

## Review

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

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## 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 hm<sup>2</sup> 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 (Krzymaniński, 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).

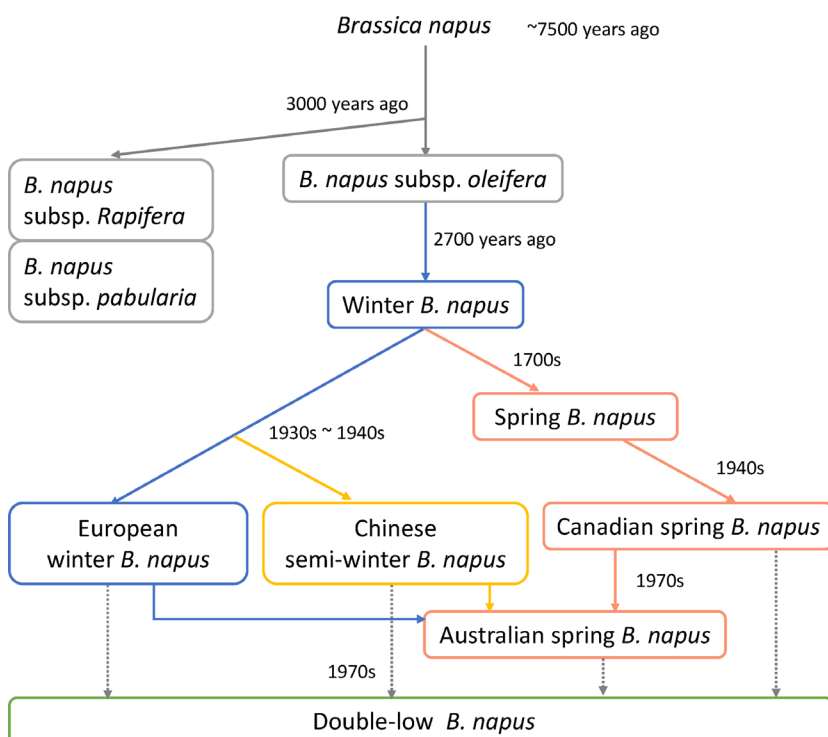
There are tens of thousands of diverse germplasm resources of rapeseed and its related species stored in the major international germplasm banks in China, the United States, the United Kingdom, Korea, India, Germany, Canada, Australia, Russia, Japan and the Netherlands (Knee *et al.*, 2011; Li *et al.*, 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.*, 2010; Qian *et al.*, 2009; Udall *et al.*, 2004). For example, some of the inbred lines derived from rutabaga (*B. napus* var.



**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.

*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.*, 2014; Zou *et al.*, 2016a). These species also have many desirable traits and high genetic diversity, as shown in Table S1

**Table 1** Exotic introgressions and genomic changes of *Brassica napus*

Crops	Hybridization method	Trait introduction	Reference
<b>Intraspecific hybridization</b>			
Spring-type × semi-winter type	Pollination	Heterosis	Qian <i>et al.</i> (2007); Yao <i>et al.</i> (2013)
Spring-type × winter-type	Pollination	Determinate inflorescence Clubroot resistance Black leg resistance Heterosis	Li <i>et al.</i> (2018b) Fredua-Agyeman and Rahman (2016); Rahman <i>et al.</i> (2011) Light <i>et al.</i> (2011) Dang and Chen (2015); Quijada <i>et al.</i> (2006)
Winter-type × semi-winter type	Pollination	Heterosis	Qian <i>et al.</i> (2009)
rutabaga ( <i>B. napus</i> var. <i>napobrassica</i> ) × spring-type	Pollination	Higher seed yield and oil content	Shiranifar <i>et al.</i> (2020)
<b>Introgressions of the genetic components of a single species within <i>Brassica</i></b>			
<i>B. napus</i> × <i>B. rapa</i>	Pollination	Early maturity Clubroot resistance Heterosis	Liu (2000) Hirani <i>et al.</i> (2016); Liu <i>et al.</i> (2018); Zhan <i>et al.</i> (2015) Zhang <i>et al.</i> (2015)
<i>B. napus</i> × <i>B. oleracea</i>	Pollination	Expanded genetic diversity <i>Sclerotinia</i> resistance Self-incompatibility Heterosis	Iftikhar <i>et al.</i> (2018) Mei <i>et al.</i> (2020) Ripley and Beversdorf (2003) Li <i>et al.</i> (2014)
<i>B. oleracea</i> × <i>B. napus</i>	Embryo rescue	Heterosis	Kaminski <i>et al.</i> (2020)
<i>B. juncea</i> × <i>B. napus</i>	Pollination	Pod shattering resistance Yellow seeds Multilocular siliques Blackleg resistance	Prakash and Chopra (1988) Liu <i>et al.</i> (2010) Chen <i>et al.</i> (2018b) Dixelius (1999); Rashid <i>et al.</i> (2018); Schelfhout <i>et al.</i> (2006)
<i>B. napus</i> × <i>B. carinata</i>	Repeated pollination Pollination	Early maturity Determinate inflorescence Blackleg resistance Pod shattering resistance	Zaman <i>et al.</i> (2019b) Tu <i>et al.</i> (2020) Fredua-Agyeman <i>et al.</i> (2014); Navabi <i>et al.</i> (2010) Dhaliwal <i>et al.</i> (2017)
<i>B. fruticulosa</i> × <i>B. napus</i>	Embryo culture		Chen <i>et al.</i> (2011)
<b>Synthetic <i>B. napus</i></b>			
<i>B. rapa</i> × <i>B. oleracea</i> and <i>B. oleracea</i> × <i>B. rapa</i>	Ovary culture Pollination and protoplast fusion Ovule culture		Song <i>et al.</i> (1993) Becker <i>et al.</i> (1995) Lu <i>et al.</i> (2001)
	Ovary culture, embryo culture	Yellow seeds	Wen <i>et al.</i> (2008)
<i>B. rapa</i> × <i>B. oleracea</i>	Ovary culture, embryo culture Embryo rescue	Large seeds <i>Sclerotinia</i> resistance	Fu <i>et al.</i> (2012b) Ding <i>et al.</i> (2019)

Table 1 Continued

Crops	Hybridization method	Trait introduction	Reference
<i>B. oleracea</i> × <i>B. rapa</i>		Yellow seeds	Gaeta <i>et al.</i> (2007); Lukens <i>et al.</i> (2006); Xiong <i>et al.</i> (2011)
	Embryo rescue	Heterosis	Rahman (2001)
<i>B. carinata</i> × <i>B. rapa</i>	Pollination	Heterosis, high linoleic acid and high linolenic acid contents, nitrogen efficiency	Girke <i>et al.</i> (2012); Samans <i>et al.</i> (2017)
			Chen <i>et al.</i> (2010); Qian <i>et al.</i> (2005); Qian <i>et al.</i> (2003); Wang <i>et al.</i> (2015); Xiao <i>et al.</i> (2010); Zou <i>et al.</i> (2018); Zou <i>et al.</i> (2010)
<i>B. juncea</i> × <i>B. carinata</i>	Pollination	Heterosis	Chatterjee <i>et al.</i> (2016)
Exotic introgressions from Brassicaceae beyond interspecific hybridizations with <i>B. napus</i>			
<i>B. napus</i> × <i>O. violaceus</i>	Protoplast fusion	Red flowers, higher oleic and linoleic acid contents	Ding <i>et al.</i> (2013); Fu <i>et al.</i> (2018); Gautam <i>et al.</i> (2016); Ge <i>et al.</i> (2009); Hua and Li (2006); Ma and Li (2007)
<i>B. napus</i> × radish cabbage	Pollination	Clubroot resistance	Zhan <i>et al.</i> (2017)
<i>B. napus</i> × <i>R. sativus</i>	Protoplast fusion	Fertility restored	Sakai <i>et al.</i> (1996)
	Flower culture method	Vigor	Metz <i>et al.</i> (1995)
	Embryo rescue	Clubroot resistance	Diederichsen <i>et al.</i> (2015)
<i>B. napus</i> × <i>I. indigotica</i>	Protoplast fusion	Resistance to influenza virus, cytoplasmic male sterile	Du <i>et al.</i> (2009); Kang <i>et al.</i> (2014); Tu <i>et al.</i> (2020)
<i>B. napus</i> × <i>S. alba</i>	Protoplast fusion	Yellow seeds	Wang <i>et al.</i> (2014)
	Electrofusion	<i>Sclerotinia</i> resistance, yellow seeds	Li <i>et al.</i> (2009)
<i>B. napus</i> × <i>L. fendleri</i>	Pollination and embryo culture	Increased linoleic acid and linolenic acid content	Du <i>et al.</i> (2008)
<i>B. napus</i> × <i>S. arvensis</i>	Protoplast fusion	Cytoplasmic male sterile	Cheng <i>et al.</i> (2008)
<i>B. napus</i> × <i>C. bursa-pastoris</i>	Pollination	Early maturity, double-low quality, <i>Sclerotinia</i> resistance	Chen <i>et al.</i> (2009); Chen <i>et al.</i> (2007); Zhang <i>et al.</i> (2013)

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*

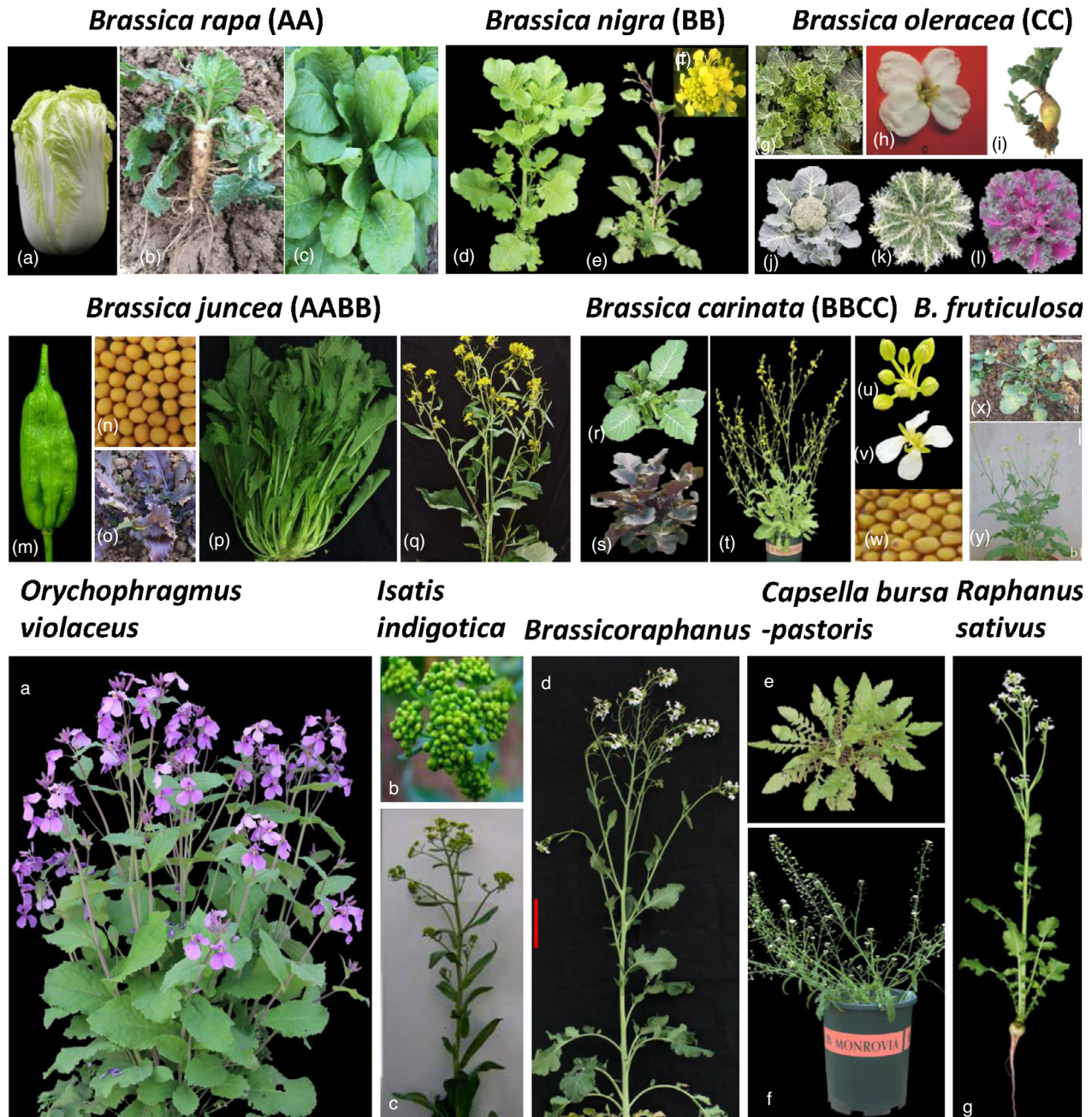
The presence of “shared” *Brassica* genomes with high levels of sequence similarity and organization between multiple species (Chalhoub *et al.*, 2014; Liu *et al.*, 2014; Parkin *et al.*, 2014), has offered a unique opportunity for germplasm improvement (FitzJohn *et al.*, 2007; Kathe *et al.*, 2019). 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 (Paritosh *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) (Dixelius, 1999; Rashid *et al.*, 2018), early maturity (Zaman, 1989), yellow seededness (Liu *et al.*, 2010), pod shatter resistance (Prakash and Chopra, 1988) and multilocular siliqua traits that have potential for high yield (Chen *et al.*, 2018b). Chinese hybrid varieties Huangzaizao, Xiangzayou 631 and Xiangzayou 518, with early maturity, yellow seeds, and a high oil content, has been bred using this approach (Yang *et al.*, 2021).

*Brassica carinata* (Ethiopian mustard,  $2n = 34$ , BBCC) is a very important oilseed crop that has formed slightly earlier than *B. napus* but later than *B. juncea* (Song *et al.*, 2021a) and been cultivated in Ethiopia and neighbouring countries for centuries (Alemayehu and Becker, 2002), and it is a promising and competitive feedstock for

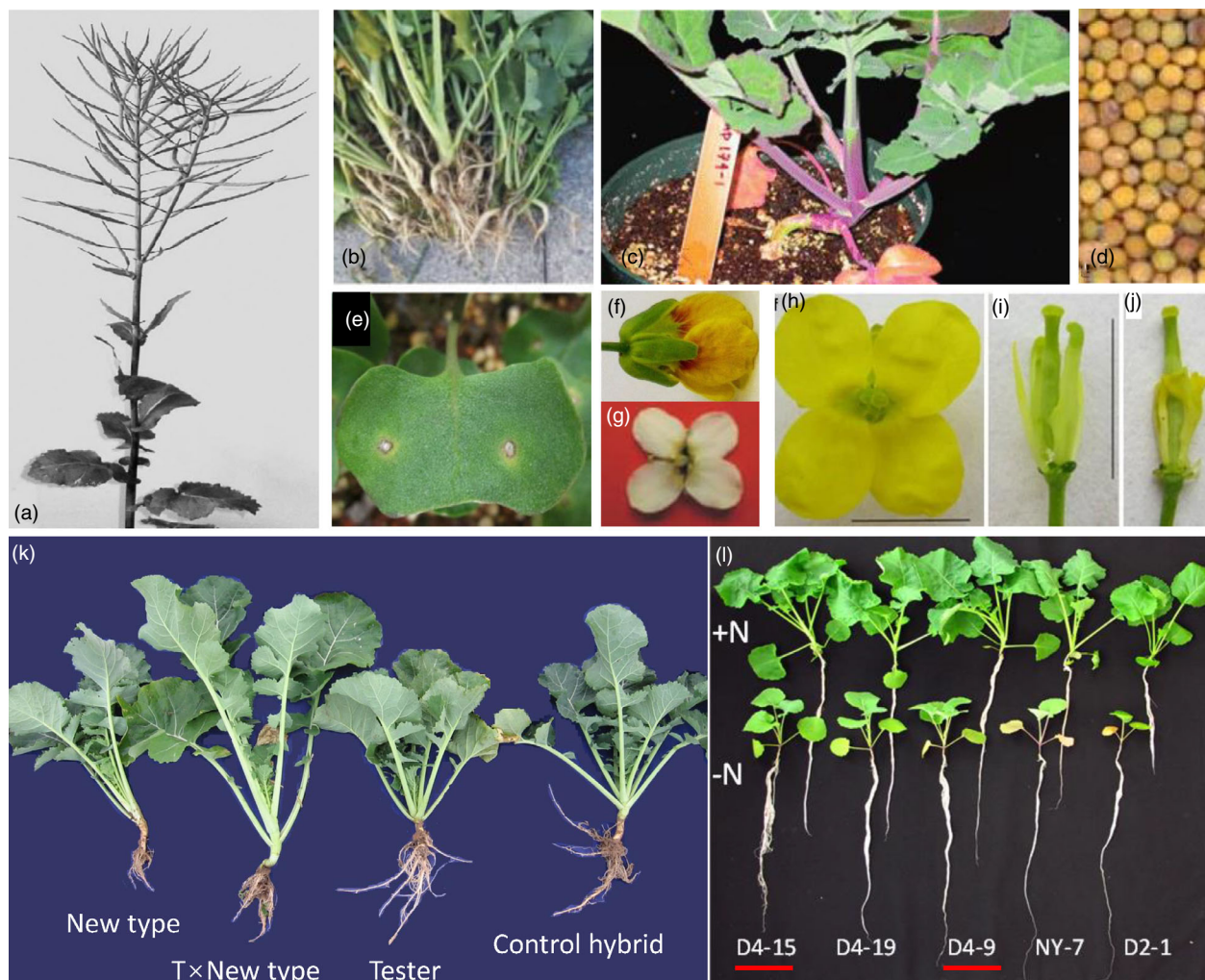


**Figure 2** Diverse germplasm from *Brassica* and its related species. A, B, and C are images of *B. rapa*, where B shows a winter-type oilseed *B. rapa* variety bred by Gansu Agricultural University; D, E, and F are images of *B. nigra*; G (Li *et al.*, 2014), H (Fu *et al.*, 2012b), I–L are images of *B. oleracea*; M–Q are images of *B. juncea*, where M shows a trilocular variety J163-4 (Xu *et al.*, 2017), N shows a variety with yellow seeds, O shows a variety with purple leaves, and P shows a leafy branching line (Muntha *et al.*, 2019); R–W are images of *B. carinata* lines, where R and S show plants in seeding stages with green and purple leaves, respectively, T shows a plants at flowering time, U shows the determinate inflorescence of *B. carinata*, V shows a milky white flower, and W shows yellow seeds (Guo *et al.*, 2012); X and Y shows the seeding stage and flowering stage of *B. fruticulosa* (Chen *et al.*, 2011). a shows flowering plants of *Orychophragmus violaceus*; b and c show flower buds and flowering plant of *Isatis indigotica* (Du *et al.*, 2009); d shows flowering plant of synthetic *Brassicoraphanus* (RRCC) (Zhan *et al.*, 2017); e and f show the seedling stage and flowering stage of *Lesquerella fendleri*; and g shows a flowering plant of *Raphanus sativus*.

bio-based fuel industries (Seepaul *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



**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).

AA and CC genome. As an example, synthetic *B. napus* (A<sup>1</sup>A<sup>1</sup>C<sup>0</sup>C<sup>0</sup>) was created by crossing diploid *B. oleracea* (C<sup>0</sup>C<sup>0</sup>) and *B. rapa* (A<sup>1</sup>A<sup>1</sup>) (superscript represents the first letter of the species name) (Table 1): some lines showed yellow seeds (Figure 3D) (Rahman, 2001; 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<sup>1</sup>A<sup>1</sup>C<sup>1</sup>C<sup>1</sup>) was created by hybridization between artificially synthesized hexaploidy (A<sup>1</sup>A<sup>1</sup>B<sup>1</sup>B<sup>1</sup>C<sup>1</sup>C<sup>1</sup>), 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<sup>1</sup>A<sup>1</sup>C<sup>1</sup>C<sup>1</sup>) was created by interspecific hybridization between *B. juncea* (A<sup>1</sup>A<sup>1</sup>B<sup>1</sup>B<sup>1</sup>) and *B. carinata* (B<sup>1</sup>B<sup>1</sup>C<sup>1</sup>C<sup>1</sup>) 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

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 *Isatis indigotica* ( $2n = 14$ , 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; Kathe *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 (RRCC) (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 (Bannerrot *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. These 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 pangenome 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<sup>1</sup>/A<sup>2</sup>/A<sup>n</sup>, B<sup>1</sup>/B<sup>2</sup>/B<sup>c</sup>, and C<sup>1</sup>/C<sup>2</sup>/C<sup>c</sup> (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<sup>1</sup>A<sup>2</sup>C<sup>1</sup>C<sup>2</sup>) 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.*,

2018; Palacios *et al.*, 2019), changes in tRNA (Wei *et al.*, 2014), and the rapid mutation of repetitive sequences (Gao *et al.*, 2014). Synthetic *B. napus* (A<sup>1</sup>A<sup>1</sup>C<sup>1</sup>C<sup>1</sup>), 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 *I. 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, AACCC) were extracted from the intergeneric allohexaploid AACCCO (2n = 66) (Gautam *et al.*, 2016) and allotetraploid 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; Seyis *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 (Golicz *et al.*, 2016; Hurgobin *et al.*, 2018; Song *et al.*, 2020), gene annotations, transcriptomes, 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://wwwdev.genoscope.cns.fr/brassicannapus/>) (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/bnapus/>) (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.

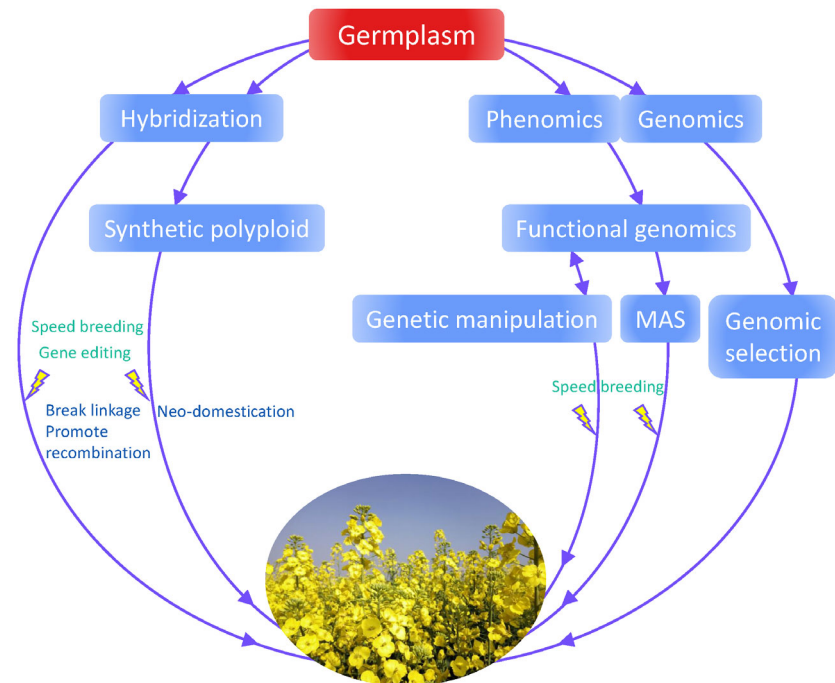
Genotyping and phenotyping are important in the analysis of the genetics architecture of traits and the improvement of crops. However, the laborious and time-consuming traditional manual scoring of phenotypes, which is much slower than high-throughput genotyping, has become the rate-limiting step (Fahlgren *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



**Figure 4** Approaches for further exploring the rapeseed gene pool. MAS represents marker-assisted selection.



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). Genome-wide 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

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

Trait	Trait related genes	Reference
Flowering time	<i>BnFLC.A2</i>	Chen <i>et al.</i> (2018c)
	<i>BnFLC.A10</i>	Hou <i>et al.</i> (2012); Yin <i>et al.</i> (2020)
Male sterility	<i>BnaSDG8</i>	Jiang <i>et al.</i> (2018)
	<i>BnaC9.Tic40</i>	Xia <i>et al.</i> (2016)
	<i>MS5</i>	Xin <i>et al.</i> (2016); Xin <i>et al.</i> (2020)
Plant architecture	<i>BnaTFL1</i>	Sriboon <i>et al.</i> (2020)
	<i>BnD14</i>	Stanic <i>et al.</i> (2021)
	<i>BnaRGA</i>	Yang <i>et al.</i> (2017)
	<i>BnaIAA7</i>	Cheng <i>et al.</i> (2021)
Seed weight and pod length	<i>BnaA9.CYP78A9</i>	Shi <i>et al.</i> (2019)
	<i>BnaEOD3</i>	Khan <i>et al.</i> (2020)
	<i>BnaUPL3.C03</i>	Miller <i>et al.</i> (2019)
Oil content	<i>BnSFAR4</i> , <i>BnSFAR5</i>	Karunaratna <i>et al.</i> (2020)
	<i>Bnaorf188</i>	Liu <i>et al.</i> (2019)
Oil and fatty acid	<i>BnaA.FAD2</i>	Okuzaki <i>et al.</i> (2018)
Phytic acid	<i>BnITPK</i>	Sashidhar <i>et al.</i> (2020)
Pod shattering resistance	<i>BnJAG</i>	Zaman <i>et al.</i> (2019a)
	<i>BnaA.ALCa</i> , <i>BnaC.ALCa</i>	Braatz <i>et al.</i> (2017)
	<i>BnIND</i>	Zhai <i>et al.</i> (2019)
Leaf colour	<i>BnaC07.HO1</i>	Zhu <i>et al.</i> (2017)
Boron absorption	<i>BnaA3.NIP5;1</i>	Hua <i>et al.</i> (2016)
	<i>BnaA9.WRKY47</i>	Feng <i>et al.</i> (2020)
	<i>BnaC4.BOR1;1c</i>	Zhang <i>et al.</i> (2017b)
Blackleg resistance	<i>LepR3</i>	Larkan <i>et al.</i> (2013)
	<i>Rlm9</i>	Larkan <i>et al.</i> (2020)

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 Chikkaput-taiah *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 silique, 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 (Lemmon *et al.*, 2018; Li *et al.*, 2018d; Yu *et al.*, 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 orphan 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 neodomestication of synthetic *Brassica* polyploids and wild species by rapidly editing genes related to domestication, genome stability, and recombination.

### Outlook

Allotetraploid *B. napus* is the youngest *Brassica* species (Song *et al.*, 2021a); it has a complex genome that is accompanied by chromosomal structural variation and characteristics that have driven and will continue to drive its evolution. In addition, the large-scale interspecific hybridization has accumulated unique resources with rich genetic diversity and genomic structural

**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) 0.34–0.81 (SY to PH)	Wurschum <i>et al.</i> (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 <i>et al.</i> (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 <i>et al.</i> (2016)
TN DH population	OC, PC, EAC, LEN, SAC, GLU	60K DNA array	RR-BLUP, BayesC $\pi$ , EG-BLUP, GBLUP, MAS	0.76, 0.66, 0.89, 0.76, 0.81, 0.79	Zou <i>et al.</i> (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 <i>et al.</i> (2017)
225 parents and 448 hybrids	SY, TSW, SE, FT, OC, PC, GLU	60K DNA array	GCA RR-BLUP GCA + SCA RR-BULP RR-BULP + <i>de novo</i> GWAS GCA BayesB GCA + SCA BayesB GCA BBR + SCA BayesB	0.35–0.82 (SY to GLU)	Werner <i>et al.</i> (2018)
67 parents and 363 hybrids	SY, FT, SN, TSW, GLU, EAC, OC, OLE, LEI, LEN	43 106 (SNP <sub>T</sub> ) + 5496 (SNP <sub>S</sub> )	GBLUP (SNP <sub>T</sub> + A + D) GBLUP (SNP <sub>S</sub> + A + D) GBLUP (SNP <sub>T+S</sub> + A + D) GBLUP (SNP <sub>T</sub> + SNP <sub>S</sub> + A + D) GBLUP (SNP <sub>T+S</sub> + A + D + E)	0.73, 0.97, 0.77, 0.65, 0.97, 0.99, 0.70, 0.99, 0.91, 0.83	Hu <i>et al.</i> (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	Koscielny <i>et al.</i> (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 <i>et al.</i> (2021)
218 plants	Sclerotinia stem rot resistance	24 634 SNP	LMM (A), LMM (A + AA), Bayes A, Bayes B, Bayes C, LASSO, BRR	0.74, 0.76, 0.56, 0.69, 0.68, 0.63, 0.70	Derbyshire <i>et al.</i> (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<sub>T</sub>, SNP markers identified with traditional *B. napus* reference genome; SNP<sub>S</sub>, 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 pangenome 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 pangenomic 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 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

**Table 4** The germplasm resources created by gene editing in *Brassica napus*

Gene	Phenotype	Gene function	Reference
<i>BnaEOD3</i> genes	Shorter siliques, smaller seeds, more seeds per silique, higher seed yield	<i>EOD3</i> ( <i>ENHANCER3 OF DA1</i> ) plays a key role in controlling the seed size and silique length in tomato and <i>Arabidopsis thaliana</i>	Khan et al. (2020)
<i>BnaSDG8.A</i> and <i>BnaSDG8.C</i>	Early flowering	<i>SDG8</i> ( <i>SET DOMAIN GROUP 8</i> ) is a pleiotropic gene involved in several plant biological processes, including flowering time and plant size	Jiang et al. (2018)
<i>BnaTFL1</i> genes	Early flowering, altered plant architecture	<i>TFL1</i> ( <i>TERMINAL FLOWER 1</i> ) is a flowering inhibitor and controls the identity of shoot meristem during the plant life span	Sriboon et al. (2020)
<i>BnD14</i>	Improved architecture and seed yield	Strigolactone receptor	Stanic et al. (2021)
<i>BnSPL3</i> genes	Developmental delay	<i>SPL3</i> ( <i>SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 3</i> ) is key floral activator which acts upstream of <i>LEY</i> , <i>FUL</i> and <i>AP1</i> in <i>Arabidopsis</i>	Li et al. (2018a)
<i>BnaRGA</i> genes	Decreased plant height	<i>RGA</i> ( <i>REPRESSOR OF GA1-3</i> ) acts as a master repressor in gibberellic signalling	Yang et al. (2017)
<i>BnaRGA</i> and <i>BnaIAA7</i> genes	Decreased plant height	Rapid turnover of IAA proteins is essential for normal auxin response	Cheng et al. (2021)
<i>BnaA03.MAX1</i> and <i>BnaC03.MAX1</i>	Semi-dwarf, more branches, more siliques, increased yield	<i>MAX1</i> ( <i>MORE AXILLARY GROWTH 1</i> ) encodes a cytochrome P450 monooxygenase (CYP711A1), which is a carlactone oxidase that catalyses the SL biosynthesis	Zheng et al. (2020)
<i>BnaA09.ZEP</i> and <i>BnaC09.ZEP</i>	Orange flowers	The nuclear-encoded plastid enzyme zeaxanthin epoxidase ( <i>ZEP</i> ) plays a critical role in carotenoid biosynthesis	Liu et al. (2020b)
<i>BnaMLPK</i>	Self-incompatibility	M-locus protein kinase ( <i>MLPK</i> ) is thought to interact with the activated <i>SRK</i> , and control self-incompatibility	Chen et al. (2019)
<i>BnS6-SMI2</i>	Self-incompatibility	<i>SCR-methylation-inducing region 2</i> ( <i>Smi2</i> ): the <i>Smi2</i> of the dominant S locus generates small interfering RNAs (siRNAs), which suppresses the expression of the recessive S locus <i>SCR</i> by siRNA-mediated DNA methylation in <i>B. rapa</i>	Dou et al. (2021)
<i>MS5</i>	Genic male sterility	<i>MS5</i> mediates early meiotic progression	Xin et al. (2020)
<i>BnAP2</i>	Typical sepal carpeloid	A-functional genes <i>AP2</i> is required for sepal and petal development	Zhang et al. (2018a)
<i>BnA10.LMI1</i>	Lobed leaves	A <i>LATE MERISTEM IDENTITY1</i> ( <i>LM1</i> )-like gene ( <i>BnA10.LMI1</i> ) encoding an HD-Zip I transcription factor is the causal gene underlying the <i>BnLLA10</i> locus, and <i>BnLLA10</i> , is responsible for the lobed-leaf shape in rapeseed	Hu et al. (2018)
<i>BnJAG</i> genes	Pod shatter resistance	The <i>Arabidopsis</i> <i>JAGGED</i> ( <i>JAG</i> ) gene is a key factor implicated in the regulatory web of dehiscence fruit	Zaman et al. (2019a)
<i>BnaA.ALC.a</i> and <i>BnaC.ALC.a</i>	Pod shatter resistance	The <i>Arabidopsis</i> myc/bHLH gene <i>ALCATRAZ</i> ( <i>ALC</i> ) enables cell separation in fruit dehiscence	Braatz et al. (2017)
<i>BnIND</i> genes	Pod shatter resistance	<i>IND</i> ( <i>INDEHISCENT</i> ) is important for the formation of both the lignified and separation layers of the valve margin	Zhai et al. (2019)
<i>BnCLV</i> genes	Multilocular silique	The <i>CLAVATA</i> ( <i>CLV</i> ) pathways act in a feedback loop to regulate many aspects of stem cell function, including cell fate, proliferation, and growth in <i>Arabidopsis</i>	Yang et al. (2018)
<i>BnaTT2</i> genes	Yellow seeds, increased oil content, higher linoleic acid, and linolenic acid	<i>TT</i> ( <i>Transparent Testa</i> ) genes are involved in the flavonoid biosynthetic pathway. <i>TT2</i> regulates proanthocyanidin biosynthesis in seeds	Xie et al. (2020)
<i>BnTT8</i> genes	Same as above	<i>TT8</i> is a central component of the well-conserved complex that controls flavonoid accumulation in various crops	Zhai et al. (2020)
<i>BnSFAR4</i> , <i>BnSFAR5</i>	Higher oil content	<i>SFAR</i> ( <i>SEED FATTY ACID REDUCER</i> ) genes have a significant effect on seed oil content	Karunaratna et al. (2020)
<i>BnaA.FAD2</i> genes	Increased oleic acid in seed	<i>FAD2</i> ( <i>FATTY ACID DESATURASE 2</i> ) catalyses the desaturation of oleic acid (C18:1) to linoleic acid (C18:2)	Huang et al. (2020); Okuzaki et al. (2018)
<i>BnITPK</i> 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)
<i>BnLPAT2</i> , <i>BnLPAT5</i> genes	Enlarged oil bodies and increased accumulation of starch in mature seeds	Lysophosphatidic 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)
<i>BnaRGA</i> genes	Drought tolerance	<i>RGA</i> ( <i>REPRESSOR OF GA7-3</i> ) is a nuclear protein that negatively regulates the gibberellin signal transduction pathway;	Wu et al. (2020b)
<i>BnALS</i> genes	Herbicide resistance	Acetolactate synthase (ALS), a key enzyme for the biosynthesis of branched-chain amino acids, is the target site of several important herbicides	Cheng et al. (2021); Wu et al. (2020a)
<i>BnWRKY11</i> and <i>BnWRKY70</i>	<i>Sclerotinia</i> resistance	Many WRKY transcription factors associates with disease resistance in <i>Arabidopsis</i>	Sun et al. (2018)

Table 4 Continued

Gene	Phenotype	Gene function	Reference
<i>CRT1a</i>	<i>Verticillium longisporum</i> resistance	Loss of function of CRT1a (calreticulin) strongly reduces plant susceptibility to <i>V. longisporum</i> in both <i>A. thaliana</i> and <i>B. napus</i>	Probsting <i>et al.</i> (2020)
<i>BnaA9.WRKY47</i>	Increased adaptation to low boron stress	WRKY-mediated gene expression is involved in various stress responses, such as pathogen defence, cold resistance, salt tolerance and nutritional stresses, and in developmental and metabolic processes	Feng <i>et al.</i> (2020)

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 findings 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.

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## Conflict of interest

The authors declare that they have no competing interests.

## Author contributions

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

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## 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.