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Crossover distribution in barley analysed through RFLP linkage data

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Abstract The pattern of recombination in barley with regard to (1) the distribution of crossover points among whole gametes, (2) the distribution of crossover points among individual chromosomes and (3) the distribution of crossover points within chromosomes has been analysed using data sets underlying two recently published restriction fragment length polymorphism (RFLP) linkage maps representing male and female meiosis, respectively. The data indicated that the process of recombination had been random with no interference. The two data sets gave similar results, indicating that male and female meiosis in barley do no differ significantly. The possibility of using RFLP data in studies of crossover distribution is stressed.

Key words *Hordeum vulgare* · RFLP · Genetic map · Recombination · Crossover

Introduction

Since publication of the first genetic map (Sturtevant 1913), mapping has been a major activity of geneticists. Until very recently map construction in most organisms has been limited by the availability of stocks with suitable morphological markers. Classical genetic maps are therefore built up from a large number of crosses where each cross gives information about only a few segregating loci. Only in exceptional cases, such as in *Drosophila*, have more than ten segregating loci been studied in a single cross (Müller 1916; Charles 1938; King and Mortimer 1990).

Due to the low number of informative loci segregating in these classical crosses, only limited information about the process of recombination in the whole genome could be gained from each cross. Important questions, such as the number of crossovers per individual meiosis and the number and distribution of crossover points on each chromosome, could not be satisfactorily answered from such data. Although the compiled genetic maps can give some information towards answering these questions, this is so only when the maps have been fully saturated with markers. After almost a century of genetic mapping, such saturated classical maps exist only for a handful of model organisms (see O'Brien 1993). Elsewhere, recombination over the whole genome can be studied only by using cytological techniques, i.e. through chiasma counts. Such chiasma data may be valuable for estimating the total amount of recombination in the genome. Occasionally, such as in the human male (e.g. Hultén et al. 1990), chiasma data can be used to resolve the pattern of recombination between chromosomes or within individual chromosomes. However, in a majority of species cytological resolution does not allow this kind of analysis.

With the use of modern DNA techniques this situation has changed drastically. Today there are several methods to detect polymorphic DNA markers that are suitable for genetic mapping. So far, the most commonly used type of markers are the so-called RFLPs (restriction fragment length polymorphisms). Besides the availability of markers, the construction of RFLP maps differs methodologically from map generation based on morphological markers. RFLP maps are usually generated from the offspring of one single cross where over one hundred, and sometimes several hundred, markers segregate. This implies that the data sets from which RFLP maps are generated are also very useful for investigating the pattern of recombination over whole chromosomes and genomes. Thus, the availability of DNA markers has provided us with a genetical tool for studying recombination over the whole genome in addition to the cytological methods.

The reasons for making RFLP maps may be purely scientific, as in model organisms, medical, as in humans

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or economic, as in the crop plants. RFLP maps have been produced for a number of organisms, particularly in crop plants such as the common bean (Vallejos et al. 1992), soybean (Keim et al. 1990), *Brassica oleracea* (Kianian and Quiros 1992), lettuce (Kesseli et al. 1990), tomato (Tanksley and Mutschler, 1990), potato (Gebhardt et al. 1991), pea (Ellis et al. 1992), rice (McCouch et al. 1988), barley (Graner et al. 1991) and maize (Coe et al. 1990). In spite of the fact that most of these maps were generated for breeding purposes, the data sets from which the maps were generated present an opportunity to study recombination in these organisms.

In the present paper we investigate the data from two different RFLP mapping projects in barley (*Hordeum vulgare*) that represent meiosis in both sexes. We have specifically examined the number and distribution of recombination events over the whole barley genome and over individual chromosomes. Some of the results from the analysis are discussed further by Nilsson et al. (1993).

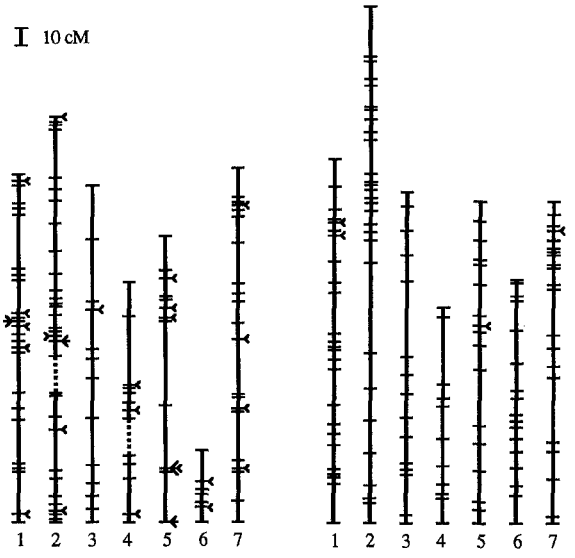

Fig. 1 Distribution of mapped markers in the published linkage maps of the data set I (*left*) and II (*right*). Corresponding chromosome numbers are at the *bottom*. The *dotted lines* indicate places where linkage was not significant but where the use of substitution lines have proven the synteni of the linked markers

Materials and methods

The data sets that are analysed were kindly provided by Dr. M. Heun (data set I) and Dr. T. Blake (data set II). The set provided by Dr. Heun is based on 113 doubled haploid individuals that were derived from anther culture of pollen from F_1 plants from the cross 'Proctor' × 'Nudinka'. A total of 154 RFLP markers was mapped to specific loci on this map with an average distance of 7.5 cM between adjacent markers. The RFLP map has been published by Heun et al. (1991).

The data provided by Dr. Blake come from the cross 'Steptoe' × 'Morex', which is one of the crosses analysed in the North American Barley Genome Project (NABGP). At present approximately 300 markers have been mapped in this cross (Kleinhofs et al. 1993). We received the results from the mapping of 139 markers using 150 doubled haploid individuals. At this stage there was an average distance of 9.8 cM between adjacent markers. This data set (II) was used to construct a preliminary map, presented at the sixth International Barley Genetics Symposium (Blake et al. 1991).

The doubled haploids used in data set II were derived using the *Hordeum bulbosum* in vitro floret culture technique (Chen and Hayes 1989). This technique involves the crossing of *H. vulgare* with pollen from *H. bulbosum*, the growth of florets in vitro, dissection of embryos from seeds and then growth of the embryos in vitro to produce plants. The genetically important part is the interspecific cross between *H. vulgare* and *H. bulbosum*, which usually generates haploid offspring containing only the chromosomes from *H. vulgare* (e.g. Pickering 1983). Thus, using this technique, haploids are produced from female gametes. This means that there is a fundamental difference between the two data sets in that data set I is based on male meiosis and data set II on female meiosis.

In the progeny derived from doubled haploids each individual represents one gamete. This means that it is possible to determine directly how an individual's genome is composed of complementary chromosome parts from its two parents. By reading the genotype at each locus along the genetic map already established, a graphical genotype is obtained for each individual. This concept was first put forward by Young and Tanksley (1989) and has many applications in plant breeding.

The two data sets are directly comparable in terms of number of mapped markers and sample size. Figure 1 shows the number of mapped markers and the distribution of markers along the published maps. The majority (91%) of the mapped markers were unique to either one or the other of the data sets; only 24 markers were common to both data sets. It can be seen that the chromosomes differ widely with respect to the number of mapped markers (e.g. from 9 to 38 in data set I). With the exception of chromosome 6 there is, however, a general agreement between the sets, e.g. in both data sets chromosomes 1 and 2 cover relatively many markers and 3 and 4 cover significantly fewer markers. Both data sets are very heterogeneous with respect to the origin of the probes, containing barley cDNA clones, oat cDNA clones, wheat genomic clones and many other clones, such as genomic clones from *Triticum tauschii* and available gene clones.

In both data sets there exist individuals in which the parental origin of 1 or more markers is not known; i.e. there are missing values. The numbers of missing values are shown in Table 1. Missing values were handled in the following way. Firstly, loci with missing values which were surrounded by loci with alleles (markers) that were all from the same parent were assumed to hold a marker from that parent. When the markers at the loci on either side of the missing value were of different parental origin, recombination must have occurred on one side of the locus. In these cases the missing allele was assigned to the parental type of the genetically nearest flanking locus. This treatment of the missing values is conservative in relation to recombination, i.e., it does not create any points of recombination that were not detectable in the original data set.

In the analyses described below we treated the observed recombination events as the only crossovers. The recombination fraction has therefore been used as an additive measure. In addition, the chromosomes are represented by linkage groups. These linkage groups certainly cover the majority of the chromosomes, but at the ends there may still occur crossingover outside the most distantly mapped markers. This means that our results are valid for a minimum number of crossovers given the published genetic maps. If the discrepancy between chiasma data and RFLP data is taken into account (Nilsson et al. 1993), such a conservative approach to the counting of crossovers seems highly motivated.

It is also important to keep in mind that the relation between the genetic and the physical distance often varies over chromosomes (Säll et al. 1993). In barley, where the majority of recombination occurs at the ends of the chromosomes, this effect is very strong (Linde-Laursen 1982). Thus, the genetic map which is discussed here is very different from the physical map in barley. Hence, all discussions below concerning the distribution of crossovers within chromosomes refer to the distribution of crossovers over the linkage group corresponding to that chromosome.

Table 1 Total number of data points (no. of probes * no. of individuals), number of missing values ("same parent" = surrounded by markers from the same parent; "different parent" = surrounded by markers from different parents) and number of singletons (positions with flanking recombination events)

Type of data	Data set I		Data set II	
Number of data points	17402		20850	
Missing values "same parent"	1064	(6.1%)	2205	(10.6%)
"different parents"	204	(1.2%)	457	(2.2%)
Sum	1268	(7.3%)	2662	(12.8%)
Singletons	72	(0.4%)	245	(1.2%)

Results and discussion

Number of crossover points in gametes and chromosomes

The overall distributions of the number of crossover points per gamete are quite similar in the two data sets (Fig. 2). Data set I has a mean of 10.8 and a variance of 10.7 and data set II has a mean of 12.1 and a variance of 13.8. The extremes are 5 and 23 and 3 and 29 for the two data sets, respectively. In this respect both sexes appear to have a similar pattern. The distributions of crossover point numbers for separate chromosomes also have the same general pattern (see Fig. 3 for chromosome 1). Table 2 shows the mean, the maximum and the variance observed in each of the seven chromosomes. In both data sets chromosome 2 showed the largest mean, while in both cases the maximum number of crossover points was found in chromosome 1 (8 in data set I and 11 in data set II).

The fact that the overall recombination pattern is similar for the two data sets is of particular interest since they represent male and female meiosis, respectively. Other cases in barley where it has been possible to compare the sexes have yielded similar results. Bennet et al. (1973) observed similar chiasma numbers in male and female, and Doll and Brown (1979) investigated the recombination frequencies between the hordein loci and found no indication of differences between the sexes.

Nilsson et al. (1993) pointed out that, in a number of organisms, the number of crossovers estimated from RFLP maps is considerably higher than the number of chiasmata observed in cytological studies. Published chiasma studies using barley (Gale and Rees 1970; Bennet et al. 1973; Nilsson and Pelger 1991) indicate lower recombination than that inferred from the present data. This effect becomes particularly clear if we compare the present RFLP data and chiasmata data with respect to the maximum number of crossovers that is observed in a single gamete. Here we find a maximum of 23 and 29 crossover points per gamete, whereas in the chiasma data presented by Nilsson and Pelger (1991) the maximum number of chiasmata per meiosis was 15. This is an enormous difference, since one crossover point per gamete represents an average of two chiasmata per meiosis. Furthermore, additional recombination events may have occurred outside the outermost markers and within long segments within the map. Because of the relative density of the maps, however, we expect few such unobserved crossovers within the maps. The reason for the inconsistency between chiasma and crossover numbers is not known, but it calls for further investigation (Nilsson et al. 1993).

Distribution of crossover points between and within chromosomes

Table 2 shows the mean and the variance of the number of crossover points for each of the seven chromosomes in the data sets. If the distribution of crossover points over each chromosome were completely random and if the position of each crossover point could be determined

Fig. 2 Distribution of crossover points per gamete. *Dotted line* (data set I) represents male meiosis while *solid line* (data set II) represents female meiosis

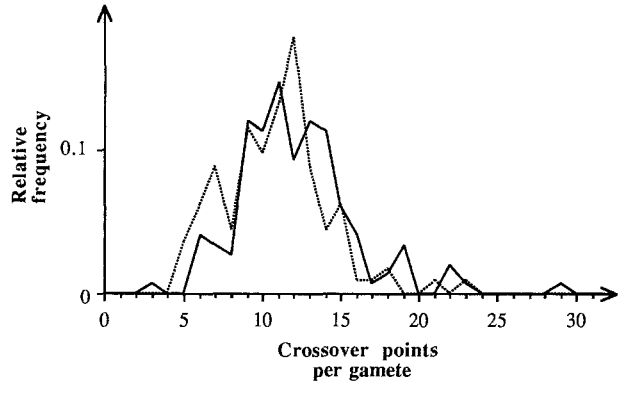

Fig. 3 Distribution of the number of crossover points in chromosome 1. *Dotted line* (data set I) represents male meiosis while *solid line* (data set II) represents female meiosis

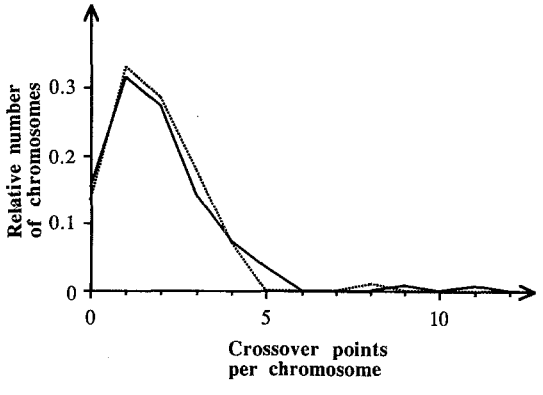

Table 2 Average number (Mean), maximum (Max), variance (Var) and expected variance under random distribution (Evar) of crossover points per chromosome

Chromosome	Data set I				Data set II			
	Mean	Max	Var	EVar	Mean	Max	Var	EVar
1	1.78	8	1.60	1.47	1.87	11	2.52	1.61
2	2.30	6	1.99	1.86	3.03	9	3.20	2.31
3	1.70	6	1.42	1.35	1.61	5	1.33	1.28
4	1.48	4	0.95	1.05	1.09	5	0.85	0.90
5	1.36	3	0.59	1.00	1.64	4	1.18	1.38
6	0.36	2	0.29	0.32	1.22	5	1.00	1.08
7	1.83	4	1.62	1.52	1.65	6	1.25	1.37

exactly, a Poisson distribution with the variance equal to the mean is expected. In the present case, where the information is limited to segments, the expected variance under the assumption of an independent distribution of number of crossover points among individual chromosomes is $\Sigma r_i - \Sigma r_i^2$, where r_i is the recombination frequency in segment i. This quantity has been called the expected variance and is also found in Table 2. It can be seen that there is no systematic difference between the observed variance and the expected variance; in 7 cases the expected variance is larger, in 7 cases it is smaller. Thus, a sign test would give a P value of 1.0.

The next step was to investigate the positional distribution of crossover points within chromosomes with 1, 2, 3 etc. crossover points. In order to test the hypothesis of an equal distribution among these different classes of crossover point number in all chromosomes, each of the seven linkage groups in the two data sets was divided into 3–5 sections of approximately equal genetic length (based on the published maps). The number of crossover points was then counted in each segment. The hypothesis of an equal crossover point distribution, irrespective of the number of crossover points found in the chromosome, was then tested by an ordinary test of homogeneity. Only crossover number classes representing a sufficient total number of crossover points were included. The results are shown in Table 3. Of the tests 10 show no significance and 3 indicate a difference between the classes. In one of these 3 cases – the second chromosome in data set I – there is a tendency that chromosomes with fewer crossover points have relatively less crossingover in the central parts of the map. The other 2 cases, however, show no obvious regularity in their differences among the classes. This is illustrated by comparing the linkage group corresponding to chromosome 1 in the two data sets. In Fig. 4 we show the relative contribution of crossover points in each segment of the linkage group from the different crossover number classes. In data set I no significant differences were observed, while data set II showed significant differences. However, the heterogeneity detected by the test does not follow a distinct pattern according to Fig. 4. Thus, the overall impression is that crossover distribution is random with respect to variation both between and within chromosomes.

Table 3 Homogeneity tests of the hypothesis of an equal distribution of crossover points in linkage groups corresponding to chromosomes with different numbers of crossover points. The table shows the chi-square value (χ^2), degrees of freedom (df) and probability value (P). In chromosome 6 in data set I there were too few markers and too few observed crossovers to perform the test

Linkage group	Data set I			Data set II		
	χ^2	df	P	χ^2	df	P
1	6.4	12	0.89	27.2	16	0.04
2	26.8	16	0.04	15.4	16	0.50
3	6.6	8	0.58	12.2	8	0.14
4	7.7	6	0.26	5.0	4	0.29
5	3.9	6	0.70	14.7	12	0.26
6	.	.	.	13.8	4	<0.01
7	7.4	12	0.83	6.4	4	0.71

These results contrast with a number of earlier investigations of the pattern of recombination of whole genomes. A number of chiasma studies, e.g. Henderson (1963), Hultén (1974), Laurie (1980) and Jones (1984), indicate a strong interference in the positioning of chiasmata. Similar results have been obtained genetically, such as in the studies of recombination over large parts of whole chromosomes in *Drosophila* by Müller (1916) and Charles (1938). Hence, positive interference is generally assumed to be the rule in eukaryotes (Bailey 1961).

There is still, of course a possibility that some species differ in this respect. Several factors may cause the observed pattern of recombination to appear random, even if the recombination events themselves show positive interference. High levels of gene conversion, for instance, could cause the apparent randomness and even negative interference. Another mechanism could be an increased amount of germ line mitotic recombination. A substantial proportion of the crossover points observed in the recombination data would, in such a case, be produced by recombination in the mitoses preceding the meiosis. Yet another factor that may counteract positive interference is variation in recombination frequencies between different meioses (Säll and Bengtsson 1989). Some cases of negative interference have been reported in barley (Søgaard 1977; Larsson 1985; Säll 1990), but the causes of these results are not known.

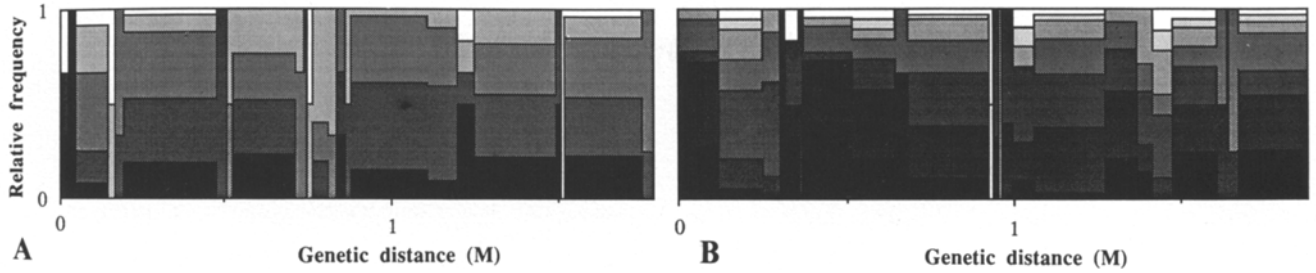

Fig. 4A, B Relative contribution of crossover points along the linkage group corresponding to chromosome 1. *Vertical divisions* represent positions of markers along the map based on recombination frequencies. *Coloured areas* represent the relative contribution of crossovers from chromosomes with a particular number of crossover points. **A** Data set I; *dark to light* areas represent chromosomes with 1, 2, 3, 4 and 8 crossover points, respectively. **B** Data set II; *dark to light* areas represent chromosomes with 1, 2, 3, 4, 5, 9 and 11 crossover points, respectively

Errors in RFLP data?

The unexpected randomness may also be due to some problem with the RFLP data. For example, the phenotype of an individual can obviously be misclassified either through scoring or typing errors. Such misclassifications would generate apparent randomness. For short chromosomal segments, we observed cases of negative interference in both data sets, an effect that is also expected if misclassifications occur. In the continuation of the NABGP mapping project this problem has received attention, and markers causing too much negative interference have been withdrawn from the map (Blake 1992). A more systematic detection of errors in genetic linkage data has also been proposed by Lincoln and Lander (1992). An algorithm for error detection is now available in their latest version of MAPMAKER, and future RFLP maps using this programme will thus provide even better data sets for crossover analyses.

We have not used this programme to reinvestigate the data since our intention was to base the analysis on the maps published by the respective authors. Instead, we have performed a simple operation to investigate the possible effects of misclassifications. In every case where 1 single marker from one of the parents was flanked on both sides by markers from the other parent this marker was changed. These positions are called "singletons". In data set I 72 such singletons were found and in data set II 245 were found (Table 1).

Table 4 shows the mean, maximum, variance and expected variance for the data sets with singletons removed. Naturally, the means decrease, but only moderately. The mean per gamete decreases from 10.8 to 9.5 in data set I and from 12.1 to 8.8 in data set II. The maximum numbers, on the other hand, decrease quite drastically. In chromosome 1, which was mentioned above, the maximum numbers observed in one single chromosome decrease from 8 and 11 to 4 and 5 in the two data sets, respectively. For whole gametes the maxima drop from 23 and 29 to 19 and 17, respectively. This change is not sufficient to explain the difference between the recombination data and chiasma data mentioned above. For data set I, the mean 9.5 is still significantly higher than the corresponding expected value of 7.0 from chiasma data (Nilsson et al. 1993).

The removal of singletons also decreases the variance in crossover number per chromosome. Furthermore, the observed variances systematically become smaller than the expected variances (12 out of 14, which corresponds to a P value of 0.013 in a two-sided sign test). This overdispersal in crossover number might indicate an underlying interference. However, the results must be interpreted with caution, since the removal of true double recombinants will have a similar effect. We therefore performed the tests of equal distribution among chromosomes with different numbers of crossovers on the changed data sets. No significant differences were observed in any of the tests (results not shown). Thus, even if it is plausible that the data sets used contain errors, the rough method of removing sigletons does not completely explain the observed pattern of randomness nor in the inconsistency with chiasma data.

Table 4 Average number (Mean), maximum (Max), variance (Var) and expected variance under random distribution (Evar) of crossover points per chromosome when the singletons have been excluded from the data set

Chromosome	Data set I				Data set II			
	Mean	Max	Var	EVar	Mean	Max	Var	EVar
1	1.68	4	1.19	1.38	1.46	5	1.27	0.99
2	1.81	4	1.05	1.44	1.69	5	1.54	1.49
3	1.49	4	0.97	1.22	1.26	4	0.93	1.03
4	1.32	4	0.72	0.96	0.89	3	0.57	0.75
5	1.20	3	0.54	0.94	1.27	3	0.71	1.11
6	0.36	2	0.29	0.32	1.02	3	0.62	0.91
7	1.69	4	1.37	1.39	1.25	3	0.64	1.03

Conclusion

In summary, we wish to point out the unique opportunity of making crossover analyses from available RFLP data sets. In many of the species concerned, almost nothing is known about the general process of crossing-over, either from cytological chiasma data or from genetic linkage data based on morphological markers. We conclude that the possibility of using RFLP data in the proposed way has generally been overlooked in most RFLP mapping projects. This is probably due to the overriding interest in using RFLP maps for breeding programmes and not in basic research.

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