Frequent nonreciprocal translocations in the amphidiploid genome of oilseed rape (*Brassica napus*)

A.G. Sharpe, I.A.P. Parkin, D.J. Keith, and D.J. Lydiate

Abstract: A RFLP map of *Brassica napus*, consisting of 277 loci arranged in 19 linkage groups, was produced from genetic segregation in a combined population of 174 doubled-haploid microspore-derived lines. The integration of this map with a *B. napus* map derived from a resynthesized *B. napus* × oilseed rape cross allowed the 10 linkage groups of the *B. napus* A genome and the 9 linkage groups of the C genome to be identified. Collinear patterns of marker loci on different linkage groups suggested potential partial homoeologues. RFLP patterns consistent with aberrant chromosomes were observed in 9 of the 174 doubled-haploid lines. At least 4 of these lines carried nonreciprocal, homoeologous translocations. These translocations were probably the result of homoeologous recombination in the amphidiploid genome of oilseed rape, suggesting that domesticated *B. napus* is unable to control chromosome pairing completely. Evidence for genome homogenization in oilseed rape is presented and its implications on genetic mapping in amphidiploid species is discussed. The level of polymorphism in the A genome was higher than that in the C genome and this might be a general property of oilseed rape crosses.

Key words: restriction fragment length polymorphism, genetic linkage map, homoeologous recombination, microspore culture, doubled haploid.

Résumé : Une carte RFLP du *Brassica napus*, comprenant 277 loci assemblés en 19 groupes de liaison, a été réalisée à partir de la ségrégation génétique chez une population de 174 lignées dihaploïdes provenant de la culture de microspores. Une intégration de cette carte avec une carte produite à la suite d'un croisement *B. napus* resynthétisé × colza a permis d'identifier les 10 groupes de liaison du génome A et les 9 groupes du génome C. La disposition colinéaire de certains marqueurs dans différents groupes de liaison suggère l'existence possible d'homéologies partielles. Des motifs RFLP indiquant des aberrations chromosomiques ont été observés chez 9 des 174 lignées dihaploïdes. Au moins quatre de ces lignées sont porteuses de translocations homéologues non-réciproques. Ces translocations résultent vraisemblablement de recombinaisons homéologues à l'intérieur du génome amphiploïde du colza et cela suggère que le *B. napus* domestiqué est incapable de contrôler de facon stricte l'appariement des chromosomes. Des indications d'une homogénéisation du génome du colza sont présentées et l'impact de ce phénomène sur la cartographie chez les espèces amphiploïdes est discuté. Le niveau de polymorphisme était plus élevé chez le génome A que chez le génome C et ceci pourrait représenter une situation générale chez les croisements du colza.

Mots clés : polymorphisme des longueurs des fragments de restriction, carte génétique, recombinaison homéologue, culture de microspores, haploïdes doublés.

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Introduction

Oilseed rape/canola (*Brassica napus*) is the main oilseed crop grown in Europe and a crop of major importance in China and North America (FAO (United Nations Food and Agriculture Organization) production year book 1992). It would be desirable to use modern marker-assisted breeding techniques, reviewed recently by Paterson et al. (1991), to improve the agronomic characteristics of oilseed rape. *Brassica* crops are ideal for the exploitation of restriction fragment length polymorphism (RFLP) markers because of the high levels of natural polymorphism (Figdore et al. 1988). The first RFLP map of *B. napus* described 120 loci ordered in 19 linkage groups (7 of which contained 3 or fewer loci) and 17 unlinked loci (Landry et al. 1991). A more recent *B. napus* RFLP map consisted of 120 loci ordered in 22 linkage groups (Ferreira et al. 1994). The genetic analysis described below has resulted in a more comprehensive RFLP map of oilseed rape. It consists of 277 loci arranged in 19 large linkage groups, with only

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1 pair and 4 single loci remaining unlinked to the major groups.

Brassica napus is very amenable to microspore culture (Lichter 1982; Lichter et al. 1988), which results in the rapid generation of true-breeding doubled-haploid (DH) lines (Henderson and Pauls 1992). The ability of microspore culture to produce true-breeding cultivars in a single generation has led to the technique being adopted widely by plant breeders who wish to develop uniform varieties (Chen and Beversdorf 1990). However, there is anecdotal evidence for segregation for altered morphology within DH lines (R. Jennaway, personal communication). This paper describes the inheritance of RFLP-defined loci by microspore-derived plants and demonstrates that spontaneous translocations occur at a high frequency in oilseed rape. These translocations are likely to contribute to the variation that is sometimes observed in DH lines of oilseed rape.

Brassica napus is an amphidiploid species with 19 chromosome pairs. Cytological evidence indicates that it has been formed by the hybridization of *B. oleracea* (n = 9) with *B. rapa* (n = 10) (U 1935). More recent investigations based on RFLP analysis have suggested that the present day *B. napus* is not a simple fusion of the diploid *B. oleracea* and *B. rapa* genomes (Song and Osborn 1992). However, it is clear that 10 linkage groups from *B. napus* pair preferentially with *B. rapa* chromosomes, while the remaining 9 *B. napus* linkage groups pair preferentially with *B. oleracea* chromosomes (Parkin et al. 1995). Domesticated *B. napus* exhibits predominantly bivalent chromosome pairing, while resynthesized *B. napus*, formed from interspecific crosses between *B. rapa* and *B. oleracea*, exhibits multivalent formation that probably reflects pairing between homoeologous chromosomes (Attia and Röbbelen 1986). The high frequency of nonreciprocal translocations reported in this paper is probably the result of residual homoeologous recombination in domesticated *B. napus*.

Materials and methods

Parental plant material

The two *B. napus* parents of the mapping cross, N-o-1 and N-o-9, were DH lines of oilseed rape derived from a Canadian spring cultivar (P. Wray and P. Dale; John Innes Centre, Norwich NR4 7UH, U.K.) and a British winter cultivar (P. Capitain and R. Jennaway; Cambridge Plant Breeders, Thriplow SG8 7RE, U.K.), respectively. N-o-72-8 is a population of 92 DH lines derived from a single F_1 plant from a N-o-9 × N-o-1 cross and N-o-69-8 is a population of 82 DH lines derived from a single F_1 plant from the reciprocal cross. The populations of DH lines were derived via microspore culture essentially as described by Chuong and Beversdorf (1985).

DNA extraction and Southern hybridization

DNA was extracted essentially as described by Sharp et al. (1988) except that "Kirby mix" (Covey and Hull 1981) was used for the initial extraction of the freeze-dried tissue. Restriction enzyme digestion, gel electrophoresis, alkaline transfer, and Southern hybridization were essentially as described in Sharp et al. (1988) except that: DNA was blotted onto Hybond N^+ nylon membranes (Amersham); 10% dextran sulphate was added to the hybridization solution; and two low stringency washes followed by two high stringency washes (in 0.2× SSC (1× SSC: 0.15 M NaCl plus 0.015 M sodium citrate), 0.1% SDS) were employed after hybridization. The DNA size standard was as described by Lydiate et al. (1986).

RFLP probes

Three libraries of small *Pst*I fragments of *Brassica* DNA were generated. DNA was isolated from the oilseed rape variety Westar (*B. napus*, "pN" probes), the turnip rape cultivar Maleksberger (Braunschweig accession No. 011008) (*B. rapa*, "pR" probes), and from the Chinese broccoli line O-al-5 (D.J. Lydiate, unpublished data) (*B. oleracea*, "pO" probes). DNA samples were digested with *Pst*I and fragments 0.6–2.0 kilobases (kb) in size were extracted from agarose gels by electroelution. The purified fragments were ligated into the *Pst*I site of pIJ2925, a derivative of pUC19 (Yanisch-Perron et al. 1985) in which flanking *Bgl*II sites have been added to the polylinker region (G.R. Janssen, personal communication), and the recombination deficient *Escherichia coli* strain TG2 (Maniatis et al. 1989) was transformed with the resulting plasmids. The inserted *Brassica* DNA was amplified using the polymerase chain reaction (Innis et al. 1990) and "oligo-labelled" with [^{32}P]dCTP (Feinberg and Vogelstein 1984).

A total of 405 *Brassica Pst*I clones were screened for low copy number and polymorphism and 103 highly informative *Brassica* RFLP probes were selected. Fifty-four *B. napus* RFLP probes ("pW" probes) selected from libraries described by Thormann et al. (1994) and 5 *Brassica* cDNA clones ("pC" probes) were also used.

Linkage analysis

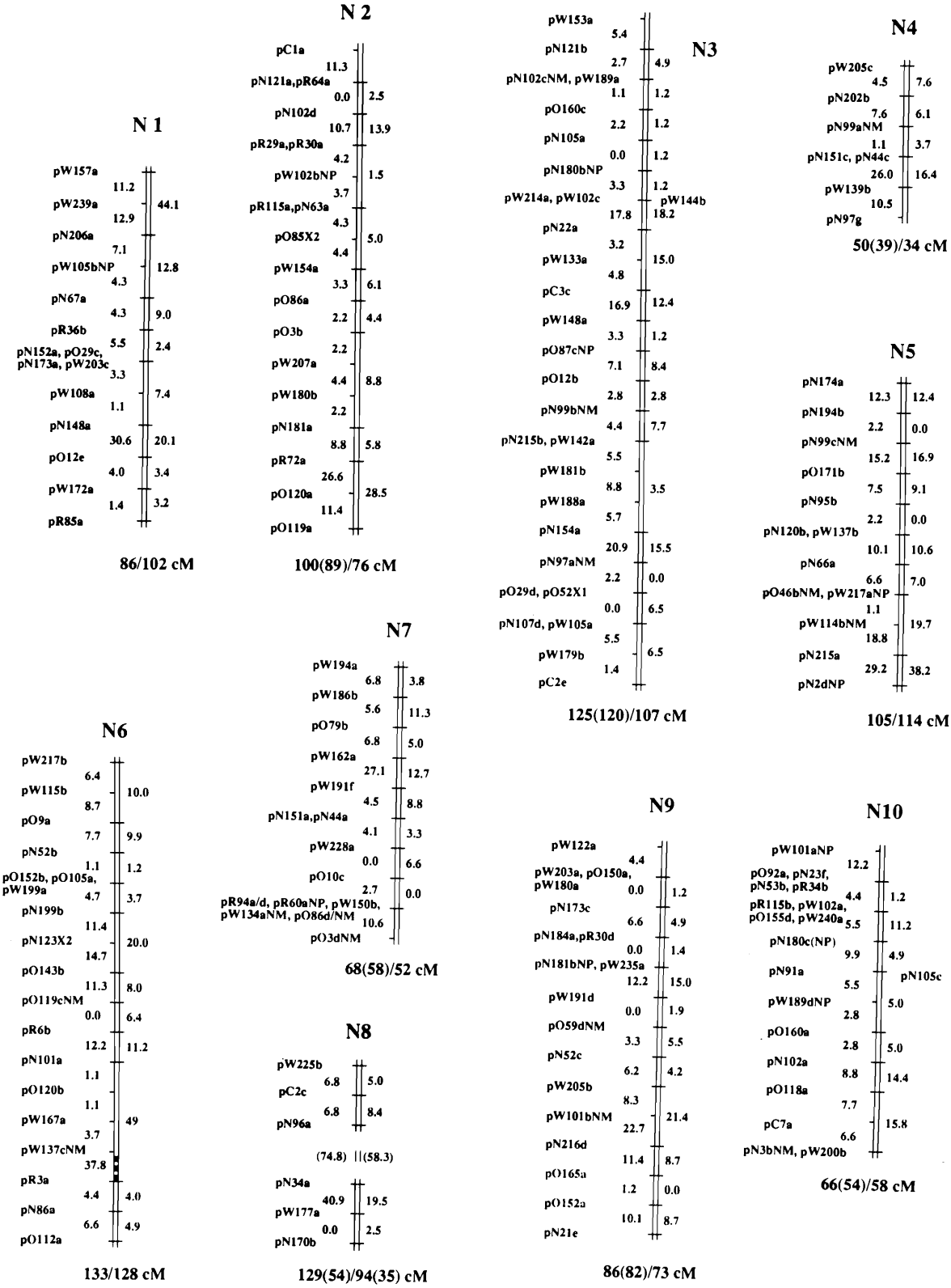
The analysis of genetic linkage was performed using simple BASIC programmes as described by Ellis et al. (1992) and MAPMAKER, versions 1.9 and 3.0 (Lander et al. 1987). A minimum LOD score of 4.0 was used to associate RFLP loci into initial linkage groups, the LOD score was reduced to bridge the five largest intervals (Fig. 1). Three-point and multipoint analyses were used to determine the most probable locus order for each linkage group. The locus order was verified using two-point analysis for every pairwise combination of loci within each linkage group (Ellis et al. 1992) and by re-examining the original scorings for single loci flanked by double crossovers. Because the DH lines were derived from single gametes and from a single round of meioses in a common F_1 parent, double crossovers flanking short map intervals should be extremely rare. Recombination frequencies were converted to map distances using Kosambi's mapping function (Kosambi 1944).

Results

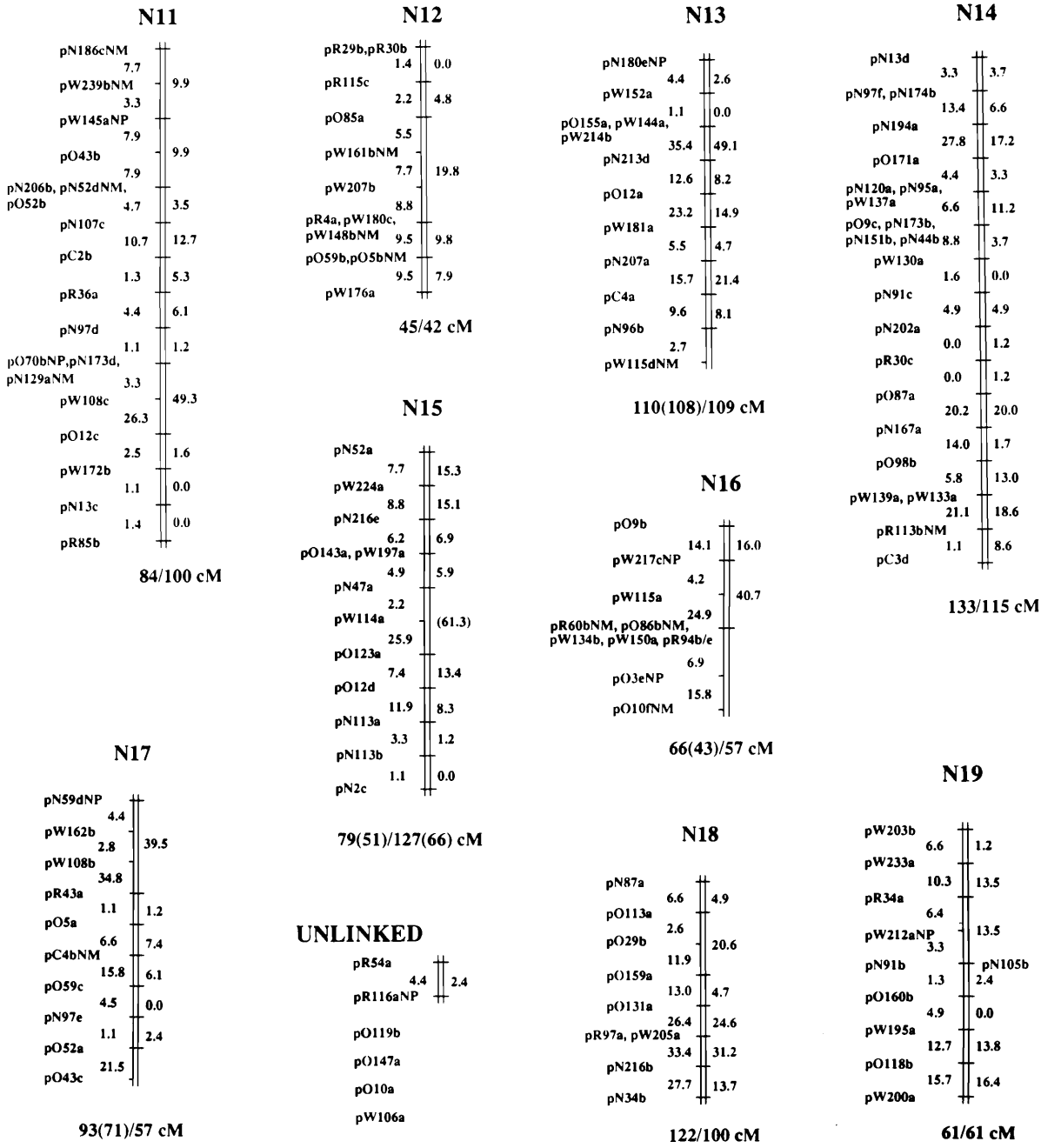
The genetic linkage maps

The genetic linkage maps of *B. napus* that were derived from populations N-o-72-8 and N-o-69-8 are shown in Fig. 1. The combined map consisted of 277 loci associated in 19 linkage groups (total map distance 1741 cM for N-o-72-8 and 1606 cM for N-o-69-8) with a further pair of loci and four independent loci that remained unassociated

Fig. 1. An integrated genetic linkage map of *B. napus* based on segregation in the N-o-72-8 and N-o-69-8 populations of DH lines. Vertical lines represent linkage groups (N1–N19) with RFLP-defined loci represented by the code for the appropriate RFLP probe followed by a lower case letter to distinguish different loci recognized by the same probe. A pair of segregating alleles was scored at each locus except for loci with identifiers ending in NP or NM, where only the alleles from the N-o-9 or N-o-1 parent, respectively, could be scored. Map distances (cM) on the left and right sides of the linkage groups are those calculated for the N-o-72-8 and N-o-69-8 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



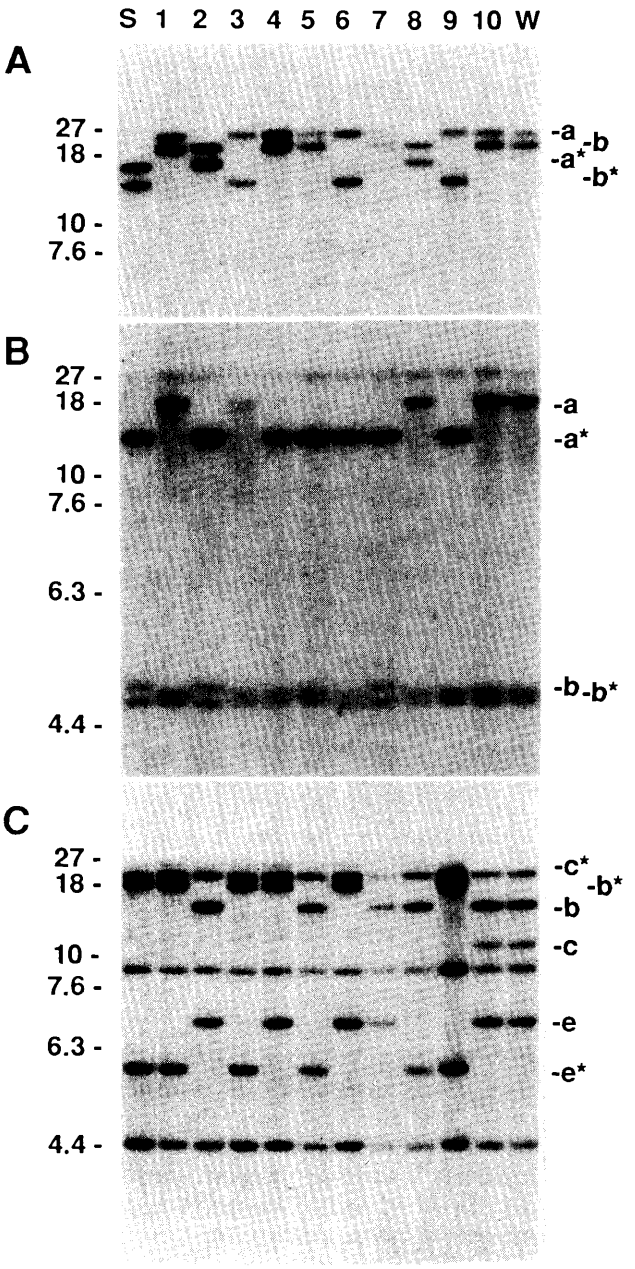
the total. All loci separated by recombination in either population are represented by identical spacing to facilitate the comparison of recombination frequencies in the two populations. All informative polymorphisms were based on genomic DNA digested with *Eco*RI, except for loci ending in "X" (followed by a number) where polymorphism was based on DNA digested with *Xba*I. Six of the map intervals were based on linkage with LOD scores < 4 in both populations, considered separately. The intervals, and LOD scores in the N-o-72-8 population, were N5 (pN215a–pN2dNP) LOD 3.8, N17 (pW108b–pR43a) LOD 3.1, N13 (pO155a–pN213d) LOD 3.0, N18 (pR97a–pN216b) LOD 2.69, N6 (pW137cNM–pR3a) LOD 2.2, and N8 (pN96a–pN34a), which exhibited essentially no linkage. Linkage across the two largest map intervals was verified in other crosses as described in the text.



with the major groups. The two maps were identical with respect to the most probable relative positioning of loci on all 19 linkage groups. The genetic distances separating loci were also very similar with only two intervals exhibiting a difference in recombination frequency that could be expected to occur, by chance, at a frequency of less than 5%: pN47a–pO123a (on N15) $0.05 > P > 0.01$ and pN167a–pO98b (on N14) $0.01 > P > 0.001$. The marked conservation of genetic distances, over equivalent regions of the two maps, was also obvious at the level of whole linkage groups and over the total map.

Linkage across the two largest map intervals (pW137cNM–pR3a on N6 and pN96a–pN34a on N8, Fig. 1) has been demonstrated independently using a complementary

Fig. 2. Autoradiographs of RFLP alleles segregating in 12 DH *B. napus* lines and detected by three *Brassica* probes. All tracks contained total DNA digested with *Eco*RI: tracks S and W, parental DNA from N-o-1 and N-o-9, respectively; and tracks 1–10, DNA from 10 DH lines of the N-o-72-8 population. Probe A (pR59) detected two polymorphic loci (*a* and *b*). Probe B (pN34) detected four loci, two polymorphic (*a* and *b*) and two monomorphic. Probe C (pC2) detected six loci, three polymorphic (*b*, *c*, and *e*) and three monomorphic. The numbers to the left of the autoradiographs represent the positions of the size standards (sizes in kilobase pairs) and the letters to the right of the autoradiographs identify segregating pairs of alleles (* indicates alleles from the N-o-1 parent). All the monomorphic loci detected by pN34 and pC2 in the N-o-72-8 and N-o-69-8 populations were polymorphic and mapped in the complementary N-fo-61-9 population (Parkin et al. 1995; A. Sharpe and D.J. Lydiate, unpublished data).



B. napus population (LOD > 4; Parkin et al. 1995). Linkage across the pN96a–pN34a interval has also been verified in three further *B. napus* populations (LOD > 3 in each case; P.M. Howell, M.J. Fray, and D.J. Lydiate, unpublished data). A pronounced clustering of marker loci can be observed in many regions of the map, with five extreme clusters containing four or more coincident loci, namely: the middle of N1, the bottom of N7, the top of N10, the upper portion of N14, and the middle of N16 (Fig. 1). The populations used to derive the integrated genetic linkage map of *B. napus* described above and the population used to develop a complementary map of *B. napus* (Parkin et al. 1995) shared a common parent, namely, the DH winter oilseed rape line N-o-9. This allowed the rigorous integration of the two *B. napus* maps based on the segregation of the same N-o-9 alleles at 211 loci in both populations.

Homoeologous loci in the A and C genomes of *B. napus*

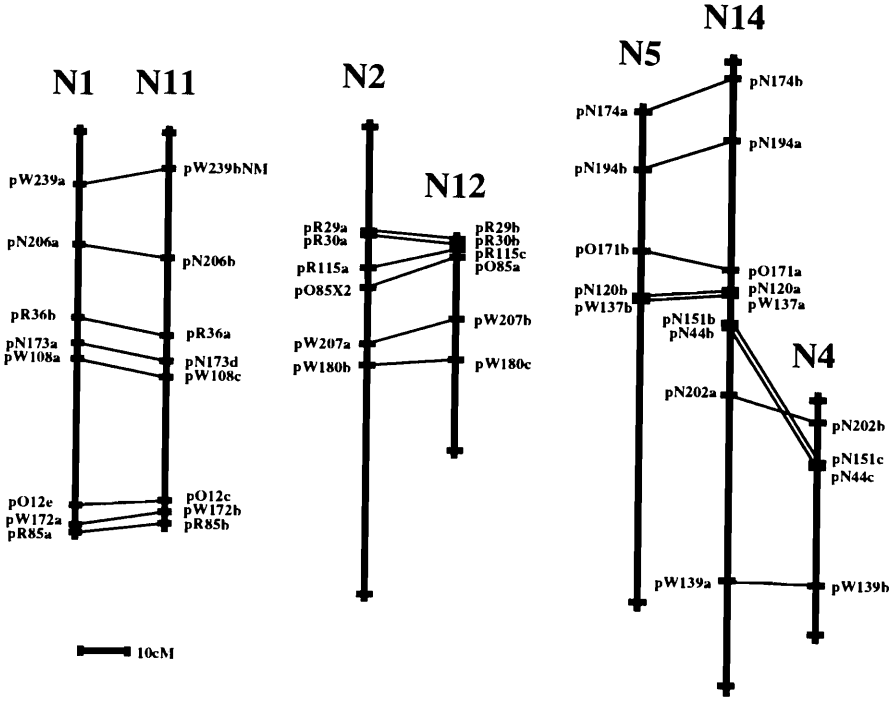
Over 80% of informative *Brassica* probes detected even numbers of loci in *B. napus*, typically two, four, six, or eight loci (Fig. 2), with six loci being most common. The loci produced Southern hybridization signals of varying strength and these loci, strongly hybridizing, weakly hybridizing, and intermediate, also occurred in pairs. The presence of the A (*B. rapa*) and C (*B. oleracea*) genomes within amphidiploid *B. napus* provides a ready explanation for the duplicate nature of *B. napus* loci.

Linkage groups N1–N10 represent the A genome of *B. napus*, while groups N11–N19 represent the C genome (Lydiate et al. 1993; Parkin et al. 1995). Pairs of linkage groups with conserved orders of related loci (that is, loci detected by a single probe) could be identified, for example: N1 with N11, N2 with N12, and N14 with N4 and N5 (Fig. 3). These linkage groups might represent pairs of homoeologous chromosomes derived from common ancestral chromosomes from the progenitor of *B. oleracea* and *B. rapa*. However, the RFLP map (Figs. 1 and 3) necessarily represents an incomplete picture of the homoeologous relationships between the different linkage groups, because less than half of the DNA fragments (and thus probably less than half of the loci) that were detected by the RFLP probes were polymorphic.

Duplicated loci and missing loci

The two alleles at a polymorphic locus produce distinctive RFLP banding patterns in populations of DH lines with one or other allele present in every line and no lines containing both alleles. Unusual RFLP patterns were observed at specific loci in particular DH lines from both the N-o-72-8 and N-o-69-8 populations. Both alleles of one locus were present in these lines, while neither allele was observed at a second (possibly homoeologous) locus (Fig. 4). After noting these unusual locus or line combinations it became apparent that groups of linked loci were segregating in an unusual manner in the same individuals (Fig. 5). These segregation patterns are consistent with the duplication of chromosomal segments and the concurrent loss of related segments from (partially) homoeologous chromosomes. These nonreciprocal translocations probably result from homoeologous recombination at meiosis in the N-o-72-8 and N-o-69-8 F_1 individuals.

Fig. 3. Pairs or sets of linkage groups with conserved orders of related loci. Vertical lines represent linkage groups with pairs of loci detected by a single probe indicated by connecting lines. Linkage groups N11, N12, and N14 belong to the C (*B. oleracea*) genome (Parkin et al. 1995) and linkage groups N1, N2, N4, and N5 are partially homologous linkage groups from the A (*B. rapa*) genome.



Frequency and distribution of nonreciprocal translocation events

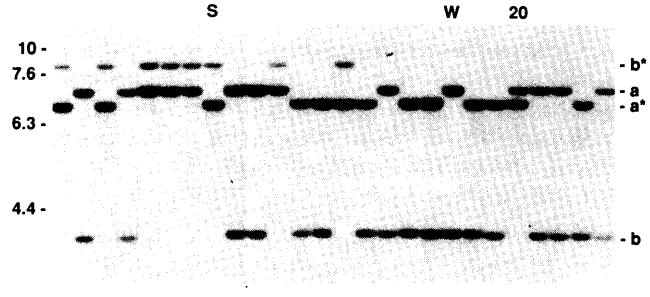
The distribution of nine aberrant chromosomes, homozygous in DH lines of the N-o-72-8 and N-o-69-8 populations, is shown in Fig. 6. Rearrangements *a*, *b*, *c*, and *h* (Fig. 6) are nonreciprocal translocations likely to have resulted from homoeologous recombination in the two F_1 parents. Rearrangements *e*, *g*, and *i* (Fig. 6) might have arisen via the same mechanism, however, the chromosomal segments homoeologous to the rearranged regions were not covered by markers in the N-o-72-8 and N-o-69-8 maps (Parkin et al. 1995). Rearrangements *d* and *f* (Fig. 6) could indicate the existence of fragmented chromosomes.

No phenotypic changes associated with any of the chromosome rearrangements have been detected, however, the DH lines are segregating for a large number of traits, making an accurate assessment difficult.

None of the chromosomal aberrations represented in Fig. 6 represented aneuploidy, because each aberrant linkage group contained a high proportion of loci that segregated normally. Thus, none of the chromosomal aberrations was solely the result of nondisjunction at meiosis in the N-o-72-8 or N-o-69-8 F_1 plants.

Anomalies restricted to linkage groups N7 and N16 have been omitted for the current analysis, because it is likely that the N-o-1 parent of the N-o-72-8 and N-o-69-8 crosses was homozygous for a reciprocal translocation involving the lower portions of the corresponding chromosomes (D.J. Lydiate and J.S. Parker, unpublished data).

Fig. 4. Autoradiograph of RFLP alleles segregating in 26 DH *B. napus* lines and detected by probe pR85. All tracks contained total DNA digested with *Eco*RI: track S, parental DNA from N-o-1; track W, parental DNA from N-o-9; and the remaining tracks, DNA from 24 DH lines of the N-o-72-8 population. Distinct alleles are segregating at two loci, pR85a and pR85b (* indicates alleles from the N-o-1 parent). DH line 20 has both alleles from locus pR85a and neither allele from locus pR85b.



In the 174 lines of the two populations, 1939 crossovers resulting from normal homologous recombination were detected on 17 linkage groups (omitting N7 and N16). The products of a maximum of nine (and a minimum of four) homoeologous recombination events were detected in the same portions of the same populations. The frequency of homoeologous recombination was thus 0.21–0.46% that of homologous recombination (or 0.0014–0.003 detectable

Fig. 5. Nonreciprocal translocations involving linkage groups N1 and N11. RFLP scoring data from 44 DH lines of the N-o-72-8 population probed with eight informative clones is represented: +, inheritance of the N-o-9 parental allele; −, inheritance of the N-o-1 parental allele; 4, inheritance of both parental alleles; 1, inheritance of neither parental allele; columns, DH lines; and rows, loci. Homoeologous sets of loci are reciprocally duplicated in or missing from the lines represented by columns 23 and 37.

N1

```
pW239a   +-+++---+---++--++--+-++-+-++++-++--+-+-+---
pN206a   +-++++++-+--+++-+++----+++-++++-++--+-+-+---
pR36b    +-++++++-+--+++++++-+-++++--++++-++--1---+---
pN173a   +-++++++-+--+++++++-+-++++--++++-++--1---+---
pW108a   +-++++++-+--+++++++----+++--++++-++--1---+---
pO12e    --+-+-+++++++--+-+----+++-+++++-++-+1+--+---
pW172a   --+-+-+++++++--+-+----4++-+++++++++-+1+-++---
pR85a    --+-+-+++++++----+----4++-+++++++++-+1+-++---

pR85b    -++-+-+---++-++-++++++1+++++++-++-++4+++----
pW172b   +++-+-+---++-++-++++++1+++-+++-++-++4+++----
pO12c    +++-+-+---++-++-++++++-+++-+++-++--+4+++----
pW108c   +++-+-++-+++--+-++++-+-+-+-+++-++--+4+++----
pN173d   +++-+-++-+++--+-++++-+-+-+-+++-++--+4+++----
pR36a    +++-+-++++++---++++-+-+-+-++++++--+4+++----
pN206b   +++-+-++++++-+-+++++++-+-+-++-+++--+-+-++--+
pW239b   +++-+-+-+-++-+-+++++++-+-+----+-+-++-+-++-++
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N11

homoeologous crossovers per chromatid) in the N-o-72-8 or N-o-69-8 F_1 plants.

Effect of genome homogenization on RFLP maps of *B. napus*

The same RFLP allele was sometimes present at a pair of distinct (often homoeologous) loci in *B. napus*. Nonreciprocal translocations, caused by homoeologous recombination, are an obvious mechanism driving this genome homogenization. The segregation of these duplicate alleles (present at pairs of distinct loci) can be mistakenly scored as segregation at single loci. The RFLP pattern for loci pW136a and pW136c (Fig. 7) elegantly demonstrates the possible confusion resulting from duplicate alleles. In the case of pW136a and pW136c, one RFLP allele was present at both loci in the N-o-9 parent and a different allele was present at both loci in the N-o-1 parent. This resulted in a segregation pattern for a pair of homoeologous loci in the DH lines of the N-o-72-8 and N-o-69-8 populations equivalent to the RFLP pattern normally associated with the segregation at a single polymorphic locus in a conventional F_2 population (Fig. 7).

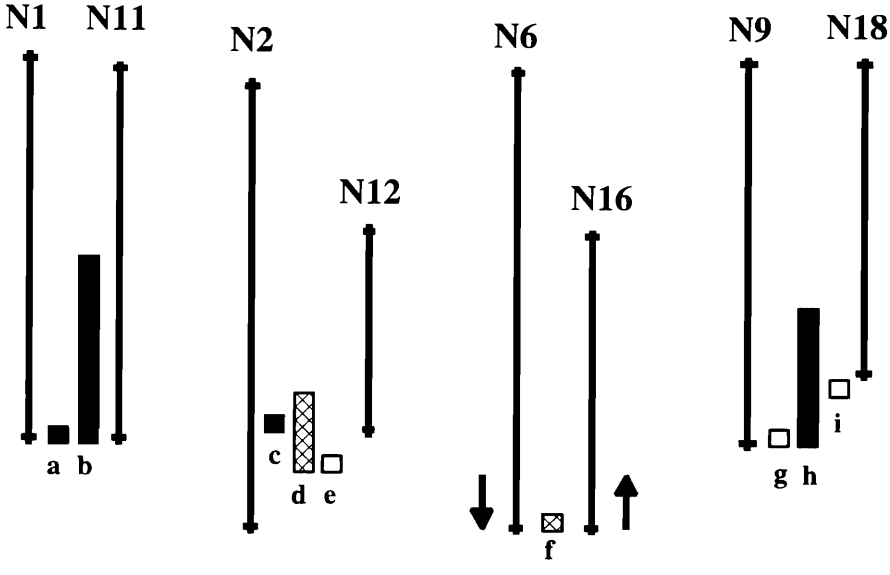
Including the scored segregation pattern of a duplicate allele in genetic linkage analysis (under the erroneous assumption that it represented a single locus) resulted in the fusion of a pair of distinct linkage groups (Fig. 8). When the duplicate alleles were present at a pair of homoeologous loci, the fused linkage group had a structure resembling a large inverted repeat (Fig. 8).

Discussion

The 19 linkage groups of the combined *B. napus* map (Fig. 1) are probably equivalent to the 19 chromosome pairs of *B. napus*. However, cytological experiments are needed to establish definitively the relationships between linkage groups and chromosomes.

In the *B. napus* map described above, there were 160 polymorphic loci assigned to the 10 linkage groups of the A genome (N1–N10) and 117 polymorphic loci assigned to the 9 linkage groups of the C genome (N11–N19). The difference between the A and C genomes, with respect to the number of mapped loci, was significant (χ^2 test of similarity, $P < 0.01$). This probably resulted from contrasting levels of polymorphism in the two genomes and might be a general property of *B. napus*. There are indications that the *B. oleracea* portion of the genome has a fairly narrow genetic base originating in *B. montana* (a wild subspecies of *B. oleracea*) that is the putative maternal parent of successful *B. oleracea* × *B. rapa* hybrids (Song and Osborn 1992; Magrath et al. 1993). In contrast, the genetic diversity in the *B. rapa* portion of the *B. napus* genome has been increased by repeated interspecific crosses between *B. napus* and *B. rapa* (Johnston 1974).

Fig. 6. Schematic representation of the distribution and extent of chromosomal aberrations. Vertical lines (N1–N18) are linkage groups. Boxes indicate the location and extent of the nine chromosomal rearrangements (*a–i*): solid boxes represent nonreciprocal translocations, open boxes represent possible nonreciprocal translocations, and hatched boxes represent the loss of chromosomal fragments (*d*) or the presence of extra incomplete chromosomes (*f*). *a*, Line 23, pR85a–pW172a duplicated / pR85b–pW172b lost; *b*, line 67, pR85b–pC2 duplicated / pR85a–pN67a lost; *c*, line 31, pR29b–pR30b duplicated / pR29a–pR30a lost; *d*, line 11, pN121a–pN63a lost / no duplication of loci on N12; *e*, line 37, pN121a–pN102d duplicated / homoeologous segment of N12 not mapped; *f*, line 18, pW217b duplicated / no loss of markers on N16; *g*, line 65, pN21e lost / homoeologous segment of N18 not mapped; *h*, line 16, pN34b–pW205a duplicated / pN21e–pN216d lost; and *i*, line 18, pO165a duplicated / homoeologous segment of N18 not mapped. N2/N12 and N6/N16 are in inverted orientation with respect to their representations in Fig. 1. Arrows indicate region of inversion with respect to locus order on N6 and N16.



RFLP analysis of the two populations of DH lines revealed a low but appreciable level of homoeologous recombination at meiosis in oilseed rape (*B. napus*). *Brassica napus* has an amphidiploid genome produced by combining two diploid progenitor species, *B. oleracea* and *B. rapa* (U 1935). These two diploid species are themselves closely related according to phylogenies based on restriction fragment length polymorphism in both chloroplast (Warwick and Black 1991) and nuclear genomes (Song and Osborn 1988). A low frequency of homoeologous recombination is probably a general property of oilseed rape cultivars. The effects of this recombination have been observed in populations derived from crosses between Tapidor and Victor (P.M. Howell and D.J. Lydiate, unpublished data) and between Mansholts Hamburger Raps and Samourai (Uzunova et al. 1995; Fig. 1, track 29). The active control of chromosome pairing is required to limit homoeologous recombination in hexaploid wheat (Riley et al. 1960) and it is likely that this is also true of amphidiploid *B. napus*. It will be interesting to compare the frequency of homoeologous recombination in newly resynthesized *B. napus* lines, where there has been no selection for stable chromosome pairing, with that in "natural" *B. napus* cultivars.

Fig. 7. Autoradiograph of RFLP alleles segregating in 12 DH *B. napus* lines and detected by probe pW136. All tracks contained total DNA digested with *Eco*RI: tracks S and W, parental DNA from N-o-1 and N-o-9, respectively; and tracks 1–10, DNA from 10 DH lines of the N-o-72-8 population. Probe pW136 detected two polymorphic loci, *a* and *c*, however, N-o-1 had the same allele (*a*/c**) at both loci and N-o-9 had a distinct allele (*a/c*) but again at both loci.

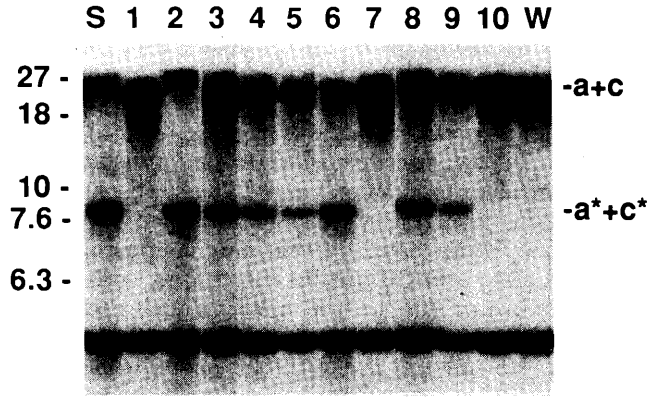
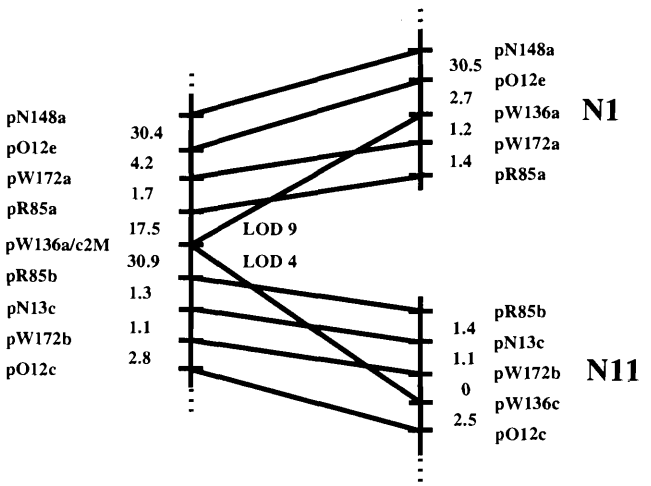


Fig. 8. The pW136a/c phantom locus produces a N1/N11 pseudolinkage-group (left). The probe pW136 detected a single RFLP allele at both the pW136a and pW136c loci of the parental line N-o-1. When the segregation of this allele was scored as segregation at a single locus, pW136a/c2M, the phantom locus was linked to the bottoms of linkage groups N1 and N11. However, when the segregation pattern of the corresponding allele from the N-o-9 parent was considered, the segregation pattern at two distinct loci, pW136a on N1 and pW136c on N11, could be deduced (right).



The distinct A and C genomes of *B. napus* appear to have been maintained throughout its evolution, based on the fact that the chromosomes of modern *B. oleracea* and *B. rapa* cultivars each pair with specific, distinct chromosomes in modern *B. napus* cultivars (Parkin et al. 1995). However, our results suggest that homoeologous recombination, resulting in nonreciprocal homoeologous translocations, occurs in modern cultivars of *B. napus* at a frequency of between 0.027 and 0.057 detectable homoeologous crossovers per gamete. Inbreeding depression could provide an explanation for this apparent paradox. *Brassica oleracea* and *B. rapa* normally exist as outbreeding populations and both species are highly sensitive to inbreeding depression. In contrast, *B. napus* normally exhibits little inbreeding depression, presumably as a result of extensive intergenomic complementation between duplicate expressed genes in the A and C genomes (Song and Osborn 1994). If genome homogenization occurs as a result of homoeologous recombination, deleterious alleles (normally masked by duplicate genes) could replace their properly functioning homoeologues. By this process, nonreciprocal homoeologous translocations would cause reduced fitness in *B. napus*. Natural selection and selection for vigorous cultivars in breeding programmes could then result in a general selection against individuals with translocations. This hypothesis is being tested by analysing contrasting pairs of microspore-derived DH lines of oilseed rape, homozygous for the presence or absence of nonreciprocal homoeologous translocations, in order to detect any differences in phenotype (P.M. Howell and D.J. Lydiate, unpublished data). Rearrangements similar to those identified in members of the N-o-72-8 and N-o-69-8 populations probably occur during the multiplication of DH lines of oilseed rape. Such rearrangements are a likely cause of the variation that sometimes disturbs the uniformity of such "DH" material.

Intergenomic complementation between duplicate genes in the A and C genomes of oilseed rape probably masks genetic variation that would otherwise be produced by recessive variant alleles at one of a pair of homoeologous loci. Nonreciprocal translocations resulting from homoeologous recombination would result in recessive variant alleles becoming established at pairs of homoeologous loci. Candidates for such pairs of duplicate homoeologous genes in *B. napus* include those controlling the production of stamenoid petals (M.J. Fray and D.J. Lydiate, unpublished data) and multivalve pods (C.M. Bowman and D.J. Lydiate, unpublished data).

The genome homogenization that results from nonreciprocal homoeologous translocations causes pairs of homoeologous/homologous loci to share common alleles. When the segregation of these shared alleles is scored simplistically, it causes the formation of fused pseudolinkage groups. In maps derived from the N-o-72-8 and N-o-69-8 populations, a phantom locus (pW136a/c2M) fused linkage groups N1 and N11 (Fig. 8). Maps derived from other *B. napus* populations are similarly complicated by phantom loci when the ends of homoeologous chromosomes share common RFLP alleles (P.M. Howell and D.J. Lydiate, unpublished data). The potential to form this type of fused pseudolinkage group is likely to be a general property of the genetic linkage analysis of amphidiploid species.

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151. Yukio Kaneko, Chiaki Kimizuka-Takagi, Sang Woo Bang, Yasuo Matsuzawa. Radish 141-160. [Crossref]

152. Danuta Babula, Małgorzata Kaczmarek, Piotr A. Ziółkowski, Jan Sadowski. Brassica oleracea 227-285. [Crossref]