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REVIEW

Cytogenetics and germplasm enrichment in *Brassica* allopolyploids in China



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Abstract

This paper reviews research advances in cytogenetics and germplasm innovation in *Brassica* allopolyploids, particularly oilseed rape (*Brassica napus*), in China. Three naturally evolved *Brassica* allotetraploid species are cytologically stable but tend to preferentially lose several chromosomes from one subgenome when induced by alien chromosome elimination. A-subgenome is extracted from *B. napus*, and the ancestral *Brassica rapa* was restituted after the total loss of C-subgenome chromosomes. Genome-wide genetic and epigenetic alterations were observed in both natural and synthetic *Brassica* allotetraploids. *B. napus* was subjected to extensive interspecific hybridization with landraces of *B. rapa* and *Brassica juncea*, which exhibit abundant phenotype variations, to widen the genetic diversity in breeding and select numerous elite germplasm resources and cultivars; these cultivars include the representative Zhongyou 821, which also parented numerous other varieties. Novel *B. napus* genotypes were obtained using *Brassica* trigeneric hybrids and allohexaploids (2n=54, AABBCC) by combining subgenomes from extant allotetraploids and diploids as bridge. Alien additions, substitutions, and translocations of the *B. napus* genome were developed by intergeneric/intertribal sexual and somatic hybridizations with several crucifers. Furthermore, mitochondrial DNA recombination promoted the production of novel cytoplasmic male sterile lines.

Keywords: *Brassica napus*, germplasm, *Brassica rapa*, *Brassica juncea*, cytogenetics

1. Introduction

Oilseed rape (*Brassica napus* L., 2n=38, AACC), which is

widely cultivated in China, was first introduced to Korea in the 1930s, to Europe in the 1940s, and to Japan after the anti-Japanese War in 1945 (Shengli Youcai) (Liu 2000). *Brassica rapa* L. (2n=20, AA) and *Brassica juncea* (L.) Czern & Coss. (2n=36, AABB) were traditionally grown for oil production; moreover, the subspecies or varieties of these two species are popular vegetables in China and throughout Asia (Wang *et al.* 2013). After the establishment of the People's Republic of China, *B. rapa* was gradually replaced as an oil crop by *B. napus*, which exhibits higher yield, improved resistance to biotic and abiotic stresses, and wider adaptability. The first *B. rapa* variety with low erucic acid content was selected from the local landrace Liho

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in Germany; this variety was then introduced to Qinghai, China in 1974 to provide germplasm for breeding cultivars with low erucic acid content. Bronowski, a variety from Poland, provides genetic resource for cultivation of oilseed rape with low glucosinolate content (Fu *et al.* 2012). These two varieties are used as primary gene donors to breed cultivars with double low quality (<1% erucic acid, <30 μmol glucosinolates g^{-1} seed meal) in China and other countries. Based on replacement of rapeseed oil varieties in China, the history of rapeseed oil production is divided into three stages or leaps, namely, substitution of native *B. rapa* by alien *B. napus* (1949–1960s); wide distribution of *B. napus* to the release of the elite cultivar Zhongyou 821 (1970s–1980s); and replacement of conventional cultivars by hybrid cultivars (1990s–present) (Liu 2000). The success of each leap could be attributed to the use of novel germplasms or selection of elite varieties or breeding parents.

2. Genetic behavior of ancestral genomes in allopolyploids

The cytological interrelationships among six cultivated *Brassica* species provide the textbook example of speciation by interspecific hybridization, also known as U-triangle, which was proposed by the Korean-Japanese scientist Nagaharu (1935). The combinations of any two of three diploid species, namely, *Brassica nigra* (L.) Koch ($2n=16$, BB), *Brassica oleracea* L. ($2n=18$, CC), and *B. rapa* L. (syn. *Brassica campestris*, $2n=20$, AA), produced three allotetraploids, including *Brassica carinata* Braun ($2n=34$, BBCC), *B. juncea* (L.) Czern. ($2n=36$, AABB), and *B. napus* L. ($2n=38$, AAC). The natural origin patterns of these allotetraploids are used to produce numerous synthetic counterparts by interspecific crosses among extant diploids with various diversities, elucidate the evolutionary origin, and develop new germplasms for breeding. The formation and evolution of three allotetraploids are affected by different phylogenetic relationships among three diploids: *B. rapa* and *B. oleracea* are closely related, but both are distantly related to *B. nigra*. In *B. napus*, abundant homeologous exchanges, ranging from large segments to single SNPs, were detected by sequence comparison with extant *B. rapa* and *B. oleracea*; these exchanges include crossovers and non-crossovers between two subgenomes. Homeologous gene expression shows genome dominance and equivalence and lack of significant bias toward either subgenome of the recent allopolyploid (Wang *et al.* 2011; Liu *et al.* 2014). The genome sequence of *B. juncea* has no obvious intergenomic exchanges but shows evident homeolog expression dominance between two subgenomes because numerous genes are dominant toward the B-subgenome (Yang *et al.* 2016). Based on the correlation between homeolog expression dominance and

evolutionary rate, the B-subgenome evolves faster than the A-subgenome, indicating the asymmetric evolution of the two constituent subgenomes. Homeolog expression dominance could be associated with human selection and utilized to produce vegetable- and oil-use varieties of this allotetraploid.

The three naturally evolved *Brassica* allotetraploid species are cytologically stable; however, their chromosomes are preferentially lost or maintained in intergeneric hybrids with other crucifers and exhibit different stabilities at species and genome levels. The stability hierarchy of the three species is *B. carinata*>*B. juncea*>*B. napus*, and that of subgenomes in each species is *B. nigra*>*B. rapa*>*B. oleracea* (Ge *et al.* 2013) (Fig. 1). The consistent performance between the hierarchies of subgenomic stability and nucleolar dominance (*B. nigra*>*B. rapa*>*B. oleracea*) in these allotetraploids (Chen and Pickard 1997) highlights the role of rRNA genes as a contributing factor in preferential stabilization of the subgenome/chromosomes from the rRNA donor parents. The relatedness of the A- and C-subgenomes could lead to tolerance of *B. napus* to lose several and, in the extreme, all C-subgenome chromosomes from its complement, thereby restituting the ancestral *B. rapa* (Tu *et al.* 2010; Zhu *et al.* 2016). In the synthesized *Brassica* allohexaploids, which do not exist in nature, the stability hierarchy of the subgenomes is B>A>C (Fig. 1). A previous study used different crossing strategies to artificially produce *Brassica* allohexaploids ($2n=54$, AABBCC), which possess the combinations of the genomes from the extant allotetraploids and diploids (Zhou *et al.* 2016).

The preferential loss of several C-genome chromosomes from the complement of *B. napus* is repeatedly induced in its intergeneric crosses with other crucifers (Chen *et al.* 2007; Du *et al.* 2008; Tu *et al.* 2010); this property enables

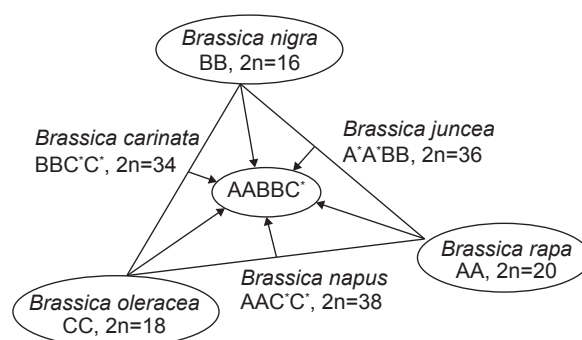


Fig. 1 Different genome stabilities in three *Brassica* allotetraploids and synthetic allohexaploids revealed in distant hybridizations and selfed progenies. Stability hierarchy among tetraploids is *Brassica carinata*>*Brassica juncea*>*Brassica napus*, and is B>A>C for the genomes in each tetraploid and hexaploid. One of two genomes in the allotetraploids (asterisks) is less stable. Modified from Ge *et al.* (2013).

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