

Review Article

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Molecular Networks and Regulatory Factors Underlying Yield Formation in Rapeseed

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Abstract This study summarizes the rapeseed yield-related genes identified through QTL mapping and genome-wide association study, introduces the roles of several major hormones, and also analyzes the key pathways and regulatory networks of the proteome and metabolome in photosynthesis, lipid accumulation, energy metabolism, and stress response. The results indicated that auxin, cytokinin and gibberellin all played significant roles in branching, grain size and seed development. The synthesis, transportation and source-reservoir relationship of carbohydrates play a decisive role in the formation of yield. Epigenetic modifications can affect gene expression and the adaptability of plants to the environment. Environmental factors such as temperature, light and moisture can also affect the stability of yield through hormones and signal transduction pathways. This study aims to establish a systematic regulatory model for the formation of rapeseed yield, providing theoretical references for future molecular breeding of high-yield, stress-resistant and high-quality varieties.

Keywords Rapeseed (*Brassica napus*); Yield formation; Molecular regulatory networks; Multi-omics integration; Genome editing

1 Introduction

Rapeseed (*Brassica napus*) is one of the world's three major oil crops and an important source of vegetable oil, feed and biofuels. It holds an important position in global food and oil security and sustainable agriculture (Lv et al., 2025). With the increase in population and the rising demand for renewable energy, increasing rapeseed production has become the focus of agricultural research. Although breeding techniques have been continuously improved, the yield per unit area of rapeseed is still lower than that of other major oil crops. Therefore, it is extremely urgent to increase production to meet the demand for fats and proteins (Canales et al., 2021; Xiong et al., 2022; Gu et al., 2024).

The yield formation process of rapeseed involves multiple factors such as genetics, phenotype and environment. Yield is determined by direct traits such as the number of pod, the number of grains per pod and the weight of a thousand grains, as well as by indirect traits such as plant height, the number of branches, flowering period and the length of the main sequence. These traits are closely related, influence each other, and are regulated by environmental factors such as light, temperature, moisture, soil, and management measures. Sufficient sunlight can increase the yield in plateau areas, while adverse conditions such as salinity, drought and high temperature can reduce the yield by altering gene expression and metabolic activities (Kourani et al., 2022; Hao et al., 2023). The genetic basis of yield traits in rapeseed also involves polygenes, quantitative trait loci (QTL), epigenetic regulation, and the interaction between genes and the environment (Lu et al., 2017; Raboanatahiry et al., 2018).

This study summarized the main molecular networks and regulatory factors for the formation of rapeseed yield, analyzed the genetic basis, key genes and regulatory mechanisms related to yield traits, and explored the interaction between environmental factors and molecular regulatory networks. By integrating multi-omics data and the latest research achievements in molecular breeding, this study aims to provide theoretical references for understanding the formation mechanism and molecular improvement of high-yield rapeseed, as well as practical directions for the cultivation of high-yield and high-quality varieties.

2 Genetic Basis of Yield Traits in Rapeseed

2.1 Major yield-related components: seed number, pod number, seed weight, and biomass allocation

The yield of rapeseed (*Brassica napus* L.) is jointly determined by multiple quantitative traits, mainly including the number of pod per plant, the number of seed per pod, the weight of a thousand grains, and biomass allocation, etc. Research shows that the number of pod and the number of seed per pod are the main factors determining the yield of rapeseed, while grain weight and biomass allocation also have a significant impact on the total yield. Agronomic traits such as plant height, the number of branches and the length of the main sequence also indirectly affect the yield. There are often genetic correlations or antagonistic relationships among different yield traits, and balanced optimization is required during breeding (Raboanatahiry et al., 2018).

2.2 Quantitative trait loci (QTL) mapping and genome-wide association studies (GWAS) in yield trait dissection

Quantitative trait loci (QTL) mapping and genome-wide association study (GWAS) are important methods for studying the genetic basis of rapeseed yield. A large number of studies have identified hundreds or even thousands of yield-related QTLs in different groups and various environments. Through meta-analysis of QTL, QTLs of multiple traits can be integrated into co-localized “core QTLs”, demonstrating the complexity and pleiotropy of yield traits. GWAS utilizes high-density SNP chips or resequencing data to precisely locate yield-related genes in natural populations and discover many new QTLs and candidate genes. Some QTLs exhibit stable performance in different environments and are important targets for molecular breeding (Khan et al., 2019; Khan et al., 2021).

2.3 Identification of core yield-related genes across diverse rapeseed germplasms

By integrating QTL mapping, GWAS and transcriptome analysis, researchers identified multiple core yield-related genes in different rapeseed germplasms. Genes such as *BnaA09g39790D* (RNA helicase), *BnaA09g39950D* (lipase), and *BnaC09g25980D* (SWEET7) are related to particle weight or particle number. Genes such as *BIG1-D*, *CAND1* and *DRG3* are involved in hormone signaling and pollen development processes, and also have an impact on yield in arid environments. Some pleiotropic genes (such as *BnaA03g23490D*, *BnaC09g46370D*) can simultaneously regulate multiple yield or quality traits. The accumulation of these superior alleles in high-yield materials indicates their importance in yield formation (Pal et al., 2021; Xiang et al., 2023; Salami et al., 2024).

3 Molecular Networks Regulating Yield Formation

3.1 Hormonal signaling pathways (auxin, cytokinin, gibberellin, and brassinosteroid regulation)

Auxin (IAA) can regulate cell division and elongation, and influence key traits such as floral organ differentiation, branching angle and seed size. Variations of auxin signaling genes such as *BnaA3.IAA7* can improve plant type and enhance heterosis (Cheng et al., 2017; Li et al., 2019). Cytokinin (CK), gibberellin (GA), and brassinolide (BR) are also involved in seed development, branching formation, and yield regulation. Transcriptomic and metabolomic studies have shown that BR can promote the expression of auxin synthesis-related genes, enabling seedlings to grow better (Ma et al., 2025). The interaction between BR and auxin has a significant effect on the branching angle and yield under high-density cultivation (Cheng et al., 2017). The GASA family genes in the gibberellin pathway are closely related to seed size. Multi-omics analysis also revealed that under adverse conditions such as drought and salt stress, hormone signals affected the growth and yield of rapeseed by regulating the expression of related genes (Mohamed et al., 2022; Tan et al., 2024; Li et al., 2025).

3.2 Carbohydrate metabolism and source–sink dynamics in yield determination

The synthesis, transportation and distribution of carbohydrates are the basis for the formation of rapeseed yield. The accumulation of photosynthetic products in leaves and the transport efficiency to grains determine grain fullness and final yield (Xiong et al., 2022). The activities of key enzymes such as Rubisco, AGPase, SuSy and SPS are regulated by nitrogen levels and water stress, and are closely related to yield (Kuai et al., 2021). Stress-resistant varieties can maintain a high carbohydrate transport capacity and sink strength under drought or waterlogging conditions, and thus have more stable yields (Kuai et al., 2020; Aubert et al., 2024). In addition, the T6P synthase (TPS) family plays a dual role in carbon allocation and drought resistance regulation, and is an

important node in source-reservoir regulation. During seed development, glucose metabolism, lipid synthesis and protein accumulation show phased changes and are jointly affected by genetics and environment (Xiong et al., 2022; Hao et al., 2023).

3.3 Integration of molecular signaling with developmental and environmental cues

Conditions such as light, temperature and nitrogen can affect flower differentiation, grain development and yield by regulating the expression of genes related to hormone synthesis, signal transduction and carbon metabolism (Xiong et al., 2022; Hao et al., 2023). For instance, high nitrogen conditions can promote auxin synthesis and accelerate the development of flower meristem, thereby increasing yield (Hao et al., 2022). Long daylight in plateau areas is beneficial for prolonging the grain development period and promoting the accumulation of photosynthetic products (Xiong et al., 2022). Multi-omics studies have found that transcription factors, hormone signals, carbon metabolism, and stress response genes jointly constitute a complex regulatory network for yield formation (Hao et al., 2023; Salami et al., 2024). Non-coding RNAs (such as lncRNA and miRNA) can also be involved in the regulation of yield traits and stress responses by regulating hormone signaling and metabolic pathways (Cheng et al., 2017; Tan et al., 2024).

4 Transcriptional and Epigenetic Regulation

4.1 Transcription factors influencing seed and silique development

LAFL family genes such as BnLEC1 (LEAFY COTYLEDON1), BnFUS3 (FUSCA3), and BnWRINKLED1 (WRI1) regulate endosperm development, lipid synthesis, and seed maturation. Conditional expression of BnLEC1 and BnL1L can significantly increase seed oil content without affecting major agronomic traits, indicating that they are crucial in fatty acid synthesis and carbon flow regulation (Tan et al., 2011). BnFUS3 and BnWRINKLED1 promote oil accumulation by regulating the expression of lipid synthesis genes (Chen et al., 2024). Transcription factors such as MYB56 can activate the expression of BnLEC1, thereby promoting seed oil accumulation (Figure 1) (Han et al., 2024). The high expression of these genes is usually closely related to high-yield and high-oil content strains (Chen et al., 2024).

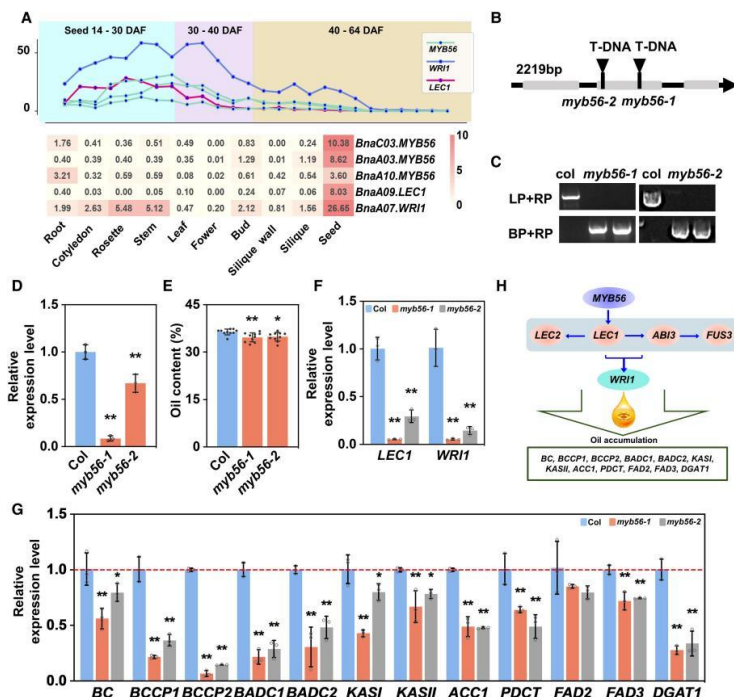


Figure 1 Functional characterization of *BnaC03.MYB56* as a positive regulator of seed oil accumulation (Adopted from Han et al., 2024)

4.2 Epigenetic modifications (DNA methylation, histone modification, and small RNAs) in yield regulation

DNA methylation plays a regulatory role in seed development, nutrient absorption and stress resistance. Genes related to DNA methylation or demethylation in rapeseed change dynamically under different tissues and stress

conditions, regulating seed development and stress response (Fan et al., 2020; Zheng et al., 2025). When nitrogen is insufficient, hypomethylation of the promoters of key nitrogen metabolism genes such as NRT1.1 and NRT2.1 will promote their upregulation, thereby improving nitrogen utilization efficiency and yield (Hua et al., 2020). Histone modifications (such as H3K4me3 and H3K27me3) also change under drought conditions, regulating the expression of osmotic regulation and stress-related genes (Prasad et al., 2025). Small RNAs (such as miR827, miR171, miR160) affect leaf senescence and root development by regulating genes such as NLA, SCL6, ARF17, thereby altering nutrient distribution and yield (Hua et al., 2020).

4.3 Gene expression networks revealed by transcriptomic and epigenomic studies

Transcriptome and epigenomic analyses revealed that yield-related traits were jointly regulated by multiple transcription factors (such as MYB, bHLH, ERF, WRKY, bZIP, ARF, etc.) and their downstream genes (Han et al., 2024). In high-yield materials, the enhanced expression of genes such as cell division, cell wall synthesis, carbohydrate metabolism and seed storage protein promoted seed development and grain weight increase (Salami et al., 2024). Epigenetic modifications further affect yield traits by regulating the activity of these genes (Hua et al., 2020; Prasad et al., 2025). Combined transcriptome and proteome analysis also indicated that pathways such as signal transduction, fatty acid synthesis, and glucose metabolism also play key roles in yield formation (Zheng et al., 2025).

5 Proteomic and Metabolomic Insights into Yield Formation

5.1 Protein interaction networks involved in photosynthesis, nutrient transport, and pod filling

Proteomics research has found that during the enrichment period of rapeseed seeds, the expression of proteins related to glycolysis, carbohydrate metabolism and fatty acid synthesis significantly increases, and these changes promote the accumulation of fats and proteins. Compared with soybeans, the expression level of fatty acid synthesis-related proteins in rapeseed at this stage was approximately three times higher, and the types and contents of proteins in the carbon assimilation and glycolytic pathways also significantly increased, indicating that rapeseed achieves high oil accumulation by enhancing glycolytic and fatty acid synthesis (Hao et al., 2023). Protein-protein interaction network analysis further indicated that multiple processes such as lipid metabolism, protein synthesis, secondary metabolism, photosynthetic system and amino acid metabolism were jointly regulated by key genes (CAC2, SNC4, ACX2, PLDGAMMA1, etc.), thereby affecting lipid formation (Chao et al., 2017).

In terms of photosynthesis and nutrient transport, transcriptome analysis of seeds and pod shells revealed enhanced gene expression related to photosynthesis, carbon metabolism, lipid synthesis and transport in high oil content varieties, which contributed to the synthesis and transport of photosynthetic products and provided a material basis for lipid accumulation (Shahid et al., 2019; Hao et al., 2023). The photosynthetic capacity of the pod wall and the supply of carbon sources have significant influences on seed filling and final yield (Li et al., 2018). Lipid transporter protein (LTP) and seed storage albumin (SSA) show staged high expression during development: LTP peaks 25 days after flowering, and SSA is highly expressed around 40 days. Both are involved in the transport and accumulation of fats and proteins. The protein-protein interaction network also involves links such as energy metabolism, electron transport chain and oxidative phosphorylation, showing the multi-level regulatory characteristics of rapeseed yield formation (Chen et al., 2022).

5.2 Metabolite profiling and pathway enrichment related to energy metabolism and lipid accumulation

Metabolomics studies have shown that during seed development and stress response of rapeseed, metabolites such as carbohydrates, amino acids and lipids undergo dynamic changes. During the critical period of seed development of high oil content varieties, the contents of carbohydrates, fatty acids and triacylglycerol significantly increased, and glycolysis, TCA cycle and fatty acid synthesis pathways were significantly enriched (Shahid et al., 2019). Efficient carbon flow to lipid conversion is the basis for massive lipid accumulation (Chao et al., 2017; Hao et al., 2023). Under low temperature, drought or nitrogen stress, rapeseed enhances stress resistance and maintains yield by regulating the accumulation of metabolites such as carbohydrates, amino acids and organic acids, activating the TCA cycle, amino acid synthesis and secondary metabolic pathways (Shen et al., 2022). For

instance, the roots of drought-tolerant varieties accumulate substances such as galactose and fumaric acid, enhancing their stress resistance (Zhi et al., 2024). When nitrogen is insufficient, significant changes occur in pathways such as sucrose, phenylalanine, amino acids and the TCA cycle, and plant hormones and flavonoid metabolites are also involved in regulation (Shen et al., 2022).

5.3 Multi-omics integration for understanding dynamic regulatory processes

Multi-omics integration analysis (including proteomics, metabolomics and transcriptomics) has revealed the complex gene-protein-metabolite network in the formation of rapeseed yield. QTL mapping, protein interaction and metabolic pathway analysis revealed that there were close connections among processes such as carbon metabolism, lipid synthesis and protein accumulation, and they were finely regulated by multiple signaling pathways. The BnIR multi-omics database integrates genomic, transcriptomic and metabolomic information, providing support for the screening of candidate genes and mechanism research. Furthermore, the combined analysis of proteomics and metabolomics can reveal the dynamic regulatory patterns under different developmental stages, tissues and environments, providing a theoretical basis for the molecular design breeding of high-yield and high-oil content rapeseed (Chao et al., 2017; Shahid et al., 2019).

6 Environmental and Stress-Responsive Regulatory Mechanisms

6.1 Impact of temperature, light, and water availability on yield-related gene expression

Temperature, light and water supply can directly alter seed development, photosynthetic efficiency and the expression of related genes. In plateau areas, longer hours of sunlight can significantly increase the 1000-grain weight and the number of pod of rapeseed, promote grain development, enhance the expression of yield-related genes, and thus achieve high yield (Xiong et al., 2022). Low temperatures will inhibit seed germination and seedling growth, resulting in reduced yields. Under low-temperature conditions, the QTL regions related to seed viability are concentrated with genes involved in DNA repair, energy generation, antioxidant response and hormone signal transduction (Luo et al., 2021; Zhang et al., 2022). During drought, especially from the flowering stage to the formation of corner fruits, the yield of rapeseed can drop by approximately 30%. Studies have shown that genes such as ABCG16, BIG1-D, and CAND1 can regulate pollen development, seed quantity, and grain weight under drought conditions, playing an important role in drought-resistant yield performance (Salami et al., 2024; Shahsavari et al., 2025).

6.2 Stress signaling pathways (ABA, ROS, MAPK) modulating reproductive success and yield stability

The stress resistance mechanism of rapeseed relies on a complex signaling network. Abscisic acid (ABA) signaling is activated under drought and low-temperature conditions, regulating downstream genes such as ABI5 and PP2Cs, promoting stomatal closure and enhancing osmotic regulation, thereby improving stress resistance (Cao et al., 2022; Nan et al., 2023; Shahsavari et al., 2025). Reactive oxygen species (ROS) accumulate under stress. On the one hand, they can induce the expression of antioxidant enzymes (CAT, GPX, SOD, etc.) and eliminate excessive ROS to protect cells. On the other hand, they can also act as signaling molecules to regulate reproductive organ development and stress response (Li et al., 2022; Mohammadi et al., 2025). The MAPK signaling pathway interacts with ABA and ROS, participates in regulating gene expression, cell cycle and reproductive development under stress, thereby affecting yield stability (Manna et al., 2023; Nan et al., 2023). For example, BnA.JAZ5 regulates stomatal density through the interaction of ABA and JA signals, enhances drought resistance, and thereby affects seed germination and final yield (Figure 2) (Cao et al., 2022).

6.3 Molecular breeding strategies for enhancing stress-resilient yield formation

Based on GWAS and transcriptome analysis, researchers have identified a large number of candidate genes and QTLs related to drought resistance, cold tolerance and salt tolerance, which can be used for molecular marker-assisted selection (MAS) or gene editing (Luo et al., 2021; Salami et al., 2024). For instance, the co-expression of genes such as NCED3, ABAR, CBF3, LOS5 and ICE1 can significantly enhance the comprehensive resistance and yield of rapeseed to various stresses (Wang et al., 2018). Genes that control epidermal waxy synthesis, antioxidant response and hormone signaling (such as CER1, MYB, CAT, GPX, etc.)

have also become important breeding targets (Zhang et al., 2025). With the development of gene editing technologies such as CRISPR/Cas9, it has become possible to cultivate new rapeseed varieties that are high-yielding and stress-resistant.

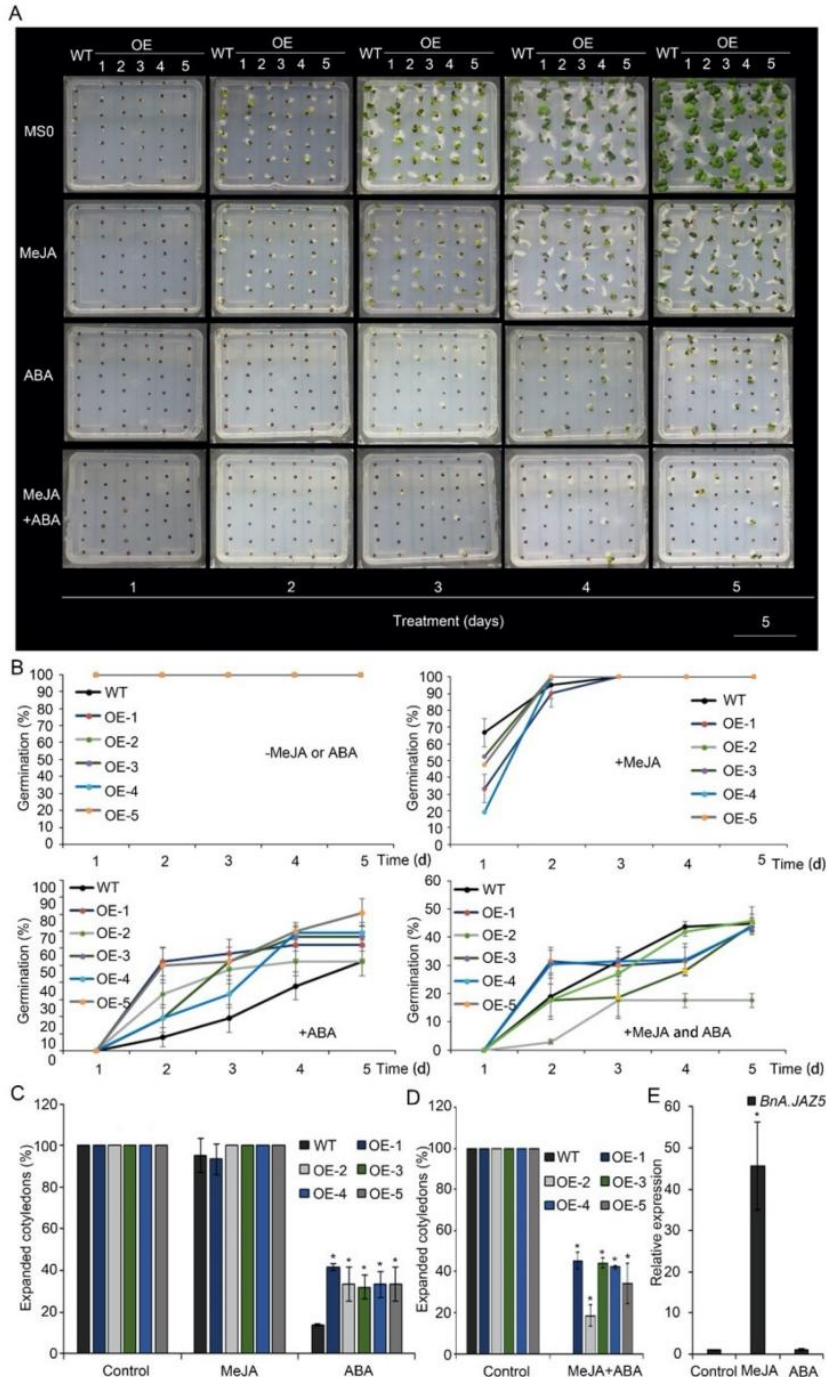


Figure 2 Seed germination of *p35S::BnA.JAZ5* plants on MS medium supplemented with 50 μ M MeJA, 9 μ M ABA or both 50 μ M MeJA and 9 μ M ABA, respectively (Adopted from Cao et al., 2022)

7 Case Study: Molecular Characterization of High-Yield Rapeseed Varieties

7.1 Study background and selection of representative cultivars

Rapeseed (*Brassica napus* L.) is one of the major oil crops worldwide, and increasing its yield has always been a key direction in breeding research. The high-yield trait of rapeseed is jointly determined by genetic factors and environmental conditions, involving a complex gene network. In recent years, with the development of technologies such as genome-wide association study (GWAS), multi-omics integration and high-throughput

sequencing, researchers have been able to screen out high-yield and low-yield varieties from large-scale germplasm resources and systematically analyze their molecular differences. For instance, among 403 core rapeseed materials, researchers utilized multi-site GWAS combined with transcriptome data to screen out 20 representative high-yield varieties and systematically evaluated their yield traits and molecular characteristics. In the Xiangride area of the Qinghai Plateau, the field performance and molecular phenotypes of varieties with different yields were compared, and it was found that the interaction between the environment and genes plays an important role in high-yield formation (Xiong et al., 2022).

7.2 Analysis of transcriptomic and proteomic data during reproductive development

During the reproductive development stage of rapeseed, transcriptome sequencing of leaves and seeds of high-yield and low-yield varieties revealed that the expression levels of genes related to cell division, cell wall formation, carbohydrate metabolism and grain filling were significantly higher in high-yield varieties (Xiong et al., 2022). The combined analysis of proteomics and transcriptomics further indicated that high-yield varieties showed an upregulation trend in cell cycle, energy metabolism, hormone signal transduction (such as MYB, bHLH, ERF, WRKY and other transcription factor families), as well as genes related to seed storage proteins and lipid transporters. These changes contribute to grain development and yield improvement (Salami et al., 2024). Furthermore, in plateau areas, prolonged sunlight exposure can increase the 1000-grain weight and the number of kernels by regulating photoperiodic gene expression and prolonging the grain development cycle (Xiong et al., 2022).

7.3 Key findings: candidate genes, signaling modules, and regulatory hubs associated with superior yield

Multi-omics integration studies have also identified a number of candidate genes and regulatory modules closely related to high yields. For instance, genes such as BnaA09g39790D (RNA helicase), BnaA09g39950D (lipase), and BnaC09g25980D (SWEET7) are significantly associated with 1000-grain weight and the number of grains per pod. In arid environments, genes such as BIG1-D, CAND1, and DRG3 affect grain formation and final yield by regulating hormone signaling and pollen development. Transcription factor families such as MYB, bHLH and WRKY, as core regulatory nodes, coordinate the processes of cell growth, energy distribution and material accumulation, and promote the formation of high-yield traits (Salami et al., 2024). High-yield varieties usually enrich these superior alleles and have a more active regulatory network, which constitutes the molecular basis of their yield advantage (Xiong et al., 2022).

8 Research Gaps and Future Directions

8.1 Integration of systems biology for modeling yield-related molecular networks

Although multi-locus GWAS, QTL mapping and transcriptome studies have identified many candidate genes and quantitative trait loci (QTNs/QTLs) related to rapeseed yield, most studies are still limited to the single-omics level and lack multi-omics integrated analysis and systematic modeling. Therefore, it is difficult to fully reveal the molecular regulatory mechanisms behind complex traits (Khan et al., 2021; Salami et al., 2024). Systems biology, by integrating multi-layer data such as genomes, transcriptomes and metabolomics, can better reveal the dynamic relationships among genes, metabolites and phenotypes, providing a theoretical basis for establishing rapeseed yield formation models (Pazhamala et al., 2021). At present, the multi-omics integration research in the field of rapeseed is still in its early stage, and there is a lack of a systematic network model for yield formation. In the future, the accumulation and sharing of multi-omics data should be strengthened, and network analysis and dynamic modeling methods suitable for complex traits of rapeseed should be developed, so as to understand the yield formation mechanism more comprehensively and achieve precise regulation (Salami et al., 2024).

8.2 Application of CRISPR/Cas genome editing for yield trait optimization

The CRISPR/Cas system has been successfully applied to the targeted editing of yield-related genes (such as BnaMAX1, BnFAD2, etc.) in rapeseed, significantly improving plant type, branch number and oleic acid content, providing a new idea for the breeding of high-yield and high-quality rapeseed varieties (Zheng et al., 2019; Wang et al., 2021). However, at present, the application of CRISPR/Cas in rapeseed yield improvement still faces some

problems, such as multi-gene redundancy, unstable editing efficiency, difficulty in obtaining de-transgenic plants, and insufficient assessment of environmental adaptability and safety (Tian et al., 2022). Most of the existing research focuses on the editing of single genes or a few genes, and there is a lack of systematic studies on the key regulatory factors in the yield formation network. In the future, CRISPR/Cas should be combined with new technologies such as systems biology and phenomics to develop high-throughput and multi-gene co-editing strategies, deeply explore the core genes affecting yield formation, and evaluate their stability and safety under multiple environmental conditions (Lin et al., 2022).

8.3 Need for cross-environmental multi-omics datasets and predictive modeling

The yield traits of rapeseed are significantly affected by genotype, environment and their interactions. It is difficult to accurately predict the yield with single environmental or single omics data (Salami et al., 2024). At present, multi-omics data across environments are still limited, and there is a lack of predictive models that can simultaneously integrate genomic, transcriptomic, metabolomic, phenotypic and environmental factors. Methods such as machine learning and neural networks have shown high accuracy in production prediction, but there is still room for improvement in the fusion of multi-omics and multi-environment data (Rajković et al., 2021; De Meyer et al., 2023). Future research should enhance multi-omics data collection in different ecological environments and establish predictive models that can integrate multi-layer information to achieve precise prediction and regulation of rapeseed yield formation (Knoch et al., 2021; Norouzi et al., 2024).

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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