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Review

The progress of intersubgenomic heterosis studies in *Brassica napus*

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The new nomenclature of *Brassica* has been suggested in a previous study by same authours where the symbols of A^r, A^j and A^n represented the A genome in the *Brassica rapa*, *Brassica juncea* and *Brassica napus*, B^b, B^j and B^c for the B genome of *Brassica nigra* (black mustard), *B. juncea* and *Brassica carinata*, C^o, C^n and C^c for the C genome of *Brassica oleracea*, *B. napus* and *B. carinata*. Numerous efforts have focused on exploring novel *B. napus* ($A^nA^nC^nC^n$) breeding stocks by the hybridization between *Brassica* species. Thereafter, most interspecific hybrids in *Brassicas* could be considered as intersubgenomic hybrids. In this review, examples are shown from recent studies on the method for construction of new-typed *B. napus* with genome composition of $A^rA^rC^cC^c$ and $A^rA^rC^nC^n$, the meiosis and embryo sac development of new-typed *B. napus*, the appearance of intersubgenomic ($A^nA^rC^nC^c$ and $A^rA^nC^nC^n$) heterosis and the mechanism for production of intersubgenomic heterosis were described.

Key words: New-typed *B. napus*, subgenome, intersubgenomic heterosis.

INTRODUCTION

In *Brassicas*, three diploid species, that is, *Brassica rapa* (AA, 2n = 20), *Brassica nigra* (BB, 2n = 16), *Brassica oleracea* (CC, 2n = 18) and three natural spontaneous amphidiploids species of *Brassica napus* (AACC, 2n = 38), *Brassica juncea* (BBCC, 2n = 36) and *Brassica carinata* (AABB, 2n = 34) have been on existence. Lots of research revealed that the three amphidiploids species of *Brassicas* were derived from the interspecific crosses between three diploids (Morinaga, 1933, 1934; UN, 1935; Snowdon, 2007). *B. napus* was the most important oilseed *Brassica* crop in the world due to good production potential and resistances. *B. napus* accounts for about 85% of oilseed rapeseed in China (Fu, 2000). *B. napus* was one of the specie that the heterosis was widely used, the first CMS male sterile line with practical value and the first hybrid variety that was successfully cultivated in China (Fan and Stefansson, 1986; Downey and Röbbelen, 1989; Fu, 2000). Lots of research revealed that the heterosis has a relationship with the genetic diversity of the parents (Diers et al., 1996; Riaz et al., 2001; Liu et al., 2002; Qian et al., 2005). The germplasm of *B. napus* was rather narrow compared with other species of *B. rapa*, *B. oleracea* and *B. carinata* for only about 400 years of domestication (Gómez-Campo, 1999). The narrow genetic basis limiting its potential for improving seed yield, otherwise, the A genome of *B. rapa* and C genome of *B. carinata* is rather different from A and C genome of *B. napus* (Prakash and Hinata, 1980; Hoenecke and Chyi, 1991; Song et al., 1995; Li et al., 2005, 2006). Introgression of A genome of *B. rapa* and C genome of *B. carinata* into *B. napus* would explore the genetic bases of *B. napus*. Recently, some efforts have been made to widen the germplasm of *B. napus* by introgressions of genomic components from the parental species (Chen and Heneen, 1989; Seyis et al., 2003; Qian et al., 2005).

THE CONCEPT OF SUBGENOME OF *BRASSICA*

Long years of evolution and artificial selection have made the A genome and C genome in *B. napus* somewhat different from the A genome in *B. rapa* and *B. juncea*, the

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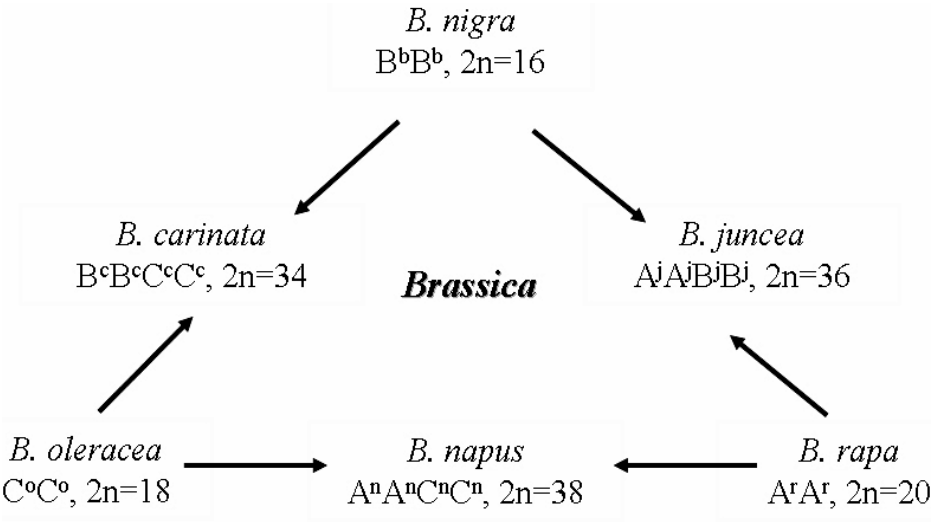

Figure 1. The letters of subgenome of *Brassicas* and their relationship.

C genome in *B. oleracea* and *B. carinata* (Inomata, 1985; Song et al., 1988). To distinguish the difference, the concept of subgenome was introduced to genus *Brassicas.* Thus, A^r, A^n and A^j was used to represent the A genome in *B. rapa*, *B. napus* and *B. juncea*, B^b, B^j and B^c for the B genome of *B. nigra* (black mustard), *B. juncea* and *B. carinata* while, C^o, C^n and C^c was used for the C genome of *B. oleracea*, *B. napus* and *B. carinata* (Qian et al., 2005; Li et al., 2004, 2006, 2007) (Figure 1). *B. napus* was the widely cultivated in the world, the limited geographical range of *B. napus* and its intensive breeding has led to a comparatively narrow genetic basis in this species. Numerous efforts have focused on exploring novel *B. napus* breeding stocks by the hybridization of *B. rapa* × *B. oleracea* or *B. napus* × *B. juncea*, *B. carinata* × *B. nigra* (Meng et al., 1998; Bing et al., 1996; Rahman, 2001; Li et al., 2004). Thereafter, most interspecific hybrids in *Brassica* could be considered as intersubgenomic hybrids, such as $A^rA^nC^n$ (*B.napus* × *B. rapa*) and $A^rB^cC^c$ (*B. carinata* × *B. rapa*).

As shown in previous studies, the positive correlations between genetic distance between parents of hybrid and mid-parent heterosis has been demonstrated for seed yield in *B. napus*. If a new-typed *B. napus*, $A^rA^rC^cC^c$ or $A^rA^rC^nC^n$ with normal meiosis can be created by interspecific hybridization and molecular selection, the heterosis would be expected in the hybrid of $A^rC^cC^nC^c$ or $A^rA^nC^nC^n$ if hybridization is carried out between the new-typed *B. napus* with genome composition $A^rA^rC^cC^c$ or $A^rA^rC^nC^n$ and the natural *B. napus* with genome composition of $A^nA^nC^nC^n$.

THE METHOD FOR PRODUCING NEW-TYPED *B. NAPUS*

Two kinds of intersubgenomic hybrids of $A^rA^nC^cC^n$ and $A^rA^nC^nC^n$ were produced by the hybridization between $A^rA^rC^cC^c$ × $A^nA^nC^nC^n$ and $A^rA^rC^nC^n$ × $A^nA^nC^nC^n$. The method for the production of new-typed *B. napus* with genome composition of $A^rA^rC^cC^c$ and $A^rA^rC^nC^n$ is as shown in Figure 2.

The procedure for producing of new-typed B. napus with genome composition of $A^rA^rC^nC^n$

Hybridization was made between *B. napus* ($A^nA^nC^nC^n$) and *B. rapa* (A^rA^r) and the trigenomic hybrids with genome composition of $A^rA^nC^n$ were obtained (Liu et al., 2002; Qian et al., 2003, 2005). The chromosome number of the trigenomic hybrids of $A^rA^nC^n$ was 29 chromosomes, which had abnormal meiosis behavior, so the chromosome of the seeds obtained by self-crossing of trigenomic hybrids might varied. The plants with 38 chromosomes were obtained by chromosome checking of all the plants that were derived from self-crossing of trigenomic hybrids of $A^rA^nC^n$. The plants with high ratio of A^r/A^n were obtained by using amplified fragment length polymorphisms (AFLP) and simple sequence repeat (SSR) molecular markers (Figure 2I). Materials with 38 chromosome and high ratio of A^r/A^n were also obtained by backcrossing between $A^rA^nC^n$ and *B. rapa* (A^rA^r). The A^r ratio of individuals in F_2 of $A^nA^nC^nC^n$ × A^rA^r and BC_1F_2 varied from 28.2 to 69.6%, with an average of 60.5%.

The procedure for producing of new-typed B. napus with genome composition of $A^rA^rC^cC^c$

In order to obtain the new-typed *B. napus* with genome composition of $A^rA^rC^cC^c$, the breeding procedure shown in Figure 2II was conducted in previous studies (Li et al., 2004, 2005, 2005, 2006, 2007). Firstly, trigenomic

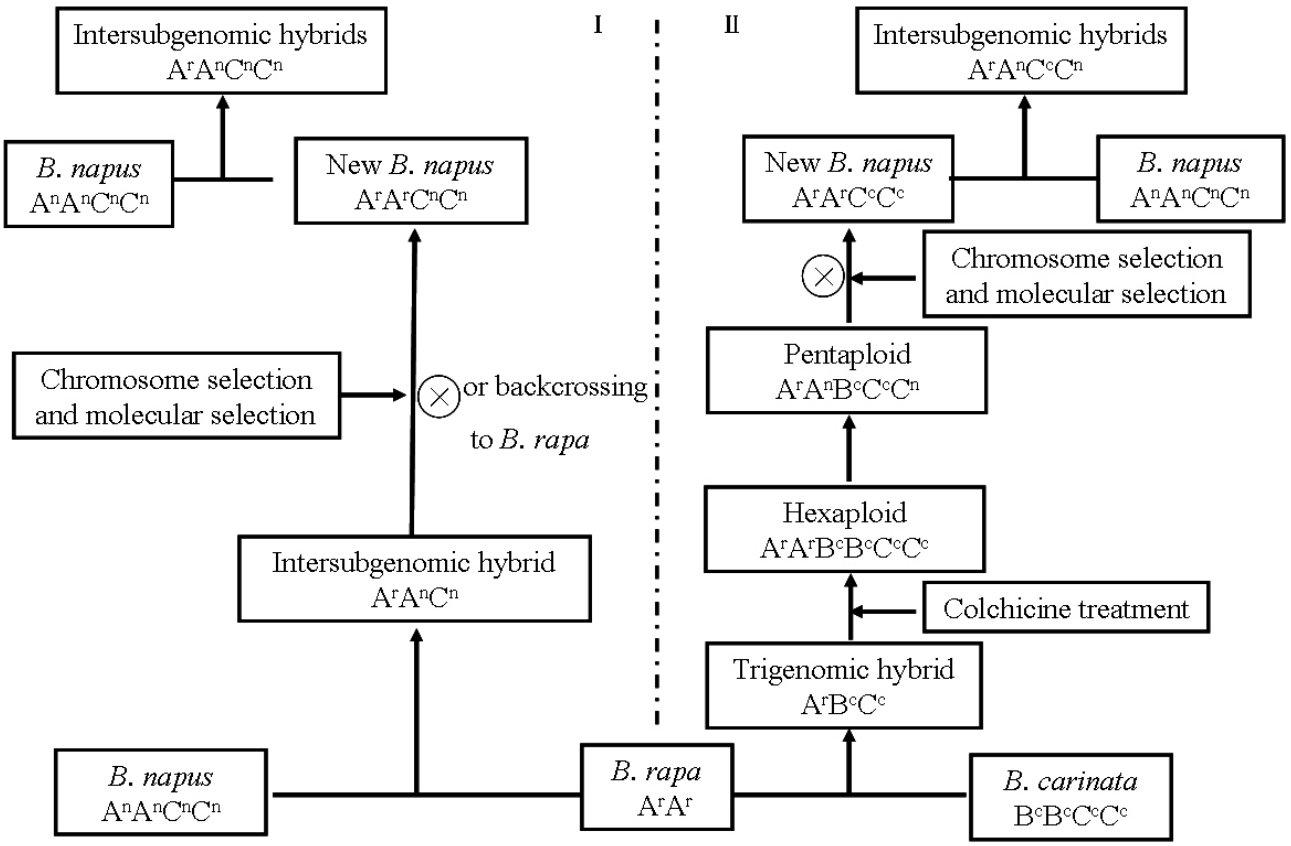

Figure 2. The procedure for producing the new-typed *B. napus*.

hybrids ($A^rB^cC^c$) were obtained by reciprocal crosses between *B. carinata* ($B^cB^cC^cC^c$) and *B. rapa* (A^rA^r), the trigenomic hybrids had the expected 27 chromosomes (Figure 3a, 3b). The trigenomic hybrids were treated with colchicine in the seeding stage and the hexaploid ($A^rA^rB^cB^cC^cC^c$, 2n = 54) were produced (Figure 3c). To generate the pentaploid hybrids with $A^rA^nB^cC^cC^n$ genomic composition, the hexaploid ($A^rA^rB^cB^cC^cC^c$) were used as female parents to pollinate the natural cultivars of *B. napus* ($A^nA^nC^nC^n$). The hybrid of hexaploid × $A^nA^nC^nC^n$ were identified to be pentaploid ($A^rA^nB^cC^cC^n$) with 46 chromosomes (Figure 3d). The $A^rA^nB^cC^cC^n$ hybrids were preferred self-crossed and the laggards appeared in profusion at anaphase I and anaphase II. GISH analysis showed that the B^c chromosomes could be lost in meiosis (Figure 3e). It indicated that the materials with 38 chromosomes without B^c chromosomes could be produced (Figure 3f).

Thousands of the plants with 38 chromosomes were performed molecular analysis. The results revealed that about 50% of the genomic components in new-typed *B. napus* were replaced by A^r and C^c subgenome of *B. rapa* and *B. carinata* (Li et al., 2007). The molecular marker analysis also showed that different material from the same combination of $B^cB^cC^cC^c$ × A^rA^r had different genetic background (Li et al., 2007). The hybridization was again made between different materials with different genetic background and the ratio of A^r and C^c was increased to 80% in new-typed *B. napus* as expected, that is, the new typed *B. napus* was almost with the genome composition of $A^rA^rC^cC^c$. The new-typed *B. napus* lines with normal meiosis behavior, normal embryo sac development process and good pollen fertility (Figure 4) indicated that those new-typed *B. napus* had balanced genetic basis (Li et al., 2006, 2007).

THE PERFORMANCE OF INTERSUBGENOMIC HETEROSIS IN *B. napus*

Hhybridization was made between $A^rA^rC^nC^n$ × $A^nA^nC^nC^n$ and $A^rA^rC^cC^c$ × $A^nA^nC^nC^n$ and the intersubgenomic hybrids of $A^rA^nC^nC^n$ and $A^rA^nC^cC^n$ were obtained, the filed experiment showed that those intersubgenomic hybrids exhibited high heterosis potential.

As for the intersubgenomic hybrids of $A^rA^nC^nC^n$, strong seed yield heterosis was observed among partial intesubgenomic hybrids. Qian et al. (2005) revealed that about 90% of 129 intesubgenomic hybrids of $A^rA^nC^nC^n$ exceeded their respective tester lines, whereas 75 and 25% of combinations surpassed Zhongyou 821 and Huaza 4 of two widely cultivated cultivars in China, respectively. The

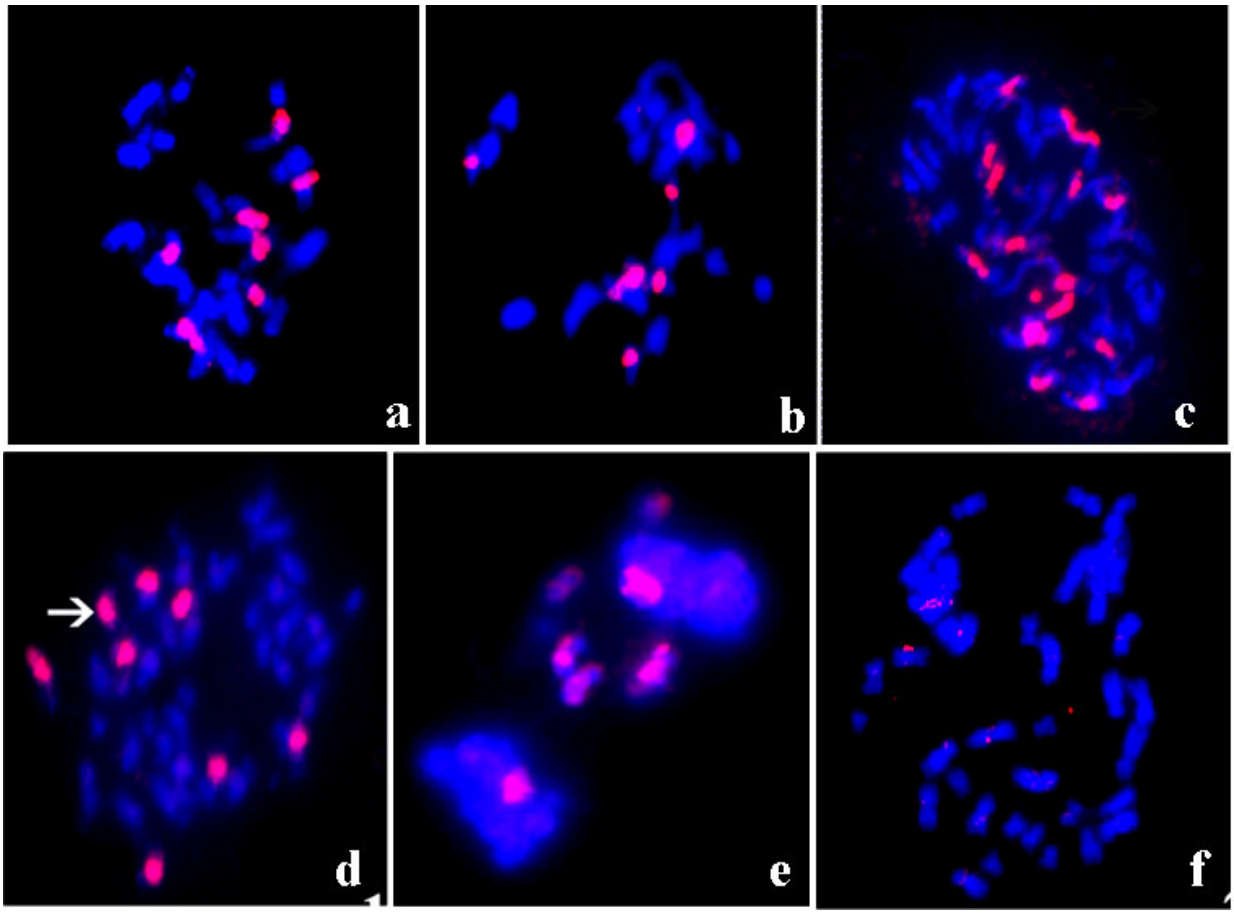

Figure 3. The chromosome identification of trigenomic hybrid, hexaploid, pentaploid and tetraploid by GISH. The DNA from the *B. nigra* (B^bB^b) was used as the probe. a and b represent the chromosome constitution from somatic and pollen mother cells of trigenomic hybrids ($A^rB^cC^c$), respectively; c and d represent the hexaploid ($A^rA^rB^cB^cC^cC^c$) and pentaploid ($A^rA^nB^cC^cC^n$), respectively; e represent the meiosis at anaphase I of pentaploid, indicating that the B^c chromosome might be lost during meiosis; f represent the plants without the B^c chromosomes. Image from Li et al. (2005 and 2004).

strong heterosis was confirmed by reevaluating 2 out of the intesubgenomic hybrids of $A^rA^nC^nC^n$ and by surveying hybrids between 20 lines of the new-typed of *B. napus* in BC_1F_5. The heterosis was from 29.17 to 95.83% and the amount of mid-parental heterosis varied from 21.73 to 86.50%, with an average of 43.15% for seed yield (Qian et al., 2005).

As for intersubgenomic hybrids of $A^rA^nC^cC^n$. Li et al. (2006) revealed that most of the intersubgenomic hybrids of $A^rA^nC^cC^n$, derived from the hybridization between new-typed *B. napus* ($A^rA^rC^cC^c$) with natural *B. napus* ($A^nA^nC^nC^n$), were grown vigorously from the seeding stage to the flowering stage (Figure 5). Seed yield of intersubgenomic hybrids was better than the control and obviously, over-standard heterosis on average were observed. Three lines of new-typed *B. napus* was selected from the F_5 generation to hybridized to five tester cultivars in order to test the potential of intersubgenomic hybrids on seed production. About 50% of intersubgenomic hybrids showed high parent heterosis (HPH) of 11.98% on the average and HPH values of two combinations was over 40%. Chen et al. (2008) revealed that the mid-parent heterosis value for seed yield exceeded 40% in their studies and the high-parent heterosis value for seed yield was over 50% in some intersubgenomic hybrids. Chen et al. (2008) also observed that eight out of nine tested hybrids showed significant higher seed yield than that of their parents.

The above mentioned phenomena suggested the strong heterosis potential of the intersubgenomic hybrids of $A^rA^nC^nC^n$ and $A^rA^nC^cC^n$.

THE POSSIBLE MECHANISM FOR PRODUCTION OF HETEROSIS IN INTERSUBGENOMIC HYBRIDS

Interaction between different genomes of *Brassicas* might be the reason for production of heterosis. Liu et al. (2002) revealed that some DNA fragments of A^r were signifi-cantly associated with biomass production in trigenomic hybrids ($A^rA^nC^n$), but those DNA fragment had no direct relationship with the hetsrosis of yield. Qian et al. (2005)

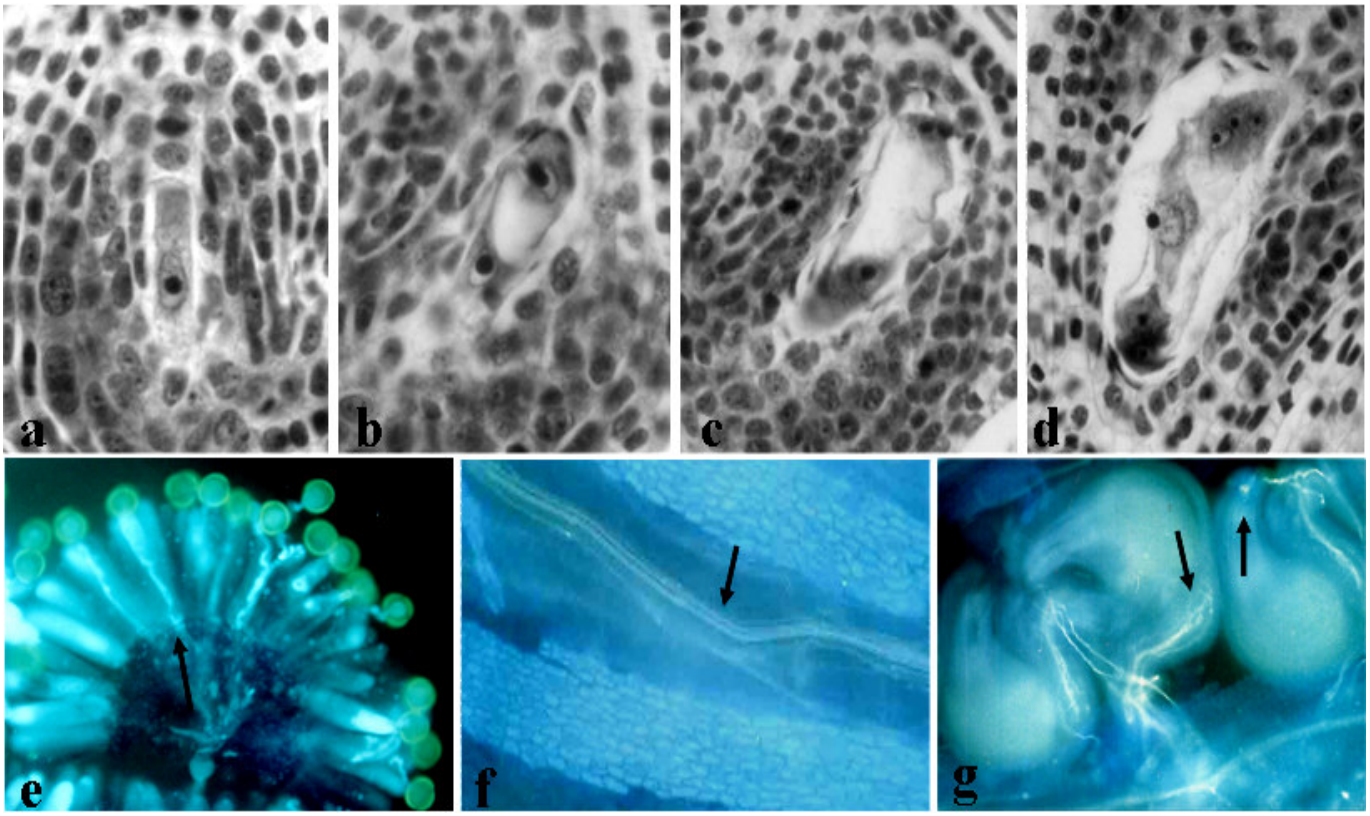

Figure 4. Observation of the embryo sac development and the pollen tube elongation in new-typed *B. napus*. a–d represents the development of embryo sac in one partial new-typed *B. napus*. a = 1-nucleate aposporous embryo sac, b = 2-nucleate aposporous embryo sac, c = 4-nucleate embryo sac, d = 8-nucleate embryo sac. e–f represents pollen germination and pollen tube elongation in one new-typed *B. napus,* e = the pollen grains germinated normally, f = the pollen tube passes through the pistillar chord. Arrow shows the pollen tube; g = pollen tube reaches the ovary and releases the contents (arrow). Image from Li et al. (2007).

detected that some DNA segments that introgressed from A^r had positive effects on seed yield of intersubgenomic hybrids of $A^rA^nC^nC^n$. Li et al. (2006) indicated that seed yield of intersubgenomic hybrids of $A^rA^nC^cC^n$ was positively correlated with the genomic proportion of A^r, C^c and A^r + C^c in the new-typed *B. napus*. The above mentioned phenomena suggested that the increasing subgenome portion of A^r and C^c in the new-typed *B. napus* might further strengthen the intersubgenomic heterosis for seed yield.

Allelic combinations present in hybrids might result in the alteration of allele expression profiles, production of novel allelic interactions, genesis of beneficial adaptations in the hybrids and give rise to heterotic phenotypes (Springer and Stupar, 2007; Chen et al., 2008). Chen et al. (2008) also found that the introgression of A^r and C^c subgenome of *B. rapa* (A^rA^r) and *B. carinata* ($B^cB^cC^cC^c$) could lead to considerable differences in the gene expression profiles of the partial new-typed *B. napus* ($A^{r/n}A^{r/n}C^{c/n}C^{c/n}$) compared with their parents. By comparing with the additive effects that appeared in rice and wheat and the dominance and overdominance effects that appeared in maize (Xiong et al., 1998; Tian and Dai, 2004; Sun et al., 2004), Chen et al. (2008) considered that dominance and overdominance effects were prominent in the intersubgenomic hybrids.

About 15.04 and 0.66% of the transcript-derived fragments (TDFs) that differentially expressed between the intersubgenomic hybrids and their parents showed significant correlation with at least one or over two of analyzed traits of yield. This indicated that allelic variation introduced from A^r/C^c subgenome may lead to many positive allelic combinations in the intersubgenomic hybrids (Chen et al., 2008). Some TDFs, such as Copia-like TDF, were activated in new-typed *B. napus.* It indicated that the DNA methylation and chromatin remodeling might be involved in the production of intersubgenomic heterosis (Hirochika et al., 2000; Zilberman et al., 2007; Chen et al., 2008). Further research revealed that 12 TDF-markers were mapped to 12 different linkage groups within the one DH population constructed by Qiu et al. (2006),.Four of these TDFs were located within the confidence intervals of eight quantitative trait loci (QTLs) for yield-related traits, which could explain the phenotype variation from 4.41 to 13.45% in the TN DH population (Figure 6). The genes or ESTs (TDFs) were also mapped within the confidence intervals of QTLs for the target traits in rice, rapeseed and maize (Mao et al., 2004; Liu et

Figure 5. Intersubgenomic hybrids growing at different developmental stages. a represent the seed setting of new-typed *B. napus*, b, c and d represent the intersubgenomic hybrids growing at seeding, flowering and maturing stages, respectively (arrow and arrow heads represent the control and intersubgenomic hybrids, respectively). Image from Li et al. (2006).

al., 2005; Huang et al., 2006; Ju et al., 2006).

OUTLOOK

The genetic analysis showed that the different new-typed *B. napus* were with richful genetic diversity compared with their parents. It indicated that introgression of A^r genome of *B. rapa* and C^c genome of *B. carinata* could significantly diversify the genetic basis of the rapeseed and play an important role in the evolution of *B. napus*. The intersubgenomic heterosis was strong in most combination of new-typed *B. napus* × natural *B. napus*. In fact, the new-typed *B. napus* was not completely the new-typed for only about 50% of A^n and C^n genome in the natural *B. napus* was replaced by A^r and C^c of *B. rapa* and *B. carinata*. The intersubgenomic heterosis could be increased by increasing A^r and C^c in the new-typed *B. napus*. The efforts for production of new-typed *B. napus* with much higher ratio of A^r and C^c are in process.

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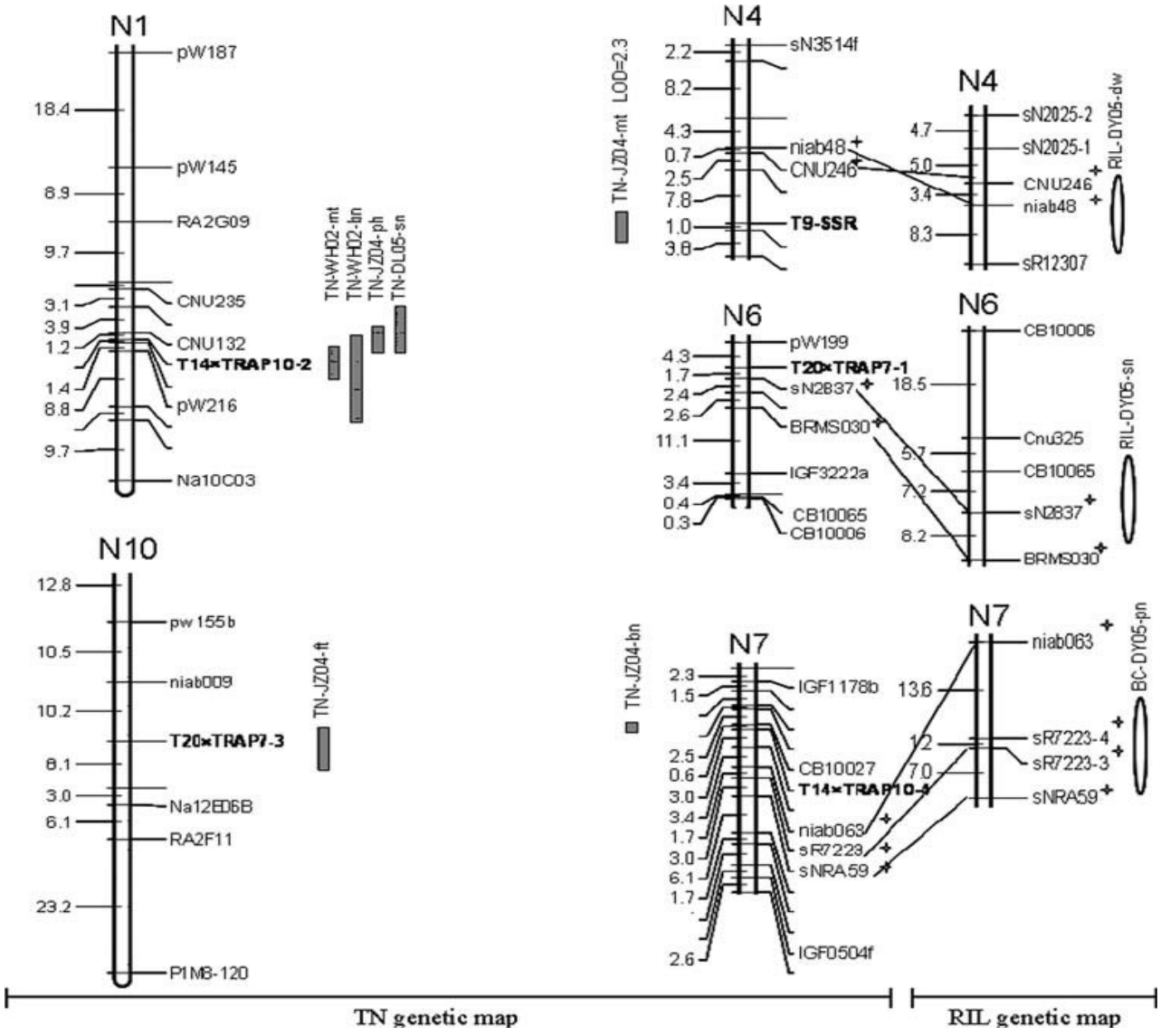

Figure 6. The TDF-markers map to yield-related QTL regions on linkage maps. Markers showed in bold are the TDF-derived markers. TN, RIL and BC represent the TN DH population, the HT RIL population and its derived RIL-BC_1 population, respectively. The bars (or ellipses) and their label indicated the QTL and their corresponding confidence intervals in different population and environments. ‘‘DL’’ signifies Dali county of Shanxi province, ‘‘DY’’ corresponds to Daye City, ‘‘JZ’’ Jingzhou City, ‘‘WH’’ Wuhan City of Hubei Province in China and the numbers following these abbreviations show the seeding year. bn represents the first branch number per plant; ft, the flowering time; ph plant height; mt mature time; sn seed number per pod. Image from Chen et al. (2008).

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