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Molecular Basis of Flower Color Variation in Rapeseed: Breeding Implications

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Abstract This study expounds the molecular reasons behind the color changes of rapeseed and also explains the usefulness of these findings in breeding. Research has found that the changes in flower color are mainly related to the synthesis of pigments such as anthocyanins, carotenoids and flavonoids, and these processes are inseparable from some important regulatory genes. Environmental and epigenetic factors can also affect the expression of flower color. If genomic tools such as molecular markers and CRISPR/Cas9 gene editing technology are combined with traditional breeding methods, rapeseed varieties with ideal flower colors can be bred more quickly and accurately. This research aims to provide valuable scientific references for improving rapeseed breeding methods and expanding the applications of rapeseed in agriculture or other fields in the future.

Keywords Flower color variation; Brassica napus; *Pigment biosynthesis*; Molecular breeding; CRISPR/Cas9

1 Introduction

The flower color of rapeseed (*Brassica napus* L.) is not only beautiful, but also plays an important role in plant growth and economic value. The color of flowers can affect whether insects come for pollination, which is crucial for the seed setting and yield of rapeseed. Flower color can also reflect the genetic status and health level of crops, which is also helpful for breeding work such as increasing yield or enhancing disease resistance. From an economic perspective, rapeseed flower fields with good colors are more likely to attract attention, which can make the crops more competitive in the market and increase commercial value (Hao et al., 2022; Wang et al., 2023).

The variation of rapeseed flower color is determined by many genes and metabolic processes together, and the genetic basis is rather complex. Some genes are involved in the synthesis of pigments, such as anthocyanins that control red and purple petals. The expression level of the *BnaA03.ANS* gene in red petals is much higher than that in white and yellow petals. The metabolomic and transcriptomic analyses by Hao et al. (2022) found that flavonoids, especially anthocyanins, are the main components causing the differences in flower color. These research results facilitate a clearer understanding of the genes and metabolic mechanisms that control flower color, and also provide a reference for the targeted selection and breeding of rapeseed with specific flower colors during breeding.

This study summarizes the genetic and biochemical mechanisms of flower color formation in rapeseed, identifies the key genes and molecular markers related to different flower colors, and discusses how these findings can be applied to the breeding of rapeseed varieties with more ideal flower colors. This study aims to understand the molecular mechanisms behind flower color changes, see what uses these changes have in breeding, and provide assistance for improving rapeseed breeding methods in the future.

2 Biochemistry of Flower Pigmentation

2.1 Biosynthetic pathways of anthocyanins, carotenoids, and flavonoids

The color of rapeseed flowers is mainly determined by the synthesis pathways of three types of pigments: anthocyanins, carotenoids and flavonoids. Luo et al. (2021) and Hao et al. (2022) indicated that anthocyanin is a type of flavonoid, and its synthesis process requires several important enzymes such as DFR (dihydroflavonol reductase) and ANS (anthocyanin synthase). Liu et al. (2020) and Li et al. (2022) found that carotenoids mainly determine yellow, orange and red colors and are synthesized from a substance called isoprene. The synthesis process requires enzymes such as CRTISO (carotenoid isomerase) and ZEP (zeaxanthin epoxidase). Flavonoids (including anthocyanins) are synthesized through the phenylpropyl pathway. According to their different structures and modification methods, various colors can be formed (Grotewold, 2006; Sánchez-Cabrera et al., 2021).

2.2 Enzymatic regulation and role of key enzymes in pigment synthesis

The two enzymes, DFR and ANS, are crucial in the synthesis of anthocyanins, and their expressions are controlled by transcription factors such as MYB and bHLH (Luo et al., 2021; Hao et al., 2022). CRTISO and ZEP can convert precursor substances into pigments during the synthesis of carotenoids. If there are problems with these genes, the color of the petals will change significantly. In 2022, Li et al. 's research found that after *BnaCRTISO* mutates, its petals turn milky white. In 2020, Liu et al. 's research discovered that silencing the *BnaZEP* gene causes petals to turn orange. The regulatory process of these enzymes is rather complex, with feedback regulation and mutual influence with other metabolic pathways (Sagawa et al., 2016).

2.3 Interaction of pigments and resulting color variation

When anthocyanins and carotenoids coexist, some special color changes are formed. Liu et al. (2020) and Li et al. (2022) found that the expression of genes related to carotenoid synthesis decreased, while the expression of genes related to flavonoid synthesis increased, and the petal color of rapeseed might change significantly. Environmental factors can also affect the changes of pigments. The content of anthocyanins will increase under strong light (Figure 1) (Luo et al., 2021). The relationship between pigments and the genes that regulate them is the key to studying and controlling flower color changes (Grotewold, 2006; Sánchez-Cabrera et al., 2021).

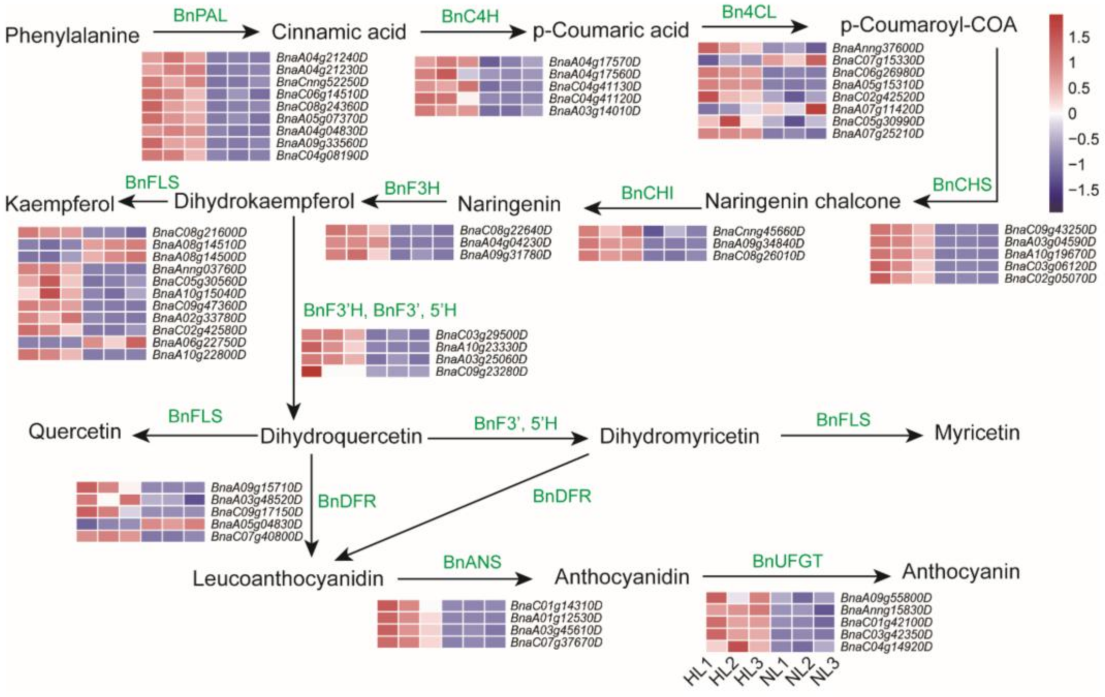

Figure 1 Change in the expression levels of anthocyanin biosynthesis-related genes in leaves of rapeseed seedlings exposed to high-light (HL) or normal-light (NL) intensity for 16 h (Adopted from Luo et al., 2021)

Image caption: Green letters above/next to the arrows represent enzymes encoded by the indicated genes in each reaction step. The key biosynthetic enzymes are as follows: BnPAL, phenylalanine ammonium lyase; BnC4H, cinnamic acid 4-hydroxylase; Bn4CL, 4-coumarate-CoA ligase; BnCHS, chalcone synthase; BnCHI, chalcone isomerase; BnCHI, flavanone-3-hydroxylase; BnF3′H, flavonoid-3-hydroxylase; BnF3’, 5’H, flavonoid-3’,5’-hydroxylase; BnFLS, flavonol synthase; BnDFR, dihydroflavonol reductase; BnANS, anthocyanin synthase; BnANR, anthocyanin reductase; and BnUFGT, uridine diphosphate glucose-flavonoid-3-O-glycosyltranferase. Colored boxes and scale indicate expression levels in the HL and NL samples. Each column represents an independent biological replicate, labeled as 1, 2, and 3 following the HL or NL designation (Adopted from Luo et al., 2021)

3 Genetic Regulation of Flower Color

3.1 Key genes controlling pigmentation in rapeseed flowers

The color of the petals of rapeseed (*Brassica napus* L.) is mainly influenced by genes related to the synthesis of flavonoids and carotenoids. Li et al. (2023) hold that *BnaA10g23330D* (also known as *BnF3'H*) is involved in the synthesis of delphinidin and peonidin, which are pigments that give the petals a purple color. Hao et al. (2022) found that the *BnaA03.ANS* gene helps synthesize anthocyanins in red petals and is indispensable. If the carotenoid isomerase gene *BnaCRTISO* mutates, it will affect the content of carotenoids and cause significant changes in the color of petals (Figure 2) (Li et al., 2022).

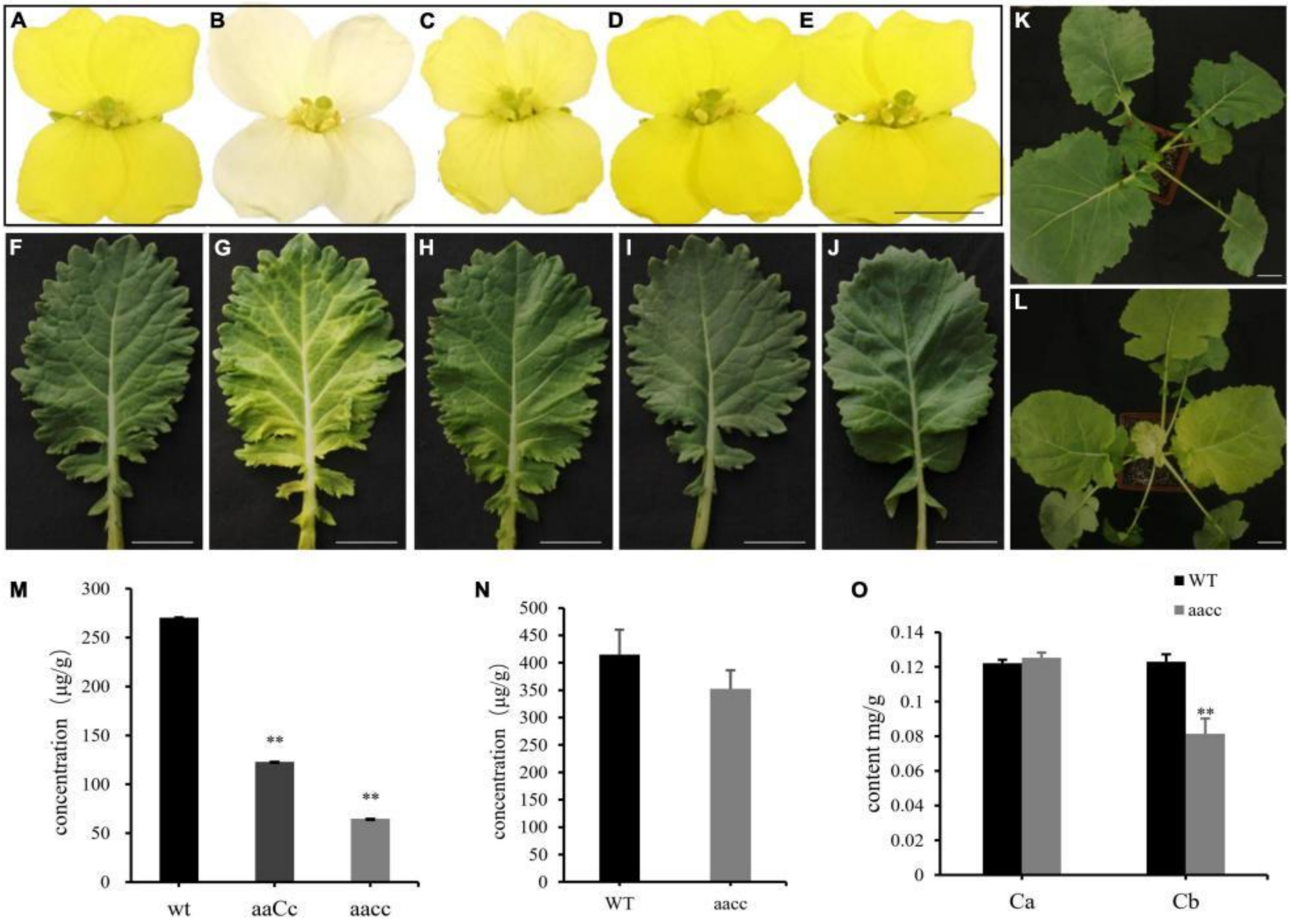

Figure 2 Mutations in the *BnaCRTISO* gene affected the color of petals and leaves (Adopted from Li et al., 2022)

Image caption: (A-J) The phenotype of flower (At the first day after flowering) and leaf in *WT*, *aacc*, *aaCc*, *AAcc*, *aaCC*, respectively. "*aaCC*," "*AAcc*," and "*aacc*" represent mutations of the target gene in *BnaA09.CRTISO*, *BnaC08.CRTISO* and both copies, respectively. (K) *WT* seeding. (L) *aacc* seeding. Bars, 1 cm. (M) The total carotenoid contents (μg/g fresh weight) of petals in *aacc*, *aaCc*, WT, respectively. (N) The total carotenoid contents of leaves in *aacc*, *WT*, respectively. (O) The content of chlorophyll *a, b* in the leaves of *WT* and *aacc*, respectively. (M-O) Data are presented as means±SE ($n \geq 3$); *t*-test was used for statistical analysis between the mutant and its *WT* (**$P > 0.01$) (Adopted from Li et al., 2022)

3.2 Regulatory mechanisms, including transcription factors

The regulation of rapeseed flower color is related to a protein combination of the MBW complex composed of three proteins: MYB, bHLH and WD40, which is the core part controlling anthocyanin synthesis. The R2R3-MYB transcription factor determines the depth and distribution range of petal color (Davies et al., 2012). The interactions among these proteins can affect when and where anthocyanin-related genes are expressed. The early study by Morita et al. (2006) also found a similar situation in morning glories, where the color of the flowers would change significantly due to mutations in the *MYB* or *WD40* genes. Park et al. (2007) argued that the bHLH transcription factor not only regulates anthocyanin synthesis but also participates in the regulatory processes of other pigments.

3.3 Epigenetic factors influencing gene expression

Epigenetic regulations such as DNA methylation and histone modification can affect the expression of genes related to anthocyanin synthesis. These modifications can alter the structure of chromatin and affect whether transcription factors can reach the target genes. Jia et al. (2021) found that the carotenoid synthesis genes that control petal color might be affected by these epigenetic factors. Davies et al. (2012) hold that environmental changes or plant development signals may also regulate the formation of the MBW complex through these mechanisms and affect the color of flowers.

4 Environmental and Epigenetic Influences

4.1 Effects of light, temperature, and soil conditions on flower color

Light can affect the synthesis of flavonoids and carotenoids, and these pigments determine the color of petals. Li et al. (2022) found that the *BnaCRTISO* gene in carotenoid synthesis changes its expression under different light conditions, causing the petal color to change from milky white to light yellow. At different temperatures, the expression patterns of genes related to flowering period and pigment synthesis will change, and the flower color will become different (Shah et al., 2018). The amount of nutrients in the soil also affects the generation of pigments, resulting in differences in the flower color of rapeseed (Jia et al., 2021).

4.2 Role of epigenetic modifications in flower pigmentation

Epigenetic regulatory methods such as DNA methylation and histone modification sometimes make genes more active, but they may also prevent them from expressing, affecting the synthesis of pigments. Recent research by Li et al. (2023) indicates that the expression of the *BnaA10g23330D* (*BnF3'H*) gene, which is crucial for anthocyanin synthesis, may be influenced by epigenetics, thereby affecting the formation of purple petals. Jia et al. (2021) found that if the *BnNCED4b* gene related to the decomposition of carotenoids is expressed abnormally, it may also change the content of carotenoids due to epigenetic regulation, causing the petals to turn white.

4.3 Interaction between genetic and environmental factors

Genes determine the basic route of pigment synthesis, and the environment affects the expression of these genes. Shah et al. 's research in 2018 and Li et al. 's research in 2022 both suggest that related genes exhibit different activities during the synthesis of carotenoids and flavonoids due to changes in light or temperature, causing alterations in petal color. Li et al. (2022) also found that if specific mutations occur in the *BnaCRTISO* gene, the plant's response to the environment will also change, resulting in different flower colors. Both the role of genes and the influence of the environment should be taken into account during breeding in order to select and breed rapeseed varieties with ideal color (Jia et al., 2021; Li et al., 2022; Li et al., 2023).

5 Evolutionary Significance of Flower Color Variation

5.1 Role of flower color in attracting pollinators

The color of flowers is crucial in attracting pollinating insects. For plants like rapeseed, it is related to whether they can reproduce smoothly. Different flower colors can affect the choice of pollinators. Different colors may attract different kinds of insects, thereby improving pollination efficiency and being helpful for plants to maintain genetic diversity (Sobel and Streisfeld, 2013; Wang et al., 2016). Davies et al. (2012) hold that the formation of flower color is mainly regulated through the anthocyanin synthesis pathway. Some transcription factors in this process can affect the amount and distribution of pigments and play a key role in this regulation.

5.2 Adaptive significance in natural and agricultural ecosystems

The variation of flower colors is useful for plants to better attract pollinators in the natural environment, which can increase the success rate of reproduction and enhance their adaptability. Flower colors can affect pollination and other agronomic characteristics in agricultural environments. Li et al. (2022) hold that different flower colors can make the fields look more beautiful, which is also beneficial for the development of agricultural tourism and the enhancement of the ornamental value of crops. Studying the genetic causes of flower color changes provides a lot of useful information for breeding work and is beneficial for breeding new rapeseed varieties that are both good-looking and of practical value (Jia et al., 2021; Li et al., 2022).

5.3 Evolutionary pathways leading to color diversification

Matar and Melzer (2021) and Hao et al. (2022) found that if the key genes controlling the synthesis of anthocyanins and carotenoids mutate, it will cause significant changes in the color of flowers. Li et al. (2022) demonstrated that mutating the *BnaCRTISO* gene with CRISPR/Cas9 technology would affect the content of carotenoids and alter the color of petals and leaves. In their 2022 study, Hao et al. demonstrated that the expression of genes and metabolites varies in petals of different colors, indicating that there is a very complex regulatory system behind the color changes. To figure out how the flower colors of rapeseed and other plants evolved, it is necessary to have an in-depth understanding of how these genes and molecular mechanisms work (Jia et al., 2021; Hao et al., 2022; Wang et al., 2023).

6 Methods for Analyzing Flower Color Genetics

6.1 Genetic mapping and quantitative trait loci (QTL) analysis

The research of Zhang and Cai (2024) suggests that genetic mapping and QTL analysis are helpful for identifying gene regions related to flower color. QTL plotting has been used to study the flowering time of rapeseed, and the flowering time is related to the flower color to some extent. The studies of Wang et al. (2016), Li et al. (2018), and Xu et al. (2021) discovered several QTLS that affect flowering time, which is helpful for understanding flower color changes. High-density SNP arrays and genome-wide association studies (GWAS) can identify which markers are related to traits more quickly and are useful for analyzing complex traits such as flower color (Wang et al., 2016; Li et al., 2018).

6.2 Use of molecular markers and marker-assisted selection (MAS)

Molecular markers such as SSR, SNP and InDel are very important in the study of flower color genetics in rapeseed. They can be used in mark-assisted selection (MAS) to help breeders accelerate the breeding process through genotype selection. Many reviews have introduced the usage and benefits of these markers in plant breeding (Collard et al., 2005). Ding et al. (2020) and Xu et al. (2021) found that some markers related to flowering time QTL have been developed and they can also be used to study flower color traits. The early research by Collard et al. (2005) indicated that breeders could select rapeseed varieties with ideal flower colors more quickly through MAS, making breeding more efficient and accurate.

6.3 Advances in omics technologies (genomics, transcriptomics, metabolomics)

Genomics, transcriptomics and metabolomics provide comprehensive information for understanding the molecular mechanisms of flower color changes. Genomics can identify candidate genes related to flower color through whole-genome resequencing (Takagi et al., 2013; Ding et al., 2020). Transcriptomics is useful for understanding which genes play a role in the synthesis of anthocyanins and reveals how these genes are regulated. Metabolomics focuses on how pigments are synthesized and analyzes the metabolites in these processes (Li et al., 2018; Ding et al., 2020).

7 Breeding Strategies for Flower Color Improvement

7.1 Conventional breeding approaches for flower color variation

The traditional methods in rapeseed flower color breeding are mainly achieved through generations of selection and hybridization. The recent research by Zhou and Xu (2024) suggests that this approach generally relies on observing the appearance of plants and selecting plants with ideal flower colors for the next step of breeding. The research by Wang et al. (2023) indicates that to select varieties with specific petal sizes, it is necessary to understand the role of major genes in order to better select and utilize different alleles. The gene *BnaCRTISO* has been found to regulate the color of petals and leaves. Its research results provide an important genetic mechanism reference for traditional breeding (Li et al., 2022).

7.2 Marker-assisted breeding for targeted traits

Marker-assisted breeding (MAB) can select plants containing good genes more quickly and accurately, improving the efficiency of breeding. The research by Wang et al. (2023) identified some SNP markers related to the petal size of rapeseed, offering the possibility of breeding varieties with specific petal sizes. The research on the *BnaC.TT2.a* gene by Zhou et al. (2016) also showed that it is related to seed coat color and fatty acid synthesis and can be used as a molecular marker for breeding. There are also some markers that can identify the genes controlling the content of linolenic acid. These examples all demonstrate that MAB is very practical in rapeseed breeding.

7.3 Application of genomic selection and hybridization strategies

Genomic selection (GS) predicts the breeding value of plants through genome-wide markers, enabling the selection of potential varieties at an early stage. Wu et al. (2019) discovered a large number of SNP and InDel variations when studying the ecological differentiation of rapeseed, indicating that GS has great prospects in rapeseed breeding. Fang et al. 's research in 2022 found that hybridization with near-isogenic lines (NILs) performed well in achieving both early flowering and high yield simultaneously, indicating that combining genetic information with traditional hybridization methods is very useful. Identifying QTL and candidate genes related to the glucosinolate content in seeds also laid the foundation for combining GS with hybridization methods in breeding (Liu et al., 2019).

8 Gene Editing and Biotechnological Tools

8.1 CRISPR-Cas9 applications for precise gene modification

In the study of Li et al. (2022), the carotenoid isomerase gene (*BnaCRTISO*) was edited using CRISPR-Cas9 technology, turning the petals milky white and the leaves yellow. This mutation led to a significant decrease in the content of carotenoids and altered the expression of many genes related to the synthesis of carotenoids and flavonoids, indicating that there is a very complex molecular mechanism behind the changes in rapeseed flower color. Wang et al. (2023) mutated the *Far-Red Elongated Hypocotyl 3* (*BnFHY3*) gene through CRISPR-Cas9 and obtained plants with smaller petals, indicating that this technology can be used to improve the size and color of petals, which is beneficial for future breeding work.

8.2 RNA interference (RNAi) and gene silencing for pigment regulation

After Hao et al. conducted RNAi treatment on the *BnaA03.ANS* gene in the petals of red rapeseed flowers in 2022, they found that the color of the flowers changed from raspberry red to rice red and zinc yellow, and the contents of pigments such as peonidin, anthocyanins, neoflavin, β-carotene, and lycopene were significantly reduced. It indicates that anthocyanins and flavonoids are crucial in the formation of red flower colors and that RNAi is effective in regulating flower colors. Liu et al. (2020) silenced the *BnaA09.ZEP* and *BnaC09.ZEP* genes, and the flowers turned orange, which also proved that RNAi can be used to improve the flower color of rapeseed (Figure 3).

8.3 Potential risks and ethical considerations

Gene editing and RNAi technologies bring about some risks and ethical issues. CRISPR-Cas9 may sometimes change in places where it should not be edited, which may affect the normal growth of plants or disrupt the ecological balance. It is not yet completely clear whether putting genetically modified plants into the natural environment will cause long-term effects. The act of modifying plant genomes also raises concerns about whether it will affect biodiversity or allow a few people to control a large amount of genetic resources. It is necessary to carefully assess the risks of these technologies and, through public discussion, find responsible solutions.

9 Case Study: Breeding Rapeseed Varieties with Desired Flower Colors

9.1 Background and objectives of the case study

The main purpose of this case study is to understand the molecular causes of flower color changes in rapeseed (*Brassica napus*) and how these findings can be applied in breeding. The flower colors of rapeseed are not only beautiful but also can attract pollinating insects and protect the reproductive parts of the flowers. The focus of the research is to identify the key genes and related metabolic pathways that control the color of petals, laying the foundation for the future cultivation of new rapeseed varieties with specific flower colors.

9.2 Methods and techniques used in breeding programs

Wang et al. (2023) identified 20 significant SNPS and 236 genes related to petal size through genome-wide association studies (GWAS), all of which can serve as molecular markers for breeding. Some studies have identified metabolites and genes with significant differences in petals of different colors through metabolomic and transcriptomic analyses. In 2023, Li et al. discovered 223 metabolites and 20 511 differentially expressed genes through UPC-MS /MS and RNA-Seq techniques, and identified the key gene *BnaF3'H* that regulates purple petals. Li et al. (2022) successfully edited the *BnaCRTISO* gene using CRISPR/Cas9 technology, altering the color of petals and leaves, indicating that there is a complex molecular regulatory mechanism behind it. Li et al. (2023) also used qRT-PCR to verify the expression of these key genes and confirmed the role of *BnaA10g23330D* in the synthesis of purple pigment.

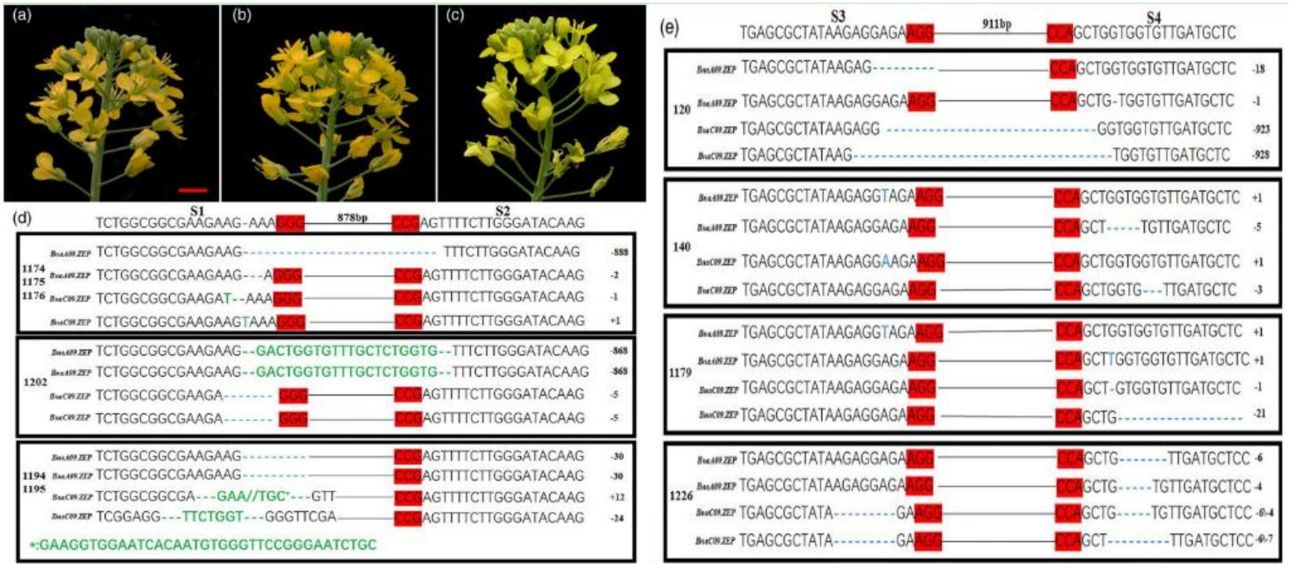

Figure 3 Mutations at the target sites in several representative knockout lines (Adopted from Liu et al., 2020)

Image caption: (a, b) Orange-flowered phenotype of one T₀ plant transformed with the CRISPR/Cas9 expression modules Crispr-*A09C09ZEP1* (a) and Crispr-*A09C09ZEP2* (b). (c) Yellow-flowered phenotype of *Brassica napus* Westar. (d, e) Sanger sequencing of the edited sites in several T₀ plants transformed with the CRISPR/Cas9 expression modules Crispr-*A09C09ZEP1* (d) and Crispr-*A09C09ZEP2* (e). All ten plants had a biallelic mutation in both *BnaA09.ZEP* and *BnaC09.ZEP*. Black letters indicate the gRNA target sites, and red-highlighted regions represent the protospacer adjacent motif. Dotted lines represent deletions, full lines represent the same sequence as in the wild-type plants and blue letters represent insertions. The numbers in the left column indicate the line number. The numbers at the end of each line indicate the type of mutation in the targeted locus (e.g. '-2' indicates a two-nucleotide deletion, '+12' indicates a 12-nucleotide insertion). Scale bar = 1.5 cm (Adopted from Liu et al., 2020)

9.3 Outcomes, challenges, and practical implications

Some key genes are involved in the synthesis of flavonoids, carotenoids and anthocyanins, which are crucial for the color of petals. Hao et al. (2022) hold that the *BnaA03.ANS* gene plays a key role in the formation of red petals. The important SNPS and differentially expressed genes (DEGs) identified by Li et al. (2023) and Wang et al. (2023) also provide useful molecular markers for targeted breeding. However, the genetic structure of rapeseed is very complex, which brings difficulties to the identification and manipulation of target genes. Li et al. (2022) also found that some genes such as *BnaCRTISO* have multiple copies, which makes it difficult for a single gene editing to produce significant effects. These research results are of great significance for cultivating ornamental rapeseed and can also help improve pollination efficiency. The development of rapeseed varieties with diverse flower colors can also enhance the field landscape effect, which is beneficial to the development of agricultural tourism (Li et al., 2022; Zeng et al., 2023).

10 Challenges and Future Directions

10.1 Challenges in achieving stable flower color traits

Li et al. (2023) demonstrated that the gene *BnaA10g23330D* (*BnF3'H*) affects the synthesis of two key components of purple petals, namely, peonidin and delphinidin, but its specific role remains to be further studied. Jia et al. 's research in 2021 found that the formation of white petals is related to the carotenoid synthesis pathway, a process involving many differentially expressed genes, which makes breeding work more complex. Li et al. (2022) demonstrated that genes like *BnaCRTISO* have multiple copies, and mutations must be carried out simultaneously on two copies to change the flower color, which makes it more difficult to achieve stable traits. Hao et al. (2022) hold that environmental factors can also affect gene expression and the accumulation of metabolites, increasing the difficulty of obtaining stable flower colors.

10.2 Integration of traditional and modern breeding techniques

Traditional breeding mainly relies on observing the appearance characteristics of plants for selection, but this method is slow and not very accurate. Modern technologies such as CRISPR/Cas9 can precisely modify genes. Li et al. (2022) successfully altered the petal and leaf colors of rapeseed by site-specific editing of the *BnaCRTISO* gene. Wang et al. 's research in 2023 found that genome-wide association studies (GWAS) identified many important SNPS and genes related to petal size and color, all of which can serve as molecular markers to assist in breeding. The combination of old and new methods can not only improve the breeding efficiency, but also cultivate rapeseed varieties with stable color and meeting the requirements more accurately.

10.3 Future perspectives in molecular breeding and market-driven innovation

Jia et al. (2021) and Li et al. (2023) have identified many differentially expressed genes and metabolites related to flower color through high-throughput sequencing techniques such as RNA-Seq and UPLC-MS/MS. Future research can focus on verifying the functions of some candidate genes such as *BnaA03.ANS* (Hao et al., 2022). Yin et al. (2019) proposed that the combination of metabolome data and genetic information is useful for identifying important regulatory pathways and thereby promoting targeted breeding efforts. Many consumers prefer rapeseed with diverse colors and good looks. Such demand will also affect the development of breeding goals. Breeding varieties with unique and stable colors can increase ornamental value, promote agricultural tourism and bring new market opportunities (Li et al., 2022).

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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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