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Inter- and intra-genomic homology of the *Brassica genomes*: implications for their origin and evolution

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Abstract In order to determine the homologous regions shared by the cultivated *Brassica* genomes, linkage maps of the diploid cultivated *B. rapa* (A genome, n = 10), *B. nigra* (B genome, n = 8) and *B. oleracea* (C genome, n = 9), were compared. We found intergenomic conserved regions but with extensitve reordering among the genomes. Eighteen linkage groups from all three species could be associated on the basis of homologous segments based on at least three common markers. Intragenomic homologous conservation was also observed for some of the chromosomes of the A, B and C genomes. A possible chromosome phylogenetic pathway based on an ancestral genome of at least five, and no more than seven chromosomes, was drawn from the chromosomal inter-relationships observed. These results demonstrate that extensive duplication and rearrangement have been involved in the formation of the *Brassica* genomes from a smaller ancestral genome.

Key words *Brassica rapa* · *B. oleracea* · *B. nigra* · Genome homology · RFLP · Linkage maps

Introduction

One way to study the evolution of plant genomes is to compare the amount of conserved gene order among related species or genera (Doebley and Wendel 1989). Using the same set of clones, it is possible to construct linkage maps for each of the species to be compared. Gene order, linkage-group conservation, and chromosome distribution can then be determined. Examples of the use of this technique for evolutionary studies in plants are common. Studies between species with the same chromosome number have been carried out in tomato and potato (Bonierbale et al. 1988; Gebhardt et al. 1991; Tanksley et al. 1992), tomato and pepper (Tanksley et al. 1988), garden pea and lentil (Weeden et al. 1992) wheat, barley and rye (Moore et al. 1993, 1995), and maize and sorghum (Hulbert et al. 1990; Binelli et al. 1992), although it has recently been confirmed that maize has x = 5 and sorghum x = 10 chromosomes (Moore et al. 1995). Complete marker-order correlation was found between the tomato and the potato genomes with the exception of only five inversions (Tanksley et al. 1992), but a high level of chromosome reordering was observed between tomato and pepper (Tanksley et al. 1988). Colinearity among diverse cereal crops is the rule, although in some cases rearrangements at different levels can be detected (Moore et al. 1995). Gene order in the three wheat genomes, A, B and D, is practically identical, except for a few changes due to gross chromosomal rearrangements. The H genome of barley is also quite similar to the wheat genomes which differs from the rye genome by at least 13 chromosomal interchanges (Moore et al. 1993, 1995). An intermediate case of linkage conservation was found in the comparison between garden pea and lentil (Weeden et al. 1992).

Comparisons of genomes between related species with different chromosome numbers have also been conducted. These include comparisons between *Brassica oleracea* and *B. rapa* (Slocum 1989), between *B. olereca* and *Arabidopsis thaliana* (Kowalski et al. 1994), and also among other cereal crops and grasses. In the latter species, the wheat genome is 15-fold and 2.5-fold larger in DNA content than those of rice and corn, respectively. In spite of great differences in DNA content and chromosome numbers, many genes and linkage groups appear to have been conserved since the divergence of these three crops and other grasses from a common ancestor (Moore et al. 1995). Not only is the gene content conserved, but the linear array of genes along the chromosome is also conserved. This indicates

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that evolution by translocations, inversions and other cytogenetic alterations is not coupled to the process leading to dramatic changes in DNA content in plants. Comparison between the crucifers *B. oleracea* and *B. rapa* by Slocum (1989) disclosed extensive genomic regions of conserved homology. As expected, the level of colinearity was less between *B. oleracea* and *A. thaliana*, another crucifer but classified in a different tribe (Kowalski et al. 1994).

In the present study, linkage maps of *B. nigra* (n = 8, B genome, Truco and Quiros 1994), *B. rapa* (n = 10, McGrath and Quiros 1991) and *B. oleracea* (n = 9, Kianian and Quiros 1992) developed by a set of common probes were compared for colinearity. Our primary objective was to ascertain the degree of homology among the genomes of these three species and then relate it to their phylogeny.

Materials and methods

Probes and hybridization conditions

The same sources of probes were used for the construction of all the maps. These were: (1) random genomic clones for a *B. napus* library (Bx clones; Hosaka et al. 1990), (2) random clones from a cDNA library of *B. napus* (provided by Dr. J. Harada, University of California at Davis; BNx clones isolated by Kianian, and LxNxx clones isolated by Landry for the construction of their *B. oleracea* linkage maps, Kianian and Quiros 1992, Landry et al. 1991), (3) low-copy clones (BGxx) from a size-selected genomic *PstI* library of *B. rapa* oliseed cv Candle by R. Bernatzky, Univeristy of Massachusetts) and (4) five clones identifying known genes: a self incompatibility gene from *B. oleracea* (pBOS5; Nasrallah et al. 1985), the genes for isocitrate lyase from *B. napus* (IL9; Comai et al. 1989), a gene coding for late embryogenesis abundant protein (LEA76; Harada et al. 1988), the omega-3 fatty desaturase gene of *A. thaliana* (CD33, Arondel et al. 1992) and the gene for napin from *B. napus* (N2; Crouch et al. 1983). In addition, a cloned RAPD fragment associated to linolenic acid content in *B. napus* (K01, Hu et al. 1995) and five probes from a gene complex on chromosome 3 of *A. thaliana* (Atx) were included (Delseny et al. 1995).

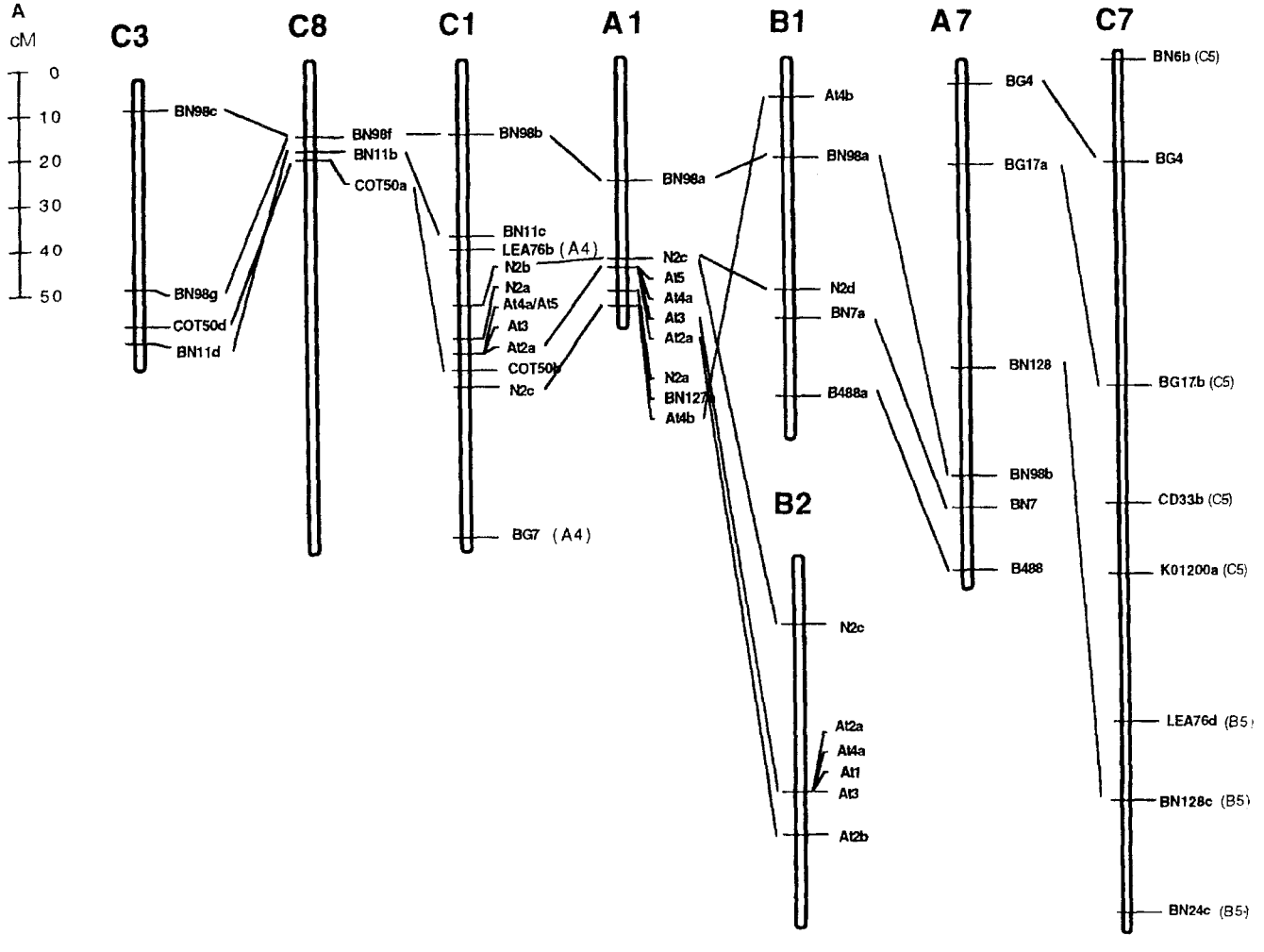
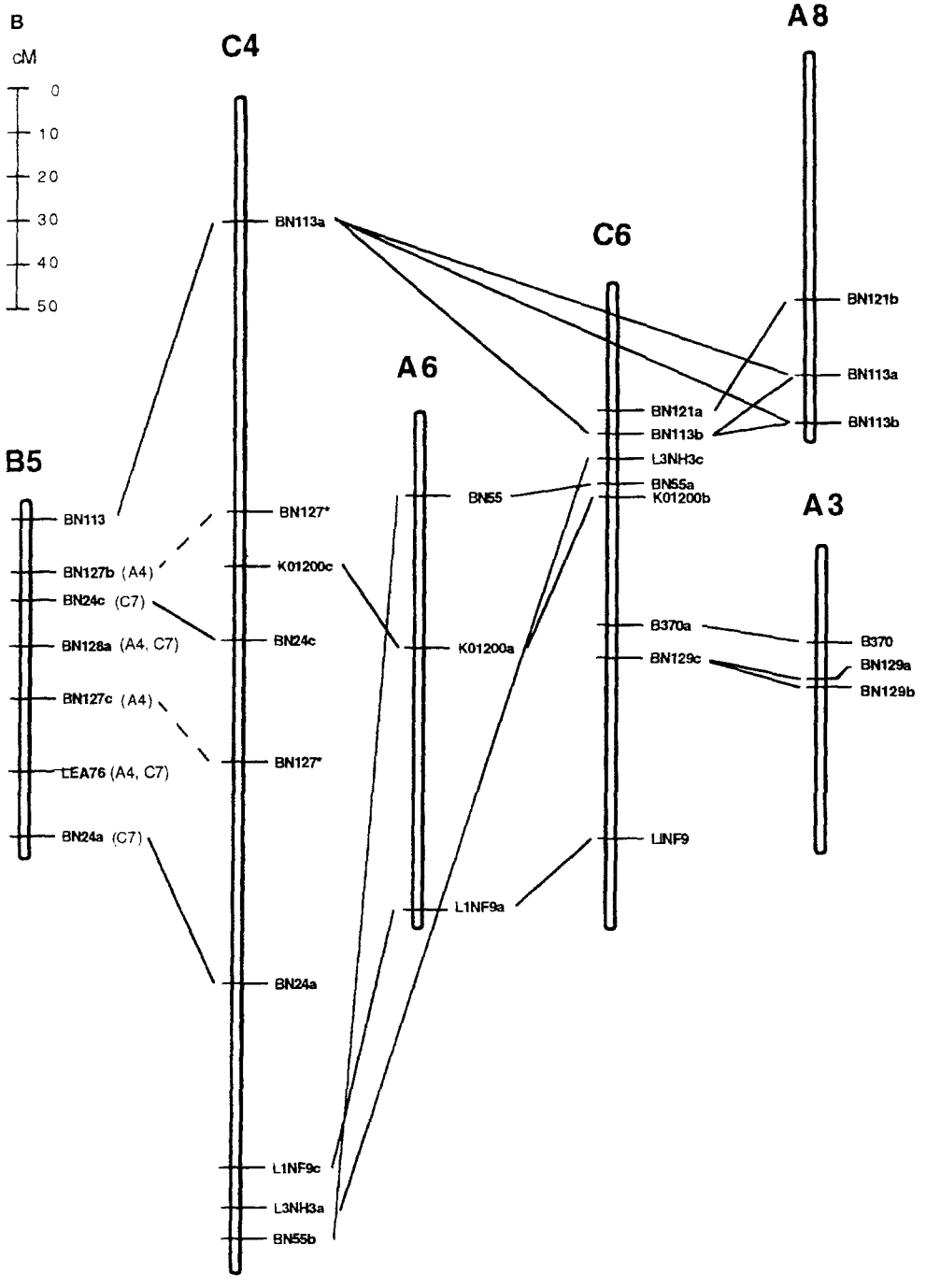


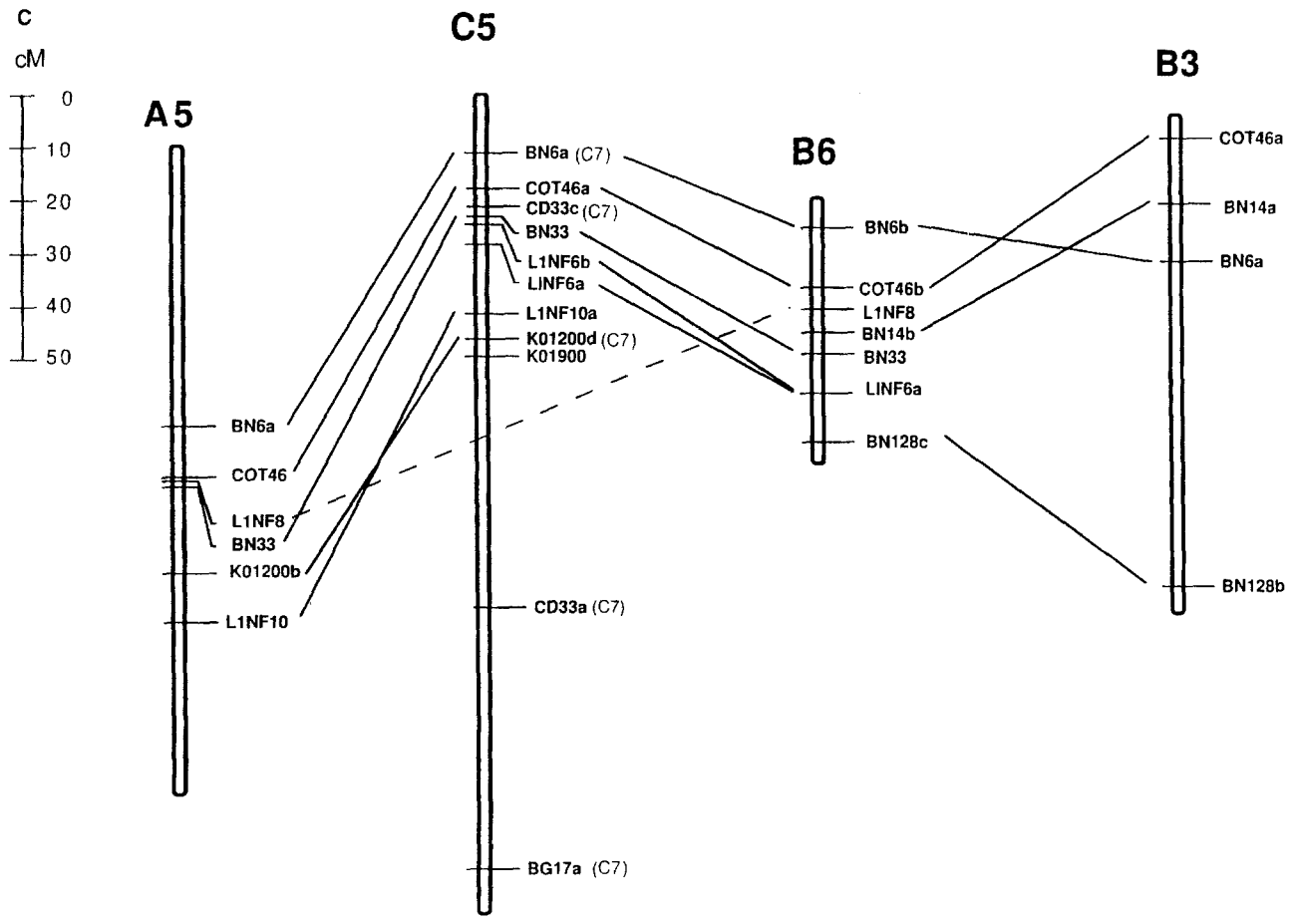
Fig. 1A–C Intergenomic homology among linkage groups of the A, B and C genomes. Only common markers and partial linkage groups are depicted for sake of simplicity. Scale in cM provided at the left corners. **A** Association cluster consisting of eight linkage groups. *A. thaliana* gene complex (*Atx* loci) is conserved in groups A1, B2 and C1. **B** Association cluster of six linkage groups. *Asterisks* on marker BN127 in group C4 indicates that it was located by *B. rapa-oleracea* addition lines since this marker did not segregate in the F_2 population of *B. oleracea*. Therefore its position on C4 is arbitrary. **C** Association cluster of four linkage groups. Group C7 in **A** associates clusters of 1B and 1C as specified by the *numbers in parenthesis*. Group A4, not shown in this figure, shares homology with B5 and C1

Hybridization and filter-washing stringency conditions were the same in the construction of all the maps and have been previously described (Kianian and Quiros 1992). New markers were mapped into these populations by using Zeta-probe GT membrances (Bio-Rad). We followed the manufactuer's instructions for hybridization and post-hybridization washing. However, the second washing in 25 mM of Na_2HPO_4 and 1% SDS was omitted for the *Arabidopsis* probes (Atx).

Construction of the maps

Previously published F_2 linkage maps for all three diploid cultivated *Brassica* species were expanded by adding markers to the original populations, and reconstructed using the program Mapmaker (Lander et al. 1987; Lincoln et al. 1992). These included a *B. rapa* map based on an F_2 population of 61 individuals (McGrath and Quiros 1991), consisting of ten linkage groups and 84 loci spanning 912 cM. This map has now been further expanded by consolidation with a *B. rapa* map produced by Schilling A and R. Bernatzky (unpublished). The second map was for *B. nigra* based on a F_2 population of 83 individuals (Truco and Quiros 1994), with 72 loci covering 511 cM in eight linkage groups. Finally, the *B. olereca* map was a composite from four F_2 populations (Kianian and Quiros 1992) consisting of nine linkage groups with 175 markers and 1738 cM. This map was expanded by adding markers to a collard × broccoli F_2 population, forming part of the composite map. In order to simplify the data presentation, markers that were not in common among species,





Legend for Fig. 1A–C please see page 1226

including the RAPD markers in the *B. nigra* map published by Truco and Quiros (1994), were omitted in the figures.

Mapmaker involves multipoint analysis and estimations of maximum likelihood on the calculation of map distances. We assembled the linkage groups using two-point data with a linkage criterion of 0.3 for the recombination frequency and a log likelihood (LOD) of 3.0 or higher. The order of the markers within a linkage group was determined using three-point analysis with a LOD 3.0 for the frame markers and LOD 2.0 or 1.0 for the rest of the markers. We confirmed the order of the markers in a linkage group by using the TRY command, moving one marker at a time, then accepting the map order which gives the highest log-likelihood.

Comparing the maps

Evolutionary comparisons between genetic maps constructed with the same set of clones are most reliable when the group of clones that is used corresponds to single-copy sequences. These markers make it possible to unambiguously assign orthologous loci in the genomes of the species compared. When duplicated sequences are frequent, as in the *Brassica* genomes, the assignment of orthologous loci in synteny comparisons is only tentative since it is unclear which fragments correspond to the same loci in the different species (McGrath and Quiros 1991). To overcome this difficulty we have considered orthologous loci for this study: namely, (1) single-copy loci and (2) duplicated loci where linkage to a second marker is conserved among species. For simplification, only common markers determined by the same probes, and only those segregating in all three populations, were included in the linkage groups depicted in the figures.

Nomenclature

Loci were named by the symbols described under the "Probes and hybridization conditions" section. Single-copy loci were designated by the name of the probe alone. For duplicated loci, each mapped locus had a low-case letter indicating the relative size of its fragments, starting with "a" for the largest fragments. The linkage groups for *B. rapa* and *B. nigra* were named arbitrarily with a prefix referring to their genomic origin, namely A and B, respectively. For *B. oleracea* the linkage groups correspond to chromosomes, prefix C, assigned by alien addition lines (McGrath et al. 1991).

Results

Marker distribution and polymorphism

It was not possible to determine accurately the number of loci identified by the different clones because the distribution of segregating fragments in codominant (at least two fragments) and dominant loci (one fragment), and non-segregating fragments (possibly monomorphic loci) was different among species.

Altogether, 85 loci were scored after testing the three species with 42 common probes. Twenty five of these loci segregated simultaneously in all three species, 29 in two and 31 in one of the species. Most of the loci were duplicated, except for the single-copy locus BN33.

Table 1 Common loci shared by A-, B- and C-genome linkage groups and the size (cM) of the fragments containing those loci on their respective linkage groups

Loci	Linkage group	cM
BN11, COT50, BN98	C3	50.3
At2, At3, At4, At5, N2, COT50, BN98	C1	53.7
At2, At3, At4, At5, N2, BN98	A1	27.1
At1, At2, At3, At4, N2	B2	66.2
At4, N2, BN98, BN7, B488	B1	65.1
BN98, BN7, B488, BG4, BG17, BN128	A7	104.0
BG4, BG17, BN128	C7	142.4
BN113, BN24, BN128, LEA76	B5	68.9
BN113, K01, BN55, L3NH3, L1NF9	C4	205.9
BN121, BN113, K01, B370, BN55, L3NH3, L1NF9	C6	92.6
K01, BN55, L1NF9	A6	88.5
BN6, COT46, K01, L1NF6, L1NF10	C5	57.3
BN6, COT46, K01, L1NF8, BN33, L1NF10	A5	26.6
BN6, COT46, L1NF8, BN33, L1NF6, BN14, BN128	B6	40.1
BN6, COT46, BN14, BN128	B3	82.5

Table 3 Distances (cM) of intragenomic segments revealed in the A, B and C genomes

Within the A genome		
CA15, IL9	A4	3.0
CA15, IL9	A10	6.5
AX58, N2, BN127	A1	20.1
AX58, N2, BN127	A4	107.1
COT1, COT49	A5	4.5
COT1, COT49	A10	2.9
Total		144.1
Within the B genome		
BN128, COT46, BN14, BN6	B3	82.5
BN128, COT46, BN14, BN6	B6	29.2
At4, N2,	B1	45.4
At4, N2,	B2	36.3
Total		193.4
Within the C genome		
BN113, L1NF9, L3NH3, BN55	C4	220.6
BN113, L1NF9, L3NH3, BN55	C6	86.8
BN98, COT50, BN11	C1	36.8
BN98, COT50, BN11	C3	50.3
BN98, COT50, BN11	C8	11.7
BN6, CD33, K01, BG17	C5	179.4
BN6, CD33, K01, BG17	C7	103.8
Total		689.4

The number of common loci segregating in two species can be broken down as follows: 38 in *B. rapa* and *B. oleracea*, 34 in *B. rapa* and *B. nigra* and 33 in *B. oleracea*, and *B. nigra*.

Homologies detected for linkage groups of the three *Brassica* genomes

Comparing all the linkage groups of the three genomes, it was possible to associate most of them on the basis of homologous segments sharing three or more marker loci. These were divided into three clusters to facilitate data presentation in Fig. 1. Figure 1A depicts a cluster of eight linkage groups. Groups A1, B2 and C1 contained the *A. thaliana* chromosome-3 gene complex. Groups B1, A7, C7, C3 and C8 shared homology with the first three groups for other loci (Tables 1 and 2). Groups C1, C3 and C8 showed intragenomic homology. Group A7 was formed by the addition of B1 and C7 markers,

Table 2 Distances (cM) of homologous segments shared among and between the A, B and C genomes

Homologous blocks	Linkage groups (cM)					
Between A and B genomes						
At4, BN98, N2	A1	(27.1)	B1	(45.4)		
LEA76, BN127	A4	(11.7)	B5	(43.5)		
BN98, BN7, B488	A7	(20.6)	B1	(55.3)		
At2, At3, At4, N2	A1	(23.4)	B2	(45.5)		
BN6, COT46, BN33	A5	(9.9)	B6	(29.8)		
Total		92.7		219.5		
Between B and C genomes						
At2, At3, At4, N2, BN98			B2	(45.5)	C1	(53.7)
LEA76, BN24, BN128			B5	(57.5)	C7	(35.5)
BN6, COT46, BN33			B6	(29.8)	C5	(57.3)
BN6, COT46			B3	(22.9)	C5	(57.3)
BN113, BN24			B5	(68.9)	C4	(161.9)
Total				223.6		365.7
Betwen A and C genomes						
At2, At3, At4, N2, BN98	A1	(27.1)			C1	(53.7)
BG4, BG17, BN128	A7	(60.7)			C7	(142.4)
BN55, K01, L1NF9	A6	(88.5)			C4	(144.5)
BN6, COT46, K01, BN33, L1NF10	A5	(35.8)			C5	(57.3)
BN121, BN113	A8	(26.7)			C6	(5.8)
BN129, B370	A3	(9.9)			C6	(7.4)
BN55, K01, L1NF9	A6	(88.5)			A6	(76.1)
Total		337.2				487.2

including most of the markers of these two groups. Group C7 served to connect the first cluster with the two others presented in Figs. 1B and C. This linkage group showed homology for three markers with group B5 that associated on the basis of other markers to five more groups (Fig. 1 B, Tables 1 and 2). On this cluster, C6 had two segments of two markers each present in groups A3, as three loci due to the duplication of marker BN129, and as three loci on A8, due to the duplication of marker BN113. Groups C4 and C6 showed intragenomic homology defined by four markers (Table 3). Group C7 (Fig. 1A) associated to C5 in the third cluster (Fig. 1C) by intragenomic homology (Table 3). C5 showed homology with A5 and B6 (Tables 1 and 2) and B6 showed intragenomic homology with B3 (Table 3). A5 had practically all the markers of C5, except for L1NF6 which was replaced by L1NF8. Both markers, L1NF6 and L1NF8, were present in B6 which also shared other markers with the first two groups and B3. Considering all these associations, 18 linkage groups, six of the A, five of the B and seven of the C genome, interconnected to each other by common loci. In addition to this major group of homology, it was possible to detect a few more associations which, for the sake of simplicity, are not shown in Fig. 1. Group C1 shared markers LEA76 and BG7 with A4, group B5 was associated to A4 by markers BN127 (two duplicated loci in B5) and LEA76 (Table 2), and group A4 showed intragenomic homology with A1 (Table 3). Group A10 shared two markers with A4 and two markers with A5 (Table 3). Groups B4 and B8 showed intragenomic homology with groups B1 and B2 for 2–6 *A. thaliana* markers located on chromosome 4 (Sadowski et al., unpublished). Other tentative associations could be constructed for C2, A2 and A9 on the basis of the self-incompatibility locus BOS5 present in these three chromosomes. This locus did not segregate in *B. nigra* (B genome). Groups B7 and C9 were small and had unique marker associations not found anywhere else in the genomes, so their connections to any of the clusters were undetermined.

In general, the genetic distances for the homologous segments in the compared linkage groups were quite large, often covering most of them, indicating large fragments of homology. Inversions were often observed for some of the associations.

Intergenomic vs intragenomic homology

Table 2 summarizes the levels of intergenomic homology. These were calculated by adding the distances in centimorgans of the chromosome segments showing homology between two genomes. Although these figures may understimate real values, they serve to compare levels of homology for the different genomes. The lowest homology was found between the A and B genomes, which shared 92.7 and 219.5 cM of their genomes, respectively. Homology between the B and C genomes was intermediate, with 223 and 365.7 cM, respectively. The highest homology was observed for the A and C genomes, with 337.2 and 487.2 cM, respectively.

Inspection of the three sets of linkage groups revealed intragenomic homology between groups A1 and A4; B3 and B6; C1, C3 and C8; C4 and C6; and C5 and C7. When only two loci in common per linkage group was considered, additional intragenomic homology regions could be detected for all three genomes (Table 3). The best estimate for intragenomic homology was obtained from *B. oleracea* since it had the largest map. This value was 689.2 cM, which corresponds approximately to 40% of the C genome.

Discussion

Although the RFLP maps used for the comparisons do not cover all three genomes entirely, they provide an adequate representation for most of their linkage groups. Larger maps have been published for *B. oleracea* (Slocum et al. 1989; Landry et al. 1992) *B. rapa* (Song et al. 1991; Chyi et al. 1992) and more recently *B. nigra* (Lagercrantz and Lydiate (1995), but comparative analysis among the three genomes has not been possible before. This is because of the previous unavailability of a B-genome map and the lack of common probes mapped in all three genomes. The main objective of the present study was to provide an initial comparative analysis of the A, B and C genomes.

The highly duplicated nature of the three genomes was revealed by the fact that of a total of 61 probes tested, including the 42 common probes to the three genomes, 17 resolved two polymorphic loci and nine revealed three or more loci. This finding further supports the notion that the diploid *Brassica* species are ancient polyploids (Quiros et al. 1994). Sometimes a probe hybridized to fragments corresponding to three segregating loci in one of the species but only to two segregating loci in another species. A similar result was found in a comparative study of linkage groups between potato and tomato (Gebhardt et al. 1991).

All three *Brassica* species shared regions of homology in their genomes. Often a single linkage group showed regions of homology with more than one group of the other species. This is in agreement with a comparative study between maps of *B. rapa* and *B. oleracea* by Slocum (1989), who found that in some cases it was possible to align linkage groups from one to the other species. Some of the linkage groups, however, also shared homologous regions that were separated into more than one group in the other species.

It is evident that extensive gene reordering has taken place during the evolution of *Brassica* species, even though there is considerable conservation among certain chromosome regions within and among the three genomes. This results in complex intra- and intergenomic chromosomal relationships where colinearity is maintained for some segments, but broken up for other chromosomal regions. The extensive map of *B.*

rapa produced by Chyi et al. (1992) illustrates this phenomenon quite well for intragenomic homology, where six of the ten chromosomes, representing approximately half of the nine genome, associate in this fashion. Similarly, in *B. oleracea* we found seven of the nine chromosomes showing homologous segments, covering also approximately 40% of the genome.

What do these findings tell us about the structure and origin of the *Brassica* genomes? The three diploid *Brassica* cultivated species are considered ancient polyploids (Prakash and Hinata 1980) derived from a common ancestor, with five (Sikka 1940) or six chromosomes, by polysomy or the duplication of whole chromosomes (Catcheside 1934; Robbelen 1960). On the basis of chromosome-pairing associations, the number of satellite chromosomes and isozyme-marker distribution in *Brassica* and *Sinapis*, a basic ancestral genomic number as low as x = 3 has been suggested by Chen and Heneen (1991, 1995). The reiteration of chromosome segments, due to RFLP loci duplication within the genomes, certainly agrees with the hypothesis that the existing *Brassica* genomes derive from a smaller ancestral genome. However, the complexity of the existing chromosomal relationships discards the possibility that autopolyploidy alone explains the higher chromosome numbers currently observed in the cultivated genomes.

On the basis of marker arrangement conservation, we attempted to draw phylogenetic relationships among the chromosomes of the three genomes. This allowed us to postulate the possible number of chromosomes in the hypothetical ancestral genome responsible for the origin the A, B and C genomes under the two following assumptions: (1) the A genome is related to the C genome and possibly derived from it, and (2) two main lineages gave rise the diploid cultivated *Brassica* species, the *B. rapa*/*B. olereca* and *B. nigra* lineage. These assumptions are supported by taxonomic studies based on chloroplast (Warwick and Black 1991; Pradhan et al. 1992) and nuclear DNA (Song et al. 1988). Given the above assumptions, at least five and no more than seven ancestral chromosomes can be postulated to explain the existing linkage groups and their homologous relationships (Fig. 2). Six ancestral chromosomes (W1–W6) are assumed to originate the B- and/or C-genome chromosomes corresponding to the linkage groups depicted in Fig. 1. In this hypothetical scheme, C-genome chromosomes give rise to A-genome chromosomes. In addition, two intermediate chromosomes, Bx and Cx, originating from W1, are postulated. Bx gave rise to chromosomes B1, B2, B4 and B8, whereas Cx probably produced A7. Bx was similar in constitution to C1. Considering groups B7 and C9, which did not show homology to any other groups, they may both originate from W6 or independently one from W6 and the other from a seventh ancestral chromosome, W7. Considering that these groups have only a few markers, it is conceivable that they may become associated to the first five ancestral chromosomes (W1–W5) as additional markers are added to them.

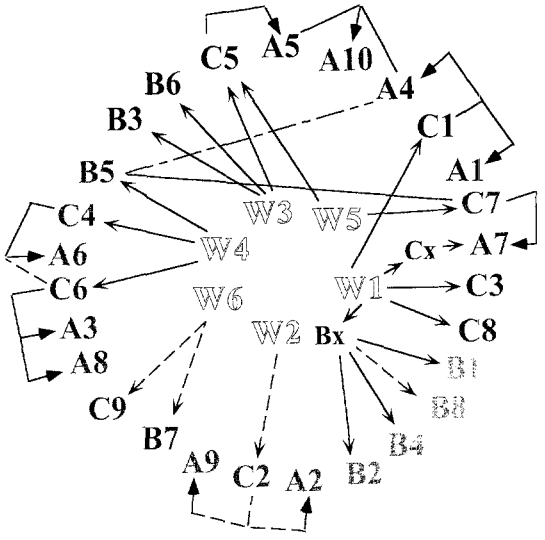


Fig. 2 Diagram showing the hypothetical origin of the chromosomes of the *Brassica* genomes A, B and C from an ancestral genome of x = 6 chromosomes (*W1* to *W6*). *Bx* and *Cx* are intermediate chromosomes. *Broken lines* indicate tentative homologies based either on two markers (B5 to A4 and B1, B4 and B8), or the presence of the self-incompatibility locus BOS5 (W2 to C2, A2, A9) or unique groups (W6 to C9 and B7)

Although hypothetical, this chromosomal relationship serves as a framework to chracterize the *Brassica* chromosomes and determine the mechanisms leading to their origin. For example, the higher level of intergenomic homology between the A and C genomes supports the conjecture that the former derived later on from an already established C genome. Although for simplicity we postulated a single ancestral genome directly giving rise to the existing chromosomes, it is possible that other intermediate steps have taken place. For example, chromosomal rearrangements due to spatial isolation may have generated more than one ancestral genome conserving chromosome numbers. By hybridization and amphiploidy, a common event in *Brassica* (U 1935), genomes of higher order may have originated resulting in conserved duplicated regions. With further evolution by homoeologous recombination, as reported by Quiros et al. (1994) and Song et al. (1995), and aneuploidy (Quiros et al. 1994), the present genomes may have become established. The homologous associations observed for a few groups derived from independent ancestral chromosomes, such as A4 and B5, B5 and C7 and B6 and C5 (Fig. 2), are a reflection of this. All these evolutionary events may have resulted in genomes with different chromosome numbers, such as the B genome (n = 8) in *B. nigra*, the C genome (n = 9) in *B. oleracea*, and the A genome (n = 10) of *B. rapa*, with similar levels of intra- and inter-genomic homology. The genome size of the diploid species has remained practically constant in spite of the existing chromosomal repatterning; 507–516 Mbp (million base pairs) for *B. rapa*, 468 Mbp for *B. nigra* and 599–662 Mbp for *B. oleracea* (Arumuganathan and Earle 1991). Thus similar

amounts of genetic information exist in each of these genomes but are packed in a different number of chromosomes.

Our results suggest that the *Brassica* genomes are differentiated from an originally smaller genome that served as a foundation to build the present-day genomes by duplicating and reshuffling the existing information. Hybridization and chromosomal rearrangements have thus played a substantial role in their evolution.

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