REVIEW FOR GENETIC DISSECTION AND CLONING OF GENES FOR SEED WEIGHT IN OILSEED RAPE

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Abstract. The seeds are generally much larger than wild seeds and are most likely to respond to selective pressure on yield, uniform germination, and seedling vitality exerted by humans during domestication. In particular, on the model plant *Arabidopsis thaliana*, we are able to clone various genes such as seed weight and size. Cloned genes responsible for seed-weight variation also control the number and size of cells in the integument, embryo, and endoderm, but mainly control cell division affecting the final weight/size of the seed. QTL mapping and cloning experiments carried out on rapeseed over the past decade have identified many seed weight QTLs, cloned some genes regulated the seed weight and dissected part of mechanism of the formation of seed weight in rapeseed. In this review, identifying main loci and cloning of some genes responsible for seed-weight variation in the *Brassica* genus from the prior studies is summarized to provide basic information on the cloning of the gene responsible for seed weight.'

Keywords: *seed weight, QTL, oilseed rape, clone, regulatory mechanisms*

Introduction

The *Brassica* genus provides a variety of important oilseed and vegetable crops for human nutrition (Warwick et al., 2006). Crop of particular agricultural are used in three diploid species, *B. rapa* (AA), *B. nigra* (BB), *B. oleracea* (CC), and three polyploid species, *B. napas* (AACC), *B. juncea* (AABB) and *B. carinata*, (BBCC). The triangle of 'U'model (Nagaharu, 1935) described the evolutionary associates among these *Brassica* species by describing in what way these genomes of the three ancestral *Brassica* species (*B. rapa*, *B. nigra*, *B. oleracea* give rise to allopolyploid genus (*Fig. 1*). Diploid ancestors hybridization resulted into allopolyploid species, i.e. *B. rapa* (AA) and *B. oleracea* (CC) hybridization give rise to *B. napus* an allopolyploid species, while *B. juncea* (AABB) formed by hybridization between *B. rapa* (AA) and *B. nigra* (BB), whereas, *Brassica carinata* (BBCC) is result of hybridization between *Brassica nigra* (BB) and *Brassica oleracea* (CC). All followed by spontaneous chromosome doubling, subsequent diversifying selection then gave rise to the vegetable and oil-use sub-varieties of *B. napus*

(AACC), *B. juncea* (AABB) and *B. carinata* (BBCC), respectively (Solangi et al., 2021). The day by day increasing rate of the worldwide population has demanded more food requirement. To meet up this food shortage, a significant improvement in crop grain yield is required. Seed weight (SW) is one of the three primary determinants traits (silique number plant^{-1}, seed number silique^{-1}, and seed weight) that influence the yield for oilseed rape and it is also one of the most significant yield traits for oilseed rape. As a result, one of the key strategies for enhancing oilseed rape yield, is to increase the seed weight (Geng et al., 2016). Seeds, like grains and oilseeds, are a direct product to eat. It has been shown that greater seed size and seed weight imply more reserve food and help seedling establishment (Ellis, 1992; Khan et al., 2012). SW has been recognized as a complicated trait governed by polygenes. The current difficulty in improving seed size is identifying genomic areas with quantitative trait loci (QTL) that influence seed size and yields directly (Namarata Dhaka et al., 2017). 17 QTLs for seed weight have been discovered on chromosome A09 of *B. napus* (Fu et al., 2015), demonstrating the genetic complexity of seed weight regulation in *Brassica* species. Understanding seed weight genetics and regulatory mechanisms is particular important for yield improvement and enhancement, as well as physiological, biochemical, and molecular components. As a result, seed weight QTL mapping investigations in numerous *Brassica* species have been conducted, and a few genes linked with these QTLs have been cloned in recent years. However, in *Brassica* species, the regulatory mechanisms governing gene expression for seed weight are yet not clear.

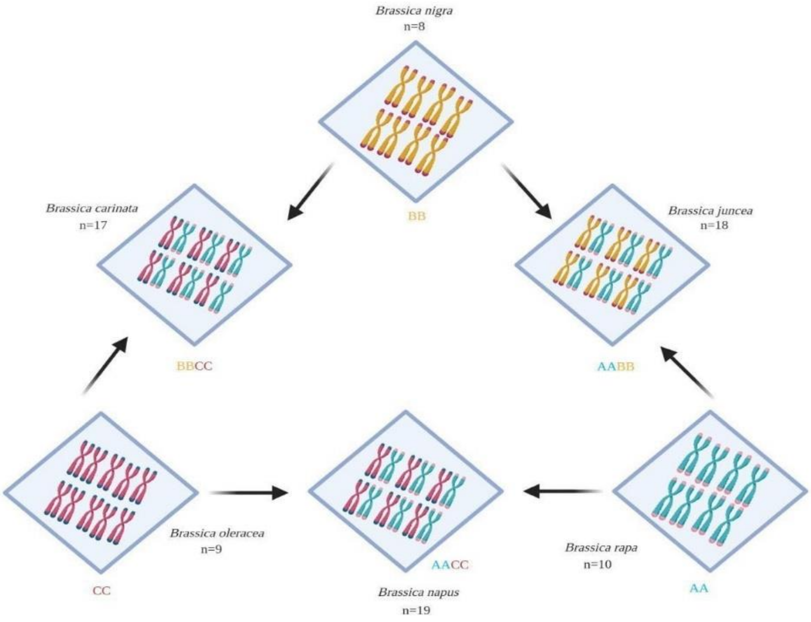

Figure 1. *The U-triangle diagram shows the genetic relationships between six Brassica genus species. Different colors represent chromosomes from each genome (Nagaharu, 1935; Solangi et al., 2021)*

Control of seed weight

The seeds are composed of embryos, endosperms and coats. Each of these three structures is genetically different. Embryos come from fertilized eggs and contain equivalent representations of maternal and paternal genes, and it develops further and becomes mature offspring at the time of seed germination. The endosperm is usually formed by the fusion of two polar nuclei and a spermatic nucleus. Therefore, it contains two doses of the maternal parental gene and one dose of the paternal parental gene. The endosperm serves as a food source for development and germination. The seed coat protects the embryo and endosperm, it comes from the integument of the ovum. Therefore, seed coat contains only maternal genes. Overall, seeds represent a complex genetic structure (Doganlar et al., 2000). Cell division, cell differentiation, and seed maturation are the three phases of seed formation. Coordinated gene regulation in the embryo, endosperm, and seed coat is required for each of these processes. Several species' seed development has been carefully examined (reviewed in Cumming, 1993; Meinke, 1994). Several researches have been carried out to look into the genetic and developmental factors that influence seed weight/size (Basnet et al., 2015). Some studies have offered fresh information on the factors that influence seed weight/size.

Evolution of seed weight

Seed weight varies widely among plant species, ranging from tiny orchid seeds (1 µg) to massive double coconut seeds (10 kg) (Boesewinkel and Bouman, 1993). The seeds of most domesticated plant species are substantially bigger (up to 10 times larger) than those of their wild counterparts (Evants, 1993). A desirable reproductive strategy for wild plants that must self-produce is to generate a large number of little seeds that may be readily spread, increasing the likelihood of finding a favourable habitat for germination and survival. Plants are required for life in the wild, yet they are incompatible with the needs of human agriculture. Humans have chosen plants that generate bigger seeds, offer consistent germination, and have high vigour under direct field planting. Compared with small seeds, although bigger seeds is not suitable for great fecundity and dispersal in the wild, have a higher yield and perform better in contemporary agriculture's mono-cultural, direct-seeded settings. Humans have chosen large seeds as a method of improving production, which is the second most evident rationale for raising seed weight during domestication. Of course, since the seed is the consumable product of such species, this only applies to wheat, soybean, sunflower, and similar species. The use of large seeds for better germination and vigor, on the other hand, is applicable to almost all crops, even those where the seed is not the principal agricultural output.

When understanding the path of domestication of plants and initiating the design of plants to change seed weight and composition, it is necessary to identify the key locations behind this variation. In domestic plants, differences in seed weight are often polygenic, and with the advent of Quantitative Trait Locus (QTL) Analysis (Tanksly, revised in 1993), it is now possible to identify the causative gene responsible for changes in seed weight with domestication in various plant species, such as *Arabidopsis* (Alonso-Blanco et al., 1999), tomatoes (Doganlar et al., 2000), and rice (Bao et al., 2014).

Associations between seed weight QTLs and other traits

Seed weight, determined by seed size, as one of the most important traits of *Brassica* species, it is not only positively related to plant productivity (Clarke and Simpson,1978; Butruille et al., 1999; Shi et al., 2009), but also positive and significantly correlated with oil content, protein content, seed germination rate and viability (Singh et al., 1996; Adamski et al., 2009; Basnet et al., 2015). The correlation between SW and SL has been studied by many researchers, but the direction of the coefficients was inconsistent (Aytac et al., 2009; Zhang et al., 2011; Yang et al., 2012). In general, longer siliques may have more sources of material, resulting in larger seeds (Chay et al.,1989; Lebowitz, 1989; Diepenbrock, 2000). There was a weak trade-off between seed number per silique (SN) and seed weight (SW) in rapeseed, since a slightly negative correlation was detected between SN and SW (Lu et al., 2011; Cai et al., 2014; Shi et al., 2015; Zhu et al., 2020). SW is also an important property that affects seedling colonization and seed dispersal (Gegas et al., 2010; Kesavan et al., 2013; Zhang et al., 2015). Seedlings of large seed plants can adapt to stressful environments, while small seed plants are thought to produce large numbers of seeds (Moles et al., 2005; Westoby et al., 2002). Seed weight also correlates with the number of seeds/ovums, ovary length, seed length and fruit length in *Arabidopsis* (Alonso-Blanco et al., 1999).

QTL mapping and genome-wide association study for seed weight of oilseed rape

Ploidy results from the rise of one genome (autopolyploid) or the combination of two or more different genomes (alploploid). It is present in a lot of blooming plants, including a lot of key crops (Masterson, 1994). Because of the polyploid genome's complexity, QTLs such as homologous sequences on distinct chromosomes and errors induced by interactions between homologous genes are difficult to locate. *B. napus* (AACC), for example, is a heteropolyploid (4x) specie and derived from replication of the whole genome with two ancestors: *Brassica rapa* and *Brassica oleracea*, and is the world's second biggest producer of vegetable oil after soybeans (Chalhoub et al., 2014). Furthermore, *Brassica juncea*, an important oilseed crop in the Indian subcontinent, is also an allopolyploid (AABB) with diploid *B. rapa* (AA) and *B. nigra* (BB) genomes, (Pradhan et al., 1993; Srivastava et al., 2001). *B. rapa* is a diploid oilseed rape with the *Brassica* A genome as well as one of the progenitors of the cultivated kinds of oilseed rape *B. napus* and *B. juncea*. Furthermore, the *Brassica* A genome is closely connected to the *Brassica* C genome in *B. oleracea* (Rana, et al., 2004).

Seed weight is an important agronomic traits for oilseed rape, since it is one of the three major component traits that determined the yield of oilseed rape, furthermore, seeds of oilseed rape are the consumed product, larger seeds may have higher oil content, higher protein content, higher seed germination rate as well as greater seed viability (Geng et al., 2016; Namrata Dhaka et al., 2017). Phenotypic diversity of seed weight in the oilseed rape, including *B. rapa* (AA), *B. napus* (AACC), and *B. juncea* (AABB), ranges from roughly 1.8 g to more than 7.0 g. Seed weight has been found to be influenced by a large number of QTLs with minor effects and a few QTLs with big impacts as a highly heritable characteristic (Namrata Dhaka et al., 2017). In *Brassica* species, quantitative trait locus (QTL) mapping and map-based cloning for seed weight trait have been conducted out using bi-parental mapping population (Butruille et al., 1999; Mahmood et al., 2005; Quijada et al., 2006; Udall et al., 2006; Li et al., 2007, 2008, 2019; Ramchiary et al., 2007; Fan et al., 2010; Wang and Guan, 2010; Chen et al., 2011; Zhang et al., 2011; Zhu et al., 2012; Yang et al., 2012; Yadava et al., 2012; Cai et al., 2012, 2014; Bagheri et al., 2013; Qi et al., 2014; Fu et al., 2015; Shi et al., 2015; Geng et al., 2016; Wang et al., 2017a, 2020; Luo et al., 2017; Namrata Dhaka et al., 2017; Dong et al., 2018; Sun et al., 2018; Shen et al., 2019; Deng et al., 2019; Xin et al., 2021; Bilgrami et al., 2023).

In recent years, with the development of high-density customized single nucleotide polymorphism (SNPs), genome wide association study (GWAS) has become a powerful tool for deciphering the genetic architecture of complex quantitative traits (Lu et al., 2017; Zhong et al., 2021a). In the current study, GWASs for seed weight identification in *B. napus* have been finished (Li et al., 2014; Bouchet et al., 2016; Khan et al., 2019; Pal et al., 2021; Zhang et al., 2023). As a result, 41 association signals on 12 chromosome of *B. napus,* including A01, A02, A05, A06, A07, A09, A10, C01, C03, C04, C05, C09 and so on.

In consideration of the importance of seed weight in *B. napus*, a group of researchers have worked on a variety of QTLs identification for seed weight. Therefore, hundreds of QTLs for these traits have been identified using bi-parental mapping population and genome wide association studies (GWAS), which are distributed throughout the 19 chromosomes of the *B. napus* genome (Quijada et al., 2006; Fan et al., 2010; Zhang et al., 2011, 2023; Yang et al., 2012; Cai et al., 2014; Ding et al., 2014; Li et al., 2014; Bouchet et al., 2016; Luo et al., 2017; Dong et al., 2018; Raboanatahiry et al., 2018, 2022; Deng et al., 2019; Khan et al., 2019; Wang et al., 2020; Xie et al., 2020; Pal et al., 2021) (*Table 1*). A few studies on QTLs identification for seed weight in *B. rapa* and *B. juncea* have been conducted out. And, only six 1000-seed weight QTLs are discovered in *B. rapa* on A02, A03, A05, A06, A09, and A10, with explained variance ranging from 6% to 17% (Li et al., 2013; Basnet et al., 2015; Bagheri et al., 2013) (see *Table 1*). In *Brassica juncea*, 21 consensus Tsw (Tsw-C) QTLs have been found on LGs A03, A04, A07, A10, B02, B03, and B08 (Mahmood et al., 2005; Ramchiary et al., 2007; Yadava et al., 2012; Namrata Dhaka et al., 2017). Few genes associated with these QTLs have been cloned, and the regulatory mechanisms controlling gene expression for seed weight in *Brassica* species are still unclear (*Table 1*). Furthermore, maternal influences, which include the maternal environment as well as the mother genotype, play an important role in seed weight determination (Pet and Garretsen, 1983; Nieuwhof et al., 1989; Doganlar et al., 2000; Bagheri et al., 2013; Li et al., 2019). By maternal effects, *APETALA2* (*AP2*) in Arabidopsis and auxin-response factor 18 (*ARF18*) in *Brassica napus* alter seed weight (Liu et al., 2015).

Clone of genes and regulatory mechanisms underlying gene expression for seed weight of *Arabidopsis* and oilseed rape

The seed weight of dicots is determined by regulating the growth of female gametophyte embryos, endosperm, integument, cell number/cell size, or both (Sundaresan et al., 2005; Alonso-Blanco et al., 1999). As a result, several cellular activities have an impact on the seed size (Fang et al., 2012). Various seed weight/size genes have been successfully cloned, particularly in the model plant *Arabidopsis*. The cloned genes largely controlled cell division, but they also controlled the cell number or size of the integument, embryo, and endosperm, and ultimately affected seed weight or seed size. Some mutants, including as ap2, arf2, da1, eod3, ttg2, and klu, regulate cell elongation in the integument surrounding the seed to control seed size (Fang et al., 2012; Ohto et al., 2005; Schruff et al., 2006; Garcia et al., 2005; Adamski et al., 2009). The HAIKU transcription factor (IKU) was first exposed to influence sperm size by influencing endosperm development (Garcia et al., 2005). IKU1, IKU2, MINI3 and SHB1 act on the same developmental pathways that influence the size of the endosperm (Luo et al., 2005; Zhou et al., 2009; Jiang et al., 2013). Genes involved in hormone signaling, such as brassinosteroid hormones, are endosperm and embryonic development (which act upstream of SHB1, IKU1, MINI3, IKU2) and AP2, MNT/ARF2, cytochrome P450

KLUH (KLU)/CYP78A5] (Jiang et al., 2013; Jiang and Lin, 2013). Signal transduction via cytokinins and ethylene also plays an important role in the regulation of seed size (Li et al., 2013; Bennett et al., 2014). Flavonoids signal from the seed mantle to the endosperm, thus influencing its spread (Doughty et al., 2014). The ubiquitin pathway controls seed size by targeting proteins for degradation (Li and Li, 2015). Polycomb group (PcG) gene clusters and other epigenetic regulators also affect seed size (Li and Li, 2015). In *Arabidopsis* mini3, iku1, iku2 and shb1 mutants, early endosperm cellularization or proliferation in the early stages of seed development affects the seed masses (Garcia et al., 2003; Luo et al., 2005; Wang et al., 2010; Zhou et al., 2009; Kang et al., 2013). The met1 gene has been determined to have a parental effect on seed size due to methylation loss of cytosine residues on CG islands (Feng et al., 2010). SUPPRESSOR2 OF DA1 (SOD2) encodes the ubiquitin-specific protease 15 (UBP15). Promotes cell division of the ovum integument and regulates seed size by developing seeds (Jiang et al., 2013). DA1 and DA2 respectively encode ubiquitin receptors and RING-type proteins with ubiquitin ligase E3 activity and determine final semen weight and organ size by limiting the period of cell proliferation (Li et al., 2008; Xia et al., 2013). The ARF2 gene is associated with auxin signaling, cell division, and the final size of seeds and other organs (Schruff et al., 2006). APETALA2 (AP2) plays an important role in determining seed size, seed weight, seed oil and protein accumulation, acting through the maternal sporophyte and endosperm genome, seed weight and seed Yields are controlled (Jofuku et al., 2005). In general, Seed weight and size are principally determined by cell division, cell quantity, and cell size regulation in the integument, embryo, and endoderm. Brassinosteroids, cytokinins, and ethylene are among the genes that govern hormonal signaling. *Arabidopsis* seed size is also influenced by flavonoids, ubiquitins, auxins, and other epigenetic regulators.

As dicotyledonous plants, the *Brassica* genus crop may has similar regulatory mechanism for seed weight or size with *Arabidopsis* (*Table 2*). There are three types of oilseed rape, including *B. rapa* (AA), *B. napus* (AACC), and *B. juncea* (AABB), only in *B. napus*, the regulatory mechanism was partially dissected. For example, the auxin response factor 18 (*ARF18*) gene on chromosome A9 of *Brassica napus* may modulate seed weight without damaging the pod. Specifically, deletion of 55-aa prevents the formation of *ARF18* homodimer leading to loss of binding activity. Therefore, the inhibitory activity of *ARF18* on the downstream auxin gene is blocked, and the SW and SL of oilseed rape (AACC) are increased (Liu et al., 2015). Another major consensus QTL qSLWA9 that controls sisique length and seed weight simultaneously on chromosome A09 of *Brassica napus*, is accurately mapped, and the candidate gene *BnaA9.CYP78A9* may influence auxin levels by affecting a well-known auxin or an unknown auxin biosynthesis or metabolism pathway. The gene expression level was elevated by a 3.7 kb CACTA-like Transposable elements (TE) acting as an enhancer inserted into 3.9-kb upstream regulatory sequence of *BnaA9.CYP78A9*, so as to promote silique elongation and seed enlargement (Yang et al., 2012; Shi et al., 2019). A cqSW.A03-2 locus controlling the seed weight was identified on A03 chromosome of *B. napus*. The candidate gene *BnaA03g37960D* encodes a histidine kinase receptor, which may perceive cytokinin molecules to regulate cytokinin signal transduction by a multistep two-component system, and thereby involves in seed weight regulation of *B. napus* (Wang et al., 2020). A potential regulation mechanism model for the maternal control of seed weight via the pod in rapeseed was proposed (Li et al., 2019). For the two major pleiotropic QTLs, the variations of the underlying causal genes in protein function and/or expression level lead to changes in expression levels of the downstream response genes (such as BnaA09g55530D) related to pod growth and development, which result in changes in pod length, photosynthetic area and photosynthate gross in the pod wall. At the same time, the mobile signal between pod wall and seed also changes, affecting the transport of photosynthate from pod wall to seed and then influencing the expression of genes related to reserves synthesis and metabolism, which finally affect seed filling, size and weight.

Some researchers discovered the differentially expressed gene (GSBRNA2T00037121001) by transcriptome analysis, which is involved in inorganic ion transport and metabolism, as well as coding a ferritin. This gene is a promising candidate for additional research into *B. napus* seed weight (Geng et al., 2018). A hot region on ChrA09 of *B. napus* was identified as tightly associated with the TSW trait by association analysis combined with bulked segregant analysis (BSA), which contained 91 candidate genes. From annotation information, four genes (GSBRNA2T00037136001, GSBRNA2T00037157001, GSBRNA2T00037129001, and GSBRNA2T00069389001) might be intriguing candidate genes for seed weight. For example, GSBRNA2T00037136001 plays a role in cell division, GSBRNA2T00037157001 in seed development, GSBRNA2T00037129001 in seed development and cell division, and GSBRNA2T00069389001 in IAA biosynthesis, all of which might be highly related to seed weight (Geng et al., 2016). Furthermore, *BnDA1*, which is similar to *Arabidopsis DA1* (DA means large in Chinese), has been discovered to encode a ubiquitin receptor that regulates seed size by regulating cell proliferation in the integuments of *B. napus*, and *BnDA1* was down-regulated in *B. napus* by over expressed of AtDA1^{R358K}, which is a functional deficiency of DA1 with an arginine-to-lysine mutation at the 358th amino acid. The seed weight and yield of transgenic plants all increased significantly (Wang et al., 2017). In addition, in *B. napu*, the phenotypes of the different allelic combinations of *BnaEOD3* copies revealed gene functional differentiation among the two subgenomes, and the different copies of *BnaEOD3* might involve in seed development. Furthermore, the *BnaEOD3* could act maternally to promote cotyledon cell expansion and proliferation to regulate seed weight in rapeseed (Khan et al., 2021).

In conclusion, the major QTLs for seed weight were mapped to A09 in nine different oilseed rape groups (*Table 1*) seed masses and genes on the A09 chromosome have been cloned in oilseed rape (*Table 2*), but in one *B. rapa* group only one SW QTL was assigned to A09. No major seed weight QTL was assigned to A09 in *B. juncea* (*Table 1*). The cloned oilseed rape has several seed mass genes, but the genetic mechanism of the *Brassica* seed mass has not yet been elucidated. In addition, the genes are not cloned in *B. juncea* and *B. rapa*. One reason is that it is more difficult to genetically control the seed yield of amphibian rapeseed. A single TSWQTL may contain one or more candidate genes. Designation of these candidate genes can narrow the range of potential target genes, and potential candidate genes belong to specific loci, but this does not mean that they control traits. There is none. QTLs may be the result of changes in other new genes that have not been studied in the model system. For example, some genes that significantly affect rice and *Arabidopsis* seed size/weight, such as GS3, GS5, GW2, MINI3, TTG2, ARF2, IKU2, are in small regions of QTL or not even in confidence intervals. Intervals previously defined by the TSW QTL (Cai et al., 2012). Therefore, there is a lot study to be done in the *Brassica* genus before we have a review explains of the seed weight regulating mechanisms.

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Table 1. *QTL mapping of seed weight in B. napus, B. juncea and B. rapa*

Cultured type	References	Parent lines	Population structure	Number of plants/families	Number and class of markers	Number of QTLs detected	LG
B. napus	Quijada et al., 2006	MF216 × P1804, RV128 × P1804	DH	150	RFLP	3	A06 C07 C09
	Fan et al., 2010	SW Hickory × JA177, J7046 × J7005	DH F2	190 190	SSR	9	A01 A02 A05 A07 A10 C04
	Zhang et al., 2011	HZ396 × Y106	DH	208	SSR	6	A02 A07 C03
	Zhu et al., 2012	DH-G-42 × DH-7-9	F2	190	SSR SRAP	3	A09 C01
	Yang et al., 2012	S1 × S2 S1 × No2127	RIL	186 + 192	SSR	5	A01 A06 A09 C09
	Cai et al., 2012	Hickory × JA177	DH	190	SSR	12	A01 A02 A04 A05 A07 A09 C02
	Ding et al., 2014	QY10× Bakow P-efficient cv. Eyou Changjia × P-inefficient cv. B 104-2	BQDH BERIL	200 124	SSR	21	
	Fu et al., 2015	SWU07×Express	DH RC-F2	261 + 233	SSR	21	A04 A05 A06 A09 C02 C05
	Li et al., 2014	ZS11× No. 73290	F2, F2:3, F2:4	184	SSR STS SNP InDel	13	A01 A03 A04 A07 A08 A09 C02 C06
	Cai et al., 2014	Inbred lines	Inbred lines	192	AFLP SSR	9	A02 A06 A07 A09 A10 C08 C09
	Bouchet et al., 2016	Inbred lines	Inbred lines	92	SNP	16	A01 A04 A05 A06 A07 A09 C02 C03 C04 C05
	Geng et al., 2016	G-42×7-9	DH	250	SLAF	4	A09
	Luo et al., 2017	Tapidor ×Ningyou7	DH	182	SNP	49	A01 A02 A03 A04 A06 A07 A08 A09 A10 C05 C06 C08 C09
	Sun et al., 2018	APL01×Holly	RIL	189	SNP, SSR	23	A01 A02 A03 A04 A06 A08 C02 C04 C06 C07 C08
	Dong et al., 2018	Inbred lines	Inbred lines	157	SNP	20	A01, A04, A09, C02, C06
	Raboanatahiry et al., 2018	22 Populations	22 Populations	Many	Many	168	A02 C07 C08
	Deng et al., 2019	ZS11×QU	DH	282	SNP	3	A09
	Khan et al., 2019	Inbred lines	Inbred lines	521	SNP	9	A02 A06 A09 A10 C04
	Wang et al., 2020	ZY50×7-5	DH	189	SNP, SSR	6	A03 A07 A08 C02
	Xie et al., 2020	No.21279 ×ZY821	DH	115	SNP	4	A07 C02 C06 C08
	Pal et al., 2021	Inbred lines	Inbred lines	113	SNP	11	A03 C02
	Zhang et al., 2023	24 Populations	24 Populations	Many	Many	57	A01 A02 A03 A04 A05 A06 A07 A08 A09 A10 C01 C02 C03 C04 C05 C06 C07 C08 C09
B. juncea	Namrata Dhaka et al., 2017	Varuna× Heera TM-4×Donskaja-IV Donskaja-IV×EH-2 EH-2× Pusajaikisan	DH	182 + 184	IP, SSR, BACSSR	6	A03 A07 A10 B03
	Yadava et al., 2012	TM-4×Donskaja-IV	DH	100	AFLP, SSR, IP	2	A03 A04

	Ramchiary et al., 2007	Varuna×Heera	DH	123	AFLP, RFLP, SSR, Gene-marker	13	A03 A04 A07 A10 B02 B08
B. rapa	Basnet et al., 2015	YS143×PC175	DH	170	AFLP SSR Myb Gene-T	2	A05
	Li et al., 2013	Chiifu 401-42×RCBr	CRF3	190	SSR SNP	4	A02, A03, A06, A10
	Bagheri et al., 2013	L58×R-o-18	F2	190	AFLP SSR	1	A09

Table 2. *Number of candidate genes for seed weight detected in different populations of Brassica napus*

Cultured type	References	Population structure	Number of plants/families	Markers	LG	The candidate gene	The molecular mechanism
B. napus	Shi et al., 2019	F_2 F_3	9737	SSR	A09	BnaA9.CYP78A9	Acts as a positive regulator whose high expression will accelerate a higher concentration of auxin and stimulate seed expansion
	Geng et al., 2018	DH	2	RNA-seq transcriptome analysis	A09	GSBRNA2T00037121001	Be involved in inorganic ion transport and metabolism and encodes a ferritin
	Geng et al., 2016	DH	250	SLAF-seq	A09	GSBRNA2T00037136001 GSBRNA2T00037157001 GSBRNA2T00037129001 GSBRNA2T00069389001	GSBRNA2T00037136001 participates in cell division; GSBRNA2T00037157001 was involved in the process of seed development; GSBRNA2T00037129001 was involved in both seed development and cell division; GSBRNA2T00069389001 participated in the process of IAA biosynthesis
	Wang et al., 2020	BC_5F_3 BC_5F_4	2732	InDel	A03	BnaA03G37960D	A histidine kinase encoding gene
	Liu et al., 2015	BC_4F_1 BC_4F_2	4000	SSR, InDel, SNP	A09	BnaA09g55580D	Encodes an auxin response factor and shows inhibitory activity on downstream auxin genes
	Wang et al., 2017				C05	BnaC05g14930D	As a ubiquitin receptor and negatively regulates seed size
	Li et al., 2019	F_2 RIL	1150 184			CYP78A9	Regulation mechanism for the maternal control of seed weight in rapeseed. The mobile signal between pod wall and seed also changes, affecting the transport of photosynthate from pod wall to seed and then influencing the expression of genes related to reserves synthesis and metabolism, which finally affect seed filling, size and weight
	Khan et al., 2021	Inbred line	1		A04 A05 C04	BnaA04g27100D BnA05g01200D BnaC04g00760D BnaC04g50960D	Act maternally to promote cotyledon cell expansion and cell proliferation to regulate seed growth in rapeseed

Conclusion

This paper reviewed the seed weight QTL of oilseed rape identified in previously published reports and elaborated the regulatory mechanisms of genes for the seed weight of oilseed rape that has been cloned. In the present, only genes for seed weight that are located on the A09 chromosome have been cloned in *B. napus*. The major QTLs of seed weight on A09 is QTL mapped in nine different populations of *B. napus*. Whereas, only one and no one SW QTL is mapped on A09 in *B. rapa* and *B. juncea*, respectively. Though, there are a few genes for seed weight in *B. napus* that have been cloned yet, however, the regulatory mechanisms of the genes for the seed weight of the *Brassica* genus are still not clear and there are no genes for seed weight being cloned in *B. juncea* and *B. rapa*.

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