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A comparison of physical distribution of recombination in chromosome 1R in diploid rye and in hexaploid triticale

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Summary. Polymorphism for six C-bands on chromosome 1R was used to study the frequency and distribution of recombination along the chromosome in a diploid rye (*Secale cereale* L.) and in a hexaploid triticale (X *Triticosecale* Wittmack) derived from it. In rye, the total recombination frequency in five segments of chromosome 1R was 93.7%. Recombination was concentrated in the distal regions of both chromosome arms and was infrequent in the proximal regions. In hexaploid triticale the total recombination frequency in the same chromosome was reduced to 51.7%. In both backgrounds the distal half of the long arm showed similar recombination frequencies, 51.4% and 45.7% for rye and triticale, respectively. The remaining about two-thirds of the chromosome length showed 42.3% recombination in rye but only 6% recombination in triticale. The results demonstrate that the genetic background in which mapping is performed not only affects the total amount of recombination, but also its distribution along the chromosome length.

Key words: – *S. cereale* – Triticale – Chromosome 1R – Genetic mapping – C-banding

Introduction

While both conventional and RFLP genetic maps show fairly even distribution of markers over the length of chromosomes (Tanksley 1988; Chao et al. 1989; Hoisington and Coe 1990), there is a growing suspicion that the physical distribution of these markers may not be as even as the maps indicate (Gale et al. 1990). This may be particularly true for such species as wheat and barley where recombination is concentrated in the distal regions of chromosome arms (Linde-Laursen 1982; Dvorak and Chen 1984; Jampates and Dvorak 1986; Curtis and Lukaszewski 1991). In consequence, genes which are physically located a considerable distance away from the centromere appear tightly linked to it. In wheat, the *Ph1* gene on chromosome arm 5BL maps about 1 cM from the centromere (Sears 1984) but is physically located in the middle of the arm (Jampates and Dvorak 1986); the *Glu-B1* gene on 1BL which maps between about 10 and 30 cM from the centromere is located about 70% of the physical arm length away from it (Curtis and Lukaszewski 1991).

In some self-pollinating species RFLP mapping is complicated by a limited amount of naturally occurring polymorphism. Much higher levels of polymorphism are found when interspecific hybrids or chromosomes from related species are used in mapping (Bernatzky and Tanksley 1986; Helentjaris et al. 1986; Chao et al. 1989; Keim et al. 1989). Because chromosome pairing in interspecific hybrids is frequently reduced, such an approach would be expected to further distort the relationship between the genetic and physical distribution of markers. Reduced pairing affinity of homologous chromosomes from different cultivars and from different species (heterohomologues) was demonstrated in wheat (Dvorak and McGuire 1981; Crossway and Dvorak 1984). Since this reduction was not evenly distributed throughout the entire chromosome complement, different chromosomes and chromosome arms were affected to varying degrees. Consequently, distortions in map distances would be expected to vary for different chromosomes and chromosomes arms, or for the same chromosome depending on the origin of its pairing partner (Dvorak and Chen 1984). At times this distortion may produce surprising results. In several different mapping efforts the *Glu-B1* gene on chromosome 1B in wheat was mapped at distances of

9.1 cM (Payne et al. 1984), 18% recombination (Curtis and Feldman 1988), 28.1 cM (Singh and Shepherd 1988) and 32.6 cM (Curtis and Lukaszewski 1991) from the centromere. There were no indications that structural rearrangements of chromosome 1B were responsible for these wide discrepancies.

Differences in chromosome pairing frequencies do not directly and proportionately translate into differences in genetic distances. In three 1B chromosomes of *T. dicoccoides* mapped against the same 1B telocentrics the combination with the lowest MI pairing showed the highest recombination frequency (Curtis and Lukaszewski 1991). As suggested by Dvorak and Chen (1984) and demonstrated by Curtis et al. (1991) reduction in MI pairing coupled with selection for euploid gametes, particularly on the male side, tends to inflate the estimates of recombination frequencies.

The genetic background in which mapping is performed may also affect the result. In hexaploid triticale varying degrees of pairing reduction for the genomes of one or both of the parental species were observed (Jung and Lelley 1985; Lelley, 1985). It is not clear, however, whether such reductions would be distributed evenly throughout the genome or would again affect different chromosomes and chromosome arms to varying degrees. It appeared that rye and a derivative hexaploid triticale would be appropriate forms to study the effect of genetic background on the physical distribution of recombination and genetic map distances in the same chromosome.

Materials and methods

There are six differences in the distribution and size of C-bands between chromosome 1R of rye lines E and H (Fig. 1). Line E is an inbred from Spain (Giraldez et al. 1979); line H is a set of individuals selected for the particular banding pattern from a commercial cv 'Dankowskie Zlote' from Poland. The F_1 hybrids between the two lines were produced and backcrossed to both parents as male and female.

Rye lines E and H were crossed to line Do1 of tetraploid wheat, and hexaploid triticales Do1E and Do1H were produced and intercrossed. Pollen from the Do1E × Do1H F_1 was used in backcrosses to both amphiploids. The Do1E amphiploid shows severe necrosis, probably due to the presence of complementary *Ne-Ner* genes (Ren and Lelley 1988). The Do1E × Do1H F_1 hybrid was moderately necrotic with low plant vigor, delayed flowering and reduced fertility, and produced shriveled seed. Despite repeated attempts it was not possible to produce enough backcross seed to complete the experiment. Consequently, in addition to BC_1 progeny, a sample of F_2 was also used in this part of the experiment.

Backcross progenies in rye and backcross and F_2 progenies in triticale were individually C-banded according to Lukaszewski and Gustafson (1983), and the C-banding patterns of chromosomes 1R were noted. Each BC_1 plant had one parental (E or H, depending on the backcross partner) chromosome 1R that was excluded from the analysis. Depending on the C-banding pattern the second 1R chromosome was classified as parental or recombined (Fig. 1). In the triticale F_2 both 1R chromosomes were included in the analysis. In the recombined chromosomes the physical location of cross-over event(s) was determined assuming the minimum number of cross-overs necessary to produce the observed C-banding pattern.

The general level of MI pairing in the E × H rye F_1 hybrid was scored in Feulgen-stained preparations. For C-banding analysis of the 1R chromosome alone anthers with metaphase I were collected from plants with appropriate banding patterns on 1R following the backcross to line E. Meiotic pairing of chromosome 1R in triticale hybrids was observed on C-banded squashes of metaphase I (MI) anthers collected from sister plants of those involved in backcrosses. The meiotic C-banding procedure was the same as that for root-tip squashes.

The consensus physical map of the distribution of C-bands on both 1R chromosomes was produced. The total chromosome length and the length of the interband regions represent the mean value of 10 measurements taken directly from a TV camera-monitor system attached to the microscope. The C-bands were sequentially numbered from the centromere to the telomere S1 to S3 in the short arm and L1 to L3 in the long arm, and the interband regions were identified by their deliminating C-bands. The relative lengths of the interband regions were expressed as a proportion of the length of a region to the total length of chromosome. The relative length of the L2-L3 region, being below the resolution limit of the technique employed, was estimated from the chromosomes recombined in this segment as being about 1% of the total chromosome length.

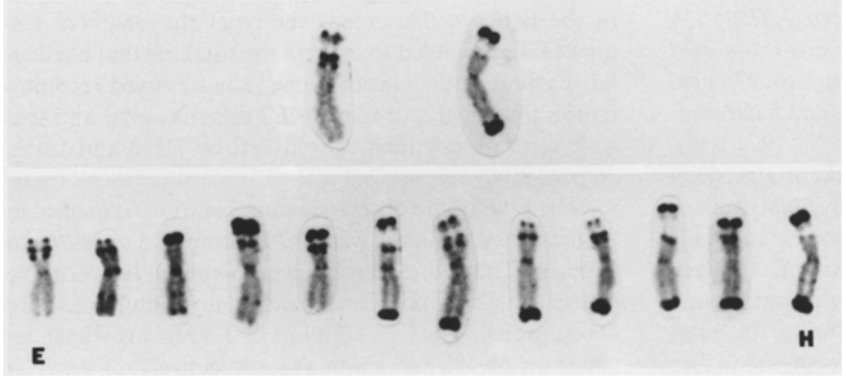

Fig. 1. C-banding patterns of the parental 1R chromosomes (*top row*) and of recombined and non-recombined chromosomes recovered in the backcross progeny in rye

Results

Metaphase I pairing frequencies

In a sample of 100 pollen mother cells (PMCs) of the E × H rye F_1 hybrid an average of 11.86 chromosome arms were paired per cell, for an 84.7% average pairing frequency. In three backcross plants with 1R chromosomes heterozygous for the presence/absence of the telomeric C-bands, the short arm of chromosome 1R (1RS) was paired in 42%, 55% and 37% of PMCs for an average MI pairing frequency of 44.7%, and the long arm of chromosome 1R (1RL) paired in 78%, 80%, and 92% of PMCs for an average MI pairing frequency of 83.3%.

In a preparation from one plant a mixture of diplotene-diakinesis and MI PMCs were present, allowing a comparison of pairing frequency of chromosome 1R between the two stages. In a sample of 135 PMCs in diplotene/diakinesis chromosome arm 1RS was paired in 86.0% of the cells compared to 42.0% of 50 PMCs at MI. Chromosome 1RL was paired in 88.9% of diplotene/diakinesis PMCs and 78.0% of MI PMCs.

In hexaploid triticale F_1 hybrids due to slow growth, poor plant vigor and poor synchrony of PMC divisions it was not possible to collect an adequate number of MI anthers for chromosome pairing analysis. In addition, very poor spreading of MI chromosomes and overall reduction of pairing of both wheat and rye chromosomes made the analysis unreliable. In a sample of 20 PMCs analyzed chromosome arm 1RS appeared to pair with a 15% frequency while 1RL with a 45% frequency.

Distribution of recombination

The total number of 1R chromosomes analyzed in rye was 206; 110 of those were from the backcross using the E × H F_1 as female, and 96 from the backcross using the F_1 as male. The differences in frequencies and distribution of cross-overs between the two populations were minor (Fig. 2) and not statistically significant. Consequently, the data from both backcross populations were pooled. Among the 206 chromosomes, 70 were classified as non-recombined (parental) of which 34 were of the H C-banding pattern and 36 of the E pattern. Among 136 recombined chromosomes, 101 required one cross-over event to produce the observed banding pattern, 27 chromosomes required two cross-over events, and 8 chromosomes three cross-over events.

In the DoIE × DoIH F_1 triticale backcross progeny only 102 chromosomes were successfully analyzed, of which 52 were from the backcross using the F_1 as female and 50 as male. Monosomics for chromosome 1R were frequent, particularly among the progeny produced in a backcross using the F_1 as female. To bring the total sample size to a level comparable to that analyzed in rye,

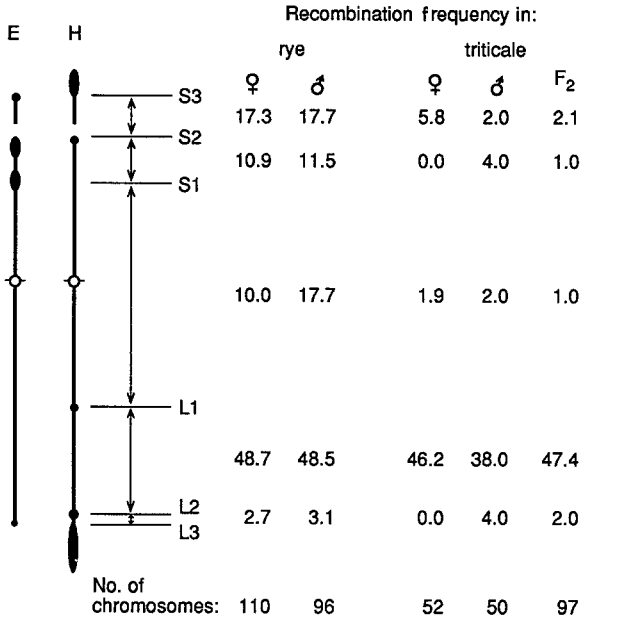

Fig. 2. Recombination frequencies in five segments along chromosome 1R in backcross progenies in rye and in backcross and F_2 progenies in hexaploid triticale

52 additional F_2 plants were karyotyped. Among those, 97 normal 1R chromosomes were present, bringing the total number of scored chromosomes to 199. The differences between both backcrosses, and between backcrosses and F_2 were minor and not statistically significant (Fig. 2), and the results for all three combinations were pooled. Among the 199 chromosomes analyzed, 106 were classifed as parental, 66 of which were of the H type and 40 of E type. Among 93 recombined chromosomes 90 required one and 3 required two cross-over events to produce the observed banding pattern.

The physical distance between the telomeric (L3) and subtelomeric (L2) C-bands on the 1RL arm of line H was too small to unequivocally determine whether both L2 and L3 bands or only the L3 band was present. The cross-overs in the L2–L3 segment were only scored in chromosomes with the L2 band present and the telomeric L3 band absent (Fig. 1). As this class represents only one of the two possible cross-over types the observed frequency was doubled to express the total for that particular segment of the chromosome. The observed recombination frequencies of the L1–L2 regions in rye and triticale were proportionately reduced by 1.5% and 1.0%, respectively.

The total of the observed recombination frequency in chromosome 1R in rye was 93.7% compared to 51.7% in triticale. The reduction in recombination between rye and triticale was not distributed evenly along the entire chromosome. The L1–L2 and L2–L3 regions which account for 26.4% and about 1%, respectively, of the rela-

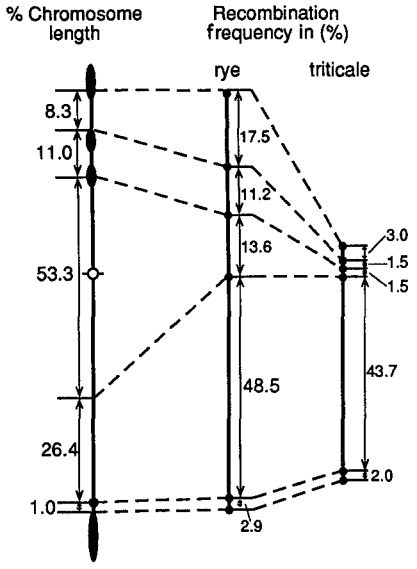

Fig. 3. Physical and genetic distribution of C-bands in chromosome 1R in diploid rye and in hexaploid triticale. Relative physical lengths of the five analyzed segments are given on the *left*

tive chromosome length (47.6% of the long arm) recombined with comparable frequency in rye and triticale (48.5% versus 43.7% for L1–L2, 2.9% versus 2.0% for L2–L3; Fig. 3). The remaining portion of the chromosome, between bands L1 and S3, comprising 52.4% of the relative length of the long arm plus the entire short arm (72.6% of the total chromosome length), supported a recombination frequency of 42.3%, or 45.1% of all recombination events observed in rye, but only a recombination frequency of 6.0%, or 11.6% of all recombination detected in triticale. This reduction in recombination in the L1-S3 segment in triticale resulted in the genetic map of chromosome 1R being 42.0% shorter than that in rye.

Discussion

The frequency of recombination in chromosome 1R in rye recorded in this study appears reasonably close to that reported by other authors, considering sample sizes, standard errors and expected variation due to genetic and environmental factors (Benito et al. 1990; Lawrence and Appels 1986; Sybenga et al. 1990). The major discrepancy is the relatively high recombination frequency observed here in the S1–S2 region proximal to the nucleolar organizing region (NOR) and in the L1-S1 region that spans the middle half of the chromosome (Fig. 3). Lawrence and Appels (1986) reported 7.2% recombination between NOR on the short arm and *Sec-3* on the long arm. Sybenga et al. (1990) reported 2.4% and Singh and Shepherd (1984) 4.6% recombination between *Sec-3* and the centromere. By comparison to the *Glu-B1* gene on wheat chromosome 1B, the probable physical location of *Sec-3* would be in the vicinity of the L1 C-band, giving an approximate value of recombination between this locus and NOR in this study of about 25%. On the other hand, the recombination frequency between the telomeric C-band S3 and NOR observed here (17.5%) is lower than the recombination frequency between *Sec-1* and NOR, 26.5%, given by Lawrence and Appels (1986). Again, in chromosome 1B *Gli-B1* was mapped 3.1% from the telomeric C-band (Curtis and Lukaszewski 1991).

The total amount of recombination for chromosome 1R in rye reported earlier (Lawrence and Appels 1986) was lower than that for comparable genetic markers in wheat. It also appears to be the case in this study. The total amount of recombination for the entire chromosome 1R in rye recorded here was 93.7% compared to 125.8% in chromosome 1B in tetraploid wheat (Curtis and Lukaszewski 1991). However, it is reasonable to assume that a fair number of recombination events, particularly in the distal half of the long arm, were not detected in this study due to the large physical distance between the L1 and L2 bands. Even with the large spacing between the markers used in this study chromosomes with two cross-overs per arm were detected. With more closely spaced markers more double cross-over events might have been detected. In chromosome 1B of tetraploid wheat two genetic markers, *Gli-B1* and *Glu-B1*, used in addition to C-bands, detected 13 additional cross-overs (5.8% recombination). In that study C-bands in the distal halves of chromosomes 1B were spaced no farther apart than 19.8% of the relative arm length compared to the distance of about 44.8% of the relative arm length of the L1-L2 region.

Telocentric chromosomes were not available for this study, and the position of the centromere on the genetic map could not be ascertained. However, the general pattern of the distribution of recombination is clear. Of the 93.7% recombination recorded in rye, in proximal parts of the chromosome 53.3% of the relative chromosome length on both sides of the centromere accounted for 13.6% of recombination. On the other hand, distal parts of the chromosome: 27.4% of the relative chromosome length in the long arm and 19.3% of the relative chromosome length on the short arm accounted for 51.4% and 28.7% of all recombination observed, respectively. This pattern in chromosome 1R in rye observed in this study is similar to that observed in chromosome 1B in tetraploid wheat (Curtis and Lukaszewski 1991), 5BL in hexaploid wheat (Jampates and Dvorak 1986) and chromosome 3L in barley (Linde-Laursen 1982). In these species recombination is concentrated in the distal parts of chromosome arms, which in consequence are overly extended on the genetic maps, and is infrequent, or ab-

sent, in the proximal regions, which are compressed on the genetic map. These species have distinctly terminal or subterminal chiasmata in MI.

This pattern of the distribution of recombination was disturbed in hexaploid triticale. The distal half of the long arm, which in rye showed 51.4% of recombination, in triticale also showed a comparable frequency, 45.7%. The rest of the chromosome, however, which in rye showed 42.3% recombination, in triticale showed only 6% recombination. It is not entirely clear what mechanisms caused such alteration of the genetic map in these two backgrounds, but it is reasonable to assume that chromosome pairing and/or differences in transmission rates were involved.

Neither in rye nor in triticale F_1 hybrids was the MI pairing of chromosomes 1R studied with adequate precision. In rye stocks comparable to those used in mapping it appeared that 1RS paired with about 45% frequency and 1RL with about 83% frequency. The long arm pairing is directly comparable to the average general pairing in the F_1 hybrid (84.7%); the short arm pairing is only about half that. It is possible that this reduction in the pairing frequency of 1RS was caused by the heterozygosity for the large telomeric C-band as reported by Naranjo and Lacadena (1980). In 11 rye lines with only one major telomeric C-band present Lukaszewski and Kaltsikes (unpublished data) observed that heterozygosity for the telomeric C-band reduced pairing of the arm involved. This reduction appeared to be more severe for the shorter than for the longer arms. The effect of telomeric C-band heterozygosity on pairing frequency may be similar to that of deficiency heterozygosity. In hexaploid wheat Curtis et al. (1991) observed that heterozygosity for a deficiency, for even a small segment, drastically reduced MI pairing of the arm involved. In deficiency homozygotes the deficient arms paired with high frequency, albeit somewhat lower than normal chromosome arms. In rye the large telomeric C-bands occupy substantial areas of the arms; proportionally larger in shorter than in longer arms. Consequently, elimination of a band from a short arm would create a greater disproportion in arm length than in a long arm with all the consequences of pairing failure.

In the Do1E × Do1H hexaploid triticale hybrids chromosome arm 1RS heterozygous for the S34 band paired with only about 15% frequency, while 1RL heterozygous for the L3 band paired with about 45% frequency. Naranjo and Lacadena (1980) showed that heterozygosity for the telomeric C-bands in chromosome 1R in tetraploid wheat-rye hybrids reduced pairing of the arm involved, and this reduction appeared to be more pronounced in the short than in the long arm. Singh et al. (1990) reported 10.2% and 64.2% pairing frequency of 1RS in two combinations in wheat. The combination with 10.2% pairing was heterozygous for the presence of the telomeric C-band; the combination with 64.2% pairing was homozygous. Singh and Shepherd (1984) reported that the chromosome 1RL in wheat background showed only 62.2% pairing frequency. It would appear, therefore, that pairing frequency of chromosome 1R in wheat background is reduced, that this reduction is greater for the S arm than for L arm, and that it can be reduced even further by C-band heterozygosity.

While there appears to be a reasonably close correspondence between the observed pairing frequency and the observed recombination frequency in 1RS in triticale (15% pairing versus 6% recombination), there was no similar correspondence for the long arm (45% pairing versus 45.7% recombination). The discrepancy between the observed pairing and recombination frequencies in triticale was probably caused by a combination of desynapsis and gametic selection. Desynapsis was not observed in rye. While pairing at diplotene/diakinesis in rye appeared higher than that in MI, particularly for the short arm, without the pulling forces as in MI it was not possible to detect whether the two arms were indeed bound by a chiasma, were involved in achiasmate association, or were only lying parallel to each other. Due to the high frequency of pairing in the long arm the frequency of 1R univalents in rye was very low. Still, desynapsis in the short arm would have easily been detected by recombined banding patterns in the unpaired short arms in rod bivalents, but it was not. On the other hand, in triticale two 1R univalents recombined for their C-banding pattern were observed.

In addition to desynapsis in triticale gametic or zygotic selection was also probably involved. Selection probably favored those gametes, which resulted from the 52% of meiocytes with paired 1R chromosomes, thus inflating the recombination estimate. On the other hand, chance inclusion of 1R univalents into gametes must have been frequent and it did not appear to be random. Among non-recombined chromosomes in the progeny of triticale there was a predominance of the H-type chromosomes over the E-type chromosomes in about a 3:2 ratio. It is not clear what factors affected such a skewed transmission. In the rye experiment, all bands except for S2 segregated in 1:1 ratio. The large E-type S2 band, however, was present in 119 chromosomes and absent in 87 chromosomes, a significant deviation from the expected 1:1 ratio ($p < 0.05$). The size of this band correlates with the amount of rDNA (R. Appels, personal communitacion), and it is possible that an increased amount of rDNA was favored by the gametes. In triticale, rye NOR is supressed, and perhaps this factor favored the H-type chromosome with a small S2 band. Poor seed set and poor germination rate of the backcross and F_2 seed in this combination would create ample opportunity for gametic and zygotic selection. All these factors indicate that the recombination frequency in chromosome 1R in

triticale was overestimated and that the actual genetic map of the chromosome is shorter than is shown in Fig. 3.

Regardless of the obvious non-randomness of the analyzed sample of 1R chromosomes in triticale, the experiment demonstrates that the genetic map of the 1R chromosome in triticale was greatly distorted compared to the map of the same chromosome in rye. This distortion was not evenly distributed. It did not appear to affect the distal half of the long arm; the remaining portion of the chromosome showed drastic reduction of crossing-over, and as a result, the markers appeared to be tightly linked.

References

Benito C, Frade JM, Orellana J, Carrillo JM (1990) Linkage and cytogenetic maps of genes controlling endosperm storage proteins and isoenzymes in rye (*Secale cereale* L.). Theor Appl Genet 79:347–352

Bernatzky R, Tanksley SD (1986) Toward a saturated linkage map in tomato based on isoenzymes and random cDNA sequences. Genetics 112:887–898

Chao S, Sharp PJ, Worland AJ, Warham EJ, Koebner RMD, Gale MD (1989) RFLP-based genetic maps of wheat homoeologous group 7 chromosomes. Theor Appl Genet 78:495–504

Crossway A, Dvorak J (1984) Distribution of nonstructural variation along three chromosome arms between wheat cultivars 'Chinese Spring' and 'Cheyenne.' Genetics 106:209–324

Curtis CA, Feldman M (1988) Increased proximal recombination frequency in common wheat by premeiotic colchicine treatment. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp. Cambridge pp 243–248

Curtis CA, Lukaszewski AJ (1991) Genetic linkage between C-bands and storage protein genes in chromosome 1B of tetraploid wheat. Theor Appl Genet 81:245–252

Curtis CA, Lukaszewski AJ, Chrzastek M (1991) Metaphase I pairing of deficient chromosomes and genetic mapping of deficiency breakpoints in common wheat. Genome 34:553–560

Dvorak J, Chen K (1984) Distribution of nonstructural variation between wheat cultivars along chromsome arm 6Bp. Evidence from the linkage map and physical map of the arm. Genetics 106:325–333

Dvorak J, McGuire P (1981) Nonstructural chromosome differentiation among wheat cultivars with special reference to differentiation of chromosomes in related species. Genetics 97:391–414

Gale MD, Chao S, Sharp PJ (1990) RFLP mapping in wheat – progress and problems. In: Gustafson JP (ed) Gene manipulation in plant improvement II. Plenum Press, New York, pp 353–363

Girladez RM, Cermeno C, Orellana J (1979) Comparison of C-banding pattern in the chromosomes of inbred lines and open pollinated varieties of rye. Z Pflanzenzucht 83:40–48

Helentjaris T, Slocum M, Wright S, Schaefer A, Niehuis J (1986) Construction of genetic linkage maps in maize and tomato using restriction fragment length polymorphism. Theor Appl Genet 72:761–769

Hoisington DA, Coe EH (1990) Mapping in maize using RFLP's. In: Gustafson JP (ed) Gene manipulation in plant improvement II. Plenum Press, New York, pp 331–352

Jampates R, Dvorak J (1986) Location of the *Ph1* locus in the metaphase chromosome map and the linkage map of the 5Bq arm of wheat. Can J Genet Cytol 28:511–519

Jung C, Lelley T (1985) Cytological and morphological expression of interactions between wheat and rye genomes in triticale. In: Bernard M, Bernard S (eds). Genetics and breeding of Triticale. EUCARPIA meeting, Clermont-Ferrand, pp 145–151

Keim P, Shoemaker RC, Palmer RG (1989) Restriction fragment length polymorphism diversity in soybean. Theor Appl Genet 77:786–792

Lawrence CJ, Appels R (1986) Mapping of the nucleolus organizer region, seed protein loci and isoenzyme loci on chromosome 1R in rye. Theor Appl Genet 71:742–749

Lelley T (1985) Triticale breeding, a new approach. In: Bernard M, Bernard S (eds) Genetics and breeding of Triticale. EUCARPIA meeting, Clermont-Ferrand, pp 133–143

Linde-Laursen I (1982) Linkage map of the long arm of barley chromosome 3 using C-bands and marker genes. Heredity 49:27–35

Lukaszewski AJ, Gustafson JP (1983) Translocations and modifications of chromosomes in triticale × wheat hybrids. Theor Appl Genet 64:239–248

Naranjo T, Lacadena JR (1980) Interaction between wheat chromosomes and rye telomeric heterochromatin on meiotic pairing of chromosome pair 1R of rye in wheat-rye derivatives. Chromosoma 81:249–261

Payne PI, Holt LM, Jackson A, Law CN (12984) Wheat storage proteins: their genetics and their potential for manipulation by plant breeding. Philos Trans R Soc Lond Ser B 304:359–371

Ren ZL, Lelley T (1988) Genetics of hybrid necrosis in rye. Plant Breed 100:173–180

Sears ER (1984) Mutations in wheat that raise the level of meiotic chromosome pairing. In: Gustafson JP (ed) Gene manipulation in plant improvement. Plenum Press, New York, pp 295–300

Singh NK, Shepherd KW (1984) Mapping of the genes controlling high-molecular-weight glutenin subunits of rye on the long arm of chromosome 1R. Genet Res 44:117–123

Singh NK, Shepherd KW (1988) Linkage mapping of genes controlling endosperm storage protein genes in wheat. 2. Genes on the long arm of group 1 chromosomes. Theor Appl Genet 75:642–650

Singh NK, Shepherd KW, McIntosh RA (1990) Linkage mapping of genes for resistance to leaf, stem and stripe rusts and *w*-secalins on the short arm of rye chromosome 1R. Theor Appl Genet 80:609–616

Sybenga J, Pamar S, van Eden J, Shewry P (1990) Mapping seed storage protein loci *Sec-1* and *Sec-2* in relation to five chromosomal rearrangements in rye (*Secale cereale* L.). Theor Appl Genet 79:201–208

Tanksley SD (1988) Molecular mapping of plant chromosomes. In: Gustafson JP (ed) Chromosome structure and function. Impact of new concepts. Plenum Press, New York, pp 157–173