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RFLP analysis of an *Aegilops ventricosa* chromosome that carries a gene conferring resistance to leaf rust (*Puccinia recondita*) when transferred to hexaploid wheat

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Abstract RFLP analysis has been used to characterise XM^v, a chromosome of *Aegilops ventricosa* present in a disomic addition line of wheat. This chromosome is known to carry a major gene conferring resistance to leaf rust (*Lr*). The analysis demonstrated that XM^v is translocated with respect to the standard wheat genome, and consists of a segment of the short arm of homoeologous group 2 attached to a group 6 chromosome lacking a distal part of the short arm. *Lr* was located to the region of XM^v with homoeology to 2S by analysis of a leaf rust-susceptible deletion line that was found to lack the entire 2S segment. Confirmation and refinement of the location of *Lr* was obtained by analysis of a spontaneous resistant translocation in which a small part of XM^v had been transferred to wheat chromosome 2A.

Key words RFLP analysis · Wheat · *Aegilops ventricosa* · Leaf rust resistance

Introduction

Leaf rust of hexaploid bread-wheat, *Triticum aestivum* L., which is caused by the pathogen *Puccinia recondita* Roberge ex Desmaz, can cause substantial yield losses in certain environments and years and is probably the most important disease of wheat worldwide. Numerous single-gene resistances have been used by breeders to control the disease, but these resistances have tended to be short-lived, with the exception of *Lr34*, which appears to give durable resistance when present in combination with other resistance genes (Singh and Rajaram 1992).

Wild Triticeae species are a rich source of novel resistances to many wheat diseases, including leaf rust. Resistance genes have been transferred from both *Aegilops* (Sears 1956; Dvorak 1977) and *Agropyron* (Knott 1968; Wienhus 1973; Sears 1972) spp. by a variety of methods, including backcrossing, *Ph1*-mediated introgression and irradiation. Dosba (1982) used *Aegilops ventricosa* (syn. *Triticum ventricosum*, 2n=4x=28, D^vM^v) to produce a set of M^v additions to wheat cv 'Moisson', among which one line (v260) was resistant to leaf rust. The homoeology of the added chromosome in v260, XM^v, has not to date been fully elucidated.

In this paper we report the development of a number of derivatives of v260, including the introduction of the leaf rust resistance gene into hexaploid wheat. Restriction fragment length polymorphism (RFLP) technology has been employed to determine the identity of XM^v relative to wheat chromosomes and to identify precisely the location of the rust resistance locus.

Materials and methods

Genetic stocks

The following genetic stocks were employed: hexaploid wheat cv 'Moisson', *Ae. ventricosa* accessions 10 (received in 1957 from Simonet) and 11 (received in 1969 from Kihara) and disomic addition line v260. A deleted addition line, XM^v-del, the interspecific chromosome substitution line, $XM^v(6D)$, and a wheat-XM^v translocation line, L22, were developed from v260 as follows. The XM^v addition stock v260 was crossed as male to 'Cappelle-Desprez' monosomic for chromosome 6A to obtain the substitution of XM^v for 6A. This was crossed and backcrossed twice to 'Moisson' to restore most of the 'Moisson' background. During this process a leaf rust-susceptible segregant arose that carried a cytologically shortened form of chromosome XM^v (Fig. 1), and this was maintained as a disomic-deleted addition line identified here as XM^v-del. Similarly, the substi-

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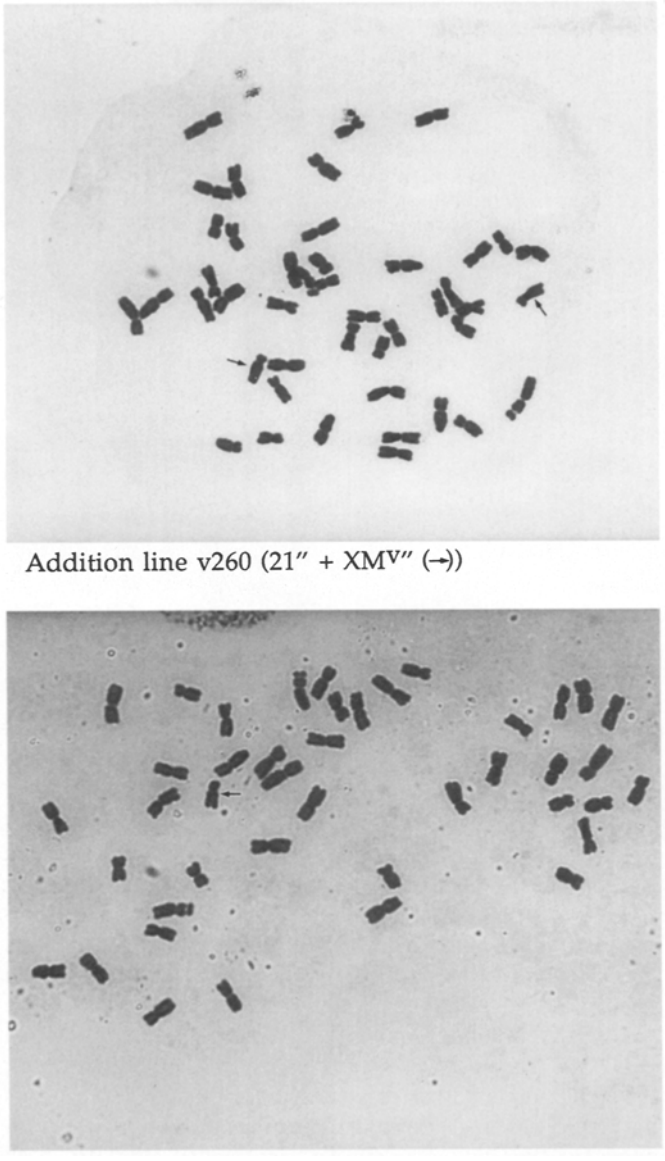

Fig. 1 Cytological characterisation of the chromosome XM^v in the addition line v260 (21″+XM^v″) and of the chromosome XM^v-del in the substitution line XM^v(6A) (40″+6A+XM^v-del)

tution line XM^v(6D) was obtained through a cross to 'Cappelle-Desprez' monosomic for chromosome 6D, followed by four crosses to 'Moisson'. L22 is resistant to leaf rust and carries a translocation between a segment of XM^v and an unknown wheat chromosome. This translocation occurred spontaneously and was discovered among the progeny of the cross v246×'Moisson' (v246 is a duplicate of v260).

RFLP analysis

DNA was extracted by the CTAB method (Rogers and Bendich 1985), while restriction digests, Southern blotting, probe labelling, hybridisation and autoradiography followed Sharp et al. (1988). PSR numbered probes were from the collection maintained at the Cambridge Laboratory, and consisted of: (1) a set of probes that recognise loci on the 12 homoeologous arms of wheat, excluding group 6 (1S: PSR168, 1L: PSR162, 2S: PSR109, 2L: PSR609, 3S: PSR305, 3L: PSR156, 4S: PSR163, 4L: PSR914, 5S: PSR628, 5L: PSR 115, 7S: PSR119, 7L: PSR121); (2) a set recognising loci on homoeologous group 6; and (3) a set recognising loci on homoeologous group 2S. The identity of the probes in (2) and (3), and the chromosomal location of the fragments they recognise are listed in Table 1.

Table 1 DNA probes, chromosomal locations of the fragments to which they hybridise and status of the fragments (present '+' or absent '–') in the addition line v260 and the v260-derived genetic stocks, XM^v-del (a deleted addition line) and L22 (a translocation line)

DNA probe	Wheat	v260	XM^v-del	L22
PSR167	6S,5B	–	–	–
PSR964	6BS,DS	–	–	–
PSR8	6S	–	–	–
PSR106	6S	–	–	–
PSR627	6AS,BS	–	–	–
PSR22	1BS,6BS	–	–	–
PSR312	6S	–	–	–
PSR141	6S	+	+	–
PSR113	6S	+	+	–
PSR371	6L	+	+	–
PSR142	6L	+	+	–
PSR915	6L	+	+	–
PSR149	6L	+	+	–
PSR605	6L	+	+	–
PSR2	6L	+	+	–
PSR154	6L	+	+	–
PSR546	6BL,DL	+	+	–
PSR928	2AS,DS	–	–	–(–2A)
PSR933	2AS,DS	+	–	+(–2A)
PSR150	2S,5L,7S	+	–	+(–2A)
PSR109	2S,5L	+	–	–
PSR666	2S	+	–	–
PSR108	2S,7S	+	–	–
PSR131	2S	+	–	–
PSR912	2S	–	–	–
PSR135	2S	–	–	–
PSR107	2S	–	–	–

PSR8=carboxypeptidase probe, PSR22=ribosomal probe, PSR2=α-amylase probe

Leaf rust reactions

Reaction to leaf rust was assessed on adult plants grown in the field under naturally occurring inoculum of the pathogen in Rennes, France, using a scale 1–9 (1=no symptom, 9=100% of the leaf covered by leaf rust). During the course of production of the genetic stocks (see above), the leaf rust population was virulent each year on cv 'Moisson' and line XM^v-del (score 7–9), but avirulent on lines carrying the complete chromosome XM^v and line L22 (score 1, exceptionally 2). Joint segregation of loci with the rust resistance was studied by analysis of individual F_3 plants bred from 13 rust resistant F_2 individuals of the cross L22×'Moisson'.

Results

Phenotypic compensating effect for chromosome 6D by XM^v

The substitution line XM^v(6D) is vegetatively vigorous and tends to be taller than euploid wheat, with lighter green

Table 2 Meiosis results for the progeny segregation of the cross 'Moisson' (21″) X F_1 double monosomic (20″+XD′+XM^{v}′)

Wheat chromosomes	Progeny of the cross 21″ X (20″ + XD′ + XM^{v}′)			
	20″+XD′+XM^{v}′	21″	21′+XM^{v} ′	20″+XD′
1D	0	9	5	2
2D	0	9	2	0
3D	0	4	4	1
4D	0	8	6	0
5D	0	12	2	2
6D	7	7	0	1
7D	0	8	2	3

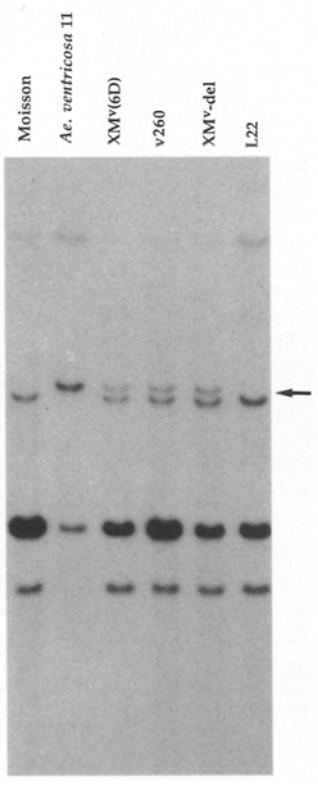

Fig. 2 Hybridisation of the probe PSR113 to *Eco*RI-restricted genomic DNA from 'Moisson', *Ae. ventricosa* 11, substitution line XM^{v}(6D), addition line v260, deleted addition line XM^{v}-del and translocation line L22. The *arrow* indicates the *Ae. ventricosa* M^{v} fragments

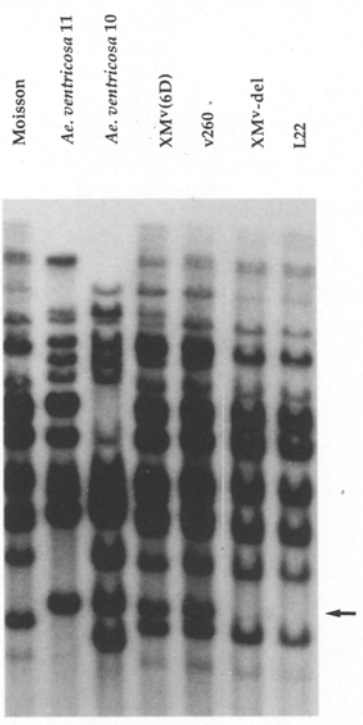

Fig. 3 Hybridisation of the probe PSR109 to *Eco*RV-restricted genomic DNA from 'Moisson', *Ae. ventricosa* 11, *Ae. ventricosa* 10, substitution line XM^{v}(6D), addition line v260, deleted addition line XM^{v}-del and translocation line L22. The arrow indicates the *Ae. ventricosa* M^{v} fragments

foliage. The fertility of the line is excellent, and the transmission through the gametes of the alien chromosome from a double monosomic (for chromosomes 6D and XM^{v}) is good (Table 2).

The relationship of XM^{v} to wheat group 6 chromosomes

The ability of chromosome XM^{v} to compensate for the absence of 6A and 6D led us first to examine homoeology with wheat group 6 chromosomes. Seventeen DNA probes which detect restriction fragments on the homoeologous group 6 chromosomes (Table 1) were hybridised to *Eco*RI, *Eco*RV, *Hin*dIII and *Dra*I digests of genomic DNA from 'Moisson', *Ae. ventricosa* 11, XM^{v}(6D), v260, XM^{v}-del and L22. Of these, all detected distinct fragments in *Ae. ventricosa* relative to 'Moisson'. All 8 *Ae. ventricosa* loci detected by probes recognising fragments located on the long arms of wheat homoeologous group 6 (6L) chromosomes were present in XM^{v}(6D), v260 and XM^{v}-del. However only two, *Xpsr113-6M^{v}* and *Xpsr141-6M^{v}*, of the 9 6S loci behaved in this way (Fig. 2). None of the 17 wheat group 6 probes detected an *Ae. ventricosa* fragment in L22. Thus, XM^{v} shares homoeology with 6L and the proximal part of 6S. However, the segment lost in XM^{v}-del, in which the gene for leaf rust resistance, *Lr*, must be located, is unrelated to wheat group 6. This conclusion was strengthened by the lack of any *Ae. ventricosa* markers with homoeology to group 6 in the leaf rust resistant line L22.

The relationship of chromosome XM^{v} to wheat group 2 chromosomes

In an ordered search for the identity of a chromosome segment with homoeology to wheat chromosomes other than those in group 6, probes detecting loci distributed in the distal regions of each of the remaining 12 wheat homoeologous group chromosome arms were used to assay the same genetic stocks. This analysis showed that PSR109, which hybridises with fragments originating from the short arm of wheat homoeologous group 2 chromosomes (Devos et al. 1993b), detects an *Ae. ventricosa* locus in XM^{v}(6D) and v260, but not in XM^{v}-del or L22 (Fig. 3), while the remaining 11 arm diagnostic probes produced RFLP profiles that were indistinguishable from those of 'Moisson' in all the lines.

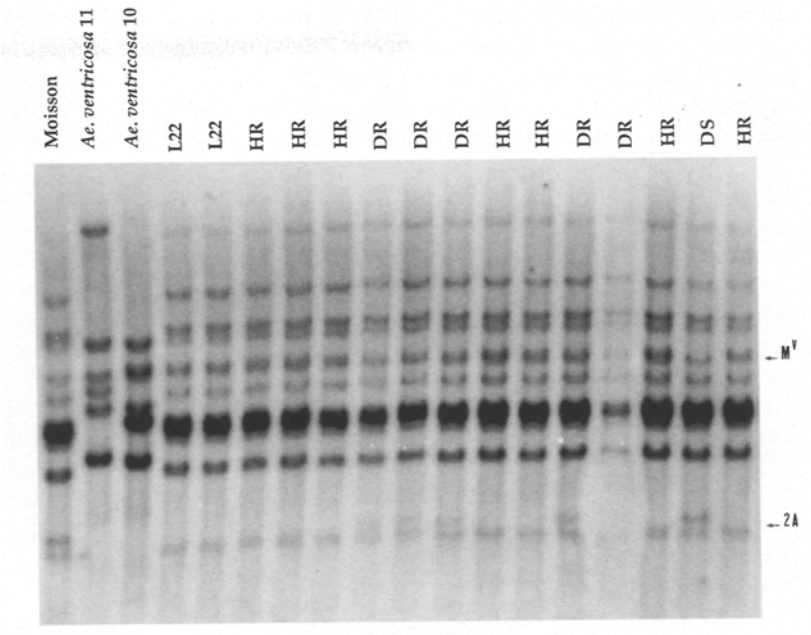

Fig. 4 Hybridisation of the probe PSR150 to *Dra*I-restricted genomic DNA from 'Moisson', *Ae. ventricosa* 11, *Ae. ventricosa* 10, L22, resistant individuals from non-segregating F_3 families (*HR*), resistant individuals from segregating F_3 families (*DR*) and a susceptible individual from a segregating F_3 family (*DS*). Diagnostic bands corresponding to the M^v genome and the chromosome *2A* are indicated by *arrows*

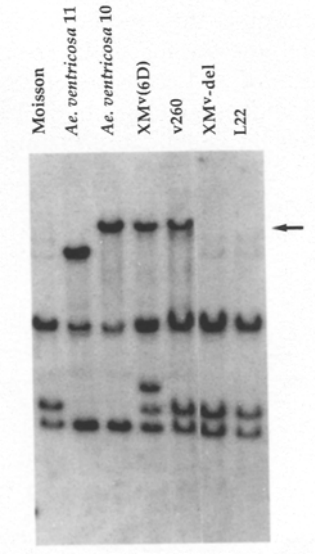

Fig. 5 Hybridisation of the probe PSR666 to *Eco*RV-restricted genomic DNA from 'Moisson', *Ae. ventricosa* 11, *Ae. ventricosa* 10, substitution line XM^v(6D), addition line v260, deleted addition line XM^v-del and translocation line L22. The *arrow* indicates the *Ae. ventricosa* M^v fragments

Nine additional probes which are able to detect loci on wheat 2S were then tested (Table 1), and all of these detected unique fragments in *Ae. ventricosa*. Three loci, *Xpsr107-M*^{v}, *135-M*^{v} and *912-M*^{v}, which define a proximal segment of the 2S wheat map, were not present in v260. Also, PSR928, which detects a distally located 2S locus, did not detect the *Ae. ventricosa* fragments in v260. The remaining 5 clones detect *Ae. ventricosa* fragments (Table 1). It was concluded that XM^v carries a distally located fragment of 2S bounded by the markers *Xpsr131-2M*^{v} and *933-2M*^{v}, XM^v-del contains no 2S markers and L22 carries only *Xpsr150-2M*^{v} (Fig. 4) and *933-2M*^{v}, which defines a genetically short distal 2S fragment, and lacks the corresponding fragments for wheat chromosome 2A. Like v260, L22 does not carry an *Ae. ventricosa* fragment hybridising to PSR928. However, L22 also lacks the corresponding *Xpsr928-2A* fragment.

These observations led to the conclusion that chromosome XM^v is translocated relative to wheat, and consists of a fragment of 2S attached to a larger segment with homoeology to wheat group 6. The 2S segment consists of a section of chromosome with homoeology to the end of wheat 2S but lacking the next terminal region, that identified by PSR928. The shortened form of XM^v, present in the deleted addition line, has lost that portion of XM^v that exactly, within the limits of resolution provided by the DNA probes available, corresponds to the 2S fragment. Finally, the origin of the translocation in L22 is consistent with a homoeologous recombination event between chromosome XM^v and chromosome 2A in the short distal region of 2S bounded by *Xpsr150* and *Xpsr666*.

Confirmation of the 2S location of *Lr* by segregation

DNA from homozygous resistant individuals from 7 non-segregating and 6 segregating F_3 families, along with 1 susceptible individual from a segregating F_3 family were probed with PSR150 (Fig. 4). This analysis showed that all 12 resistant plants carried *Xpsr150-2M*^{v}, which was absent in the susceptible plant. Of the 6 individuals from the segregating families 5 carried *Xpsr150-2A*, while all 7 homozygous resistant individuals carried only *Xpsr150-2M*^{v}.

The identity of the *Ae. ventricosa* progenitor of stocks carrying chromosome XM^v

The RFLP profile of *Eco*RV digests of XM^v(6D) and v260 probed with PSR666 shows the presence of an *Ae. ventri-*

cosa fragment (Fig. 5). However, this fragment is clearly not part of the profile of *Ae. ventricosa* 11, the supposed parent of v260, but rather is part of the profile of *Ae. ventricosa* 10. This suggests that the latter accession, and not the former, was the *Ae. ventricosa* parent used in the cross with *T. aethiopicum*, which was the progenitor of the addition lines. A similar conclusion was drawn by Gale et al. (1984) from comparisons of the α-amylase profiles of derivatives of VPM1, which was supposedly derived from the cross (*Ae. ventricosa* 11×*T. persicum*)×*T. aestivum* (Maia 1967). PSR150-generated profiles (Fig. 4) also show this pattern, but in addition, they reveal that, in L22, the *Ae. ventricosa* 10 fragment replaces one fragment in 'Moisson', which corresponds to one located on chromosome 2A of cv 'Chinese Spring'.

Discussion

Comparative studies of gene location within the Triticeae have in general shown that there is a high degree of homoeology between these related genomes within the tribe. However, the availability of plentiful genetic markers provided by RFLP technology has begun to reveal that complete colinearity has been frequently disrupted by evolutionary intragenomic translocation events. Within wheat itself, major rearrangements have been shown to have occurred between certain chromosomes (Naranjo et al. 1987; Naranjo 1990; Naranjo and Fernandez-Rueda 1991; Liu et al. 1992; Devos et al. 1993b), and more dramatically, most of the chromosomes of rye have been shown to have been rearranged with respect to the standard wheat genome (Devos et al. 1993a). The initial expectation was that chromosome XM^v would prove to be fully homoeologous with wheat homoeologous group 6, since XM^v compensates well phenotypically for chromosome 6D. However, the RFLP analysis shows conclusively that chromosome XM^v carries a segment with homoeology to the distal short arm region of wheat group 2 chromosomes and has lost a segment corresponding to the distal part of the short arm of group 6. It is of interest that the deleted addition line has lost all of the group 2 but none of the group 6 markers. Thus, chromosome XM^v-del may have spontaneously broken at the same 2/6 breakpoint, which may therefore represent a fragile site.

Two possible models for the structure of chromosome XM^v in the addition line v260 are proposed (Fig. 6). In the first, the 2/6 breakpoint is present on the short arm of 6, generating a translocation of the form 2S-6S.6L (terminology of Koebner and Miller 1986), while the second requires both a translocation and a deletion event to give 2S-6L.6S(del). To be consistent with observations of the chromosome morphologies of XM^v in v260 and of XM^v-del, the former model requires that the physically longer arm of XM^v consists of 2S-6S, while the shorter arm has homoeology to 6L. In the latter model, the longer arm carries the genetic information of 6L. As no loss of 6L mark-

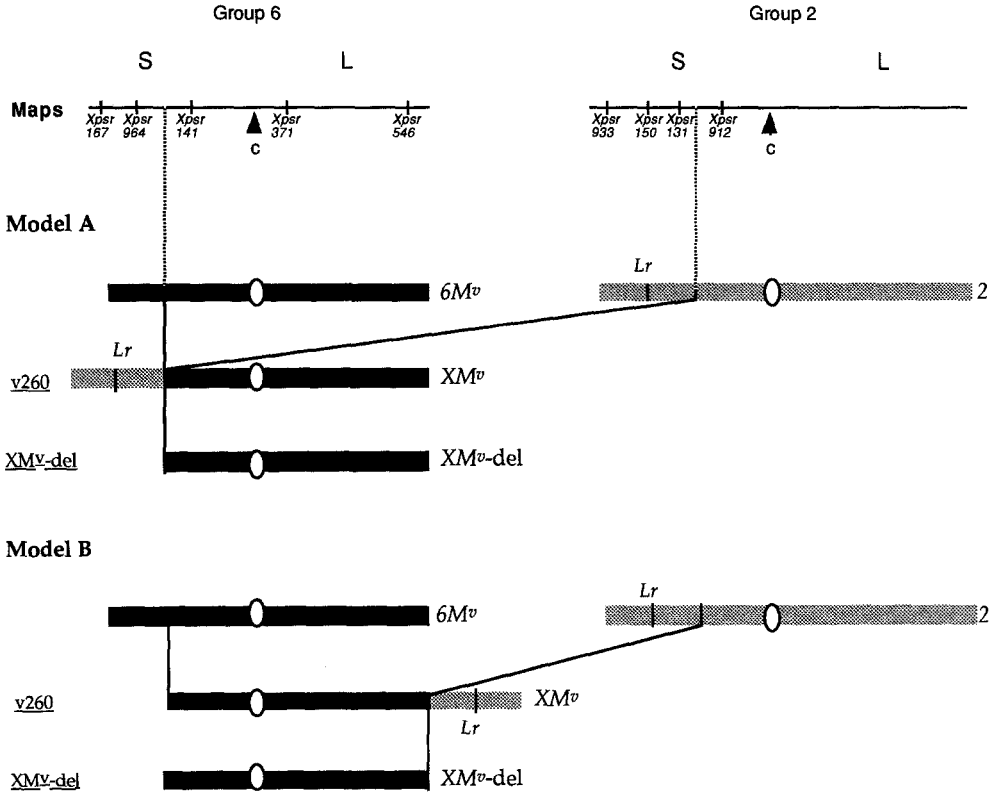

Fig. 6 Two possible models for the structure of chromosomes XM^v and XM^v-del when present in the addition line v260 and in the deleted addition line XM^v-del

ers was observed and as the former model requires only one event rather than two for the latter (translocation and deletion), the more probable hypothesis is that chromosome XM^v has the structure 2S-6S.6L.

An interesting issue is whether the 2/6 translocation in chromosome XM^v pre-existed in *Ae. ventricosa*, or whether it was induced de novo during the production of the addition lines. To distinguish between these two possible origins would require mapping within *Ae. ventricosa* to demonstrate whether or not *Xpsr131-M^v* and *912-M^v* are linked. Both possibilities have precedents in wheat-alien cytogenetics. Pre-existing rearrangements have been demonstrated between the genomes of wheat and rye, as alluded to above, and de novo translocations have been observed both among the addition line chromosomes of *Thinopyrum elongatum* (syn. *Agropyron elongatum*), as shown by isozyme analyses (Hart and Tuleen 1983), and in progeny of wheat×triticale crosses, as shown by C-banding (Lukaszewski and Gustafson 1983). An intriguing coincidence is that the distal portion of wheat chromosome 2BS has been translocated to the distal end of 6BS (Devos et al. 1993b); however, the breakpoint in this case is between *Xpsr150-2B* and *933-2B*, and is therefore not identical to the more proximal breakpoint in *XM^v* (between *Xpsr131-M^v* and *912-M^v*).

The translocation in L22 has occurred between chromosomes XM^v and 2A, and appears to be a homoeologous recombinant of the form 2AL.2AS-2M^{v}S, where the M^v segment includes the loci *Xpsr150-2M^v* and *933-2Mv*. By extrapolation from the wheat map (Devos et al. 1993b), the expectation is that the XM^v fragment carrying the *Lr* gene is genetically short. It is of interest that the breeder's line VPM1, which also had as a parent *Ae. ventricosa* 10, has recently been shown to carry *Lr37* located distally on chromosome *2AS*. This gene is likely to have originated from *Ae. ventricosa* rather than from the other parents in the pedigree of VPM1, since it is closely linked to genes for resistance to two other rust pathogens (Bariana and McIntosh 1993). Such clusters of genes for resistance can remain unbroken when recombination is suppressed, as occurs within an introgressed segment of non-wheat origin. If the *Lr* gene present in XM^v derivatives is identical to *Lr37*, then the 2A/XM^v recombination has occurred twice, although not necessarily in the same place in independent pedigrees. Nonetheless, since the frequency of recombination between homoeologous chromosome segments from the M^v and A genomes will remain limited, both *Xpsr150* and *Xpsr933* should serve as almost completely linked markers for *Lr* in future breeding experiments.

The lack of an M^v fragment with homology to PSR928 in chromosome XM^v or any of its derivatives indicates that the distal end of the segment with homoeology to 2S is located elsewhere in M^v genome. The current map of this region on chromosome 2A is consistent with *Xpsr928* being located distal to *Xpsr933* (KM Devos, personal communication), and there are precedents for this segment being predisposed to translocation in both the B (Devos et al. 1993b) and the R genomes (Devos et al. 1993a).

Although the exchange of homoeologous segments, at least via recombination, is generally inhibited in a normal wheat background by the presence of *Ph1* and other genes that suppress allosyndesis, nevertheless exchanges similar to the one in L22, which involve less than a complete chromosome arm, have been observed (Miller et al. 1988; King et al. 1991). Furthermore, RFLP analysis has shown that introgressed alien segments do recombine with their wheat homoeologues with a low, but detectable frequency (unpublished data). Such recombinants are thought to have occurred as a result of rare allosyndetic events, and will only be recovered when an easily selectable trait, such as disease resistance, has been transferred.

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