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Construction of *Brassica* B genome synteny groups based on chromosomes extracted from three different sources by phenotypic, isozyme and molecular markers

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Abstract The three B genomes of *Brassica* contained in *B. nigra*, *B. carinata* and *B. juncea* were dissected by addition in *B. napus*. Using phenotypic, isozyme and molecular markers we characterized 8 alien B-genome chromosomes from *B. nigra* and *B. carinata* and 7 from *B. juncea* by constructing synteney groups. The alien chromosomes of the three different sources showed extensive intragenomic recombinations that were detected by the presence of the same loci in more than one synteny group but flanked by different markers. In addition, intergenomic recombinations were observed. These were evident in euploid AACC plants of the rapeseed phenotype derived from the addition lines carrying a few markers from the B genome due to translocations and recombinations between non-homoeologous chromosomes. The high plasticity of the *Brassica* genomes may have been an powerful factor in directing their evolution by hybridization and amphiploidy.

Keywords *Brassica* · B-genome addition lines · *Phoma* resistence · Molecular markers · Chromosome synteny

Introduction

Cytogenetic and molecular investigations have revealed the secondary polyploid nature of cultivated diploid *Brassica* species *B. nigra* (BB, 2n=16), *B. oleracea* (CC, 2n=18) and *B. compestris* (AA, 2n=20) (Röbbelen 1960; Armstrong and Keller 1981; Attia and Röbbelen 1986; Song et al. 1988; Kianian and Quiros 1992). This distinctive structural characteristic of the *Brassica* genomes results in extensive duplications of chromosome segments sharing regions of homoeology within and between genomes (Slocum 1989; McGrath and Quiros 1991; Kianian and Quiros 1992). Duplicated homoeologous regions provide the opportunity for autosyndetic and allosyndetic chromosome pairing under conditions imposed by hybridization. By such means, the *Brassica* genome is extremely plastic, able to exchange chromosomal segments by non-homoeologous recombination (Quiros et al. 1994). This ability results in new chromosomal combinations that may have been instrumental in the origin and evolution of the existing genomes.

The B genome of *Brassica* is an important source of agronomically useful traits, including genes for disease resistance (Sacristan and Gerdemann 1986; Struss et al. 1991a; Chevre et al. 1991). The amphidiploid species *B. carinata* (BBCC, 2n=34) and *B. juncea* (AABB, 2n=36) were derived from hybridization between *B. nigra* with *B. oleracea* and *B. compestris*, respectively (U 1935). The possibility of introgressing genes from the B genome into the A or C genomes opens up opportunities for genetic improvement of rapeseed and other *Brassica* crops (Zhu et al. 1992; Struss et al. 1995).

Genetical and structural studies on the B genome have been done mostly in diploid *B. nigra* species by establishing marker synteny and linkage groups (This et al. 1990; Chevre et al. 1991; Struss et al. 1991a, 1992; Truco and Quiros 1994). Little is known about the B genomes included in the amphidiploids *B. carinata* and *B. juncea*. Only recently have Song and Osborn (1994) conducted the first comparative analyses of the same *Brassica* genomes in natural and synthetic amphidiploids.

In the present paper, a comparative analysis of synteny groups extracted from the three B-genome carriers, diploid *B. nigra* and amphidiploids *B. carinata* and *B. juncea*, has been conducted by the addition of these chromosomes to

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B. napus. This study made it possible to estimate genomic changes due to homoeologous recombinations within the *Brassica* B genome.

Materials and methods

Monosomic *B. napus*/B-genome chromosome addition lines were created by reciprocal interspecific hybridization of *B. nigra* (BB, 2n=16) and *B. napus* (AACC, 2n=38), *B. compestris* (AA, 2n=10) and *B. carinata* (BBCC, 2n=34) as well as *B. oleracea* (CC, 2n=18) and *B. juncea* (AABB, 2n=36). The added B-genome chromosomes were then transferred into the *B. napus* cv 'Andor' as the recipient parent by recurrent backcrossing (Struss et al. 1991b). For characterization of the B-genome chromosomes phenotypic and molecular markers were applied.

Phenotypic markers

Fatty acids

Fatty acid composition was determined on half seeds by gas chromatography (GC) according to Thies (1974).

Sinigrin

Glucosinolate profiles were assessed on 200 mg defatted seed meal using high performance liquid chromatography (HPLC) as described by Kräling et al. (1990).

Phoma resistance

Monosomic addition lines, euploid sister plants, the parents of the lines and the rapeseed cultivar 'Jet Neuf' were used for testing resistance to *Phoma lingam*. An aqueous pycnospore suspension of *Phoma lingam* at a concentration of 10^7 spores/ml was used as inoculum. Ten to 12 plants of each line were inoculated at the three-leaf stage by wounding the petiole using a needle and then placing 10 µl suspension on the wounded area. Plants were kept in a growth chamber at 20°C and 100% humidity for 3 days. Disease symptoms were scored on the stem 10 weeks after inoculation on a scale of 1 (no symptom) to 9 (collapse).

Isozyme markers

Crude extracts of young leaves, buds or seeds were used for horizontal starch gel electrophoresis. The enzymes assayed were phosphoglucoisomerase (PGI), triose phosphate isomerase (TPI), aconitase (ACO), phosphoglucomutase (PGM), alcohol dehydrogenase (ADH), shikimic acid dehydrogenase (SDH), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (6-PGDH), and leucine amino peptidase (LAP), following the protocols reported by Chevre et al. (1991).

Molecular markers

Restriction fragment length polymorphisms (RFLPs)

Total genomic DNA was extracted from young leaves of the monosomic addition lines following a modified protocol of Rogers and Bendich (1988). Aliqouts of 2–5 µg DNA were digested with restriction endonuclease *Eco*RI and *Hin*dIII, separated in 1% agarose gel and transferred to hybond-N nylon membranes. Hybridization was conducted with probes from genomic and cDNA libraries of *B. oleracea* and *B. napus* according to Truco and Quiros (1994). The addition lines were grouped according to their common markers.

Random amplified polymorphic DNA (RAPDs)

Genomic DNA was used as template for the amplification of random DNA sequences using 10-mer primers. Between 50 and 100 mg leaf tissue was collected using the tops of sterile 1.5-ml Eppendorf tubes to pinch out five discs of tissue into the tube. The tissue was macerated in the tube using liquid N2. Five hundred microliters extraction buffer 2×CTAB (100 m*M* TRIS-HCl pH 8.0, 20 m*M* EDTA pH 8.0, 1.4 *M* NaCl, 1% PVP Mr. 40,000, 2% CTAB) and 7 µl proteinase K were added to the tube. The samples were incubated at 60°C for 30 min. One volume (500 µl) chloroform-isoamyl EtOH (24:1) was added, and the tubes were vortexed gently for 10 s. The extracts were centrifuged for 10 min at 13,000 rpm and 4°C. The supernatant was transferred to a fresh tube and mixed with 500 µl isopropanol by gentle vortexing and then centrifuged for 15 min at 13,000 rpm and 15°C. The pellet was washed with 70% ethanol (1 ml), vacuum-dried and resolved in 100 µl 1×TE. For polymerase chain reaction (PCR) the DNA was diluted 20 times.

Primers were provided by UC Davis (Quiros et al. 1991) and Operon technologies (Almeda, Calif.). The PCR technique was applied as reported by Williams et al. (1990) with minor modification described by Quiros et al. (1991).

Results

The phenotypic markers sinigrin content of the seeds and resistance to *Phoma lingam* were present on two or three B-genome chromosomes, depending on the B-genome source, whereas erucic acid was present in 1 or 2 chromosomes (Fig. 1). A single locus for erucic acid content of seeds was detected in *B. nigra* and two loci each in *B. carinata* and *B. juncea* (Fig. 1). The content of erucic acid in the B-genome donor species was 37% in *B. nigra*, 41% in *B. carinata* and 22% in *B. juncea*. 'Andor' the recipient *B. napus* rapeseed variety of the B-genome alien chromosomes, is a 00-quality cultivar that does not contain erucic acid in its seed oil. The addition lines showed a range of 5% to 40% erucic acid in their seeds.

In all three B genomes, 2 chromosomes with sinigrin genes were disclosed. In *B. nigra*, sinigrin constituted 99% of the glucosinolates in the seeds at a concentration of 62 µmol/g air-dry meal; in *B. carinata* this was 94%, at 77 µmol/g; and in *B. juncea* it was 98%, at 90 µmol/g. 'Andor' only contained a total of 10.23 µmol/g and was free of sinigrin. Sinigrin concentrations in the addition lines ranged from 1.7 to 7.5 µmol/g seed.

Three chromosomes carrying *Phoma lingam* resistance genes were resolved in *B. nigra* and *B. carinata*, whereas only 2 were found in *B. juncea* (Fig. 1). It was of particular interest that each of these genes contributed a level of resistance similar to that of the donor parent.

Sinigrin content and *Phoma* resistance loci were mapped together on the same chromosome, except for the third *Phoma* resistance locus on *B. nigra*, which was mapped on chromosome 4. Erucic acid content also mapped on the same chromosome with these 2 loci in 1 chromosome of each of the B-genome donor species (Fig. 1). Seven to eight B-genome chromosomes from each donor species was effectively defined by the isozyme and DNA-based markers. Similar to the phenotypic markers, most of the isozyme loci were represented in more than 1 chromosome, except for PGM-3 (Table 1, Fig. 1).

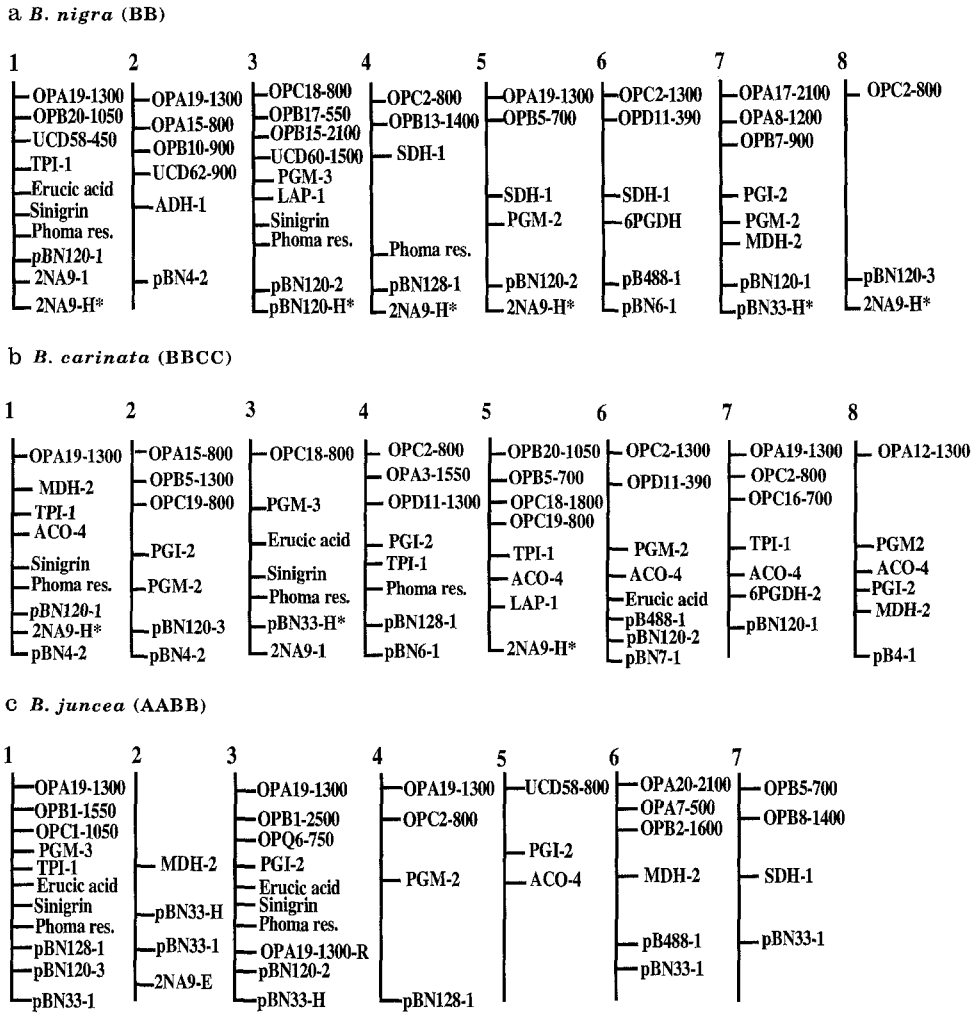

Fig. 1a–c Synteny groups constructed by phenotypic, isozyme, RFLP nad RAPD markers for the B genomes extracted from three different sources: **a** *B. nigra*, **b** *B. carinata* and **c** *B. juncea*. Numbering is arbitrary

Table 1 Number of B-genome chromosomes mapping for isozyme markers in three series of *B. napus* addition lines

Isozyme	Genome combinations		
	B.AC	A.BC	C.AB
ACO-4	–	5	1
ADH-1	1	–	–
LAP-1	1	1	–
MDH-2	1	2	2
6PGDH-2	1	1	–
PGI-2	1	3	2
PGM2,3	3	3	2
SDH-1	3	–	1
TPI-1	1	4	1

Most of the isozyme markers mapped in the lines derived from *B. nigra* agreed with results reported previously (This et al. 1990; Chevre et al. 1991). The exceptions were the presence of 2 identical loci for PGM-2 and 3 loci for SDH on different alien chromosomes. The same deviation was obsereved for TPI-1 found on a single chromosome from the *B. nigra*-derived lines, and 4 different chromosomes in both *B. juncea* and *B. carinata* lines. PGI-2 was found in a single chromosome in the *B. nigra* lines, on 2 chromosomes in *B. juncea* and on 3 in the *B. carinata* lines.

A total of ten isozyme disclosed seven to eight different synteny groups in the B-genome chromosomes derived from the three donor species. These were further described by the DNA-based markers.

A total of 220 plants were assayed for RAPDs, allowing the selection of 54 alien addition plants with B-genome chromosomes (Table 2). A total of 53 RAPD markers were localized over all 8 chromosomes of *B. nigra* and *B. carinata* and over 6 of *B. juncea* (Fig. 1). When RAPD primers were assayed for B-genome specificity, 135 of 180 primers were not polymorphic between the B genome and the A and C genomes of *B. napus*, while 45 primers yielded specific products distinguishing the B genome from the AC genomes. Among these informative primers, the amplification products of 14 primers, called selective primers, disclosed polymorphisms between the three B genomes derived from *B. nigra*, *B. carinata* and *B. juncea* (Table 3). These primers were used for the identification of B-genome chromosomes from the three different sources.

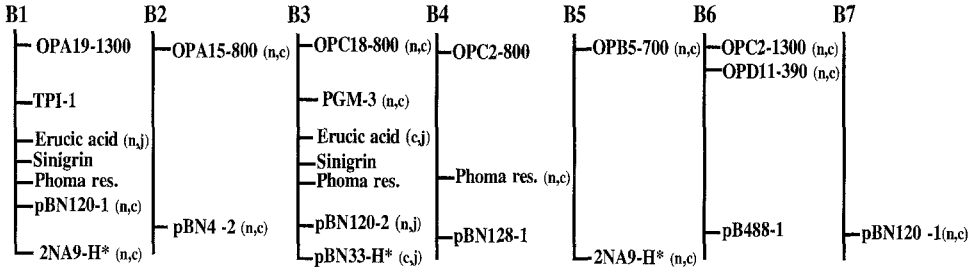

Fig. 2 Consensus synteny maps containing the same marker association in two (indicated in *parenthesis*: *n=B. nigra, c=B. carinata, j=B. juncea*) or three B-genome species

Table 2 Efficiency of RAPD markers for the identification of B-genome addition lines of *B. napus*

Genome combination	Number of plants	Primers used	Number of selected plants
B×AC; AC×B	80	A8, A15, A17, A19, B5, B7, B10, B10, B15, B17, B20, C2, C18, D11, UCD58, 60, 62	21
A×BC; BC×A	50	A3, A12, A15, A19, B5, B20, C2, C16, C18, C19, D11	18
C×AB	90	A7, A19, A20, B1, B2, B5, B8, C1, C2, Q6, UCD58	15

Table 3 Classification of RAPD primers based on polymorphism between AC and B genomes of *Brassica*

Primer	Non-informative	Informative	Selective[a]
A1–A20	13	7	4
B1–B20	15	5	1
C1–C20	16	4	3
D1–D20	16	4	1
H1–H20	17	3	–
I1–I20	19	1	–
J1–J20	15	5	–
Q1–Q20	11	9	3
R1–R20	13	7	2
Total	135	45	14

[a] Polymorphism within the three B genomes of *Brassica* can be recognized

For RLFP markers 35 probes were used for the characterization the B-genome chromosomes. Specific RFLP markers were found for 8 B-genome chromosomes of *B. nigra* and *B. carinata* and for 7 chromosomes of *B. juncea* (Fig. 1).

In agreement with the results obtained with the phenotypic and isozyme markers, in general the DNA-based markers also showed that some of the loci were present in more than 1 chromosome, often in association with different flanking markers. For example, the enzyme PGM locus *Pgm-2* was found on 2 chromosomes of *B. nigra*, each associated with different isozyme and molecular markers (Fig. 1a). The same locus was also located on 3 *B. carinata* chromosomes, 2 of which also carried the locus *Aco-4*, while the rest of the other markers on these chromosomes were different. The third *Pgm-2* chromosome exhibited other flanking markers (Fig. 1b), disclosing extensive synteny rearrangements.

By comparing the synteny groups from all three sources, we attempted to determine consensus synteny groups that may represent the arrangement of the wild-type markers of the B genome. This was done by looking for common markers shared by chromosomes from at least two of the three different B-genome donors (Fig. 2). This comparison enabled the tentative identification of a minimum of 4, and possibly 5 out of the 8 B-genome chromosomes. Two additional groups, B5 and B7, were also resolved, except that these two shared the same pBN120 and 2NA9 loci with B1. Therefore, B5 and B7 may have derived from B1 as intragenomic recombinants. For some of the phenotypic markers it was not possible to determine whether the multiple loci present in 2 or 3 chromosomes were identical, derived by recombination or duplicated loci due to the lack of information on their mode of inheritance. The small number of common segregating loci precluded the assignment of the existing *B. nigra* linkage groups established by Truco and Quiros (1994) to these synteny groups.

The selfed progeny of monosomic addition lines produced 20% monosomic and 2% disomic addition plants, with the remainder being euploids of 38 chromosomes with the rapeseed phenotype of recipient *B. napus* parent. However, some of these euploid sister plants contained erucic acid and sinigrin in the seed and stem resistance to *Phoma lingam*. These plants were backcrossed to 'Andor' in order to test the occurrence of translocations or substitutions. The meiotic analysis of the hybrids in 98% of the PMCs studied showed 19 II at metaphase I. The lack of univalents suggests that these plants are the result of intergenomic translocation between B-genome chromosomes and those of the A and C genomes. By subsequently using B-genome-specific RFLP and RAPD markers we were able to verify the occurrence of translocations in our material (Struss et al. 1995). Four translocation lines were detected by RAPD primer OPU9, and 4 translocation lines could

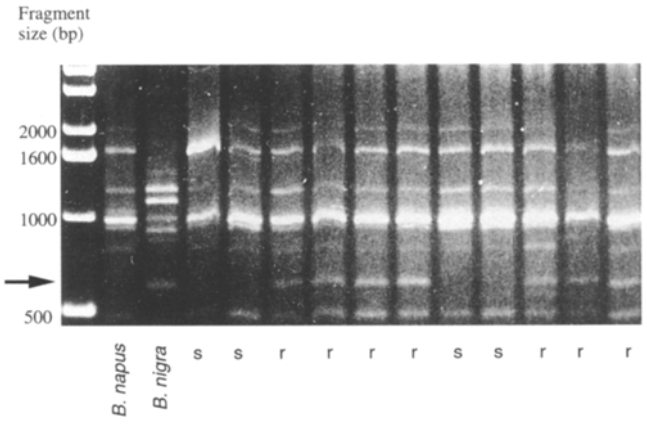

Fig. 3 RAPD markers amplified by primer OPU9 displaying a 600-bp fragment (*arrow*) associated to *Phoma* resistance in translocation lines derived from B-genome addition lines (*r* resistant, *s* susceptible)

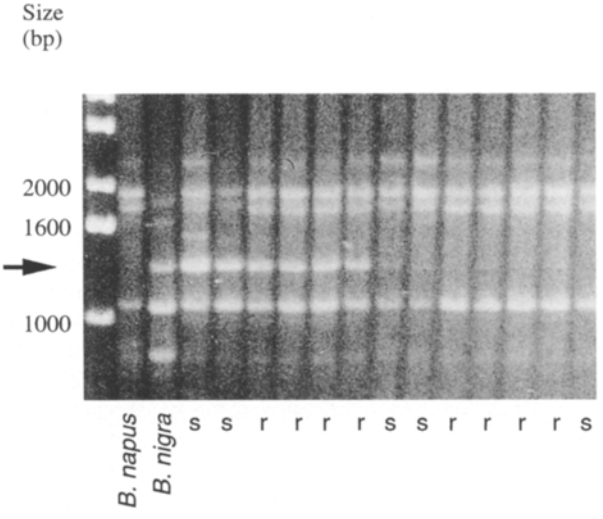

Fig. 4 RAPD markers amplified by OPT12 displaying a B-genome specific marker of 1,300 bp (*arrow*) independent of disease reaction to *Phoma lingam* translocation lines derived from B-genome addition lines (*r* resistant, *s* susceptible)

detected in the F_1 carrying resistance genes to *Phoma lingam* (Fig. 3). Some of the addition lines seemed to contain more than one translocated *B. nigra* chromosome segment. For example, in the same material we could not distinguish between resistant and susceptible plants when using a second RAPD primer (OPT12). This latter primer, however, detected a translocation from *B. nigra*-genome chromosome segments that was independent of any association to the resistance genes of *B. nigra* (Fig. 4). A B-genome-specific RFLP for probe pRP1104 also revealed translocations in this material. A fragment of 16 kb typical of the B genome was present in euploids containing erucic acid and sinigrin in their seeds (Fig. 5).

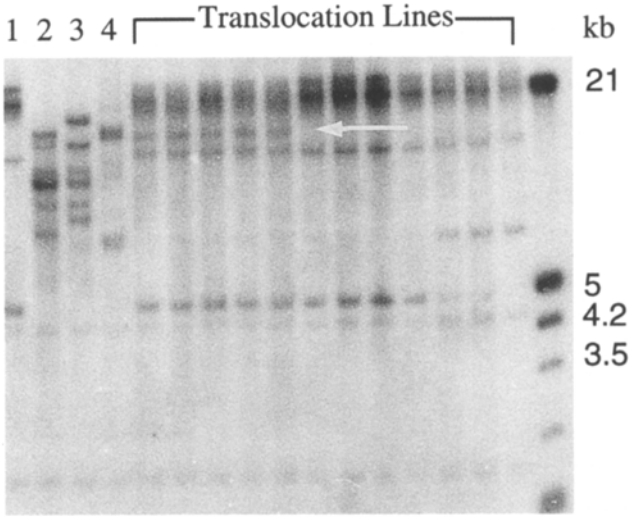

Fig. 5 Hybridization pattern of RFLP probe (pRP1004) revealing translocation lines carrying sinigrin and erucic acid genes of the B genome of *Brassica* (*arrow*); *1 B. napus, 2 B. nigra, 3 B. juncea, 4 B. carinata*

Discussion

In the present study, 8 different B-genome chromosomes of *B. nigra*, the 8 of *B. carinata* and 7 of *B. juncea* were identified. Extensive intragenomic rearrangements were observed for the B-genome chromosomes extracted from the three B genomes of *Brassica* in the *B. napus* addition lines. Evidence for chromosomal rearrangements is provided by the presence of the same loci for all three type of markers in more than 1 chromosome derived from the same sources. Points of chromosome breakage differed for all three sources of B-genome chromosomes, resulting in a varying number of chromosomes carrying a given locus. These rearrangements most likely resulted from the peculiar mode of origin of this material – from trigenomic interspecific hybrids in which all three genomes had been combined in a haploid condition (ABC; n=27 chromosomes) and from which the B-genome chromosome addition lines were derived in three different sets (Struss et al. 1991b). In these primary amphihaploid trigenomic hybrids, genomes were exposed to auto- as well as allosyndetic pairing, leading to the observed intra- and intergenomic recombinations. *Brassica* chromosomes are known for their frequent homoeologous pairing in haploids (Attia and Röbbelen 1986). Due to the divergence of these genomes, which is reflected in both different chromosome numbers and rearrangements of colinear segments (Quiros et al. 1994), the pairing of B-genome chromosomes with those of the A and C genomes is relatively infrequent in disomic hybrids and amphiploids (Attia and Röbbelen 1986; Song and Osborn 1988; Warwick and Black 1991). Only a few chromosomes have been observed microscopically to undergo autosynthedic pairing in the B genome (Prakash 1973, Attia and Röbbelen 1986). The presence of con-

served colinear segments within and between genomes seems to be sufficient to allow homoeologous pairing under certain conditions, such as haploidy, which accounts for the observed intragenomic recombinations in the present addition lines. Another possible source of chromosomal rearrangement is by misdivision of univalents at meiosis, leading to random chromosome break and fusion and consequently intra- and intergenomic recombinations. Sears (1972), Lukaszewski and Gustafson (1983) have reported this type of recombination in wheat/rye addition lines. Sharpe et al. (1995) observed a similar phenomenon for the chromosomes of the A and C genomes in *B. napus*.

The euploid intergenomic translocation lines were obtained from addition lines (Struss et al. 1995). These translocation lines possessed 2n=38 chromosomes and expressed B-genome traits such as erucic acid and sinigrin content in the seeds and resistance to *Phoma lingam*. Euploid *B. napus* plants carrying *B. nigra* traits are of particular interest to the plant breeder. The meiotic analysis of pentaploid plants AACC B (2n=46) and monosomic addition lines did not reveal intergenomic chromosome pairing (Struss et al. 1991b). Ren et al. (1990) observed rye chromatin segments translocated into wheat via monosomic wheat-rye addition lines without pairing between rye and wheat chromosomes. In our material the resistance to *Phoma lingam* was successfully introduced from the B genome into *B. napus* (AACC), most likely by intergenomic translocation. Possibly, the mechanisms for the integration of the alien chromatin is allosyndetic pairing similar to that observed in wheat or in the trigenomic haploid ABC (n=27). In any case, the present euploids can be directly used in breeding programs of *B. napus*.

Structural changes have also occurred during the evolution of the B genome in *B. nigra* and in the derived amphidiploid species. Such changes have been described by Hoenecke and Chyi (1991) in their comparison of the linkage maps of the A genome in *B. compestris* and *B. napus*. However, in BBC and BBA addition lines derived from hybridization between *B. nigra* and *B. carinata* as well as *B. nigra* with *B. juncea* pairing between B-genome chromosomes of *B. nigra* with those from *B. carinata* or *B. juncea* is close to normal (Struss, unpublished data). This indicates a high level of homoeology between the chromosomes of the three B genomes of *Brassica* despite differences at the level of the linkage groups or DNA bases as reported by Song and Osborn (1994).

The fatty acid analyses showed that in *B. nigra* 1 and in both *B. carinata* and *B. juncea* 2 genes control erucic acid production in the seed oil. In *B. napus* erucic acid is controlled by 2 genes with additive effects (Jönsson 1977) and in the amphidiploid *B. carinata* 2 loci have also been reported for erucic acid synthesis (Fernandez-Escobar et al. 1988). In *B. compestris* (Dorrel and Downy 1964) and *B. oleracea* (Chen et al. 1988) erucic acid is determined by 1 gene only. Since an erucic acid gene was found on a single *B. nigra* chromosome, 1 gene is evidently responsible for erucic acid production in *B. nigra*. The 2 genes detected in the B genomes of both *B. carinata* and *B. juncea* could be assigned to either evolutionary changes in the B genomes of these species, or to intergenomic introgression from the C genome in *B. carinata* and from the A genome in *B. juncea*, resulting in an additional gene for erucic acid in the respective B genomes.

With respect to sinigrin all three B genomes of *Brassica* are alike in that sinigrin production in seeds is controlled by 2 genes.

Similarly, no differences could be observed between the B genomes of *Brassica* for resistance against *Phoma lingam*.Three genes were found in *B. nigra* and *B. carinata* and 2 in *B. juncea*, where 7 of 8 B-genome chromosomes have been identified so far. Presumably, in *B. juncea* 3 genes are also responsible for resistance to *Phoma lingam*, the third gene being located on the last unmapped B-genome chromosome of *B. juncea*.

Based on the comparison of the three B-genome synteny maps for the addition lines, we found more common markers between the B genomes of *B. nigra* and *B. carinata* than between these two with *B. juncea*. However, this is probably due to the fact that the *B. juncea*-derived synteny groups contained fewer markers than those of the other two genome species.

The results of the present study provide further evidence of the extensive of plasticity of the *Brassica* genomes due to homoeologous recombination. In particular, synthesis of the trigenomic hybrids depends on extensive reshuffling of the chromosomes, which may create useful new combinations of evolutionary significance. Although only B-genome chromosomes addition lines were surveyed in this investigation, it is likely that the A- and C-genome chromosomes display the same type of behavior. The *Brassica* genomes likely evolved from smaller ancestral genomes of n=5 (Catcheside 1934) or n=6 (Sikka 1940; Röbbelen 1960), and an increase in chromosome number may have occurred by hybridization, thereby providing the opportunity for homeologous recombination. By means of natural selection desirable recombinants may have been established to form the A, B and C genomes of the diploid species. These, as supported by our data, have undergone further rearrangement, probably by similar mechanisms, during hybridization and synthesis of the existing natural amphidiploids species. Our results illustrate the evolutionary differences between the three B genomes of *Brassica* and also confirm the occurrence of intergenomic translocations of chromosome segments in *Brassica*, thereby providing an effective means for the introduction of alien variation into the various *Brassica* crops.

References

Armstrong K, Keller WA (1981) Chromosome pairing in haploids of *Brassica compestris*. Theor Appl Genet 59:49–52

Attia T, Röbbelen G (1986) Cytogenetic relationship within cultivated *Brassica* analyzed in amphihaploids from the three diploid ancestors. Can J Genet Cytol 28:323–329

Catcheside DG (1934) The chromosomal relationship in the Swede and turnip groups of *Brassica*. Ann Bot 601:33

Chen BY, Heneen WK, Jönnson R (1988) Independent inheritance of erucic acid content and flower color in the C-genome of *Brassica napus* L. Plant Breed 100:147–149

Chevre AM, This P, Eber F, Deschamps M, Renard M, Delseny M, Quiros CF (1991) Characterization of disomic addition lines *Brassica napus-Brassica nigra* by isozyme, fatty acid, and RFLP markers. Theor Appl Genet 81:43–49

Dorrel DC, Downey RK (1964) The inheritance of erucic acid content in rapeseed (*Brassica compestris*). Can J Plant Sci 44: 499–504

Fernandez-Escobar J, Dominguez AM, Martin A, Fernandez-Martinez JM (1988) Genetics of the erucic acid content in interspecific hybrids of Ethiopian mustard (*Brassica carinata* Braun) and rapeseed (*B. napus* L.). Plant Breed 100:310–315

Hoenecke M, Chyi YS (1991) Comparison of *Brassica napus* and *B. rapa* genomes based on restriction fragment length polymorphism mapping. In: McGregor DI (ed) Proc 8th Int Rapeseed Congr, vol 4. GCIRC, Saskatoon, Canada, pp 1102–1107

Jönsson R (1977) Breeding for improved oil and meal quality in rape (*Brassica napus* L.) and turnip rape (*Brassica compestris* L.). Hereditas 87:205–218

Kianian SF, Quiros CF (1992) Generation of a *Brassica oleracea* composite map linkage arrangements among various populations and evolutionary implications. Theor Appl Genet 84:544–554

Kräling K, Röbbelen G, Thies W, Herrmann M, Ahmady MR (1990) Variation of seed glucosinolates in lines of *Brassica napus*. Plant Breed 100:33–39

Lukaszewski AJ, Gustafson JP (1983) Translocations and modifications of chromosomes in triticale wheat hybrids. Theor Appl Genet 64:239–248

McGrath JM, Quiros CF (1991) Inheritance of isozyme and RFLP markers in *Brassica compestris* and comparison with *B. oleracea*. Theor Appl Genet 82:668–673

Prakash S (1973) Haploidy in *Brassica nigra* Koch. Euphytica 22:613–614

Quiros CF, Hu J, This P, Chevre AM, Delseny M (1991) Development and chromosomal localization of genome specific markers by polymerase chain reaction in *Brassica*. Theor Appl Genet 82:627–632

Quiros CF, Hu J, Truco MJ (1994) DNA-Based marker maps of *Brassica*. In: Philipps RL, Vasil IK (eds) DNA based markers in plants. Kluwer Academic Publ, Dordrecht, 11:199–222

Ren ZL, Lelley T, Röbbelen G (1990) The use of monosomic rye addition lines for transferring rye chromatin into bread wheat. I. The occurrence of translocations. Plant Breed 105:257–264

Röbbelen G (1960) Beiträge zur Analyse des *Brassica*-Genoms. Chromosoma 1:205–228

Rogers SO, Bendich AJ (1988) Extraction of DNA from plant tissues. Plant Mol Biol Manual A6:1–10

Sacristan MD, Gerdemann M (1986) Different behavior of *Brassica juncea* and *B. carinata* as sources of *Phoma lingam* resistance in experiments of interspecific transfer to *Brassica napus*. Plant Breed 97:304–314

Sears ER (1972) Chromosome engineering in wheat. Stadler Genet Symp 4:23–28

Sharpe AG, Parkin IAP, Keith DJ, Lydiate DJ (1995) Frequent nonreciprocal translocations in the amphidiploid genome of oilseed rape (*Brassica napus*). Genome 38:1112–1121

Sikka SM (1940) Cytogenetics of *Brassica* hybrids and species. J Genet 40:441–509

Slocum MK (1989) Analyzing the genomic structure of *Brassica* species using RFLP analysis. In: Helentjaris T, Burr B (eds) Development and application of molecular markers to problems in plant genetics. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, N.Y.

Song KM, Osborn TC (1994) A method for examining expression of homologous genes in plant polyploids. Plant Mol Biol 26:1065-1071

Song KM, Osborn TC, Williams PH (1988) *Brassica* taxonomy based on molecular restriction fragment length polymorphisms (RFLPs). I. Genome evolution of diploid and amphidiploid species. Theor Appl Genet 75:784–749

Struss D, Quiros CF, Röbbelen G (1991a) Construction of different B-genome addition lines of *Brassica napus* L. In: McGregor DI (ed) Proc 8th Int Rapeseed Congr, vol 2. GCIRC, Saskatoon, Canada, pp 358–363

Struss D, Bellin U, Röbbelen G (1991b) Development of B-genome chromosome addition lines of *B. napus* using different interspecific *Brassica* hybrids. Plant Breed 106:209–214

Struss D, Quiros CF, Röbbelen G (1992) Mapping of phenotypic and molecular markers on *Brassica* B-genome chromosomes using addition lines of rapeseed. Plant Breed 108:320–32

Struss D, Plieske J, Quiros CF (1995) Evidence of intergenomic B-genome translocation in *B. napus* using molecular markers. In: Murphy D (ed) Proc 9th Int Rapeseed Congr, vol 4. GCIRC, Cambridge, England, pp 1125–1127

Thies W (1974) New methods for the analysis of rapeseed constituents. In: DGF, Proc 4th Int Rapeseed Congr. GCIRC, Giessen, pp 275–282

This P, Ochoa O, Quiros CF (1990) Dissection of the *Brassica nigra* genome by monosomic addition lines. Plant Breed 105:211–220

Truco MJ, Quiros CF (1994) Structure and organization of the B genome based on a linkage map in *Brassica nigra*. Theor Appl Genet 89:590–598

U N (1935) Genome analysis in *Brassica* with special reference to the experimental formation of *B. napus* and peculiar mode of fertilization. Jpn J Bot 7:389–452

Warwick SI, Black LD (1991) Molecular systematics of *Brassica* and allied genera (subtribe *Brassicinae*, *Brassiceae*) – chloroplast genome and cytodeme congruence. Theor Appl Genet 83:839–850

Williams JG, Kubelik AE, Levak KJ, Rafalski JA, Tingey SC (1990) DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. Nucleic Acids Res 18:6531–6535

Zhu J, Struss D, Röbbelen G (1993) Studies on Resistance to *Phoma lingam* in *Brassica napus-Brassica nigra* addition lines. Plant Breeding 111:192–197