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# Comparison of wheat physical maps with barley linkage maps for group 7 chromosomes

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**Abstract** Comparative genetic maps among the Triticeae or Gramineae provide the possibility for combining the genetics, mapping information and molecular-marker resources between different species. Dense genetic linkage maps of wheat and barley, which have a common array of molecular markers, along with deletion-based chromosome maps of *Triticum aestivum* L. will facilitate the construction of an integrated molecular marker-based map for the Triticeae. A set of 21 cDNA and genomic DNA clones, which had previously been used to map barley chromosome 1 (7H), were used to physically map wheat chromosomes 7A, 7B and 7D. A comparative map was constructed to estimate the degree of linkage conservation and synteny of chromosome segments between the group 7 chromosomes of the two species. The results reveal extensive homoeologies between these chromosomes, and the first evidence for an interstitial inversion on the short arm of a barley chromosome compared to the wheat homoeologue has been obtained. In a cytogenetically-based physical map of group 7 chromosomes that contain restriction-fragment-length polymorphic DNA (RFLP) and random amplified polymorphic DNA (RAPD) markers, the marker density in the most distal third of the chromosome arms was two-times higher than in the proximal region. The recombination rate in the distal third of each arm appears to be 8–15 times greater than in the proximal third of each arm where recombination of wheat chromosomes is suppressed.

**Key words** Comparative maps · Deletion lines · Molecular-tagged chromosome regions (MTCRs) · *Triticum aestivum* · *Hordeum vulgare*

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## Introduction

The plant family Gramineae with some 10 000 species contains various crops of commercial interest including wheat, barley, rice, maize, oat, sorghum and sugarcane. Restriction-fragment-length polymorphism (RFLP) linkage maps have been developed for the diploid species of rice (McCouch et al. 1988; Saito et al. 1991), barley (Graner et al. 1991; Heun et al. 1991; Kleinhofs et al. 1993) and *Triticum tauschii* (Gill et al. 1991b; Lagudah et al. 1991). In hexaploid wheat, both genetic maps (Chao et al. 1989; Liu and Tsunewaki 1991) and chromosome-arm maps have been constructed (Anderson et al. 1992; Devey and Hart 1993).

Recently, cytologically-based physical maps of the group 7 chromosomes of *Triticum aestivum* L. that rely on deletion mapping and the *Aegilops cylindrica* system to induce terminal deletions have been reported (Werner et al. 1992; Hohmann et al. 1994). Despite the fact that the chromosomes of the A, B and D genomes of wheat differ in their size, and in the amount and distribution of heterochromatin, these data suggested that the relative physical position of genes in homoeologous chromosomes has been largely conserved. Furthermore, by comparing physical with linkage maps, cytogenetically based physical maps can be constructed which define the subregion distribution of markers and recombination events (for a review see Gill and Gill 1994). The construction of these maps will be a critical first step for map-based cloning of agronomically useful genes in cereals, especially from those with large genomes. With the recent demonstration of collinear genetic mapping

of genes across cereal genomes (Ahn and Tanksley 1993; Ahn et al. 1993), the availability of various deletion stocks in wheat, but not in barley, offers the possibility of constructing cytogenetically based physical maps across the cereal crops. Here, we prove that physical maps of wheat are collinear to linkage maps of barley and discuss the implications of these results on the genomic structure of wheat and barley.

## Materials and methods

### DNA probes

RFLP probes were generously provided 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, ABG), and Dr. E. S. Lagudah, CSIRO, Canberra (designated CS). Probes which are designated MWG were selected from barley (Graner et al. 1991). The mapped loci were designated *Xpsr*, *Xksu*, *Xbcd*, *Xcdo*, *Xwg*, *Xabc*, *Xabg*, *Xcs* and *Xmwg* respectively.

### Plant material

Chinese Spring (CS) lines homozygous for deletions (Endo 1988; Endo and Gill 1995) were analyzed. The breakpoint for each deleted chromosome was calculated as a fractional length (FL) of the distance from the centromere for a sample of at least five C-banded chromosomes. However, FL values were not precise because of their indirect calculation. Therefore, they should be regarded as an approximate estimation of the breakpoints.

### Restriction-fragment-length polymorphism (RFLP) 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 1% agarose gels and blotted onto Nylon membranes. Random priming and hybridization were performed as described (Hulbert et al. 1990; Lagudah et al. 1991).

### Map construction

Two linkage maps of barley were used in the present study. The first map is based on the progeny of 71 $F_1$ anther-derived doubled haploid lines from a cross between the cultivars Igri and Franka (I/F; for details see Graner et al. 1991). The second map is based on the progeny of 150 $F_1$ anther-derived doubled haploid plants from a cross of the cultivars Streptoe and Morex (S/M), which were produced by the *Hordeum bulbosum* technique (for details see Kleinhofs et al. 1993). The procedure for construction of the physical map was essentially as described by Werner et al. (1992). Briefly, a locus was assigned to a chromosome arm by Southern analysis of the nullitetrasomic and ditelosomic stocks (Sears 1954, 1966) of wheat. 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 loci were allocated within specific chromosome regions between the breakpoints of adjacent deletions by scoring for the presence or absence of chromosome arm-specific bands. The chromosome regions that were tagged with molecular marker(s) were designated as MTCRs (molecular-tagged chromosome regions). We have constructed a cytogenetically based physical map of the group 7 chromosomes of common wheat by utilizing a total of 54 homozygous deletion stocks (Hohmann et al. 1994). The data allow the division of the three chromosomes into 60 subregions. One consensus map was generated from the three physical maps of chromosomes 7A, 7B and 7D (Hohmann et al. 1994). The consensus map was compared with two linkage maps of *Hordeum vulgare* (Graner et al. 1991; Kleinhofs et al. 1993). For an unequivocal presentation, these comparisons contain those loci that have been mapped in both physical and linkage maps. Physical and linkage maps were aligned at the approximate location of the centromere.

## Results

### Physical mapping of homoeologous group 7 loci

For physical mapping, we selected 39 RFLP clones, derived from wheat, barley, oat or *Triticum tauschii*, that had been previously used for linkage mapping of barley chromosome 1. We focussed on (1) evenly distributed markers to cover most of the two chromosome arms and (2) markers that were clustered around the centromere of the linkage maps. Of 39 DNA clones used, a total of 21, including 14 genomic DNA and seven cDNA clones, identified loci when used to physically map wheat chromosomes. No polymorphisms in the individual genomes of wheat were detected with 18 barley clones, eight of which were expected to identify loci in the region of the centromere.

Fourteen barley RFLP probes had not previously been used to map particular chromosome arms in hexaploid wheat. The majority of the probes, 16 out of 21 (76.2%), detected polymorphic loci in all three genomes of hexaploid wheat (Table 1). All of the loci were collinear on homoeologous chromosome arms in hexaploid wheat. The remaining five probes could only be used for mapping one or two genomes because of the lack of corresponding fragments in the complementing genomes.

### Physical maps of chromosomes 7A, 7B and 7D

The mapped loci provide a good physical coverage of the centromeric, interstitial and telomeric regions of the group 7 chromosomes of wheat. For chromosome 7A, six short-arm and six long-arm chromosome regions were tagged by 19 molecular markers (Fig. 1). The untagged segments with fractional-length (FL) values included those in the proximal region of the long arm (FL 0.0–0.33) and in the interstitial regions of both the short (FL 0.45–0.66) and long arms (FL 0.49–0.83). For chromosome 7B, 18 deletion lines were examined including ten deletions for the long arm and two for the short arm, as well as six for the long arm of chromosome 4A (Fig. 1) which represents 7BS chromatin (Liu et al. 1992; Werner et al. 1992). Twelve molecular-tagged chromosome regions (MTCRs) were established with 18 RFLP

**Table 1** Origin, number and polymorphisms detected with clones used for physical mapping of group 7 chromosomes of wheat

| Clone designation | Origin | Type | Number of clones | No. of polymorphisms | | |
|---|---|---|---|---|---|---|
| | | | | A | B | D |
| MWG808, MWG905, MWG2031, MWG2062, MWG2080, ABG476 | *H. vulgare* | Genomic DNA | 6 | 6 | 6 | 6 |
| RIS44, ABC151, cMWG705 | *H. vulgare* | cDNA | 3 | 3 | 3 | 3 |
| CDO475, CDO673 | *A. sativa* | cDNA | 2 | 2 | 2 | 2 |
| PSR129, PSR150 | *T. aestivum* | cDNA | 2 | 2 | 2 | 2 |
| WG380, WG719, WG834 | *T. aestivum* | Genomic DNA | 3 | 3 | 3 | 3 |
| Subtotal | | | 16 | 16 | 16 | 16 |
| MWG89 | *H. vulgare* | Genomic DNA | 1 | 1 | 0 | 1 |
| ABC310 | *H. vulgare* | cDNA | 1 | 1 | 0 | 0 |
| MWG903 | *H. vulgare* | Genomic DNA | 1 | 0 | 1 | 0 |
| cMWG704 | *H. vulgare* | cDNA | 1 | 0 | 0 | 1 |
| KSUA1 | *T. tauschii* | Genomic DNA | 1 | 0 | 0 | 1 |
| Subtotal | | | 5 | 2 | 1 | 3 |
| MWG528, MWG530, MWG555, MWG649, MWG681, MWG714, MWG725, MWG739, MWG836, MWG851, MWG957, MWG967, MWG2041, ABG380, ABG461 | *H. vulgare* | Genomic DNA | 15 | 0 | 0 | 0 |
| ABC156, ABC167, ABC455 | *H. vulgare* | cDNA | 3 | 0 | 0 | 0 |
| Subtotal | | | 18 | 0 | 0 | 0 |
| Total RFLP | | | 39 | 18 | 17 | 19 |

markers. For chromosome 7D, nine deletion lines were analyzed, three for the short arm and six for the long arm. Seven of eleven chromosome regions were tagged by using 20 markers. For one short-arm marker, *Xabg476.1*, duplicated loci (*Xabg476-7A.2*, *Xabg476-7B.2* and *Xabg476-7D.2*) were detected on the long arm in the subarm regions FL 0.33–0.40, FL 0.33–0.45 and FL 0.10–0.30 of chromosomes 7A, 7B and 7D, respectively.

## Comparison of the physical map of hexaploid wheat with linkage maps of barley

Despite the fact that chromosomes 7A, 7B and 7D differ in size, as well as in the amount and distribution of heterochromatin, the relative position of mapped homologous loci was conserved and mostly collinear. This allowed the construction of a consensus physical map which can be utilized for the physical allocation of orthologous loci across the Triticeae genomes (Fig. 2).

The comparison of barley linkage maps with the consensus physical map of the group 7 chromosomes of wheat demonstrated that there was collinearity for most of the markers (Fig. 2). The arm locations of the markers were identical in wheat and barley. The synteny of markers in the long arm is conserved. In the short arm, the order of four proximal markers (*Xpsr150/Xcmwg705/Xmwg808/Xabg476.1*) and another pair of markers (*Xabc151/Xmwg89*) appears to be reversed between wheat and barley. These four proximal markers in the I/F linkage map and the pair of markers in the S/M linkage map are tightly linked. Based on the marker synteny between wheat and barley we determined the location of the centromere on the I/F map between markers *Xpsr150* and *Xmwg903* (Fig. 2). Similarly, the centromere on the S/M map was placed between markers *Xabg476.1* and *Xwg719*.

## Marker density

A cytogenetically-based physical map allows the allocation of markers that reveal polymorphism to proximal, interstitial and distal chromosome regions of the short and long arms of chromosomes 7A, 7B and 7D (Fig. 3). The marker *Xabg476.1* is assigned to the most proximal 31% of the short arm. The marker *Xcmwg704* is located in the intersitial 35% and *Xmwg89* in the most distal 33% of the short arm. Together with 97 markers that were previously mapped by Hohmann et al. (1994) the cytogenetically based physical map contains 111 clones which detect 118 loci, and 100 (85%) of the loci are collinear. From physical and linkage mapping, the proximal, interstitial and distal chromosome regions harbor 23 (21.3%), 31 (28.7%) and 54 (50.0%) of the

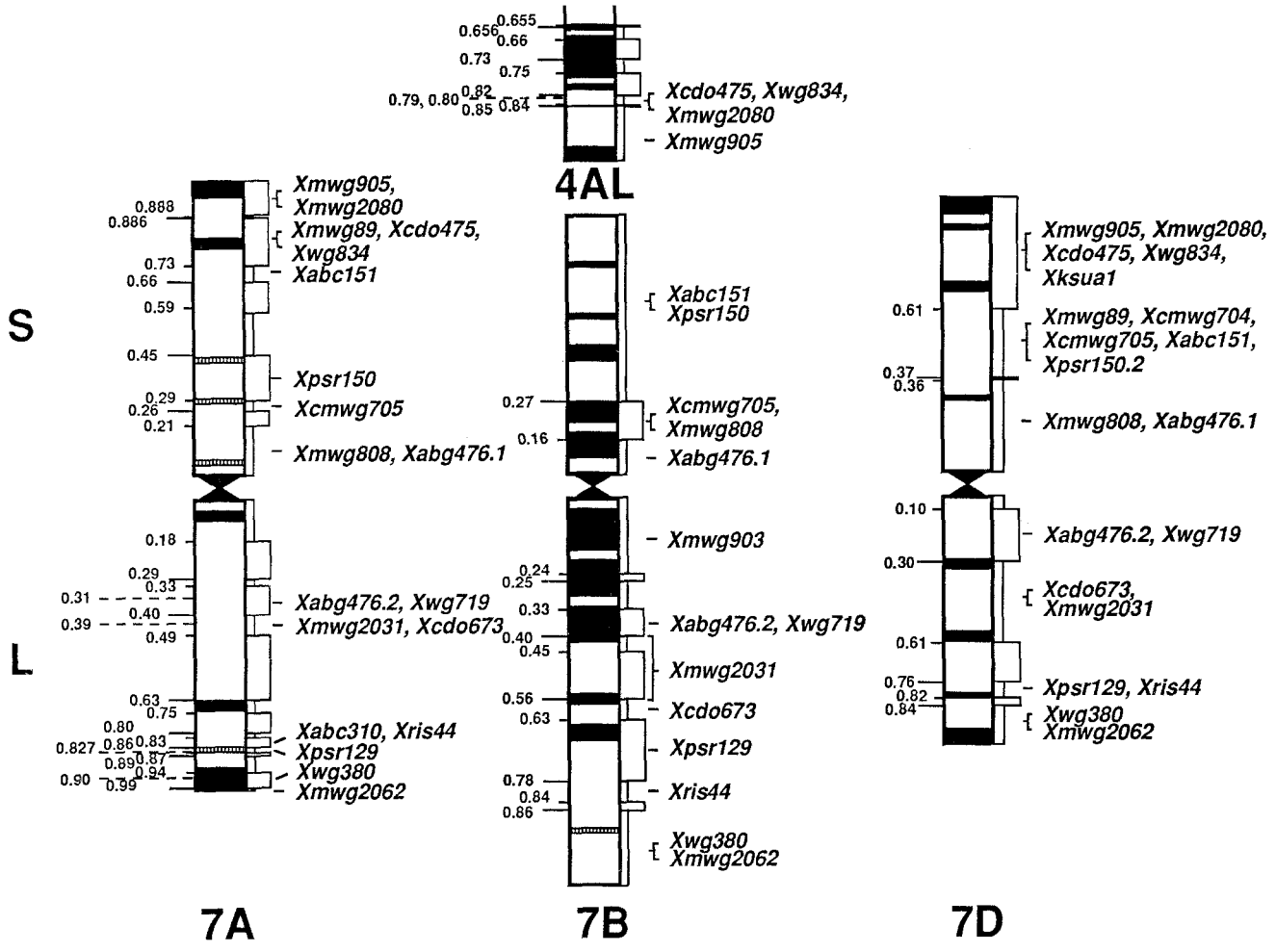


**Fig. 1** Physical maps of C-banded wheat chromosomes 7A, 7B and 7D and the distal region of chromosome arm 4AL of wheat. Fractional length (FL) measurements are shown on the left and marker allocation on the right. Some FL values (*dashed lines*) calculated from C-banded chromosomes were not in agreement with the linear order on the physical map

short-arm markers, respectively (Table 2). The average number of markers per 1% of FL can be calculated for each of the regions by dividing the length of the region by the number of markers allocated to that region. The number of loci that show polymorphism is two-times higher in the most distal region compared to the proximal regions of both the short and long chromosome arms. Markers in proximal regions are highly conserved with low polymorphism between wheat and barley.

## Recombination frequency

The proximal third of the short and long arms of homoeologous group 7 chromosomes have a genetic length of about 4 cM to 5 cM (Table 2). MWG704 and MWG2031 map at a distance of 17 cM and 7 cM from the centromere, respectively, in barley 7H (Fig. 3). Physically the orthologous wheat loci are located in interstitial chromosome regions at FL 0.37–0.61 (*Xcmwg704*) or FL 0.45–0.49 (*Xmwg2031*) (Fig. 2).

Average genetic distances corresponding to 1% FL were calculated for each of the chromosome regions by dividing the genetic distance by the length of the region in the FL (Table 3). Considering that the genetic length of the short arm is 140 cM and that of the long arm is 70 cM at the minimum, the recombination rate in the distal third of each arm for the markers studied is 8–15 times greater than in the proximal third of each arm. Recombination in proximal regions of wheat chromosomes is suppressed. A higher marker density in distal regions is correlated with higher rates of recombination in the distal regions of chromosomes and a lower density of markers in the proximal regions is correlated with a lower recombination frequency.

## Landmark loci

Considering comparative mapping of loci we have a long-term objective to identify landmark loci that characterize subarm regions of the chromosome arms. Landmark loci are defined as markers that map across the three genomes of wheat with collinearity and are not

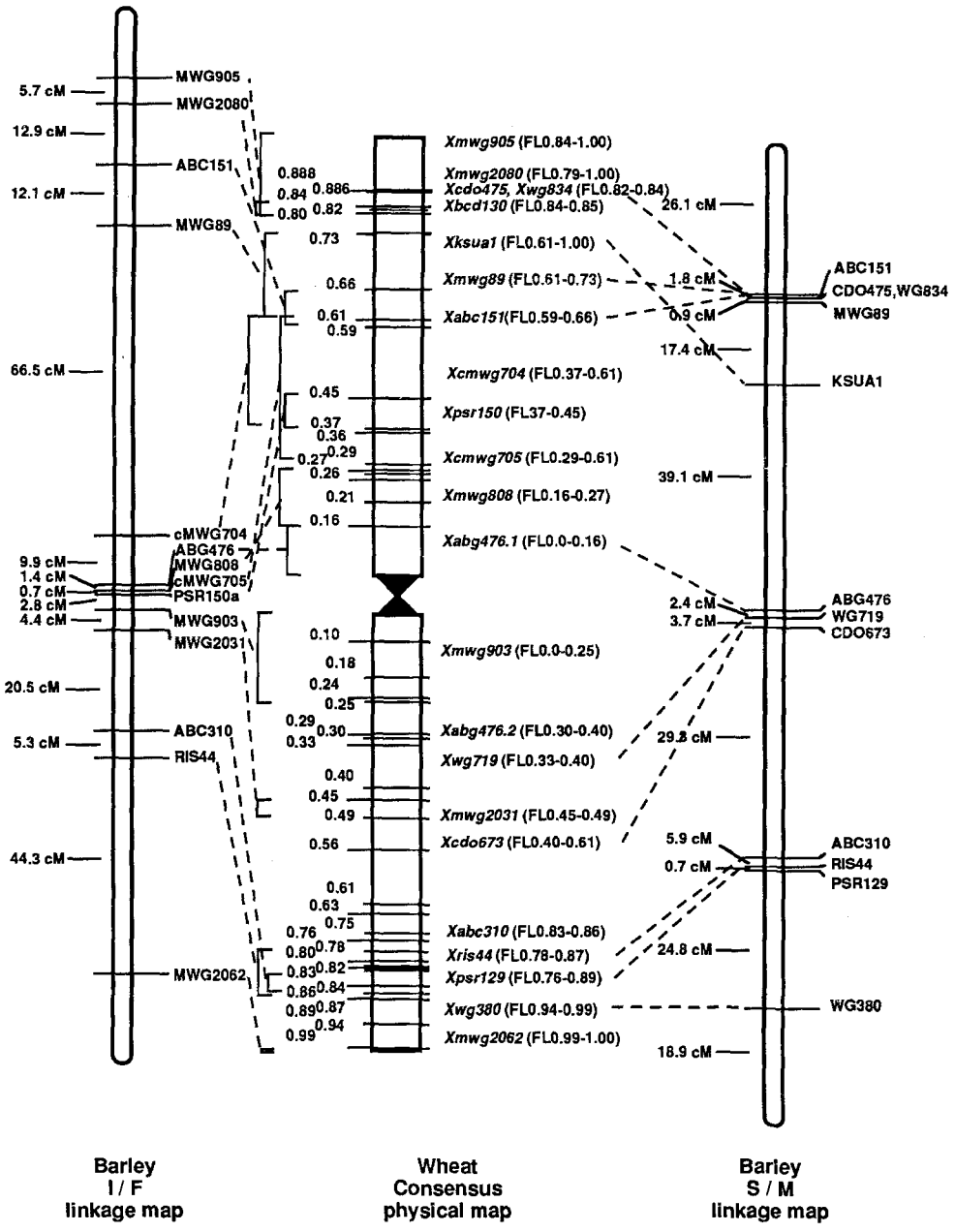


**Fig. 2** Comparison of the consensus physical map of wheat (center) and linkage maps (left and right) from barley chromosome 1 (7H). left: linkage map based on the linkage I/F (Igri/Franka) map; right: linkage map based on Kleinhofs et al. (1993). The linkage maps include only markers that were localized on the physical map

duplicated. In general, these markers reveal one single RFLP band for each of the genomes with different restriction enzymes. In Table 3 we tentatively specified ten landmark loci, five loci each for the short and long arms, that will be useful for targeting specific genes to specific regions of homoeologous group 7 chromosomes.

## Discussion

### Comparison of the physical map of hexaploid wheat with linkage maps of barley

A comparison of the physical map of hexaploid wheat with different linkage maps of wheat (Chao et al. 1989; Liu and Tsunewaki 1991), *T. tauschii* L. (Gill et al. 1991b; Lagudah et al. 1991) and barley (Graner et al. 1991; Heun et al. 1991; Kleinhofs et al. 1993) that have an array of molecular markers in common can assist in the construction of an integrated molecular marker-based map for the Triticeae. The physical and linkage order of molecular markers along the homoeologous group 7 chromosomes is almost identical in wheat and barley. Minor deviations could be detected in two subregions of the short arm with respect to the proximal interval *Xpsr150/Xcmwg705/Xmwg808/Xabg476.1* on the I/F map, as well as the more distal interval *Xmwg89/Xabc151* on both the I/F and S/M maps. In order to further delineate the physical size of these putative inversions, analysis of an increased number of markers in common to both linkage and physical maps are required. However, the markers in the proximal region

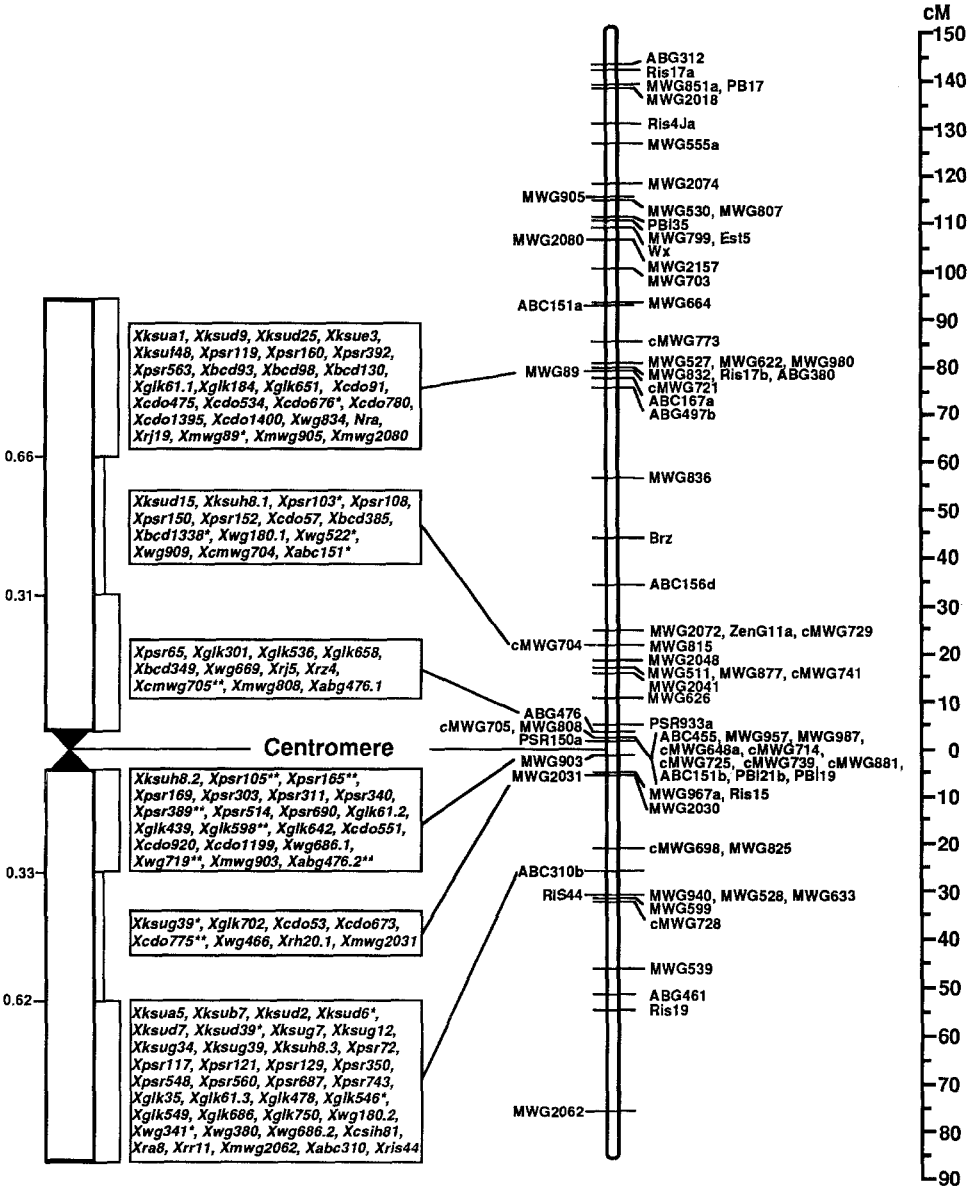


**Fig. 3** Comparison of the physical consensus map of wheat (left) with the linkage I/F (lgri/Franka) map (right) of barley depicting physical positions of all mapped group 7 loci. Markers that were located in more distal regions in one of the wheat chromosomes 7A, 7B or 7D (see Fig. 1) are indicated by one *asterisk* and markers that were mapped in more proximal regions in one of the chromosomes by *two asterisks*. Note: marker ABC151 has been mapped proximal to MWG89 in the physical map but distal to it in the linkage map

**Table 2** Comparison of subarm regions for the number of markers and recombination frequencies in group 7 chromosomes of wheat and barley

| Chromosome arm | FL[a] interval | Length in FL | Number of markers | | Approximate genetic distance | | Number of markers per 1% of FL | Genetic distance per 1% of FL |
|---|---|---|---|---|---|---|---|---|
| | | | Total | % | cM | % | | |
| 7S | 0–0.31 | 0.31 | 23 | 21.30 | 4 | 2.82 | 0.74 | 0.13 |
| 7S | 0.31–0.66 | 0.35 | 31 | 28.70 | 72 | 50.70 | 0.89 | 2.06 |
| 7S | 0.66–1.0 | 0.34 | 54 | 50.00 | 66 | 46.48 | 1.59 | 1.94 |
| Σ 7S | 0–1.0 | 1.0 | 108 | 100.00 | 142 | 100.00 | 1.08 | 1.44 |
| 7L | 0–0.33 | 0.33 | 23 | 29.49 | 5 | 6.76 | 0.70 | 0.15 |
| 7L | 0.33–0.62 | 0.29 | 11 | 14.10 | 21 | 28.38 | 0.38 | 0.72 |
| 7L | 0.62–1.0 | 0.38 | 44 | 56.41 | 48 | 64.86 | 1.16 | 1.26 |
| Σ 7L | 0–1.0 | 1.0 | 78 | 100.00 | 74 | 100.00 | 0.78 | 0.74 |

[a] FL, fractional length

**Table 3** Probes and deletion stocks exploited to identify landmark loci for short and long arms of group 7 chromosomes of wheat

[a] Average of proximal and distal fractional length (FL) values of the interval in which the locus is mapped
[b] Marks the distal boundary of the deletion interval region in which the locus is mapped
[c] Marks the proximal boundary of the deletion interval region in which the locus is mapped

| Probe | Arm location of loci detected | FL position[a] | Diagnostic deletion stock[b] | | |
|---|---|---|---|---|---|
| | | | 7A | 7B | 7D |
| MWG808 | 7S | 0.122 | 7AS.6(FL0.21) | 7BS.1(FL0.271) | 7DL.5(FL0.36) |
| BCD349 | 7S | 0.165 | 7AS.4(FL0.26) | 7BS.1(FL0.271) | 7DL.5(FL0.36) |
| PSR152 | 7S | 0.415 | 7AS.8(FL0.45) | 4AL.2(FL0.75) | 7DL.1(FL0.37) |
| CDO676 | 7S | 0.670 | 7AS.2(FL0.73) | 4AL.2(FL0.75) | 7DL.4(FL0.61)[c] |
| MWG905 | 7S | 0.880 | 7AS.1(FL0.888) | 4AL.1(FL0.85)[c] | 7DL.4(FL0.61)[c] |
| CDO1199 | 7L | 0.194 | 7AL.3(FL0.29) | 7BL.14(FL0.24) | 7DS.5(FL0.30) |
| PSR690 | 7L | 0.258 | 7AL.7(FL0.33) | 7BL.12(FL0.25) | 7DS.5(FL0.30) |
| CDO673 | 7L | 0.498 | 7AL.10(FL0.49) | 7BL.7(FL0.63) | 7DS.2(FL0.61) |
| RIS44 | 7L | 0.780 | 7AL.8(FL0.83) | 7BL.6(FL0.84) | 7DS.3(FL0.82) |
| CSIH81 | 7L | 0.912 | 7AL.15(FL0.99) | 7BL.3(FL0.86)[c] | 7DS.7(FL0.84)[c] |

are tightly linked and reversing their order in the linkage map will conform them to the physical map. The genetic cluster of markers around the centromere is clearly resolved in the physical map.

Detailed knowledge of the correlation between linkage and physical distance is crucial for various aspects of both molecular genetics and cytogenetics, as well as for practical plant breeding. In this respect, the present study provides further evidence of uneven recombination frequencies along the chromosome, as has been shown for wheat (Jampates and Dvorak 1986; Curtis and Lukaszewski 1991; Werner et al. 1992), barley (Linde-Laursen 1982), rye (Lukaszewski 1992) and *T. tauschii* (Gill et al. 1993; Kota et al. 1993; Hohmann et al. 1994). Although, the present results rest on the analysis of species from two different genera, at least two lines of evidence lead to the conclusion that these observations apply to both wheat and barley. (1) Linkage maps of both species display marker clusters around the centromeres of most chromosomes (Graner et al. 1993; Hart et al. 1993; Kleinhofs et al. 1993). (2) A recent comparison of physical and linkage maps of barley chromosome 5 (1H) based on the analysis of set of microisolated translocation chromosomes showed drastically reduced recombination frequencies in proximal regions and an increase in the physical marker density for distal regions of the chromosome (Sorokin et al. 1994). Also, the consensus physical map for homoeologous group 7 chromosomes of wheat shows a relative increase in marker density from proximal to distal portions.

## Physical mapping

We have mapped 118 RFLP and RAPD loci, 53 on the short arm and 65 on the long arm. We molecularly tagged 53 chromosome regions (88.3%) out of 60 regions. The wheat genome consists of 16 000 million base pairs per haploid genome (Arumuganathan and Earle 1991) and the entire length of the haploid set of chromosomes is 235.4 μm (Gill et al. 1991a). The length of chromosome 7A is 11.3 μm (Endo and Gill 1984). To-date, 29 different chromosome regions have been distinguished on chromosome 7A (Endo and Gill 1995) implying that the average size is 0.39 μm per region, which corresponds to twice the resolution of the light microscope. With 95 RFLP loci mapped onto chromosome 7A the average number of loci per region is 3.3. On the average we have mapped a marker every 0.12 μm or every 8.1 Mb. The highest marker density detected is in the long-arm chromosome region at FL 0.86–0.87 with six markers. In that region a marker has been mapped for every 0.01 μm or every 800 kb. Any gene of interest in such a region will thus be accessible to map-based cloning strategies.

## Comparative mapping

Comparative genetic mapping with RFLP probes has shown significant conservation among several related crop species. Conserved linkages with nearly identical gene content and gene order have been reported between tomato and potato (Bonierbale et al. 1988; Tanksley et al. 1992), maize and sorghum (Hulbert et al. 1990; Whitkus et al. 1992; Berhan et al. 1993), rice and maize (Ahn and Tanksley 1993), and between rice, maize and wheat (Ahn et al. 1993), based on RFLP linkage maps. A high degree of linkage conservation, and the fact that probes from one species can be used in another, (Tanksley et al. 1992) will accelerate integrative mapping studies. With a close relationship between species of the Gramineae and the availability of a large number of RFLP clones it is possible to integrate different genetic maps of barley into a physical consensus map of wheat. Landmark loci, which represent cDNA clones and single- or low-copy genomic DNAs that correspond to highly conserved coding regions, are a helpful tool in the allocation of orthologous loci across the Triticeae genomes. Genomic segments with conserved gene synteny will be useful in the genetic mapping of orthologous genes. These regions may be of significance in understanding genome evolution among the Triticeae by

analyzing structural rearrangements in chromosomes, recombination hot spots, suppression of recombination, gene distribution, gene duplication and elimination events. The correlation of chromosome function and structure of defined chromosome regions will provide information for strategies of gene transfer of orthologous loci of disease resistance and quantitative traits.

Yet another potential of comparative maps is the localization of the centromere in those plant species where no telosomic stocks are available. Ahn et al. (1993) have discussed the possibility of locating rice centromeres by comparative mapping using the information of mapped loci in wheat. The centromeric position is often conserved (Ahn and Tanksley 1993). We have roughly localized the centromere on the linkage map of barley. The attempt to use barley clones for hybridization to proximal DNA fragments of wheat chromosomes in more detail failed due to the absence of polymorphisms in restriction fragment length. Obviously clones from the centromere region of barley are highly conserved with a low polymorphism between barley and wheat. Therefore, in comparative maps the density of common proximal markers is reduced.

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