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Comparative RFLP mapping of *Hordeum vulgare* and *Triticum tauschii*

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Abstract *Hordeum vulgare* (barley) and *Triticum tauschii* are related, but sexually incompatible, species. This study was conducted to determine the extent of homology between the genomes of barley and *T. tauschii* using a common set of restriction fragment length polymorphism (RFLP) markers. Results showed that >95% of low-copy sequences are shared, but 42% of the conserved sequences showed copy-number differences. Sixty-three loci were mapped in *T. tauschii* using RFLP markers previously mapped in barley. A comparison of RFLP marker order showed that, in general, barley and *T. tauschii* have conserved linkage groups, with markers in the same linear orders. However, six of the seven linkage groups of *T. tauschii* contained markers which mapped to unrelated (i.e., non-homoeologous) barley chromosomes. Additionally, four of the *T. tauschii* linkage groups contained markers that were switched in order with respect to barley. All the chromosome segments differing between *T. tauschii* and barley contained markers that were detected by multi-copy probes. The results suggest that the observed differences between the *T. tauschii* and barley genomes were brought about by duplications or deletions of segments in one or both species. The implications of these findings for genetic mapping, breeding, and plant genome evolution are discussed.

Key words Comparative mapping, · RFLP · Barley *Triticum tauschii* · Genome evolution

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Introduction

Barley (*Hordeum vulgare*) and *Triticum tauschii* are related species belonging to the Triticeae tribe of the Gramineae family. Although barley and *T. tauschii* are sexually incompatible, the genomes of the two species share a number of common features. Barley is an inbreeding diploid cereal with a genome size of approximately 5.5×10^9 base pairs (bp), organized into seven chromosomes (Bennett and Smith 1976). *T. tauschii's* genome is also organized into seven basic chromosomes with a genome size of roughly $3.6–4.9\times10^9$ bp (Bennett and Smith 1976).

T. tauschii is the diploid progenitor of the D genome of common wheat, an allohexaploid species (2n=6x=AABBDD) (Kihara 1944; McFadden and Sears 1944, 1946). The other two genomes found in common wheat each have a basic chromosome number of seven and approximately the same number of DNA base pairs as in *T. tauschii* (Bennett and Smith 1976). Genome comparison studies using isozymes (Benito et al. 1985; Hart 1987) have shown that each chromosome in barley is genetically related (homoeologous) to three chromosomes in common wheat (one chromosome from each genome). Furthermore, a comparison of isozyme, morphological, and a limited number of restriction fragment length polymorphism (RFLP) markers revealed the same gene order (synteny) among homoeologous chromosome groups of barley and wheat (Kam-Morgan et al. 1989; Sharp et al. 1989). However, the exact details of the homoeology between barley and wheat are not known since most of these comparisons were based solely upon expressed DNA sequences, which are known to comprise only a small portion of eukaryotic genomes.

Comparative RFLP mapping has been used to compare the genomes of related, but sexually incompatible, plant species, such as tomato and pepper (Tanksley et al. 1988), tomato and potato (Bonierbale et al. 1988; Gebhardt et al. 1991), sorghum and maize (Hulbert et al. 1990), wheat and rye (Liuyc et al. 1992; Devos et al. 1993), rice and maize (Ahn and Tanksley 1993), and rice and wheat (Ahn et al.

1993). In a comparison between wheat and rye, Devos et al. (1993) observed extensive gene rearrangements in rye relative to the wheat genome. However, a conservation in gene order was reported between barley and wheat (Kam-Morgan et al. 1989; Sharp et al. 1989; Liao and Niks 1991), but these studies cannot be considered conclusive because of the small number of probes used.

The present study was conducted to better determine the extent of homology between the genomes of barley and *T. tauschii* using RFLP markers distributed throughout each of their genomes. Comparing these two diploid species is easier than comparing hexaploid wheat and barley because the genomes are of similar size and no complications from polyploidy exist. We set out to answer three questions: (1) What proportion of low-copy sequences is shared between the genomes of barley and *T. tauschii*? (2) Are there changes in the copy numbers of certain sequences between the genomes of barley and *T. tauschii*? (3) Has gene order on chromosomesbeen conserved between the genomes of barley and *T. auschii*?

Materials and methods

Plant materials

Two accessions from *T. tauschii*, TA 1691, var. *meyeri* and TA 1704, var. *typica*, and 60 F_2-derived F_3 families from a cross between TA 1691 and TA 1704 (Gill et al. 1991) were used for mapping in *T. tauschii*. For barley, cultivars 'Steptoe' and 'Morex' were used to screen for polymorphisms. The barley RFLP map, described in Kleinhofs et al. (1993), was constructed in a doubled haploid population (Chen and Hayes 1989) derived from a cross between 'Steptoe' and 'Morex'.

DNA extraction, restriction digestion, Southern blotting and hybridization

DNA was extracted from young leaves according to McCouch et al. (1988). For Southern blotting, approximately 10–12 µg of DNA was digested with *Eco*RI, *Eco*RV, *Dra*I, and *Xba*I following the manufacturer's instruction using two units of enzyme per µg of DNA. DNA was run on a 0.9% agarose gel as described in Bernatzky and Tanksley (1986), and alkaline blotted onto Hybond-N^+ nylon membranes (Amersham) for 3–6 h. Probes were labelled with ^{32}P by random priming (Feinberg and Volgelstein 1983). Hybridization and washing were according to the procedures described in Bernatzky and Tanksley (1986). Homologous hybridizations of barley clones to barley DNA and wheat clones to *T. tauschii* DNA were washed at 0.2×SSC and 0.1% SDS, while hybridizations of heterologous probes were washed at a lower stringency of 0.5×SSC and 0.1% SDS.

Clones

The cDNA clones used were from oats (**CDO**; Heun et al. 1991), wheat (**PSR**;Chao et al. 1989, Sharp et al. 1989), and barley (**ABC**; Kleinhofs et al. 1993, **BCD**; Heun et al. 1991). Genomic DNA clones used were from *T. tauschii* (**KSU** or **DG**; Gill et al. 1991), wheat (**WG**; Heun et al. 1991), and barley (**ABG**; Kleinhofs et al. 1993 and **BG**; Lapitan, unpublished). All genomic DNA clones were from a *Pst*I digest. Inserts were prepared by polymerase chain reaction as explained in Nkongolo et al. (1993). Primers used for **ABG, BG, WG,** and **KSU** clones were as described in Heun et al. (1991). M13 forward and M13 reverse primers were used for **ABC, BCD,** and **CDO** clones.

Genetic mapping

Ninety-eight markers from the barley map (Kleinhofs et al. 1993) were screened for polymorphisms in *T. tauschii*. Fifty-two clones segregating in the *T. tauschii* cross were mapped against the existing markers in the database (Gill et al. 1991) using the MAPMAKER program (Lander et al. 1987). Clones segregating for more than one locus were designated with the marker name followed by a letter (for example, BCD266A and BCD266B). Genetic distances were calculated using the Kosambi function, with mapping parameters set at LOD=3.0 and theta=0.5. Markers KSUA1, KSUA3, KSUD14, KSUD22, KSUF2, KSUF15, KSUH11, PSR106, PSR128, and PSR154 were previously mapped in *T. tauschii* by Gill et al. (1991). All markers on the barley RFLP map had been mapped by the North American Barley Genome Mapping Project (NABGMP) (Kleinhofs et al. 1993).

Results

Proportion of low-copy sequences shared between barley and *T. tauschii*

The proportion of low-copy-number sequences shared between the genomes of barley and *T. tauschii* was determined using a total of 155 *Pst*I genomic clones selected at random, including both barley and *T. tauschii* clones. A clone was defined as containing a low-copy-number sequence if it hybridized to a few discrete bands (1–10 bands) on genomic blots. Each clone was hybridized to genomic blots containing restriction enzyme digested DNA from barley and *T. tauschii* and scored for presence or absence in the two species. When no hybridization was detected with a heterologous probe (i.e., a barley clone on *T. tauschii* DNA and a *T. tauschii* clone on barley DNA) that probe was scored as absent in the other species if several criteria were met. First, the probe should have been labelled with a minimum specific activity of 3×10^7 cpm/µg. Second, the hybridization of a probe to the source DNA (i.e. a barley probe to barley DNA and a *T. tauschii* probe to *T. tauschii* DNA) and to the molecular weight standard, lambda, in the same reaction should have given signals. Third, signals should not have been detected in the DNA of the other species even after a long exposure time (about 2 weeks). These guidelines ensured that the absence of signals was due to the absence of a heterologous sequence with 85% or greater homology at the stringency used (0.5 SSC) (Beltz et al. 1983) rather than to a failure in the hybridization procedure.

We observed that the majority of the clones tested were present in the genomes of both barley and *T. tauschii*. Ninety-five percent (21/22) of the *T. tauschii* clones hybridized to barley DNA, and 98% (130/133) of barley clones hybridized to *T. tauschii* DNA. This indicates that a high proportion of low-copy-number sequences is conserved between the genomes of barley and *T. tauschii*.

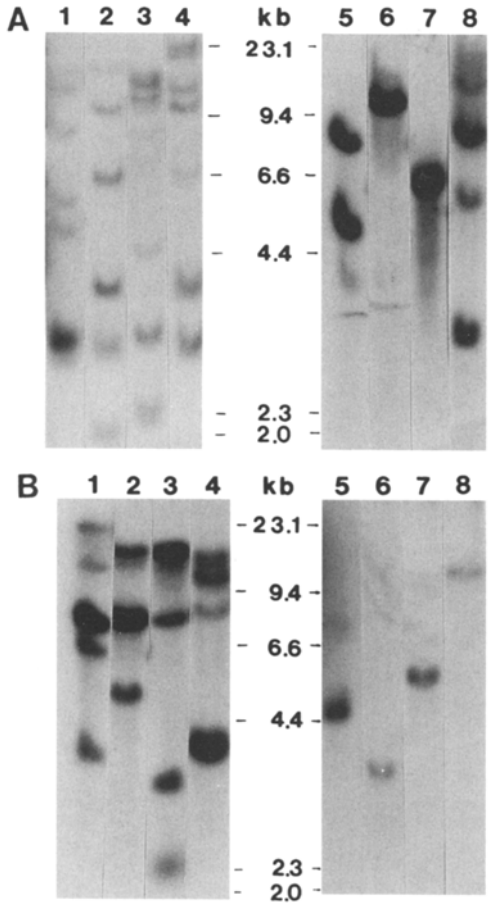


Fig. 1A, B Autoradiograms showing examples of copy-number comparisons between barley and wheat. *Lanes 1, 2, 3, 4* contain DNA from barley, and *lanes 5, 6, 7,* and *8* contain DNA from *T. tauschii*. DNA was cut with the following restriction enzymes: *lanes 1* and *5*, *Eco*RI; *2* and *6*, *Eco*RV; *3* and *7*, *Dra*I; *4* and *8*, *Xba*I. DNA was probed with KSUD14 (**A**) and ABG705 (**B**)

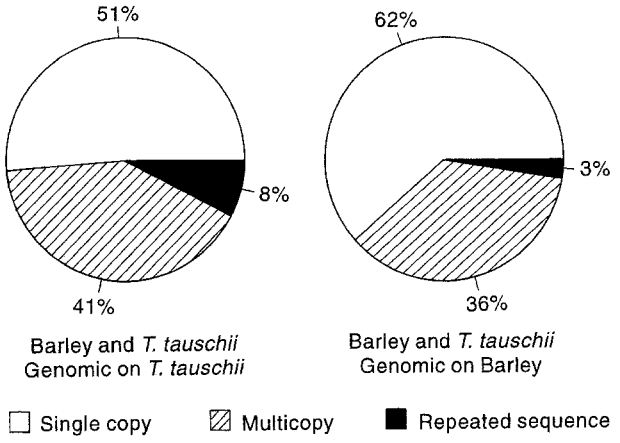


Fig. 2 Proportion of genomic clones classified as single-copy, multi-copy, and repeated in the genomes of barley and *T. tauschii*. A set of 78 barley and *T. tauschii* genomic clones was used by hybridizing each clone to barley and *T. tauschii* DNA

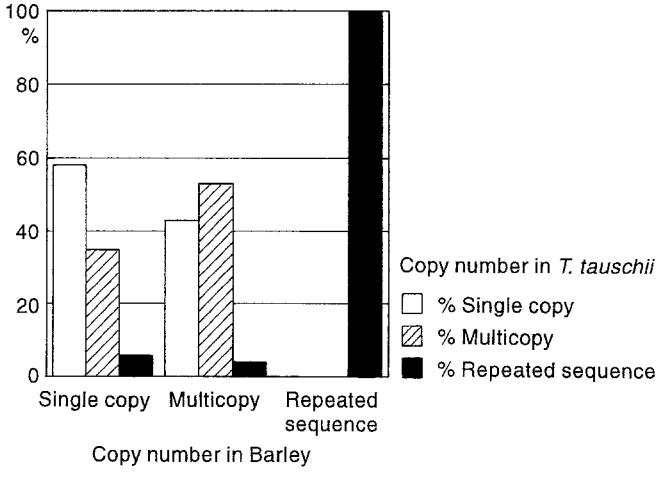
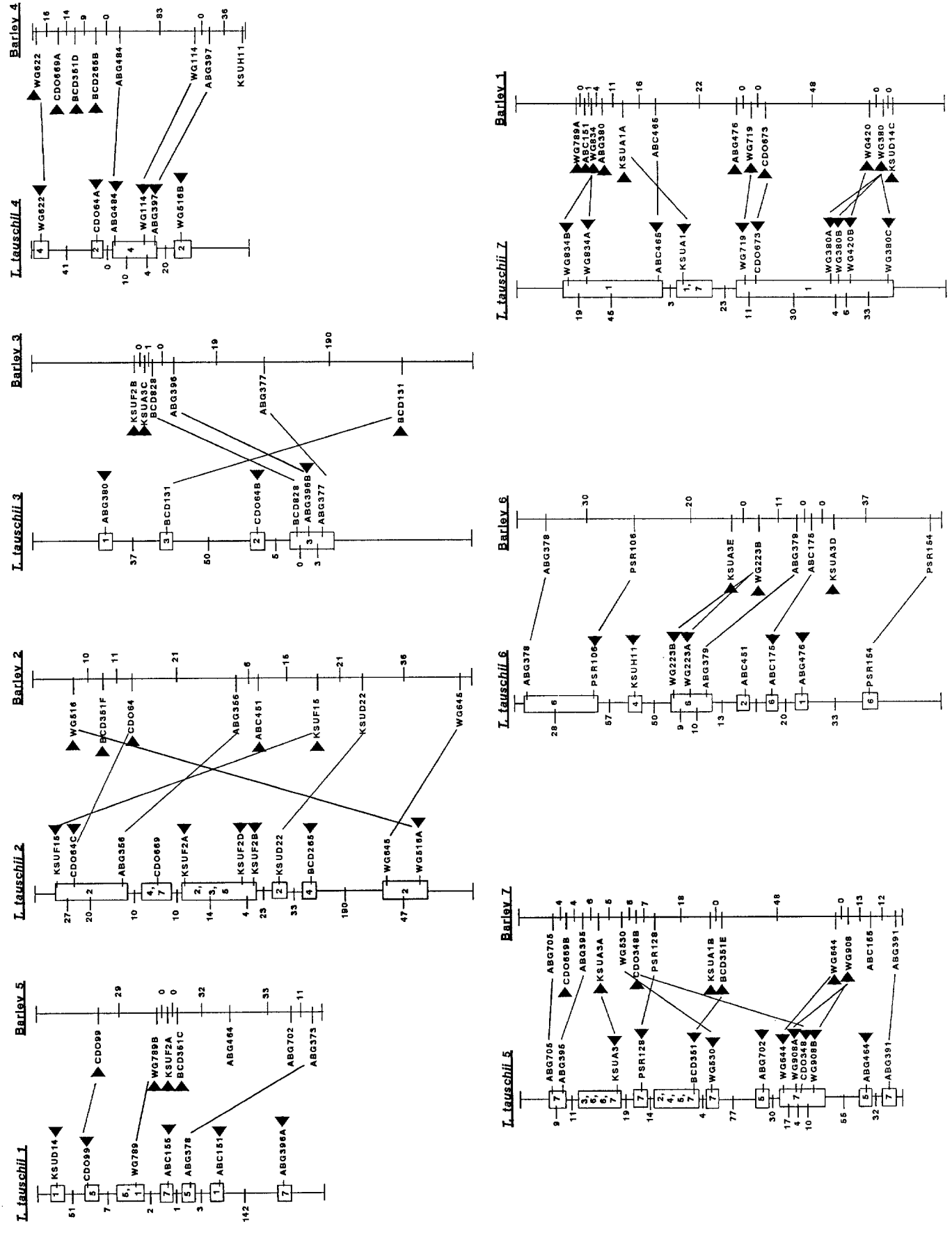


Fig. 3 Differences in copy numbers of conserved DNA sequences between barley and *T. tauschii*. The bar graphs represent the proportion of clones in *T. tauschii* containing single-copy, multi-copy, and repeated sequences. The X-axis indicates the corresponding copy numbers in barley

Copy numbers of conserved sequences in barley and *T. tauschii*

To compare the copy numbers of conserved sequences in the genomes of barley and *T. tauschii*, a set of 78 genomic clones (from the barley and *T. tauschii Pst*I libraries) which hybridized to both barley and *T. tauschii* DNA was used. The clones, consisting of 57 barley and 21 *T. tauschii* clones, were hybridized to filters containing barley and *T. tauschii* DNA cut with four restriction enzymes and classified as single-copy, multi-copy, or repeated. A single-copy clone was defined as one which hybridized to only one band with three or more restriction enzyme digests. A multi-copy clone hybridized to two or more bands in two or more enzyme digests, and a repeated sequence clone showed a smear with all enzyme digests. Fig. 1 illustrates two examples of copy-number comparisons between barley and *T. tauschii*. Fig. 1 A shows hybridization of a *T. tauschii* genomic clone insert (KSUD14) to barley and *T. tauschii* DNA. This clone hybridized to at least two bands with two restriction enzymes in *T. tauschii* and several bands in barley. Therefore, it was classified as multi-copy in both *T. tauschii* and barley. Fig. 1 B shows a barley genomic clone (ABG705) which was multi-copy in barley and single-copy in *T. tauschii*. When hybridizing with a heterologous probe, a lower stringency condition was used in post-hybridization washes (0.5×SSC vs 0.2×SSC for homologous probes) to allow detection of DNA sequences that may be poorly conserved in the other species.

The proportion of *Pst*I genomic clones falling into each category in the genomes of barley and *T. tauschii* is depicted in Fig. 2. The majority of the clones hybridized to single-copy or multi-copy sequences, while a small proportion of clones hybridized to repeated sequences in both species. The relative proportions of single-copy, multi-


T. tauschii 1
Barley 5
T. tauschii 2
Barley 2
T. tauschii 3
Barley 3
T. tauschii 4
Barley 4
T. tauschii 5
Barley 7
T. tauschii 6
Barley 6
T. tauschii 7
Barley 1

copy, and repeated sequences are similar in the two genomes (i.e., not significantly different at P=0.05). However, when individual clones were compared for copy numbers in the two genomes, 42% showed differences. Of clones that were single-copy in barley, approximately 58% were also single-copy, while 35% were multi-copy and 6% were repeated in *T. tauschii* (Fig. 3). Of clones that were multi-copy in barley, 53% were also multi-copy, while 43% were single-copy and 4% were repeated in *T. tauschii*. All clones that were repeated in barley were also repeated in *T. tauschii*.

Comparison of gene order between barley and *T. tauschii*

Fifty-two markers previously mapped in barley (Kleinhofs et al. 1993) were polymorphic and mapped in *T. tauschii*. Markers were evenly distributed on the seven linkage groups of *T. tauschii* and barley (Fig. 4). The numbered boxes in the linkage groups of *T. tauschii* in Fig. 4 indicate the corresponding chromosome location of the markers in barley. Two features were apparent when the *T. tauschii* and barley maps were compared. First, almost all the *T. tauschii* linkage groups comprised markers that mapped to a few different barley chromosomes. For example, *T. tauschii* chromosome 1 had markers that mapped to chromosomes 1, 5 and 7 of barley (Fig. 4). The only exception was *T. tauschii* 7 where all markers had at least one locus map to barley 1. Second, although markers in the *T. tauschii* linkage groups came from more than one barley chromosome, in six of seven *T. tauschii* linkage groups, the majority of those markers mapped to only one barley chromosome. In chromosome 2 of *T. tauschii*, for example, 6 of 11 loci mapped to barley chromosome 2. Similar observations were found in the other *T. tauschii* chromosomes, with the exception of chromosome 1. Four of six loci in *T. tauschii* 3 were in barley 3; four of six loci in *T. tauschii* 4 were in barley 4; 11 of 13 loci in *T. tauschii* 5 were in barley 7; seven of ten loci in *T. tauschii* 6 were in barley 6; and all ten loci in *T. tauschii* 7 were in barley 1. In *T. tauschii* chromosome 1, three loci mapped to barley 5, but the other three loci mapped to barley 1. One marker, WG789, mapped to barley chromosomes 1 and 5. Based on homoeology studies involving isozymes (Benito et al. 1985; Hart 1987), *T. tauschii* chromosome 1 is homoeologous to barley chromosome 5. Therefore, the observation of as many loci in *T. tauschii* 1 with homology to barley chromosome 1 as with barley chromosome 5 was not expected. *T. tauschii* linkage group chromosome 1 was lined up against barley chromosome 5 in Fig. 4 because no other linkage group in *T. tauschii* appears to be homoeologous to barley chromosome 5.

A comparison of the linear order of common markers in homoeologous chromosomes showed that the marker orders are very similar (Fig. 4). Common markers between *T. tauschii* 1 and barley 5, *T. tauschii* 4 and barley 4, and *T. tauschii* 6 and barley 6, are co-linear. In the other chromosomes, slight changes in the order of markers in *T. tauschii* chromosomes with respect to barley occurred. For example, switches were observed in the positions of KSUF15 and WG516A in chromosome 2. Other *T. tauschii* chromosomes where switches were seen with respect to the homoeologous barley chromosomes included *T. tauschii* 3, 5 and 7.

All loci that differed in chromosome location or order between *T. tauschii* and barley were detected by multi-copy probes (indicated by arrowheads in Fig. 4) in *T. tauschii*, barley, or both. There were nine probes in *T. tauschii* and six in barley that mapped to multiple loci. The multiple loci detected by a probe were designated with a letter following the probe name (e.g., KSUF2A, B). We observed that, oftentimes, if a marker mapped to multiple loci in one or both species, one of the loci was in the same position in homoeologous chromosomes of barley and *T. tauschii*, while the other copies did not have corresponding loci in the other species. WG789 is an example. It mapped to chromosomes 1 and 5 in barley and to one locus in chromosome 1 of *T. tauschii*. The order of WG789 in barley chromosome 5 relative to markers CDO99 and ABG373 is the same as in *T. tauschii* chromosome 1. However, WG789A in barley does not have a corresponding locus mapped in *T. tauschii* chromosome 7.

It was also found that some multi-copy probes in barley or *T. tauschii* did not have corresponding loci in the homoeologous chromosome of the other species (i.e., orthologous loci). ABG380 in *T. tauschii* 3 and barley 1, is one example. Oftentimes, not all bands detected by a multi-copy probe can be mapped. It is possible that orthologous loci between the two species are not mapped due to lack of polymorphisms.

Markers from the barley map cover 918 cM, whereas the same markers in *T. tauschii* cover 1 332 cM. A paired t-test with homoeologous chromosomes as pairs, showed no significant difference (P=0.29) between the genetic lengths of barley and *T. tauschii* chromosomes (Table 1). Also, when selected intervals, consisting of pairs of markers adjacent to each other and co-linear in the two maps (Table 1), were compared, there was no significant difference (P=0.39) between *T. tauschii* and barley. There are cases where recombination was higher in barley (CDO99-ABG373; WG622-ABG397), or higher in *T. tauschii* (KSUD22-WG645; ABG378-PSR154; WG719-WG380), and cases where they were nearly equal (CDO64-ABG356; BCD828-ABG377; ABG705-KSUA3; PSR128-BCD351).

Fig. 4 RFLP map of *T. tauschii* chromosomes and the homoeologous barley chromosomes. *Numbered boxes* in *T. tauschii* chromosomes indicate the corresponding chromosome locations in barley. A comparison of co-linearity of markers between barley and *T. tauschii* is shown by *lines* across homoeologous chromosomes. Markers with an *arrowhead* are multi-copy in that particular species. Markers without an *arrowhead* are single-copy in the respective species, except for markers ABC175, ABG464, ABG484, ABG702, ABG705, KSUH11, PSR106, PSR128, and PSR154 in barley for which copy-number data were unavailable. *Numbers* on the left and right sides of each chromosome indicate the genetic distances between markers

Table 1 Comparison of genetic lengths of homoeologous chromosomes and common intervals between *T. tauschii* and barley RFLP maps

Chromosome number (*T. tauschii*/barley)	Total chromosome length (cM)		Interval length (cM)		
	T. tauschii	Barley	Interval	*T. tauschii*	Barley
1/5	97	105	CDO99-ABG373	61	105
2/2	377	120	CDO64-ABG356	20	21
			KSUD22-WG645	223	36
3/3	96	211	BCD828-ABG377	3	19
4/4	76	158	WG622-ABG397	55	122
5/7	280	124	ABG705-KSUA3	20	14
			PSR128-BCD351	14	18
6/6	231	99	ABG378-PSR154	231	99
7/1	175	101	WG719-WG380	84	48

Discussion

Comparison of barley and *T. tauschii* genomes

The genomes of *T. tauschii* and barley were compared in terms of similarities in the composition of low-copy-number DNA sequences, the copy numbers of conserved sequences, and the order of RFLP markers in linkage groups. The results showed that the genomes of these two species share a very high proportion (>95%) of low-copy sequences. However, many of the conserved sequences have different copy numbers in the two genomes. Only 58% of the sequences compared have the same copy numbers in *T. tauschii* and barley. For those showing changes, most were from single-copy to multi-copy or multi-copy to single-copy in one species compared to the other. These results suggest the occurrence of duplications and/or deletions in the evolution of the two genomes.

Positioning of 52 markers previously mapped in barley onto the *T. tauschii* map revealed conserved linkage groups between *T. tauschii* and barley. Each linkage group of *T. tauschii* mostly comprised markers that mapped to one barley chromosome, with the exception of *T. tauschii* 1/barley 5. Furthermore, the linear order of markers in the conserved linkage groups was maintained. Based on these comparisons, *T. tauschii* chromosomes 1, 2, 3, 4 ,5, 6, and 7 were found to be similar to barley chromosomes 5, 2, 3, 4, 7, 6 and 1, respectively. It was also noted that *T. tauschii* chromosome 1 contained as many markers that mapped to barley chromosome 1 as those that mapped in barley chromosome 5. The results, except those for *T. tauschii* 1, agree with previously established homoeologous relationships between barley and *T. tauschii* based on isozyme markers (Benito et al. 1985; Hart 1987).

There were also a few differences observed between the homoeologous chromosomes of *T. tauschii* and barley. First, except for chromosome 7, all of the chromosomes of *T. tauschii* contained markers that mapped to non-homoeologous barley chromosomes. The presence of three out of seven markers in *T. tauschii* chromosome 1 that belong to a second barley chromosome (chromosome 1) may be a result of duplication and is explained a little later in this section. Secondly, within conserved linkage groups, a change in the order of some markers was observed in *T. tauschii* compared to barley. Interestingly, all DNA segments involved in these changes comprised only one or two markers whose orders in *T. tauschii* differed with respect to barley, despite the relatively large number and even distribution of mapped markers compared. Clusters of three or more markers that had different orders or chromosomal positions in the two species were not found, as would be expected if chromosomal rearrangements such as translocations had occurred. In other comparative mapping studies where translocations and inversions were reported, the segments involved in rearrangements in one species contained several markers representing contiguous loci in the other species (Bonierbale et al. 1988; Tanksley et al. 1988; Devos et al. 1993).

The observations that all of the loci involved in the changes in marker order or chromosome positions come from multi-copy probes provide a clue for a possible mechanism for these changes. These observations suggest that DNA segments common to barley and *T. tauschii* underwent duplications in one or both species after their divergence from a common ancestor, and new copies were inserted at new sites. It is also just as likely that a deletion of a locus from a multi-copy marker in one or the other species occurred after the species diverged in evolution. This would explain why in many of the multi-copy probes, one locus has the same exact position in barley and *T. tauschii*, while the other copies of the same probe do not have corresponding loci in the other species. In cases where a multi-copy probe does not have orthologous loci in the two species, it may also be possible that the orthologous locus is non-polymorphic, and therefore unmappable, in one of the species. This statement is supported by our observation that in some multi-copy probes in barley, one of the bands can be assigned to a barley chromosome (in a wheat-barley addition line) that is homoeologous to a *T. tauschii* chromosome containing a locus for those individual probes. An example is shown in Fig. 5. ABG476, a multi-copy probe in barley, mapped to chromosome 1 in barley and chromosome 6 in *T. tauschii*. Figure 5 shows that the major band of this probe is located in chromosome arm 1S of barley as expected from the map. However, a second

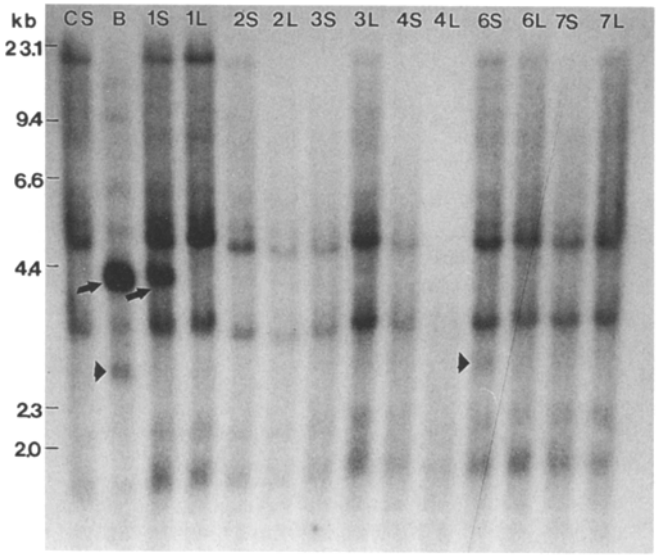


Fig. 5 Autoradiogram showing hybridization of ABG476 to a Southern blot containing DNA from wheat cv 'Chinese Spring' (*CS*), barley cv 'Betzes' (*B*), and 12 wheat/barley ditelosomic addition lines. Barley chromosome arms are indicated above the lanes. *1S*= wheat plus barley chromosome arm 1S, *1L*=wheat plus barley chromosome arm 1L, etc. *Arrows* point to a barley band seen in wheat/barley ditelosomic 1S. *Arrowheads* point to barley band seen in wheat/barley ditelosomic 6S

band, which is much weaker, is also present in barley chromosome arm 6S, which suggests that the mapped locus in *T. tauschii* corresponds to this minor band in barley.

The results from the present study show that the genomes of barley and *T. tauschii* are generally similar, despite the fact that these species are sexually incompatible. Unlike findings in the comparative mapping of wheat and rye, indicating the occurrence of translocations in the A and B genomes of wheat and the R genome of rye (Devos et al. 1993; Liucj et al. 1992), translocations do not seem to have played an important role in the evolution of the genomes of barley and *T. tauschii*. The few differences observed between these two species are most likely due to duplications and/or deletions of sequences. This is consistent with our findings that although low-copy sequences are conserved in the genomes of barley and *T. tauschii*, many of these sequences have undergone changes in copy numbers which may have been brought about by duplications and deletions.

The mechanism(s) responsible for generating duplications or deletions is unknown. It is possible that transposons may have been involved. Deletion of DNA may result from the excision of a transposon. Duplicated sequences may be generated from the insertion of a transposon into a target site. However, sequences duplicated during transposon insertion are generally short (4–10 bp long; see Freeling 1984 for review), while target sequences detected by Southern hybridization are usually several hundred base pairs long. Transposons have not been isolated in barley or *T. tauschii*, although a retrotransposon-like sequence has been found in wheat (Harberd et al. 1987; Liu et al. 1992). Unequal crossing-over between homologous chromosomes and gene conversion are other possible mechanisms that could explain duplication and deletion of sequences within a chromosome (Smith 1975; Dover 1982; Arnheim 1983). However, neither of these can explain the presence of duplicated sequences in non-homoeologous chromosomes.

Implications for genetic mapping, breeding, and plant genome evolution

The high degree of conservation observed between homoeologous chromosomes of barley and *T. tauschii* indicates that most DNA markers can be used interchangeably between the two species to saturate specific chromosome regions lacking markers. The same set of single-copy RFLP markers may be useful for tagging genes for important traits in barley and *T. tauschii*, but caution must be taken when using multi-copy markers. In such instances, the loci mapped in the two species may not be orthologous and, therefore, will map to non-homoeologous chromosomes.

RFLP mapping has allowed comparisons between the genomes of species that are closely, as well as distantly, related. In monocots, extensive comparisons have now been made between barley and *T. tauschii* (this study), wheat and rye (Devos et al. 1993), rice and maize (Ahn and Tanksley 1993), and rice and wheat (Ahn et al. 1993; Kurata et al. 1994). These studies have revealed conserved linkage groups, even between species that are as remotely related as rice and maize (Ahn and Tanksley 1993), and rice and wheat (Ahn et al. 1993). Duplications and deletions of sequences appear to be important in the evolution of plant genomes, as shown in the present study and others (Helentjaris et al. 1988; Hulbert et al. 1990; Ahn and Tanksley 1993). Other processes, such as translocations and inversions, have also been involved in the evolution of some plant genomes, particularly polyploid species (Ahn and Tanksley 1993; Devos et al. 1993). As more comparisons between other monocot species are conducted, it will be possible to obtain a better picture of these evolutionary processes. The identification of conserved linkage groups might also be important in identifying genes for traits in monocot species.

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