

Identification of the A and C genomes of amphidiploid *Brassica napus* (oilseed rape)

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

Abstract: A genetic linkage map consisting of 399 RFLP-defined loci was generated from a cross between resynthesized *Brassica napus* (an interspecific *B. rapa* × *B. oleracea* hybrid) and "natural" oilseed rape. The majority of loci exhibited disomic inheritance of parental alleles demonstrating that *B. rapa* chromosomes were each pairing exclusively with recognisable A-genome homologues in *B. napus* and that *B. oleracea* chromosomes were pairing similarly with C-genome homologues. This behaviour identified the 10 A genome and 9 C genome linkage groups of *B. napus* and demonstrated that the nuclear genomes of *B. napus*, *B. rapa*, and *B. oleracea* have remained essentially unaltered since the formation of the amphidiploid species, *B. napus*. A range of unusual marker patterns, which could be explained by aneuploidy and nonreciprocal translocations, were observed in the mapping population. These chromosome abnormalities were probably caused by associations between homoeologous chromosomes at meiosis in the resynthesized parent and the F₁ plant leading to nondisjunction and homoeologous recombination.

Key words: genetic linkage map, homoeologous recombination, *Brassica rapa*, *Brassica oleracea*, genome organization.

Résumé : Une carte génétique comprenant 339 marqueurs RFLP a été réalisée suite à un croisement entre un *Brassica napus* resynthétisé (un hybride interspécifique entre le *B. rapa* et le *B. oleracea*) et le colza « naturel ». La majorité des loci présentent une transmission disomique des allèles parentaux. Ceci montre que les chromosomes du *B. rapa* reconnaissent et s'apparient exclusivement avec leurs homologues du génome A chez le *B. napus* tout comme les chromosomes du *B. oleracea* s'apparient avec leurs homologues du génome C chez le *B. napus*. Ce comportement a permis d'identifier les 10 groupes de liaison du génome A et les 9 groupes de liaison du génome C chez le *B. napus*. De plus, ceci indique que les génomes nucléaires de *B. napus*, *B. rapa* et *B. oleracea* sont demeurés essentiellement inchangés depuis la formation de l'espèce amphiploïde *B. napus*. Différents motifs inhabituels ont été observés dans cette population et ceux-ci pourraient être le résultat d'aneuploïdie ou de translocations non-réciproques. Ces anomalies chromosomiques sont vraisemblablement causées par suite d'associations entre chromosomes homéologues survenant lors de la méiose chez le parent synthétique et chez les individus F₁ menant ainsi à la non-disjonction et à la recombinaison homéologue.

Mots clés : carte génétique, recombinaison homéologue, *Brassica rapa*, *Brassica oleracea*, organisation génomique.

[Traduit par la Rédaction]

Introduction

The hypothesis that *Brassica napus* is an amphidiploid species formed from interspecific hybridization between two diploid progenitors, *B. rapa* (the A genome) and *B. oleracea* (the C genome), was first proposed by U (1935) based on cytological evidence. *Brassica napus* can be resynthesized from new interspecific crosses between current representatives of *B. rapa* and *B. oleracea* (Prakash and Hinata 1980). The general high fertility of crosses between

resynthesized *B. napus* lines and established oilseed rape cultivars (Chen and Heneen 1989) has substantiated U's hypothesis. However, phylogenies based on polymorphism in organelle genomes (Palmer et al. 1983; Song and Osborn 1992) have suggested that the main maternal ancestor of "natural" *B. napus* was distinct from modern *B. rapa* and *B. oleracea* and might have been more closely related to *B. montana*, a wild member of the *B. oleracea* complex. Restriction fragment length polymorphism (RFLP) maps of *B. rapa* (Chyi et al. 1992; Song et al. 1991) and *B. oleracea* (Landry et al. 1992; Slocum et al. 1990) have been generated and some collinearity between the A and C genomes has been identified (Teutonico and Osborn 1994). Comparisons between high density RFLP maps of *B. rapa*, *B. oleracea*, and *B. napus* should allow the identification of the A- and C-genome linkage groups of

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Fig. 2. A genetic linkage map of *B. napus* based on segregation in the N-fo-61-9 population 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. In the case of N16 all loci were coincident, because N61-9 was monosomic for the chromosome represented by N16, see text. A pair of segregating alleles were scored at each locus, except for loci with identifiers ending in: NP or NM, where only the allele from the N-o-9 or SYN1 parent, respectively, could be scored; (NP), where the N-o-9 allele was scored and the corresponding SYN1 allele was duplicated at a second homoeologous locus; (NM), where the SYN1 allele was scored and the corresponding N-o-9 allele was duplicated at a second homoeologous locus; and (2P–2M), where a single allele in N-o-9 and a single allele in SYN1 were both duplicated at the same pair of homoeologous loci (see text). The 12 loci in parentheses were monomorphic but were positioned on the basis of translocations and aneuploidy. Map distances in cM are on the right side of the linkage groups with total map lengths at the bottom. All loci separated by recombination are represented with even spacing. All informative polymorphisms were based on genomic DNA digested with *EcoRI*, except for loci ending in “X” (followed by a number), where polymorphism was based on DNA digested with *XbaI*. ●, Loci with *B. oleracea* alleles; ▲, loci with *B. rapa* alleles.

B. napus and the detection of any gross rearrangements distinguishing the linkage groups of the diploid and amphidiploid species. However, the marker densities on published maps of *B. napus* (Landry et al. 1991; Ferreira et al. 1994) are comparatively low and intergenomic comparisons have been complicated by widespread intragenomic duplications in the diploid species (Song et al. 1991; Slocum et al. 1990). In the present study we describe the construction of a dense RFLP map of *B. napus* using a highly polymorphic cross between a resynthesized *B. napus* line and an established winter oilseed rape cultivar. The use of a resynthesized *B. napus* line and regular chromosome pairing in the F₁ allowed the diploid origin of the *B. napus* linkage groups to be identified and established that the A and C genomes in *B. napus* are homologous to those in *B. rapa* and *B. oleracea*.

Materials and methods

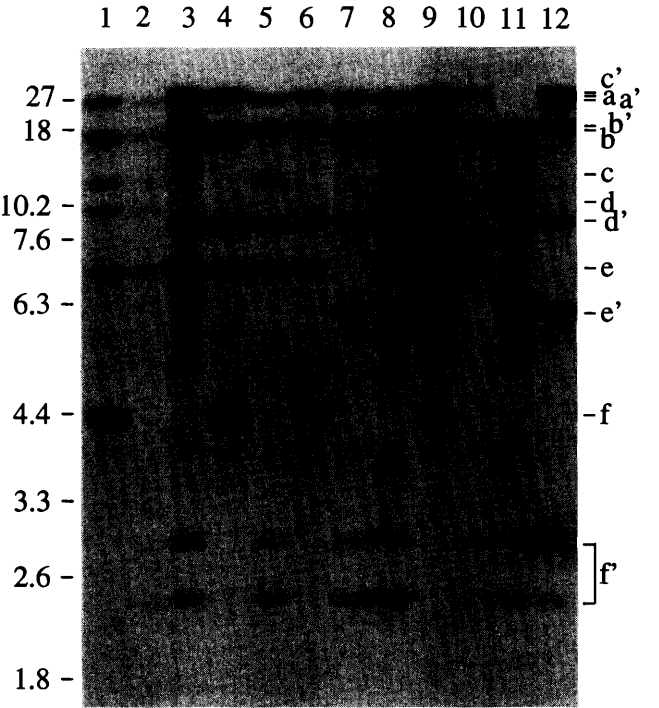
Parental plant material

The two parents of the mapping cross, SYN1 and N-o-9, were doubled-haploid (DH) lines of *B. napus*. SYN1 was a resynthesized line (T. Hodgkin, Scottish Crop Research Institute, Dundee DD2 5DA, U.K.) produced by embryo rescue from an interspecific cross involving R-c-17, a line of *B. rapa* ssp. *chinensis* pollinated with O-al-23, a line of *B. oleracea* ssp. *alboglabra*. N-o-9 was a British winter cultivar of oilseed rape derived from microspore culture (P. Capitain and R. Jennaway, Cambridge Plant Breeders, Thriplow SG8 7RE, U.K.). N-fo-61-9 is a population of 50 DH lines derived from a single F₁ plant from a SYN1 × N-o-9 cross. The populations of DH lines were derived via microspore culture essentially as described by Chuong and Beversdorf (1985).

DNA extraction, Southern hybridization, and RFLP probes

DNA was extracted as described by Sharpe et al. (1995) and 0.6 mg of total DNA was routinely extracted from 0.5 g of freeze-dried leaf material. Restriction enzyme digestion, gel electrophoresis, alkaline transfer, and Southern hybridization were carried out as described by Sharpe et al. (1995). A total of 162 highly informative *Brassica* RFLP probes were employed. These probes included selections from four libraries of small *PstI* fragments of *Brassica* genomic DNA, two *B. napus* libraries (“pN” and “pW” probes), a *B. rapa* library (“pR” probes), and a *B. oleracea* library

Fig. 1. Autoradiograph of RFLP alleles segregating in 12 DH *B. napus* lines and detected by pC2. All tracks contained total DNA digested with *EcoRI*: tracks 1 and 12, parental DNA from N-o-9 and SYN1, respectively; tracks 2–11, DNA from 10 DH lines of the N-fo-61-9 population. Probe pC2 detected six polymorphic loci (a–f). 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 SYN1 parent). The line represented in track 11 carried neither allele at locus pC2a and two copies of the N-o-9 allele of locus pC2b.

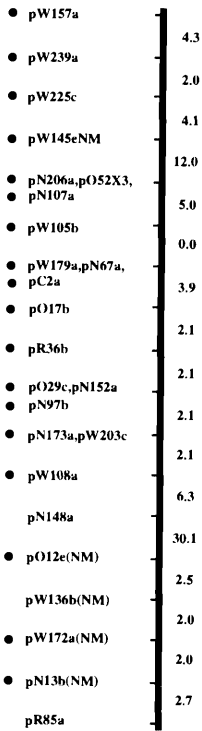


(“pO” probes), and five *Brassica* cDNA clones (“pC” probes) (Sharpe et al. 1995).

Linkage analysis

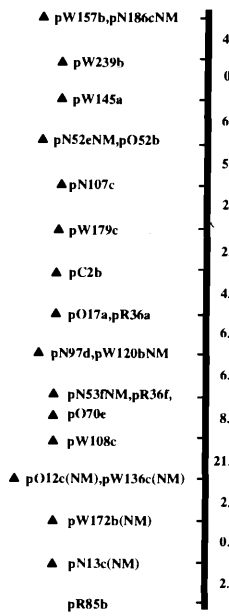
The analysis of genetic linkage was performed using simple BASIC programmes as described by Ellis et al. (1992) and MAPMAKER, versions 1.9 and 3.0 (Lander et al. 1987). A LOD score of 4.0 was used to associate RFLP loci into initial

N1



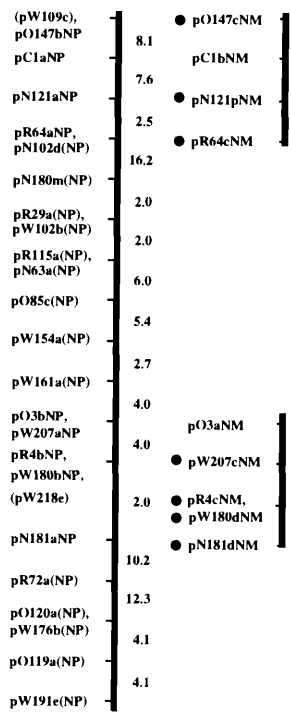
85 cM

N11



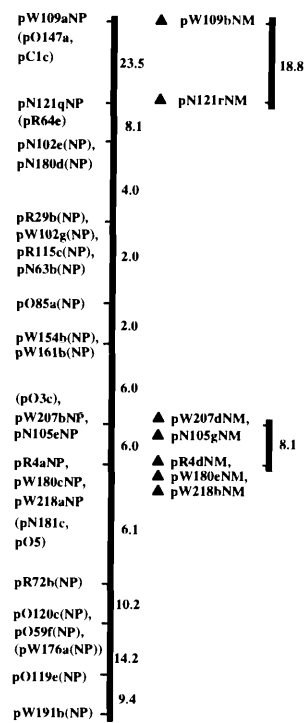
72 cM

N2



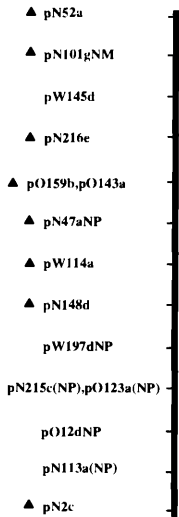
93 cM

N12



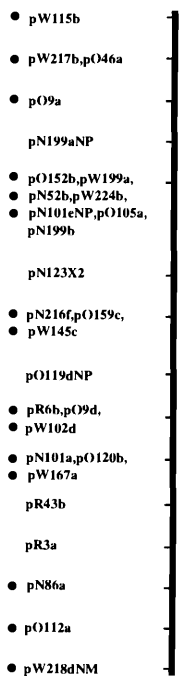
111 cM

N15



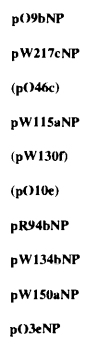
87 cM

N6

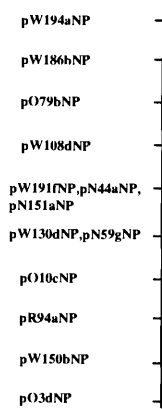


125 cM

N16

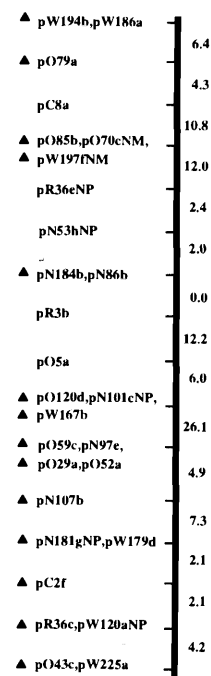


N7



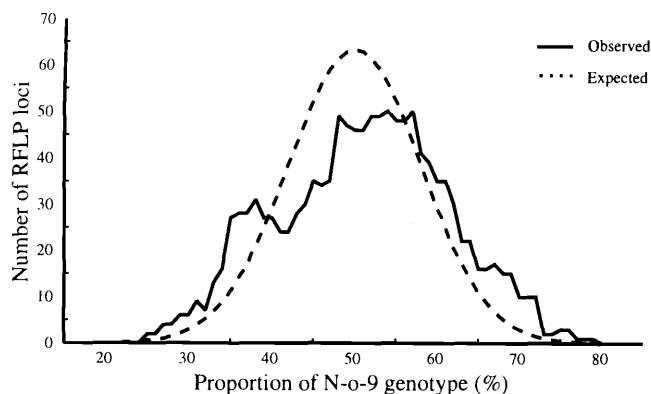
76 cM

N17



103 cM

Fig. 3. Frequency distribution of allele ratios at loci in the N-fo-61-9 population. The graphs represent 5% windows taken at 1% intervals.



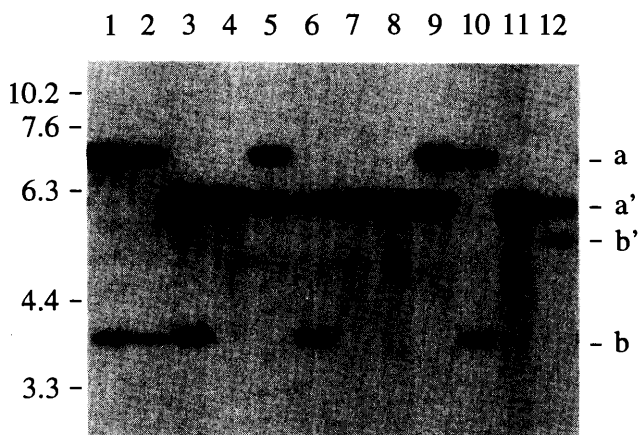
linkage groups. Three-point and multipoint analyses were used to determine the most probable locus order for each linkage group. The locus order was verified by re-examining the original scorings for single loci flanked by double crossovers. Because the DH lines were derived from single gametes and from 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

Disomic inheritance of RFLP alleles

A resynthesized *B. napus* line (SYN1) was pollinated with a DH oilseed rape cultivar (N-o-9) and plants from the resulting F_1 population (N-fo-61) were subjected to microspore culture in order to produce recombinant DH progeny. A total of 162 informative *Brassica* clones were used to assay polymorphic RFLP-defined loci in a population of 50 DH lines derived from a single F_1 plant (N61-9). The genotypes of the DH lines were equivalent to the genotypes of the single gametes from which they were cultured. The overwhelming majority of RFLP alleles segregated in a way characteristic of disomic inheritance, that is, one of a pair of parental alleles was present in each of the DH lines, with no lines carrying both alleles and no lines carrying neither allele (Fig. 1). The disomic inheritance of pairs of alleles at genetic loci is a reflection of the regular bivalent pairing of chromosomes. The fact that the F_2 progeny of a cross between an oilseed rape cultivar ("natural" *B. napus*) and a resynthesized *B. napus* line (a new interspecific hybrid between *B. rapa* and *B. oleracea*) exhibited disomic inheritance of parental alleles demonstrated that, in the F_1 parent, particular chromosomes from *B. oleracea* were exclusively pairing with particular chromosomes from *B. napus* and particular chromosomes from *B. rapa* were similarly pairing with particular chromosomes from *B. napus*. This observation suggested that the bulk of the genome of *B. napus* consisted of distinct C-genome (*B. oleracea*) and A-genome (*B. rapa*) chromosomes.

Fig. 4. Autoradiograph of RFLP alleles segregating in 12 DH *B. napus* lines and detected by pN63. All tracks contained total DNA digested with *Eco*RI: tracks 1 and 12, parental DNA from N-o-9 and SYN1, respectively; tracks 2–11, DNA from 10 DH lines of the N-fo-61-9 population. Probe pN63 detected a pair of homoeologous loci, *a* (N2) and *b* (N12). The SYN1 allele *b'* was not present in any DH lines of the N-fo-61-9 population, while the homoeologous SYN1 allele *a'* was present in zero, one, or two copies in the DH lines and segregated with N-o-9 alleles from both loci.



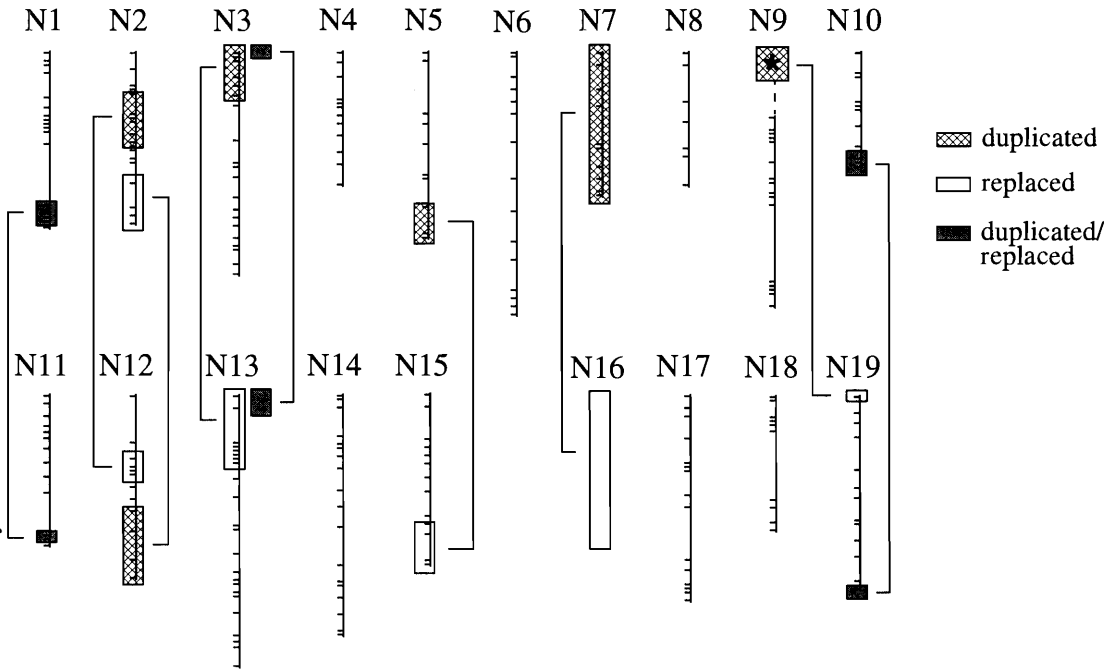
A genetic linkage map of *B. napus*

Southern hybridization analysis of the N-fo-61-9 population of DH lines with 162 RFLP probes detected 399 polymorphic loci. The segregation of parental alleles at these loci was scored and the data was subjected to genetic linkage analysis to produce a genetic map of *B. napus* (Fig. 2). The map contained 392 loci assigned to 19 substantial linkage groups, with an additional group of 4 coincident loci, 1 pair of loci, and 1 isolated locus remaining unlinked to the main groups. The 19 linkage groups covered a total of 1656 cM. The extent of allele imbalance in the 399 scored loci of the N-fo-61-9 population was greater than that expected to occur by chance (χ^2 , $P < 0.001$) (Fig. 3).

The diploid origin of *B. napus* loci

The *B. oleracea* and *B. rapa* parents of the resynthesized *B. napus* line SYN1 were individual plants from partially inbred lines. The diploid origin of most of the RFLP alleles from SYN1 could be deduced by comparing the Southern hybridization patterns of SYN1 with those of the two parental lines, *B. oleracea* (O-al-23) and *B. rapa* (R-c-17). The disomic inheritance of RFLP markers in the N-fo-61-9 population meant that *B. oleracea* alleles from SYN1 identified C-genome loci in *B. napus* and *B. rapa* alleles from SYN1 identified A-genome loci in *B. napus*. The diploid origin of the SYN1 alleles was established unambiguously at 240 (of the 399) polymorphic loci scored in the N-fo-61-9 population (Fig. 2). The diploid equivalents of all 19 *B. napus* linkage groups could be determined because each linkage group contained either only A-genome loci or only C-genome loci (Fig. 2). Linkage groups N1–N10 of *B. napus* are equivalent to *B. rapa* linkage groups, while N11–N19 are equivalent to *B. oleracea* linkage groups.

Fig. 5. Nonreciprocal translocations and aneuploidy in the N61-9 F₁ plant. The diploid origin of the SYN1 alleles affected by translocations in N61-9 (both the duplicated alleles and the alleles that were replaced) could be determined, allowing the direction of the translocations to be deduced. *, The cluster of four loci that remained unassociated with the main linkage groups in the N-fo-61-9 genetic map (pN52g, pN213e, pR116e, and pW157c) have been positioned on the end of N9 in maps derived from other populations (A.G. Sharpe and D.J. Lydiate, unpublished data).

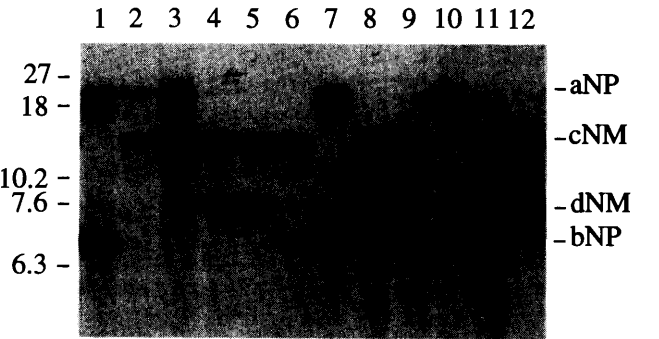


There was extensive collinearity of marker loci between large segments of A-genome chromosomes and their potential partial homoeologues in the C genome. The linkage groups of the A and C genomes have been interspersed in Fig. 2 so that the most collinear regions of the different linkage groups are adjacent to one another; for example, N1 and N11 could be complete homoeologues while N3 and N13 appear to be partial homoeologues, with the upper 70% of both linkage groups being very similar while the lower portions appear completely unrelated.

Genome homogenization through nonreciprocal translocations

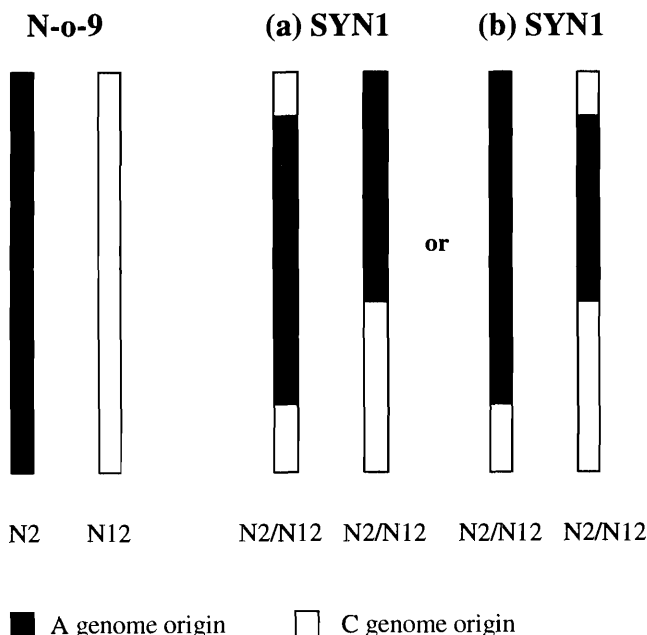
A number of the loci positioned on the genetic linkage map presented in Fig. 2 did not exhibit simple disomic inheritance of distinct parental alleles. A characteristic unusual segregation pattern occurred at several loci. In this pattern, one allele from the SYN1 parent was not present in any of the N-fo-61-9 population (or the N61-9 F₁ plant) and a second (homoeologous) allele from SYN1 was present at a high frequency and in variable dosage (one or two copies) (Fig. 4). Typically, N-o-9 parental alleles segregated with the two copies of the duplicated SYN1 allele. The loci in Fig. 2 with codes ending in “(NP)” exhibited this type of segregation pattern. Loci of this type occurred in linked clusters, and the clusters were not interrupted by simple loci with unique parental alleles, suggesting that the segregation pattern was a characteristic of large chromosomal

Fig. 6. Autoradiograph of RFLP alleles segregating in 12 DH *B. napus* lines and detected by pR4. All tracks contained total DNA digested with *Eco*RI: tracks 1 and 12, parental DNA from N-o-9 and SYN1, respectively; tracks 2–11, DNA from 10 DH lines of the N-fo-61-9 population. Probe pR4 detected a pair of homoeologous loci bNP/cNM and aNP/dNM; however, these loci exhibited tetrasomic inheritance with each DH line inheriting any pair of the four alleles.



regions. There were five regions of the genome of N61-9 where pairs of homoeologous loci shared a single SYN1 allele and where a potentially homoeologous SYN1 allele was missing (Fig. 5, hatched and open boxes, respectively). These marker patterns are consistent with the duplication of chromosomal segments and the concomitant replacement

Fig. 7. Schematic representation of the possible chromosomal configurations in the N61-9 F_1 plant for the chromosomes represented by linkage groups N2 and N12. The N61-9 plant was formed from the fusion of two gametes; the gamete from N-o-9 carried a N2 chromosome that was completely of A-genome origin and a N12 chromosome that was completely of C-genome origin, while the gamete from SYN1 carried a pair of hybrid N2/N12 chromosomes formed by homoeologous recombination. There were two possible configurations, *a* and *b*, for these hybrid chromosomes.

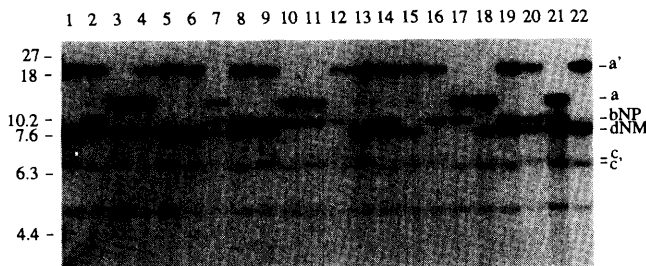


of homoeologous segments. The most obvious explanation for this observation is the occurrence of homoeologous recombination in the SYN1 parent at meiosis leading to several nonreciprocal homoeologous translocations in the gamete that SYN1 donated to the N61-9 F_1 plant.

Three pairs of homogenized chromosomal segments were also identified in the genome of N-o-9 (Fig. 5, shaded boxes). Corresponding loci on distinct linkage groups shared common RFLP alleles along each pair of potentially homoeologous segments. These regions also probably represented nonreciprocal translocations but the direction of the translocation (the chromosomal origin of the duplicated segment) could not be established because the translocation was already fixed in the N-o-9 parent. If unrestrained, these nonreciprocal translocations would homogenize the *B. napus* genome and obscure the diploid origin of the related segments of partially homoeologous chromosomes. The homogenization of the tops of linkage groups N3 and N13 in both parents of N61-9 (SYN1 and N-o-9) caused pairs of homoeologous loci in this region to exhibit the segregation pattern expected from a single heterozygous locus in a normal F_2 population.

When the segregation patterns of RFLP alleles present at duplicate loci were scored simplistically (under the erroneous assumption that they represented segregation at single loci) and included in normal linkage analyses, clusters

Fig. 8. Autoradiograph of RFLP alleles segregating in 22 DH *B. napus* lines and detected by pO79. All tracks contained total DNA digested with *Eco*RI: tracks 11 and 22, parental DNA from N-o-9 and SYN1, respectively; tracks 1–10 and 12–21, DNA from 20 DH lines of the N-f0-61-9 population. Probe pO79 detected three polymorphic loci, pO79a (N17), pO79c (N3), and pO79bNP/dNM (N7). The pO79dNM allele was present in zero, one, or two copies in the DH lines, obscuring its segregation with the pO79bNP allele. The line represented in track 4 carried both alleles at locus pO79a, probably as a result of a translocation involving N7 and N17 (see Fig. 9).



of duplicate loci formed phantom linkage groups and phantom ends to established linkage groups. The preponderance of loci with highly unbalanced allele ratios in the N-f0-61-9 population (Fig. 3) made it impractical to use allele frequency as a means of identifying duplicate loci.

Tetrasomic inheritance of alleles on N2 and N12

Clusters of linked loci in two distinct regions of linkage groups N2 and N12 exhibited tetrasomic inheritance. Tetrasomic inheritance was typified by a segregation pattern in which any pair of a set of four alleles (from two polymorphic homoeologous loci) was inherited by the DH individuals (Fig. 6). The segregation patterns of the N-o-9 parental alleles from these tetrasomic sets could be mapped straightforwardly. They were linked to loci in the regions of N2 and N12 that had been rearranged as a result of nonreciprocal translocations (Fig. 5). In the N-f0-61-9 population, the segregation patterns of only the N-o-9 parental alleles could be scored unambiguously at the loci affected by nonreciprocal translocations in the SYN1 gamete (Fig. 4). Thus the genetic linkage maps for groups N2 and N12 were based solely on the inheritance of N-o-9 parental alleles by the individuals of the N-f0-61-9 population. This demonstrated the utility of constructing single chromosome maps of chromosomes forming multivalent associations. The physical association between loci on a single parental chromosome ensures that genetic linkage is maintained.

Partial linkage maps for the nonhomogenized regions of chromosomes N2 and N12 from the SYN1 parent are represented alongside the complete N2 and N12 linkage groups in Fig. 2. Two possible chromosomal configurations in the N61-9 F_1 plant would explain the segregation patterns of the RFLP alleles associated with linkage groups N2 and N12 (Fig. 7). It is likely that these chromosomes were generated by one homoeologous single crossover and one homoeologous double crossover between N2 and N12 at meiosis in the SYN1 parent.

Fig. 9. Scoring data recording the presence or absence of an additional copy of N7 in the haploid genomes of DH lines of the N-fo-61-9 population. Rows represent loci and columns represent the DH lines. In the scoring matrix: —, two copies of the locus; 0, one copy of the locus; T, one copy of the N7 locus and a duplicate copy of the homoeologous locus on N17 (see Fig. 8); and *, missing data point. In the deduced haploid copy number of N7, “T” represents a line with one unrearranged copy of N7 plus a second copy carrying a nonreciprocal translocation involving the top of N17 and “F” represents a line with one unrearranged copy of N7 plus an additional fragment of N7.

pO79dNM	--0-0*-T*-----0T-----00--0000-----T0--0*-00-----
pW186dNM	---0-0--*T-----0T-----00--0000-----T0--0*-00-----
pW194cNM	---0-0--*T-----0T-----00--0000-----T0--0*-00-----
pW108dNM	---0-0-----0-----00--0000-----0--0*000-----
pN44dNM	---0-0*-*-*-0*-----00--000*-*-0--0-0*-00-----*
pW130dNM	---0-0-----0-----00--0000-----0--00-00-----
pW150bNM	--0-0-----0-----00--0000-----0--00-00-----
pO3dNM	--0-0-----0--0--00--0000-----0--00-0*-***
Haploid copy No. of N7	222121222T222221T2F222112F111122222T1221*211222222

Nondisjunction in resynthesized *B. napus*

There were a number of loci (those on N16, Fig. 2) where the allele frequency for the N-o-9 parental allele was very high in the N-fo-61-9 population and a SYN1 allele was missing from the N61-9 F₁ plant and its progeny. Those of the above loci that were polymorphic in a cross between N-o-9 and a spring oilseed rape cultivar were mapped to linkage group N16 (Sharpe et al. 1995). Probes pO3, pO10, pR94, pW130, and pW150 all detected loci on the bottom halves of both N16 and N7 (Fig. 2), suggesting that the corresponding chromosomes might be partial homoeologues. Markers on N7 also exhibited unusual segregation patterns in the N-fo-61-9 population. A coherent linkage group was constructed based on the segregation patterns of alleles from the N-o-9 parent. However, these alleles did not segregate simply with alleles from the SYN1 parent. Instead, the probes that detected loci on N7 each hybridized to an allele from SYN1 that was present in zero, one, or two copies in individuals of the N-fo-61-9 population (Fig. 8).

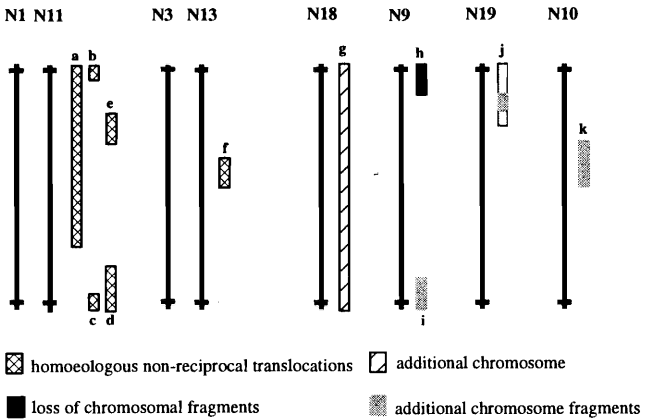
The segregation patterns for loci on N7 were consistent with there being three copies of the chromosomes represented by N7 in the N61-9 F₁ plant, one from the N-o-9 parent and two from the SYN1 parent. The haploid copy number of the chromosomes equivalent to N7 was determined for each DH line of the N-fo-61-9 population by collating the scorings from the corresponding N-o-9 and SYN1 alleles for each locus (Fig. 9). Considering the haploid chromosome complement, 14 lines carried a single copy of N7, 31 lines carried two copies of N7, and 5 lines carried one normal copy of N7 and one rearranged copy of N7 (Fig. 9).

The above data could be explained by a nondisjunction event at meiosis in the SYN1 parent that resulted in a gamete with two copies of the N7 chromosome and no copies of the N16 chromosome. Fusion of this gamete with a normal gamete from N-o-9 would then have resulted in N61-9 having three copies of N7 (two from SYN1 and one from N-o-9) and one copy of N16 (from N-o-9).

Homoeologous recombination, nondisjunction, and chromosome fragmentation at meiosis in the N61-9 plant

The effects of chromosomal aberrations inherited by the N61-9 F₁ plant on the segregation of RFLP alleles in the

Fig. 10. Schematic representation of the *B. napus* map showing the distribution and extent of chromosomal aberrations in the 10 atypical DH lines of the N-fo-61-9 population. Vertical lines (N1, etc.) are linkage groups and boxes indicate the location and extent of the 11 chromosomal rearrangements. *a*, Line 33, pW157b–pO12c duplicated / pW157a–pN148a replaced; *b*, line 24, pW157b duplicated / pW157a replaced; *c*, line 28, pR85b duplicated / pR85a replaced; *d*, line 34, pR85a–pN148a duplicated / pR85b–pO12c replaced; *e*, line 9, pO52X3–pN206a duplicated / pO52b replaced; *f*, line 6, pC3c–pO79c duplicated / pW112c replaced; *g*, line 4, tetrasomic for N18; *h*, line 20, pW122a–pN173c lost, no corresponding duplication; *i*, line 4, pO165a–pN23b duplicated, no corresponding loss of loci; *j*, line 35, pO119f duplicated (duplication possibly extends from pO70dNM to pN213b at the top of the linkage group), no corresponding loss of loci; *k*, line 3, pW240a–pN23f duplicated, no corresponding loss of loci.



N-fo-61-9 population have been discussed. Unusual marker patterns restricted to individual N-fo-61-9 lines, and therefore individual gametes of the N61-9 F₁ plant, were also observed. These probably resulted from aberrant events in particular meiotic nuclei of the N61-9 individual. Six lines of the N-fo-61-9 population (Numbers 6, 9, 24, 28, 33, and 34, Fig. 10) exhibited RFLP patterns indicative

of nonreciprocal translocation events (Fig. 10, *a-f*) probably resulting from homoeologous recombination in the N61-9 F_1 plant. In each case, there were linked groups of duplicated loci (both the SYN1 allele and the N-o-9 allele were present in the same gamete), while linked groups of homoeologous loci were missing (neither allele could be detected).

A nondisjunction event probably resulted in line 4 being tetrasomic, with four copies of N18 (Fig. 10, *g*). All loci on N18 appeared to be duplicated (both SYN1 and N-o-9 alleles present in the same gamete) but no loci were missing.

Chromosome fragmentation events at meiosis in N61-9 appear to have resulted in additional copies of pieces of N9, N19, and N10 being inherited by lines 4, 35, and 3, respectively, (Fig. 10, *i, j*, and *k*). These lines had linked sets of duplicated loci that did not extend over entire linkage groups and the homoeologous loci appeared normal.

A segment of the chromosome equivalent to N9 appeared to be missing from line 20 (Fig. 10, *h*). Neither parental allele could be detected at a set of linked loci and no loci were obviously duplicated.

Discussion

A RFLP map of *B. napus*, consisting of 399 loci positioned on 19 substantial linkage groups, has been produced. This genetic linkage map, derived from the N-fo-61-9 population, has been integrated with a linkage map produced from an oilseed rape cross (Sharpe et al. 1995). The same 19 linkage groups were conserved in both maps and probably correspond to the 19 chromosome pairs of amphidiploid *B. napus*. RFLP-defined loci on 15 of the linkage groups exhibited disomic inheritance of parental alleles. The unusual segregation patterns of loci on other linkage groups were probably caused by nonreciprocal translocations (in the case of N2 and N12) and aneuploidy (in the case of N7 and N16). These chromosome abnormalities in N2/N12 and N7/N16 were almost certainly caused by homoeologous recombination and nondisjunction, respectively, during meiosis in the resynthesized parent of the N-fo-61 cross.

The disomic inheritance of parental alleles in the N-fo-61-9 population indicated regular chromosome pairing in a F_1 hybrid between resynthesized *B. napus* and "natural" *B. napus*. That is, at meiosis in the F_1 hybrid, the chromosomes from *B. rapa* must each have paired with individual (A genome) chromosomes of *B. napus* and the chromosomes from *B. oleracea* must each have paired with particular (C genome) chromosomes of *B. napus*. This allowed the identification of the 10 A-genome linkage groups (N1-N10) and the 9 C-genome linkage groups (N11-N19) of *B. napus*. The existence of homologous chromosomes in a F_1 hybrid between established *B. napus* and resynthesized *B. napus* indicates that the A and C genomes of *B. napus* have remained relatively unchanged since the initial hybridization(s) that produced the ancestors of oilseed rape and that the A and C genomes of modern cultivars of *B. rapa* and *B. oleracea* are very similar to those of the diploid ancestors of established *B. napus*. However, the results do not preclude the possibility that A-genome chromosomes contain homoeologous segments originally from the C-genome, or visa versa, but indicate that any such

introgressed segments do not prevent preferential chromosome pairing. The *B. napus* linkage group designations used above are particularly informative, because, for the first time, they reflect the diploid origin of the groups and the likely homoeologous relationships between the chromosomes of the A and C genomes. We propose that this nomenclature should be adopted universally as the various genetic maps of the *Brassica* A and C genomes become integrated.

The average number of loci on the linkage groups of the A (20, SD 8) and C (23, SD 7) genome in the N-fo-61-9 map were similar: $P = 0.40$ for t test of the likelihood of the observed difference occurring by chance. The average lengths of the linkage groups of the A (86 cM, SD 21) and C (100 cM, SD 31) genome were also similar within *B. napus*: $P = 0.30$ for t test of the likelihood of the observed difference occurring by chance. In contrast, published maps of the diploid species suggest that the genetic size of the A genome (approximately 2000 cM; Chyi et al. 1992; Song et al. 1991) is typically twice the size of the C genome (approximately 1000 cM; Landry et al. 1992; Slocum et al. 1990). The genetic maps of *B. napus* derived from the N-fo-61-9 population and a comparable map derived from an oilseed rape cross (Sharpe et al. 1995) indicate that the frequency of recombination is effectively equal in the A and C genomes of *B. napus*. This suggests that the recombination machinery of *B. napus* acts equally on chromosomes of both genomes and that the frequency of recombination is comparable to that observed in *B. oleracea*.

There were two pairs of *B. napus* linkage groups that appeared to be homoeologous along their whole length, namely, N1 with N11 and N2 with N12. The extensive collinearity between most other regions of the A and C genomes suggested that all the remaining linkage groups of the A genome also had homoeologous segments in the C genome. Many of the chromosomal abnormalities identified in the F_1 plant and its gametes could be explained by pairing between homoeologous chromosomal segments at meiosis in the F_1 and its resynthesized parent, leading to homoeologous recombination and nondisjunction. Mapping the distribution of nonreciprocal translocations in F_1 plants resulting from homoeologous recombination in resynthesized *B. napus* has confirmed the partially homoeologous nature of many of the chromosomes of the A and C genomes (R. Ruiter and D.J. Lydiate, unpublished data). The identification of homoeologous relationships between the linkage groups of the *Brassica* A and C genomes will elucidate the chromosomal rearrangements that have occurred during the divergence of *B. rapa* and *B. oleracea* from a common ancestor. An understanding of the distribution of homoeologous regions will also make possible the efficient transfer of genes between species using interspecific crosses and marker-assisted breeding.

A high frequency of homoeologous recombination (approximately 10% of total recombination) is a common feature of resynthesized lines of *B. napus* (U. Lagercrantz and D.J. Lydiate, unpublished data). Indeed, homoeologous recombination has been shown to occur, though at a comparatively low frequency (approximately 0.3% of total recombination), in cultivars of oilseed rape (Sharpe et al. 1995). Segregation for the frequency of homoeologous

recombination between the lines of the N-fo-61-9 population is being used to analyze the genetic control of chromosome pairing in *B. napus*. This research holds out the tantalizing possibility of identifying a *Brassica* gene equivalent to the *Ph1* locus of wheat (Riley et al. 1960). The population is also producing insights into the genetic control of self-incompatibility in *B. napus* (I.A.P. Parkin and D.J. Lydiate, unpublished results). Control of chromosome pairing and suppression of self-incompatibility were probably two key characteristics necessary for *B. napus* to become established as a stable amphidiploid species.

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