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Characterization of deletions in common wheat induced by an *Aegilops cylindrica* chromosome: detection of multiple chromosome rearrangements

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Abstract An *Aegilops cylindrica* chromosome induces terminal deletions of chromosomes in wheat as identified by C-banding. We are constructing high-density physical maps of wheat chromosomes and have detected additional chromosome rearrangements. Among 63 lines with chromosomal subarm deletions in group 7 chromosomes, 7 lines (11.1%) were shown to harbor additional chromosome rearrangements. Two other lines were also omitted from the physical mapping because of the nature of the breakpoint calculations. The presence or absence of chromosome-specific restriction fragment length polymorphism (RFLP) or random amplified polymorphic DNA (RAPD) markers indicated that additional interstitial deletions are present in 3 lines (4.8%) with deletions in the short chromosome arms and in 4 lines (6.3%) with deletions in the long chromosome arms. We also used chromosome pairing analysis of F_1 plants of deletion lines with double ditelosomic lines of 'Chinese Spring' wheat to detect small terminal deletions. The deletion of the most distal 1% of chromosome arm 7AL was associated with a pairing reduction of 60%.

Key words High-density physical map · Chromosome pairing · Gametocidal genes · Interstitial deletions · Translocations

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Introduction

Gametocidal genes or chromosomes have been indentified in genus *Aegilops* (Endo 1990), *Ae. speltoides* (Tsujimoto and Tsunewaki 1984) and other *Aegilops* species (Tsujimoto and Tsunewaki 1983; Tsujimoto and Tsunewaki 1985a). Some of these gametocidal genes were also found to induce chromosome aberrations in common wheat (Endo 1985, 1988; Tsujimoto and Tsunewaki 1985b; Tsujimoto and Noda 1988). Most of the induced genetic anomalies resulted in chromosome breakage and the deletion of chromosome segments. The resulting deletion lines have been used in studies of fine cytological mapping of genes on wheat chromosomes or chromosome arms (Endo and Mukai 1988; Endo et al. 1991; Mukai and Endo 1992). Deletion lines have been used in restriction fragment length polymorphism (RFLP) analysis to construct physical maps of the wheat genome (Werner et al. 1992; Kota et al. 1993; Gill et al. 1993a) and in the fine cytological mapping of genes (Gill et al. 1993b; Ogihara et al. 1994). Recently, a high-density physical map of group 7 chromosomes from *Triticum aestivium* L. based on deletion mapping and using the *Aegilops cylindrica* system to induce terminal deletions has been reported (Hohmann et al. 1994). Among 402 deletion lines described in 'Chinese Spring' wheat (Endo and Gill 1995) 63 lines carried subarm deletions in group 7 chromosomes. Of a total of 63 deletion lines 54 carried terminal deleted chromosomes that resulted from a single breakpoint and the concomitant loss of the distal fragment. Of the physical map with 60 chromosome subarm regions, 23 short- and 37 long-arm regions, 51 regions were molecularly tagged by 97 markers.

In this article we report details on 9 lines with deleted chromosomes that have additional interstitial deletions or peculiar fraction lengths that had been eliminated from the construction of physical maps. Furthermore, we show that chromosome pairing analysis can be utilized to detect small terminal deletions in deletion

lines. The implications of these modifications for physical mapping are discussed.

Materials and methods

Plant material

Individual chromosome arm deletions in wheat cultivar 'Chinese Spring' (CS) were isolated as described by Endo (1988) and Endo and Gill (1995). Individual chromosome arm deletions in CS were isolated from a backcross progeny of a monosomic addition line of an *Aegilops cylindrica* chromosome to CS (Endo 1988). Plants with chromosomal aberrations, mainly deletions, were identified by C-banding (Endo 1986). The breakpoint (BP) for each deleted chromosome was calculated as a fractional length (FL) of the distance from the centromere from a sample of at least five C-banded chromosomes. However, FL values are not accurate because of their indirect calculation. Therefore, they should be regarded as an approximate estimation of the breakpoints. Deletion chromosomes were designated by the deleted chromosome arm followed by a dash and an identification number. Deletion lines were designated the same way, but a point was used instead of the dash. For example, deletion line 7AS.1 has deletion chromosome 7AS-1. Several aneuploid stocks for group 7 chromosomes, nulli-tetra (NT) and ditelosomic (DT) stocks (Sears 1954; 1966) were exploited for the allocation of molecular markers. The cytologically longer arm of chromosome 7D (7DL) is genetically 7DS and homoeologous to chromosome arms 7AS and 7BS. We will use the generally accepted genetic nomenclature to describe group 7 arms.

RFLP and RAPD analysis

The extraction of genomic DNA from leaf tissue of the deletion and aneuploid stocks followed the procedure of Appels and Moran (1984). Ten-microgram samples of total genomic DNA digested with *Bam*HI, *Dra*I, *Eco*RI, *Eco*RV or *Hin*dIII restriction endonucleases were electrophoresed in a 1% agarose gel and blotted onto a Nylon membrane. Random priming and hybridization were performed as described previously (Hulbert et al. 1990; Lagudah et al. 1991).

RFLP probes were generously supplied by Dr. M. Gale, Cambridge Laboratory, Norwich (designated PSR), Dr. K. S. Gill, Kansas State University (designated KSU), Dr. M. Sorrells, Cornell University, Ithaca (designated BCD, CDO, WG), Dr. A. Kleinhofs, Washington State University, Pullman (designated ABC), Dr. K. Tsunewaki, Kyoto University, Kyoto (designated TAG) and Dr. E. S. Lagudah, CSIRO, Canberra (designated CS). The mapped loci were designated *Xpsr*, *Xksu*, *Xbcd*, *Xcdo*, *Xwg*, *Xabc*, *Xglk*, and *Xcs* respectively. Random amplified polymorphic DNA (RAPD) reactions and marker designation were performed according to Hohmann et al. (1994).

Map construction

The procedure for construction of the physical map has been described by Werner et al. (1992). Briefly, a locus was assigned to a chromosome arm by Southern analysis of the NT and DT stocks. RFLP loci were allocated within specific chromosome regions between breakpoints of adjacent deletions by scoring the presence or absence of chromosome arm-specific bands.

Results and discussion

Molecular detection of multiple chromosome rearrangements

Deletion lines represent one of the efficient tools for the construction of physical high-density maps of chromosomes. The *Aegilops cylindrica* system has been shown to be an effective method for inducing single terminal deletions (Endo 1988; Werner et al. 1992; Kota et al. 1993; Gill et al. 1993a). Of the homoeologous group 7 chromosomes of wheat, 70 different terminal deletions were identified, 63 lines in homozygous condition (Endo and Gill 1995). Among these, we identified 9 lines (14.3%) that contained either additional chromosome rearrangements or peculiar FLs by using 97 RFLP and RAPD markers (Hohmann et al. 1994). Twenty-four clones that have been unambiguously allocated to specific chromosome segments in 54 single terminal deletion lines (Fig. 1) have been exploited to detect further modifications in the deleted chromosomes of these 9 lines.

The Southern hybridization experiments with 18 clones were associated with signals that were not in agreement with the identification of single terminal deficiencies in deleted chromosomes of 7 lines (11.1%). With 12 genomic clones, KSUB7, KSUD2, KSUD15, KSUG34, PSR350, TAG61, TAG536, TAG750, WG180, WG522, WG669, and WG686, and 6 cDNA clones, PSR103, PSR108, PSR150, PSR152, BCD349 and BCD1338, we had obtained evidence for additional interstitial deletions. In 3 lines with terminal deletions in the short arms of chromosomes 7AS-7, 7AS-10 and 7BS-1 (Table 1) and in 4 lines with deletions in the long arm of chromosomes 7BL-11, 7BL-13, 7BL-5 and 7DS-1 (Table 2) additional "chromosomes segment-specific" RFLP bands within certain chromosome regions were missing. For example, in the physical mapping of lines 7AS.7 (FL 0.87) with genomic or cDNA clones of *T. aestivum* (WG669), *Ae. squarrosa* (PSR108, KSUD15) and barley (BCD349), chromosome-specific bands were absent in regions with FL of 0.0–0.21, 0.21–0.26, 0.45–0.59 and 0.66–0.73 (Table 1), indicating the presence of interstitial deletions (Fig. 2). In the cases of 7BL-13, 7BL-5 and 7DS-1 submicroscopic chromosome segments were either translocated to another unknown chromosome or, more likely, the actual breakpoint is more distal and combined with further 'subterminal' interstitial deletions. In addition, from Southern hybridization experiments we have evidence for the retention of subterminal interstitial segments in lines 7BL.5 within segment FL 0.84–0.86 and line 7DS.1 within segment 0.84–1.00 (Table 2, Fig. 3). Apparently, the same chromosome segment (FL 0.84–0.86) appears to be present in 7BL.13 as well.

The breakpoints in deleted chromosomes of 2 lines, 7AS.12 (FL 0.83) and 7AL.17 (FL0.71), had to be reallocated more distally with six markers, KSUD9, BCD93, WG341, WG380, CSIH81 and PSR743, to chromosome regions of FL 0.88–1.00 (Table 1) and FL 0.94–0.99 (Table 2), respectively. This is probably because of the inaccuracy of FL calculations or possibly because of interstitial deletions that were not detected with the DNA marker used in this study. There were 7 other deletion chromosomes that had similar contradictory FL values.

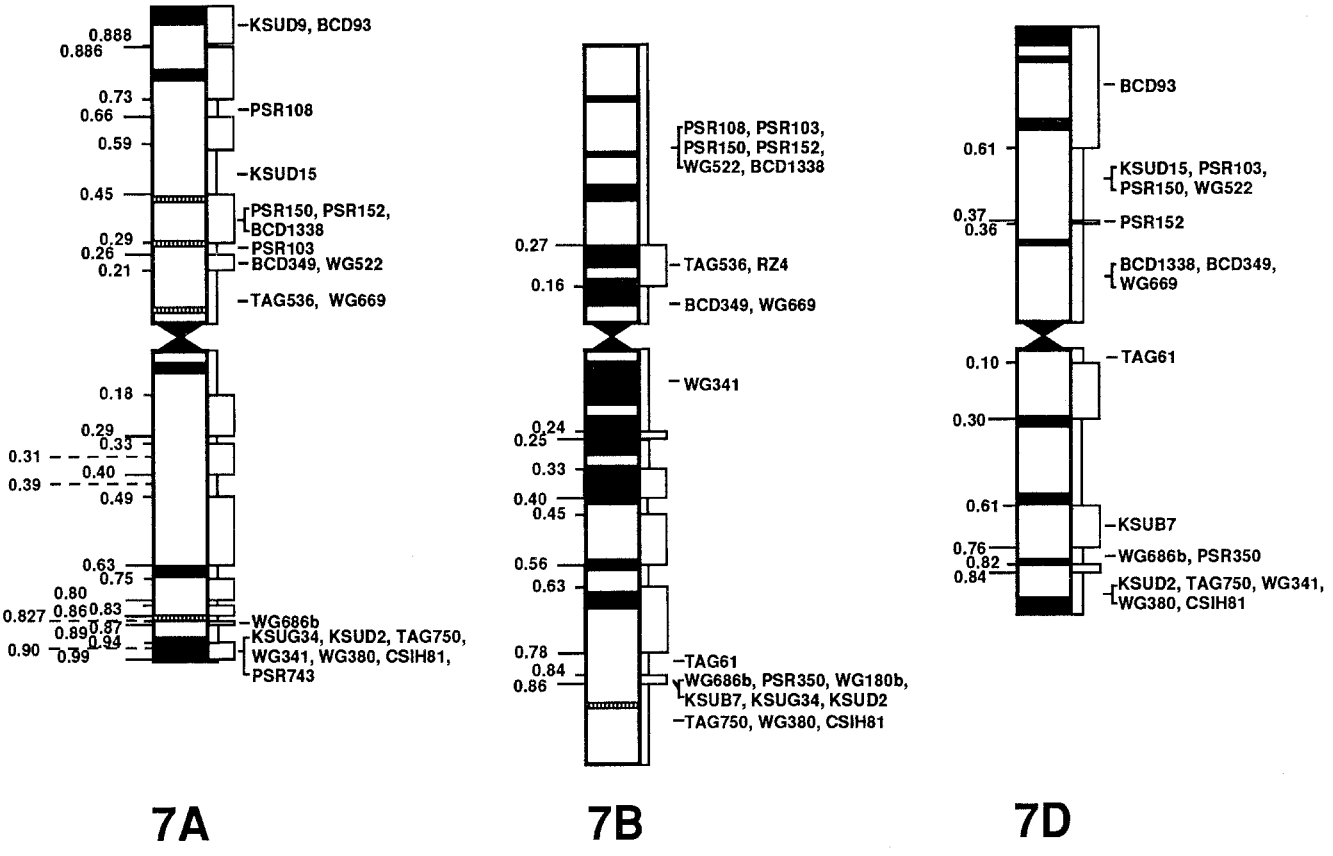

Fig. 1 Physical allocation of RFLP and RAPD markers that detect additional interstitial deletions and additional distal markers in deletion lines of group 7 chromosomes of wheat. Fraction length (FL) measurements are shown on the *left* and marker allocation on the *right*. Some FL values (*dashed line*) calculated from C-banded chromosomes were not in agreement with the linear order in the physical map

Implications for physical mapping

The presence of interstitial deletios and/or translocations have an impact on physical mapping and the linear order of markers along the chromosome. For example, from the hybridization signals of probe TAG536 (Table 3) and RAPD marker RZ4 (Fig. 4) on deleted chromosomes of the short arm of 7B, these 2 markers would either map distal to the breakpoint at FL 0.271

Table 1 Physical mapping of short arm deletions of wheat chromosome 7A and 7B using 16 RFLP markers and four short arm deletion lines, 7AS.12, 7AS.7, 7AS.10 and 7BS.1[a] (n.d. not determined due to the lack of polymorphism)

Marker[b]	Chromosome region	Deletion line			
	FL (of chromosome)	7AS.12 (FL 0.83)	7AS.7 (FL 0.87)	7AS.10 (FL 0.449)	7BS.1 (FL 0.271)
PSR119, PSR160	FL 0.88–1.00 (7A)	–	+	–	+
KSUD9, BCD93	FL 0.88–1.00 (7A)	+	+	–	+
CDO475	FL 0.73–0.87 (7A)	+	+	–	+
PSR108	FL 0.66–0.73 (7A)	+	–	–	–
ABC151	FL 0.59–0.66 (7A)	+	+	–	–
KSUD15	FL 0.45–0.59 (7A)	+	–	–	n.d.
PSR152	FL 0.29–0.45 (7A)	+	+	+	+
PSR150	FL 0.29–0.45 (7A)	+	+	+	–
BCD1338	FL 0.29–0.45 (7A)	+	+	–	+
PSR103	FL 0.26–0.29 (7A)	+	+	–	+
WG522	FL 0.21–0.26 (7A)	+	+	–	+
BCD349	FL 0.21–0.26 (7A)	+	–	+	+
WG669	FL 0.00–0.21 (7A)	+	–	+	+
TAG536	FL 0.16–0.27 (7B)	+	+	+	–

[a] + and –: Presence and absence of the respective RFLP marker. Bold signs indicate additional modifications
[b] Markers that detect additional modifications are underlined

Table 2 Physical mapping of long arm deletions of wheat chromosomes 7A, 7B and 7D using 14 RFLP markers and five long arm deletion lines, 7AL.17, 7BL.11, 7BL.13, 7BL.5 and 7DS.1[a] (n.d. not determined due to the lack of polymorphism)

Marker[b]	Chromosome region (FL of chromosome)			Deletion line				
	7A	7B	7D	7AL.17 (FL 0.71[c])	7BL.11 (FL 0.86)	7BL.13 (FL 0.79)	7BL.5 (FL 0.69)	7DS.1 (FL 0.14)
CDO775	0.63–0.75	0.56–0.63	0.76–0.82	+	+	+	+	–
KSUG7, PSR72	0.75–0.80	0.63–0.78	0.76–0.82	+	+	+	–	–
TAG61[d]	n.d.	0.78–0.84	0.76–0.82	n.d.	–	+	–	n.d.
WG686b	0.86–0.87	0.78–0.84	0.76–0.82	+	+	–	–	+
PSR350	n.d.	0.78–0.84	0.76–0.82	n.d.	+	–	–	–
WG180b	n.d.	0.78–0.84	n.d.	n.d.	+	–	–	n.d.
KSUB7[d]	n.d.	0.84–0.86	0.61–0.76	n.d.	+	+	–	+
KSUG34	0.94–0.99	0.78–0.84	n.d.	+	–	–	+	n.d.
KSUD2	0.94–0.99	0.84–0.86	0.84–1.00	+	–	–	+	–
TAG750	0.94–0.99	0.86–1.00	0.84–1.00	+	+	–	–	+
WG341[d]	0.84–0.86	0.00–0.24	0.84–1.00	+	+	–	–	–
WG380, CSIH81	0.94–0.99	0.84–0.86	0.84–1.00	+	+	–	–	–
PSR743	0.94–0.99	0.86–1.00	n.d.	–	–	–	–	n.d.

[a] + and –: presence and absence of the respective RFLP marker. Bold signs indicate additional modifications
[b] Marker(s) that detect additional modifications are underlined
[c] FL of this deletion is not comparable to others because the chromosome also has a deletion in the short arm
[d] Marker(s) with non-colinear distribution on chromosomes 7A, 7B and 7D

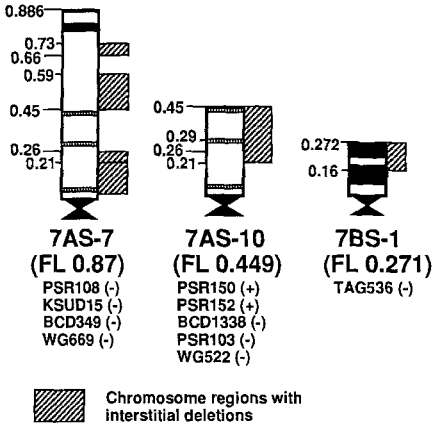

Fig. 2 Additional interstitial deletions in terminally deleted short arms of homologous group 7 chromosomes of wheat detected by physical mapping with molecular markers. The markers that were associated with the absence or presence of "chromosome segment-specific" RFLP bands are indicated with (–) or (+)

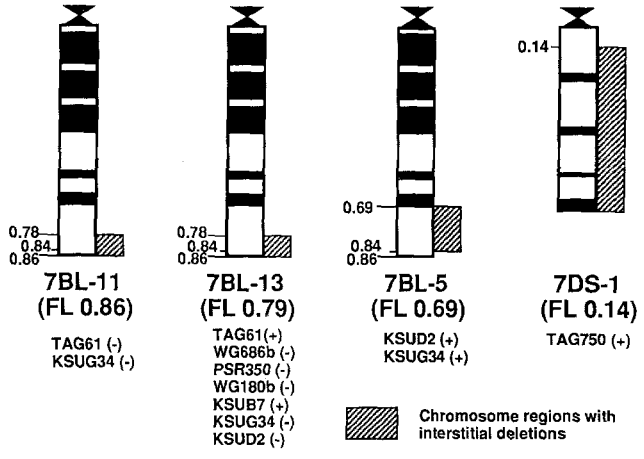

Fig. 3 Additional interstial deletions and additional distal markers in terminally deleted long arms of group 7 chromosomes of wheat detected by physical mapping with molecular markers. The markers that are associated with the absence or presence of "chromosome segment-specific" RFLP bands were indicated with (–) or (+)

(in line 7BS.1) or proximal to the breakpoint at FL 0.272 (in line 7BS.2), depending on the deletion line (Fig. 5). In addition, with line 7BS.1 we obtained positive hybridization signals with more distal probes, indicating that the distal part of chromosome 7BS-1 carried chromatin of 7BS that is originally located distal to the breakpoint at FL 0.271. Obviously, the deleted chromosome 7BS-1 contained an interstitial deletion and was therefore, omitted from the construction of the physical map.

Most of the additional submicrospic modifications were detected in neighboring regions of the primarily cytologically detected terminal deletion breakpoint induced by the gametocidal gene. At the moment it is not clear, whether these modifications were primarily caused by the induction of the terminal deletion itself or were the consequences of the repair of the deleted chromosome arm. In summary, the proximal region of the short arm (FL 0.0–0.29) and subterminal regions of the long and short arms (FL 0.78–1.00) accounted for most of the additional chromosome rearrangements.

In contrast, in the *Ae. speltoides* system the frequency of lines homozygous for the deleted segment is much lower and the chromosome arms of some deletion

Table 3 Physical mapping of short arm deletions of wheat chromosome 7B using 11 RFLP or RAPD markers and three deletion lines, 7BS.1, 7BS.2 and 7BS.3[a]

Marker[b]	Localization in chromosome region of 7BS	Deletion line		
		7BS.1 (FL 0.271)	7BS.2 (FL 0.272)	7BS.3 (FL 0.16)
PSR103	FL 0.27–1.0	+	–	–
PSR152	FL 0.27–1.0	+	–	–
BCD98	FL 0.27–1.0	+	–	–
BCD1338	FL 0.27–1.0	+	–	–
WG522	FL 0.27–1.0	+	–	–
RZ4	FL 0.16–0.27	–	+	–
TAG536	FL 0.16–0.27	–	+	–
PSR65	FL 0.16–0.27	+	+	–
TAG658	FL 0.16–0.27	+	+	–
BCD349	FL 0.0–0.16	+	+	+
WG669	FL 0.0–0.16	+	+	+

[a] + and –: presence and absence of the respective RFLP marker. Bold signs indicate additional modifications
[b] Marker(s) that detect additional modifications are underlined

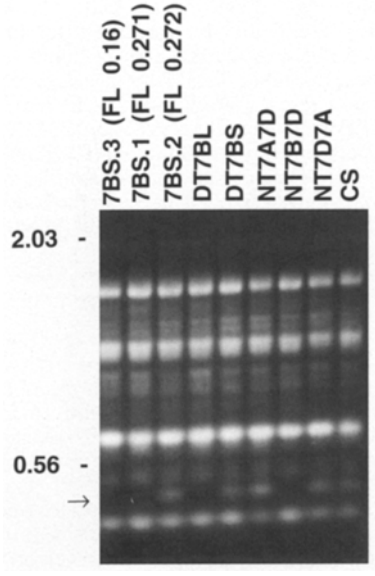

Fig. 4 Deletion mapping of the short arm of chromosome 7B with RAPD marker RZ4. The polymorphic band is indicated by an *arrow*

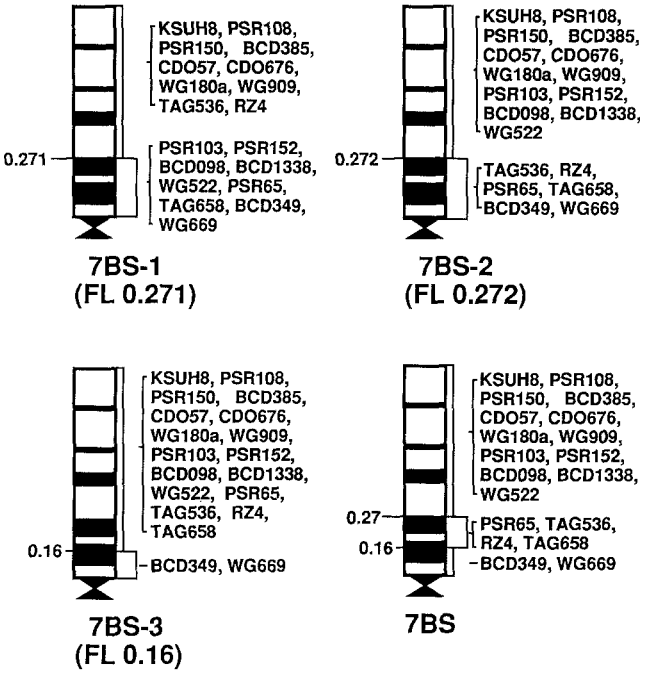

Fig. 5 Physical maps of the short arm of chromosome 7B from three different deletion lines, 7BS.1, 7BS.2 and 7BS.3, and one map constructed from lines 7BS.2 and 7BS.3

lines were found to be highly rearranged (Ogihara et al. 1994). Among 19 deletions reported for chromosome 5AL only 4 lines (q7, q9, q22 and q32) were single terminal deletions without any detectable additional chromosome rearrangements. All of the other lines carried either 'pinpoint' mutations, with 1 line being a translocation, 10 lines with an RFLP pattern that could be interpreted by the presence of additional interstitial deletions and 4 lines with both translocations and interstitial deletions. However, the *Ae. speltoides* system with a high frequency of induced interstitial deletions may be helpful in indentifying new lines with deletions of genes of interest. 'Pinpoint' mutations are useful for gene cloning in genomic subtraction experiments.

For a construction of a fine physical map of chromosome arms, single terminal deletions are more advantageous than double or interstitial deletions. In particular, additional interstitial deletions physically close to the first deletion may give rise to an alternate order of marker sequence in that region. The presence of "chromosome segment-specific" RFLP bands on Southern blots, although the specific chromosome segment is cytologically absent on the relevant group 7 chromosome, can be interpreted by a translocation of this segment to another unknown chromosome.

A high number of molecular markers will increase the probability of detecting additional chromosome rearrangements. In the *Ae. cylindrica* system we had initially detected the 9 lines described here with 36 markers. None of the 61 markers that we mapped later detected new modifications. Fine physical maps with high marker densities should enhance the structural analysis of wheat chromsomes and might be practical for gene tagging through map-based cloning (Gill and Gill 1991).

Chromosome pairing

Full synapsis of deficient and complete homologoues at pachytene in maize (*Zea mays* L.) but not at metaphase I (MI) was analyzed by McClintock (1931) and Stadler (1933). Chromosome pairing between deleted chromosomes and their complete homologous chromosome (arm) at MI was reported by Curtis et al. (1991). Pairing analysis of deficient chromosomes with their complete homologues at MI can provide information on (1) pair-

Table 4 Frequency (%) of telosome pairing and multivalent formation in F_1 hybrids between three different 7AL deletion lines and a double ditelosomic 7A line (DDT7A)

Cross	Number of PMCs	Number of paired telosomes			Multivalents
		2	1	0	(III + IV)
CS/DDT7A	150	84.0	12.0	4.0	0.0
7AL.15 (FL 0.99)/DDT7A	100	24.0	62.0	14.0	0.0
7AL.9 (FL 0.94)/DDT7A	233	4.7	84.6	10.7	0.0
7AL.10 (FL 0.49)/DDT7A	200	1.0	75.5	23.5	0.0

ing initiation at zygotene (Moens et al. 1989) and (2) the distribution of pairing initiation sites along the chromosome. The chromosome pairing configurations at MI can also indicate the presence of single breakage events or more complex rearrangements. The study of chromosome pairing in MI of crosses between homozygous deletion lines and double ditelosomic (DDT) lines would enable the detection of additional chromosome rearrangements within the deletion lines. In crosses involving lines 7AL.9, 7AL.10 and 7AL.15 no meiotic irregularities, like multivalent formation or bridges at anaphase II, were observed. The long arm of chromosome 7A in deletion line 7AL.15 (FL 0.99) was paired with the 7AL telosome in 24.0% of the PMCs (Table 4). In the control (CS/DDT7A), 84.0% of the telosomes were paired. Therefore, the deletion of 1% of the long arm of chromosome 7A was associated with a reduction in pairing frequency of 60.0%. A deficiency of 6% of the long arm of chromosome 7A accounted for a pairing frequency of 4.7%. In the cross 7AL-10/DDT7A, where 51% of the long arm of chromosome 7A was deleted, only 1% of this chromosome arm paired.

The reduced chromosome pairing of deficient chromosome arms of wheat with their respective telosomes was observed earlier by Curtis et al. (1991). In the long arm of chromosome 7A we found a more drastic drop in the pairing frequency, with 24% pairing by a 1% deletion and 1% pairing by a 49% deletion. A small deletion of 1% of the chromosome arm could account for an improper alignment of telomeres and cause a clear reduction in pairing. Curtis et al. (1991) calculated a declined pairing frequency as the deficiency length increased. The 8% deficiency reduced pairing to 29.8% with the long arm of chromosome 4A and the 23% deficiency reduced to 3.8%. Chromosome arms with 34%, 36% and 39% deletions did not pair with the telosome at all. Pairing in the long arm of chromosome 5B was rare (2.7%) in plants heterozygous for a 49% deficiency of that arm. Homologous pairs of deficient chromosomes showed near-normal levels of MI pairing (Curtis et al. 1991). Obviously, there is an inability of homologues of unequal length to initiate synapsis, which leads to pairing failure. Curtis et al. (1991) observed that small differences in length between deficiency breakpoints and the telomere have drastic effects on pairing and that large differences in length between deficiency breakpoints and the centromere do not. Our data on chromosome 7A support their observation on chromosome 4A. They concluded that the telomere attachment points of deficient and complete arms to the nuclear membrane remain the same but that the lack of homology in the distal regions of the arm prevents synapsis. The telomeres of wheat are of importance for primary initiation of the synaptonemal complex formation between homologues (Holm 1986). Studies on the chromosome pairing of deficient or deleted chromosomes imply that the accurate alignment of telomeric regions is obviously critical for MI pairing (Curtis et al. 1991).

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