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Towards a Canola Quality Resynthesized Rapeseed (*Brassica napus* L.): *B. oleracea* Genotypes as a Basic Resource

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ABSTRACT

Brassica oleracea is a well known species of the *Brassica* genus. With the other *Brassica* species, namely *B. rapa*, *B. nigra*, *B. juncea*, *B. carinata* and *B. napus*, it forms the so called U triangle. Genotypes derived from several locally distributed members of the genus *Brassica* have become one of the most important vegetable oil resources worldwide because of substantial progress in breeding and cultivation practices. Efforts to develop low erucic character in several *Brassica* species led to the discovery of low-erucic acid mutants in the species *Brassica rapa* (AA), *B. napus* (AACC) and *Brassica juncea* (AABB). In amphidiploid *B. carinata* (BBCC) low erucic acid mutants were not known up to the 1990's. Using different strategies low erucic acid forms were successfully selected in the subsequent years. Up to now low erucic acid forms of *B. nigra* (BB) have not been cited in the literature. *B. oleracea* genotypes displaying low erucic acid were discovered at the end of the 1990's. These genotypes were used to develop 0-quality resynthesized rapeseed forms via interspecific crosses with different quality *B. rapa* forms. The diploid cabbages, one of the progenitors of rapeseed (*B. napus*), are highly useful as basic breeding material of *Brassica napus*. With this respect, the low erucic acid cabbage genotypes with their potential use in *Brassica* breeding and further use will be discussed in this review.

Keywords: *Brassica*, rapeseed breeding, interspecific hybridization
Abbreviations: RS-lines, resynthesized rapeseed lines

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INTRODUCTION

The genus *Brassica* is economically the most important genus in the Brassicaceae family (syn. Cruciferae). Several *Brassica* species/types can be classified as significant oilseed crops, vegetables and forage crops. *Brassica* species, such as mustard, are used in the production of condiments. Further they are widely used in the national cuisines of many countries and they are recognized as a valuable source of dietary fiber. Besides a low content of fats their vegetable forms contain vitamins, minerals and fiber also a large number of novel phytochemicals, some of which provide protection against carcinogenesis (Steinmetz and Potter 1996).

On the global level, *Brassica* crops are economically the most important oilseeds. The oilseed Brassicas are found within *Brassica juncea*, *Brassica carinata*, *Brassica rapa* (syn. *Brassica campestris*) and *Brassica napus*. Low glucosinolate and low erucic acid varieties are increasingly commonly referred as canola, a more pleasant-sounding name. Canola, which is most often *B. napus*, has received much attention worldwide and may soon become the most popular oilseed crop (Snowdon *et al.* 2007).

Presently, canola-quality *B. rapa* and *B. juncea* varieties are also available. Canola oil is widely used in cooking since it is very low in saturated fat, making it appealing to healthconscious consumers.

While most research in *Brassica* crops has been performed on oilseed and vegetable biotypes, rapid-cycling *Brassica* biotypes of various species have startet to gain attention in recent years. In addition to Brassica crops and rapid-cycling models, the genus contains several weedy species, of which *B. rapa* is the most important (Cardoza and Stewart 2004).

Cytogenetic relationships between *Brassica* species

The chromosomal relationships among the A, B and C genomes of the diploid *Brassica rapa* (genome AA, 2n = 20; turnip rape, turnip, Chinese cabbage), *B. nigra* (genome BB, 2n = 16; black mustard) and *B. oleracea* (genome CC,

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Invited Mini-Review

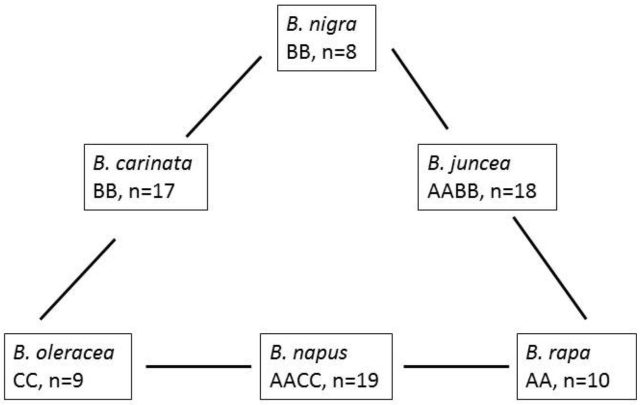

Fig. 1 The *Brassica* triangle of species, as described by U (1935), representing the A, B and C genomes and their respective amphidiploids that arose from spontaneous chromosome doubling via meiotic nondisjunction after interspecific hybridizations in regions of overlapping geographical distribution of the respective diploid progenitors.

2n = 18; cabbage, cauliflower, broccoli, kale, kohlrabi, brussel sprouts) and their natural spontaneous amphidiploids *B. carinata* (genome AABB, 2n = 34; Abyssinian or Ethiopian mustard), *B. napus* (genome AACC, 2n = 38; oilseed rape, swede) and *B. juncea* (genome BBCC, 2n = 36; Indian or brown mustard) were elucidated through interspecific crosses and meiotic analyses made by the Asian cytogeneticists Morinaga and U in the early 20th century (Morinaga 1933, 1934; U 1935). Because the *Brassica* amphidiploid species can be generated synthetically with the help of embryo rescue techniques, this complex of the three diploid species and their polyploids (**Fig. 1**) is today one of the most useful model systems for investigations of polyploidy in crop plants (e.g. Song *et al.* 1995; Lukens *et al.* 2006). Colchicine treatment can also be used to artificially synthesize autotetraploid *Brassicas*, which can potentially be used to compare the corresponding effects of gene dosage, autoploidy, alloploidy and amphiploidy on gene regulation and expression (Snowdon 2009).

History of canola quality

B. napus was cultivated by ancient civilisations in Asia and the Mediterranean. Its use has been recorded as early as 2000 BC in India and has been grown in Europe since the 13th century, primarily for its use as lamp oil (Colton and Sykes 1992). *B. napus* was first grown commercially for use as a lubricant on war ships. Traditionally, *B. napus* is unsuitable for human food or animal feed due to the presence of two naturally occurring toxicants, erucic acid and glucosinolates.

Early rapeseed cultivars had high levels of erucic acid in the oil and glucosinolates in the meal. The presence of these components in rapeseeds caused serious health concerns. The high levels of erucic acid are responsible for producing fatty deposits in the heart, skeletal muscles, and adrenals of rodents as well as for impairing their growth. Plant breeding programs initiated in Canada resulted in the identification of Liho, a rapeseed line containing low levels of erucic acid in 1959. A program of backcrossing and selection was conducted to transfer the low erucic acid trait into agronomically adapted cultivars (Przybylski *et al.* 2005). This led to the first low erucic acid cultivar of *B. napus*, 'Oro', in 1968 and the first low erucic acid *B. rapa* cultivar, 'Span', in 1971. Because of the health concerns related to high levels of erucic acid, over 95% of the rapeseed grown in Canada in 1974 were low erucic acid varieties. Glucosinolates were also considered detrimental in rapeseed meal fed to poultry, swine, and ruminants. The hydrolyzed products of glucosinolates, namely, isothiocyanates and other sulphur-containing compounds, were shown to interfere with the uptake of iodine by the thyroid gland, contribute to liver disease, and reduce growth and weight gain in animals. Consequently, plant breeders realized that if rapeseed meal was to be used as animal feed, the glucosinolate content should be reduced. A Polish line with a low-glucosinolate trait, Bronowski, was identified by Dr. Krzymanski in the late 1950s. Breeding efforts to introduce this trait into low erucic acid lines made by Dr. Baldur Stefansson at the University of Manitoba resulted in the release of the world's first low erucic acid, low glucosinolate cultivar of *B. napus*, often called the double-zero rapeseed. This was followed in 1977 by the release of the first low erucic acid, low glucosinolate cultivar of *B. rapa*, Candle, by Dr. Keith Downey of the National Research Council of Canada in Saskatoon (Przybylski *et al.* 2005).

Detection of *B. oleracea* genotypes displaying edible oil quality

Due to substantial progress in breeding and cultivation practice in rapeseed and mustards-derived from several locally distributed members of the genus *Brassica*-have become one of the most important source of vegetable oil worldwide. Especially in several European countries with cool-temperate climates oilseed rape (*B. napus*) with 'double-low' seed quality (canola) dominates field crop production (Seyis *et al.* 2004). Regarding this quality characters, low-erucic acid mutants were found in *B. rapa* (AA) (Downey 1964), *B. napus* (AACC) (Stefansson *et al.* 1961, 1964) and *B. juncea* (AABB) (Kirk and Oram 1978).

First low erucic acid mutants of amphidiploid *B. Carinata* (BBCC) were developed in the 1990's. Different strategies, such as the selection of transgressive segregants in the crossing progeny of diverse *B. carinata* accessions (Alonso *et al.* 1991), induced mutations and interspecific crosses with low-erucic *B. napus* and *B. juncea* (Getinet 1987; Fernández-Escobar *et al.* 1988) were used to reduce the erucic acid content. Low erucic acid forms have been successfully selected using the first and last mentioned method (Alonso 1991; Getinet *et al.* 1994). Low-erucic acid forms of the monogenomic species *B. nigra* have not been detected yet.

B. oleracea genotypes displaying zero erucic acid character were first mentioned by Lühs *et al.* (2000). Two of these genotypes, namely Ladozshkaya and Kashirka, were described by Seyis *et al.* (2004). The description include their vernalization requirement, flowering biology, fatty acid composition and glycosinolate content. Kashirka and Ladozhskaya both display vernalization requirement (14 weeks at 5°C for Kashirka and up to 18 weeks at 5°C for Ladozshkaya. Both genotypes are self-compatible and seed set could be achieved after pollination by hand. Their flowers are typical *Brassica* flowers, leaves are small and transverse broad elliptic, the oleic acid content of Kashirka and Ladozskaya is 57.40 and 56.21% respectively, heir glucosinolate content measured with NIRS (Near Infrared Restriction Spectroscopy) is 63.4 and 129.5 µmol g/DM, respectively.

Further, Seyis and Friedt (2010a) described the fatty acid composition of three *B. oleracea* genotypes including Kashirka and Ladozskaya; the third accession was Eisenkopf. They obviously emphasized the varying fatty acid composition of these genotypes which ranged from zero up to over 45% of erucic acid. They identified three groups on the basis of erucic acid content: low, intermediate and high erucic acid group. They further underlined the possibility of using this basic material as a genetic resource for quality and yield improvement in oilseed rape breeding.

In addition to fatty acid composition of these genotypes, the genomic Southern analysis and PCR-amplifications of different *Brassica* species including Ladozhskaya (Lühs *et al.* 1999) revealed that the progeny of the *B. oleracea* accession Ladozshkaya DS 8395 had a completely different pattern with no signal in the selection for zero of this cabbage meaning partial or complete deletion of the *KCS* gene. The latter result was verified through PCR analysis with a KCS-specific primer pair, where the 1.25 kb fragment characteristic for all other genotypes was not amplified in the case of zero erucic acid mutant.

Resynthesized rapeseed as a tool for broadening genetic diversity

Genetic diversity of oilseed rape is considered to be low because of the short cropping history and the strong breeding focus on seed quality characters, i.e. low erucic acid and glucosinolate contents which narrowed down the genetic base (Friedt and Snowdon 2009). The resynthesis of oilseed rape from its diploid progenitors cabbage and turnip is therefore practised in order to broaden the genetic base of oilseed rape (Becker *et al.* 1995; Seyis *et al.* 2003a; Basunanda *et al.* 2007), although resynthesized rapeseed lines exhibit a low yield potential and inferior seed quality. According to Snowdon *et al.* (2007) resynthesis has repeatedly been used for gene introgression into cultivars, e.g., resistance to various diseases resistances or yellow seed color.

Several studies have been started with the objective of resynthesizing rapeseed (*B. napus* L.) from its diploid progenitors.

Breeding for agronomic and economic values tends to bias the exploitation of genetic variation (Friedt *et al.* 2007). Therefore, it is necessary to continuously integrate diverse germplasm into the breeding process in order to maintain a high level of genetic diversity. The, resynthesis of novel *B. napus* genotypes through artificial crosses between the diploid parents, assisted by embryo rescue, has repeatedly been shown to be useful for broadening the genetic basis of rapeseed. Both progenitor species exhibit an extremely broad genetic anod phenotypic diversity that are the potential for a huge variety of different RS rapeseed forms (Chen and Heneen 1989; Song *et al.* 1993; Lühs *et al.* 2000). The relatively high extent of intergenomic recombination between A and C genome chromosomes in early generations of RS rape further increases the potential for development of novel genotypes through resynthesis (Song *et al.* 1993; Lydiate *et al.* 1995).

The resynthesis of *B. napus* genotypes through interspecific hybridization between the diploid parents, assisted by embryo rescue, has repeatedly been shown to be useful for broadening the genetic basis of rapeseed. For example, Becker *et al.* (1995) investigated genetic distances between resynthesized lines and *B. napus* varieties by RFLP and allozyme markers and suggested that resynthesized lines might be a valuable source for broadening the genetic base of the breeding material of Seyis *et al.* (2003a), who analysed genetic distances of six families of resynthesized lines, spring oilseed and fodder rape cultivars by means of AFLP marker. Udall *et al.* (2004) described the introgression of resynthesized *B. napus* into hybrid spring canola as a source of novel alleles for the improvement of canola spring hybrids. However, poor agronomic performance and undesired seed quality traits such as high seed erucic acid and glucosinolate contents in resynthesized lines complicate their direct introduction of resynthesized lines into hybrid breeding programs. Backcrossing genetically diverse resynthesized lines into well adapted breeding material to establish a heterotic genepool for hybrid breeding is a labor intensive approach and a long-term perspective, and appropriate resynthesized lines would have to be carefully selected (Girke *et al.* 2012).

Becker *et al.* (1995) suggested the use of resynthesized rapeseed to develop a complementary genepool for hybrid breeding of European winter oilseed rape. To introduce canola quality, crosses with adapted material and subsequent backcrossing to resynthesized material are required, followed by recurrent selection for agronomically important genes.

Hybrids produced from crosses between genetically diverse resynthesized rapeseed and adapted oilseed types showed a high yield potential (Seyis *et al.* 2005a). The relationship between genetic distance and heterosis in oilseed rape was investigated by Diers *et al.* (1996) using RFLP markers. A similar study was performed by Riaz *et al.* (2001) using Sequence Related Amplified Polymorphic (SRAP) markers. The latter study demonstrated that crosses among genotypes from genetically divergent clusters tended to show higher levels of heterosis for seed yield and other traits.

Resynthesized rapeseed forms as a resource in *B. napus* hybrid breeding

The availability of genetically distant plant material is of great importance for hybrid breeding programs based on exploiting expected heterosis effects. These effects increase when parents with relatively different genetic base are used. An advantage of hybrids compared with open-pollinated cultivars is the yield stability under unfavourable conditions due to their heterozygous genotype (Wricke and Weber 1986; Léon 1991).

Due to the present transition from pure line breeding to hybrid breeding, genetic diversity in oilseed rape is receiving new attention, as heterotic pools of accessions with sufficiently large genetic distance need to be formed for maximum hybrid performance (Snowdon *et al.* 2007). Significant relationships between parental genetic distance and hybrid oilseed rape performance have been described (Diers *et al.* 1996; Riaz *et al.* 2001; Shen *et al.* 2006), but were not considered in detail. For improvement of hybrid performance, Quijada *et al.* (2004) suggested the introgression of European winter oilseed rape genomic segments into Canadian spring canola, as superior hybrid performance was found in testcrosses between these two genepools. A different strategy for increasing hybrid performance of oilseed rape has been proposed by Li *et al.* (2006), who found considerable heterosis in crosses between natural *Brassica napus* parents and a new type of *Brassica napus* containing the A subgenome of *B. rapa* and the C subgenome of *B. carinata* thus realizing intersubgenomic heterosis.

Heterosis effects are generally higher in crosses of genetically distant rapeseed materials. Lefort-Buson *et al.* (1987) determined higher yields in spring rapeseed hybrids, which were developed from genetically divergent spring rapeseed cultivars than traditional rapeseed varieties. The advantage of hybrid cultivars over cultivars derived from pure line breeding is not only the use of heterosis for increasing yield, also yield stability is high due to the heterozygous structure of hybrids (Paulmann and Frauen 1991). The superiority of hybrids specially becomes obvious in unfavourable conditions. Based on three year results Becker (1987) showed that the relative level of heterosis in the unfavourable year was two fold higher compared with the favorable year. The potential for hybrid rapeseed cultivars is well documented (Schuster and Michael 1976; Sernyk and Stefansson 1983; Grant and Beversdorf 1985; Lefort-Buson *et al.* 1987; Brandle and McVetty 1990). For this aim different pollination systems were developed (Buzza 1995). Cytoplasmatic male sterility (CMS systems) like the Ogu/INRA CMS-System (Renard *et al.* 1997), and the Male sterility system (MSL system) (Paulmann and Frauen 1998). As oilseed rape breeders today are seeking for genetic diversity in their hybrid breeding programmes resynthesized *B. napus* (RS lines) forms are gaining interest (Girke 2002; Lühs *et al.* 2002). Because of the low yield potential of RS lines their use is more directed to developing semi-synthetic rapeseed forms (Kräling 1987; Friedt *et al.* 2003) or backcross breeding procedures to introgress the novel genetic diversity.

Seyis *et al.* (2010b) conducted a study to determine the general combining ability (GCA) of different rapeseed material. Nine high-erucic acid RS lines and three old spring rapeseed cultivars were used as pollinators of male-sterile double-low spring rapeseed lines (MSL system). Yield performance of the single-cross hybrids was tested in a two year field trial in Rauischholzhausen/Germany. It revealed that the semi-synthetic rapeseed hybrids based on

RS lines had a higher yield potential. The developed test hybrids had 1-15% higher yield compared with the control cultivar, 'Senator'.

The same material was sown by the same investigators (Seyis *et al.* 2005a) in field trials organized in the locations of Rauischholzhausen and Hohenlieth/Germany and in Dyngby/Denmark. The yield performance of the single-cross hybrids again revealed a high yield potential of semi-synthetic rapeseed hybrids based on the RS lines.

In 1995 and 1996, Girke *et al.* (1999) investigated 12 F_1-hybrids between the spring rapeseed "Korall" and resynthesized rapeseed lines in field trails established in two locations Svalöv, Sweden and Dyngby, Denmark. Mid-parent heterosis was calculated as 32%. The hybrids revealed an average heterosis of 9.5% in comparison with the higher yielding parent. Some of the crosses exceeded the yield of their superior parent up to 21%. In consideration of the small number of the investigated resynthesised genotypes, these results indicated the potential that resynthesized oilseed rape might offer to hybrid breeding.

Development of zero erucic acid resynthesized rapeseed

Seyis *et al.* (2005b) were the first to report the existence of resynthesized rapeseed forms displaying low erucic acid content. They used the embryo rescue technique to develop amphidiploid RS-lines using the *B. oleracea* genotypes Kashirka and Eisenkopf and the *B. rapa* form Asko. The erucic acid content of developed RS lines varied between 43.09 and 63.14%.

Seyis *et al.* (2003b) crossed two spring type (Reward and apetalous turnip rape) and two winter type *B. rapa* forms (Q3F and SWSP) with the *B. oleracea* genotypes Kashirka and Lazdozshkaya. Totally 468 hybrids were obtained in this study and individual plants of different crossing combinations were analyzed for fatty acid composition and those erucic acid contents displayed nearby zero.

Further, during a TUBİTAK project, Seyis *et al.* (2010c) developed 227 resynthesized rapeseed forms using the two cabbage accessions Kashirka and Ladozshkaya and the two inter *B. rapa* forms 15591 and 15080 displaying 00-quality. The developed RS lines obtained from different crossing combinations were used to develop rapeseed hybrids by crossing them with the male sterile lines MSL 004C, MSL 007C, MSL 501C and MSL 506C. The first two male sterile lines were winter forms and the last two lines were spring forms. The authors were able to obtain seed from 19 hybrids based on the mentioned RS lines. The erucic acid content of the developed hybrids was determined as near zero and their oleic acid content ranged from 55.56% to 73.14.

SYNTHESIS

The major problem of the use of resynthesized rapeseed forms in quality breeding is their high glucosinolate content arising from the same character originating from the *B. oleracea* parent. To introduce canola quality in RS-lines, crossing with adapted material and subsequent backcrossing to resynthesized material are required, followed by recurrent selection for agronomic performance (Girke *et al.* 2012).

Another approach should be the reduction of the glucosinolate content of the *B. oleracea* parent. Applicable methods may be the irradiation of *B. oleracea* seeds or interspecific hybridization of *B. oleracea* with related *Brassica* species, because the selection of cabbage genotypes with low glucosinolate content may be a long and uncertain approach since no such material has been detected so far. Yet another method could be the cultivation of the low erucic acid genotypes *in vitro* since tissue culture causes the well known somaclonal variation, which may lead to a breakdown in the high glucosinolate level.

As explained in this paper, RS lines can be used only in the development of intraspecific or semisynthetic hybrids or in the development of interspecific rapeseed hybrids based on RS lines using male sterile *B. napus*, because of the low yield performance of these lines.

The presence of the three *B. oleracea* genotypes displaying low erucic content offers new possibilities to increase the yield performance of *B. napus*. As found by Seyis *et al.* (2005a) rapeseed hybrids based on RS-lines are higher yielding compared with the presently breeding material. The material used in this study was spring-type.

However, the low erucic acid *B. oleracea* genotypes are winter types. If they can be selected regarding their seed yield performance, their use in developing new RS-lines can offer the way for the further yield improvement in *B. napus*, because of using winter types the expected yield heterosis will be higher.

CONCLUSIONS

B. napus, the source of a highly nutritional vegetable oil and at the same time a valuable renewable resource for the biofuel industry, is currently the most important oilseed crop in Europe and Asia, and the second most important oilseed worldwide following soybean. Patterns of genetic and phenotypic diversity were studied in winter-type and spring-type *B. napus* gene bank collections, including oilseed, fodder and vegetable rape varieties of diverse geographical origins. *Brassica* oilseeds have become a significant agricultural product during the past 30 year and are now the world's third-leading source of both vegetable oil (after soybean and oil palm) and oil meal (after soybean and cotton). In Europe and Asia oilseed rape (predominantly from *Brassica napus* L.) is today the most important source of vegetable oil for human nutrition and as a renewable fuel. The dramatic increase in demand for *Brassica* oils places increasing pressure on plant breeders to continuously improve seed and oil yields, the overall agronomical performance and the quality of the oil and of the meal that remains after oil extraction (Snowdon 2009).

The described *B. oleracea* material can be the base of both quality and yield breeding of *B. napus* in future, because the *B. oleracea* gene pool together with that of *B. rapa* offers a indispensable source for its genetic diversity.

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