# Reconstruction of allopolyploid Brassicas through non-homologous recombination: introgression of resistance to pod shatter in *Brassica napus*

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(*Received 15 November 1989 and in revised form 12 March 1990*)

**Summary**

Pod shattering of rapeseed (*Brassica napus*) causes serious yield loss. Genetic resistance to shattering has been introgressed into *B. napus* from *B. juncea*. This followed from allosyndetic pairing between chromosomes of B and C genomes in the interspecific F1 hybrid, *B. juncea* × *B. napus* ($2n = 37$, AABC). The reconstituted *B. napus* plant showed regular meiosis with 19 bivalents and had pollen and seed fertility of 84 and 23% respectively. An approach is suggested for achieving introgression from monogenomic diploids to digenomic allopolyploids that exploits non-homologous recombination.

## 1. Introduction

An important way of introducing useful genes for crop improvement into the gene pool is by wide crossing. At the interspecific level, the chances of gene introgression improve when the species involved share some chromosome homology. Our study of interspecific hybrids of *Brassica carinata* × *B. juncea*, *B. napus* × *B. carinata* and *B. juncea* × *B. napus* has revealed considerable intergenomic homologies as expressed by bivalents in excess of the number expected from autosyndetic pairing. We have exploited these homologies in a programme to introgress gene(s) for non-dehiscence of siliquas into rapeseed *B. napus*. The incorporation of such resistance into *B. napus* is important because shattering detracts from yield. Preliminary results of this work were reported by Prakash & Chopra (1988).

## 2. Materials and methods

*B. juncea* and *B. napus* used in this study were experimental allopolyploids as follows:

*B. napus*(706), $2n = 38$, AACC, was obtained from the cross *B. campestris* ssp. *oleifera* var. brown sarson ($2n = 20$, AA) × *B. oleracea* var. *botrytis* ($2n = 18$, CC). It is a medium duration strain (155 days) and has good yield.

*B. juncea*(BN), $2n = 36$, AABB, was produced from the cross *B. campestris* ssp. *oleifera* var. brown sarson × *B. nigra* ($2n = 16$, BB). The allopolyploid has high resistance to shattering.

The F1 hybrid of the cross *B. juncea*(BN) × *B. napus*(706) was backcrossed twice to *B. napus*(706). In the BC3 generation, a plant with high resistance to shattering but otherwise like *B. napus* was obtained.

## 3. Results

The F1 hybrid *B. napus* × *B. juncea* ($2n = 37$, AABC) was a vigorous plant, morphologically intermediate between the parents. The leaves were petiolate like those of *B. juncea*, but the inflorescence and flowers resembled those of *B. napus*. At meiotic metaphase, cells with 10II + 17I were preponderant. However, 9·3% cells had the maximum pairing of 14II + 19I. The hybrid had a pollen fertility of 29%. The siliquas were non-shattering but most of them were empty. Occasional siliquas contained 1 or 2 seeds. The backcross to *B. napus* yielded 3 types of plants: (1) some resembling *B. juncea*, (2) some intermediate between *B. juncea* and *B. napus*, and (3) some resembling *B. napus*. The napus-like plants had poor fertility of pollen (43·57%) and seed (9%). Out of 117 such plants, only one was non-shattering. This plant was backcrossed with *B. napus*. The BC3 progeny consisted of 69 plants which closely resembled *B. napus*. They were cytologically examined and seven had 19II at metaphase 1 and were indistinguishable from *B. napus*. One was non-shattering. This plant matured in 153 days and had pollen fertility of 84% but the seed fertility was low (23%).

## 4. Discussion

Among cultivated Brassicas, consistent shattering of pods at maturity is common in *B. napus* (Kadkol *et al.* 1985). All the exotic strains of this species express this character in India where the harvest coincides with a hot and dry season. In experimentally produced allopolyploids also, the synthesized *napus* shattters even when the parental *B. campestris* (AA) and *B. oleracea* (CC) are non shattering. The fact that the reciprocal product also shatters (Prakash, unpublished) shows that the cytoplasm does not have a determining influence. Obviously, the expression of the shattering character is caused by interaction of genes in the A and C genomes. Additionally, the cause of shattering is evidently due to specific genomic interaction between A and C: neither the interaction of A and B (as in *B. juncea*) nor that of B with C (as in *B. carinata*) leads inevitably to shattering. In natural *B. juncea* and *B. carinata*, considerable genetic variation for pod shattering is observed; the range is from highly non-shattering to highly shattering types.

The interspecific hybrid *B. juncea* × *B. napus* (AABC) is non-shattering because of the B genome. The resistant plant identified in the progeny of the brackcross with *B. napus* has $2n = 38$, is a regular bivalent former and is indistinguishable from the parental *B. napus* morphologically and cytologically. It is reasonable to infer that this plant carries an introgressed segment of the B genome that is responsible for suppression of shattering. The introgression probably occurred in the AABC hybrid by non-homologous recombination between allosyndetically paired chromosomes of the B and C genomes. The cytology of AABC hybrids has been studied by Moninaga (1929) and Sasaoka (1930). They reported that bivalent formation in the hybrid was confined to pairing between A genome chromosomes (10II); the chromosomes of the B and C genomes remained unpaired (17I). In our study, 90·7% PMCs showed the meiotic configuration 10II + 17I while in 9·3% of cells 14II + 9I were found. The additional four bivalents can be attributed to three possibilities (1) autosyndesis in the B genome, (2) autosyndesis in the C genome, and (3) allosyndesis between B and C genomes. Mizushima (1950*a*, *b*) found up to four bivalents in BC hybrids and up to four quadrivalents in synthetic *B. carinata* (BBCC, $2n = 34$). Considering the number and frequency of bivalents in haploids of *B. nigra* (2II, 0·137; Prakash, 1973) and *B. oleracea* (2II, 0·074; Thompson, 1956), Mizushima (1980) argued that in spite of the possibility of two autosyndetic bivalents each in *B. nigra* and *B. oleracea*, the probability of four autosyndetic pairs in BC hybrid was only 0·010 (0·137 × 0·074). In BC hybrids, however, bivalents are observed with a frequency of 0·106 (Mizushima, 1950*a*). This is ten times more than the probability of four autosyndetic bivalents. Mizushima (1980) proposed that the 4 bivalents in BC hybrids were of allosyndetic origin. It is likely, therefore, that the 4 bivalents observed by us in the hybrid AABC result from allosyndetic pairing of B with C chromosomes. This conclusion is supported by the heteromorphic nature of the bivalents. Song *et al.* (1988) found distinct differences in the size of chromosomes of *B. nigra* (small) and *B. oleracea* (relatively large). Effective allosyndetic pairing appears to be a rare event because only one resistant plant was obtained. The possibility of chromosome substitution or addition can be ruled out because meiosis in the derived plant was normal.

The allopolyploid *Brassica* species lack several desirable attributes such as early flowering and maturity, reduced biomass and increased siliqua number in *B. carinata*; resistance to white rust (*Albugo candida*) in *B. juncea* and lodging resistance imparting thick stout stem, reduced apical dominance and resistance to *Phoma* and black leg (*Leptospharia maculans*) in *B. napus*. These characters are available in monogenomic species, namely *B. nigra*, *B. oleracea* and *B. campestris* Attempts at transfers of these attributes are plagued by low seed production. An alternative approach would be to exploit recombination in interspecific hybrids between digenomic species. The advantages of this approach are: (*a*) improved seed set due to buffering provided by two sets of one genome and (*b*) 'forced' pairing and exchange between homoeologous genomes. The validity of this approach is suggested not only by the introgression of shattering resistance reported in this paper but also by other reconstituted allopolyploids that we have been able to produce, the details of which will be published separately.

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