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The distribution of RFLP markers on chromosome 2(2H) of barley in relation to the physical and genetic location of 5S rDNA

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Abstract. The 5S rDNA locus on the long arm of barley chromosome 2(2H) was genetically mapped in two crosses in relation to 30 other RFLP loci. Comparison of the genetic maps with the previously published physical position of the 5S rDNA, determined by in-situ hybridization, showed that there was a marked discrepancy between physical and genetic distance in both crosses, with recombination being less frequent in the proximal part of the arm. Pooled information from the present study and other published genetic maps showed that at least 26 of the 44 (59%) RFLPs that have been mapped on 2(2H)L lie distal to the 5S rDNA locus even though this region is only 27% of the physical length of the arm. The distribution of RFLP markers is significantly different from expected ($P < 0.01$), implying that the low-copy sequences used for RFLP analysis occur more frequently in distal regions of the arm and, or, that sequences in distal regions are more polymorphic.

Key words: Barley – RFLP – 5S rDNA – Genetic mapping – Physical mapping

Introduction

The development and application of RFLP-based high-resolution genetic maps of cereals will benefit from an understanding of the relationship between the distribution of genes and the distribution of recombination events along chromosomes. This information will help define the physical distances between linked loci, and will be valuable in developing strategies for marker-mediated selection and gene cloning.

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RFLP-based genetic maps of barley (*Hordeum vulgare* L.) are developing rapidly (Graner et al. 1991; Heun et al. 1991), but these maps provide little information on the physical positions of genetic markers. It is important to investigate physical location because previous studies in wheat, rye and barley all show that the distribution of recombination events is highly non-random, with most occurring in distal regions (see Discussion).

Information on the physical position of genetic markers can be obtained by incorporating cytological markers such as nucleolus organizer regions (NORs), C-bands and in-situ hybridization sites into genetic maps. The present paper describes the distribution of RFLP markers on barley chromosome 2(2H) in relation to the physical and genetic location of sequences encoding 5S ribosomal RNA. 5S rDNA was reported on chromosome 2(2H) of barley by Kolchinsky et al. (1990, 1991) using wheat/barley single chromosome addition lines. More recently, Leitch and Heslop-Harrison (1993) described four 5S rDNA sites in the barley genome using in-situ hybridization, and designated the site on the long arm of chromosome 2(2H) as *5SDna-H3*.

Materials and methods

The mapping populations

Genetic maps were constructed using two F_2 populations each consisting of 120 plants. One population was from a cross between the barley cvs Betzes and Golden Promise and the second was from a cross between cv Captain and *H. spontaneum* (IPSR accession 2370).

RFLP analysis

The probes detecting RFLP are listed in Table 1. With the exception of pTa794, where *Taq*I digests were employed, *Eco*RI, *Eco*RV, *Dra*I or *Hin*dIII digests were used to identify RFLP. DNA extraction, Southern blotting by alkaline transfer to Hy-

Table 1. Clones mapped on barley chromosome 2(2H)

Probe	Locus	Type	Size (kb)	Wheat location[a]	Mapped in	
					Wheat[a]	Rye[a]
PSR102	*Xpsr102*	Wheat cDNA	0.57	2L	+	+
PSR108	*Xpsr108*	Wheat cDNA	0.85	2S, 7S	−	−
PSR109	*Xpsr109*	Wheat cDNA	0.65	2S, 5L	+	+
PSR126	*Xpsr126*	Wheat cDNA	0.75	2S	−	−
PSR150	*Xpsr150*	Wheat cDNA	0.70	2S, 5L, 7S	+	−
PSR331	*Xpsr331*	Wheat gDNA	0.70	2L	+	+
PSR540	*Xpsr540*	Wheat gDNA	2.00	2L, 7BS	+	+
PSR566	*Xpsr566*	Wheat gDNA	2.50	2S	+	−
PSR630	*Xpsr630*	Wheat gDNA	2.20	2L	+	+
PSR666	*Xpsr666*	Wheat gDNA	1.30	2S	+	+
PSR687	*Xpsr687*	Wheat gDNA	2.00	2L, 7L	−	+
PSR901	*Xpsr901*	Wheat gDNA	1.40	2L	+	+
pST3	*XSs2*	Wheat cDNA[b]	0.92	2S	−	+
pTa794	*X5SDna-H3*	Wheat 5S rDNA	0.41	1S, 5S[c]		
PSRB9	*XpsrB9*	Barley gDNA	0.90			
PSRB24	*XpsrB24*	Barley gDNA	1.20			
PSRB30	*XpsrB30*	Barley gDNA	1.00			
PSRB31	*XpsrB31*	Barley gDNA	1.70			
PSRB141	*XpsrB141*	Barley gDNA	1.60			
BCD175	*XBCD175*	Barley cDNA	0.70			
BCD266	*XBCD266*	Barley cDNA	1.50			
BCD410	*XBCD410*	Barley cDNA	0.80			
CDO366	*XCDO366*	Oat cDNA	1.40			
CDO373	*XCDO373*	Oat cDNA	0.90			
CDO588	*XCDO588*	Oat cDNA	1.60			
WG645	*XWG645*	Wheat gDNA	2.60			
WG996	*XWG996*	Wheat gDNA	1.00			
MWG858	*XMWG858*	Barley gDNA	1.00			
MWG865	*XMWG865*	Barley gDNA	0.60			
MWG878	*XMWG878*	Barley gDNA	1.80			

Probes with a PSR prefix are wheat cDNA or wheat genomic clones from the Cambridge Laboratory, IPSR. Probes with a PSRB prefix are barley *Pst*I genomic clones from the Cambridge Laboratory, IPSR. Probes with the prefix BCD, CDO or WG were previously mapped in barley by Heun et al. (1991). Probes with the prefix MWG were previously mapped in barley by Graner et al. (1991) and Graner (personal communication). pTa794 consists of part of the 120-bp coding region and the non-transcribed spacer of wheat 5S rDNA and was isolated by Gerlach and Dyer (1980)

[a] Chromosome location and the list of mapped probes are from Devos et al. (1993a)

[b] Type-two sucrose synthase cDNA. Probe from Dr. P. Carbonero

[c] Physical locations determined using in-situ hybridization by Mukai et al. (1990)

bond N+ membrane (Amersham), probe labelling with ^{32}P and hybridization was as described in Devos et al. (1992) except that denaturation of the labelled probe was by addition of 1/10 vol 3 M NaOH for 5 min. The barley chromosome arm location of PSRB, BCD, CDO, WG and MWG probes was determined using Chinese Spring/Betzes ditelosomic addition lines (Islam 1983). Linkage maps were made using the MAPMAKER v2.0 program (Lander et al. 1987) with the Kosambi mapping function. A map of six loci (*XSs2, Xpsr126, Xpsr102, Xpsr901, Xpsr630* and *Xpsr331*) in the Captain × *H. spontaneum* cross was previously described by Devos et al. (1993a).

Results

RFLP mapping

A total of 54 probes were tested for RFLP in Betzes and Golden Promise, and 36 probes in Captain and *H. spontaneum*. Twenty-one RFLPs were identified in the Betzes × Golden Promise cross (39% of the probes), and 22 in the Captain × *H. spontaneum* cross (61% of the probes) giving a total of 30 2(2H) markers. Eleven loci, including *X5SDna-H3*, were mapped in both crosses.

*Taq*I-digested DNA from the parental lines and from individuals of the F_2 populations gave multiple bands when probed with pTa794. However, in the Betzes × Golden Promise population the band pattern of individual F_2 plants was either identical to Betzes, identical to Golden Promise, or was a combination of the two (Fig. 1). The ratio of plants in these three categories was not significantly different from 1:1:2, showing that a single locus was segregating. The F_2 plants of the Captain × *H. spontaneum* population could be scored for the presence or absence of a band specific to Captain. The

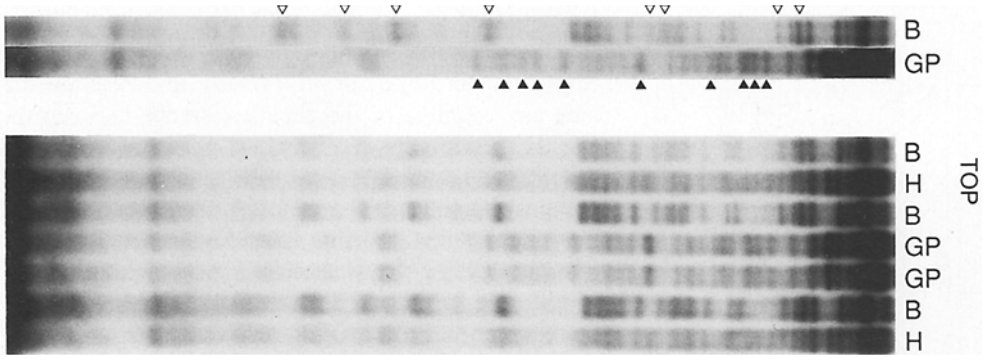

Fig. 1. *Taq*I digests of DNA from the Betzes × Golden Promise population probed with pTa794. The two tracks on the left are the parental varieties. Examples of Betzes-specific bands are indicated by *open arrowheads*, and Golden Promise-specific bands by *solid arrowheads*. The seven tracks on the right show individual F_2 plants and their respective genotypes

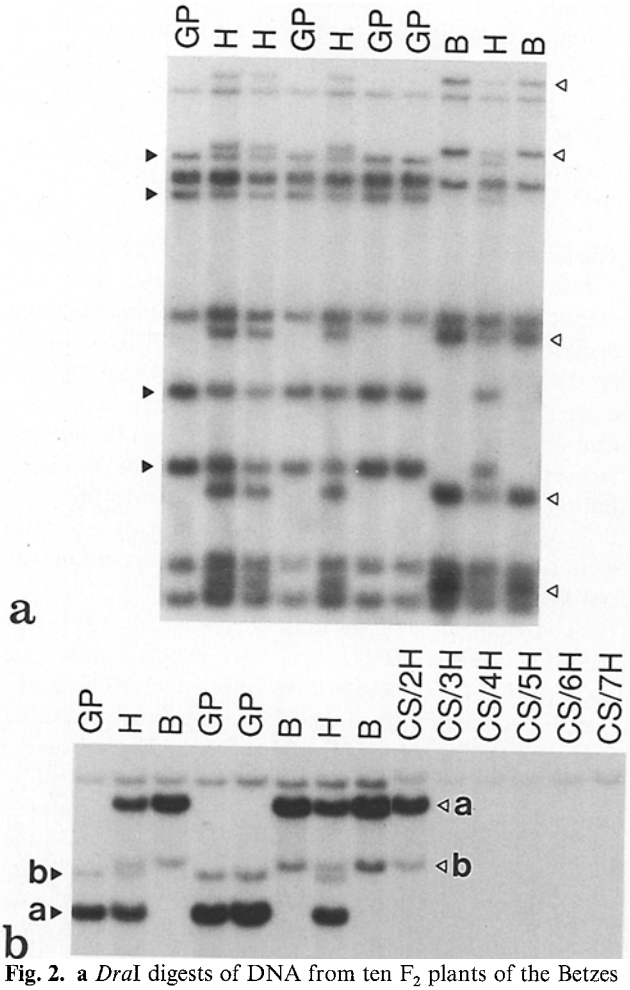

Fig. 2. **a** *Dra*I digests of DNA from ten F_2 plants of the Betzes × Golden Promise population probed with PSR109. **b** *Hin*dIII digests of DNA from eight F_2 plants of the Betzes × Golden Promise population and from Chinese Spring/Betzes whole-chromosome addition lines probed with PSRB31. Betzes bands are indicated by *open arrowheads*, Golden Promise bands by *solid arrowheads*. The *a* and *b* polymorphisms cosegregated in all but one individual (data not shown), showing that this probe detected two closely-linked loci (*XpsrB31a* and *Xpsr31b* in Fig. 3)

segregation of this polymorphism was not significantly different from a 3:1 ratio which again showed segregation of a single locus. In both crosses the locus detected with pTa794 was linked to RFLP markers specific to the long arm of chromosome 2(2H), identifying it as *X5SDna-H3*, the 5S rDNA site found on the long arm of chromosome 2(2H) by in-situ hybridization using digoxigenin-labelled pTa794 (Leitch and Heslop-Harrison 1993).

Apart from pTa794, most probes gave two to four bands in individual F_2 plants which identified single loci. Two probes, PSR109 (Fig. 2a) and PSRB9, gave multiple bands with several differences but in both crosses bands specific to each parent always cosegregated, showing that each probe detected only a single locus. The map position of *Xpsr109* and *XpsrB9* in relation to other RFLP markers makes it likely that the same loci were scored in both crosses. PSRB31 (Fig. 2b) detected two closely-linked loci in the Betzes × Golden Promise cross.

Comparison of the two barley crosses

The genetic maps of chromosome 2(2H) in the two barley crosses are shown in Fig. 3 together with the physical position of the 5S rDNA. The 11 loci mapped in both crosses gave the same locus order in both cases. However, the overall map of the Captain × *H. spontaneum* cross was longer than that of the Betzes × Golden Promise cross (181 cM vs 167 cM), principally due to a higher frequency of recombination in the proximal part of the short arm. The map positions of the BCD, CDO, WG and MWG probes were consistent with published results (Graner et al. 1991; Heun et al. 1991; Graner personal communication). Ten of the PSR probes mapped in barley, as well as pST3, have also been mapped in wheat or rye (see Table 1). The order of loci was the same in all three species, although the genetic distances between loci in pericentromeric regions was greater in barley.

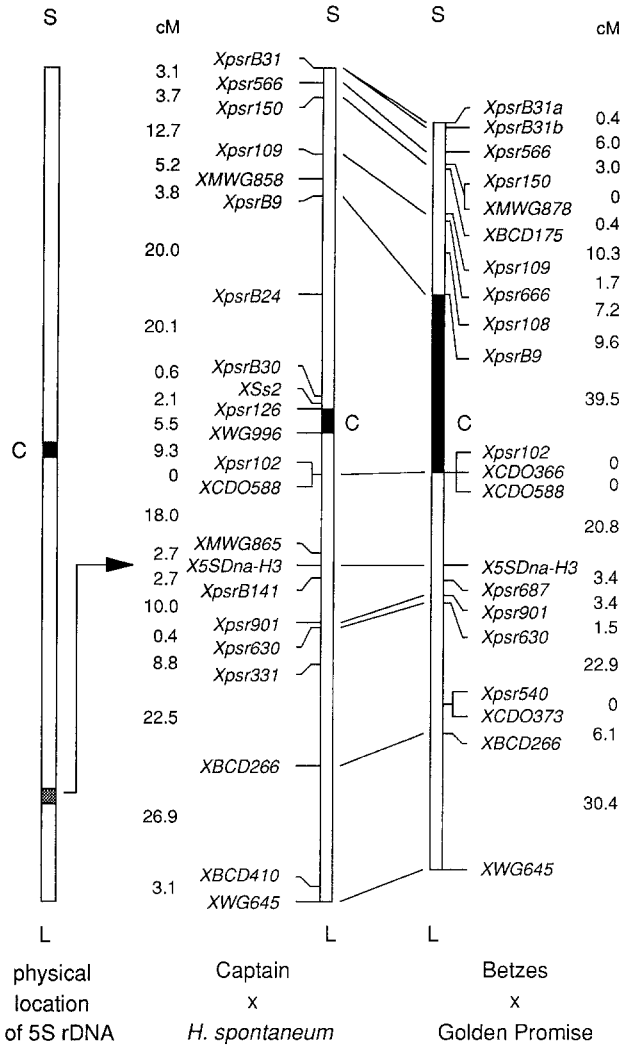

Fig. 3. Genetic maps of chromosome 2(2H) together with the physical location of the 5S rDNA. *Lines* between the two genetic maps identify the 11 probes mapped in both crosses, and the *solid black segments* show the interval spanning the centromere. The arm ratio of the 2(2H) chromosome shown on the left and the physical position of the 5S rDNA (the measured position of the pTa794 in-situ hybridization signal) are from Leitch and Heslop-Harrison (1993). The overall order is the most likely, and the positions of common markers are consistent with other published maps

Comparison of physical and genetic distances

Comparison of the genetic map of the Captain × *H. spontaneum* cross with the physical map (Fig. 3) showed that recombination was substantially less frequent in the centromere→*X5SDna-H3* interval compared to the *X5SDna-H3*→telomere interval, so that the *X5SDna-H3* locus was closer to the centromere on the genetic map than would be expected from its physical position. The *X5SDna-H3* locus was no more than 33% of the genetic map length from the centromere compared to 73% of the physical length. Furthermore, this is a minimum estimate since it includes the whole of the map interval containing the centromere (*Xpsr126*→*XWG996*), and does not include any estimate of the genetic distance between the most distal long arm marker (*XWG645*) and the telomere.

Physical and genetic distances in the Betzes × Golden Promise cross could not be compared as accurately because probes for the pericentromeric region were not polymorphic, despite being tested with 12 additional restriction enzymes. As a result the centromere could only be located to the 39.5 cM interval between *XpsrB9* and the *Xpsr102-XCDO366-XCDO588* locus (Fig. 3). However, comparison with the Captain × *H. spontaneum* map makes it likely that the centromere is genetically closer to the *Xpsr102* cluster, indicating a reduction in pericentromeric recombination in the long arm similar to that of the Captain × *H. spontaneum* cross.

The distribution of RFLP markers on the long arm of chromosome 2(2H) relative to the physical position of the 5S rDNA

The RFLP maps in Fig. 3 contain seven markers mapped in barley by Heun et al. (1991), five of which were also mapped by the North American barley genome mapping project (NABGMP) in the cross Steptoe × Morex. In addition, the most recent NABGMP map (NABGMP circular 9.9.92) also includes the 5S rDNA locus on the long arm of chromosome 2(2H). Thus, data from these three crosses can be combined to give an estimate of the distribution of long arm RFLP markers relative to the position of the 5S rDNA. Data from Graner et al. (1991) were not included because the centromere position was not known.

The centromere on the map of Heun et al. (1991) was placed between *XCDO537* and *XWG996* by hybridizing these probes to Chinese Spring/Betzes ditelosomic addition lines, identifying *XWG996* as the most proximal long-arm marker. On the NABGMP map the centromere was placed between *XBmy2* located on the short arm by Kreis et al. 1988) and *XWG996*. This interval includes two other loci, which were both assumed to be on the long arm. It was also assumed that all markers proximal to *XCDO373* in the map of Heun et al. (1991) were proximal to the 5S rDNA, which is reasonable given that *XCDO373* was unlinked to the more proximal markers in their cross.

On the above interpretation the numbers of RFLP markers proximal or distal to the 5S rDNA are 20 and 30 respectively, though the latter region occupies only 27% of the physical length of the arm. The expected ratio in a sample of 50 probes is 36 to 14, assuming a random distribution of single and low-copy sequences along the chromosome arm and random sampling during library

construction. The discrepancy in the ratios is significant (χ^2 1*df*=10.6 $P<0.01$). However, a significant difference is not observed when the smaller sample of expressed genes (cDNAs and cDNA-derived PCR primers) are considered (χ^2 1*df*=2.7 n.s.), although half (14 out of 28) occur in the 5S rDNA to telomere interval.

An accurate alignment of RFLP maps with the genetic map of morphological markers is not yet possible but *XMWG865*, which maps 2.7 cM proximal to *X5SDna-H3*, has the same genetic map location as the 2-row/6-row *hex-v* locus in the cross Igri × Franka (Graner personal communication). Comparison with the 2(2H) map of morphological markers (Shahla and Tsuchiya 1990) suggests that 8 of the 16 morphological markers mapped on the long arm of chromosome 2(2H) are likely to be located distal to the 5S rDNA. Combining this information with the distribution of cDNA polymorphisms indicates a significant excess of markers in the region distal to the 5S rDNA (χ^2 1*df*=4.9 $P<0.05$).

Discussion

The relationship between physical and genetic length in cereal chromosomes

The relationship between physical and genetic length along barley chromosome arm 2(2H)L is consistent with results from other chromosome arms in cereals (Linde-Laursen 1979, 1982; Dvořák and Chen 1984; Payne et al. 1984; Snape et al. 1985; Jampates and Dvořák 1986; Lawrence and Appels 1986; Kleinhofs et al. 1988; Gustafson et al. 1990; Curtis and Lukaszewski 1991; Wang et al. 1991; Lukaszewski 1992; Werner et al. 1992; Leitch and Heslop-Harrison 1993). Most of these studies involved chromosome arms bearing NORs, but it seems clear that the lower frequency of recombination in proximal regions is a general feature of the chromosomes of wheat, rye and barley.

Comparison of published genetic maps of wheat or rye with barley suggests, however, that compression of the genetic map around the centromere is less marked in barley than in wheat or rye. This is illustrated in the present work by comparison of the genetic distance between *XSs2* and *Xpsr331*, which was 17 cM in rye (Devos et al. 1993a) and 60 cM in the Captain × *H. spontaneum* cross. This behaviour should make the ordering of loci in proximal map regions easier in barley. It would be of interest to determine if the difference between barley and wheat or rye is due to differences in the distribution of recombination along the chromosome or to differences in the physical spacing of low-copy sequences.

5S rDNA probes should be useful for studying the relationship between physical and genetic distance in other barley crosses since eight different band patterns were found in *Taq*I digests of DNA from 11 additional diverse varieties probed with pTa794. This indicates that barley 5S rDNA sequences have a reasonably high level of RFLP, as reported by Khvyrleva et al. (1987). 5S rDNA probes such as pTa794 will be particularly useful if RFLP for the 1(7H) S, 3(3H)L and 4(4H) L sites recognizable by in-situ hybridization can also be identified.

The distribution of RFLP markers on chromosome 2(2H)L

The significant excess of RFLP markers in the distal region of the long arm of chromosome 2(2H) of barley indicates that the single and low-copy sequences used for RFLP analysis are more frequent in distal regions and, or, that sequences in distal regions are more polymorphic. Studies on cereals suggest that both may be contributory factors.

Firstly, analysis of wheat/rye recombinants using restriction enzymes sensitive to cytosine methylation shows a higher frequency of unmethylated *Not*I and *Mlu*I sites in distal regions of the chromosome (Moore et al. 1993). Genomic DNA libraries produced by methylation-sensitive enzymes such as *Pst*I also sample from these unmethylated islands, implying that genomic libraries will be relatively enriched for sequences from distal chromosome regions. There is also evidence that unmethylated islands are associated with genes (Moore et al. 1993), implying that distal regions of cereal chromosomes may be relatively gene rich, as has been reported for human chromosomes (Saccone et al. 1992). If so, cDNA libraries may also be relatively enriched for sequences from distal chromosome regions.

Secondly, there is evidence that wheat genomic probes that do not detect homoeologous sequences in related species are more frequently located in distal regions of the wheat genetic maps (Devos et al. 1993a). This suggests that distal chromosome regions are evolving more quickly and hence would be expected to be more polymorphic. This would also lead to a higher frequency of RFLP markers in distal chromosome regions.

Determining the relative importance of these two factors requires genotypes in which defined chromosome regions are added or deleted. The most useful for barley are probably wheat/barley recombinant chromosomes (Shepherd and Islam 1992) since the physical size and position of the barley segments can be determined by in-situ hybridization (Mukai and Gill 1991; Schwarzacher et al. 1992). Assignment of probes to the chromosome sub-regions requires a restriction-fragment difference between the wheat and barley homoeoalleles, but such differences are common and the vast majority of probes should be assignable by this method. The only class of probes not easily assignable would be those that are single or low-copy in barley but highly repeated in wheat. Barley deletion stocks might also be usable provided that

they are viable and the break points can be located precisely. In wheat, the use of deletions seems preferable since they are readily tolerated and a large number have already been defined in relation to C-band pattern (Werner et al. 1992).

It would be valuable to relate the results of such studies to the distal localization of recombination observed in cereal chromosomes. For example, if distal regions are found to be relatively gene rich, this would provide an interesting parallel with yeast (*Saccharomyces cerevisiae*) where data from the sequencing of chromosome III suggests that regions rich in transcribed genes have higher levels of recombination (Oliver et al. 1992).

Homoeologous relationships of the 2(2H) 5S rDNA site

With the exception of gross translocation differences (Devos et al. 1993b; Liu et al. 1992) there is generally a close correspondence between the order of loci on chromosomes of wheat, rye and barley when probes which cross hybridize between these three species are analyzed (Devos et al. 1992, 1993a; Laurie et al. 1992). However, this general rule of colinearity does not apply to the 2(2H) 5S rDNA site, which has no counterpart in wheat or rye. In contrast, the other 11 homoeologous group-2 clones whose map locations can be compared between barley and wheat or rye (Table 1) occur in the same order. This colinearity suggests either that there has been a small interstitial translocation of a 5S rDNA site to the long arm of chromosome 2(2H) since the evolutionary divergence of wheat, rye and barley or, more probably, that extensive sequence amplification and deletion of 5S rDNA sequences has taken place, as has been proposed for other *Triticeae* lineages (Scoles et al. 1988).

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