Review
Exploring the gene pool of *Brassica napus* by genomics-based approaches

Dandan Hu1, Jinjie Jing1, Rod J. Snowdon2,3, Annaliese S. Mason2,3, Jinxiong Shen1, Jinling Meng1 and Jun Zou1,4

1National Key Laboratory of Crop Genetic Improvement, College of Plant Science & Technology, Huazhong Agricultural University, Wuhan, China
2Department of Plant Breeding, IFZ Research Centre for Biosystems, Land Use and Nutrition, Justus Liebig University, Giessen, Germany
3Plant Breeding Department, INRES, The University of Bonn, Bonn, Germany

Summary
De novo allopolyploidization in *Brassica* provides a very successful model for reconstructing polyploid genomes using progenitor species and relatives to broaden crop gene pools and understand genome evolution after polyploidy, interspecific hybridization and exotic introgression. *B. napus* (AACC), the major cultivated rapeseed species and the third largest oilseed crop in the world, is a young *Brassica* species with a limited genetic base resulting from its short history of domestication, cultivation, and intensive selection during breeding for target economic traits. However, the gene pool of *B. napus* has been significantly enriched in recent decades that has been benefit from worldwide effects by the successful introduction of abundant subgenomic variation and novel genomic variation via intraspecific, interspecific and intergeneric crosses. An important question in this respect is how to utilize such variation to breed crops adapted to the changing global climate. Here, we review the genetic diversity, genome structure, and population-level differentiation of the *B. napus* gene pool in relation to known exotic introgressions from various species of the Brassicaceae, especially those elucidated by recent genome-sequencing projects. We also summarize progress in gene cloning, trait-marker associations, gene editing, molecular marker-assisted selection and genome-wide prediction, and describe the challenges and opportunities of these techniques as molecular platforms to exploit novel genomic variation and their value in the rapeseed gene pool. Future progress will accelerate the creation and manipulation of genetic diversity with genomic-based improvement, as well as provide novel insights into the neo-domestication of polyploid crops with novel genetic diversity from reconstructed genomes.

Keywords: polyploid crop, *Brassica*, gene pool, exotic introgressions, genomic changes, genomic-based improvement.

Introduction
Rapeseed is an important oilseed crop cultivated worldwide, with a yield of approximately 75 million tons and 37.58 million ha2 acreage in recent years. Rapeseed accounts for 13% of worldwide oil production and is third behind oil palm (35%) and soybean (28%) (USDA). The widely cultivated double-low rapeseed (low erucic acid and low glucosinolate content in seeds), also known as canola (*Brassica napus*), not only provides a healthy and nutritionally balanced edible oil for humans, but is also one of the most important sources of protein in animal feed. Rapeseed is also a soil-improving crop that can improve the soil nutrient status (Agegnehu et al., 2014; Chen et al., 2018a), accumulate beneficial bacteria (Zhang et al., 2017a), and suppress disease (Fang et al., 2016a) when incorporated into many crop rotation systems, and it is an important source of bioenergy, including biodiesel and industrial oil. Rapeseed breeding and industrial development are inseparable from the innovative utilization of germplasm resources. Here, we summarize the research progress to date, challenges, countermeasures and future perspectives on the evaluation, innovation and utilization of *B. napus* germplasm resources, as well as the progress of genomic-based tools such as molecular marker-assisted selection (MAS), whole genome-wide predictions and genome editing.

The origin, evolution, and genetic diversity of *Brassica napus*

*Brassica napus* (2n = 38, AACC) is an allotetraploid that was formed by interspecific crosses between the diploid ancestors of *B. rapa* (2n = 20, AA) and *B. oleracea* (2n = 18, CC) in the last 10 000 years (An et al., 2019, Bancroft et al., 2011, Chalhoub et al., 2014; Kimber and McGregor, 1995; Prakash and Hinata, 1980; Sun et al., 2017; UN, 1935). There are records to indicate that *B. napus* may have multiple independent origins, including the generally speculated origin in Europe (Chalhoub et al., 2014; Prakash et al., 2011) and the possible origin in Asia (Liu, 2000). Unfortunately, it is challenging to determine its precise origins.
without wild *B. napus*. Studies have shown that the A genome of *B. napus* may have evolved from a European turnip ancestor (*B. rapa ssp. rapa*) (Lu et al., 2019; Yang et al., 2016) and that the C genome may have been contributed by the wild Brassica species *B. montana* (2n = 18) (Song et al., 1997) or by the common ancestor of Kohlrabi, cauliflower, broccoli, and Chinese kale (Lu et al., 2019). The European origin has been supported by recent population evolutionary analysis based on genomic and transcriptome sequences (An et al., 2019; Lu et al., 2019).

As a young allotetraploid species with less than 500 years of cultivation history (Allender and King, 2010), *B. napus* was initially cultivated as vegetables including *B. napus* subsp. *rapifera* (swede and rutabaga) and *B. napus* subsp. *pabularia* (fodder rape and Siberian kale) for human consumption and animal fodder, and was then gradually domesticated as an oilseed crop (*B. napus* subsp. *oleifera*) after the industrial revolution (Allender and King, 2010; An et al., 2019; Applequist and Ohlson, 1972; Damania et al., 1997). The ‘double-low’ (low glucosinolate and erucic acid content in seeds) breeding performed since the 1950s (Krzywanski, 1978; Stefansson and Kondra, 1975) and local genetic improvements for early maturity and heterosis, such as those made in China (Fu et al., 1989; Liu, 2000; Song et al., 2020; Zou et al., 2019) (Figure 1), have rapidly established rapeseed as a major global oil crop and greatly improved its industrial value and status.

The oilseed types of *B. napus* can be divided into spring types (no vernalization requirement; grown mainly in North America, Scandinavia and Eastern Europe), semi-winter types (low to moderate vernalization requirement; grown in China and Europe) and winter types (strict vernalization requirement; grown mostly in Europe) (Liu, 2000). Winter-type *B. napus* is the original type that was first cultivated in Europe in the late Middle Ages (Fussell, 1955). Then, spring-type *B. napus* was differentiated in approximately 1700 (Bonnema, 2012) and spread to England in the late 18th century, followed by Canada in the 1940s and Australia in the 1970s (Cowling, 2007). The Chinese semi-winter type of *B. napus* originated in Poland and made its way to China through Japan (Wu et al., 2018).

There are tens of thousands of diverse germplasm resources of rapeseed and its related species stored in the major international germplasm banks in China, the United States, the United Kingdom, Korea, India, Germany, Canada, Australia, Russia, Japan and the Netherlands (Knee et al., 2011; Li et al., 2020a). However, we should take into account that *B. napus* is the youngest Brassica species with limited genetic diversity (Cowling, 2007; Fu and Gugel, 2010) due to the limited history of cultivation and domestication (Prakash et al., 2011), traditional breeding methods, and long-term double-low breeding in the 1950s and 1980s (Friedt and Snowdon, 2010). Therefore, to break through this breeding block and further expand the genetic diversity of *B. napus*, innovative germplasm improvement based on hybridization, genomic analysis, (pre) breeding and genetic manipulation is imperative.

**Broadening the genetic diversity of the Brassica napus gene pool**

Approaches such as hybridization, physical and chemical mutagenesis, and genetic engineering have often been used to introduce novel variation and to broaden the genetic basis of rapeseed; the former, which includes intraspecific and interspecific hybridization, has been the most extensive and achievable way to date, and is still ongoing in various breeding programs worldwide.

**Germplasm innovation and utilization based on intraspecific hybridization**

Crosses are frequently made between *B. napus* lines from groups with different subspecies, ecotypes or complementary traits to produce new germplasm or to increase heterosis (Kebede et al., 2020a).

---

**Figure 1** Cultivation and domestication process and genetic groups of Brassica napus. The arrow from European winter *B. napus* to Australian spring *B. napus* represents the introductions from Europe to Australia, including both winter type and spring type *B. napus*. The arrow from Chinese semi-winter *B. napus* to Australian spring *B. napus* also included the introductions from Japan to Australia.
2010; Qian et al., 2009; Udall et al., 2004). For example, some of the inbred lines derived from rutabaga (B. napus var. napobrassica) × spring-type B. napus crosses gave higher seed yield and had greater oil content than their spring-type B. napus parent (Shiranifar et al., 2020). Besides, through hybridization between winter-type B. napus and spring-type B. napus, clubroot (Rahman et al., 2011) and blackleg resistance (Light et al., 2011) from winter-type B. napus have been introduced into spring-type B. napus, and a determinate inflorescence strain that is beneficial for reducing plant height has been obtained (Li et al., 2018b). In addition, hybrids derived from spring-type, semi-winter type, and winter-type B. napus showed strong heterosis (Table 1), and the spring × winter-type hybrids have been successfully used in commercial breeding after solving flowering problems (Dang and Chen, 2015).

Germplasm innovation and exotic introgressions based on interspecific hybridization

Interspecific hybridization is important in promoting speciation, evolution, and the production and transfer of rich genomic variation, and has often been used for crop genetic improvement and enrichment of the available germplasm pool (Abbott, 1992; Mallet, 2005; Rieseberg and Carney, 1998). Compared with B. napus, other Brassica species show rich genetic diversity (Warwick, 2011) and obvious genetic differences and subgenomic variation relative to B. napus (Chalhoub et al., 2014; Parkin et al., 2018).

Table 1  Exotic introgressions and genomic changes of Brassica napus

| Crops                                       | Hybridization method | Trait introduction                | Reference                                      |
|---------------------------------------------|----------------------|-----------------------------------|-----------------------------------------------|
| Intraspecific hybridization                 |                      |                                   |                                               |
| Spring-type × semi-winter type              | Pollination          | Heterosis                         | Qian et al. (2007); Yao et al. (2013)         |
| Spring-type × winter-type                   | Pollination          | Determinate inflorescence         | Li et al. (2018b)                             |
|                                            |                      | Clubroot resistance               | Fredua-Agyeman and Rahman (2016); Rahman et al. (2011) |
|                                            |                      | Black leg resistance              | Light et al. (2011)                           |
|                                            |                      | Heterosis                         | Dang and Chen (2015); Quijada et al. (2006)   |
| Winter-type × semi-winter type              | Pollination          | Heterosis                         | Qian et al. (2009)                            |
| rutabaga (B. napus var. napobrassica) × spring-type | Pollination          | Higher seed yield and oil content | Shiranifar et al. (2020)                      |
| Introsgressions of the genetic components of a single species within Brassica |                      |                                   |                                               |
| B. napus × B. rapa                          | Pollination          | Early maturity                    | Liu (2000)                                    |
|                                            |                      | Clubroot resistance               | Hirani et al. (2016); Liu et al. (2018); Zhan et al. (2015) |
|                                            |                      | Heterosis                         | Zhang et al. (2015)                           |
| B. napus × B. oleracea                      | Pollination          | Expanded genetic diversity        | Iftikhar et al. (2018)                        |
|                                            |                      | Sclerotinia resistance            | Mei et al. (2020)                             |
|                                            |                      | Self-incompatibility              | Ripley and Beversdorf (2003)                  |
|                                            |                      | Heterosis                         | Li et al. (2014)                              |
| B. oleracea × B. napus                      | Embryo rescue        | Heterosis                         | Kaminski et al. (2020)                        |
| B. juncea × B. napus                        | Pollination          | Pod shattering resistance         | Prakash and Chopra (1988)                     |
|                                            |                      | Yellow seeds                      | Liu et al. (2010)                             |
|                                            |                      | Multilocular silique              | Chen et al. (2018b)                           |
|                                            |                      | Blackleg resistance               | Dixelius (1999); Rashid et al. (2018); Schelfhout et al. (2006) |
|                                            |                      |                                  |                                               |
| B. napus × B. carinata                     | Repeated pollination  | Early maturity                    | Zaman et al. (2019b)                          |
|                                            | Pollination          | Determine inflorescence           | Tu et al. (2020)                              |
|                                            |                      | Blackleg resistance               | Fredua-Agyeman et al. (2014); Navabi et al. (2010) |
|                                            |                      | Pod shattering resistance         | Dhaliwal et al. (2017)                        |
| B. fruticulosa × B. napus                  | Embryo culture       |                                  | Chen et al. (2011)                            |
| Synthetic B. napus                          |                      |                                   |                                               |
| B. rapa × B. oleracea and B. oleracea × B. rapa | Ovary culture        | Large seeds                       | Fu et al. (2012b)                             |
|                                            | Pollination and protoplast fusion | Yellow seeds                       | Wen et al. (2008)                             |
|                                            | Ovule culture        |                                  |                                               |
|                                            | Ovary culture, embryo culture | Yellow seeds                       |                                               |
| B. rapa × B. oleracea                       | Ovary culture, embryo culture | Large seeds                       | Fu et al. (2012b)                             |
|                                            | Embryo rescue        | Sclerotinia resistance            | Ding et al. (2019)                            |
Exotic introgressions from Brassicaceae beyond interspecific hybridizations with *B. napus*

| Crops | Hybridization method | Trait introduction | Reference |
|-------|----------------------|--------------------|-----------|
| *B. oleracea × B. rapa* | Embryo rescue | Yellow seeds | Gaeta et al. (2007); Lukens et al. (2006); Xiong et al. (2011) |
| *B. carinata × B. rapa* | Pollination | Heterosis, high linoleic acid and high linolenic acid contents, nitrogen efficiency | Chatterjee et al. (2016) |
| *B. juncea × B. carinata* | Pollination | Heterosis | Chatterjee et al. (2016) |

Exotic introgressions from Brassicaceae beyond interspecific hybridizations with *B. napus*

- *B. napus × O. violaceus*: Protoplast fusion, Red flowers, higher oleic and linoleic acid contents, Du et al. (2009); Kang et al. (2014); Tu et al. (2020)
- *B. napus × radish cabbage*: Pollination, Clubroot resistance, Diederichsen et al. (2015)
- *B. napus × R. sativus*: Protoplast fusion, Fertility restored, Sakai et al. (1996)
- *B. napus × L. indigotica*: Embryo rescue, Clubroot resistance, Metz et al. (1995)
- *B. napus × I. indigotica*: Protoplast fusion, Resistance to influenza virus, cytoplasmic male sterile, Du et al. (2009); Kang et al. (2014)
- *B. napus × S. alba*: Protoplast fusion, Yellow seeds, Wang et al. (2014)
- *B. napus × L. fendleri*: Pollination and embryo culture, Sclerotinia resistance, yellow seeds, Li et al. (2009)
- *B. napus × S. arvensis*: Protoplast fusion, Increased linoleic acid and linolenic acid content, Du et al. (2008)
- *B. napus × C. bursa-pastoris*: Protoplast fusion, Cytoplasmic male sterile, Cheng et al. (2008)
- *B. napus × C. bursa-pastoris*: Pollination, Early maturity, double-low quality, Sclerotinia resistance, Chen et al. (2009); Chen et al. (2007); Zhang et al. (2013)

2014; Zou et al., 2016a). These species also have many desirable traits and high genetic diversity, as shown in Table 1 and Figure 2 (Quezada-Martinez et al., 2021; Warwick, 2011). These traits have been or could be further introduced into the *B. napus* gene pool to provide genetic diversity, and germplasm types suited to changing environments and industry requirements. It is reported that the root exudates of the wild or related species would be a benefit for the improvement of the agricultural output and reduction of environmental impacts (Preece and Penuelas, 2020). We would also pay attention on the advantageous root exudates of these wild or related species and introducing it to *B. napus*.

**Germplasm introgressions from species that share a genome with Brassica napus**

The presence of “shared” Brassica genomes with high levels of sequence similarity and organization between multiple species (Chalhoub et al., 2014; Liu et al., 2014; Parkin et al., 2014), has offered a unique opportunity for germplasm improvement (Fitzjohn et al., 2007; Katche et al., 2019). The diploid progenitor *B. rapa* can spontaneously hybridize and backcross with *B. napus* (Table 1) (Hansen et al., 2001) and has most commonly been used in the breeding of Chinese semi-winter-type *B. napus* (Liu, 2000; Zou et al., 2019) as well as Canadian spring-type *B. napus* (Attri and Rahman, 2018). Modern genome sequencing analysis has also clearly identified abundant imported components from *B. rapa* in Chinese *B. napus* varieties; the latter shows unique footprints of differentiation that have arisen during the process of artificial selection, breeding and environmental adaptation, resulting in a semi-winter-type subpopulation with obvious genomic differences from its European ancestors (Sun et al., 2017; Wu et al., 2018; Zou et al., 2019).

Although the diploid progenitor *B. oleracea* shows low cross-compatibility with *B. napus* (Myers, 2006; Quazi, 1988), with frequent sterility in the resulting interspecific hybrids (Li et al., 2014), several useful traits including self-incompatibility (Ripley and Beversdorf, 2003), *Sclerotinia* resistance (Ding et al., 2013; Mei et al., 2020), expanded genetic diversity (Bennett et al., 2008; Iftikhar et al., 2018) and improved heterosis potential (Li et al., 2014) have been successfully transferred into *B. napus*.

With the deterioration of the global climate, the allotetraploid rapeseed *B. juncea* (2n = 36, AABB) has become a possible alternative to *B. napus* in the low moisture regions (Pantosh et al., 2014) of Canada and Australia, and is often used for the improvement of *B. napus* in terms of blackleg disease resistance (Figure 3E) (Dixielus, 1999; Rashid et al., 2018), early maturity (Zaman, 1989), yellow seededness (Liu et al., 2010), pod shatter resistance (Prakash and Chopra, 1988) and multilocular silique traits that have potential for high yield (Chen et al., 2018b). Chinese hybrid varieties Huanqiaizao, Xiangzayou 631 and Xiangzayou 518, 36, AABB) has become a possible alternative to *B. napus* in the low moisture regions (Pantosh et al., 2014) of Canada and Australia, and is often used for the improvement of *B. napus* in terms of blackleg disease resistance (Figure 3E) (Dixielus, 1999; Rashid et al., 2018), early maturity (Zaman, 1989), yellow seededness (Liu et al., 2010), pod shatter resistance (Prakash and Chopra, 1988) and multilocular silique traits that have potential for high yield (Chen et al., 2018b). Chinese hybrid varieties Huanqiaizao, Xiangzayou 631 and Xiangzayou 518, early maturity, double-low quality, *Sclerotinia* resistance (Chen et al., 2009; Chen et al., 2007; Zhang et al., 2013).
et al., 2019). Desirable traits, such as determinate inflorescences, which are suitable for mechanized production (Figure 3A) (Tu et al., 2020), blackleg resistance (Fredua-Agyeman et al., 2014; Navabi et al., 2010; Navabi et al., 2011), and pod shatter resistance (Dhaliwal et al., 2017), have been introduced from B. carinata to B. napus.

**Synthetic Brassica napus** as a subpopulation with a novel genomic composition

In addition to introducing certain superior genes or alleles, a creative approach for germplasm innovation has involved the synthesis of B. napus through hybridization between species with...
AA and CC genome. As an example, synthetic *B. napus* (A'AC'C'C') was created by crossing diploid *B. oleracea* (C'C) and *B. rapa* (A'A') (superscript represents the first letter of the species name) (Table 1): some lines showed yellow seeds (Figure 3D) (Wen et al., 2008), large seeds and white flowers (Figure 3G) (Fu et al., 2012b), and improved *Sclerotinia* resistance (Ding et al., 2019). The second kind of synthetic *B. napus* (A'AC'C'C') was created by hybridization between artificially synthesized hexaploidy (A'A'B'B'C'C, created by *B. carinata* and *B. rapa*) (Jiang et al., 2007; Tian et al., 2010) and *B. napus*, followed by more than 10 rounds of self-pollination, MAS, cytological observation, and trait selection (Hu et al., 2019; Li et al., 2006; Xiao et al., 2010). Lines with high linoleic and linolenic acid content, nitrogen use efficiency (Figure 3L) (Wang et al., 2015), and disease resistance have been selected from this gene pool, and some lines have been used in the breeding of Chinese hybrid varieties Youyan 50 (Zhang et al., 2014) and Huayouza72. In another approach, synthetic *B. napus* (A'AC'C'C') was created by interspecific hybridization between *B. juncea* (A'A'B'B) and *B. carinata* (B'B'C'C) followed by chromosome doubling and several generations of self-pollination and trait selection (Chatterjee et al., 2016). These synthetic *B. napus* have shown abundant genetic and phenotypic variation, significant genetic differentiation when compared to traditional *B. napus*, and strong subgenomic heterosis potential as a subpopulation of *B. napus* (Figure 3K) (Abel et al., 2005; Chen et al., 2010; Girke et al., 2012; Hu et al., 2020; Seyis et al., 2006), and they comprise a rich source of genetic variation for the improvement of established *B. napus* types.

**Exotic introgressions based on intergeneric and intertribal hybridization**

Beyond *Brassica*, rich genetic resources in the Brassicaceae (Warwick, 2011) are valuable for introducing favourable traits to *B. napus* as well as for exploring new crops. For example, the ornamental plant *Orychophragmus violaceus* contains a low

---

**Figure 3** Rich favourable trait variation of *Brassica napus* lines with introgressions from other species. A shows a plant at the seeding stage with a determinate inflorescence (Tu et al., 2020); B shows clubroot-resistant seedlings in the field (Zhan et al., 2015); C shows a plant with purple stems (Navabi et al., 2011); D shows yellow seeds (Wen et al., 2008); E shows a plant with blackleg resistance (Rashid et al., 2018); F shows a red flower (Fu et al., 2018); G shows a white flower (Fu et al., 2012b); H, I, and J show the flowers of a male sterile line, where I and J are flowers with sepals and petals removed (Kang et al., 2014); K shows the subgenomic heterosis of new-type *B. napus*; and L shows the growth contrast of N-efficient new-type *B. napus* lines D4-15 and D4-9 under high-N and low-N conditions at the seedling stage (Wang, 2014).
erucic acid content and a high number of branches, pods and seeds (Figure 2a) (Luo et al., 1994) and can potentially produce special industrial fatty acids in seed oil (Li et al., 2018c). Radish (Raphanus sativus, 2n = 18, RR) has clubroot resistance (Zhan et al., 2017) and cytoplasmic male sterility traits (Ogura, 1968). The medicinal plant Sinapis alba (2n = 14, Figure 2b,c) shows resistance to diseases caused by bacteria and viruses (Kang et al., 2020). White mustard (Sinapis alba, 2n = 24) has yellow seeds, resistance to biotic and abiotic stresses, pod shatter resistance, and beneficial ingredients for humans (Kumari et al., 2020). Some Brassicaceae species with insect resistance have also been identified, as reviewed in Herve (2018).

The development of tissue culture and protoplast fusion technologies promotes intergeneric and even intertribal hybridization in rapeseed by introducing various favourable traits and creating new germplasm (FitzJohn et al., 2007; Katche et al., 2019) (Table 1). B. napus lines with additional chromosome fragments of O. violaceus that showed red flowers (Figure 3F) and higher oleic and linoleic acid contents were created by intergeneric hybridization between O. violaceus and B. napus (Table 1). Radish cabbage (RCC) (Figure 2d), raparadish (AARR), allopolyploid alien addition lines and substitution lines with chromosomes from R. sativus (Chen and Wu, 2008; Hagimori et al., 1992; Karpechenko, 1928; Lange et al., 1989; Metz et al., 1995) have been created as a bridge to transfer cytoplasmic male sterility (Bannerrrot et al., 1974), fertility-restorers (Sakai et al., 1996), beet cyst nematode resistance (Peterka et al., 2004), and clubroot resistance (Diederichsen et al., 2015; Zhan et al., 2017) traits from R. sativus to B. napus. A complete set of B. napus monosomic alien addition lines was obtained with each line carrying a chromosome of I. indigotica and showed obvious virus resistance (Du et al., 2009; Kang et al., 2014). Through crossing with I. indigotica, S. alba, and S. arvensis, B. napus lines with cytoplasmic male sterility traits were created (Figure 3H–J) (Cheng et al., 2008; Kang et al., 2014; Wang et al., 2014). In addition, after crossing Capsella bursa-pastoris (2n = 32) (Figure 2e,f) with double-high B. napus, new double-low B. napus lines with Sclerotinia resistance and early maturity were selected (Chen et al., 2007; Zhang et al., 2013).

**Reconstructed B. napus genome by exotic germplasm introgressions**

With the development of genetics and genomics technologies (van Dijk et al., 2018; Luo et al., 2020; Minoche et al., 2015; Sedlazeck et al., 2018), especially the de novo assembly of the genomes and pangenome of B. napus and its related species (Table S2), an increasing number of studies have shown that introgressions of exotic germplasm not only broaden the genetic base of B. napus but can also lead to major genomic changes. Changes vary with the relationship between species, the degree of exotic introgression, and the selection stress on the hybrid progeny (Table 1). Therefore, in-depth studies on genomic structural changes caused by ancient events and new introgressions of related species, as well as their influence on traits and heterosis, will provide a theoretical framework for understanding and manipulating the reconstructed rapeseed genome.

**Genomic variation in B. napus and related species**

*Brassica napus* is an allotetraploid with a relatively complex genome (1130 Mb) (Chalhoub et al., 2014). Since the first genome assembly of B. napus was released, high-quality genomes of five cultivars have been revealed based on state-of-the-art sequencing technologies, with improvements in the size of the assembly from 634.19 Mb to 1008 Mb and an average N50 scaffold size from 777.3 Kb to 57.88 Mb, respectively (Table S2). In addition, a 1.8 Gb pangeneome of eight varieties containing approximately 150 000 genes was constructed (Song et al., 2020). These genomic analyses showed that the A and C genomes of B. napus are highly homologous, and homeologous exchange events (HES) are ongoing processes that have greatly promoted the generation of novel, large-scale structural variation in B. napus (Chalhoub et al., 2014). Significant differentiation, such as asymmetric subgenomic evolution, different subgenomic recombination frequencies, and small- to mid-scale chromosomal structural variations between different ecological types, has also been detected in B. napus (An et al., 2019; Chawla et al., 2021; Kianian and Quiros, 1992; Samans et al., 2017; Song et al., 2020; Zou et al., 2019). Moreover, this genetic variation has been linked to quantitative trait loci for very different traits including chlorophyll content (Qian et al., 2016), flowering time (Vollrath et al., 2021; Wu et al., 2018), germination (Nguyen et al., 2016) and disease resistance (Dolatabadian et al., 2020; Gabur et al., 2020).

For the rest of the *Brassica* species, high-quality reference genomes have been released (Table S2). Because of the differences in interspecific hybridization events, speciation and polyploidization, geographic isolation, domestication, and cultivation, comparative genomics analysis based on genomes have revealed abundant subgenomic variation between the A, B, and C genomes present in different species, that is, A/A′C/A′′′, B′B/B′′′, and C/C′C″ (Chalhoub et al., 2014; Liu et al., 2014; Perumal et al., 2020; Song et al., 2021a; Wang et al., 2011; Yang et al., 2016). Genome assembly has greatly promoted the functional genomics and breeding of crops, but the existing genome resources are far from comprehensive. In future, focusing on pangenomic variation at the genome structural level using multiple reference genomes to detect presence–absence variation may shed further light on individual genomic differences between lines, genetic groups and ecotypes as a basis for breeding.

**Genome changes caused by interspecific hybridization**

Both genomic introgressions of related species and resynthesis of *Brassica* species have led to rich subgenomic variation within *Brassica*, and new genetic variation has additionally been created by interspecific hybridization-induced "genomic shock". Numerous chromosomal structural variations, including inversions and translocations, the disappearance of parental alleles, the generation of new alleles, and the imprinting of transposon activity, have been detected in B. napus lines with B. rapa introgressions (Zou et al., 2011). These genetic variations arose from the introduction of existing subgenomic variation, as well as from new variation induced by interspecific hybridization; in addition, considerable variation associated with heterosis was revealed by QTL analysis (Fu et al., 2012a; Zou et al., 2011).

Synthetic B. napus (A′A′′C/C′C″) is known to be meiotically unstable with frequent chromosomal exchanges between the A and C subgenomes, which can result in genomic rearrangements and structural variants (Song et al., 1995; Szadkowski et al., 2010; Xiong et al., 2011). Other changes may involve gene expression and epigenetic modifications (Chen and Pikaard, 1997; Gaeta et al., 2007; Lukens et al., 2006; Ran et al., 2016; Xu et al., 2009), transposable element activation and small RNA changes (Albertin et al., 2006; Fu et al., 2016; Hurgobin et al., 2006;
2018; Palacios et al., 2019), changes in IRNA (Wei et al., 2014), and the rapid mutation of repetitive sequences (Gao et al., 2014). Synthetic B. napus (AACCcD), whose genome was mostly replaced by B. rapa and B. carinata, showed a stable genome after generations of self-pollination and recurrent selection but still contained numerous structural variation that was significantly different from that of traditional B. napus (Hu et al., 2019; Zou et al., 2018). The characteristics of these different structural variations and their influence on genome stability, trait improvement, and heterosis are worth further study.

Genomic changes caused by distant hybridization

For the genetic changes caused by intergeneric hybridization, male parental chromosome elimination is very common in offspring (Chaudhary et al., 2013; Houben et al., 2011; Tayeng et al., 2012). In hybridizations between Brassica species and other genera, progeny usually retain the chromosomes from Brassica female parents and eliminate partial or total chromosomes from male parents, as reviewed in Li (2020). In addition, the elimination of C genome chromosomes has also been observed in the hybridization between B. napus and L. indigotica (Tu et al., 2010), Lesquerella fendleri (Du et al., 2008), O. violaceus (Cheng et al., 2002; Hua and Li, 2006), and Crambe abyssinica (Zhu et al., 2016). Compared with intra- and interspecific hybridization, genomic changes in intergeneric hybridization are more difficult to capture (Li, 2020), and aneuploid progeny may have increased genomic instability, including chromosome missegregation, mitotic recombination, mutations, and increased DNA damage (Gautam et al., 2016). For example, two new kinds of B. napus (2n = 38, AACCcO) were extracted from the intergeneric allo-hexaploid AACCcOO (2n = 66) (Gautam et al., 2016) and allotraploid ACPP (2n = 38) (Chen et al., 2009) after loss of the entire O genome from O. violaceus and the Ca genome from C. bursa-pastoris. This new B. napus showed the same chromosome composition as its B. napus parents, but genomic changes, including alien introgression, loss and gain of DNA segments, transposon mobilization, and extensive DNA methylation alteration, occurred after polyploidization and aneuploidization (Gautam et al., 2016; Zhang et al., 2013).

Challenges and approaches for further exploring and expanding the rapeseed gene pool

Notably, the gene pool of B. napus was significantly enriched with genetic and genomic diversity through various crosses, which introduced valuable traits, and provided innovative approaches for heterosis breeding. However, we should also note that exploring this diversity for breeding utilization has been hindered by technical limitations. First, the offspring from crosses, especially from distant crosses, often have genome instability, unusual chromosome and allele segregation, and linkage drag of deleterious traits, which requires generations of backcrossing, targeted trait selection (Becker et al., 1995; Seys et al., 2003), and recurrent selection (Hu et al., 2019) to remove. Second, due to the limited studies of the donor species, most of the improvements in these germplasms are based on inefficient and inaccurate blind selection without the assistance of genomic information. Finally, the acquisition of large-scale interspecific hybridization is still difficult even with the help of modern techniques, and innovative and high-throughput methods to create genetic variation are needed. With recent biotechnological developments, there has been rapid progress in dissecting the rapeseed genome diversity, population differentiation, and gene functions, and in manipulating genes and genomes with marker-assisted selection, transgenics, and genome editing. It is time to further improve the breeding potential of this germplasm, especially germplasm with exotic introgression, with the assistance of genome-based approaches (Figure 4).

High throughput genotyping and phenotyping

The rapid development of genome sequencing technology has greatly promoted genomic analysis and provides a foundational tool for crop improvement by facilitating rapid selection in modern breeding (Bevan et al., 2017). First, abundant genomic information is available for Brassica and Brassicaceae germplasm, including high-quality reference genomes (Table S2), organelle genomes (Mohd Saad et al., 2021), pangenomes (Golizz et al., 2016; Hurgobin et al., 2018; Song et al., 2020), gene annotations, transcriptions, and high-throughput genotypes for thousands of cultivars and breeding lines that have been identified by SNP chips and sequencing approaches (An et al., 2019; Cheng et al., 2016; Lu et al., 2019; Schmutzer et al., 2015; Wu et al., 2018, Zhang et al., 2017c). These data were stored in public platforms for sharing and remaining including the Brassica Database (http://39.100.233.196), the Brassica napus Genome Browser (https://www.dev.genoscope.cns.fr/brassicanapus/ (Chalhoub et al., 2014)), BnPedigome (http://ibi.zju.edu.cn/bnpedigome/index.php) (Zou et al., 2019), BnaSNPDB (http://rapeed.zju.edu.cn:3838/bnasnpdb) (Yan et al., 2020), and BnPiR (http://cbi.hzau.edu.cn/bnaplus/) (Song et al., 2021b). High-throughput genotyping by whole-genome sequencing, target segment sequencing and SNP-chip array is ongoing for Brassica germplasm, and these data resources and genotyping techniques are becoming increasingly inexpensive and convenient for exploring Brassica pangenomic variation, and especially for identifying and introducing favourable genes and alleles into the B. napus gene pool.

Genotyping and phenotyping are important in the analysis of the genetics architecture of traits and the improvement of crops. However, the laborious and time-consuming traditional manual scoring of phenotypes, which is much slower than high-throughput genotyping, has become the rate-limiting step (Fahlgren et al., 2015). In recent years, fast, affordable, accurate and non-destructive high-throughput phenotyping platforms based on various imaging techniques, remote-sensing tools, cloud storage, and machine learning have received widespread attention (Araus and Kefauver, 2018; Shakoor et al., 2017; Yang et al., 2020) and have been used in many crops in the field or lab. For rapeseed, researchers have begun to investigate the use of high-throughput phenotyping to dynamically screen plant growth architecture within rapeseed intervarietal substitution lines and associated populations, using image-based traits that reflect shoot growth and predict the final yield (Knoch et al., 2020; Li et al., 2020b). In addition, an unmanned aerial vehicle-based hyperspectral imaging technique has been used to estimate rapeseed seedpods maturity (Singh et al., 2021), flower number (Wan et al., 2018), plant vegetation fraction and flower fraction (Fang et al., 2016b). However, this technique is being developed and needs to be improved.

Genes/QTLs, MAS, GS and their applications in (pre) breeding

The vast amounts of genotyping and phenotyping information now available have greatly facilitated functional genomics
research with thousands of QTLs and candidate genes identified based on high-density genetic maps, genome-wide association analysis, and QTL-seq (Harper et al., 2012; Liu et al., 2020a; Luo et al., 2017; Ogura and Busch, 2015; Raman et al., 2016; Wei et al., 2016). 57 QTL and 787 marker–trait associations for 47 image-based traits were identified based on high-throughput phenotyping (Knoch et al., 2020; Li et al., 2020b). In addition, some important genes were cloned, and their functions were verified, including the genes reviewed in (Hu et al., 2017), the abiotic stress-responsive genes reviewed in (Chikkaputtaiah et al., 2017), and genes related to flowering time, male sterility, plant architecture, seed weight, pod length, oil and fatty acid contents, pod shatter resistance, blackleg resistance, leaf colour, and nutrition absorption (Table 2).

Functional genomics has resulted in many trait-related markers being developed and has been applied in genetic improvement based on marker-assisted selection, whereby single- or multigenes traits can be tracked using linked markers. This method has been successfully applied in almost all crop breeding programs for gene pyramiding and gene transgression (Dubcovsky, 2004; Hickey et al., 2019; Maharajan et al., 2018). In rapeseed, MAS technology has typically been used for selecting lines with recessive genic male sterility (Huang et al., 2012; Wang et al., 2007), self-compatibility (Tochigi et al., 2011), clubroot resistance (Zhan et al., 2015), sclerotinia stem rot resistance (Ding et al., 2021), and high oleic acid content (Spasibionek et al., 2020; Zhao et al., 2019). Combined with the speed-breeding technique that shortens the breeding life cycle through controlled light and temperature (Hickey et al., 2019), the MAS method will accelerate the improvement of rapeseed. However, we should note that many traits are qualitative and complex, and many functional genes, especially genes with small effects, are far from being fully studied, and this complexity could restrict the utilization of MAS. Except for these important agronomic and quality traits, identifying genes controlling cross-compatibility and recombination perhaps will accelerate the germplasm resource innovation based on hybridization.

In addition to MAS, the genome-wide selection (GS, or genome-wide prediction), which predicts the breeding value of the testing population according to its genotype and the prediction model developed based on the genotype and phenotype of the training population, has become a popular tool in plant breeding since the late 2000s (Bernardo, 2016). Genome-wide selection has also been studied in many crops and applied in maize and soybean (Bernardo, 2016). Prediction using different models, marker sizes, traits, heterosis, and genetic effects, has been investigated with DH populations and hybrid populations, and the results support the high potential of the genomic prediction in rapeseed (Table 3). In addition, the high prediction ability for hybrids whose parents contain exotic introgression of related species was also presented (Table 3, Hu et al., 2020). Genomewide selection was influenced by population size, the genetic relationship between the training set and prediction set, marker number, and the environment, which suggests that we can construct and improve the prediction models with suitable training populations, universal and affordable phenotypic and genotypic information, in-depth and multidimensional omics, meteorology, and advanced algorithms.

Despite the vast amounts of genetic, phenotypic and functional genomics information, these methods have been underutilized because they are not well integrated but are scattered across different programs and populations. Recently, researchers reviewed previous studies in rice, constructed a comprehensive map of rice quantitative trait nucleotides with inferred effects, and developed a genome navigation system for use in breeding (Wei et al., 2021). In addition, accumulated data from *B. napus* or even *Brassica* overall should also be unified and incorporated to develop an integrated platform with automated, unified, and incorporated genotyping and phenotyping. Importantly, high-speed universal applications across wide genetic backgrounds will
be convenient and time-saving in taking full advantage of the genetic information in MAS and GS, providing opportunities for genome-guided breeding.

Genetic manipulation

Despite introducing valuable traits through hybridization and MAS during breeding, genetic manipulation techniques, including transgenic production and gene editing that can precisely introduce or modify desired traits have gradually become key technologies in functional genomics and modern crop breeding. Transgenic technology which can specifically introduce a gene that is nonexistent in the target species has already been applied in B. napus breeding (reviewed by Ton et al., 2020 and Mohd Saad et al., 2021), resulting in varieties and lines with desirable traits such as herbicide resistance (Smyth and Phillips, 2001), hybrid breeding systems (male sterility or restoration) (Mariani et al., 1992), increased levels of the anticancer compound glucoraphanin (Liu et al., 2012), novel components such as docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA) (Walsh et al., 2016), insect resistance (reviewed by (Herve, 2018)), and abiotic stress-responsive tolerance (reviewed by Chikkapatia et al., 2017).

Recently, gene editing has become the most popular and promising technique for functional genomics, and it promises to revolutionize crop improvement by creating new non-transgenic varieties in a fast, efficient, and technically simple way without the use of transgenes (Schenke and Cai, 2020; Shelake et al., 2019; Songstad et al., 2017; Subedi et al., 2020). Gene editing makes it possible to generate targeted deletions, insertions, gene knock-outs, and point mutations, to modulate gene expression by targeting transcription factors or epigenetic machinery to DNA, or to target and modify RNA (Broeders et al., 2020). This method has been successfully used in dozens of species to create desirable traits in major crops (Ezure and Miura, 2018; Malzahn et al., 2017; Manghwar et al., 2020; Manghwar et al., 2019; Metje-Sprink et al., 2020; Zaman et al., 2019b), and dozens of gene-edited crops have been approved by a few countries (Editorial, 2021). During the process of studying gene function in B. napus, gene-edited lines with a higher seed yield, early flowering, improved architecture, orange flowers, pod shatter resistance, multilocular siliques, yellow seeds, a higher oil content, an improved fatty acid composition in the seed, environmental stress tolerance, herbicide resistance, and disease resistance have been created (Table 4). The application of these techniques will accelerate functional genomics and result in the development of crops with desired traits that can contribute to increased yield potential under a changing global environment (Lyzenga et al., 2021).

In addition, gene editing has been used to construct genome-wide mutant libraries in rice (Lu et al., 2017; Meng et al., 2017), soybean (Bai et al., 2020), and maize (Liu et al., 2020c); these libraries are of great value for functional genomics and crop improvement and could be rapidly developed for other crops (Zhang et al., 2018b). Despite the use of small-scale variations, gene editing is beginning to be used to promote recombination at specific genomic regions in yeast and tomato, which is promising for generating recombinant individuals and breaking genetic linkage (Lyzenga et al., 2021). Gene editing has also been used for de novo domestication of wild tomato, groundcherry, and allotetraploid rice with several edited domestication traits (Lemon et al., 2018; Li et al., 2018b; Xie and Liu, 2021; Zsögön et al., 2018); this method maintains the genetic diversity and valuable traits of the wild plant while increasing yield productivity, and avoids the lengthy crossings and selections of naturally occurring genetic mutations required for traditional domestication (Zhu and Zhu, 2021). Despite the great challenges of decoding the genetic/epigenetic basis of beneficial agronomic traits and integrating functional genomics discoveries with genome editing designs, these attempts highlight the potential of rapidly creating novel crops with a domesticated plant ideotype from wild plants and orphans crops using advanced biotechnologies (Hickey et al., 2019; Xie and Liu, 2021; Zsögön et al., 2017). For Brassica species, through the use of gene editing, we may be able to (i) create lines with desirable traits or mutation libraries; (ii) accelerate the introgression of elite traits by interspecific hybridization and MAS processes with increased recombination rates or targeted recombination; and (iii) facilitate the neo-domestication of synthetic Brassica polyploids and wild species by rapidly editing genes related to domestication, genome stability, and recombination.

**Table 2** Important trait related genes cloned in Brassica napus in recent years

| Trait | Trait related genes | Reference |
|-------|---------------------|-----------|
| Flowering time | BnFLC.A2 | Chen et al. (2018c) |
| | BnFLC.A10 | Hou et al. (2012); Yin et al. (2020) |
| | BnaSDG8 | Jang et al. (2018) |
| Male sterility | BnaC9.Tc40 | Xia et al. (2016) |
| | MSS | Xin et al. (2016); Xin et al. (2020) |
| Plant architecture | BnaTFI | Sirboon et al. (2020) |
| | BnD14 | Stanic et al. (2021) |
| | BnaRGA | Yang et al. (2017) |
| | BnaAA7 | Cheng et al. (2021) |
| Seed weight and pod length | BnaA9.CYP7B9 | Shi et al. (2019) |
| | BnaC0D3 | Khan et al. (2020) |
| | BnaCPL3.C03 | Miller et al. (2019) |
| Oil content | BnSFAR4, BnSFAR5 | Karunarthna et al. (2020) |
| | Bnaorf188 | Liu et al. (2019) |
| Oil and fatty acid phytic acid | BnaA.FAD2 | Okuzaki et al. (2018) |
| Pod shattering resistance | BnaC.ALC.a | Bratz et al. (2017) |
| | BnaCALC.a | Zhai et al. (2019) |
| Leaf colour | BnaC07.H01 | Zhu et al. (2017) |
| Boron absorption | BnaA3.NPS1 | Hua et al. (2016) |
| | BnaA9.WRKY47 | Feng et al. (2020) |
| | BnaC4.BOR1.1c | Zhang et al. (2017b) |
| Blackleg resistance | LepR3 | Larkan et al. (2013) |
| | Rhn9 | Larkan et al. (2020) |
Exploring the gene pool of *Brassica napus*

Table 3  Studies of genome-wide selection in *Brassica napus*

| Populations                        | Traits                   | Marker       | Model                  | Prediction ability | Reference                  |
|------------------------------------|--------------------------|--------------|------------------------|--------------------|----------------------------|
| 391 winter type DH lines           | SY, PH, FT, PC, OC, GLU  | 253 SNP      | RR-BLUP, BayesB         | 0.41–0.84 (GLU to PH) | Wurschum et al. (2014)     |
| TN DH population                   | FT                       | 1248 SNP     | RR-BLUP, RKHS, Bayesian LASSO, BayesA, Bayes B, Random Forest, SVM (linear kernel), SVM (Gaussian kernel) | 0.638, 0.639, 0.639, 0.645, 0.644, 0.611, 0.593, 0.651 | Li et al. (2015) |
| 477 parents and 950 hybrids        | SY, OY, OC, GLU, FT, SE, LS | 24 403 SNP   | RR-BLUP                | 0.45, 0.75, 0.81, 0.61, 0.56, 0.29, 0.39 | Jan et al. (2016) |
| TN DH population                   | OC, PC, EAC, LEN, SAC, GLU | 60K DNA array | RR-BLUP, BayesC, EG-BLUP, GBLUP, MAS | 0.76, 0.66, 0.89, 0.76, 0.81, 0.79 | Zou et al. (2016b) |
| TN DH population and 318 hybrids   | SY                       | 60K DNA array | GBLUP (A), GBLUP (A + D), GBLUP (A + D + E) | 0.49 (A), 0.65 (A + D), 0.72 (A + D + E) | Liu et al. (2017) |
| 225 parents and 448 hybrids        | SY, TSW, SE, FT, OC, PC, GLU | 60K DNA array | GCA RR-BLUP, GCA + SCA RR-BLUP, RR-BLUP + de novo GWAS | 0.35–0.82 (SY to GLU) | Werner et al. (2018) |
| 67 parents and 363 hybrids         | SY, FT, SN, TSW, GLU, EAC, OC, OLE, LEI, LEN | 43 106 SNP (SNP) + 5496 (SNP) | GBLUP (SNP + A + D), GBLUP (SNP + A + D), GBLUP (SNP + A + D), GBLUP (SNP + SNP + A + D) | 0.73, 0.97, 0.77, 0.65, 0.97, 0.99, 0.99, 0.91, 0.83 | Hu et al. (2020) |
| A DH population with 148 lines     | SY, FT, MAT, FD, TSW, OC, PC, GLU, SAT | 368 SNP | GBLUP | 0.14, 0.54, 0.58, 0.53, 0.66, 0.42, 0.55, 0.56, 0.47 | Koscielnyn et al. (2020) |
| 377 parents and 750 hybrids        | SY, OY, SE, PC, FT, OC, GLU, LA, Biovolume, PH, MPH-LA, MPH-PH, MPH-Biovolume | 13 201 SNP + 19 479 transcripts + 154 primary metabolites | GBLUP, RKHS | 0.32, 0.53, 0.27, 0.53, 0.64, 0.70, 0.61, 0.61, 0.59, 0.46, 0.42, 0.37 | Knoch et al. (2021) |
| 218 plants                         | Sclerotinia stem rot resistance | 24 634 SNP | LMM (A), LMM (A + AA), Bayes A, Bayes B, Bayes C, LASSO, BR | 0.74, 0.76, 0.56, 0.69, 0.68, 0.63, 0.70 | Derbyshire et al. (2021) |

SY, seed yield; PH, plant height; LA, leaf area; FT, flowering time; FD, flowering duration; MAT, number of days to maturity; PC, protein content; OC, Oil content; GLU, glucosinolate content; OY, oil yield; SE, seedling emergence; LS, lodging resistance; EAC, erucic acid content; SAT, saturated fatty acid content; LEN, linolenic acid content; SAC, stearic acid content; SN, seed number per pod; TSW, thousand seeds weight; OLE, oleic acid content; LEI, linoleic acid content. BLUP, best linear unbiased prediction; RR-BLUP, ridge regression BLUP; BBR, Bayesian Ridge Regression; GBLUP, genomic best linear unbiased prediction; EG-BLUP, extended GBLUP; LMM, linear mixed models; RKHS, reproducing kernel Hilbert space regression based on Gaussian kernels; MAS, marker-assisted selection; MPH, middle parent heterosis; GCA, general combining ability; SCA, specific combining ability; A, additive effects; D, dominance effects; E, epistatic interaction effects; SNP, SNP markers identified with traditional *B. napus* reference genome; SNP, species specific introgression SNP markers.

 variants (Song et al., 1995; Udall et al., 2005). However, this germplasm was created based on traditional breeding techniques that are often imprecise and long-term processes (Subedi et al., 2020), and their value in trait improvement and heterosis utilization will be improved and fully exploited with the assistance of omics analysis, genome-wide selection, speed breeding, and gene editing technology. First, it is very important to comprehensively dissect the complex genomic structures and pan-genome diversity across the *Brassica* species, which could help build a genome-wide atlas for genome-based improvement. In the future, further reductions in long-reads sequencing costs and increases in population sizes that can be used to detect pan genomic variations are needed for this approach. Second, functional genomics and genome-editing approaches for important genes and pathways should be further advanced with reference to model plant species. Caution needs to be taken when using this approach due to gene subfunctionalization and genome structural variations in this young polyploid species; the functions, structures, copy numbers, and physical positions of the genes could change due to polyploidization, genomic structural variations caused by interspecific and intraspecific crosses, and domestication, adaptation and selection. Third, practical whole genome-wide predictions along with marker-assisted selection on target traits should be explored and performed at the population level to improve breeding values with high efficiency and low costs. High-throughput phenomics and genomics, population genetics, and rapidly developed functional genomics will yield comprehensive and precise (pre) breeding. Last, and very
| Gene          | Phenotype                                          | Gene function                                                                 | Reference                  |
|--------------|---------------------------------------------------|-------------------------------------------------------------------------------|---------------------------|
| BnaEOD3 genes | Shorter siliques, smaller seeds, more seeds per siliqua, higher seed yield | EOD3 (ENHANCER3 OF DA1) plays a key role in controlling the seed size and siliqua length in tomato and Arabidopsis thaliana | Khan et al. (2020)        |
| BnaSDG8.A and BnaSDG8.C | Early flowering | SDG8 (SET DOMAIN GROUP 8) is a pleiotropic gene involved in several plant biological processes, including flowering time and plant size | Jiang et al. (2018)       |
| BnaTFL1 genes | Early flowering, altered plant architecture | TFL1 (TERMINAL FLOWER 1) is a flowering inhibitor and controls the identity of shoot meristem during the plant life span | Sibboon et al. (2020)     |
| BnD14 genes   | Improved architecture and seed yield              | Stigloactone receptor                                                         | Stanic et al. (2021)      |
| BnSPL3 genes  | Developmental delay                                | SPL3 (SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 3) is a key floral activator which acts upstream of LEY, FUL and AP1 in Arabidopsis | Li et al. (2018a)         |
| BnaRGA genes  | Decreased plant height                            | RGA (REPRESSOR OF GA1-3) acts as a master repressor in giberrellic signalling  | Yang et al. (2017)        |
| BnaRGA and BnaAA7 genes | Decreased plant height | Rapid turnover of IAA proteins is essential for normal auxin response | Cheng et al. (2021)       |
| BnaA03.MAX1 and BnaC03.MAX1 | Semi-dwarf, more branches, more siliques, increased yield | MAX1 (MORE AXILLARY GROWTH 1) encodes a cytochrome P450 monoxygenase (CYPI711A1), which is a carlactone oxidase that catalyses the SL biosynthesis | Zheng et al. (2020)       |
| BnaA09.ZEP and BnaC09.ZEP | Orange flowers | The nuclear-encoded plastid enzyme zeaxanthin epoxidase (ZEP) plays a critical role in carotenoid biosynthesis | Liu et al. (2020b)        |
| BnaMLPK genes | Self-incompatibility                               | M-locus protein kinase (MLPK) is thought to interact with the activated SRR and control self-incompatibility | Chen et al. (2019)        |
| BnS6-SM2 genes | Self-incompatibility                               | SCR-methylation-inducing region 2 (Sm2): the Sm2 of the dominant S locus generates small interfering RNAs (siRNAs), which suppresses the expression of the recessive S locus SCR by siRNA-mediated DNA methylation in B. rapa | Dou et al. (2021)          |
| MS5 genes     | Genic male sterility                              | M5S mediates early meiotic progression                                         | Xin et al. (2020)         |
| BnAP2 genes   | Typical sepal carpeloid                           | A-functional genes AP2 is required for sepal and petal development            | Zhang et al. (2018a)      |
| BnA10.LMI1 genes | Lobed leaves | A LATE MERISTEM IDENTIFY1 (LM1)-like gene (BnA10.LMI1) encoding an HD-Zip I transcription factor is the causal gene underlying the BnLILA10 locus, and BnLILA10 is responsible for the lobed-leaf shape in rapeseed | Hu et al. (2018)          |
| BnIAG genes   | Pod shatter resistance                            | The Arabidopsis JAGGED (JAG) gene is a key factor implicated in the regulatory web of dehiscence fruit | Zaman et al. (2019a)      |
| BnaA.ALC.a and BnaA.ALC.a | Pod shatter resistance | The Arabidopsis myc/bHLH gene ALCATRAZ (ALC) enables cell separation in fruit dehiscence | Braatz et al. (2017)      |
| BnIND genes   | Pod shatter resistance                            | IND (INDEHISCENT) is important for the formation of both the lignified and separation layers of the valve margin | Zhai et al. (2019)        |
| BnCLV genes   | Multilocular silique                               | The CLAVATA (CLV) pathways act in a feedback loop to regulate many aspects of stem cell function, including cell fate, proliferation, and growth in Arabidopsis | Yang et al. (2018)        |
| BnaTT2 genes  | Yellow seeds, increased oil content, higher linoleic acid, and linolenic acid | TT2 (Transparent Testa) genes are involved in the flavonoid biosynthetic pathway. TT2 regulates proanthocyanidin biosynthesis in seeds | Xie et al. (2020)         |
| BnTT8 genes   | Same as above                                      | TT8 is a central component of the well-conserved complex that controls flavonoid accumulation in various crops | Zhai et al. (2020)        |
| BnSFAR4, BnSFAR5 | Higher oil content                              | SFAR (SEED FATTY ACID REDUCER) genes have a significant effect on seed oil content | Karunarathna et al. (2020) |
| BnaA.FAD2 genes | Increased oleic acid in seed | FAD2 (FATTY ACID DESATURASE 2) catalyses the desaturation of oleic acid (C18:1) to linoleic acid (C18:2) | Huang et al. (2020); Okuzaki et al. (2018) |
| BnITPK genes  | Reduced phytic acid in seeds                      | Enzyme ITPK (inositol tetrakisphosphate kinase) catalyses the penultimate step for the synthesis of PA in plants | Sashidhar et al. (2020) |
| BnLAT2, BnLAT5 genes | Enlarged oil bodies and increased | Lysophosphatic acid acyltransferase (LPAT), a key enzyme in the Kennedy pathway, catalyses fatty acid chains into 3-phosphoglycerate and promotes further production of oil in the form of triacylglycerol | Zhang et al. (2019) |
| BnaRGA genes  | Drought tolerance                                 | RGA (REPRESSOR OF GA7-3) is a nuclear protein that negatively regulates the gibberrellin signal transduction pathway | Wu et al. (2020b)         |
| BnALS genes   | Herbicide resistance                              | Acetolactate synthase (ALS), a key enzyme for the biosynthesis of branchedchain amino acids, is the target site of several important herbicides | Cheng et al. (2021); Wu et al. (2020a) |
| BnWRKY11 and BnWRKY70 | Sclerotinia resistance | Many WRKY transcription factors associates with disease resistance in Arabidopsis | Sun et al. (2018)         |
Importantly, along with the accumulating genome sequences, genotypes, phenotypes, populations, germplasms, and other genomic and genetic resources, an automatic and integrated platform could be developed and would significantly improve theoretical and breeding research in rapeseed. This platform will require international efforts regarding sharing, integrating, and exchanging data. These finding would revolutionize rapeseed genomic improvement, contribute to the sustainable development of the rapeseed industry, and provide new insights into the genome evolution and breeding design of *B. napus* and even other novel *Brassica* allopolyploids.

**Acknowledgements**

This work was supported by the National Natural Science Foundation of China (31861133016, 31970564) and the Deutsche Forschungsgemeinschaft (DFG, grants MA6473/2-1, MA6473/3-1 and SN14/22-1). ASM is also partially funded by the National Natural Science Foundation of China (32000397). We acknowledged Dr. Jochen C. Reif from Department of Breeding Research, Leibniz Institute of Plant Genetics and Crop Plant Research (IPK) for his constructive suggestion for this review. We acknowledged the reviewers and editors for their constructive and helpful revision suggestions.

**Conflict of interest**

The authors declare that they have no competing interests.

**Author contributions**

IZ conceptualized the manuscript; DH, JJ, and IZ drafted the manuscript; DH prepared Figures, Tables and Supplementary Tables; JJ prepared Figure 1, Figure 3, and Table 1; IZ, RJS, ASM, JS, and JM contributed to critical revisions of the manuscript. All authors approved the final version for submission.

**References**

Abbott, R.I. (1992) Plant invasions, interspecific hybridization and the evolution of new plant taxa. Trends Ecol. Evol. 7, 401–405.

Abel, S., Möllers, C. and Becker, H.C. (2005) Development of synthetic *Brassica napus* lines for the analysis of “fixed heterosis” in allopolyploid plants. Euphytica, 146, 157–163.

Agegnehu, G., Lakev, B. and Nelson, P.N. (2014) Copping sequence and nitrogen fertilizer effects on the productivity and quality of malting barley and soil fertility in the Ethiopian highlands. Arch. Agron. Soil Sci. 60, 1261–1275.

Albertin, W., Ballau, T., Brabant, P., Chevre, A.M., Eber, F., Malosse, C. and Thiellement, H. (2006) Numerous and rapid nonstochastic modifications of gene products in newly synthesized *Brassica napus* allotetraploids. Genetics, 173, 1101–1113.

Alemayehu, N. and Becker, H. (2002) Genotypic diversity and patterns of variation in a germplasm material of Ethiopian mustard (*Brassica carinata* A. Braun). Genet. Resour. Crop Ev. 49, 573–582.

Allender, C.J. and King, G.J. (2010) Origins of the amphiplioid species *Brassica napus* L. investigated by chloroplast and nuclear molecular markers. BMC Plant Biol. 10, 54.

An, H., Qi, X.S., Gaynor, M.L., Hao, Y., Gebken, S.C., Mabry, M.E., McAlvay, A.C. et al. (2019) Transcriptome and organellar sequencing highlights the complex origin and diversification of allotetraploid *Brassica napus*. Nat. Commun. 10, 2878.

Applequist, L.A. and Ohlson, R. (1972) Rapsed. Missouri, USA: Elsevier.

Araus, J.L. and Kefauver, S.C. (2018) Breeding to adapt agriculture to climate change: affordable phenotyping solutions. Curr. Opin. Plant Biol. 45, 237–247.

Attri, R. and Rahman, H. (2018) Introgresion of allelic diversity from genetically distinct variants of *Brassica rapa* into *Brassica napus* canola and inheritance of the *B. rapa* alleles. Crop Pasture Sci. 69, 94–106.

Bai, M.Y., Yuan, J.H., Kuan, H.Q., Gong, P.P., Li, S.N., Zhang, Z.H., Liu, B. et al. (2020) Generation of a multiplex mutagenesis population via pooled CRISPR-Cas9 in soybean. Plant Biotechnol. J. 18, 721–731.

Bancroft, I., Morgan, C., Fraser, F., Higgins, J., Wells, R., Clisold, L., Baker, D. et al. (2011) Dissecting the genome of the polyploid crop *oilsed rape* by transcriptome sequencing. Nat. Biotechnol. 29, 762–766.

Bannenrot, H., Boulidard, L., Couderon, Y. and Temple, J. (1974) Transfer of cytoplasmic male sterility from *Raphanus sativus* to *Brassica oleracea*. In Proc. Euphrasia Meet Cruciferae (Willis, A. B. and North, C., eds), pp. 52–54. Dunedin: Scottish Hortic Res Inst, Invergavrie.

Becker, H.C., Engqvist, G.M. and Karisson, B. (1995) Comparison of rapeseed cultivars and researcherized lines based on allozyme and RFLP markers. Theor. Appl. Genet. 91, 63–67.

Bennett, R.A., Thiagarajah, M.R., King, J.R. and Rahman, M.H. (2008) Interspecific cross of *Brassica oleracea* var. albaglbra and *B. napus*: effects of growth condition and sique age on the efficiency of hybrid production, and inheritance of eradic acid in the self-pollinated backcross generation. Euphytica, 164, 593–601.

Bernard, R. (2016) Bandwagons I, too, have known. Theor. Appl. Genet. 129, 2323–2332.

Bevan, M.W., Uauy, C., Wulff, B.B.H., Zhou, J., Krasileva, K. and Clark, M.D. (2017) Genomic innovation for crop improvement. Nature, 543, 346–354.

Bonnema, G. (2012) Diversity and taxonomy of brassica oil crops. In *Genetics, Genomics and Breeding of Oilseed Brassicas* (Edwards, D., Batley, J., Parkin, I.A. and Kole, C., eds), pp. 47–72. Boca Raton, FL: CRC Press.

Braatza, J., Harloff, H.J., Mascher, M., Stein, N., Himmelbach, A. and Jung, C. (2017) CRISPR-Cas9 targeted mutagenesis leads to simultaneous modification of different homoeologous gene copies in polyploid *oilsed rape* (*Brassica napus*). Plant Physiol. 174, 935–942.

Broeders, M., Herrero-Hernandez, P., Ernst, M.P.T., van der Ploeg, A.T. and Pijnappel, W. (2020) Sharpening the molecular scissors: advances in gene-editing technology. iScience, 23, 100789.

Chalhoub, B., Denoeud, F., Liu, S.Y., Parkin, I.A.P., Tang, H.B., Wang, X.Y., Chiquet, J. et al. (2014) Early allopolyploid evolution in the post-Neolithic *Brassica napus* oilseed genome. Science, 345, 950–953.
Chatterjee, D., Baner, S., Gupta, M., Bhardwaj, S., Salahuddin, B.A. and Banerjee, S.S. (2016) Resynthesis of *Brassica napus* through hybridization between *B. juncea* and *B. carinata*. Theor. Appl. Genet. 129, 977–990.

Chaudhary, H.K., Patnaik, P.K., Kalia, V. and Rather, S.A. (2013) Use of asymmetry in flowering for easy and economical polyploid induction in wheat following *Imperata cylindrica*-mediated chromosome elimination approach. *Plant Breed.* 132, 155–158.

Chauhan, S., Mane, H., Girish, P., Palliyakunnel, S., Ahmed, M., Reddy, B.M. and Reddy, G.V. (2013) Transcriptomic analysis reveals widespread intragenic structural variants in a recent allopolyploid oilseed crop plant. *Plant Biotechnol. J.* 19, 240–250.

Chen, C.P., Xiao, L. and Du, D.Z. (2018b) Advances in multilocule rapeseed. *Chin. J. Oil Crop Sci.* 40, 446–451. [In Chinese with English abstract].

Chen, F., Yang, Y., Li, B., Liu, Z., Khan, F., Zhang, T., Zhou, G. et al. (2019) Functional analysis of M-Locus protein kinase revealed a novel regulatory mechanism of self-incompatibility in *Brassica napus*. *Int. J. Mol. Sci.* 20, 3303.

Chen, H.F., Wang, H. and Li, Z.Y. (2017) Production and genetic analysis of partial hybrids in intertribal crosses between *Brassica* species (*B. rapa*, *B. napus*) and *Capsella bursa-pastoris*. *Plant Cell Rep.* 36, 1791–1800.

Chen, H.G. and Wu, J.S. (2008) Characterization of fertile amphiploid between *Raphanus sativus* and *Brassica albovagina* and the crossability with *Brassica* species. *Genet. Resour. Crop Ev.* 55, 143–150.

Chen, J.P., Ge, X.H., Yao, X.C., Feng, Y.H. and Li, Z.Y. (2011) Synthesis and characterization of fertile amphiploids from a cross between *Capsella bursa-pastoris* and *Euphytia*, *Afr. J. Biotechnol.* 10, 12171–12176.

Chen, J.H., Cai, F., Xiong, Q., Feng, C.C., Liu, L., Lu, W. et al. (2018b) A 2.833-kb insertion in *BnFLC.C2* during breeding selection generated early-flowering rapeseed. *Mol. Plant*. 11, 222–225.

Chen, L., Dong, F.M., Cai, J., Xin, Q., Fang, C.C., Liu, L., Wan, L. et al. (2018c) Broad-spectrum resistance of *B. juncea* to *B*. *atroviolacea* and *B*. *napus* through hybridization between *Brassica* species. *Genet. Resour. Crop Ev.* 55, 143–150.

Chen, L.P., Ge, X.H., Yao, X.C., Feng, Y.H. and Li, Z.Y. (2011) Synthesis and characterization of interspecific trigenomic hybrids and allohexaploids between three cultivated *Brassica* allotetraploids and wild species *Brassica fruticeola*. *Afr. J. Biotechnol.* 10, 483–492.

Chen, Z.J. and Pikaard, C.S. (1997) Epigenetic silencing of RNA polymerase I transcription: a role for DNA methylation and histone modification in nucleolar dominance. *Genes Dev.* 11, 2124–2136.

Cheng, B.F., Seguin-Swartz, G. and Somers, D.J. (2002) Cytagenetics and molecular characterization of intergeneric hybrids between *Brassica napus* and *Orychophragmus violaceus*. *Genome*, 45, 110–115.

Cheng, F., Sun, R., Hou, X., Zheng, H., Zhang, F., Zhang, Y., Liu, B. et al. (2016) Subgenome parallel selection is associated with morphotype diversification and convergent crop domestication in *Brassica rapa* and *B. carinata*. *Crop Pasture Sci.* 67, 483–492.

Cheng, H., Hao, M., Ding, B., Mei, D., Wang, W., Wang, H., Zhou, R. et al. (2021) Base editing with high efficiency in allopolyploid oilseed rape by A3A-PBE system. *Plant Biotechnol. J.* 19, 87–97.

Cheng, J.H., Li, Y.C., Hu, Q., Mei, D.S., Li, Y.D., Xu, Y.S. and Wang, W.M. (2008) Molecular identification and distinctness of *N* seedling male sterile cytoplasm in *Brassica napus*. *Acta Agron. Sin.* 34, 1946–1952. [In Chinese with English abstract].

Chikkaputtinaiah, C., Debbarma, J., Baranu, I., Navickova, L., Borouh, H.P.D. and Curr, V. (2017) Molecular genetics and functional genomics of abiotic stress-responsive genes in oilseed rape (*Brassica napus* L.): a review of recent advances and future. *Plant Biotechnol. Rep.* 11, 365–384.

Cowling, W.A. (2007) Genetic diversity in *Australasian canola* and implications for crop breeding for changing future environments. *Field Crop Res.* 104, 103–111.

Damania, A.B., Valkoun, J., Wilcox, G. and Quaile, C.O. (1997) *The Origins of Agriculture and Crop Domestication*: The Harlan Symposium. California, CA: ICARDA, PGR, FAO and UC/GRCP Publishers.

Dang, B. and Chen, J. (2015) Genetic diversity increases heterosis-The sprinter *Brassica napus* project. In 14th International Rapeseed Congress, pp. 43. Saskatoon, Saskatchewan, Canada 43.

Derbyshire, M.C., Khen try, Y., Severn-Ellis, A., Mwape, V., Saad, N.S.M., Newman, T.E., Taiwo, A. et al. (2021) Modeling first order additive x additive epistasis improves accuracy of genomic prediction for sclerotinia stem rot resistance in canola. *Plant Genome*, e20088.

Dhaliwal, I., Mason, A.S., Baner, S., Bhardwaj, S., Kaur, B., Gurung, A.M., Salisbury, P.A. et al. (2017) Cytogenetic and molecular characterization of *B. napus* introgression lines of *Brassica napus* L. *Genes Genomes Genet.* 7, 77–86.

Diederichsen, E., Li, Y., Luo, P., Zeitler, T. and Chen, J. (2015) Resynthesis of *B. napus* through hybridization between *B. juncea* and *B. carinata*. *Genome Res.* 25, 34–45.

Dandan Hu

Dolatabad Amin, A., Bley, P.E., Timraz, S., Hurbolin, B., Edwards, D. and Batley, J. (2020) Characterization of disease resistance genes in the *Brassica napus* pangeneome reveals significant structural variation. *Plant Biotechnol. J.* 18, 969–982.

Dou, S.W., Zhang, T., Tu, J.X., Shen, J.X., Yi, B., Wen, J., Fu, T.D. et al. (2021) Generation of novel self-incompatible *Brassica napus* by CRISPR/Cas9. *Plant Biotechnol. J.* 19, 875–877.

Du, X.Z., Gu, H.X., Zhao, Z.G. and Li, Z.Y. (2008) Chromosome elimination and fragmentation introgression and recombination producing intertribal partial hybrids from *Brassica napus* x *Lesquerella fendleri* crosses. *Plant Cell Rep.* 27, 261–271.

Du, X.Z., Ge, X.H., Yao, X.C., Zhao, Z.G. and Li, Z.Y. (2009) Production and cytagenetic characterization of intertribal somatic hybrids between *Brassica napus* and *batsis indicotica* and backcross progenies. *Plant Cell Rep.* 28, 1105–1113.

Dubcovsky, J. (2004) Marker-assisted selection in public breeding programs: the wheat experience. *Crop Sci.* 44, 1895–1898.

Editorial (2021) Next-generation crop engineering. *Nat. Plants*, 7, 241.

Eure, H. and Miura, K. (2018) Genome editing technologies for plant physiology. *Plant Physiol. Biochem.* 131, 1.

Fahlgren, N., Feldman, M., Gehan, M.A., Wilson, M.S., Shyu, C., Bryant, D.W., Hill, S.T. et al. (2015) A versatile phenotyping system and analytics platform reveals diverse temporal responses to water availability in *Setaria*. *Mol. Plant*. 8, 1520–1535.

Fang, S., Tang, W., Peng, Y., Gorg, Y., Dai, C., Chai, R. and Liu, K. (2016b) Remote estimation of vegetation fraction and flower fraction in oilseed rape with unmanned aerial vehicle data. *Remote Sens.* 8, 416.

Fang, Y., Zhang, L., Jiao, Y., Liao, J., Luo, L., Ji, S. et al. (2016a) Tobacco rotaped with rapeseed for soil-borne Phytophthora pathogen biocontrol: mediated by rapeseed root exudates. *Front. Microbiol.* 7, 894.

Feng, Y.N., Cui, R., Wang, S.L., He, M.L., Hua, Y.P., Shi, L., Ye, X.S. et al. (2019) Synchronous improvement of subgenomes in allopolyploid: a case of *Sclerotinia* resistance improvement in *Brassica napus*. *Mol. Breed.* 39, 10.

Diederichsen, E., Zou, J., Meng, J. and Frauen, M. (2015) Clubroot control in *Brassica* species. *Int. J. Mol. Sci.* 384.

FitzJohn, R.G., Armstrong, T.T., Newstrom-Lloyd, L.E., Wilton, A.D. and FitzJohn, R.G. (2016) Resynthesis of *B. napus* through hybridization between *B. juncea* and *B. carinata*. *Genome Res.* 25, 34–45. [In Chinese with English abstract].

Fredua-Agyeman, R., Coriton, O., Huteau, V., Parkin, I.A., Chevre, A.M. and Rahman, H. (2014) Molecular cytagenetic identification of *B. napus*.
Katche, E., Quezada-Martinez, D., Katche, E.I., Vasquez-Teuber, P. and Mason, A.S. (2019) Interspecific hybridization for Brassica crop improvement. Crop Breed. Genet. Genom. 1, e1900077.

Kebede, B., Thiagarajah, M., Zimmerli, C. and Rahman, M.H. (2010) Improvement of open-pollinated spring rapeseed (Brassica napus L.) through introgression of genetic diversity from winter rapeseed. Crop Sci. 50, 1236–1243.

Khan, M.H.U., Hu, L.M., Zhu, M.S., Zhai, Y.G., Khan, S.U., Ahmar, S., Amoo, O. et al. (2020) Targeted mutagenesis of EOD3 gene in Brassica napus L. regulates seed production. J. Cell Physiol. 236, 1996–2007.

Kiani, S.F. and Qiu, Q.F. (1992) Trait inheritance, fertility, and genomic relationships of some n ~ 9 Brassica species. Genet. Resour. Crop Ev. 39, 165–175.

Kimer, D.S. and McGregor, D.I. (1995) The species and their origin, cultivation and world production. In Brassica Oilseeds: Production and Utilization (Kimer, D.S. and McGregor, D.I., eds), pp. 1–9. Wallingford, CT: CABI Publishing.

Knee, E.M., Rivero, L., Crist, D., Grotewold, E. and Scholl, R. (2011) Germplasm and molecular resources. In Genetics and Genomics of the Brassicaceae (Schmidt, R. and Bancroft, I., eds), pp. 437–467. New York, NY: Springer.

Knoch, D., Abbadi, A., Grandke, F., Meyer, R.C., Samans, B., Werner, C.R., Koscielny, C.B., Gardner, S.W., Technow, F. and Duncan, R.W. (2020) Linkage mapping and whole-genome predictions in canola (Brassica napus) subjected to differing temperature treatments. Crop Pasture Sci. 71, 229–238.

Kryzmasj, J. (1978) Double low winter rape for Poland (Brassica napus). In International Rapeseed Conference. June 12–16, 1978. Malmoe (Sweden).

Kumar, P., Singh, K.P. and Rai, P.K. (2020) Draft genome of multiple resistance donor plant Sinapis alba: an insight into SSRs, annotations and phylogenetics. PLoS One, 15, e0231002.

Lange, W., Toxopeus, H., Lubberts, J.H., Dolstra, O. and Harrewijn, J.J.L. (1989) The development of raparadish (X Brassicoraphanus, 2n = 38), a new crop in agriculture. Euphytica, 40, 1–14.

Larkan, N.J., Lydiate, D.J., Parkin, I.A.P., Nelson, M.N., Epp, D.J., Cowling, W.A., Lu, K., Wei, L.J., Li, X.L., Wang, Y.T., Wu, J., Liu, M., Zhang, C. et al. (2020) High-throughput phenotyping accelerates the dissection of the dynamic and complex genetic network underlying flowering time variation in oilseed rape. Plant Biotechnol. J., 21, 1–19. [In Chinese with English abstract].

Li, H., Long, Y., Zhang, L., Dalton-Morgan, J., Batley, J., Yu, L., Meng, J. et al. (2015) Genome-wide analysis of flowering time trait in multiple environments via high-throughput genotyping technique in Brassica napus L. PLoS One, 10, e0119425.

Li, M.T., Chen, X. and Meng, J.L. (2006) Interspecific heterosis in rapeseed production with a partial new-typed Brassica napus containing subgenome A' from B. rapa and C' from Brassica carinata. Crop Sci. 46, 234–242.

Li, Q.F., Zhou, Q.H., Mei, J.Q., Zhang, Y.J., Li, J.N., Li, Z.Y., Ge, X.H. et al. (2014) Improvement of Brassica napus via interspecific hybridization between B. napus and B. oleracea. Mol. Breeding. 34, 1955–1963.

Li, T., Yang, X., Yu, Y., Si, X., Zhai, X., Zhang, H., Dong, W. et al. (2018) Domestication of wild tomato is accelerated by genome editing. Nat. Biotechnol. 36, 1160–1163.

Liu, X.J., Teigtgen, A.M., Shirani, A., Ling, J., Busta, L., Cao, H.R., Zheng, W. et al. (2018) Discontinuous fatty acid elongation yields hydroxylated seed oil with improved function. Nat. Plants, 4, 711–720.

Liu, Z.Y. (2020) Interspecific hybridization and germplasm innovation in Brassica Crops. J. Plant Genet. Resour. 21, 20–25. [In Chinese with English version].

Light, K.A., Gororo, N.N. and Salisbury, P.A. (2011) Usefulness of winter canola (Brassica napus) race-specific resistance genes against blackleg (causal agent Leptosphaeria maculans) in southern Australian growing conditions. Crop Pasture Sci. 62, 162–168.

Liu, H.L. (2000) Genetics and Breeding of Rapeseed. Beijing: China Agricultural University Press.

Liu, H.J., Jian, L., Xu, J., Zhang, Q., Zhang, M., Jin, M., Meng, Y. et al. (2020c) High-throughput CRISPR/Cas9 mutagenesis streamlines trait gene identification in maize. Plant Cell, 32, 1397–1413.

Liu, J., Hao, W.J., Liu, J., Fan, S.H., Zhao, W., Deng, L.B., Wang, X.F. et al. (2019) Novel chimeric mitochondrial gene confers cytoplasmic effects on seed oil content in polyploid rapeseed (Brassica napus). Mol. Plant, 12, 582–596.

Liu, F., Zhao, Y., Liu, G., Wang, M., Hu, D., Hu, J., Meng, J. et al. (2017) Hybrid performance of an immortalized F1 rapeseed population is driven by additive, dominance, and epistatic effects. Front. Plant Sci. 8, 815.

Liu, S., Huang, H.B., Yi, X.Q., Zhang, Y.Y., Yang, Q.Y., Zhang, C.Y., Fan, C.C. et al. (2020a) Dissection of genetic architecture for glucosinolate accumulations in leaves and seeds of Brassica napus by genome-wide association study. Plant Biotechnol. J. 18, 1472–1484.

Liu, S.Y., Liu, Y.M., Yang, X.H., Tong, C.B., Edwards, D., Parkin, I.A.P., Zhao, M.X. et al. (2014) The Brassica oleracea genome reveals the asymmetrical evolution of polyploid genomes. Nat. Commun. 5, 3930.

Liu, Y.P., Xu, A.X., Liang, F.H., Yao, X.Q., Wang, Y., Liu, X., Zhang, Y. et al. (2018) Screening of clubroot-resistant varieties and transfer of clubroot resistance genes to Brassica napus using distant hybridization. Breed. Sci. 68, 256–267.

Liu, Y., Ye, S., Yuan, G., Ma, X., Heng, S., Yi, B., Ma, C. et al. (2020b) Gene silencing of BnaA09.ZEP and BnaC09.ZEP confers orange color in Brassica napus flowers. Plant J. 104, 932–949.

Liu, Z.S., Guan, C.Y., Chen, S.Y., Liu, S.Y. and Yan, L. (2010) Transfer of superior traits from Brassica juncea into Brassica napus. Agric. Sci. Technol. 11, 49–52.

Liu, Z., Hirani, A.H., McVetty, P.B., Daayf, F., Quinon, C.F. and Li, G. (2012) Reducing progoitrin and enriching glucoraphanin in Brassica napus seeds through silencing of the GSL-ALK gene family. Plant Mol. Biol. 79, 179–189.

Lu, C.M., Zhang, B., Kakihara, F. and Kato, M. (2001) Introgression of genes into cultivated Brassica napus through resynthesis of B. napus via oxyle culture and the accompanying change in fatty acid composition. Plant Breed. 120, 405–410.

Lu, K., Wei, L.J., Li, X.L., Wang, Y.T., Wu, J., Liu, M., Zhang, C. et al. (2019) Whole-genome resequencing reveals Brassica napus origin and genetic loci involved in its improvement. Nat. Commun. 10, 1154.

Lu, Y.M., Ye, X., Guo, R.M., Huang, J., Wang, W., Tang, J.Y., Tan, L.T. et al. (2017) Genome-wide targeted mutagenesis in rice using the CRISPR/Cas9 system. Mol. Plant, 10, 1242–1245.

Lukens, L.N., Pires, J.C., Leon, E., Vogelzang, R., Oslach, L. and Osborn, T. (2007) Whole-genome resequencing reveals a novel genetic system. Mol. Breed. 19, 1165–1177.

Lun, K., Wang, L., Ke, W., Jiang, L., Li, K. et al. (2021) Hierarchical gene expression analysis in response to root-knot nematode infection. Front. Plant Sci. 12, 748.

Luo, C., Fernie, A.R. and Yan, J.B. (2020) Single-cell genomics and epigenomics: technologies and applications in plants. Trends Plant Sci. 25, 1030–1040.

© 2021 The Authors. Plant Biotechnology Journal published by Society for Experimental Biology and The Association of Applied Biologists and John Wiley & Sons Ltd., 1–20.
Wan, L., Neik, T.X. and Batley, J. (2020) The use of genetic and gene technologies in shaping modern rapeseed cultivars (Brassica napus L.). Genes, 11, 1161.

Tu, Y.Q., Sun, J., Ge, X.H. and Li, Z.Y. (2010) Production and genetic analysis of partial hybrids from intertrial sexual crosses between Brassica napus and L. germplasm in hybridization between Brassica napus and Brassica carinata. J. Plant Genet. Resour. 21, 74–82. [In Chinese with English abstract].

Udal, J.A., Quijada, P.A., Polewicz, H., Vogelzang, R. and Osborn, T.C. (2004) Phenotypic effects of introgressing Chinese winter and resynthesized Brassica napus L. germplasm into hybrid spring canola. Crop Sci. 44, 1990–1996.

Udal, J.A., Quijada, P.A. and Osborn, T.C. (2005) Detection of chromosomal rearrangements derived from homeologous recombination in four mapping populations of Brassica napus L. Genetics, 169, 967–979.

UN (1935) Genomic analysis in Brassica with special reference to the experimental formation of B. napus and peculiar mode of fertilization. Jpn. J. Bot. 7, 389–452.

Vollrath, P., Chawla, H.S., Schiessl, S.V., Gabur, I., Lee, H.T., Snowdon, R.J. and Wei, L.J., An, Z.S., Mason, A.S., Xiao, M.L., Guo, Y., Yin, J.M., Li, J.N. (2021) Brassicaceae in agriculture. In Wang, J., Gao, Y.N., Kong, Y.Q., Jiang, J.J., Li, A.M., Zhang, Y.T. and Wang, G.C., He, J.P., Hong, D.F., Xie, Y.Z., Xu, Z.H., Liu, P.W. and Yang, G.S. (ª2021 The Authors.

Warwick, S.I. (2011) Genome-wide regression models considering general combining ability predict hybrid performance in oilseed rape with similar accuracy regardless of trait architecture. Theor. Appl. Genet. 131, 743–754.

Xia, S.Q., Wang, Z.X., Zhang, H.Y., Hu, K.N., Zhang, Z.Q., Qin, M.M., Dun, X.L. et al. (2016) Altered transcription and nonfunctionalization of duplicated genes rescue the harmful effects of a chimeric gene in Brassica napus. Plant Cell, 28, 2060–2078.

Xiao, Y., Chen, L., Zou, J., Tian, E., Xiao, W. and Meng, J. (2010) Development of a population for substantial new type Brassica napus diversified at both A/C genomes. Theor. Appl. Genet. 121, 1141–1150.

Xiong, Z., Gaeta, R.T. and Pires, J.C. (2011) Homoeologous shuffling and chromosome compensation maintain genome balance in resynthesized allopolyploid Brassica napus. Proc. Natl Acad. Sci. USA, 108, 7908–7913.

Xu, P., Cao, S.Q., Hu, K.N., Wang, X.H., Huang, W., Wang, G., Lv, Z.W. et al. (2017) Trifoliate phenotype in Brassica juncea L. resulted from interruption of ClAVATA1 gene homologue (BnCvi1) transcription. Sci. Rep. 7, 3498.

Yao, Y.M., Liu, H.D., Xu, L. and Du, D.Z. (2013) Enhancing the heterosis of spring rapeseed varieties (Brassica napus L.) by using semi-winter rapeseed varieties as parents. Acta Agron. Sin. 39, 118–125. [In Chinese with English abstract].
Zhang, W.S., Hu, D.D., Raman, R., Guo, S.M., Wei, Z.L., Shen, X.Q., Meng, J.L., Zhang, X.L., Ge, X.H., Shao, Y.J., Sun, G.L. and Li, Z.Y. (2013) Genomic change, accounting for important agronomic and seed quality traits in Brassica and related species.

Zhan, Z.X., Nwafor, C.C., Hou, Z.K., Gong, J.F., Zhu, B., Jiang, Y.F., Zhou, Y.M., Zhang, Q., Chen, H.F., He, M.L., Zhao, Z.Q., Cai, H.M., Ding, G.D., Shi, L., Zhai, Y.G., Cai, S.L., Hu, L.M., Yang, Y., Amoo, O., Fan, C.C. and Zhou, Y.M. (1989) Introgression in Brassica and related species.

Zaman, M.W. (1989) Introgression in Brassica napus for adaptation to the growing conditions in Bangladesh. Theor. Appl. Genet. 77, 721–728.

Zaman, Q.U., Chu, W., Hao, M.Y., Shi, Y.Q., Sun, M.D., Sang, S.F., Mei, D.S., Zaman, M.W. (1989) Introgression in Brassica napus L. Biometabolites, 9, 725.

Zhu, B., Tu, Y.Q., Zeng, P., Ge, X.H. and Li, Z.Y. (2016) Extraction of the constituent subgenomes of the natural allopolyploid rapseed (Brassica napus L.). Genetics, 204, 1015–1027.

Zhu, L.X., Yang, Z.H., Zeng, X.H., Gao, J., Liu, J., Yi, B., Ma, C.Z. et al. (2017) Heme oxygenase 1 defects lead to reduced chlorophyll in Brassica napus L. Plant Mol. Biol. 93, 579–592.

Zhu, X.G. and Zhu, J.K. (2021) Precision genome editing heralds rapid de novo domestication for new crops. Cell, 184, 1133–1134.

Zou, J., Hu, D.D., Mason, A.S., Shen, X., Wang, N., Grandke, F. et al. (2020) Targeted mutagenesis of BnTA8 homologs controls yellow seed coat development for effective oil production in Brassica napus L. Plant Biotechnol. J. 18, 1153–1168.

Zou, J., Fu, D.H., Gong, H.H., Qian, W., Xia, W., Pres, J.C., Liu, Y.V. et al. (2020) De novo genetic variation associated with retrotransposon activation, genomic rearrangements and trait variation in a recombinant inbred line population of Brassica napus derived from interspecific hybridization with Brassica rapa. Plant J. 68, 212–224.

Zou, J., Hu, D.D., Liu, P.F., Raman, H., Liu, Z.S., Liu, J.X., Parkin, I.A.P. et al. (2016a) Co-linearity and divergence of the A subgenome of Brassica juncea compared with other Brassica species carrying different A subgenomes. BMC Genomics, 17, 18.

Zou, J., Hu, D., Mason, A.S., Shen, X., Wang, X., Wang, N., Grandke, F. et al. (2018) Genetic changes in a novel breeding population of Brassica napus synthesized from hundreds of crosses between B. rapa and B. carinata. Plant J. 16, 507–519.

Zou, J., Mao, L., Qiu, J., Wang, M., Jia, L., Wu, D., He, Z. et al. (2019) Genome-wide selection footprints and deleterious variations in young Asian allotetraploid rapseed. Plant Biotechnol. J. 17, 1998–2010.

Zou, J., Zhao, Y., Liu, P., Shi, L., Wang, X., Wang, M., Meng, J. et al. (2016b) Seed quality traits can be predicted with high accuracy in Brassica napus using genomic data. PLoS One, 11, e0166624.

Zou, J., Zhu, J.L., Huang, S.M., Tian, E.T., Xiao, Y., Fu, D.H., Tu, J.X. et al. (2010) Broadening the avenue of intersubgenomic heterosis in oilseed Brassica. Theor. Appl. Genet. 120, 283–290.

Zhao, Q., Wu, J., Cai, G.Q., Yang, Q.Y., Shahid, M., Fan, C.C., Zhang, C.Y. et al. (2019) A novel quantitative trait locus on chromosome A9 controlling oleic acid content in Brassica napus. Plant Biotechnol. J. 17, 2313–2324.

Zheng, M., Zhang, L., Tang, M., Liu, J., Liu, H., Yang, H., Fan, S. et al. (2020) Knockout of two BnMAX1 homologs by CRISPR/Cas9-targeted mutagenesis improves plant architecture and increases yield in rapseed (Brassica napus L.). Plant Biotechnol. J. 18, 644–654.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Favourable traits reported in different Brassica species.

Table S2 Summary of the publicly available genome assemblies of Brassica and related species.