Theor Appl Genet (1995) 90: 665–670

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Analysis of self-incompatibility interactions in 30 resynthesized *Brassica napus* lines. I. Fluorescence microscopic studies

Received: 5 August 1994 / Accepted: 11 November 1994

Abstract Thirty *Brassica napus* lines have been developed through interspecific hybridization of *B. oleracea* and *B. campestris* lines with defined S-allele constitutions. These lines, which represent 29 different S-allele combinations, were tested in a diallel of test-pollinations to determine the activity of the introgressed S-alleles and intergenomic dominance relationships. Some consistent trends were observed: *B. oleracea* S-alleles high in the dominance series (e.g. S_8, S_{14}, S_{29}) were always active in the resynthesized *B. napus* lines, whereas recessive S-alleles (S_2, S_{15}) lost their activity in some test combinations. The *B. campestris* S-alleles were active in most cases, although 2 alleles were partially inactivated by the recessive *B. oleracea* allele S_{15}.

Key words *Brassica napus* · Self-incompatibility
S-allele · Interspecific hybridization

Introduction

Brassica napus (2n=38) is a natural allotetraploid derived from the diploid species *Brassica oleracea* (2n=18) and *Brassica campestris* (2n=20). Whereas the diploid progenitor species each possess an effective self-incompatibility (SI) system, their natural amphidiploid *B. napus* is self-compatible. Self-incompatible plants are a rare event and could be detected in old cultivars of swedes and oilseed rape (Olsson 1960). This is probably caused by the introgression of S-alleles from *B. oleracea* or *B. campestris* in the pedigree of these cultivars. Synthetic *B. napus*, obtained through interspecific hybridization, is self-incompatible (Olsson 1953). S-loci of both parental species can contribute to this reaction (Hodgkin 1986).

The SI system of *Brassica* is sporophytically controlled by a single, multiallelic S-locus. More than 50 alleles have been reported in *B. oleracea*, and complex interactions are present between S-alleles. Dominance relationships are not fully linear, and the activity of a specific allele can be different in the pollen or stigma (Thompson and Taylor 1966; Ockendon 1975; Wallace 1979; Visser et al. 1982). Due to competitive interaction plants heterozygous for recessive S-alleles can become self-compatible (Thompson 1972). Self-incompatibility interaction can also be influenced by genetic background or environmental factors, especially in the case of weak S-alleles (Ockendon 1975).

S-Allele interaction in *B. campestris* has been less well-investigated, but corresponding phenomena can be found in this species (Nou et al. 1993). Self-compatible genotypes (e.g. var 'sarson') are also present in *B. campestris*, probably due to the presence of recessive modifier genes (Hinata et al. 1983).

SI is widely used in the production of F_1 hybrids in vegetable forms of *B. oleracea* and *B. campestris*. It may also be used as an outbreeding system in hybrid or synthetic cultivars of field crops like *B. napus*. Important prerequisites are the introgression of S-alleles into the genome of *B. napus* and the analysis of their interactions. Gowers (1989) and Gemmell et al. (1989) analysed self-incompatible lines of swedes and oilseed rape and suggested that interspecific interactions had occurred between S-loci. Resynthesized *B. napus* with a known S-allele constitution would be a more promising material to determine the nature of interspecific S-allele interactions. So far investigations with such a material have been based on only a small number of synthetic rapeseed forms (Hodgkin 1986; Chen et al. 1988). We therefore produced 30 different synthetic *B. napus* lines containing weak to strong (recessive to dominant) S-alleles from both parental species. This set enables the analysis of intra- and interspecific S-allele interactions by means of fluorescence microscopy. Correlation of these interactions with glycoprotein patterns of the stigma will be discussed in a separate paper.

Communicated by H. F. Linskens

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Table 1 *Brassica oleracea* and *B. campestris* material used for the resynthesis of *B. napus*

Code	Line number	Taxonomy	S-Allele	Classification[a]
a. *B. oleracea*				
B.ol. 1	I 85-241		S_8	Dominant
B.ol. 4	W S 2	subvar *laciniata* L.×var *gemmifera* DC.	S_2	Recessive
B.ol. 5	W S 4	subvar *medullosa* Thell.	S_4	Less dominant
B.ol. 7	W S 14	subvar *medullosa* Thell.	S_{14}	Dominant
B.ol. 8	W S 15	subvar *medullosa* Thell.×var *gemmifera* DC.	S_{15}	Recessive
B.ol. 10	W S 32	var *fructicosa* Metz.	S_{32}	Dominant
B.ol. 11	W S 45	var *gemmifera* DC.	S_{45}	Dominant
B.ol. 13	I 85-349	ssp *alboglabra*	S_2	Recessive
B.ol. 14	I 85-362	ssp *alboglabra*	S_{29}	Dominant
b. *B. campestris*				
B. camp. 2	I 85-326		S_a	
B. camp. 3	I 85-382	ssp *rapifera*	S_b	
B. camp. 4	I SD-87-320	ssp *chinensis*	S_c	
B. camp. 5		ssp *nipposinica*	S_d	
B. camp. 6	Tokyo-King	ssp *pekinensis*	$S_{e/f}$	
B. camp. 7	Yellow Sarson	ssp *trilocularis*	–	Self-compatible

[a] According to Visser et al. (1982) and Thompson and Taylor (1966)

Materials and methods

Seeds of *B. oleracea* and *B. campestris* were kindly provided by Dr. D. Ockendon (Wellesbourne) and Dr. T. Hodgkin (Invergowrie). Nine *B. oleracea* lines and 4 *B. campestris* lines were homozygous for different S-alleles. The commercial F_1 hybrid chinese cabbage cv 'Tokyo King' (S-allele heterozygous) and an accession of the self-compatible 'Yellow Sarson' (S-allele status unknown) completed the *B. campestris* set (Table 1).

B. napus was resynthesized by interspecific hybridization of these *B. oleracea* and *B. campestris* lines followed by in-ovule embryo culture (Plümper 1991). The amphihaploid hybrids were treated with colchicine and amphidiploid shoots were bud-self-pollinated. The C_1 and C_2 generations of these resynthesized *B. napus* lines were used in subsequent investigations. The designation of the *B. napus* lines consists of the *B. oleracea* code followed by the *B. campestris* code (e.g. *B. napus* line RS 1/2 is derived from the cross *B.ol.* 1×*B. camp.* 2).

Thirty resynthesized lines of *Brassica napus* representing 29 different S-allele combinations were analysed for their incompatibility behaviour. A complete diallel set of test-pollinations between *B. napus* lines with one S-allele in common was carried out. Self-pollinations and cross-pollinations with the parental *B. oleracea*- and *B. campestris*-lines were also performed. The experiments were carried out in an insect-proof greenhouse. Self- and cross-pollinations were done on a minimum of six newly opened and emasculated flowers. If the results were not sufficiently clear, additional pollinations were made.

Pistils were removed 24 h after pollination and then fixed and stained with aniline blue according to Naether (1971). Pollen germination and pollen-tube growth were analysed using UV-light fluorescence. Some pistils were left on the plant until maturity in order to correlate the SI response with seed set.

Results

All interspecific hybrids were vigorous plants exhibiting a pollen fertility comparable to that of natural *B. napus*. Only line RS 5/6 showed a bad pollen quality. Bud self-pollination resulted in seed set for every genotype, indicating that the time course of the SI response is regulated as in the parental lines.

Three types of stigma reactions could be differentiated

Incompatible reaction

Pollen tubes were inhibited just after pollen germination and were not able to penetrate the stigma surface (Fig. 1a). In some cases, especially with *B. oleracea* as a pollen parent, pollen germination was completely inhibited. Nevertheless, pollen of the same plant germinated well on the stigma of a compatible control plant. The incompatible reaction was correlated with no seed set.

Compatible reaction

A large number of pollen grains germinated, and the pollen tubes penetrated the stigma surface (Fig. 1b). Pollen-tube growth was strictly orientated down the style, reaching the ovules. This reaction resulted in a normal seed set.

Partial compatible reaction

As well as a large number of well-grown pollen tubes, inhibited pollen tubes were also found (Fig. 1c). Pollen tubes which penetrated the stigma surface did not grow strictly down the style. This type of reaction was declared as being partial compatible and resulted in a normal seed set.

After self-pollination of open flowers all 27 *B. napus* lines originating from 2 self-incompatible ancestors showed self-incompatibility. Only *B. napus* with the genome of the self-compatible *B. campestris* var 'Yellow Sarson' exhibited compatible (RS 10/7) or partial compatible reactions (RS 8/7, RS 11/7, Fig. 2).

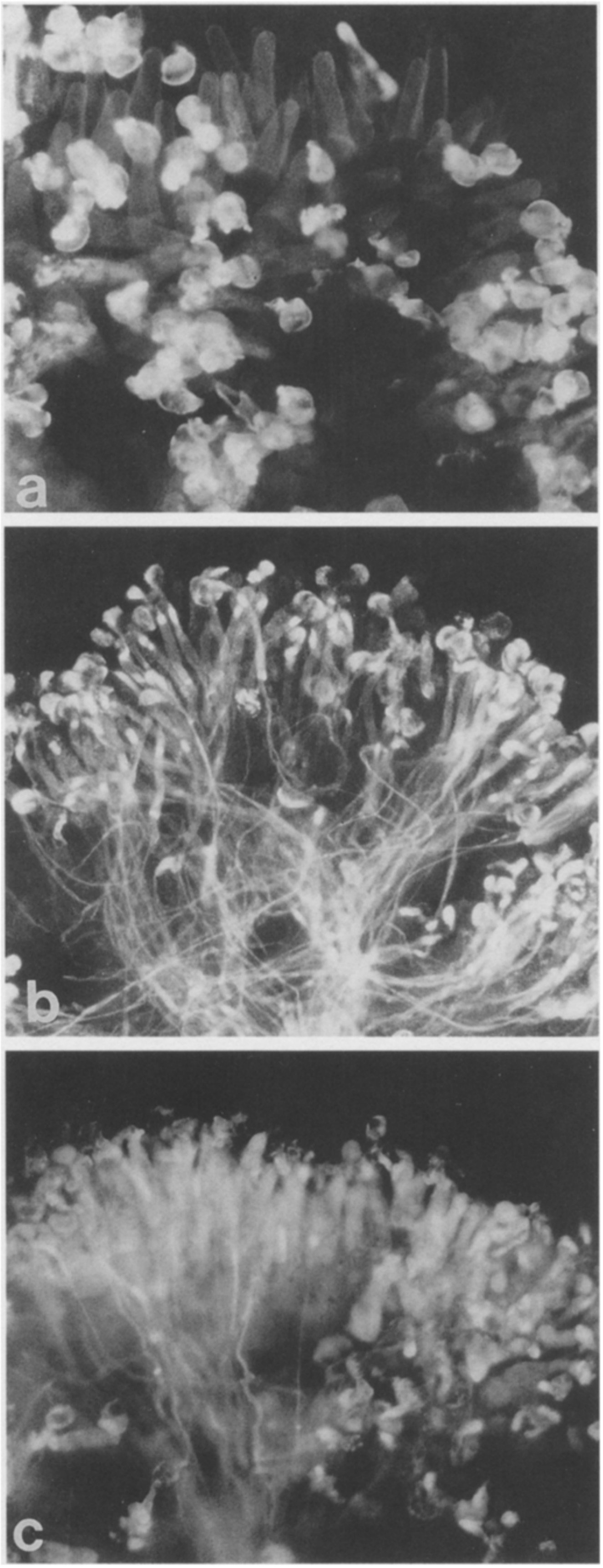

Fig. 1a–c Fluorescence micrographs showing the different types of stigma reactions. **a** Incompatible reaction, **b** compatible reaction, **c** partial compatible reaction

Identification of *B. campestris* alleles S_e and S_f in resynthesized *B. napus* lines

The heterozygous F_1 hybrid cultivar ‘Tokyo King’ produces two genetically different gametes (S_e, S_f). Only one allele is present in the amphihaploid hybrids. After colchicine treatment the amphidiploids were homozygous for this allele. In test-pollinations with *B. campestris* lines homozygous for S_e and S_f, the S-allele constitution of all lines could be identified (Fig. 3). Only Line RS 5/6 showed unclear reactions due to its bad pollen quality.

Activity of *B. oleracea* S-alleles in the *B. napus* genome

The *B. napus* lines with a dominant S-allele from *B. oleracea* (*B.ol.* 1, 7, 10, 11) demonstrated incompatible reactions upon reciprocal cross-pollinations with their *B. oleracea* parent and with *B. napus* lines carrying an identical S-allele (Fig. 2). The exceptions are RS 10/7 and RS 11/7, which derived from crosses with the self-compatible *B. campestris* var ‘Yellow Sarson’.

B. napus lines with weak *B. oleracea* S-alleles (low in the dominance range) (S_2, S_4, S_{15}) showed incompatible as well as compatible and partial compatible reactions. In nearly all cases the pollen of the resynthesized *B. napus* was compatible with the stigmas of the *B. oleracea* parent, whereas the reciprocal test resulted in an incompatible reaction. Cross pollinations between *B. napus* lines with 1 recessive S-allele in common resulted in incompatible as well as compatible and partial compatible reactions.

In reciprocal pollinations with the *B. oleracea* parent line, RS 8/7 (combining the recessive *B. oleracea*-allele S_{15} with the compatible genome of *B. campestris* ‘Yellow Sarson’) showed compatible reactions. RS 10/7 and RS 11/7, which carry *B. oleracea* S-alleles that are higher in the dominance range, were incompatible with the pollen and stigma of the *B. oleracea* parent. *B. napus* line RS 8/7 was compatible in many cross combinations even if compared to RS 10/7 and RS 11/7 with the same *B. campestris* parent.

Activity of the *B. campestris* S-alleles in the *B. napus* genome

Nearly all of the resynthesized *B. napus* lines derived from self-incompatible *B. campestris* genotypes were incompatible in reciprocal test pollinations with their *B. campestris* parent (Fig. 4). Only in RS 13/2 and RS 8/4 did both reciprocal tests result in compatible or partial compatible reactions. Incompatible reactions predominated in cross-pollinations between *B. napus* lines with one S-allele in common. The activity of the alleles S_c and S_d (*B. camp.* 4 and *B. camp.* 5) was reduced only when in combination with *B. oleracea* allele S_{15} (*B. ol.* 8).

The 3 *B. napus* lines with the genome of self-compatible ‘Yellow Sarson’ (RS 8/7, RS 10/7, RS 11/7) reacted compatibly in reciprocal test-pollinations with this *B. cam-*

Fig. 2 Activity of the *B. oleracea* S-alleles in resynthesized *B. napus*

a) S_8 (B. ol. 1)

♀ ♂	RS 1/2	RS 1/4	B. ol. 1
RS 1/2	SI	SI	SI
RS 1/4	SI	SI	SI
B. ol. 1	SI	SI	SI

b) S_2 (B. ol. 4)

♀ ♂	RS 4/2	RS 4/5	RS 4/6	B. ol. 4
RS 4/2	SI	SI	SI	comp
RS 4/5	SI	SI	SI	SI
RS 4/6	*(comp)*	*(comp)*	SI	SI
B. ol. 4	comp	comp	comp	SI

c) S_4 (B. ol. 5)

♀ ♂	RS 5/2	RS 5/4	RS 5/6	B. ol. 5
RS 5/2	SI	SI	SI	SI
RS 5/4	SI	SI	SI	SI
RS 5/6	comp	SI	SI	SI
B. ol. 5	*(comp)*	comp	comp	SI

d) S_{14} (B. ol. 7)

♀ ♂	RS 7/2	RS 7/4	RS 7/5	RS 7/6	B. ol. 7
RS 7/2	SI	SI	SI	SI	SI
RS 7/4	SI	SI	SI	SI	SI
RS 7/5	SI	SI	SI	SI	SI
RS 7/6	SI	SI	SI	SI	SI
B. ol. 7	SI	SI	SI	SI	SI

e) S_{15} (B. ol. 8)

♀ ♂	RS 8/2	RS 8/4	RS 8/5	RS 8/6	RS 8/7	B. ol. 8
RS 8/2	SI	comp	comp	comp	comp	comp
RS 8/4	comp	SI	SI	comp	SI	SI
RS 8/5	comp	SI	SI	comp	comp	SI
RS 8/6	*(comp)*	SI	*(comp)*	SI	SI	comp
RS 8/7	comp	*(comp)*	comp	comp	*(comp)*	comp
B. ol. 8	comp	comp	comp	comp	comp	SI

SI = (self-) incompatible
(comp) = partial compatible
comp = compatible

f) S_{32} (B. ol. 10)

♀ ♂	RS 10/2	RS 10/4	RS 10/6	RS 10/7	B. ol. 10
RS 10/2	SI	SI	SI	comp	SI
RS 10/4	SI	SI	SI	SI	SI
RS 10/6	SI	SI	SI	*(comp)*	SI
RS 10/7	comp	comp	comp	comp	comp
B. ol. 10	SI	SI	SI	SI	SI

g) S_{45} (B. ol. 11)

♀ ♂	RS 11/5	RS 11/6	RS 11/7	B. ol. 11
RS 11/5	SI	SI	SI	SI
RS 11/6	SI	SI	SI	SI
RS 11/7	(comp)	SI	(comp)	SI
B. ol. 11	SI	SI	SI	SI

h) S_2 (B. ol. 13)

♀ ♂	RS 13/2	RS 13/4	RS 13/6	B. ol. 13
RS 13/2	SI	SI	SI	SI
RS 13/4	SI	SI	SI	SI
RS 13/6	*(comp)*	*(comp)*	SI	*(comp)*
B. ol. 13	comp	comp	comp	SI

i) S_{29} (B. ol. 14)

♀ ♂	RS 14/2	RS 14/3	RS 14/6	B. ol. 14
RS 14/2	SI	SI	SI	SI
RS 14/3	SI	SI	SI	SI
RS 14/6	SI	SI	SI	SI
B. ol. 14	SI	SI	SI	SI

pestris genotype. Test-pollinations between these *B. napus* lines were also compatible.

Discussion

Unlike natural *B. napus* all rapeseed lines resynthesized from self-incompatible genotypes of *B. campestris* and *B. oleracea* are self-incompatible. In general, both parental loci can contribute to the incompatibility reaction. In our investigation interspecific interactions between the S-loci occurred, which is in agreement with the results of Hodgkin (1986), who studied only one genotype. Our results show that the diversity of interspecific interactions is no less complex than that of the well-known intraspecific allele interactions. This is not surprising as alleles of the *B. campestris* and *B. oleracea* S-loci show a sequence homology of up to 92% (Dwyer et al. 1991).

The interaction phenotype was mainly influenced by the dominance rank of the S-alleles. Dominant S-alleles of both loci were always codominant in the pollen as well as in the stigma. Partial compatible or compatible reactions were restricted to *B. napus* genotypes containing recessive

Fig. 3 Identification of the *B. campestris* alleles S_e and S_f in resynthesized *B. napus* lines with F_1 cv 'Tokyo King' (*B. campestris* 6) as *B. campestris* parent

♀ ♂	RS 4/6	RS 5/6	RS 7/6	RS 8/6	RS 10/6	RS 11/6	RS 13/6	RS 14/6	B.c.6 Se	B.c.6 Sf
RS 4/6	SI	(comp)	comp	comp	comp	SI	comp	comp	SI	comp
RS 5/6	comp	SI	comp	comp	comp	comp	comp	(comp)	(comp)	comp
RS 7/6	comp	SI	SI	SI	SI	comp	SI	SI	comp	SI
RS 8/6	comp	SI	SI	SI	SI	comp	SI	SI	comp	SI
RS 10/6	comp	-	SI	SI	SI	comp	SI	SI	comp	SI
RS 11/6	SI	-	comp	comp	comp	SI	comp	comp	SI	comp
RS 13/6	comp	(comp)	SI	SI	SI	comp	SI	SI	comp	SI
RS 14/6	comp	-	SI	SI	SI	comp	SI	SI	comp	SI
B.c.6 Se	SI	-	comp	comp	comp	SI	comp	comp	SI	comp
B.c.6 Sf	comp	-	SI	SI	SI	comp	SI	SI	comp	SI

RS 4/6	RS 5/6	RS 7/6	RS 8/6	RS 10/6	RS 11/6	RS 13/6	RS 14/6
Se	Sf ?	Sf	Sf	Sf	Se	Sf	Sf

Fig. 4 Activity of the *B. campestris* S-alleles in resynthesized *B. napus*

a) S_a (B. camp. 2)

♀ ♂	RS 1/2	RS 4/2	RS 5/2	RS 7/2	RS 8/2	RS 10/2	RS 13/2	RS 14/2	B.c. 2
RS 1/2	SI	SI	SI	SI	SI	SI	comp	SI	(comp)
RS 4/2	SI	SI	comp	SI	SI	SI	(comp)	SI	SI
RS 5/2	comp	comp	SI	SI	SI	comp	SI	SI	SI
RS 7/2	SI	SI	SI	SI	SI	SI	SI	SI	SI
RS 8/2	SI	SI	SI	SI	SI	SI	(comp)	comp	SI
RS 10/2	SI	SI	SI	SI	SI	SI	SI	SI	SI
RS 13/2	SI	SI	SI	SI	SI	SI	SI	(comp)	comp
RS 14/2	comp	SI	SI	SI	SI	SI	SI	SI	SI
B.c. 2	SI	SI	SI	SI	SI	SI	(comp)	SI	SI

b) S_b (B. camp. 3)

♀ ♂	RS 14/3	B. c. 3
RS 14/3	SI	SI
B. c. 3	SI	SI

SI = (self-) incompatible
(comp) = partial compatible
comp = compatible

c) S_c (B. camp. 4)

♀ ♂	RS 1/4	RS 5/4	RS 7/4	RS 8/4	RS 13/4	B. c. 4
RS 1/4	SI	SI	SI	SI	SI	SI
RS 5/4	SI	SI	SI	SI	SI	SI
RS 7/4	SI	SI	SI	comp	SI	SI
RS 8/4	(comp)	comp	comp	SI	(comp)	(comp)
RS 13/4	SI	SI	SI	SI	SI	SI
B. c. 4	SI	SI	SI	comp	SI	SI

d) S_d (B. camp. 5)

♀ ♂	RS 4/5	RS 7/5	RS 8/5	RS 11/5	B. c. 5
RS 4/5	SI	SI	SI	SI	SI
RS 7/5	SI	SI	SI	SI	SI
RS 8/5	SI	(comp)	SI	SI	comp
RS 11/5	SI	SI	(comp)	SI	SI
B. c. 5	SI	SI	SI	SI	SI

S-alleles and, in contrast to what takes place with dominant S-alleles, reciprocal differences occurred. Partial compatibility can also be found in early stages of stigma development of self-incompatible *Brassica* species. Self-pollination at this stage circumvents the SI-reaction and is normally used to produce self seed. The partial compatible reactions on stigmas of open flowers reported here can be explained as a weakened SI-reaction due to competitive interaction between recessive alleles of 2 different loci. Thompson and Taylor (1966) and Thompson (1972) found similar effects in heterozygous plants of *B. oleracea*.

In our study all plants were homozygous at both S-loci. In heterozygous plants S-allele interaction is expected to be more complex. Preliminary results with heterozygous *B. napus* plants indicate that dominant S-alleles are also expressed (Beschorner 1993).

The self-compatibility mechanism has been less well-investigated than SI. In some cases self-compatibility results from the action of suppressor or modifier genes that are unlinked to the S-locus. They show recessive or incomplete dominant inheritance. The self-compatibility of *B. campestris* var 'Yellow Sarson' is caused by a recessive modifier gene '*m*' (Hinata et al. 1983). The weakening of self-incompatibility in resynthesized *B. napus* lines with the genome of *B. campestris* var 'Yellow Sarson' is probably caused by this modifier gene having an interspecific epistatic effect on the activity of *B. oleracea* S-alleles. Surprisingly, the results with *B. oleracea* S-allele S_{15} resemble this modifying effect. Although S_{15} is classified as recessive, it was able to inactivate *B. campestris* S-alleles in many cases. In combination with recessive S-alleles, S_{15} can also lead to self-compatibility in heterozygous *B. oleracea* plants (Thompson 1972).

Results of Chen et al. (1988) showed that resynthesized *B. napus* plants were self-incompatible when derived from crosses between self-compatible *B. oleracea* ssp. *alboglabra* and self-incompatible *B. campestris*. In this case a mutation of the S-gene of *B. oleracea* ssp. *alboglabra* was presumed. Studies on the genetics of compatibility in this genotype and its interspecific interactions in resynthesized *B. napus* are in progress at our institute.

Self-compatibility in natural *B. napus* can not be explained through the action of modifier genes because hybrids between compatible and resynthesized incompatible genotypes are always SI. Goring et al. (1993) identified a 1-bp deletion in the S-receptor kinase-domain of a self-compatible *B. oleracea* line that resulted in a non-functional enzyme. The same mutation has been found in several *B. napus* cultivars and located on their *B. oleracea* genome. The fate of the *B. campestris* S-locus in natural *B. napus* still remains unclear.

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