Theor Appl Genet (1998) 96:780–785

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Structural rearrangement in chromosome 2M of *Aegilops comosa* has prevented the utilization of the Compair and related wheat-*Ae. comosa* translocations in wheat improvement

Received: 23 September 1997 / Accepted: 9 October 1997

Abstract The genetic constitutions of chromosome 2M of *Aegilops comosa* and the derived wheat-*Ae. comosa* translocations were analyzed by molecular cytogenetic techniques. Hybridization of 15 RFLP markers covering the entire length of the group-2 chromosomes revealed that chromosome 2M was structurally rearranged compared to the homoeologous chromosomes of wheat by either a pericentric inversion or a terminal intrachromosomal translocation. The breakpoint of the rearrangement was located in a region between the loci *Xpsr131* and *Xcdo405*, resulting in the translocation of 47% of 2MS to 2ML. This aberrant structure of 2M allowed homoeologous recombination between 2M and its wheat counterpart only in the translocated segment on 2ML. C-banding and genomic in situ hybridization analyses confirmed that all translocation chromosomes consisted of the complete 2MS arm, a large part of 2ML, and very small distal segments derived from 2AS or 2DS, as expected from the aberrant structure of chromosome 2M. Thus, the translocation in the line 2A-2M#4/2 can be described as T2AS-2M#1L·2M#1S and the translocations in the lines Compair and 2D-2M#3/8 as T2DS-2M#1L·2M#1S. RFLP analysis determined the breakpoints in these translocation chromosomes to be within the telomeric 16% of the wheat chromosome arms. The breakpoint of the 2A/2M translocation was between *Xbcd348* and *Xcdo783*, and that of the 2D/2M translocation was between *Xcdo783* and *Xpsr666*. Because the translocation chromosomes retain the structural aberration found in chromosome 2M, further exploitation of the wheat-*Ae. comosa* translocations for cultivar improvement is questionable.

Key words Wheat · *Aegilops comosa* · Translocation · Homoeologous recombination · RFLP · C-banding · Genomic in situ hybridization

Communicated by G. Wenzel

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Introduction

Many attempts have been made to introduce alien genes from related species to hexaploid bread wheat, *Triticum aestivum* L. em Thell. (2n = 6x = 42, genome constitution AABBDD) (for review, McIntosh 1991; Jiang et al. 1994a; Friebe et al. 1996b). There are many examples of successful gene transfer by induced homoeologous pairing in wheat. In successful transfer lines, the major portion of the recombinant (or translocation) chromosome is derived from wheat and a part of the arm with targeted gene is derived from the alien species (Friebe et al. 1996b). However, if the major portion of the recombinant chromosome is derived from an alien chromosome with a structural aberration, then induced recombination is inefficient in eliminating undesirable traits brought together with the gene of interest.

Riley and co-workers were the first to use induced homoeologous recombination (Riley et al. 1968a, b). They transferred genes conferring resistance to stripe rust (*Yr8*) caused by *Puccinia striiformis* f. sp. *tritici* Westend and to stem rust (*Sr34*) caused by *P. recondita*

from *Aegilops comosa* Sibth. and Smith (2n = 2x = 14, MM) to wheat. The resulting 2D/2M translocation stock was designated as Compair. Twenty years later, Miller et al. (1988) independently isolated spontaneous non-Robertsonian translocations involving chromosomes 2A/2M or 2D/2M. Meiotic pairing analyses suggested that the translocation chromosomes consisted of the complete short arm, centromere, and a large portion of the long arm derived from chromosome 2M, and segments derived from the short arms of either chromosomes 2A or 2D of wheat (Riley et al. 1968a; Miller et al. 1988). In addition, all 2A/2M and 2D/2M translocations involved segment exchanges between the long arm of 2M and the short arms of either 2A or 2D of wheat. These results indicated the presence of a structural rearrangement that suppressed recombination in a major portion of chromosome 2M. In fact, these translocations have not been used intensively in cultivar development (McIntosh et al. 1995).

For many years, we have used chromosome banding and genomic in situ hybridization (GISH) analyses for identifying alien chromatin in wheat (for review, Friebe et al. 1996b). Chromosome banding permits the identification of the chromosomes involved in these translocations (Friebe et al. 1996b), and GISH allows the determination of translocation breakpoints (Friebe et al. 1993; Mukai et al. 1993). In this paper, as was also demonstrated by Hohman et al. (1996), we introduce the application of cytogenetically based physical maps (CBPMs) of wheat (Werner et al. 1992; Gill et al. 1993, 1996a, b; Kota et al. 1993; Hohmann et al. 1994; Delaney et al. 1995a, b; Mickelson-Young et al. 1995) for analyzing the genetic constitutions of translocation chromosomes. A CBPM consists of an ideogram of a C-banded chromosome with deletion breakpoints and the location of molecular markers assigned by deletion analysis. The advantage of employing molecular markers mapped in a CBPM is that the markers not only detect the breakpoints of translocations but also integrate molecular data with cytological maps. By combining molecular cytogenetic and RFLP analyses, we are able to report here the chromosome structure of *Ae. comosa* chromosome 2M and the location of the physical and genetical breakpoints in the derived 2A/2M and 2D/2M translocation chromosomes. We furthermore discuss the problem encountered when homoeologous recombination is applied to an alien chromosome with a structural aberration.

Materials and methods

The lines used in this study and their origin are listed in Table 1. For C-banding analysis the protocol described by Gill et al. (1991) was used. GISH analysis was performed as described by Jiang et al. (1994b). Chromosome images were taken with a Zeiss Axioplan epuifluorocence microscope using a CCD camera (Photometrics) and the IPLab Spectrum Multiprobe software (Signal Analytics Corp.) For restriction fragment length polymorphism (RFLP) analysis, 15 RFLP markers were selected to cover almost the entire physical length of chromosomes belonging to wheat homoeologous group 2. RFLP probes were kindly provided by Drs. M. Gale, Cambridge Laboratory, Norwich, UK (designated as PSR), and M. Sorrells, Cornell University, Ithaca, NY, USA (BCD and CDO). KSU clones are maintained by the Wheat Genetics Resource Center, Kansas State University. All but 1 (PSR934) of the markers were previously mapped in CBPMs (Delaney et al. 1995a, b). The locus *Xpsr934* was allocated to the region between *XksuF15* and *XksuH16* from the linkage analysis by Nelson et al. (1995). Southern hybridization was as described by Delaney et al. (1995a).

Table 1 Plant materials used in the present study

Accession[a]	Wheat cultivar	Description[b]	Source	Reference[c]
Wheat aneuploid				
TA3263	*T. aestivum* cv Chinese Spring	M2A-T2B	WGRC	a
TA3264	*T. aestivum* cv Chinese Spring	M2A-T2D	WGRC	a
TA3265	*T. aestivum* cv Chinese Spring	N2B-T2A	WGRC	a
TA3268	*T. aestivum* cv Chinese Spring	N2D-T2B	WGRC	a
TA3103	*T. aestivum* cv Chinese Spring	Dt2AS	WGRC	b
TA3114	*T. aestivum* cv Chinese Spring	Dt2BL	WGRC	b
TA3123	*T. aestivum* cv Chinese Spring	Dt2DS	WGRC	b
TA3124	*T. aestivum* cv Chinese Spring	Dt2DL	WGRC	b
TA6624	*T. aestivum* cv Chinese Spring	DS2M(2D)	R. A. McIntosh	c
TA7653	*T. aestivum* cv Chinese Spring	DA2M	R. A. McIntosh	c
TA7654	*T. aestivum* cv Chinese Spring	DA2MS	S. Reader	c
Wheat-*Ae. comosa* translocation				
TA2915	*T. aestivum* cv Compair	T2D-2M	R. A. McIntosh	c
TA5552	*T. aestivum* cv Hobbit 'sib'	T2A-2M#4/2	R. A. McIntosh	d
TA5553	*T. aestivum* cv Hobbit 'sib'	T2D-2M#3/8	R. A. McIntosh	d

[a] Accession numbers of the Wheat Genetics Resource Center (WGRC), Kansas State University
[b] Abbreviation of the genetic stocks is according to Raupp et al. (1995)
[c] a, Sears (1954); b, Sears (1966); c, Riley et al. (1966); d, Miller et al. (1988)

Results

C-banding analysis

The *Ae. comosa* chromosome 2M is submetacentric and can be distinguished from all wheat chromosomes by its characteristic arm ratio and C-banding pattern. C-banding analysis confirmed the 2D/2M translocation in the line Compair and revealed that the translocation consists of the complete short arm, most of the long arm with the centromere derived from chromosome 2M, and a distal segment with a telomeric C-band derived from 2DS (Fig. 1). Thus, the translocation chromosome can be described as T2DS-2M#1L·2M#1S (for the guidelines of nomenclature, see Raupp et al. 1995). The C-banding pattern of the translocation chromosome in 2D-2M#3/8 was very similar to that of Compair and also can be described as T2DS-2M#1L·2M#1S. In line 2A-2M#4/2, C-banding analysis identified the translocation chromosome as T2AS-2M#1L·2M#1S, lacking the telomeric C-band of 2ML but with the diagnostic C-band derived from the distal region of 2AS.

GISH analysis

The translocation breakpoint was cytologically determined by hybridizing mitotic metaphase spreads of wheat-*Ae. comosa* translocation lines with genomic DNA of *Ae. comosa* and genomic wheat DNA as a blocker (1 : 30) (Fig. 2). The entire short arm and most of the long arm was labelled except for a tiny unlabelled wheat segment at the tip of the long arm in the Compair translocation. The unlabelled wheat segment was only detected in extended prophase chromosomes. Similar GISH patterns were also observed for the translocation chromosomes in lines 2D-2M#3/8 and 2A-2M#4/2, indicating that the wheat segments in these translocations are very small.

RFLP analysis

All but 1 (KSUH16) probe used in this study detected at least one fragment for each 2A, 2B, 2D, and 2M chromosome, suggesting that overall homoeology between chromosome 2M and wheat homoeologues is conserved. The probe KSUH16 detected homoeoloci on chromosome 2B when a different restriction enzyme was used (Delaney et al. 1995a). Five loci (from *Xbcd348* to *Xpsr131* in Fig. 3) mapped on the short arms of the wheat chromosomes but mapped on the long arm of chromosome 2M of *Ae. comosa*, indicating a structural rearrangement in chromosome 2M, which can be either a pericentric inversion or a terminal intrachromosomal translocation. If the aberration is a pericentric inversion, the size of the long arm segment not involved in the inversion is small (less than 11% of long arm). The detected breakpoint of the structural aberration was between *Xcdo405* and *Xpsr131* located in the fraction length (FL) 0.53–0.75 region on the wheat CBPM (Fig. 3).

The homoeologous recombinations leading to the wheat-*Ae. comosa* translocations apparently occurred

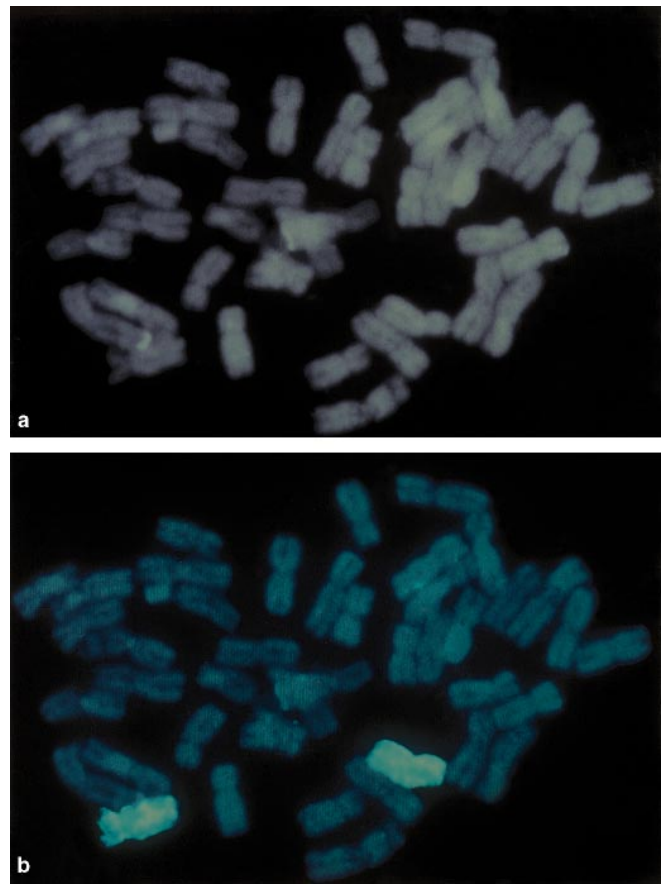

Fig. 2a, b GISH analysis of wheat-*Ae. comosa* translocation in germ plasm Compair using *Ae. comosa* genomic DNA as the probe. **a** Mitotic metaphase chromosomes of Compair stained by DAPI; **b** same cell after GISH, in which the translocation chromosome pair in Compair is completely labelled (similar to complete 2M chromosomes, not shown), indicating that the wheat segment must be tiny and not detected by GISH

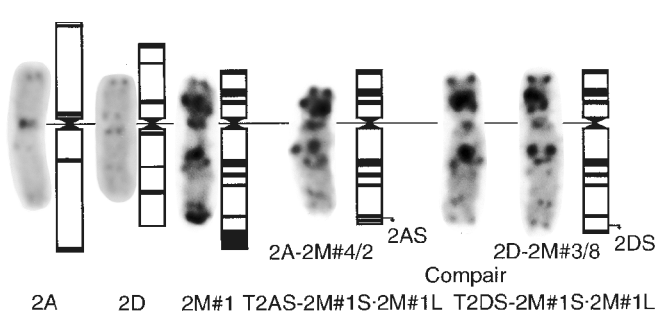

Fig. 1 C-banding patterns and ideograms of the chromosomes involved in the wheat-*Ae. comosa* translocations

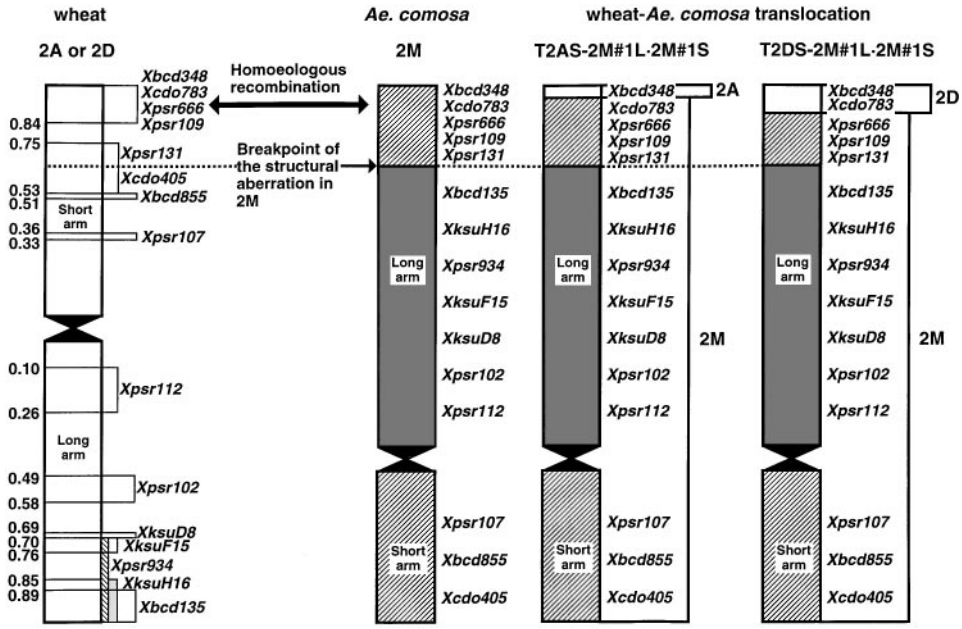

Fig. 3 Physical maps of consensus group-2, 2M, T2AS-2M#1L·2M#1S and T2DS-2M#1L·2M#1S chromosomes. FL values are shown on the *left* on consensus group-2 chromosome. All of the wheat-*Ae. comosa* translocation occurred between the distal 16% of the wheat chromosome arm (2AS or 2DS) and the segment translocated to 2ML

between the 2ML and the short arm of either 2A or 2D of wheat in the small chromosomal region distal to *Xpsr666*, which corresponds to 16% of the group-2 short arm in wheat (Fig. 3). All three translocations retained the entire 2MS arm and most of 2ML. The breakpoint of the translocation in T2AS-2M#1L·2M#1S was between *Xbcd*348 and *Xcdo783*. Two independently isolated 2D/2M translocations (Compair and 2D-2M#3/8) had breakpoints in the same region between *Xcdo783* and *Xpsr666*, which was adjacent and proximal to the breakpoint of T2AS-2M# 1L·2M#1S translocation.

Discussion

The structure of chromosome 2M

RFLP analysis demonstrated that a large segment of 2ML is homoeologous to the group-2 short arms of wheat (Fig. 3), indicating that chromosome 2M is rearranged as a result of either a pericentric inversion or a terminal intrachromosomal translocation. So far, no segment homoeologous to a group-2 long arm has been detected on 2MS. The CBPM of the group-2 wheat chromosome (Delaney et al. 1995a) was used to estimate the size of the chromosome fragment involved in the rearrangement. The detected breakpoint of the aberration was defined by the region between *Xpsr131* and *Xcdo405*, which is in the FL 0.53–0.75 interval on the CBPM (Fig. 3). Thus, at most, 47% of the short arm was translocated to the long arm. Another breakpoint, if any, should be distal to *Xbcd135*, within the telomeric 11% of the group-2 long arm (Fig. 3). The aberration detected in this study explains the submetacentric structure of chromosome 2M (Fig. 1). The ancestral 2M chromosome may have been more metacentric, as is the case for most of wheat chromosomes. During evolution, chromosome 2M experienced a structural rearrangement. As a result, up to 47% of the short arm was transferred to the long arm, and less than 11% of the long arm was transferred to the short arm. Friebe et al. (1996a) reported that chromosomes 2M of *Ae. comosa* subsp. *comosa* and $2M^h$ of *Ae. comosa* subsp. *heldreichii* were submetacentric for all the accessions studied. The rearrangement detected in this study seems at least shared in this species. Some other *Aegilops* species also have a submetacentric to acrocentric group-2 chromosome; 2 U of *Ae. umbellulata* (Friebe et al. 1995) and 2C of *Ae. cylindrica* (Endo 1996). Although their evolutionary relationship remains to be studied, C-banding analysis of metaphase-I chromosomes indicated homology between the long arm of chromosome 2C and the group-2 short arm of wheat (Friebe et al., unpublished).

Because of the rearrangement in chromosome 2M, homoeologous recombination between chromosome 2M and its wheat homoeologue is only possible between the segment translocated to 2ML and the short arm of the wheat group-2 chromosome. Homoeologous recombinations in any other region will lead to a duplication/deficiency of genetic material and will result in genetically unbalanced progeny. Segment exchange only involving the translocated region is expected through homoeologous recombination.

Wheat-*Ae. comosa* translocation

C-banding analysis identified the wheat-*Ae. comosa* translocations as T2AS-2M#1L·2M#1S for the 2A/2M translocation (2A-2D#4/2) and T2DS-2M#1L·2M#1S for the 2D/2M translocations (Compair and 2D-2M#3/8), confirming the results of previous studies based on meiotic pairing analysis (Riley et al. 1968a; Miller et al. 1988). Because these translocations originated from homoeologous recombination, homoeologous pairing between the short arm of wheat (2AS or 2DS) and 2ML occurred. As described above, the long arm of 2M has a chromosome segment that genetically belongs to the short arm of 2M, which allowed homoeologous recombination between 2ML and either 2AS or 2DS. GISH analyses revealed that the wheat segments in all three translocation chromosomes are very small and within the detection limit of the technique. Diagnostic C-bands from chromosome arms 2AS or 2DS were identified in distal regions of the translocated chromosome arms 2AS-2M#1L and 2DS-2M#1L (Fig. 1), and the region including these C-bands lacked a signal in GISH analysis when *Ae. comosa* genomic DNA was used as the probe (Fig. 2). RFLP analysis confirmed these results and tagged the breakpoints with molecular markers. The structure of the wheat-*Ae. comosa* translocation chromosomes are illustrated in Fig. 3. The translocation chromosomes have a small portion of wheat chromatin at the tip of their long arms; the remaining part corresponds to the chromosome 2M that retains the structural rearrangement. This structure hinders further recombination with wheat chromosomes. Even if the translocation chromosome pairs fully with the wheat homoeologue, any recombination in the short arm or in the long arm proximal to the breakpoint of the rearrangement in 2M (between *Xpsr131* and *Xcdo405*) will be genetically unbalanced because of duplication/deficiency. Generally, the target gene of alien transfer by homoeologous recombination should be located in a chromosome region that is not involved in major structural aberrations. Otherwise the gene would be associated with a large amount of alien chromatin, or the recombinant chromosome would be of the non-compensating type. The alternatives for transferring these genes in structural aberrations would be the use of radiation treatment that causes the random breakage of chromosomes (Sears 1993) or genetically induced chromosome breakage by a gametocidal chromosome (Endo et al. 1994). In both cases, stringent selection for the recovery of compensating transfer is required.

The translocation chromosomes in lines Compair and 2D-2M#3/8 had smaller wheat chromatin than the translocation in line 2A-2M#4/2. This is in agreement with Miller et al. (1988) who predicted this result from a pairing study between translocation lines and double ditelosomics of the corresponding wheat chromosome. They reported that the 2D/2M translocation formed a bivalent at a slightly higher rate than the 2A/2M translocation. From the CBPM of group-2 chromosomes, the size of the wheat segment retained on the translocation chromosome is estimated to be less than 16% of the corresponding chromosome arms. Although the wheat segment is small, the translocation chromosomes paired with the wheat chromosome at high frequencies. Riley et al. (1968a) reported that more than 75% of the pollen mother cells showed 21 bivalents in the F_1 between 'Chinese Spring' and Compair. Miller et al. (1988) observed 73–100% pairing between the translocation chromosome and the 2AS or 2DS telosome. These observations confirmed Lukaszewski and co-workers' conclusion that the absence of homology in the distal region of chromosome arms prevents recognition of proximal homologous segments in meiosis and consequently chiasmata pairing (Curtis et al. 1991; Lukaszewski 1997; Friebe et al. unpublished).

RFLP mapping demonstrated that a high level of homoeology in terms of gene synteny was retained among the group-2 chromosomes of wheat (Devos et al. 1993; Nelson et al. 1995). The exception was the distal region of the short arm of chromosome 2B. Although chromosomes 2A and 2D retained synteny towards the end of short arm, the distal region of chromosome arm 2BS lacked homoeoloci. Devos et al. (1993) reported five homoeoloci on 2AS and 2DS but missing on 2BS, indicating a deletion in the telomeric region on 2BS. Furthermore, they found a marker (PSR899) that detected a putative translocation between the 2B and 6B chromosomes and a successive inversion on 2BS. Nelson et al. (1995) obtained a similar result–that the distal region on 2AS did not have homoeoloci on 2BS but homoeoloci were present on 2DS. The identity of the 2BS terminal segment between the durum and wheat parents they used for mapping explained these results. A possible inversion on 2BS was also indicated by Nelson et al. (1995). Our RFLP analysis clearly demonstrated that the structural aberration(s) of chromosome 2B has occurred in the distal 16% of its short arm (Fig. 3) because the loci proximal to *Xpsr666* showed synteny among wheat chromosomes (Devos et al. 1993) and that homoeologous recombination between chromosome 2M and its wheat homoeologue occurred in this distal segment. The structural aberration in chromosome 2B may prevent homoeologous pairing between the 2B and 2M chromosomes, and this may be the reason why Miller et al. (1988) could not isolate a 2B/2M translocation.

Acknowledgements We are grateful to John Raupp and Justin Faris for critical reading of the manuscript. We thank Drs. M. D. Gale, and M. Sorrells for generous sharing of RFLP probes. Contribution numbers 98-98-J from the Kansas Agricultural Experiment Station, Kansas State University, Manhattan, KS 66506-5502, and contribution number 550 from the Laboratory of Plant Genetics, Graduate School of Agriculture, Kyoto University, Japan. One of us (BSG) thanks the DAAD and Prof. R. G. Herrmann, Botanical Institute,

University of Munich, for financial support and local hospitality during his sabbatical leave in Germany, where part of this work was carried out.

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