Regulatory mechanisms of rapeseed petal color formation: Current research status and future perspectives

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A B S T R A C T

Flower color, an important rapeseed character, has great practical value and research significance. It has become an area of intensive research in recent years. This paper summarizes the latest research progress on rape flower color in terms of variety, source, pigment composition, formation mechanism, and omics. Moreover, it provides an overview of rape flower color breeding and omics.

Rape with high ornamental value is important in agricultural tourism in addition to its common uses as an edible oil, animal feed, honey, and fertilizer (Pu et al., 2019; Xiao et al., 2022; Gan et al., 2022). China has fully implemented the rural revitalization plan since 2017. In recent years, Guangdong, Wuyuan, and other regions in China have developed rape as a tourism resource (Wang, 2018), which has greatly increased the local GDP. Currently, the rape flower color used for tourism is relatively simple, and the demand for multicolored rape is increasingly growing (Huang et al., 2017).

In addition to ornamental tourism, colored rapeseed can also be used to attract pollinators and promote pollination efficiency (An, 1989; Noda et al., 2013). It can also protect the flower organs and avoid pests (Ma, 2001; Li et al., 2007; Wen et al., 2010; Simms and ucher, 1996; Irwin et al., 2003; Caruso et al., 2010). Furthermore, it can be used as an indicator character to identify seed purity and for marker assisted selective breeding (Wu, 2018). However, the genetic mechanism of rape flower color formation has not yet been fully unified. Since very few studies have reported the genetic model, further research is required.

In this paper, the current research progress of the rape flower color has been reviewed to clarify the regulatory mechanism of rape flower color. This will provide a reference for the selection of new flower color materials and promote research on the colored rape flower, as well as promoting both tourism development and local economic benefits.

1. Current status of color rape breeding

The color of rape flowers is an area of intensive focus in rape breeding. The traditional rape flower colors were mostly yellow and white (Pu et al., 2020). However, in recent years, breeders have obtained orange, red, purple, and other color lines of rape through artificial breeding (Zhang et al., 2000a,b; Liu et al., 2020), distant hybridization (Liu et al., 2014), mutagenic breeding (Zhao et al., 2021), genetic engineering, and other methods (Huang et al., 2002; Liang et al., 1994; Fu et al., 2018). The appearance of different flower colors is regulated by one or several kinds of pigments, such as carotenoids and flavonoids, due to their varied pigment composition and content. This paper collected photos of eight common colored rape flowers (Fig. 1). Yellow-white chimeras, micro purple white flowers, pink flowers, orange flowers, and purple flowers were mostly obtained by distant hybridization with cruciferous plants. Because yellow and white rape are the most common and have been extensively studied, more attention is now being paid to other colors, such as pink, orange, and purple. The yellow and white chimera and the micro purple silk white flowers have limited potential as ornamental rapeseed due to their low probability of occurrence.

2. Types and sources of rape flower color mutants

Flower color is a noticeable genetic feature in plants. The flower color of rape usually refers to the color of its mature petals (Zhu et al., 2019). The variation in rape flower color mainly includes natural mutation,

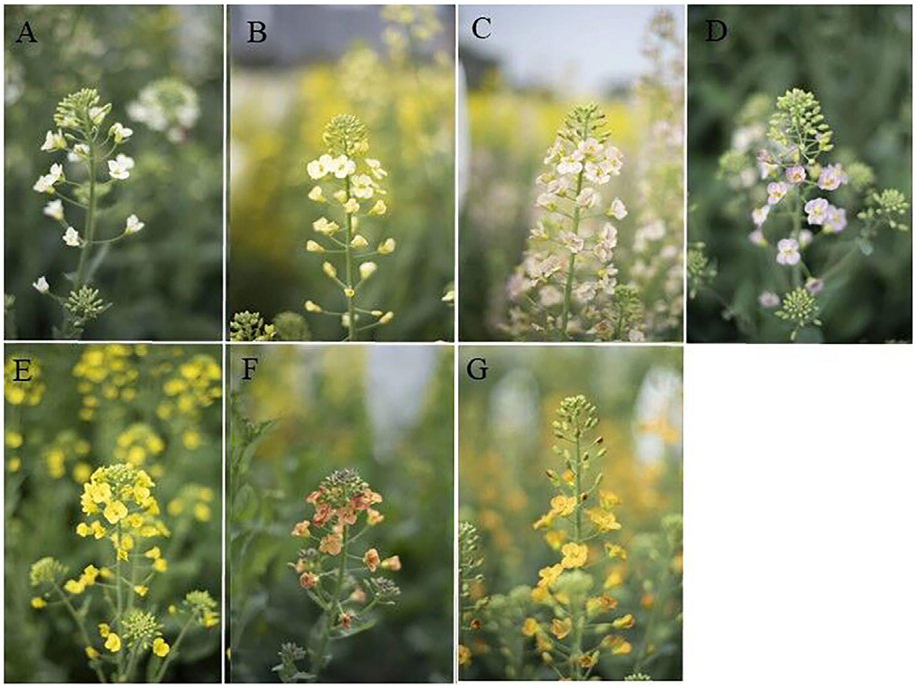

Fig. 1. Colored petals in rapeseed (Brassica napus L.). A: White flower; B: Light yellow flower; C: Pink flower; D: Purple flower; E: Yellow flower; F: Red flower; G: Orange flower. The materials of C, D, F are provided by Professor Fu Donghui of Jiangxi Agricultural University.

Table 1
Types and sources of rape flower color mutants.

Variety	Method	Flower Color	Source	Reference
97088	Natural mutations	Golden	Institute of Industrial Crops, Jiangsu Academy of Agricultural Sciences, Nanjing, China	Zhang et al. (2000)
Mutant O271	Natural mutations	Orange	National Center of Rapeseed Improvement in Wuhan, Huazhong Agricultural University, Wuhan, China	Liu et al. (2020)
ZS9 mutant ywf	EMS mutagenesis	Light yellow	National Center of Rapeseed Improvement in Wuhan, Huazhong Agricultural University, Wuhan, China	Zhao et al., 2021
PRN1 PRN2-4	Gene transfer	Yellow and white chimeras Milky	Biology Department of Hubei University, Wuhan, China	Huang et al. (2002)
K1039	Gene transfer	Light purple silk white	Southwest University, Chongqing, China	Liu et al., 2014
D1 , D2	Gene transfer	Dark yellow	Sichuan University, Chengdu, China	Liang et al. (1994)
H3	Gene transfer	Red	National Center of Rapeseed Improvement in Wuhan, Huazhong Agricultural University, Wuhan, China	Fu et al., 2018

artificial mutation, and gene transfer as shown in Table 1. The new colors that appear in natural mutations are mainly orange, golden yellow, and milky white. Artificial mutagenesis often makes the flower color pale and damages the flower organs (Chen et al., 2019). New flower colors, such as purple, pink, and red, can be obtained through gene transfer (Yin and Guan, 2013).

3. Research progress on the molecular mechanism of rape color

Since there are multiple types of rape flowers with even more complex genetic patterns, the conclusions from different studies were inconsistent due to the different experimental materials as shown in Table 2. Regarding the genetic analysis of white flower rape, although most researchers have concluded that white flower traits are regulated by incomplete dominant genes, some studies have shown that white flower traits are regulated by two pairs of major genes and multiple genes. Studies on the various colors of rapeseed have shown that flower color is controlled by one or more pairs of genes and is affected by factors, such as the chromosome and cytoplasm (Huang et al., 2017).

The flower color is determined by the pigment type and petal tissue structure with the pigment playing a key role. According to the structure and synthesis of pigments, pigments are divided into three categories, including carotenoids, flavonoids, and alkaloids (Liu et al., 2021; Camara, 2004; Gandía-Herrero, 2013; Gandía-Herrero et al., 2005; Felker et al., 2010; Markham, 2000).

To explain the mechanism of flower color regulation, color-related genes were investigated. It was found that the presentation of flower color is closely related to the carotenoid and flavonoid pathway-related genes. Tian et al. (2009) suggested that the phytoene synthase (*PSY*), phytoene desaturase (*PDS*), zeta-carotene desaturase (*ZDS*), and other carotenoid biosynthesis-related genes, as well as the carotenoid decomposition-related genes 9-cis-epoxycarotenoid dioxygenase (*NCED3*) and carotenoid cleavage dioxygenase (*CCD1*), regulated the flower color of rapeseed. Using a map-based cloning method, Zhang et al. (2015) obtained the carotenoid cleavage double oxygenase gene *BnaC3.CCD4,* which regulates the traits of cabbage-type rape white flowers. Zhang et al. (2018) constructed an approximate gene line and located the pyruvate carboxylase (*BjPC1*) and *Bjpc2* genes that regulate the traits of mustard-type rapeseed white flowers and found that both genes affected the carotenoid content. Jia et al. (2021) revealed that *BnNCED4b* encodes a protein involved in carotenoid degradation that is expressed at abnormally high levels in canola. Therefore, the formation of white rapeseedis closely related to the metabolism of carotenoids.

Table 2
Genetic pattern of rape flower color.

Flower color	Test materials	Main findings	Reference
White flower	*Raphanus sativus*, Rape	Inheritance of white-flowered trait is closely related to chromosome formation	Sernyk and Stefansson (1982)
White flower	*Brassica napus*	AABB is normal yellow; AAbb is orange; aaBB is light yellow; aabb is light orange, and aacc is milky white	Sylven (1927)
White flower	*Brassica napus*	White-flowered trait is controlled by a pair of incomplete dominant genes	Qi and Fu (1992)
White flower	*Brassica napus*	The traits of white flowers are controlled by two pairs of active genes and polygenes and are inherited as quantitative traits	Tian et al. (2009)
White flower	*Brassica campestris, Brassica alboglabra*	The hybridization of yellow cabbage with white-flowered kale showed imposed, superior, and cytoplasmic effects with the white flower showing dominance to the yellow flower. When the yellow cabbage type rape is crossed with the milky yellow flower kale, the yellow flower is dominant.	Zhang et al. (2015)
Light yellow flower	*Brassica napus*	The yellowish trait is controlled by one pair of recessive alleles.	Heyn (1977)
Orange flower	*Brassica napus*	The orange trait is controlled by two pairs of recessive genes.	Yao et al. (2017)
Yellow and white chimeras	*Brassica napus*	Yellow-white chimeras are controlled by recessive genes and are locally expressed.	Yu et al. (2004)
Orange yellow flower	*Brassica napus*	Orange-yellow is recessive to bright yellow and is controlled by two pairs of overlapping nuclear genes.	Zhou et al. (2009)
Golden flower	*Brassica napus*	The white flower versus yellow flower is controlled by one pair of incomplete dominant gene WW with the heterozygous Ww manifesting as the milky white flower. Yellow to golden flowers are controlled by two pairs of dominant genes with overlapping effects, Y1Y1Y2Y2. There are three pairs of genetic differences between white flowers and golden flowers, among which the white flower gene has a dominant effect on both the yellow flowers and golden flowers.	Zhang et al. (2000)
Light purple silk white flower	*Brassica napus, Raphanus sativus*	Purple striped flowers are caused by incomplete dominance of genes and manifest as an intermediate phenotype of both parents	Liu et al., 2014

Lee et al. (2014) studied the carotenoid isomerase gene (*BrCRTISO1*), which regulates the traits of the rapeseed milkweed. Wu et al. (2018) determined the carotenoid content of the petals of rapeseed with different flower colors (golden, yellow, earth yellow, and white flowers) and screened five different genes (*BnPSY*, lycopene β-cyclase (*BnLYCB*), lycopene epsilon cyclase (*BnLYCE*), zeaxanthin epoxidase (*BnZEP*), and *BnNCED* that are closely related to the synthesis or degradation of carotenoids.

Xu (2007) showed that the flavonoid biosynthesis-related flavonoid 3′ hydroxylase (*BnF3′H*) gene in rapeseed is primarily expressed in the petals. Qiao (2020) screened 13 key genes related to anthocyanin biosynthesis, including nine structural genes, three regulatory genes and one transporter gene. Research shows that the high expression of genes on the anthocyanin pathway control the phenotype of orange color.

As shown in Table 3, although there have been many studies on the genes related to the carotenoid pathway, more attention should be paid to the genes related to the flavonoid pathway in the future.

Fig. 2 shows the pathway of carotenoids and flavonoids. The flowering mechanism of white flowers, pale yellow flowers, and orange flowers in rape is relatively clear. The carotenoid content in the petals is significantly changed due to the preferential expression, mutation, or deletion of carotenoid-related genes, thereby resulting in different flower colors. Pink flowers and red rape have also been reported to be closely related to the metabolism of carotenoids and anthocyanins. Although the mechanism of flower color formation of yellow-white chimeric and purple rapeseed are not yet clear, purple canola color could possibly be due to the expression of anthocyanin biosynthesis-related genes, which can be focused on by future research.

Currently, there is no bluerapeseed, which may be due to the lack of the gene flavonoid 3′5′ hydroxylase (*F3′5′H*) (Noda et al., 2013) that can catalyze the synthesis of delphinidin. Therefore, such genes that regulate blue flowers can be introduced into rapeseed, or the genome editing technology *CRISPR/Cas9* can create new flower colors, such as cyan or green. Yuan et al. (2016) showed that there is a competitive relationship between the flavonoid synthesis gene flavonol synthase (*FLS*) and the anthocyanin synthesis gene leucoanthocyanidin dioxygenase (*ANS*) in the flower color formation pathway, with the *FLS* gene being preferentially expressed in some parts of the petals. Through this research, we can

Table 3
Genetic mechanism of rape flower color.

Flower color	Test materials		Mechanism	Reference
White	WP, *BnNCED4b* gene overexpression material	Yellow flower material	*BnNCED4b* participates in carotenoid degradation and decreases the lutein and zeaxanthin contents in the petals, thus, significantly decreasing the content of total carotenoids	Jia et al. (2021)
White	2127, *BnaC3.CCD4* gene preferred expression material		*BnaC3.CCD4* catalyzes oxidative cracking and significantly reduced the contents of purpurine, other carotenoids (α-carotene and lutein among others) and total carotenoids in the petals	Zhang et al. (2015)
Light yellow	Ywf, *BnaA08.PDS3* gene mutant material		*BnaA08.PDS3* promotes carotenoid accumulation, thereby significantly decreasing the contents of purpurine, lutein, zeaxanthin, and total carotenoids in the petals	Zhao et al., 2021
Yellow and white chimeras	*B. oleraceavar. alboglabra*		Yellow-white chimeras are associated with the C-genomic variation in artificial rapeseed.	Zhao et al. (2013)
Orange	O271, gene *BnaA09.ZEP, BnaC09.ZEP* missing material		*BnaA09.ZEP and BnaC09.ZEP* are responsible for continuous epoxidation of zeaxanthin, which significantly increases the lutein content in the petals and decreases the purple flavin content	Liu et al. (2020)
Pink	77, *BnaA07g15980D* and *BnaA07g17500D* introns retain variable shear material		Anabolic changes in carotenoids and anthocyanins	Zhou et al. (2021)
Red	Transcriptional regulator *OvPAP2* to 35S promoter *Orychophragmus violaceus* M4		Although the anthers turn red, the petals do not significantly turn red. In rotary petal-specific promoter plants, both the petals and anthers are red and are stable in the inbred offspring.	Fu et al., 2018
Purple	Radish KR53		Associated with anthocyanins and radish genotypes	Liu et al., 2014

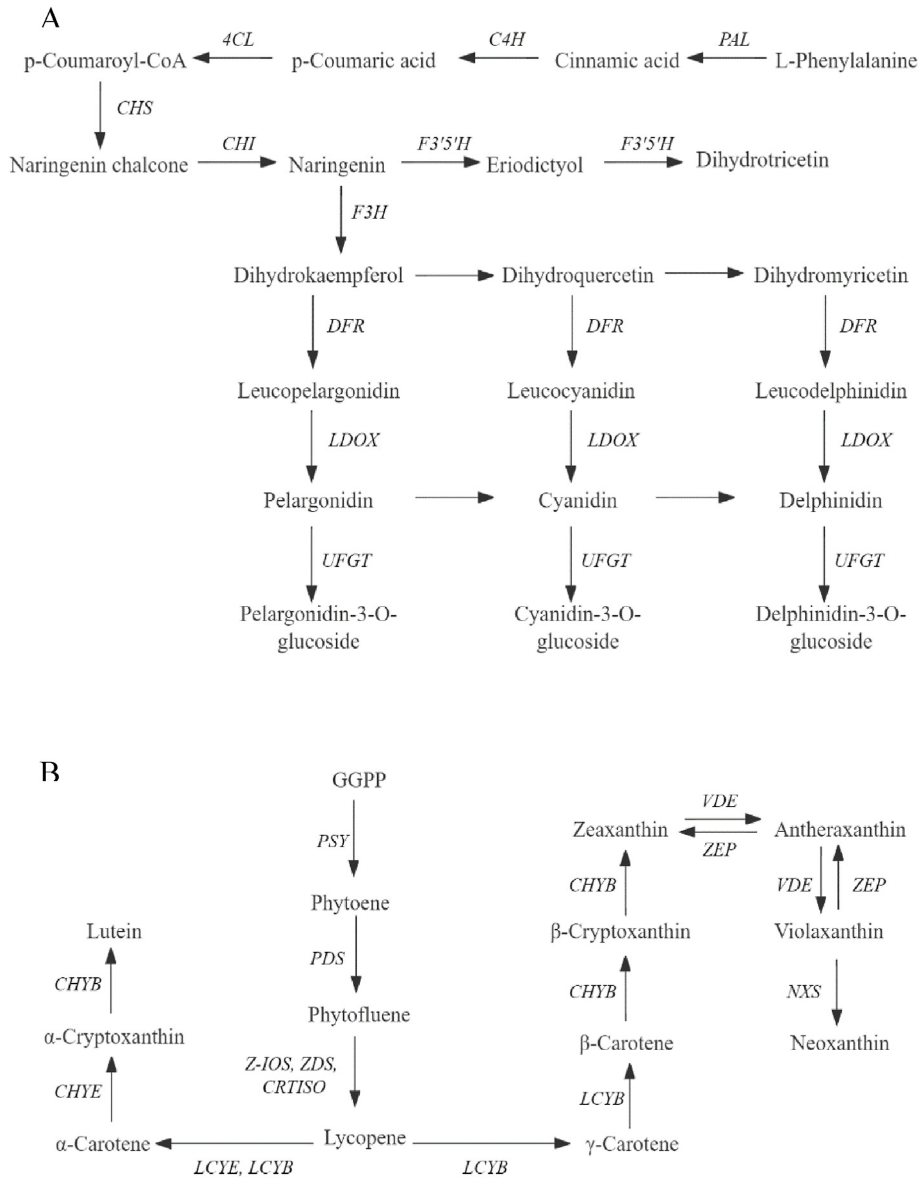

Fig. 2. Metabolic pathway diagram. A: Pathway of carotenoids; B: pathway of flavonoids.

use fixed-point gene editing technology to silence the expression of *FLS* gene, screen, and breed new flower color varieties.

4. Correlation between rape flower color and other characters

4.1. Marker-assisted breeding

Based on the constructed genetic linkage map, the marker sites related to flower color traits were gradually excavated. Dong et al. (2005) studied the RAPD marker most closely linked to the rapeseed white flower gene, while Liu (2005) obtained the RAPD marker linked to the yellow flower. Using flower color as an indicator trait, researchers can screen for hypoeric acid rapeseed, develop cytoplasmic male sterile rape varieties in the field, and identify seed purity.

4.2. Correlation between flower color and high erucic acid content in rape

The breeding goals of rapeseed are mainly high yield, high quality and high resistance. Double low (low erucic acid and sulfuric glycosides) is the goal of high-quality rapeseed breeding. Woods and Séguin-Swartz (1998) showed that the white flower traits of rapeseed are closely related to its high erucic acid content. Liu et al. (2004) screened an RAPD marker linked to both yellow flowers and a gene for low erucic acid. Pu et al. (2020) showed that the erucic acid content of orange red and peach red rape was <1.

4.3. Close linkage between rape flower color and genes related to male sterility

Studies by Kato and Tokumasu (1976) have shown that the genes that regulate rape flower color are closely related to the embryonic development-related genes, with embryos that only carry the yellow flower gene more likely to develop into vibrant seeds than those that contain the white flower gene. Heyn et al. (1908) found that the canola white flower trait is regulated by two pairs of master genes, one of which is linked to the cytoplasmic male sterility (*ogu CMS*) recovery gene. Chen and Heneen (1990) showed that the white-flowered trait is regulated by genes on the C-genome and is inherited independently of the genes that regulate male infertility traits. Li et al. (1999) found that the viability of male gametes in the orange-colored homozygote plants was relatively low. Although rape flower color and sterility genes are inherited independently, the flower color can be used to assess the degree of impurities in the field to ensure the purity of seed parents.

4.4. Utilization of rape flower color as a trait marker

Seed purity directly affects yield. The inheritance of rape flower color traits has both dominant and recessive qualities and also has certain quantitative genetic characteristics, including certain transition types. If recessive genes are introduced into restorer lines, this can not only ensure their purity but also improve those of the first generation hybrids. However, if the dominant gene is introduced into the restorer line, the purity of the first generation can be effectively identified (Zhang et al., 2000a,b; Li et al., 1999; Peng, 2008).

5. Research prospects

In recent years, the research methods for rape flower color have become more comprehensive and precise, increasing numbers of genes that regulate flower color have been deeply studied. Although there are many types of rape flower color with different genetic backgrounds, the current research is not comprehensive enough, which has certain constraints on the actual promotion. In the future, we should focus on the following aspects in depth: (1) The specific varieties of rape flower color have not been completely unified, so the flower color should be clearly classified. (2) Compared with the flower color of other plants, the range of rape flower color is narrow. Currently, there are no blue, green and other colors, so new colors can be created by using CRISPIR/Cas9 technology. (3) The traditional distant hybridization has poor fertility and unstable flower colors. Therefore, the combination of cross breeding and genetic engineering should be combined to open up new breeding ideas. (4) The flower color regulatory pathway of white, light yellow and orange rape is enriched in the carotenoid synthesis pathway. However, there is little research on other colors, such as purple, red, yellow, and white chimeras and the pathway of flavonoid synthesis, which deserve more attention. (5) Currently, most of the reports on rape flower color are related to pigment metabolome and transcriptome, which can be combined with proteomics, hormone metabolome and other multi-omics to explore the molecular mechanism of rape flower color formation. (6) The research on the relationship between fatty acids, glucosinolates, yield, oil content and flower color of rape is relatively lacking. It is necessary to determine the quality differences in yellow, white, orange, purple and other rape varieties to explore the rules between flower color and various characters, so as to select colorful rape varieties with excellent comprehensive agronomic properties, and (7) The demonstration program of colorful rape cultivation technology and landscape supporting technology can be carried out in different places to promote the development of local tourism industry.

Declaration of competing interest

All authors disclosed no relevant relationships.

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