# Conserved patterns of chromosome pairing and recombination in *Brassica napus* crosses

**I.A.P. Parkin and D.J. Lydiate**



**Abstract**: The patterns of chromosome pairing and recombination in two contrasting *Brassica napus* $F_1$ hybrids were deduced. One hybrid was from a winter oilseed rape (WOSR) × spring oilseed rape cross, the other from a resynthesized *B. napus* × WOSR cross. Segregation at 211 equivalent loci assayed in the population derived from each hybrid produced two collinear genetic maps. Alignment of the maps indicated that *B. napus* chromosomes behaved reproducibly as 19 homologous pairs and that the 19 distinct chromosomes of *B. napus* each recombined with unique chromosomes from the interspecific hybrid between *Brassica rapa* and *Brassica oleracea*. This result indicated that the genomes of the diploid progenitors of amphidiploid *B. napus* have remained essentially unaltered since the formation of the species and that the progenitor genomes were similar to those of modern-day *B. rapa* and *B. oleracea*. The frequency and distribution of crossovers were almost indistinguishable in the two populations, suggesting that the recombination machinery of *B. napus* could cope easily with different degrees of genetic divergence between homologous chromosomes. Efficient recombination in wide crosses will facilitate the introgression of novel alleles into oilseed rape from *B. rapa* and *B. oleracea* (via resynthesized *B. napus*) and reduce linkage drag.

*Key words*: integrating genetic maps, microspore culture, segregation distortion, recombination frequency, locus distribution.

**Résumé** : L'appariement chromosomique et la recombinaison ont été étudiés chez deux hybrides $F_1$ du *Brassica napus* présentant un fort contraste. Un hybride résultait du croisement entre un colza d'automne (WOSR) et un colza de printemps alors que le second hybride provenait d'un croisement entre un *B. napus* de synthèse et WOSR. La ségrégation de 211 loci équivalents a été analysée chez ces deux populations et ceci a permis d'assembler deux cartes génétiques qui sont colinéaires. L'alignement de ces cartes indique que les chromosomes du *B. napus* se comportent de façon reproductible comme 19 paires de chromosomes homologues et que les 19 chromosomes distincts du *B. napus* se recombinent avec des chromosomes uniques chez l'hybride interspécifique entre le *Brassica rapa* et le *Brassica oleracea*. Ce résultat indique que les génomes des espèces diploïdes ayant produit l'amphidiploïde qu'est le *B. napus* sont demeurés essentiellement identiques depuis la formation de cette espèce et que les génomes des espèces donatrices étaient semblables à ceux du *B. rapa* et du *B. oleracea* contemporains. La fréquence et la distribution des enjambements est à peu de choses près identique chez les deux populations ce qui suggère que la machinerie enzymatique de recombinaison du *B. napus* s'accommode aisément des différents degrés de divergence génétique entre chromosomes homologues. Une recombinaison efficace chez des croisements éloignés facilitera l'introgression dans le colza d'allèles nouveaux provenant du *B. rapa* et du *B. oleracea* (en passant par un *B. napus* de synthèse) et réduira la taille des segments introgressés.

*Mots clés* : intrégration de cartes génétiques, culture de microspores, distorsion de la ségrégation, fréquence de recombinaison, distribution des loci.

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## Introduction

*Brassica napus* is an important crop species grown extensively in Canada, Europe, and China as oilseed rape/canola. It is an amphidiploid species formed from interspecific hybridizations between *Brassica rapa* (the A-genome donor) and *Brassica oleracea* (the C-genome donor) (U 1935). *Brassica napus* has a fairly narrow genetic base, probably as a consequence of successful hybridizations being rare (Palmer et al. 1983). It is possible to introduce variation from the diploid progenitor species into *B. napus* by generating new interspecific hybrids between the modern-day representatives of *B. rapa* and *B. oleracea*. The stable introgression of such diversity and the elimination of linkage drag depend upon regular bivalent pairing and homologous recombination between the chromosomes of cultivated oilseed rape and those of newly resynthesized *B. napus* at meiosis in hybrid plants.

Molecular markers can be used to probe genome structure (Moore et al. 1995; Lagercrantz and Lydiate 1996) and also to increase the speed and efficiency of breeding programmes (Paterson et al. 1991; Lydiate et al. 1995). *Brassica* species have high levels of natural polymorphism (Figdore et al. 1988), and *B. napus* linkage maps based on restriction fragment length polymorphisms (RFLP) have been developed by a number of groups (Landry et al. 1991; Ferreira et al. 1994; Uzunova et al. 1995; Sharpe et al. 1995). However, although

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**Fig. 1.** An integrated genetic map of the *Brassica napus* genome based on segregation in the N-fo-61-9 (Parkin et al. 1995) and N-o-72-8 (Sharpe et al. 1995) populations of DH lines. Vertical lines represent linkage groups, and locus codes are as described by Parkin et al. (1995). Regions of the genome where the maps from the two populations could be integrated are represented by solid lines, and additional mapped regions are represented by dotted lines. Only loci common to both maps (215 in total) are represented in the integrated regions of the genome. Map distances (centimorgans (cM)) on the left and right sides of the linkage groups are those calculated from the N-fo-61-9 and N-o-72-8 populations, respectively. Total map lengths are represented at the bottom of the linkage groups, with the lengths of regions where the two maps can be compared in parentheses, where these are different from the total. No linkage data were available for N16 in the N-fo-61-9 population, because the parental $F_1$ was monosomic for this chromosome (Parkin et al. 1995); the corresponding data derived from the sister N-fo-61-13 population (Parkin 1995) have been used instead.



five of the published genetic maps of *B. napus* have been aligned to date (Parkin et al. 1995; Sharpe et al. 1995; Fray et al. 1997; Howell et al. 1996; Kelly et al. 1997), these do not include the earlier maps, because different laboratories have used distinct markers and because of the extensive inter- and intra-genomic duplication in the *B. napus* genome. The high levels of genome duplication within diploid *Brassica* species (Slocum et al. 1990; Song et al. 1991; Chyi et al. 1992) have also made it difficult to distinguish the A and C genomes within *B. napus*, but the two distinct genomes have recently been identified (Parkin et al. 1995; Bohuon et al. 1996).

It is important to demonstrate that *B. napus* chromosomes behave as 19 distinct homologous pairs in intervarietal $F_1$ hybrids of oilseed rape. It is also important to determine whether each of the 19 chromosomes from the haploid genome of oilseed rape recognize and recombine with unique chromosomes from newly resynthesized *B. napus*. In this paper we describe genetic segregation in populations derived from two contrasting *B. napus* hybrids. The two $F_1$ hybrids shared a common parent (a doubled haploid line of winter oilseed rape) but, while one resulted from a cross with spring oilseed rape, the other was derived from a cross with resynthesized *B. napus*. The investigations have allowed the meiotic patterns of chromosome pairing and recombination in the two hybrids to be deduced.

## Materials and methods

### Populations and genetic maps

The N-fo-61-9 population of 50 doubled haploid (DH) lines was derived from an $F_1$ individual from a cross between a resynthesized *B. napus* plant and a DH winter oilseed rape plant, N-o-9-8 (Parkin et al. 1995). The N-o-72-8 population of 92 DH lines was derived from an $F_1$ individual from a cross between the same winter oilseed rape plant (N-o-9-8) and a DH plant of spring oilseed rape (Sharpe et al. 1995). The populations were scored at a large number of marker loci detected by a common set of 162 RFLP probes (Sharpe et al. 1995; Parkin et al. 1995).

### Statistical analyses

The segregation ratio of parental alleles is expected to be 1:1 for normal disomic inheritance in a population of DH lines. Each locus was tested for the significance of unbalanced allele ratios using a $\chi^2$ test of similarity (1 df). The significance of differences in recombination frequency for equivalent intervals in the two populations (N-fo-61-9 and N-o-72-8) was estimated using Fisher's exact test, $2 \times 2$ contingency table (Yates 1934; Fisher 1935; Casagrande et al. 1978), which compared the ratio of recombinant individuals to the total number of scored individuals for each population. The observed distribution of map distances separating adjacent markers was compared with the distribution expected for randomly dispersed markers to test whether the loci mapped in the experimental populations were randomly distributed in the genome. The expected distribution of interval sizes was calculated according to Dietrich et al. (1992) as described in Lagercrantz and Lydiate (1995).

## Results

### Integration of the N-fo-61-9 and N-o-72-8 maps

The N-fo-61-9 genetic linkage map of *B. napus* was derived from meiosis in a resynthesized *B. napus* × winter oilseed rape hybrid and was composed of 392 RFLP-defined loci assembled into 19 linkage groups (N1–N19) with a total length of 1656 cM (Parkin et al. 1995). The N-o-72-8 genetic linkage map of *B. napus* was derived from meiosis in a winter oilseed rape × spring oilseed rape hybrid and was composed of 270 loci distributed over 19 linkage groups with a total length of 1741 cM (Sharpe et al. 1995). The two maps were generated independently and only compared after completion.

The N-fo-61-9 and N-o-72-8 populations shared a common parent (N-o-9-8) and this allowed the identification of common alleles in the two populations at 211 equivalent polymorphic loci. Linkage group N16 was not involved in the integration process, because the corresponding chromosome was monosomic in the $F_1$ plant from which the N-fo-61-9 population was derived (Parkin et al. 1995). The two maps were aligned using these 211 common loci and the integrated map of the two populations is shown in Fig. 1. All linkage groups were completely collinear with the exception of N6, where the two markers at the top of the linkage group were in opposite orientations in the two maps. The simple way in which the two maps were integrated indicated regular and specific chromosome pairing in the two contrasting *B. napus* hybrids.

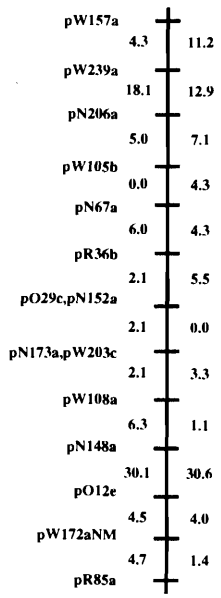
### Genomic differences in the distribution of polymorphic loci

The polymorphic loci mapped in the N-o-72-8 population were unevenly distributed between the A (160) and C (110) genomes (a $\chi^2$ test of similarity gave $p < 0.01$; Sharpe et al. 1995). In contrast, in the N-fo-61-9 population, the numbers of polymorphic loci mapped to the A (204) and C (188) genomes were not significantly different. The N-fo-61-9 population (which had 181 unique loci) was more polymorphic over the whole *B. napus* genome than the N-o-72-8 population (which had only 59 unique loci).

### Segregation distortion

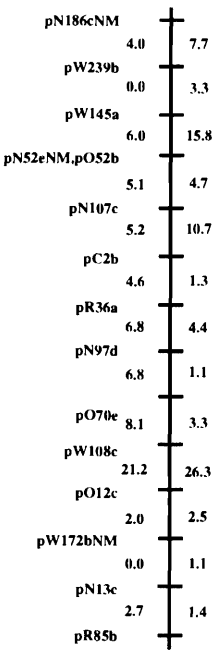
The frequency distribution of loci with varying degrees of segregation distortion was not random ($p < 0.01$) in either

## N1



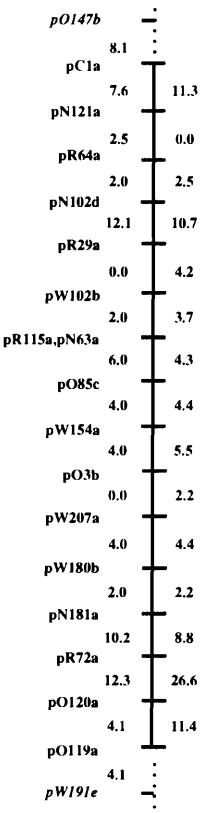

85/86 cM

## N11



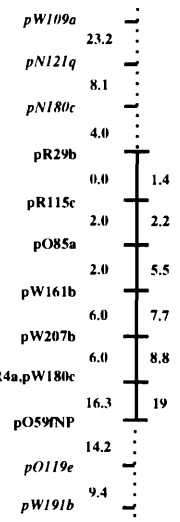

72/84 cM

## N2



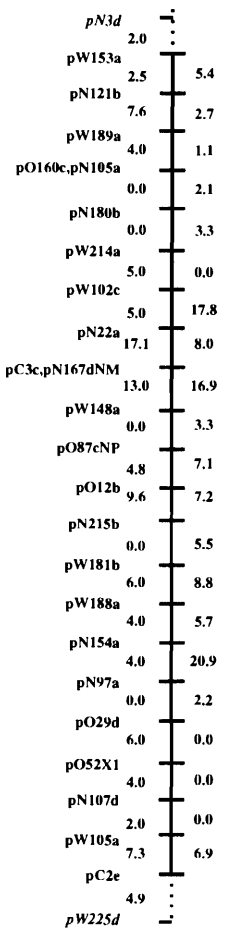

85(73)/100 cM

## N12



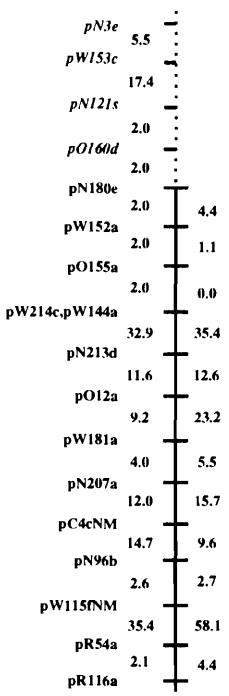

92(32)/45 cM

## N3



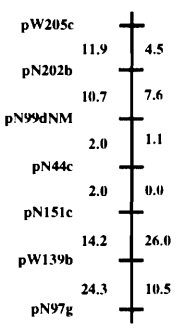

106(99)/125 cM

## N13



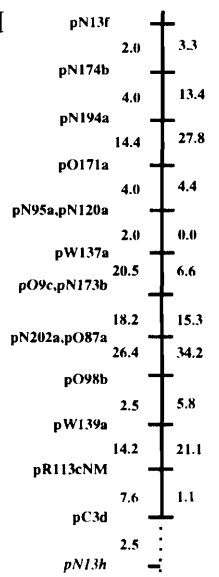

158(131)/172 cM

## N4



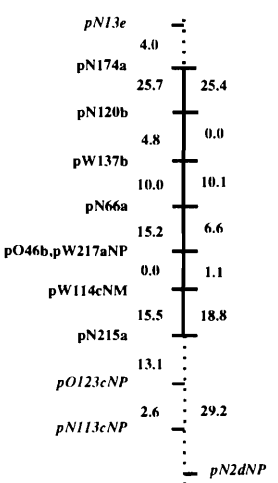

65/50 cM

## N14




118(116)/133 cM

## N5




91(71)/105(76) cM

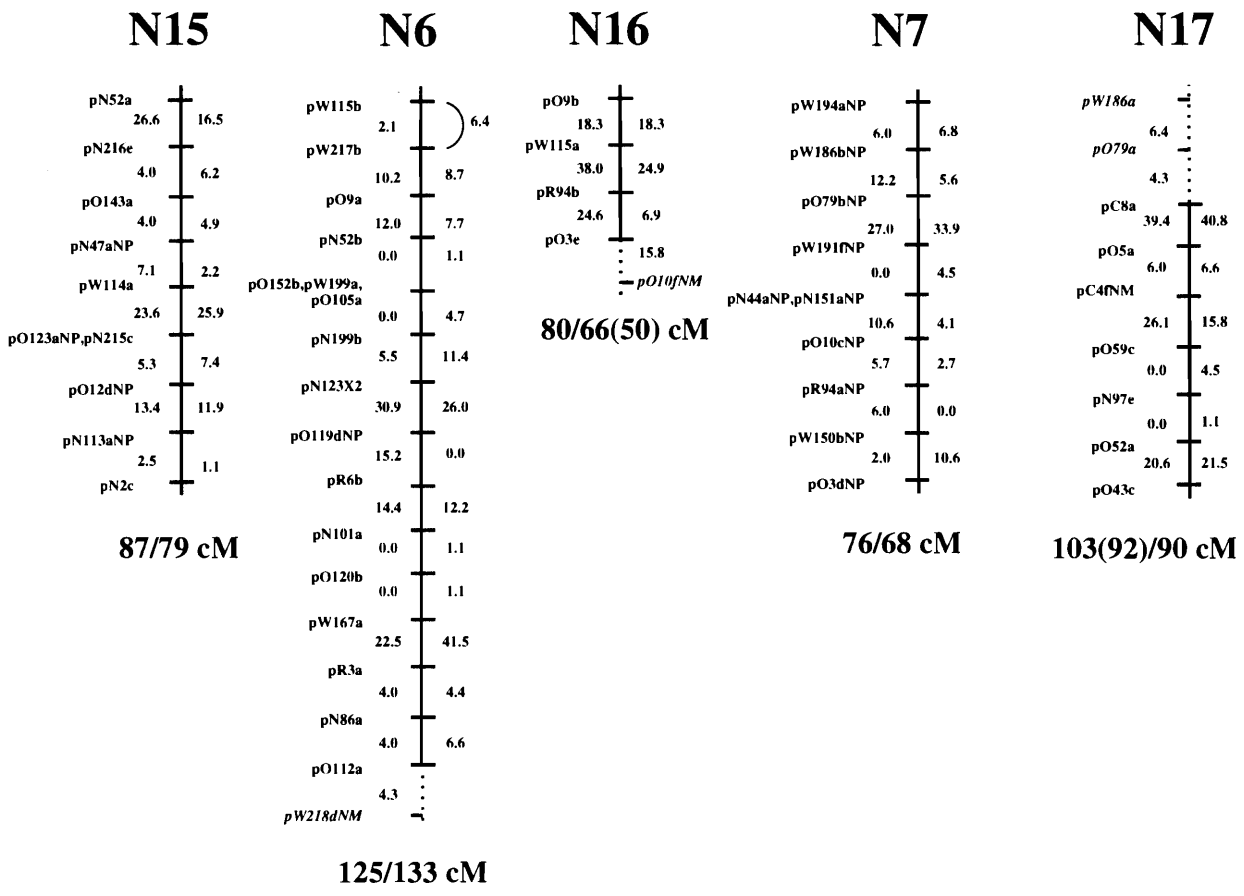
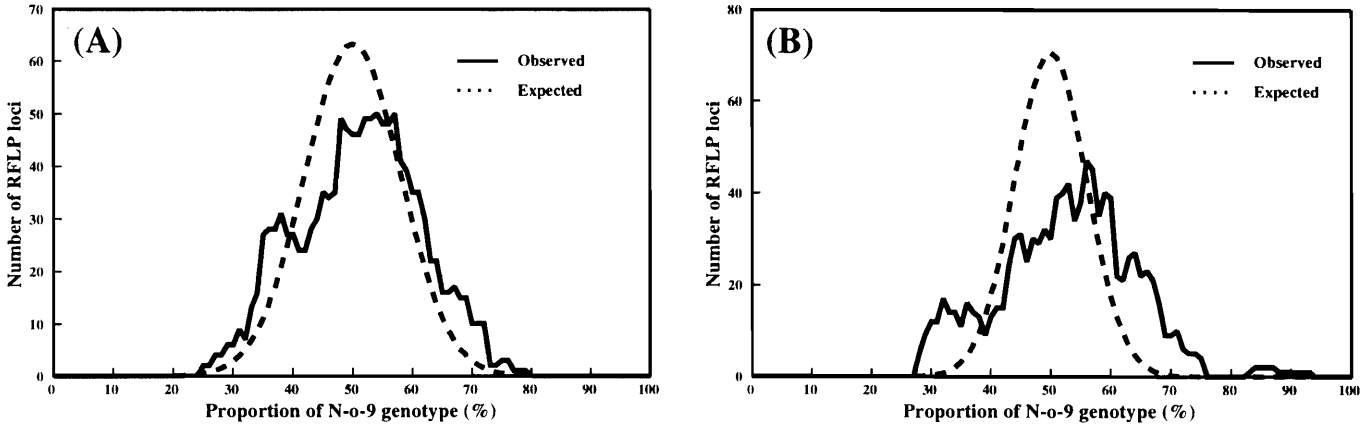


**Fig. 2.** Frequency distributions of loci with varying degrees of segregation distortion in the two mapping populations. Graphs represent 5% windows taken at 1% intervals. (A) The observed distribution of 392 loci assayed in the 50 individuals of the N-fo-61-9 population is compared with the theoretical binomial distribution ($n = 50$, $p = 0.5$). (B) The observed distribution of 270 loci assayed in the 92 individuals of the N-o-72-8 populations is compared with the binomial distribution ($n = 92$, $p = 0.5$).




of the two microspore-derived populations (Fig. 2). There was an excess of loci exhibiting a significant degree of segregation distortion in each population (particularly in N-o-72-8).

Plotting the degree of segregation distortion for loci arranged in linkage groups revealed peaks and plateaus (Fig. 3). Comparing the patterns of segregation distortion in equivalent linkage groups derived from the two populations demonstrated that the peaks in segregation distortion usually occurred at different genomic locations in the two populations (Table 1). It is likely that the peaks of allele imbalance represent genes influencing responsiveness to microspore culture, embryo competitiveness, and (or) plantlet survival during in vitro culture.

### Comparative analysis of recombination in the two contrasting $F_1$ hybrids

The frequency and distribution of recombination were compared in the two populations to test for differences in the meiotic products formed by the two contrasting $F_1$ hybrids. The overall recombination frequency of the *B. napus* genome and the overall recombination frequencies of each of the 19 linkage groups (including N16) were compared in the two populations by calculating the total number of crossovers detected in each population using scoring data from the 215 common loci (Fig. 1; Table 2). This analysis indicated that the recombination frequencies in the two $F_1$ hybrids were very similar. The recombination frequencies in each of 195 equivalent intervals of the aligned *B. napus* maps (the N-fo-61-9 and N-o-72-8 maps) were compared to test for differences in the distribution of crossovers in the two populations. The differences observed in nine of the intervals (4.6%) had a probability of $P < 0.05$, and of these intervals, two had probabilities of $0.01 < P < 0.05$ and another two had probabilities of $P < 0.001$. With the exception of the latter two, the differences in recombination frequency were almost exactly those expected by chance alone. There was no discernable difference between the two populations in the distribution of crossovers over the vast majority of the *B. napus* genome.

**Table 1.** Peaks and plateaus of allele imbalance ($p < 0.05$) along the length of the linkage groups.

| Pattern of distortion | Location and direction of distortion[a] |
|---|---|
| N-o-72-8 peak[b] | N1(+), N2(+), N6(+), N6(+), N7(+), N11(+), N19(+), N3(−), N6(−), N7(−), N9(−), N13(−) |
| N-fo-61-9 peak[c] | N8(+), N12(+), N14(+), N15(+), N15(+), N19(+), N1(−), N4(−), N17(−) |
| Peak in both populations[d] | N11(+), N1,[e] N2[e] |
| N-o-72-8 plateau[f] | N10(+) |
| N-fo-61-9 plateau[f] | N3(+) |

[a]The direction of the imbalance is indicated in parentheses after the linkage group name: +, excess of N-o-9 allele; −, excess of N-f-2/N-o-1 allele.

[b]A peak in the degree of allele imbalance significant in only the N-o-72-8 population.

[c]A peak in the degree of allele imbalance significant in only the N-fo-61-9 population.

[d]A peak in the degree of allele imbalance coincident in both populations.

[e]A peak in the degree of allele imbalance that is coincident in both populations but there is an excess of different parental alleles in each population.

[f]The allele imbalance shows a plateau along the linkage group that is significant in only one population as indicated.

### The relative distributions of crossovers and RFLP loci

The frequency distribution of interval sizes in the N-o-72-8 and N-fo-61-9 maps (and in the *B. oleracea* genetic map of Bohuon et al. (1996)) was compared with the frequency distribution expected from a model in which the spatial distributions of both crossovers and loci were random (Fig. 4). Clearly, the combined spatial distributions of crossovers and loci did not fit the random model in any of the three popula-

**Fig. 3.** Variation in the degree of segregation distortion at linked loci on integrated linkage groups, illustrating similar and contrasting selection pressures in the two populations. Map distances are from the tops of linkage groups (as represented in Fig. 1) and the mean genetic lengths of corresponding intervals assayed in the two populations have been used. (A) N11 exhibited selection for the N-o-9 allele at two, possibly equivalent, loci (one at each end of the linkage group) in both populations. (B) N14 exhibited selection for the N-o-9 allele in the centre of the linkage group but only in the N-fo-61-9 population. (C) N1 exhibited selection for the N-o-9 allele in the N-o-72-8 population but against the N-o-9 allele in the N-fo-61-9 population (possibly at more than one locus) at the top of the linkage group.

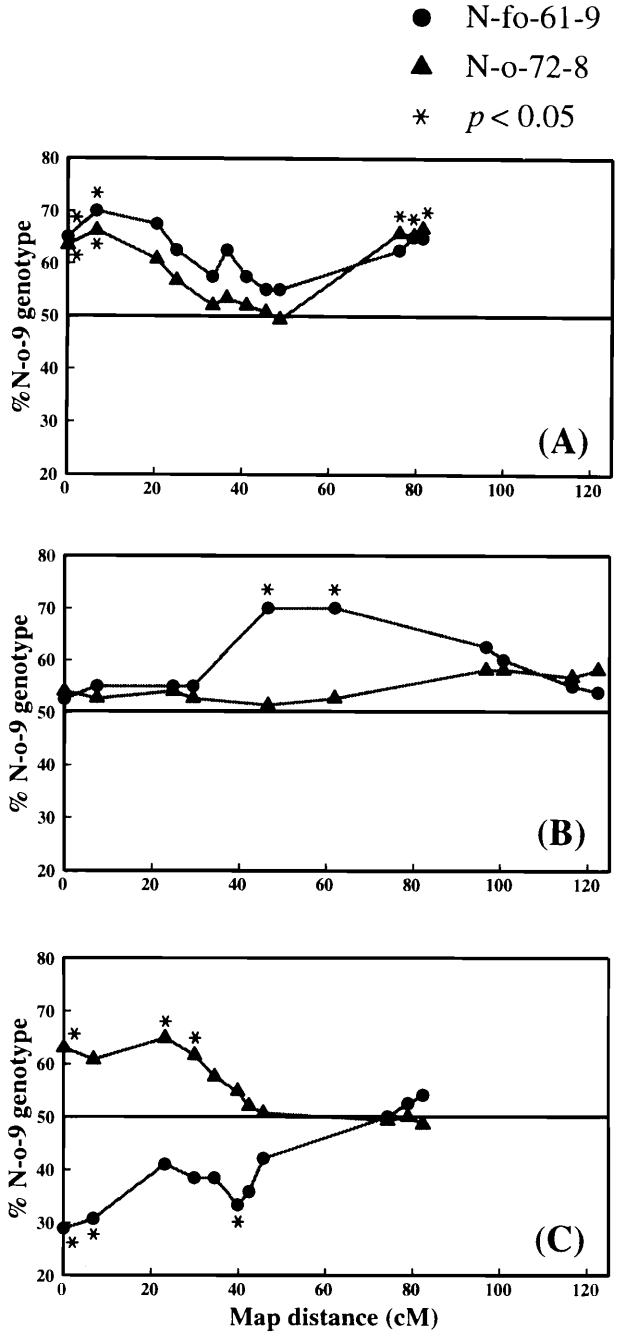



**Table 2.** Comparison of the number of observed crossovers for each of the 19 linkage groups in the two $F_1$ hybrids.

| Linkage group | Crossovers per linkage group | | | |
|---|---|---|---|---|
| | N-fo-61-9[a] | N-o-72-8[b] | $\chi^2$ | $P$[c] |
| N1 | 39 | 73 | 0.01 | 0.92 |
| N2 | 36 | 85 | 1.58 | 0.21 |
| N3 | 48 | 110 | 1.62 | 0.20 |
| N4 | 30 | 43 | 1.11 | 0.29 |
| N5 | 32 | 64 | 0.15 | 0.70 |
| N6 | 56 | 112 | 0.26 | 0.61 |
| N7 | 32 | 52 | 0.31 | 0.58 |
| N8 | 18 | 69 | 8.04 | 0.004 |
| N9 | 39 | 65 | 0.24 | 0.62 |
| N10 | 21 | 49 | 0.83 | 0.36 |
| N11 | 33 | 73 | 0.77 | 0.38 |
| N12 | 9 | 30 | 2.52 | 0.11 |
| N13 | 58 | 133 | 1.96 | 0.16 |
| N14 | 50 | 114 | 1.60 | 0.20 |
| N15 | 40 | 69 | 0.10 | 0.75 |
| N16[d] | 39[d] | 34[d] | 8.46[d] | 0.004[d] |
| N17 | 40 | 64 | 0.83 | 0.36 |
| N18 | 25 | 45 | 0.01 | 0.92 |
| N19 | 24 | 55 | 0.80 | 0.37 |
| Total | 630 | 1305 | 22.7 (17 df) | 0.16 |

[a]Crossovers detected in the 50 DH individuals of the N-fo-61-9 population using the 211 loci common to the N-fo-61-9 and N-o-72-8 maps.

[b]Crossovers detected in the 92 DH individuals of the N-o-72-8 population using the 211 loci common to the N-fo-61-9 and N-o-72-8 maps.

[c]Probability of the difference between the N-fo-61-9 and N-o-72-8 populations in the observed number of crossovers per linkage group having occurred by chance.

[d]Linkage group N16 could not be mapped in the N-fo-61-9 population (see Fig. 1).

tions (N-o-72-8: $\chi^2 = 705.6$, df = 15; N-fo-61-9: $\chi^2 = 70.8$, df = 9; *B. oleracea*: $\chi^2 = 3192.4$, df = 12), although the N-fo-61-9 population was closer to random than the other two. Localized clusters and shortages of loci and (or) crossovers would result in an observed distribution of interval sizes with excesses of both very small and very large intervals. This was the pattern observed in the N-o-72-8 population. The shortfall of coincident loci observed in the *B. oleracea* population might have a trivial explanation, namely, scoring error introducing phantom crossovers between coincident loci.

## Discussion

The meiotic patterns of chromosome pairing and recombination were deduced in two contrasting $F_1$ hybrids of *B. napus*: one derived from a cross between a winter oilseed rape (OSR) cultivar and a spring OSR cultivar and the other derived from a cross between the same winter OSR cultivar and a newly resynthesized *B. napus* line (i.e., a chromosome doubled interspecific hybrid between *B. rapa* and *B. oleracea*). The populations of DH lines derived from the two contrasting $F_1$

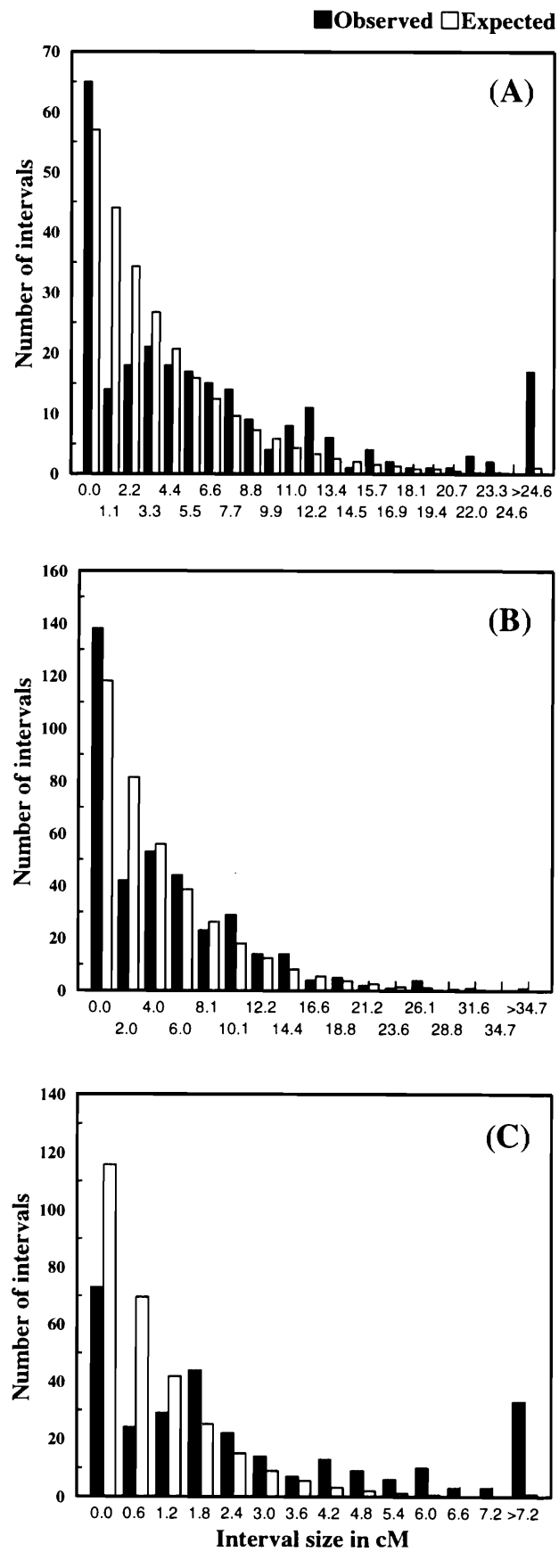



**Fig. 4.** Frequency distributions of interval sizes in genetic maps of *B. napus* and *B. oleracea*. The distributions observed in the N-o-72-8 (A), N-fo-61-9 (B), and *B. oleracea* (C) populations (solid bars) were compared with the theoretical distributions based on a model in which the spatial distributions of both the loci and the crossovers were random (open bars). The data for the *B. oleracea* population was taken from Bohuon et al. (1996). The numbers on the *x*-axes represent the upper limits of interval size in centimorgans.

hybrids via microspore culture were used to produce genetic linkage maps that could be aligned almost perfectly. This near-perfect alignment of maps indicated not only that the genetic analysis was accurate and robust in determining the linear order of loci, but also that *B. napus* chromosomes reproducibly behaved as 19 distinct homologous pairs in the two contrasting $F_1$ hybrids. Furthermore, each of the 19 chromosomes of the haploid genome of oilseed rape recognized and recombined with unique chromosomes from newly resynthesized *B. napus*. This result confirmed the conclusions of Parkin et al. (1995) and Bohuon et al. (1996), namely, that the genomes of the diploid progenitors of *B. napus* have remained essentially unaltered since the interspecific hybridization(s) that formed *B. napus*, and that these diploid genomes were extremely similar to genomes of modern-day *B. rapa* and *B. oleracea*.

Closer analysis of the genetic maps derived from the two $F_1$ hybrids suggested that not only the pattern of chromosome pairing but also the frequency and distribution of recombination were almost indistinguishable. This suggests that the recombination machinery of *B. napus* had no difficulty in coping with the increased genetic divergence of the parents of the winter OSR × resynthesized *B. napus* cross compared with the winter OSR × spring OSR cross. Recombination in maize is similarly insensitive to differences in the genetic divergence of parental genotypes (Williams et al. 1995), although reduced recombination in interspecific hybrids involving tomato has been interpreted as resulting from the high levels of heterozygosity in the hybrids (Paterson et al. 1990). The observation that crossovers were distributed similarly over the whole *B. napus* genome in the two $F_1$ hybrids also suggested the absence of any of the localized problems in chromosome pairing that might be expected to result from inversions or other such rearrangements. Resynthesized *B. napus* lines are being used to introduce useful diversity into oilseed rape (Parkin et al. 1994; Magrath et al. 1994). The constant pattern of recombination in contrasting $F_1$ hybrids of *B. napus* suggests that this introgression of novel alleles into oilseed rape from *B. rapa* and *B. oleracea* (via resynthesized *B. napus*) should not be limited by either differences in sequence homology or differences in the chromosomal structure. Efficient recombination in wide crosses will also reduce any problems associated with linkage drag.

The frequency distributions of loci with varying degrees of segregation distortion in the populations derived from the two hybrids each showed an excess of loci with unbalanced allele frequencies (Fig. 2). The proportions of loci with significant levels of allele imbalance ($p < 0.05$) were 35 and 11% for the N-o-72-8 and the N-fo-61-9 populations, respectively. These proportions were similar to those reported for other *B. napus* populations of DH lines (Ferreira et al. 1994; Uzunova et al. 1995). In contrast, the frequency distribution

of varying degrees of segregation distortion observed in a conventional backcross population of *B. napus* was much more similar to that expected by chance (Howell et al. 1996). The localized peaks of allele imbalance in the microspore-derived populations might represent genes influencing responsiveness to microspore culture, embryo competitiveness, and (or) plantlet survival during tissue culture. The identification of unique regions of pronounced segregation distortion in the two populations probably reflects contrasting allelic differences in the parents of the two $F_1$ hybrids, and indicates that responsiveness to and survival of microspore culture is probably influenced by a large number of genes.

The distribution of marker loci along the *B. napus* linkage groups was not random in any of the three genetic maps tested. This result suggests that either the sequences that gave rise to informative RFLP probes are physically clustered or that crossovers occur preferentially in particular map intervals or both. These results are in line with similar investigations in tomato (Tanksley et al. 1992), wheat (Devos and Gale 1993), and *Brassica nigra* (Lagercrantz and Lydiate 1995), where significant clustering of marker loci was evident. However, marker clustering was less extreme and less localized in *B. napus* (and particularly in the N-fo-61-9 population) than in the systems investigated previously, suggesting a reasonable correspondence between physical and genetic distances at low resolution.

The aligned map of the *B. napus* genome derived from the N-fo-61-9 and N-o-72-8 maps contained 455 loci detected by 162 informative RFLP probes. The N-o-72-8 population revealed an additional 59 polymorphic loci despite being less polymorphic than the N-fo-61-9 population, indicating that the RFLP probes probably recognize additional loci monomorphic in both populations. The alignment of linkage maps derived from meiosis in two contrasting $F_1$ hybrids indicated the reproducibility of chromosome pairing in the *B. napus* genome. This stable genome organization has allowed the integration of further *B. napus* maps generated using the common set of RFLP probes (Fray et al. 1997; Howell et al. 1996; Kelly et al. 1997).

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