

HYPOTHETICAL MODEL FOR *BRASSICA* GENOME STRUCTURE AND EVOLUTION

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ABSTRACT

Based on existing information developed by comparative gene mapping of the *Brassica* genomes A, B and C a hypothetical model on the events leading to their origin and evolution is proposed. This model assumes an ancestral genome of $x=5$ or 6 chromosomes undergoing duplication by amphiploidization.

The *Brassica* genomes and their relationships: The diploid species of *Brassica* range in genomic numbers from $x=7$ to $x=12$. The three diploid cultivated species are: 1) *B. nigra* ($2n=2x=16$, B genome), black mustard 2) *B. oleracea*, ($2n=2x=18$, C genome), cabbage group, and 3) *B. rapa* (syn. *B. campestris*) ($2n=2x=20$, A genome) turnips, rapeseed and oriental vegetables (Prakash and Hinata 1980). On the basis of limited cytological, biochemical and molecular data, it is believed that the B genome is more distantly related to both A and C genomes than the latter two are to each other (Vaughan, 1977; Attia and Robbelen, 1986; Song *et al.*, 1988, Warwick and Black (1991).

Secondary polyploidy: A common assumption is that the $x=8, 9$ and 10 cultivated species have evolved in an ascending dysploid series from a common primitive genome, 'Urgenome' (Haga, 1938). Although there are not known *Brassica* species in nature with genomes of less than $x=7$ chromosomes, Sikka (1940) postulated that the ancestral genome consisted of five basic chromosomes, whereas Catcheside (1934) and Robbelen (1960) believed that this number was actually six. This ancestral genome presumably originated the $x=8, 9$ and 10 chromosome genomes by polyploidy which was further modified by hybridization and chromosomal rearrangements resulting in a wide range of chromosome numbers (Sikka 1940). Thus, as a corollary of this hypothesis, the cultivated diploids are considered secondary polyploids or paleopolyploids (Catcheside 1934, Prakash and Hinata, 1980). The lowest chromosome number observed in the tribe *Brassicaceae* is $x=7$, thus based on these earlier studies, it is regarded ancestral to higher genomic numbers. The lowest chromosome number in the family *Cruciferae* is $x=4$ for species of the tribe *Lepidieae*.

Research from our and other laboratories have demonstrated that indeed the *Brassica* genomes are highly duplicated (Kianian and Quiros 1992a, Song *et al.* 1988, 1990, Hoencke and Chyi 1991). It has been estimated that 50% of RFLP loci are duplicated in the diploid species. These findings supports the hypothesis that *Brassica* diploids are actually secondary polyploids derived from ancestral genomes of fewer chromosomes.

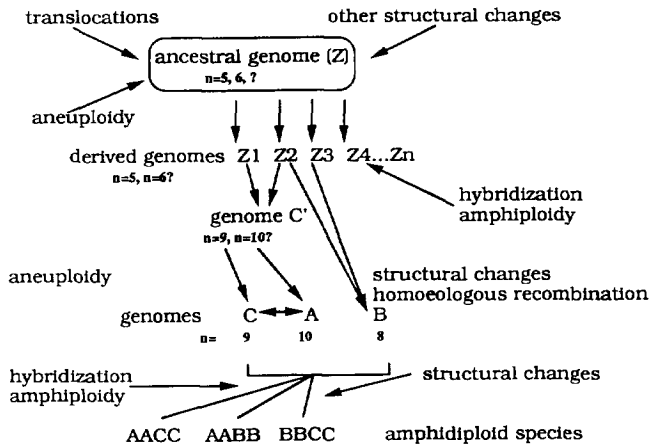
Comparative studies of the A, B and C genomes: In order to perform comparative studies of the three genomes, we constructed F2 linkage maps for *B. oleracea* (Kianian and Quiros, 1992a) and *B. nigra* (Truco and Quiros 1994). Together with the *B. rapa* map developed earlier (McGrath and Quiros 1991), we have now maps sharing common RFLP loci for the three cultivated genomes. We found extensive rearrangements for the markers, but it is also possible to detect conserved regions, which is in agreement with the previous observations of Slocum (1989) comparing the genomes A and C. The introduction of the B genome into the comparison discloses similar level of marker arrangement conservation between the B genome with the A and C genomes.

Structural composition of the genomes: The highly rearranged and dispersed duplicated chromosomal segments observed in the three genomes, argues against simple polysomy, or reiteration of whole chromosomes in the *Brassica* genomes. Thus these genomes cannot simply be described by formulae including a few founder chromosomes being reiterated twice or thrice in the same genome as described by Robbelen (1960). The intra-genomic conservation of non-homologous chromosomes is not as high as one would expect to assume initial autopolyploidization of a $x=5$ original genome followed by chromosome loss as presumed by Sikka (1940). Similarly, the presence of 8, 9 or 10 chromosomes in the B, C and A genomes cannot be explained by the loss (or addition) of one or two chromosomes. Furthermore, the DNA content of the three diploid species, regardless of genomic number is similar (ranging from 470 to 660 Mbp/1C) (Arumuganathan and Earle 1991). Therefore, they contain the same amount of genetic information but packed in different number of chromosomes.

Model explaining the origin and evolution of the *Brassica* genomes: Sikka (1940) mentioned two main forces molding the *Brassica* genomes departing from an ancestral genome of $x=5$. The first one was hybridization and the second one was chromosomal structural changes. Hybridization in *Brassica* is

well documented by the existence of natural amphidiploid species. Tolerance of changes in genomic numbers has been demonstrated by the development of alien addition lines (Quiros *et al* 1993). As far as chromosomal rearrangements is concerned, reciprocal translocations are well documented in *Brassica* species. These are known to generate not only duplications and deletions but also aneuploids. With the information we have in hand at this moment, we propose the following model summarizing the possible events leading to the origin of the A, B and C genomes of *Brassica*.

Departing from a hypothetical ancestral genome of $x=5$ or 6 chromosomes (Z genome), the species containing this genome by divergence due to spatial isolation may have suffered chromosomal structural modifications adapting them to different niches. These changes in chromosome structure may have originated a series of new genomes of similar chromosome numbers (z_1 to z_n). By hybridization of these new species, ancestral amphidiploids may have originated which through further chromosomal rearrangement and aneuploidy could have originated the present genomic numbers observed in the A, B and C genome. Because of their origin, these genomes are expected to have conserved chromosome segments and extensive duplications, which will result in further modification by homoeologous recombination. Subsequent amphiploidy of the A, B and C genome resulted in the synthesis of the three cultivated amphidiploid species. Therefore, it is likely that these events, changes in chromosome structure and number, hybridization, and amphiploidy have taken place in cycles of higher complexity during the evolution of the *Brassica* species.



Model summarizing the possible origin and evolution of the *Brassica* genomes of the cultivated species.

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