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ORIGINAL PAPER

Analysis of introgression of *Aegilops ventricosa* Tausch. genetic material in a common wheat background using C-banding

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Abstract Seven *Triticum aestivum* (cv. Moisson)–*Aegilops ventricosa* addition lines and four VPM-1 lines were studied by C-banding, and compared with the parental common wheat cultivars Marne-Desprez (hereafter Marne), Moisson, and *A. ventricosa* lines 10 and 11. All of the VPM-1 lines had similar C-banding patterns and carried the same major 5B:7B translocation as the parental Marne cultivar. According to the C-banding analysis, the VPM-1 lines carry a complete 7D(7D^{v}) chromosome substitution and a translocation involving the 5D and 5D^{v} chromosomes. However, the translocation of the 2N^{v}/6N^{v} chromosome of *A. ventricosa* to the short arm of the 2A chromosome of wheat that had been identified in an earlier study using molecular analysis (Bonhomme A, Gale MD, Koebner RMD, Nicolas P, Jahier J, Bernard M in Theor Appl Genet 90:1042–1048, 1995; Jahier J, Abelard P, Tanguy AM, Dedryver F, Rivoal R, Khatkar S, Bariana HS Plant Breed 120:125–128, 2001) was not detected in our study. However, the appearance of a small pAs1 site at the tip of the chromosome 2A short arm in VPM-1 could be indicative of a minor translocation of the *A. ventricosa* chromosome. The 5B:7B translocation was also found in all seven *T. aestivum–A. ventricosa* addition lines, although it was not present in the parental common wheat cultivar Moisson. These lines showed different introgression patterns; besides the addition of the five N^{v}-genome chromosomes, they also possessed different D(D^{v}) genome substitutions or translocations. A whole arm translocation between chromosome 1N^{v} and 3D^{v} was identified in lines v86 and v137, and also in the *A. ventricosa* line 10. This observation lends further support to the idea that *A. ventricosa* line 10, rather than line 11, was used to develop a set of wheat *A. ventricosa* addition lines.

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Introduction

The gene pool of the *Aegilops* genus can be used in wheat breeding as a source of agronomically important genes, primarily those involved in pathogen resistance and tolerance to unfavorable environmental factors (Gill et al. 1985; Kimber and Feldman 1987; van Slageren 1994). A number of useful genes from various *Aegilops* species have already been introduced into the common wheat background (Maia 1967; Friebe et al. 1996; McIntosh et al. 1998; Schneider et al. 2008). Alien genes can be transferred into cultivated wheat by developing addition or substitution lines and by inducing intergenomic translocations. However, successful manipulation of genetic material requires a comprehensive understanding of the genetic structure of the species that is being manipulated.

Aegilops ventricosa Tausch. is a tetraploid species with the genome constitution D^{v}D^{v}N^{v}N^{v}. It carries many valuable genes, such as resistance to eyespot (Dosba and Doussinault 1981; Gale et al. 1984; Kimber and Feldman 1987; Huguet-Robert et al. 2001; Jahier et al. 2001), cereal cyst nematode (Jahier et al. 1996; Seah et al. 2000; Jahier et al.

2001), Hessian fly (Delibes et al. 1997; El Khlifi et al. 2003), and leaf, yellow and stem rust (Bariana and McIntosh 1994; Bonhomme et al. 1995; Tanguy et al. 2005).

A line denoted as 'VPM1' was produced by Nicole Maìa and René Ecochard (Maia 1967) as a result of a complex cross between *A. ventricosa, T. persicum,* and *T. aestivum* cv. Marne in order to transfer resistance genes from *A. ventricosa* to bread wheat. These genes are still effective in European, Australian, and North American wheat varieties (Bariana and McIntosh 1994; Delibes et al. 1997; McIntosh et al. 1998; Bartos et al. 2004). Mapping of the rust resistance genes *Yr17, Lr37,* and *Sr38* using molecular markers revealed the presence of a small translocation between the *A. ventricosa* chromosome $2N^v$ and chromosome 2AS of bread wheat (Bariana and McIntosh 1994; Bonhomme et al. 1995). Gale et al. used an alpha-amylase isozyme marker to map the VPM-1 line, and suggested that VPM-1 may also possess a large segment of chromosome 7D from *A. ventricosa* (Gale et al. 1984).

A set of N^v chromosome addition lines was developed by Dosba et al. (1978, 1980) by crossing *A. ventricosa* line 11 and *T aestivum* cv. Moisson, as described in Dosba and Doussinault (1981) and Dosba (1982). Among these lines, disomic additions of $2N^v$, $4N^v$, $5N^v$, and $6N^v$ and other unknown chromosomes were identified with biochemical and molecular markers (Bourgeois et al. 1978; Dosba et al. 1978; Delibes et al. 1981; Tanguy et al. 2005). Besides the N^v-chromosome additions, these lines may also carry other putative substitutions or translocations, but these genetic changes could not be determined due to the limited number of markers used in these studies (Delibes et al. 1981).

The aim of this study was to investigate the VPM-1 and wheat–*A. ventricosa* addition lines and their parental forms using conventional C-banding and fluorescence in situ hybridization (FISH) in order to determine their karyotype structures.

Materials and methods

Four VPM-1 lines (*A. ventricosa*/*T. persicum*//*T. aestivum* cv. Marne[3]): VPM-C1-1-2-4K6-3-6-3-3 (line 7480), VPM-C1-1-3-5R5-2-1-3-1 (line 7483), VPM-1-1-1-2-R4 (line 7492), VPM-1-1-35 (line 7496), seven *T. aestivum–A. ventricosa* addition lines : v86, m97, v137, v172, v208, v260, v278, and their parental wheat cultivars Marne and Moisson, *T. persicum* and *A. ventricosa* were examined. The addition lines were produced on either *Aegilops* cytoplasm [(*A. ventricosa* line 11 × *T. aethiopicum* A1) × *T. aestivum* cv. Moisson] − [v-type], or wheat cytoplasm [(*T. aestivum* cv. Moisson × *A. ventricosa* line 11) × *T. aestivum* cv. Moisson) − [m-type] Dosba et al. (1978, 1980). Since previous analysis of line v260 using molecular markers suggested that *A. ventricosa* line 10 rather than line 11 was used to produce the addition lines (Bonhomme et al. 1995), both lines 10 and 11 were included in our study. The seeds of *A. ventricosa* lines 10 and 11 and the *T. aestivum* × *A. ventricosa* addition set were kindly provided by Dr J. Jahier (INRA-Rennes, France).

A standard C-banding method was used to analyze the cultivars (Badaeva et al. 1994). The slides were analyzed on a Leitz Wetzlar microscope, and the selected metaphase spreads were captured using a Leica DFC 280 (Digital FireWire Color Camera System for Analysis and Documentation) digital camera. The images were processed using Adobe Photoshop software, version 7.0. Wheat chromosomes were classified according to standard genetic nomenclature (Badaeva et al. 1990; Gill et al. 1991), and *A. ventricosa* chromosomes were classified according to (Badaeva et al. 2002).

Two DNA probes, the B-genome specific pSc119.2 and the D-genome specific pAs1, were used. The pSc119.2 probe is a 120-bp sequence isolated from rye *Secale cereale* (Bedbrook et al. 1980) and subcloned by McIntyre (McIntyre et al. 1990). The pAs1 clone is a 1-kb sequence from *A. squarrosa* (Rayburn and Gill 1986) inserted into the pUC8 plasmid. The probes were labeled with biotin or digoxigenin by nick-translation according to manufacturer's protocols (Roche, Germany). FISH was carried out as described in Salina et al. 2006. The slides were examined on a Zeiss Axiom II Imaging microscope (Carl Zeiss, Oberkochen, Germany). Images were processed using Adobe Photoshop software. The wheat and *A. ventricosa* chromosomes were identified on the basis of their labeling patterns and classified according to (Bardsley et al. 1999; Badaeva et al. 2002; Schneider et al. 2003).

Results and discussion

C-banding analysis revealed that the four VPM-1 lines carried major translocations between the 5B and 7B chromosomes, and these results were in agreement with earlier observations (Bourgeois et al. 1978). The same translocation was detected in many wheat cultivars from Europe and Asia and was designated T5B:7B-1 in order to distinguish it from another major translocation between similar chromosomes found in *T. dicoccoides* (Badaeva et al. 2007).

According to the C-banding analysis, chromosome 7D in all four VPM-1 lines was substituted by chromosome $7D^v$ of *A. ventricosa*. The presence of a large fragment of the *A. ventricosa* chromosome $7D^v$ was previously predicted based on the observation that there was independent segregation of the eyespot resistance gene and α-amylase marker allele in the F_3 families resulting from a cross between VPM-1 and a line lacking eyespot resistance (Gale et al. 1984). Chromosome

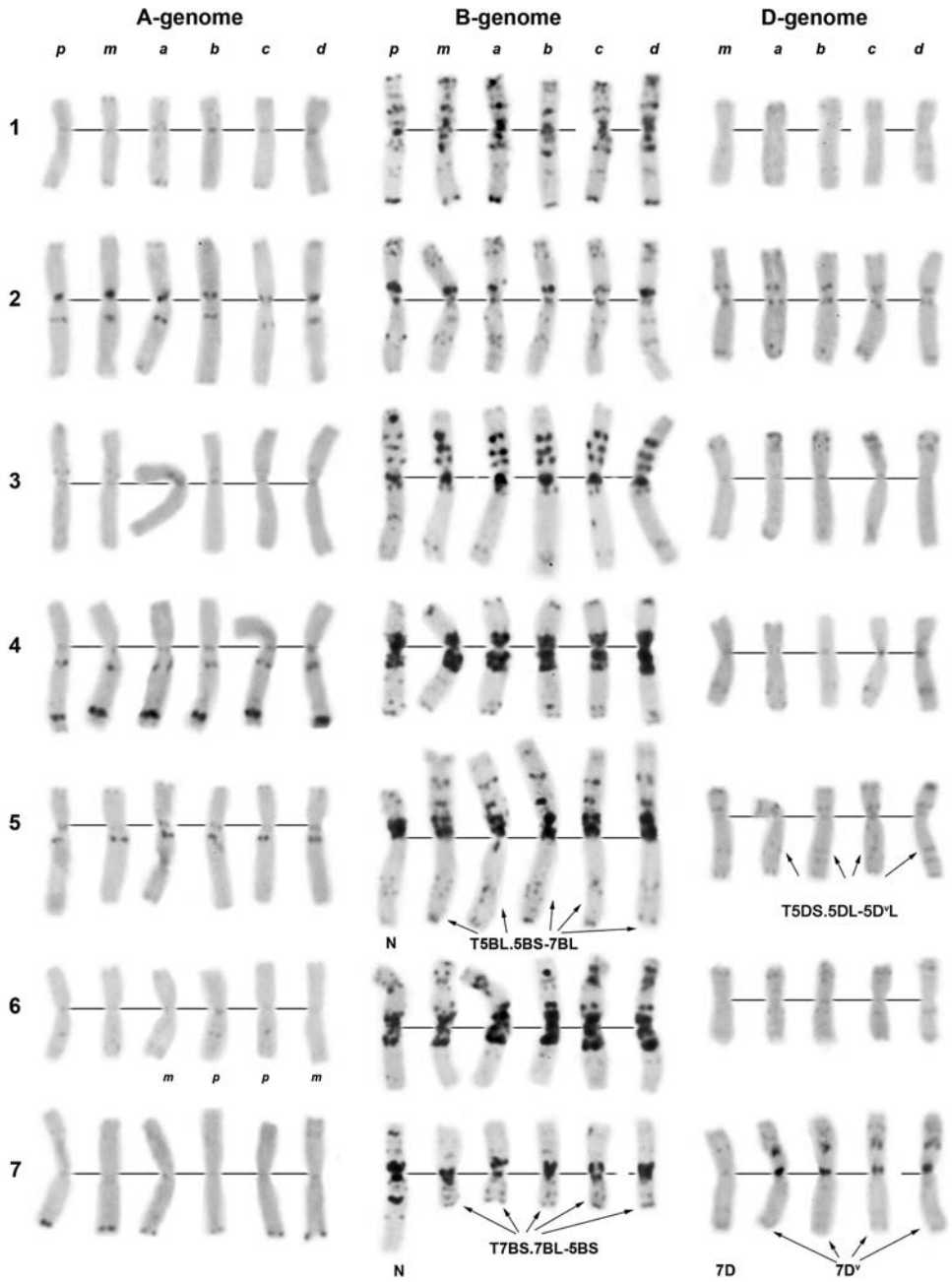

Fig. 1 Comparison of C-banding patterns in different VPM-1 lines: *p T. persicum*, k-19726; *m* Marne, *a–d* VPM-1: *a* 7480, *b* 7492, *c* 7483, *d* 7496

5D in the VPM-1 lines had two distinct interstitial C-bands in the middle of the long arm (Fig. 1, indicated with arrows). This banding pattern is characteristic of the long arm of chromosome 5D^{v} of *A. ventricosa* (Bardsley et al. 1999; Badaeva et al. 2002), and we suggested that VPM-1 could carry an additional major translocation between the long arms of chromosomes 5D and 5D^{v}. Chromosome 2A in the four VPM-1 lines was not different from the normal in the arm ratio or C-banding patterns.

Comparison of the karyotypes of the VPM-1 lines 7480, 7483, 7492, and 7496 with the parental wheat cultivar Marne (Fig. 1*m*) revealed similarities in their C-banding patterns (Fig. 1*m, a–d*), except for chromosomes 1A and 6A, which were polymorphic. Only one small C-band was observed in the distal part of the long arm of chromosome 6A (lines 7480 and 7496, Fig. 1*a,d*), as in Marne. Chromosome 6A in lines 7483 and 7492 had a clear C-band in the middle, and a small C-band in the distal region of the long arm (Fig. 1*b,c*). Two distinct telomeric C-bands were observed in the Marne chromosome 1A, and they were either absent (7492) or significantly smaller in the VPM group. Chromosome 6B in all of the VPM-1 lines was similar to the Marne chromosome 6B; however, they lack a large terminal C-band in the satellite in the VPM-1 lines.

In order to find out whether these differences are associated with the loss of heterochromomatin in the Marne

chromosomes, or whether the differences were inherited from the second parent, we compared VPM-1 with *T. persicum.* Unfortunately, the original line was not available for analysis and we used another accession of this species. This is justified because *T. persicum* is characterized by low levels of C-banding polymorphisms (E.D. Badaeva, unpublished). Similarly to VPM-1, the chromosome 1A of *T. persicum* had no telomeric C-bands, and the terminal C-band was also absent in the satellite of chromosome 6B (Fig. 1*p*). Moreover, the C-banding pattern of chromosome 6A in lines 7492 and 7496 was almost identical to the chromosome 6A of *T. persicum*. These observations indicate that VPM-1 may combine genetic material from all three parental species.

In the next step of the analysis, we compared VPM-1 with normal wheat and *A. ventricosa* using FISH with pSc119.2 and pAs1 probes. The labeling patterns of most VPM-1 chromosomes were similar to those of wheat, except for chromosomes 5D and 7D (Fig. 2). The distribution of the pAs1 probe on chromosome 7D of VPM-1 was more similar to the $7D^v$ chromosome of *A. ventricosa*, than those of wheat. These results are in agreement with the results of the C-banding analysis. Chromosome 5D of VPM-1 carried a prominent pAs1 signal in the distal region of the long arm, as did chromosome $5D^v$ of *A. ventricosa.* However, two smaller pAs1 sites were found proximal to the major pAs1 signal which are absent in *Aegilops* chromosome, but present in chromosome 5D of common wheat (Fig. 2). Based on this observation, we concluded that the distal third of the long arm of chromosome 5D of VPM-1 could be translocated from the long arm of the $5D^v$ chromosome.

Analysis of chromosome 2A in VPM-1 produced more controversial results. It has previously been argued that this chromosome contains a fragment of the *A. ventricosa* chromosome $2N^v$ that carries multiple resistance genes, *Yr17, Lr37,* and *Sr38* (Bariana and McIntosh 1994; Tanguy et al. 2005). Although the segment carried resistance genes and possessed markers characteristic of chromosome 2, it was physically attached to the *A. ventricosa* chromosome $6N^v$, therefore this chromosome was designated $2N^v/6N^v$ (Bonhomme et al. 1995; Tanguy et al. 2005).

The chromosome 2A of some common wheat varieties had a small pSc119.2 site at the telomere of the long arm, which was similar to VPM-1. However, in VPM-1, we also found a small pAs1 site at the telomere of the short arm, which is normally absent (Schneider et al. 2003) (Fig. 2). The terminal part of the long arm of the *A. ventricosa* chromosome $2N^v/6N^v$ is heavily labeled with the pAs1 probe (Bardsley et al. 1999; Badaeva et al. 2002), therefore the appearance of an unusual pAs1 site in the short arm of chromosome 2A of VPM-1 could be indicative of a minor $2A/2N^v/6N^v$ translocation.

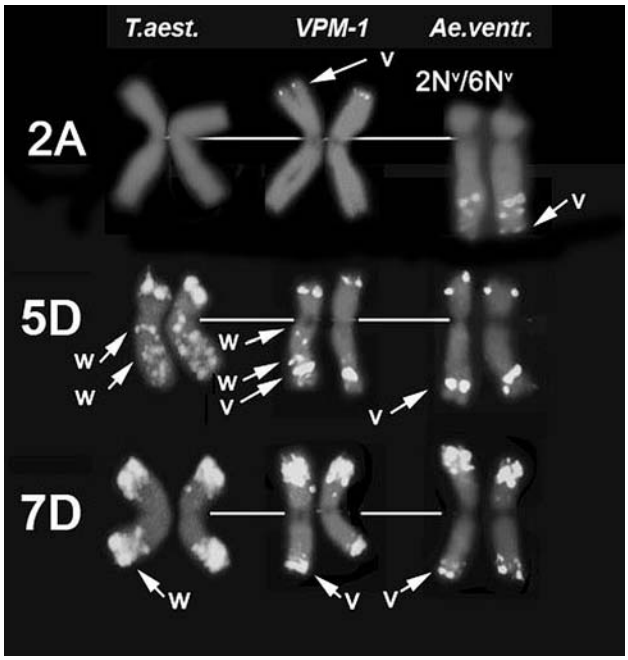

Fig. 2 The pAs1 labeling patterns of chromosomes 2A, 5D, and 7D of VPM-1 (in the *middle*) in comparison with cv. Renan (*T. aestivum*, *left*) and *A. ventricosa* line 11 (*right*). Sites specific for wheat are designated *w,* and *v* for *Aegilops*

Seven wheat–*A. ventricosa* addition lines with either wheat—m97, or *A. ventricosa* cytoplasm—v86, v137, v172, v208, v260, and v278, were analyzed using C-banding. All lines had 44 chromosomes, were similar with respect to their C-banding patterns, and carried the same major T5B:7B translocation (Fig. 3) as the VPM-1 lines. Pericentric inversion of chromosome 5A was found in lines v137 and v260 (Fig. 3*a,e*). All lines except v208 carried additional substitutions or translocations between the D and D^v chromosomes (Fig. 4).

The presence of the T5B:7B translocation in the wheat–*A. ventricosa* set is consistent with the results of Dosba (1980), who identified two translocations, T5B:7B and T1B:6B, in one of the addition lines (v255). At the same time, the parental Moisson cultivar had a normal karyotype (Fig. 5). It may be assumed that this translocation could have been inherited from the *T. aethiopicum* that was used as the bridge species in some crosses (Dosba 1982). However, other studies did not identify this translocation (Belay and Merker 1999; Kawahara and Taketa 2000). Translocation between the 5B and 7B chromosomes could have occurred de novo in the course of hybridization of these species. However, distinct differences between the C-banding patterns of chromosomes 2B, 4B, and 3B in Moisson and the *T. aestivum* × *A. ventricosa* addition lines led us to conclude that a wheat cultivar other than Moisson was used in the crosses.

Five different disomic additions of the N^v-genome chromosome were found in the materials studied. The line v172

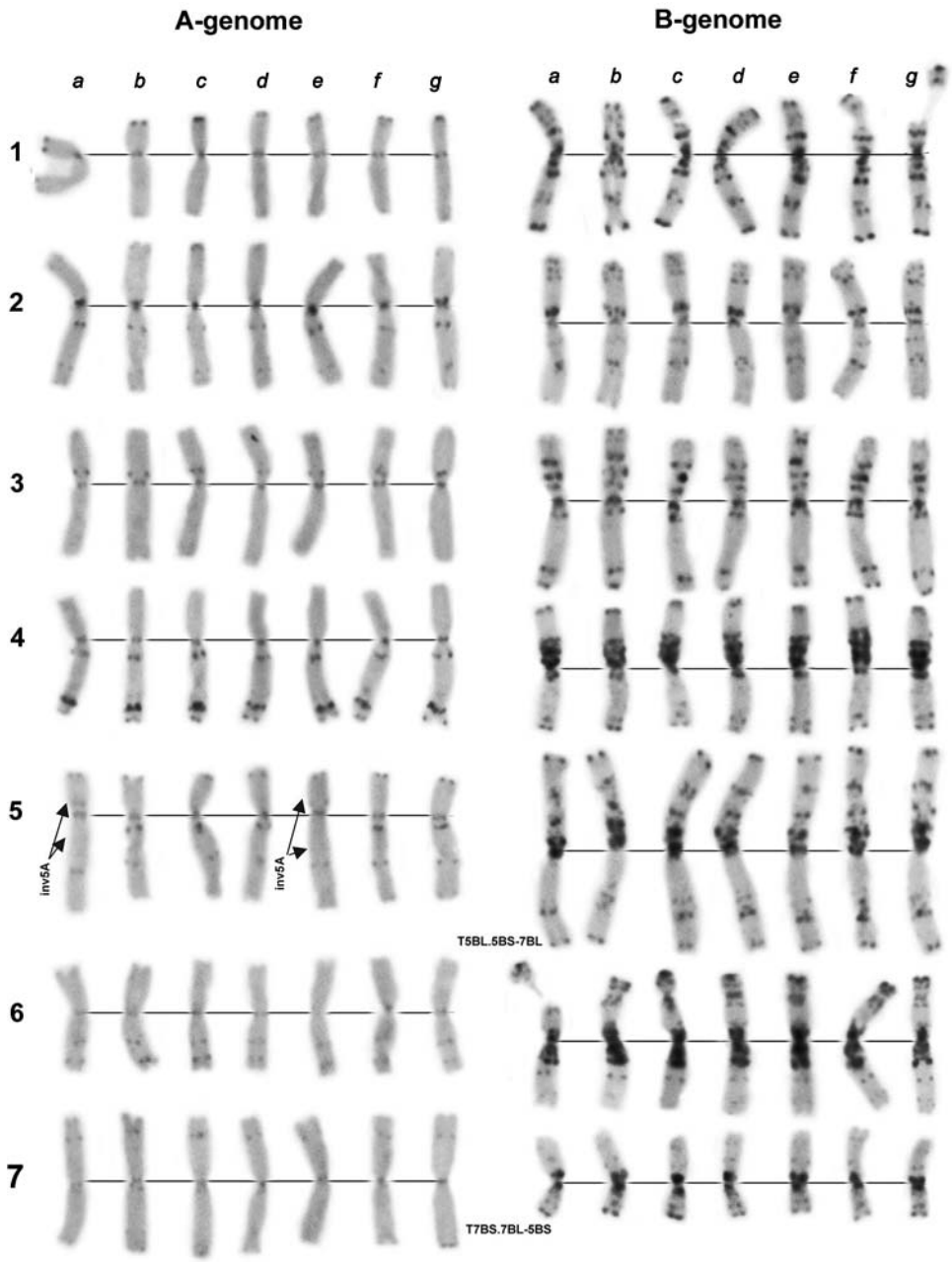

Fig. 3 Comparison of A and B-genome chromosomes in wheat–*A. ventricosa* addition lines: *a* v137, *b* v86, *c* v278, *d* v208, *e* v260, *f* m97, *g* v172. *1–7* homoeologous groups

had the 7N^v chromosome addition. C-banding analysis confirmed the presence of the *A. ventricosa* chromosome, which was earlier designated 2N^v (Badaeva et al. 2002). Therefore, our current results allowed us to correctly classify this chromosome. The line v172 also carried a 1D(1D^v) substitution (Fig. 4*f*).

The genome constitution of line v260 was studied in detail using molecular markers, and the added chromosome was classified as 6N^v (Bonhomme et al. 1995; Tanguy et al. 2005). The same chromosome was also present in m97. However, these lines differed in their introgression patterns of the D^v-genome chromosomes. A complete 4D(4D^v) substitution was found in m97 (Fig. 4*f*), while in v260, we revealed a 2D(2D^v) substitution and 5D-5D^v and 6D-6D^v translocations (Fig. 4*e*). It is noteworthy that according to previous molecular analyses (Bonhomme et al. 1995; Tanguy et al. 2005), chromosome 6N^v of line v260 carries a segment of 2N^v and was designated 2N^v/6N^v. However, it was not known whether this translocation occurred de novo in the course of wheat-*Aegilops* hybridization, or whether it was already present in *A. ventricosa.* Chromosome 6N^v of *A. ventricosa* was almost identical to the 6N^v chromosome of the addition lines in terms of its morphology and C-band distribution (Fig. 4). This finding favors the hypothesis that

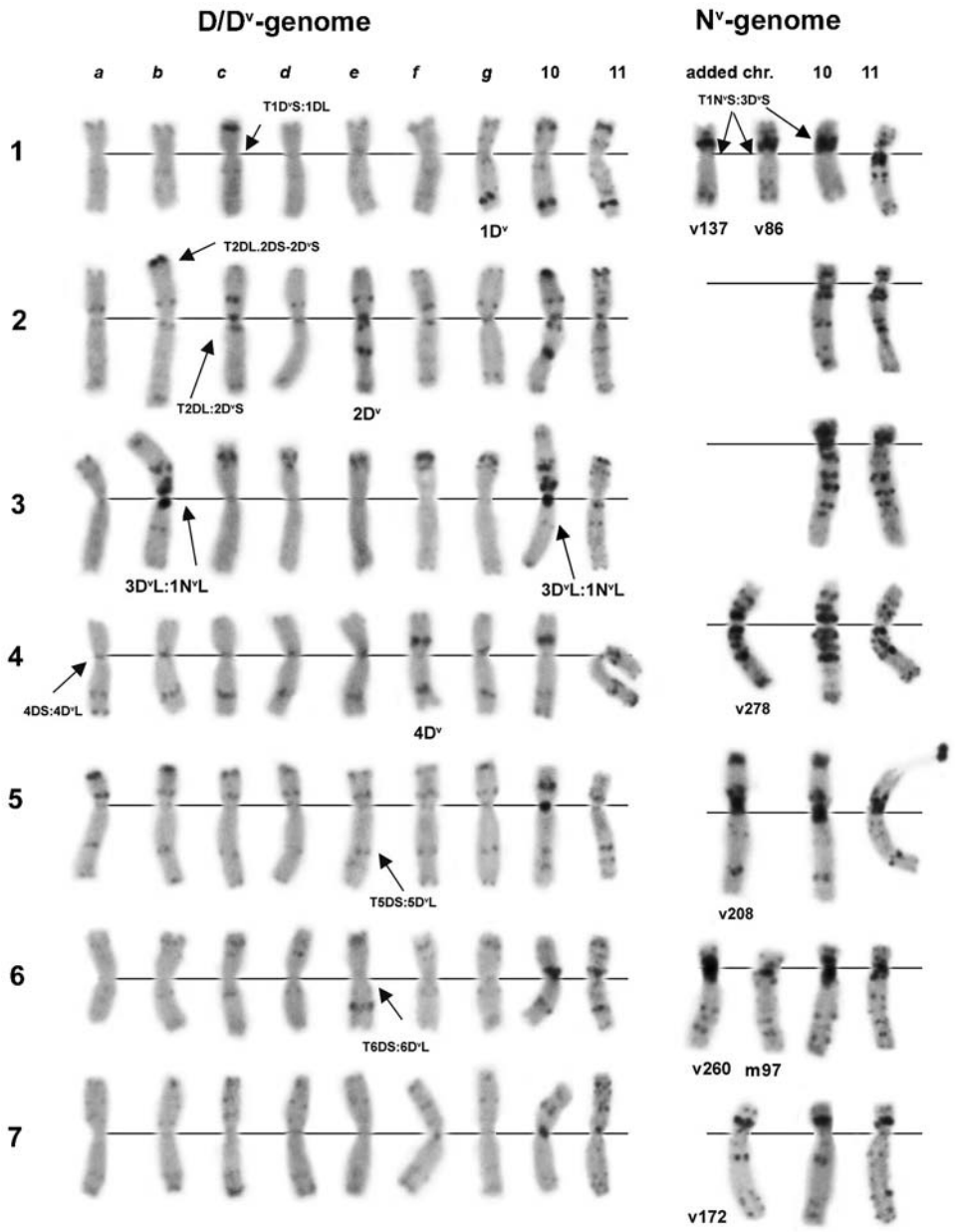

Fig. 4 Comparison of D and N^v-genome chromosomes in wheat–*A. ventricosa* addition set: *a* v137, *b* v86, *c* v278, *d* v208, *e* v260, *f* m97, *g* v172, 10 and 11 are *A. ventricosa* lines 10 and 11. *1–7* Homoeologous groups. Translocations between the D and D^v genome chromosomes are indicated with *arrows*

the translocation between 2N and 6N chromosomes was already present in *A. ventricosa*, or even in the *A. uniaristata* genome (Iqbal et al. 2000).

The v208 line carried a disomic addition of the $5N^v$ chromosome, which was previously assigned to the homoeologous group 5 based on the relative positions of the 18S–26S and 5S rDNA loci (Bardsley et al. 1999; Badaeva et al. 2002). The added chromosome was the same as in *A. ventricosa*, indicating that no changes have occurred during the production of the addition lines. In contrast to other wheat–*A. ventricosa* lines, v208 does not possess any D^v genome substitutions or translocations.

The added N^v-genome chromosome of line v278 was presumably assigned to group 4 on the basis of biochemical analyses. Delibes et al. (1981) detected CM-4 and Aph3 markers in this line, and alkaline phosphatase isozymes are known to be associated with group 4 chromosomes (Salinas et al. 1981). Our results confirmed that the added chromosome belongs to homoeologous group 4 because it is similar to chromosome $4N^v$ of *A. ventricosa* and the 4N chromosome of *A. uniaristata* in terms of its morphology, the amount and distribution of heterochromatin (Fig. 4), and the pAs1 labeling patterns (Bardsley et al. 1999; Iqbal et al. 2000; Badaeva et al. 2002). Besides the $4N^v$ addition, line v278 also possessed large translocations involving the 1D-$1D^v$ and 2D-$2D^v$ chromosomes (Fig. 4*c*).

Similar biochemical markers, CM-4 and Aph3, were found in line v137. However, the meiotic behavior of F_1

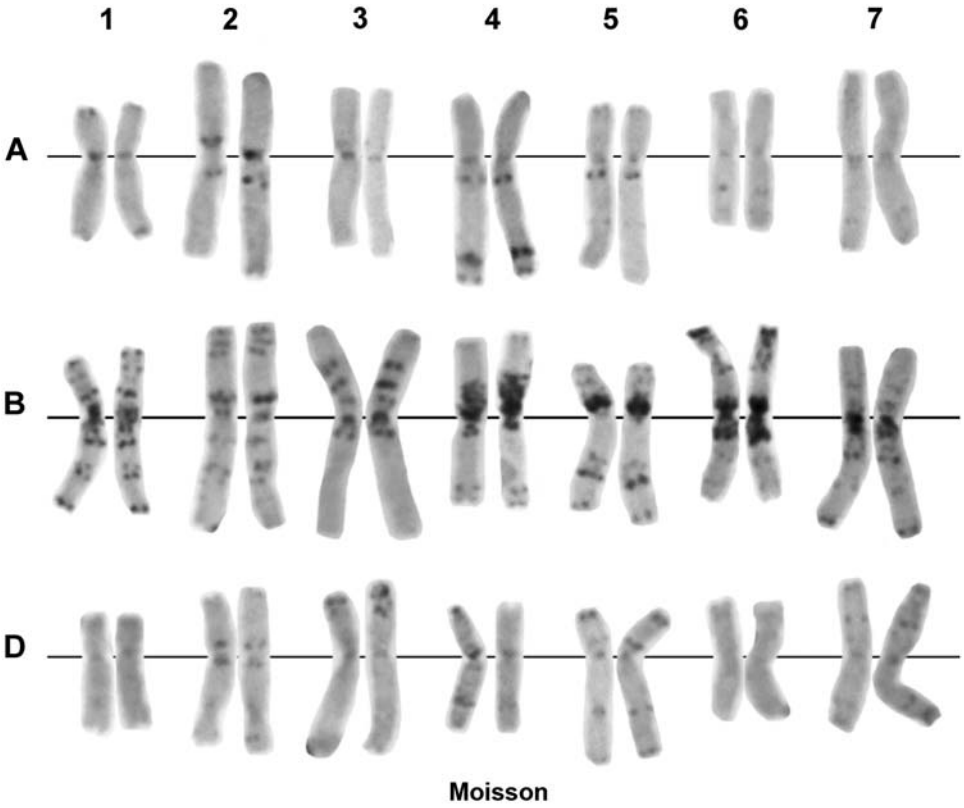

Fig. 5 C-banded karyotype of *T. aestivum* cv. Moisson

hybrids between v137 and other lines with a 4N^{v} addition showed a lack of complete homoeology (Delibes et al. 1981). The authors suggested that these lines may either possess additional chromosome substitutions or translocations, or that the added chromosome has an extensive translocation that does not affect the region carrying the marker. Analysis of v137 using C-banding revealed a T1N^{v}S:3D^{v}S chromosome of *A. ventricosa* and a translocated 4DS:4D^{v}L chromosome (Fig. 4*a*). The latter may probably explain the presence of the CM-4 and Aph marker alleles that are characteristic of the *A. ventricosa* group 4 chromosome, although it belongs to the D^{v} genome.

An added *A. ventricosa* chromosome was modified as a result of the intergenomic T1N^{v}:3D^{v} translocation that is common in this species (Bardsley et al. 1999; Badaeva et al. 2002). This translocation was found in line 10, but was absent in line 11 (Fig. 4). It is unlikely that the 1N:3D translocation occurred de novo during the production of the addition lines, therefore our observation lends further confirmation to the idea that the *A. ventricosa* line 10 rather than line 11 was used as the parent of the wheat–*A. ventricosa* addition set.

A similar T1N^{v}S:3D^{v}S addition was found in line v86. This line also contained a pair of reciprocally rearranged chromosomes, T1N^{v}L:3D^{v}L, which were substituted for the wheat chromosome 3D. This line also carried an additional minor translocation between the short arms of chromosomes 2D and 2D^{v} (Fig. 4*b*).

The results shown above suggest that hybridization of species that share common genomes can induce an extensive exchange of genetic material between closely related chromosomes. According to meiotic analysis, the D-genome of *A. ventricosa* is only slightly modified relative to its diploid progenitor (Kimber and Zhao 1983). The D-genome of common wheat is also very similar to *A. tauschii*. We might expect that wheat–*A. ventricosa* D-genome chromosome pairing could have occurred in the F_1 hybrid plant, giving rise to recombinant D-D^{v} genome chromosomes. Indeed, a high level of pairing was observed in wheat–*A. ventricosa* hybrids (Garcia-Olmedo et al. 1984; Huguet-Robert et al. 2001). In contrast, the N^{v} genome is quite distant from the A- and B-genomes, and they rarely pair at meiosis (Cunado et al. 1986). Therefore, no spontaneous translocations between A/N^{v} or B/N^{v} chromosomes have been recorded in introgression lines. The introgression of the D^{v} genome in wheat–*A. ventricosa* hybrids should be taken into account when interpreting the results of biochemical or molecular analyses, because *Aegilops*-specific markers may be attributed to both the N^{v}-genome chromosome, and the D^{v}-genome chromosome. These results underline the use of complementary markers, such as biochemical, molecular, and cytological markers in the production and characterization of addition and introgression lines, particularly if the parental species share a common genome which interferes with meiotic pairing in hybrids.

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