* Eriks. and E. Henn. was originally identified in the A genome diploid wheat species *Triticum boeoticum* accession G-21 (Gerechter-Amitai et al. 1971) and *T. monococcum* L. accession RL5244 (Kerber and Dyck 1973). This gene was transferred to tetraploid and hexaploid wheats through interspecific hybridizations. The *T. monococcum* source was backcrossed to the tetraploid Stewart and a selection carrying *Sr22* was then backcrossed to the hexaploid Marquis (Kerber and Dyck 1973), whereas the *T. boeoticum* source was backcrossed to the tetraploid Spelmar (Gerechter-Amitai et al. 1971) and then to the hexaploid Steinwedel (The 1973). Genetic and pathological tests showed that the *T. monococcum*- and *T. boeoticum*-derived hexaploid lines possessed the same rust resistance gene (The 1973; The and McIntosh 1975). Monotelosomic analysis at the hexaploid level demonstrated that *Sr22* was located in chromosome 7AL, 27±4 crossover units from the centromere and 41 units from *Pm1*, a gene conditioning low reaction to *Erysiphe graminis* f. sp. *tritici* (The and McIntosh 1975).

Sr22 is effective against all pathotypes of the stem rust pathogen in Australia. The *Sr22* from the *T. boeoticum* source was transferred to Schomburgk (Rathjen 1987). Empirical observations during the breeding of Schomburgk, and its subsequent use as a parent, showed a lower than expected recovery of advanced lines with the *Sr22* allele during several generations of field evaluation and selection by the F_2 progeny method (Rathjen, unpublished). This could result from either gametocidal effects or a yield penalty associated with the presence of *T. boeoticum* chromatin carrying *Sr22*. Reduced transmission of *Sr22* was reported by Kerber and Dyck (1973) for the *T. monococcum* source and by The and McIntosh (1975) for pooled data involving both the *T. monococcum* and *T. boeoticum* derivatives.

The effect of a number of genes for stem rust resistance, including *Sr22*, upon grain yield was evaluated using near-isogenic lines in a number of genetic backgrounds and over a range of environments (The et al. 1988). Although the mean yield of lines with *Sr22* was not significantly lower than their *sr22* controls, the effect was not consistent across genetic backgrounds. For particular combinations, resistant lines yielded approximately 10% less than susceptible counterparts.

The objectives of this study were to use DNA markers to determine the amount of *T. boeoticum* chromatin associated with *Sr22* in Schomburgk and a series of near-isogenic (The et al. 1988) and backcross-derived lines (The, unpublished). This investigation also provides a prelimi-

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Table 1 Lines involved in the transfer of *Sr22* from *T. boeoticum* G-21 to the bread wheat Schomburgk. The genome constitutions and genotypes at the *Sr22/sr22* locus are included for each line. The pedigrees of bridging lines are also shown

Line	Genomes	Pedigree	*Genotype*
T. boeoticum G-21	AA	Source of *Sr22*	*Sr22Sr22*
Spelmar	AABB		*sr22sr22*
C68.9	AABB	*T. boeoticum* /2*Spelmar	*Sr22Sr22*
Steinwedel	AABBDD		*sr22sr22*
W3589	AABBDD	C68.9/2*Steinwedel	*Sr22Sr22*
Oxley	AABBDD		*sr22sr22*
Warigal	AABBDD		*sr22sr22*
Aroona	AABBDD		*sr22sr22*
Schomburgk	AABBDD	W3589/Oxley//2*Warigal/3/2*Aroona	*Sr22Sr22*

Table 2 Pedigrees of the near-isogenic (NIL) and backcross (BC) lines with respect to *Sr22* tested by RFLP analysis. NILs comprised a resistant and a susceptible line derived from the BC_5F_2 generation while resistant backcross lines were compared to the susceptible recurrent parent

Recurrent parent	Full pedigree of *Sr22* derivatives	Type
Condor	W3589/6*Condor	NIL
Lowan	//4*Lowan	BC
Lark	//3*Lark	BC
ZL27	//3*WD100/3/4*ZL27	BC
Kiata	//3*WD154/3/3*Kiata	BC
Oxley	W3589/Oxley//5*Oxley	NIL
Vulcan	/3/4*Vulcan	BC
Vasco	/3/2*Vasco	BC
QT3730	/3/2*QT3730	BC
Egret	//6*Egret	NIL
Lilimur	/3/3*Wyuna/4/2*Lilimur	BC
IW562	/3/3*Cranbrook/4/4*IW562	BC
Wt211/7	//Wt211/7/3/5*Wt211/7	NIL
WtW31/S20	/3/4*WtW31/S20	BC
Tatiara	/3/4*Tatiara	BC
Warigal	//2*Warigal/3/2*Aroona/4/2*Aroona/5/2*Warigal	BC
Wt20/5	/5/4*Wt20/5	BC
Cook	//Oxley/3/4*Cook	BC
CO1213	/4/4*CO1213	BC
CO1568	/4/4*CO1568	BC
CO1650	/4/4*CO1650	BC
K441	/4/3*K441	BC
K1056	/4/3*K1056	BC
QT4118	/4/2*QT4118	BC
Teal	W3589/6*Teal	NIL

nary investigation of recombination between chromosome 7A of *T. aestivum* and the introgressed segment of *T. boeoticum*.

Materials and methods

Plant materials

Genetic materials tested by RFLP analyses were:-

(1) lines included in the transfer of *Sr22* from *T. boeoticum* to the bread wheat Schomburgk (Table 1).
(2) near-isogenic (NIL) and backcross (BC) lines for *Sr22*. The near-isogenic lines were produced in five genetic backgrounds where each pair of lines was selected from a single heterozygous BC_5F_2 plant (The et al. 1988). Backcross lines were produced in 20 genetic backgrounds (Table 2) and lines carrying *Sr22* were compared with the recurrent parent. The hexaploid W3589 was the donor of *Sr22* in all lines.
(3) fifty-six progeny of a single self-fertilised plant derived from a single backcross between W3589 (donor of *Sr22*) and Vasco (recurrent parent). The parental plant was identified as heterozygous at 16 RFLP loci.
(4) the alternative hexaploid sources of *Sr22*, namely: W3589=Steinwedel*2//Spelmar*2/*T. boeoticum* G-21 and W3534=Marquis*5//Stewart*3/*T. monococcum* RL5244.

Seeds of Oxley, Warigal, Aroona and Schomburgk were obtained from the Waite Institute while all other lines were produced at the Plant Breeding Institute, University of Sydney. A single seed of each line was sown for DNA extraction and RFLP analysis. Seedlings were scored for the presence of red coleoptile, conditioned by the gene *Rc1*, located on 7A (Sears 1954).

RFLP analysis

DNA was extracted from plants by a mini-prep procedure. DNA was digested with six restriction enzymes *Bam*HI, *Dra*I, *Eco*RI, *Eco*RV, *Hin*dIII and *Xba*I (Promega). Digested DNA was electrophoresed on a 1.0% agarose (Pharmacia) gel in TAE buffer and transferred to Hybond-N^+ (Amersham) nylon membranes. DNA probes, previously mapped to chromosomes of homoeologous group 7 (Chao et al. 1989; Gill et al. 1991; Heun et al. 1991; Liu and Tsunewaki 1991), were kindly provided by the Australian Triticeae Mapping Initiative collection at The University of Sydney. PCR-amplified inserts were la-

belled with [^{32}P]dCTP by random primer labelling (Feinberg and Vogelstein 1983).

Reaction to stem rust

All lines with *Sr22* used in RFLP analysis were progeny tested with an appropriate culture of *P. graminis* f. sp. *tritici* to verify their genotypic status with respect to *Sr22*. These selected cultures varied with the particular host genetic background.

Results

Pedigree of Schomburgk

Evidence for transmission of chromatin from *T. boeoticum* to Schomburgk was revealed by 22 RFLP probes known to map to chromosomes of homoeologous group 7. These included markers for both the short and long arms (Table 3; Fig. 1). RFLPs were identified between *T. boeoticum* and bread wheat at *Xpsr119* and *Xpsr121* [distal 7AS and distal 7AL, respectively (Chao et al. 1989)], but there was no evidence of transmission of either locus from *T. boeoticum* to W3589 and Schomburgk. It is therefore probable that the distal regions of both arms of chromosome 7A of Schomburgk comprise *T. aestivum* chromatin, while the proximal regions are of *T. boeoticum* origin.

Table 3 Marker loci at which there was evidence of transmission of chromatin from *T. boeoticum* to the bread wheat Schomburgk, via the bridging lines C68.9 and W3589. Loci within the *Xpsr*, *Xcnl* and *Xglk* sets are listed in approximate map order from distal 7AS to distal 7AL

Locus	Chromosome/ arm location	Reference[a]
Xpsr108	7AS 7BS 7DS	1
Xpsr150	7AS 7BS 7DS	1
Xpsr152	7AS 7BS 7DS	1
Xpsr103	7AS 7BS 7DS	1
Xpsr165	7AL 7BL 7DL	1
Xpsr117	7AL 7BL 7DL	1
Xpsr72	7AL 7BL 7DL	1
Xpsr129	7AL 7BL 7DL	1
Xcnl.WG719	7HS	2
Xcnl.CDO358	7HS	2
Xcnl.WG669	7HS	2
Xcnl.CDO673	7HS	2
Xcnl.WG686	7HL	2
XksuA5	7DL	3
XksuD6	7D	3
XksuD15	7D	3
XksuE9	4D	3
Xglk439	7B	4
Xglk478	7B	4
Xglk598	7B	4
Xglk750	7B	4
Xglk686	7A	4
Rc1	7A	5

[a] References to loci and locations: 1 Chao et al. (1989), 2 Heun et al. (1991), 3 Gill et al. (1991), 4 Liu and Tsunewaki (1991), 5 Sears (1954)

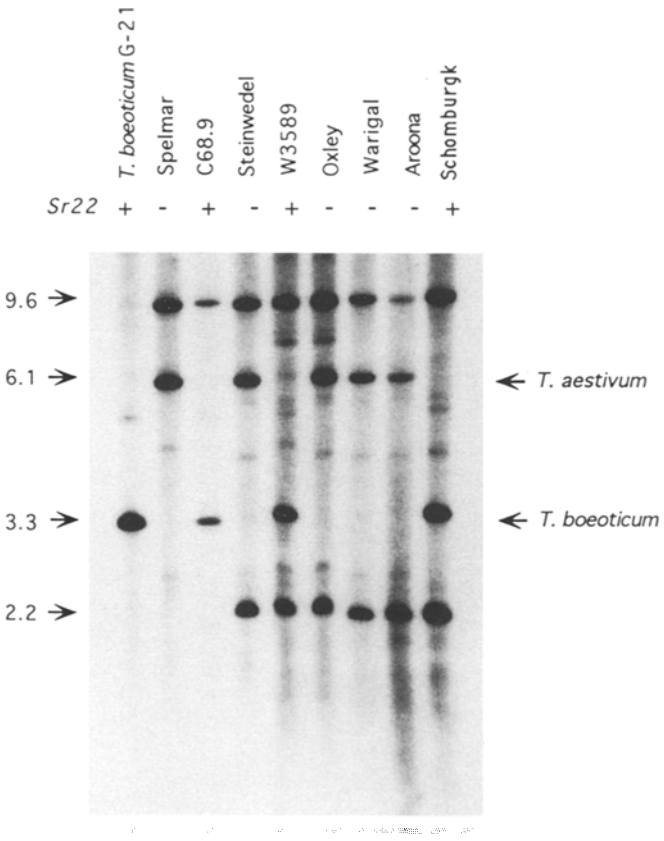

Fig. 1 *Dra*I digests of DNA from the varieties included in the transfer of *Sr22* from *T. boeoticum* to the bread wheat variety Schomburgk, probed with PSR129. The names of the various varieties and the presence or absence of *Sr22* are indicated above each lane. Bands of the 7A chromosomes of *T. aestivum* and *T. boeoticum*, and their sizes (kb), are indicated

Near-isogenic and backcross lines

The NILs and backcross lines were tested for the presence of the *T. boeoticum* alleles at 18 RFLP loci. The RFLP probes were selected to provide a full coverage of the loci identified as positive for *T. boeoticum* in Schomburgk. In contrast to the results for Schomburgk, there was evidence of recombination between chromosomes 7A of bread wheat and *T. boeoticum*. Four linkage patterns among lines carrying *Sr22* were identified, namely: (type 1) *T. boeoticum* at all loci (i.e., similar to Schomburgk), (type 2) wheat at all short arm loci and the proximal long arm locus *Xpsr165* and *T. boeoticum* at the remaining long arm loci, (type 3) wheat at all short and long arm loci, with the exception of *Xglk750* and (type 4) heterozygous at all loci (Table 4, Fig. 2). These data are consistent with *Sr22* being located in 7AL (The and McIntosh 1975) while the genotypes of the type-3 group indicate that both the *Sr22* and the *Xglk750* loci are distal of *Xpsr129*.

Progeny of heterozygous *Sr22* Vasco derivative

Three lines derived from a single backcross of Vasco to W3589 were included in the testing of the backcross lines

Table 4 Hybridization patterns in near-isogenic and backcross derived lines carrying the *Sr22* gene. "+" and "–" indicate presence and absence of the *T. boeoticum* hybridization pattern, respectively, and "±" indicates a heterozygous locus

Hybridization pattern	*Xpsr108, 152, 103, 165* *Xcnl.WG719, 669, CDO673, 358* *XksuD15, E9, Xglk439, 598* *Rc*	*Xpsr117, 129* *Xcnl.WG686* *XksuA5, D6*	*Xglk750*
Type 1[a]	+	+	+
Type 2	–	+	+
Type 3	–	–	+
Type 4	±	±	±

[a] Type 1: Condor, Egret, Wt 211/7, Oxley, Teal, Lark, Vulcan, Kiata, Lowan, ZL27, Tatiara, Wt 20/5, IW562, Lilimur, Vasco b and c, QT3730, Warigal derivatives
Type 2: Wt W31/S20 derivative
Type 3: Cook, K1056, CO1213, CO1568, CO1650, K441, QT4118 derivatives
Type 4: Vasco a derivative

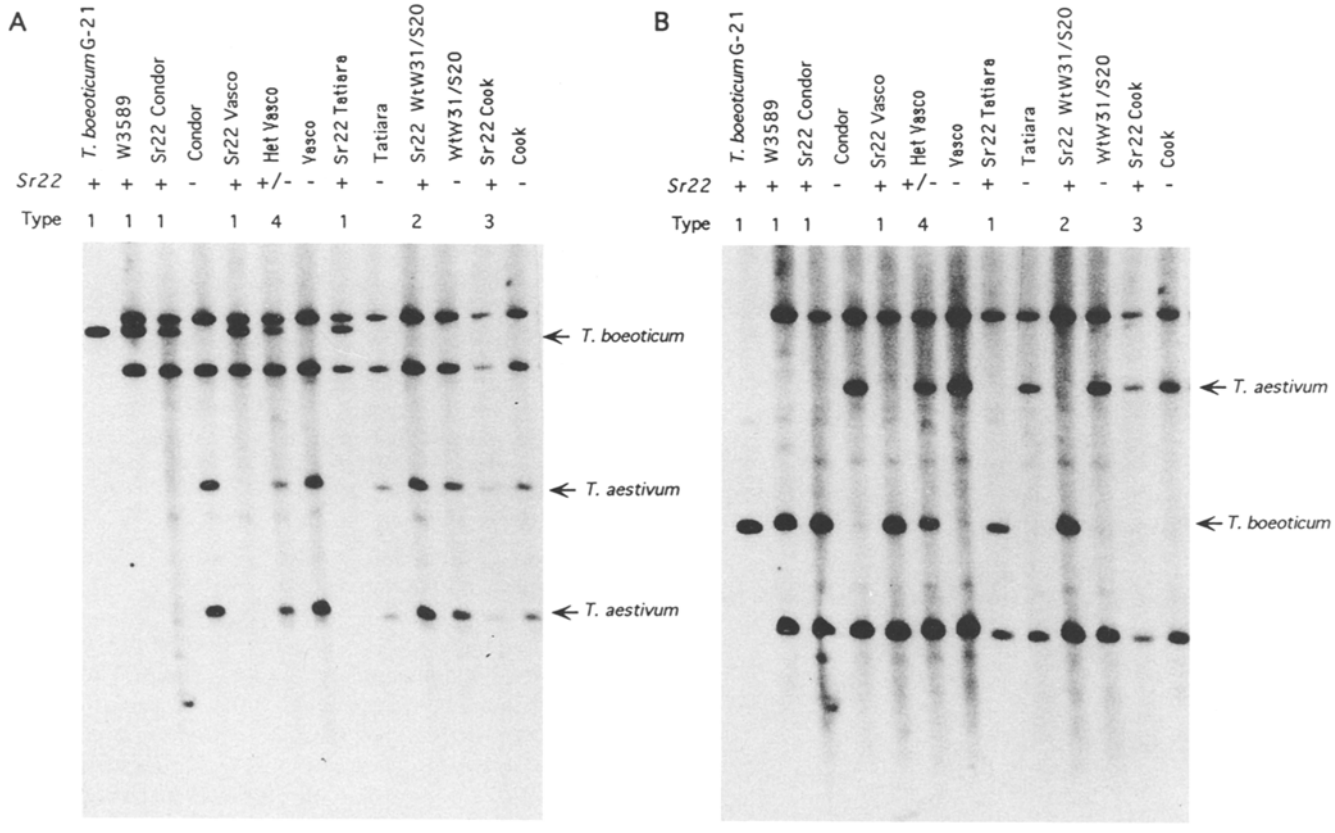

Fig. 2 *Dra*I digests of DNA from *Sr22* and control lines probed with (**A**) PSR165 and (**B**) PSR129. Lines representative of types 1–4 (Table 4) are included, together with the donor of *Sr22*. The names of the various varieties and the presence or absence of *Sr22* are indicated above each lane. Bands of the 7A chromosomes of *T. aestivum* and *T. boeoticum* are indicated

to identify the presence of *T. boeoticum* chromatin. Two of these lines (Vasco b and c) were type 1, while the third line (Vasco a) was heterozygous at all loci tested and classified type 4 (Table 4). Fifty-six progeny of the heterozygous plant were tested with 12 probes to cover the range *Xpsr108* to *Xglk750*. One recombinant was identified between *Xpsr165* and *Xpsr117* (Table 5). The frequencies of the genotypes homozygous *T. boeoticum*: heterozygous: homozygous wheat were consistent with a single gene segregation ratio of 1:2:1, namely:

(1) short-arm probes and *Xpsr165* 16:24:16 χ^2_2=1.14, P>0.50

(2) long-arm probes distal to *Xpsr 165* 16:23:17 χ^2_2=1.82, P>0.30

indicating no evidence for gametocidal effects. The pairing behaviour of chromosomes during metaphase-I was examined in pollen mother cells obtained from six plants identified as heterozygous at all loci. Chromosomes paired regularly and, although univalents were observed at a low frequency, the incidence was not significantly different from that observed in plants homozygous for wheat chromatin.

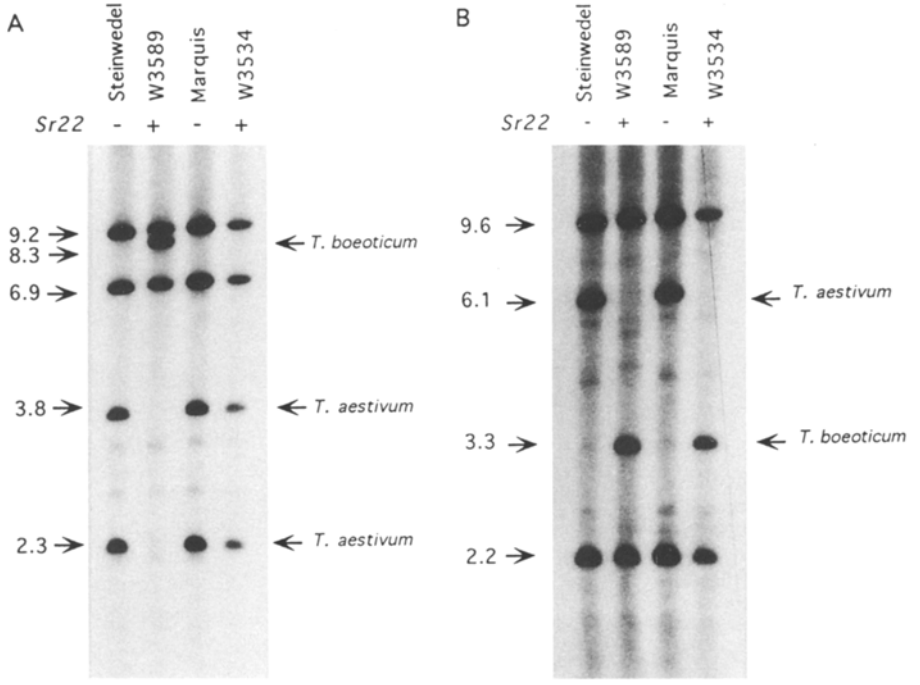

Fig. 3 *Dra*I digests of DNA from the hexaploid lines carrying the alternative sources of *Sr22* probed with (**A**) PSR 165 and (**B**) PSR129. Steinwedel was the recurrent hexapoid parent in the transfer of *Sr22* from *T. boeoticum* to W3589 (The 1973) and Marquis the recurrent hexapoid parent in the transfer of *Sr22* from *T. monococcum* to W3534 (Kerber and Dyck 1973). The names of the various varieties and the presence or absence of *Sr22* are indicated above each lane. Bands of the 7A chromosomes of *T. aestivum* and *T. boeoticum*, and their sizes (kb), are indicated

Table 5 Genotypes at 14 loci of a recombinant line identified among the progeny of a selfed heterozygote derived from W3589/Oxley//5*Oxley/3/2*Vasco

Genotype	Locus
Homozygous *T. boeoticum*	–
Heterozygous	*Rc1, Xpsr108, 152, 103, 165, Xcnl.WG719,XksuD6, E9, Xglk439*
Homozygous wheat	*Xpsr117, 129, Xcnl.WG686, XksuA5, Xglk750*

Table 6 Evidence for the presence of chromatin of the diploid A genome donor in hexaploid wheats derived from the alternative sources of *Sr22*. "+" indicates the presence of the alien allele

Loci	Steinwedel	W3589	Marquis	W3534
Xpsr108, 152, 165	–	+	–	–
Xpsr129, WG686, ksuD6	–	+	–	+

Comparison of *T. boeoticum* and *T. monococcum* sources of *Sr22*

Restriction patterns of W3589 and W3534, the hexaploid lines carrying *Sr22* derived from *T. boeoticum* G-21 and *T. monococcum* RL5244, respectively, were compared at six loci. The bread wheats Steinwedel and Marquis, the recurrent parents in the development of W3589 and W3534, respectively, were also included. RFLPs were detected between W3589 and Steinwedel for both long- and short-arm probes, as expected on the basis of the pedigree of Schomburgk (Table 3). By contrast, RFLPs were detected between W3534 and Marquis only at loci located on the long arm distal to *Xpsr165*. W3534 and W3589 showed the same restriction patterns at these distal loci, whereas W3534, Marquis and Steinwedel produced the same patterns at proximal long-arm loci and all short-arm loci (Table 6, Fig. 3) and were similar to type 2 lines listed in Table 4.

Discussion

RFLP analysis of two sets of genetic material, namely the pedigree components of cv Schomburgk and near-isogenic and backcross lines possessing *Sr22*, demonstrated a large interstitial segment of chromatin transferred from *T. boeoticum* to bread wheat along with *Sr22*. The map of chromosome 7A based on deletion stocks of Chinese Spring and RFLP probes (Werner et al. 1992) enabled estimation of the size of *T. boeoticum* chromatin transferred to Schomburgk. The presence of the *T. boeoticum* allele at *Xpsr129* and *Xpsr108* indicated that at least 80% of 7AL and 45% of 7AS of Schomburgk and type-1 near-isogenic and backcross lines (Table 4) consist of *T. boeoticum* chromatin. This is a conservative estimate of the amount of *T. boeoticum* present, as the relationship between the PSR probes and other probes tested has not been fully established by either linkage analysis or physical mapping. The relationship between physical and genetic maps of the chromosomes of homoeologous group 7 was discussed by Werner et al. (1992) and the region defined by *Xpsr129* and *Xpsr108* represents a genetic distance of at least 50 cM for chromosomes 7B and 7D (Chao et al. 1989).

Only a single recombinant between the *Xpsr108* and *Xpsr129* loci was identified among the 56 progeny of the selfed heterozygous Vasco-derived line in the absence of

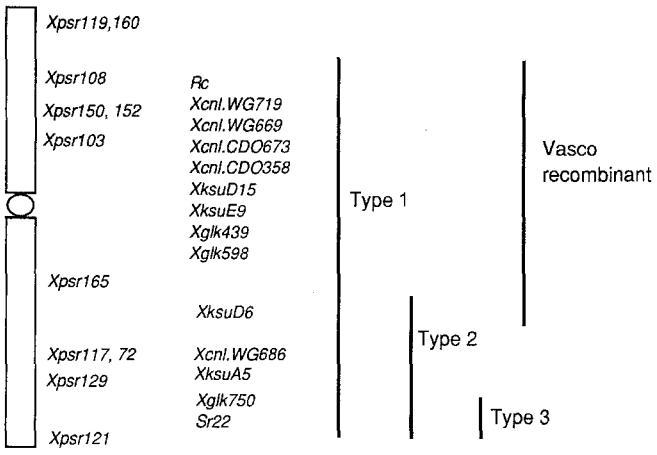

Fig. 4 Schematic diagram of chromosome 7A showing the approximate physical positions of *Xpsr* loci (Werner et al. 1992), at left, and other marker loci identified as being transmitted from *T. boeoticum* to Schomburgk. These loci are grouped according to genotypes of recombinant lines identified through NIL and backcross analysis, but are not ordered within groups. The *bold lines* at the right indicate the presence of *T. boeoticum* chromatin in the various recombinant lines

selection for the *Sr22* allele. Therefore, the low level of recombination observed in the breeding of Schomburgk and the near-isogenic and backcross lines cannot simply be attributed to linkage drag associated with selection for *Sr22*, but rather to a barrier to recombination between the 7A chromosomes of *T. aestivum* and *T. boeoticum*. Recent information suggests that *T. urartu* was the donor of the A genome to domesticated tetraploid (*T. turgidum*) and hexaploid (*T. aestivum*) wheats, whereas the domesticated diploid wheat *T. monococcum* spp. *monococcum* was domesticated from *T. monococcum* spp. *aegilopoides* (syn. *T. boeoticum*) (Dvorak et al. 1988).

There was no cytological evidence, such as a higher than expected frequency of univalents during metaphase-I, to suggest reduced pairing between the wheat 7A chromosome and the chromosome carrying an interstitial segment of *T. boeoticum*. Kerber and Dyck (1973) also observed normal chromosome pairing for hybrids carrying *Sr22* from *T. monococcum*. Similarly, Lucas and Jahier (1987) described a high level of association between chromosomes of *T. urartu* and *T. boeoticum* during meiosis. There was no evidence of gametocidal effects among the progeny of the heterozygous Vasco derivative and this is in contrast to The and McIntosh (1975) who noted reduced transmission of the *Sr22* allele. It is possible that this discrepency results from background genetic effects. Kerber and Dyck (1973) reported inconsistent gametic transmission of *Sr22*, and McIntosh (1991) also described the influence of genetic background upon gametophytic effects in relation to alien sources of disease resistance genes.

The low level of recombination between chromatin of *T. aestivum* and *T. boeoticum* prevents construction of a detailed linkage map including all loci tested. Nevertheless, as recombination was identified in four separate regions, pooling data presented in Tables 4 and 5 enables loci to be assigned to particular regions (Fig. 4). To some extent this allows integration of the four genetic maps (Chao et al. 1989; Gill et al. 1991; Heun et al. 1991; Liu and Tsunewaki 1991) upon which the analyses were based. Seven of the backcross-derived lines with *Sr22* were recombinant between *Xpsr129* and *Xglk750* and carried the *T. boeoticum* allele at *Xglk750* but not at *Xpsr129* or any other loci (Type 3). This places *Sr22* and *Xglk750* distal to *Xpsr129*. The type-3 recombinants were related (Table 2) and it is likely that a single recombination event occurred during the breeding of the Cook backcross line which was transmitted to the other six lines. The type-2 genotype described in Table 4 resulted from recombination between *Xpsr165* and *Xpsr117*, the region in which the single recombination event was observed among the progeny of the heterozygous Vasco line. In the former line, *XksuD6* co-segregated with *Xpsr117* (Table 4), whereas in the latter it co-segregated with *Xpsr165* (Table 5). *XksuD6* is therefore located between *Xpsr165* and *Xpsr117*.

The and McIntosh (1975) located *Sr22* on chromosome 7AL 27±4 crossover units from the centromere, a distance indicative of a much higher frequency of recombination than observed here. The line W3534, including *Sr22* derived from *T. monococcum*, was used for monotelosomic analysis (The and McIntosh 1975), while W3589, including *Sr22* derived from *T. boeoticum*, was used for the breeding of near-isogenic and backcross lines. A comparison of the restriction patterns of W3589 and W3534, with their recurrent wheat parents, indicates that 7AL of W3589 comprises *T. boeoticum* chromatin from *Xpsr108* in 7AS to *Xglk750* in 7AL. This represents most of chromosome 7A, including over half of the short arm and nearly all the long arm. In contrast, the amount of *T. monococcum* 7A transferred into W3534 accounts for only the distal part of 7AL (distal to *Xpsr165*). It is probable that the high levels of recombination between the centromere and *Sr22* reported by The and McIntosh (1975) was due to recombination between the proximal wheat segment of 7AL rather than between the *T. monococcum* region and wheat. Alternatively, the contrasting results may be due to a greater frequency of recombination between chromosomes 7A of *T. monococcum* and wheat than between *T. boeoticum* and wheat.

This study has demonstrated a very low level of recombination between the 7A chromosomes of *T. aestivum* and *T. boeoticum* associated with the *Sr22* gene. Nevertheless, several lines carrying a smaller introgressed segment than occurs in the variety Schomburgk were identified. These recombinants may prove useful in overcoming the negative effects, such as reduced pollen transmission and delay in time to heading (58.7 days for homozygous wheat types compared to 64.7 and 65.8 days for heterozygous and homozygous *T. boeoticum* types, respectively, among the progeny of the heterozygous Vasco line), associated with *Sr22*. The inclusion of only a small segment of *T. boeoticum* would also facilitate the transfer of genes located elsewhere on chromosome 7A to varieties carrying *Sr22*. The identification of DNA markers associated with *T. boeoticum* and *Sr22* will enable further selection of recombinant lines and also allow pyramiding *Sr22* with other genes conferring resistance to stem rust.

The technique described here to map and analyse the *Sr22* region may have broad application in the mapping of agronomically important traits in wheat and related chromosomes. The approach is similar to the use of near-isogenic lines for finding markers linked to a gene of interest. However, it utilises breeders lines rather than specifically prepared backcross material. For many characters important to wheat improvement extensive breeding and selection has already been performed. Where good pedigree information and a broad range of lines carrying the gene of interest are available, a type of NIL analysis can be made. This approach is clearly more complex than the use of NILs and may require more complex analyses. However, as described here, it is technically and conceptually feasible. Further, this approach makes use of the valuable resource of decades of research in agronomy, breeding and genetics of wheat.

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