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A *Brassica campestris-alboglabra* addition line and its use for gene mapping, intergenomic gene transfer and generation of trisomics

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Summary. *Brassica campestris-alboglabra* monosomic addition lines were developed from a trigenomic *Brassica* hybrid (2 n = 3 x = 29, AAC) obtained by backcrossing a resynthesized *B. napus* (2 n = 4 x = 38, AACC) line to its parental *B. campestris* (2 n = 2 x = 20, AA) line. One addition line was characterized genetically with three loci specific for the alien chromosome and cytologically by meiotic analysis. The following results were obtained. (1) The same chromosome in the *B. alboglabra* (2 n = 2 x = 18, CC) genome carried the three loci, E_C, W_C and *Lap-1C*^{c}, which control the biosynthesis of erucic acid, white flower colour and the faster migrating band of leucine aminopeptidase, respectively. The linear order and possible positions of the three loci were inferred. The meiotic behaviour of the alien chromosome was documented and its transmission frequency was assessed. (2) Intergenomic recombination frequently occurred in the monosomic addition line, resulting in the introgression of one or two loci from the alien chromosome into the *B. campestris* genome. (3) *B. campestris* trisomics were found in the progeny of the monosomic addition line. (4) The removal of the other eight C-genome chromosomes from the trigenomic *Brassica* hybrid led to a dramatic increase in the erucic acid content of the monosomic addition line. (5) No offspring of the trigenomic *Brassica* hybrid showed evidence of intergenomic recombination and introgression of the W_C locus into the *B. campestris* genome. It is questioned whether such a difference might be due to a possible regulating mechanism for homoeologous chromosome pairing.

Key words: *Brassica campestris-alboglabra* addition line – Trisomics – Gene mapping – Intergenomic recombination – Homoeologous pairing

Introduction

The genus *Brassica* encompasses many diploid and allopolyploid species. One of the allopolyploid species, *B. napus* (2 n = 4 x = 38, AACC), is an amphidiploid that originated during evolution from spontaneous interspecific hybridization between the diploid species *B. campestris* (2 n = 2 x = 20, AA) and *B. oleracea* (2 n = 2 x = 18, CC), as illustrated by U (1935). Cytogenetic studies have further suggested that these two diploid *Brassica* species together with *B. nigra* (2 n = 2 x = 16, BB) constitute an aneuploid series evolved from a common archetype with a lower basic chromosome number of x = 6 (Prakash and Hinata 1980). Thus, interchromosomal homoeologies exist within as well as between diploid genomes.

One approach to studying chromosome homoeologies is to dissect the diploid *Brassica* genomes by developing interspecific alien chromosome addition lines. Optimally, each chromosome additon line would have a single chromosome from one diploid species with the entire diploid complement of another species as a background. Such addition lines would greatly facilitate the genetical and cytological characterization of alien chromosomes, e.g. by identifying gene linkage groups and assigning these groups to specific chromosomes (Hosaka et al. 1990; This et al. 1990). Chromosome addition lines may also be useful for intergenomic gene transfer.

The common methodology for developing a set of alien chromosome addition lines is recurrent backcross-

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ing of an amphidiploid to a parental diploid species. Screening for addition lines is then carried out amongst the resulting aneuploid progeny. The addition lines may be identified by the unique morphological features of each alien chromosome or by genome-specific markers that distinguish the various alien chromosomes. The small size of the *Brassica* chromosomes makes it difficult to cytologically recognize each particular alien chromosome. Therefore, genome-specific markers have been used for the characterization of different *B. campestris-oleracea* addition lines (Quiros et al. 1987; McGrath and Quiros 1990; McGrath et al. 1990).

Genome specificity of genetic markers can be easily ascertained in a newly synthesized amphidiploid by comparing it with the two parental diploids. Such a case is the newly synthesized *Brassica napus* (Chen et al. 1989, 1990), which we have used in an effort to generate chromosome addition lines. The present report is concerned with the genetical and cytological characterization of one of the five *B. campestris-oleracea* addition lines we have obtained so far.

Materials and methods

Plant materials

Brassica napus was resynthesized by interspecific hybridization between *B. campestris* and *B. alboglabra* (a form of *B. oleracea*) (Chen et al. 1988 b). The resynthesized *B. napus* line No2305 was used for developing *B. campestris-alboglabra* alien chromosome addition lines. The C-genome of No2305 was contributed by the *B. alboglabra* line No4003, which had high erucic acid content, white flowers and black seeds. The A-genome originated from *B. campestris* line Sv85-38301, which had zero erucic acid content (0–3%), yellow flowers and yellow seeds (Chen and Heneen 1989). Thus, the high-erucic, white-flowered and black-seeded traits of No2305 were due to expression of genes found in the *B. alboglabra* genome.

The lack of zero-erucic genotypes in *B. alboglabra* or *B. oleracea* makes it difficult to study the inheritance of erucic acid content in the species itself. However, the inheritance pattern of both erucic acid content and white flower colour in the *B. alboglabra* genome has been shown by using resynthesized *B. napus* lines (Chen et al. 1988 a; Chen and Heneen 1989). These traits were each governed by a single locus, namely E_C and W_C, respectively, in the *B. alboglabra* genome. Furthermore, these two loci were genetically independent. Erucic acid content was almost additively inherited in the monogenic hybrid but showed a partial dominance for high content in the digenic hybrid. White flower colour was dominant over yellow. Thus, erucic acid content and white flower colour are qualitative traits under monogenic control in the resynthesized *B. napus* lines No7076 (Chen et al. 1988 a) and No2305 (Chen and Heneen 1989), which were both derived from zero-erucic and yellow-flowered *B. campestris* and high-erucic and white-flowered *B. alboglabra*. This makes these two characters ideal genetic markers for the *B. alboglabra* chromosome(s) in such resynthesized *B. napus* lines. In addition, isozyme markers specific for the *B. alboglabra* genome have also been identified in the resynthesized *B. napus* material (Chen et al. 1989, 1990).

The resynthesized *B. napus* line No2305 was backcrossed to the parental *B. campestris* line. The resulting trigenomic hybrid ($2n=3x=29$, AAC) was either selfed or successively backcrossed to the parental *B. campestris* line to generate aneuploid progeny. Aneuploid seeds derived from selfing and backcrossing were pooled. These aneuploid seeds were assayed for erucic acid content, and the resulting plants were further studied for isozymes, flower colour and seed colour. Chromosome number was also determined for these aneuploid plants to screen out monosomic addition lines.

Assays for erucic acid content and isozymes

Aneuploid seeds were analysed for erucic acid content by the half-seed technique in order to be able to raise plants from these seeds (Jönsson and Uppström 1986). The methods for assaying isozymes and the nomenclature for isozyme loci and alleles have been described previously (Chen et al. 1989, 1990). It has been possible to assay several isozyme systems in the aneuploid plants, but only the results concerning the leucine aminopeptidase isozyme locus *Lap-1C*^{c} specific for the *B. alboglabra* genome are discussed in the present paper.

Cytological methods

For mitotic chromosome counting, root tips were taken from 3- to 4-week-old plants raised in pots in the greenhouse. The root tips were put on wet filter paper in a petri dish on ice for about 8 h, and then fixed in Farmer's solution (3 parts absolute ethanol: 1 part glacial acetic acid, v:v). Preparations were made according to the Feulgen squash method (Darlington and La Cour 1960). For meiotic analysis, flower buds were also fixed in Farmer's solution supplemented with ferric chloride as a mordant, and then stored in 70% ethanol. The flower buds were stained in Snow's carmine at 60 °C for 3 h. Squashing was done in Hoyer's medium to obtain permanent slides.

Pollen stainability was determined as the percentage of pollen grains stained with 1.5% acetocarmine. More than 300 pollen grains from two flowers were counted for each plant. Normal pollen grains were fully round and densely stained, being easily distinguished from shrunken and lightly stained ones.

Results

Segregation pattern of three characters specific for the B. alboglabra genome and development of one monosomic addition line ($2n=21$)

The joint segregation pattern of the three characters, erucid acid content, flower colour and leucine aminopeptidase, in the aneuploid progeny derived from the trigenomic *Brassica* hybrid ($2n=3x=29$, AAC) is presented in Fig. 1. It can be seen that a zero-erucic seed (less than 3%) always gave rise to a plant that was yellow flowered and lacked the LAP isozyme band specific for the *B. alboglabra* genome; on the other hand, a high-erucic seed (more than 12%), without exception, developed into a plant that was white flowered and showed the presence of the LAP isozyme band specific for *B. alboglabra*. Therefore, the three loci, E_C, W_C and *Lap-1C*^{c}, controlling erucic acid content, white flower colour and the leucine aminopeptidase isozyme band, respectively, were simultaneously transmitted or lost in the aneuploid progeny comprising 110 plants.

High-erucic and white-flowered resynthesized *B. napus*
Genome: AACC
Genotype: $e_Ae_Aw_Aw_A$Lap-1A^{aa}
$E_CE_CW_CW_C$Lap-1C^{cc}

x

Zero-erucic and yellow-flowered *B. campestris*
AA
$e_Ae_Aw_Aw_A$Lap-1A^{aa}

↓

F_1 trigenomic hybrid
Genome: AAC
Genotype: $e_Ae_Aw_Aw_A$Lap-1A^{aa}
E_CW_CLap-1C^{c}

↓ Selfed and backcrossed to the *B. campestris* parent

Erucic acid (%)	0-3				12-29			
Flower colour	White		Yellow		White		Yellow	
LAP isozyme	+	−	+	−	+	−	+	−
Observed progeny	0	0	0	54	56	0	0	0

Fig. 1. The joint segregation of erucic acid content, flower colour and leucine aminopeptidase (LAP) isozyme in the aneuploid progeny derived from selfing of the F_1 trigenomic *Brassica* hybrid (2 n = 3 x = 29, AAC) and backcrossing it to the *B. campestris* parent. The symbols + and − indicate the presence or absence of the *Lap-1C^c* locus, respectively

As already pointed out by Chen et al. (1990), when two loci are carried by the same C-genome chromosome, they will show simultaneous presence or loss in the offspring from the trigenomic hybrid (2 n = 29, AAC) if their physical linkage is not broken up by recombination following auto- or allosyndesis. If the two loci are located on separate C-genome chromosomes, a concurrent presence or loss of these chromosomes could lead to the same result, but this is unlikely to occur in a large sample. Thus, what is presented in Fig. 1 indicates that the three loci E_C, W_C and *Lap-1C^c* are most likely located on the same chromosome in the *B. alboglabra* genome. This has been further verified by the development of the relevant monosomic addition line.

One plant of the aneuploid progeny was identified mitotically as having 21 chromosomes, which was confirmed by meiotic analysis. The seed which gave rise to this plant contained 24.4% erucic acid, and the plant was white flowered and showed the presence of the LAP isozyme band specific for the *B. alboglabra* genome. Thus, this plant was most probably a *B. campestris-alboglabra* monosomic addition line (2 n = 21) in which the alien chromosome was the carrier of these three loci. This was verified by studies made on seeds obtained from selfing this plant.

The progeny of the selfed monosomic addition line (2 n = 21)

The seeds obtained after selfing the monosomic addition line were yellow in colour, indicating the irrelevance of the alien chromosome to black seed colour in *B. alboglabra*. This conclusion has been verified in a subsequent study (Chen et al. in preparation).

Fifty-nine seeds/plants of the progeny obtained after selfing the monosomic addition line were studied for erucic acid content, flower colour, LAP isozyme, chromosome number and pollen stainability (Table 1). As indicated in Table 1, eight possible locus combinations (phenotypes) would be expected with respect to these three loci if pairing and recombination occurred between the alien chromosome and its homoeologues. However, only four locus combinations were realized.

The phenotype of the plants of locus combination 1 was high erucic, white flowered and exhibited the LAP isozyme band specific for *B. alboglabra*. All 18 plants of locus combination 1 had 21 chromosomes, thus indicating the transmission of the alien chromosome that resulted in the simultaneous occurrence of the three loci.

On the other hand, the phenotype of the plants of locus combination 2 was zero erucic, yellow flowered

Table 1. Locus combinations (phenotypes), chromosome numbers and pollen stainability in progeny obtained after selfing the *B. campestris-alboglabra* monosomic addition line (2 n = 21) in comparison with the *B. campestris* parent

Locus combination			Number of		Pollen stainability	
W_C	*Lap-1C*^{c}	E_C	Chromosomes (2 n)	Plants	Mean (%)	Range (%)
1 +	+	+	21	18	58	5–87
2 −	−	−	20	23	84	42–98
2 −	−	−	21	3	68	61–73
3 +	−	−	20	12	81	1–95
3 +	−	−	21	1	92	
4 +	+	−	20	2	61	25–97
5 +	−	+		0		
6 −	+	+		0		
7 −	−	+		0		
8 −	+	−		0		
Total				59		
B. campestris			20	5	99	98–100

The symbols '+' and '−' indicate the presence or absence of each respective locus

and negative for the LAP isozyme band specific for *B. alboglabra*. Twenty-three plants of this locus combination had 20 chromosomes. Evidently, the loss of the alien chromosome in these plants led to the simultaneous absence of the three loci. Three plants of locus combination 2 had 21 chromosomes, however. Since no introgression of erucic locus E_C into the *B. campestris* genome was observed, it would be improbable for the extra chromosome in these 3 plants to be the *B. alboglabra* chromosome that had lost all three loci due to intergenomic recombination. Instead, these 3 plants were most likely *B. campestris* trisomics.

The phenotype for locus combination 3 was zero erucic, white flowered and negative for the LAP isozyme band specific for *B. alboglabra*. Twelve plants of this locus combination had 20 chromosomes. The white flower colour of these plants indicated the presence of locus W_C, even though they had lost the alien chromosome. Intergenomic recombination and introgression of locus W_C into the *B. campestris* genome can easily explain the origin of these plants. Only 1 plant of locus combination 3 had 21 chromosomes. This plant was possibly a *B. campestris* trisomic in which 1 chromosome had undergone the intergenomic crossover mentioned above, thus carrying locus W_C.

The 2 plants of locus combination 4 with 2 n = 20 were zero erucic, white flowered and had the LAP isozyme band specific for *B. alboglabra*. The presence of the two loci, W_C and *Lap-1C*^{c}, in these 2 plants could be the result of an intergenomic crossover involving a larger segment of the alien chromosome, thus leading to the simultaneous introgression of these two loci into the *B. campestris* genome.

Four of the eight possible locus combinations were not observed. For example, there never occurred a yellow-flowered monosomic addition line plant in which the alien chromosome carried the two loci, E_C and *Lap-1C*^{c}, without locus W_C. Such a recombined alien chromosome should have resulted from the observed intergenomic recombination leading to the introgression of W_C into *B. campestris*. It is surprising that the addition line failed to transmit the recombined alien chromosome to its progeny.

It is difficult to assess the influence of the alien chromosome on pollen stainability in the addition line because of the wide ranges of pollen stainability observed in the addition line plants (locus combination 1) and in their diploid sibling *B. campestris* plants (locus combination 2).

Intergenomic recombination frequencies

Hypothetically, the *B. campestris* genome in the 18 plants of the monosomic addition line (locus combination 1, Table 1) may be carrying one or both of the two loci, W_C and *Lap-1C*^{c}, as a result of intergenomic introgression; however, this can not be ascertained due to the presence of the alien chromosome. Estimates of the maximum intergenomic recombination frequencies were thus based on the remaining 41 progeny plants (Table 1). We suppose that the intergenomically recombined gametes are viable and transmitted by both male and female sides. The maximum recombination frequencies for loci W_C and *Lap-1C*^{c} between the alien chromosome and its *B. campestris* homoeologue, therefore, were estimated to be $1-(26/41)^{1/2} \approx 0.204$ and $1-(39/41)^{1/2} \approx 0.025$, respectively. If the 18 plants of locus combination 1 are included, the minimum intergenomic recombination frequencies for the two loci should be estimated accordingly as $1-(44/59)^{1/2} \approx 0.136$ and $1-(57/59)^{1/2} \approx 0.017$.

Since the monosomic addition line failed to transmit the intergenomically recombined alien chromosome to the progeny, half of the recombined phenotypes were not realized. Therefore, the actual maximum recombination frequencies for the two loci W_C and *Lap-1C*^{c} should be $0.204 \times 2 = 0.408$ and $0.025 \times 2 = 0.05$, respectively, while the minimum recombination frequencies should be $0.136 \times 2 = 0.272$ and $0.017 \times 2 = 0.034$, respectively.

Transmission of the alien chromosome

Upon selfing, the monosomic addition line transmitted the alien chromosome to its progeny at a frequency of $(18/59) \approx 30.5\%$ (Table 1), which was the pooled transmission through male and female gametes. No disomic addition lines (2 n = 22) were recovered.

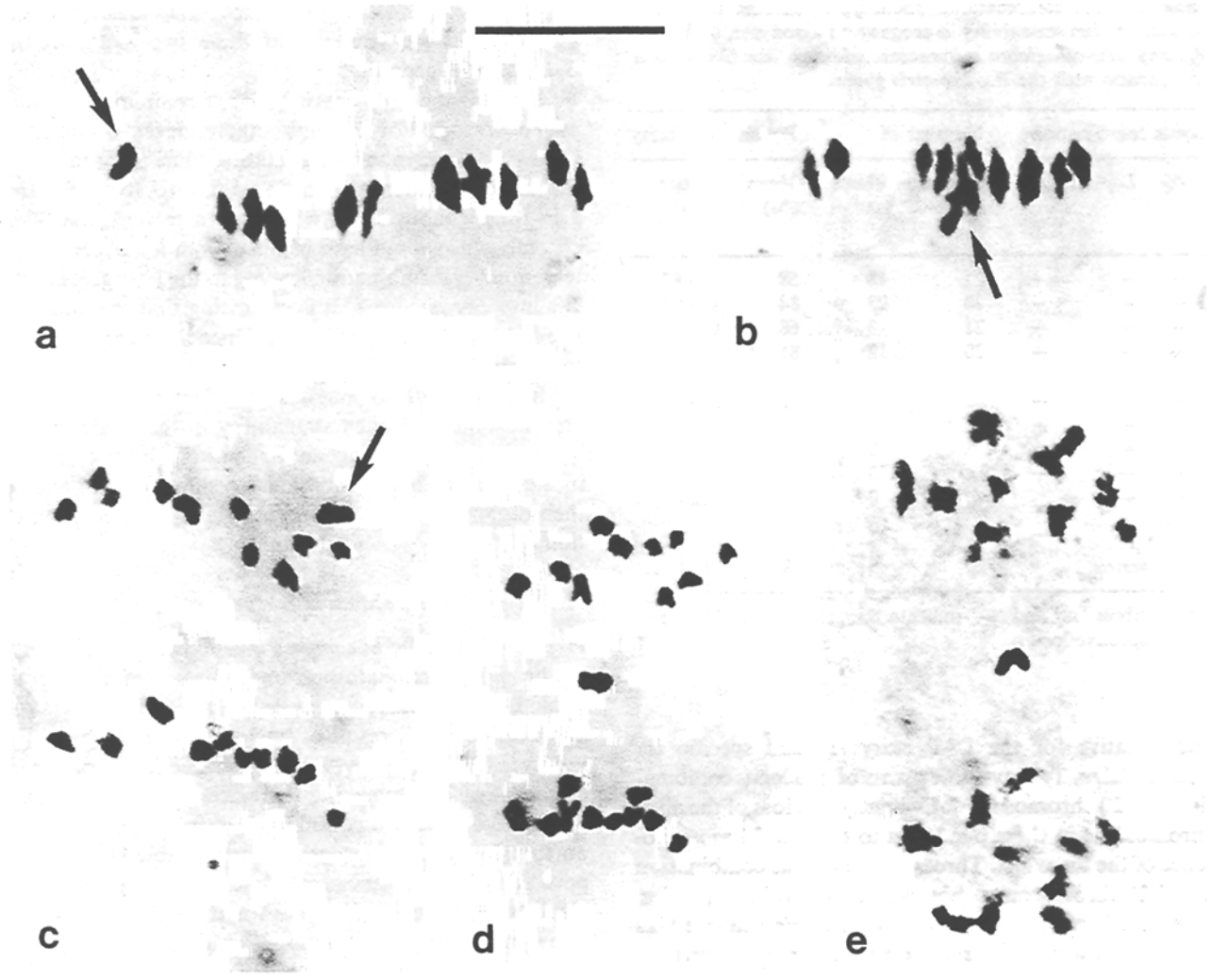

Fig. 2a–e. Meiosis of *B. campestris-alboglabra* monosomic addition line (2 n = 21). **a** Metaphase I: 10 II + 1 I (*arrow*). **b** Metaphase I: 1 III (*arrow*) + 9 II. **c** Anaphase I: 10/11 segregation. Note the large size of the alien chromosome (*arrow*). **d** Anaphase I showing 10/10 segregation and the lagging alien chromosome. **e** Anaphase/telophase I: The V-shape of the lagging alien chromosome indicates its median centromere. *Bar*: 10 μm

Cytological observations

Chromosome configurations were examined in the pollen mother cells (PMCs) at diakinesis and the first metaphase of meiosis in the monosomic addition line (Table 2). It was revealed that 88% of the PMCs had ten bivalents and one univalent (Fig. 2a) whereas the remaining 12% showed nine bivalents and one trivalent (Fig. 2b). When the alien chromosome was a univalent, it was usually not aligned on the equatorial plate.

The behaviour of the alien chromosome from anaphase I to telophase I was recorded in the addition line (Table 2). The variable behaviour of the alien chromosome was classified into five categories that occurred at different frequencies: (1) it passed undivided to either of the two poles (Fig. 2c) and was included in one of the two telophase nuclei in 31.9% of the PMCs; (2) it lagged undivided (Fig. 2d, e) and was not included in either of the two telophase nuclei in 23.6% of the PMCs; (3) it divided equationally with the two sister chromatids moving to opposite poles or the same pole or lagging behind in 33.6% of the PMCs; (4) it misdivided in 2.2% of the PMCs; (5) it underwent breakage other than misdivision in 8.7% of the PMCs.

The alien chromosome in the addition line was large (Fig. 2c, d) and had a median centromere (Fig. 2a, e).

Erucic acid content

The erucic acid contents of resynthesized *B. napus* line No2305, the resulting trigenomic hybrid (AAC) and the monosomic addition line are presented in Table 3. Com-

Table 2. Cytological observations at diakinesis, the first metaphase (MI), and the first anaphase and telophase (AI and TI) of meiosis in the *B. campestris-alboglabra* monosomic addition line (2 n = 21)

Diakinesis or MI			AI and TI		
Chromosome configuration	PMC		Behaviour of the alien univalent chromosome	PMC	
	No.	%		No.	%
10 II + 1 I	67	88	1 Entering one pole undivided	73	31.9
9 II + 1 III	9	12	2 Lagging behind undivided	54	23.6
Total	76	100	3 Equational division	77	33.6
			4 Misdivision	5	2.2
			5 Breakage	20	8.7
			Total	229	100

Table 3. Erucic acid contents of the resynthesized *B. napus* line, the trigenomic *Brassica* hybrid and the *B. campestris-alboglabra* monosomic addition line (2 n = 21)

Material	Genome	2n	Genotype	Erucic acid (%)		
				No. of seeds	Mean	Range
B. napus line No 2305	AACC	38	$e_A e_A E_C E_C$	10	24.4	23–26
The trigenomic hybrid	AAC	29	$e_A e_A E_C$	5	13.9	11–15
The monosomic addition line	AA + 1	21	$e_A e_A E_C$	18	26.3	22–31

pared with the trigenomic hybrid, the monosomic addition line showed a dramatic increase in erucic acid content.

Discussion

There are several advantages to the use of *B. campestris-alboglabra* addition lines for the characterization of the *B. alboglabra* genome. (1) By using such alien chromosome addition lines, one is exploiting intergenomic divergence, which is generally larger than intragenomic variation. (2) Resynthesized *B. napus* can easily be produced in desirable genomic combinations by carefully choosing the *B. campestris* and *B. alboglabra* (or *B. oleracea*) genotypes, which will greatly facilitate genetic analyses of specific traits in the addition lines. (3) During the process of developing addition lines, desirable gene transfer may be accomplished from the alien *B. alboglabra* chromosome to the *B. campestris* genome or vice versa.

These advantages have been exemplified in the present study. For example, the resynthesized *B. napus* line No2305 was produced in the desirable genomic combination between a zero-erucic, yellow-flowered and yellow-seeded *B. campestris* line and a high-erucic, white-flowered and black-seeded *B. alboglabra* line, which made it possible to carry out genetic analyses of these traits in the *B. alboglabra* genome. The gene for white flowers in the *B. alboglabra* line has been successfully transferred to *B. campestris*. In a conventional Mendelian experiment, it would not have been possible to study the joint inheritance pattern of erucic acid content, flower colour and seed colour since there are no zero-erucic, yellow-flowered and yellow-seeded *B. alboglabra* or *B. oleracea* genotypes available.

As to the segregation of the three loci, E_C, W_C and *Lap-1C*^{c}, only two of the eight possible phenotypes were observed in the 110 aneuploid plants derived from the trigenomic *Brassica* hybrid (AAC) (Fig. 1). This fact can be simply explained as an indication of the presence or absence of the carrier chromosome for these three loci. Thus, there is no evidence of intergenomic recombination regarding this chromosome. Otherwise, the introgression of locus W_C into the *B. campestris* genome, for example, would have resulted. In striking contrast, some of the recombined phenotypes occurred frequently in the progeny of the selfed monosomic addition line (Table 1). In particular, the 12 plants of locus combination 3 with 2 n = 20 revealed frequent introgression of locus W_C into the *B. campestris* genome, which was possibly a result of intergenomic recombination.

The discrepancy between the intergenomic recombination frequencies in the trigenomic hybrid and the monosomic addition line could be due to a chromosome pairing control mechanism similar to that in wheat (Riley et al. 1959). Such a pairing regulation mechanism has been reported in the amphidiploid *B. juncea* (Prakash 1974). Thus, intergenomic pairing involving the carrier chromosome of the three loci in the trigenomic hybrid (2 n = 29, AAC) might have been suppressed by a mechanism regulating homoeologous chromosome pairing. Suppose that the regulating mechanism was controlled by one or a few of the other eight chromosomes of the C-genome. Such a regulating mechanism would not function in the monosomic addition line (2 n = 21), consequently allowing frequent intergenomic recombination and the introgression of the white flower locus W_C into the *B. campestris* genome. Using the small progeny size of hyperploids as a criterion in a similar study, Quiros et al. (1987) observed intergenomic recombination frequencies between 6% and 20% for different isozyme loci. They also obtained disomic addition lines that were not recovered in the present study.

We reported previously the independent inheritance of erucic acid content and flower colour in the *B. albo-*

glabra genome of a resynthesized *B. napus* line (Chen et al. 1988a). The independent inheritance of these two traits can be due to the location of the two loci on separate chromosomes of the *B. alboglabra* genome, or to the distance between them if located on the same chromosome. Our present results conclusively demonstrate that the two loci are located on the same chromosome. Thus, it is the distance between the two loci that has resulted in the independent inheritance of the two traits.

The linear order of the three loci E_C, W_C and *Lap-1C*^{c} on the same chromosome can be deduced from the intergenomic recombination frequencies. Thus, locus W_C must lie most distally from the centromere since the recombination frequency was the highest for this locus. The lower frequency and simultaneous introgression of locus *Lap-1C*^{c} with locus W_C indicated that these two loci were located on the same arm, with locus *Lap-1C*^{c} being closer to the centromere. Since there was no intergenomic crossover observed for erucic locus E_C, this locus must be nearest to the centromere if carried by the same arm as the other two loci or located on the other arm of the chromosome. Because of the tight linkage between the erucic locus and the centromere, erucic acid content is the most reliable character for indicating the transmission of the carrier chromosome in the progeny of the monosomic addition line.

Using the marker genes, we were able to identify a few plants with the chromosome number of 2 n = 21 in the progeny of the selfed monosomic addition line to be presumptive *B. campestris* trisomics; these plants would otherwise have been difficult to distinguish from the monosomic addition line. However, identification of the cytological mechanism for the origin of these trisomics needs to be addressed.

In the process of developing addition lines, both the genomes of *B. campestris* and the alien chromosomes of *B. alboglabra* may not remain intact due to possible intra- and intergenomic recombination. The large range of pollen stainability observed among the diploid *B. campestris* siblings in the progeny of the selfed monosomic addition line (Table 1) was probably a result of such intergenomic recombination since the parental *B. campestris* line showed a much smaller range of pollen stainability. Furthermore, some of the diploid siblings were morphologically different from the parental *B. campestris* with regard to such traits as plant size, branching habit, leaf colour and shape.

The biosynthetic pathway to the main fatty acids in rapeseed follows two directions from oleic acid, one for carbon chain elongation towards eicosenoic and erucic acids, and the other for carbon chain desaturation towards linoleic and linolenic acids (Jönsson and Uppström 1986). Compared with that of the trigenomic *Brassica* hybrid (AAC), the dramatic increase in the erucic acid content of the monosomic addition line (Table 3) is likely to be due to the removal of the other eight C-genome chromosomes, some of which are most likely involved in the genetic control of the biochemical processes that leads to carbon chain desaturation.

We are currently trying to generate the whole set of *B. campestris-alboglabra* addition lines. The development of DNA markers is also underway. Our aim is to combine the genetic characterization of such addition lines with cytological studies, which will shed some light on the evolution of *Brassica* genomes.

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