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Identification of Genes Involved in Flower Color Formation in Rapeseed

Wenzhong Huang ✉, Zhongmei Hong
CRO Service Station, Sanya Tihitar SciTech Breeding Service Inc., Sanya, 572025, Hainan, China
✉ Corresponding email: wenzhong.huang@hitar.org

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Abstract This study introduces the genetic mechanism and regulatory mode of flower color formation in rape (*Brassica napus*), and explains several key genes involved in the synthesis of anthocyanins, flavonoids and carotenoids, such as *BnaPAP1*, *BnaTTG1* and *BnaCRTISO*, which are the core basis for the diversification of petal colors. This study, through comparative analysis with other closely related species, revealed the significant role of polyploidization and changes in regulatory patterns in the evolution of flower color, emphasizing the practical value of flower color in breseding. In the future, as long as we continue to combine these genomic tools and conduct in-depth research on the interaction between genes and the environment, there is hope to precisely control flower color traits and meet the demands of rapeseed in both practical and ornamental aspects.

Keywords Rapeseed (*Brassica napus*); Flower color; Gene identification; Anthocyanins and carotenoids; CRISPR-Cas9

1 Introduction

The flower color of rapeseed (*Brassica napus*) is a very important trait, which is related to its appearance and also has a great deal to do with agricultural applications. Rapeseed, as a major oil crop, is well known to all for its role in agriculture. Xiao et al. (2021) found that in recent years, its ornamental value has also begun to attract more attention, especially in tourist attractions, where the colorful rapeseed flowers can very well catch the eyes of tourists. The function of flower colors is not only for aesthetic purposes, but also different flower colors can affect the behavior of insects in collecting flower powder, which is very helpful for pollination. Flower color can also serve as a certain reference for breeding, which is helpful for selecting more attractive varieties with more stable yields. Jia et al. (2021) found that changing the color of flowers can make breeding work more effective and cultivate more new varieties with wide uses and high value.

Li et al. (2023) found that the formation of flower color is related to some specific metabolic processes, such as the synthesis of flavonoids and carotenoids, which is one of the key steps. Zeng et al. (2023) can more clearly identify the genes and metabolites that affect flower color through new technologies such as transcriptomics and metabolomics, thus enabling a deeper understanding of how flower color changes. However, there are still some difficulties in the research. For instance, the relationship between genes and the environment is very complex and difficult to figure out completely. Also, in different growth environments, how to make the desired flower colors stably manifest is also a big problem (Yin et al., 2019).

This study aims to clarify the molecular reasons behind the changes in flower color by using methods such as transcriptomics, metabolomics and genetic analysis, and also hopes to select some candidate genes that are useful for breeding from them. This study aims to identify the key genes and regulatory methods that affect the flower color of rapeseed, laying a foundation and providing theoretical support for cultivating new rapeseed varieties with rich flower colors and stable performance.

2 Genetic Basis of Flower Color in Rapeseed

2.1 Key pigments contributing to flower color in rapeseed

The color of rapeseed flowers is mainly determined by several pigments such as anthocyanins, flavonoids and carotenoids. Hao et al. (2022) found that components such as pelargonidin and cyanidin in anthocyanins can turn petals red or purple. Flavonoids such as quercetin and luteolin are present in relatively high amounts in white and yellow petals. Jia et al. (2021) hold that carotenoids, such as lutein and zeaxanthin, are the key to the formation of yellow petals, especially the flower color of ornamental varieties. Zeng et al. 's research in 2023 indicates that some flavonols, such as tamarixetin and kaempferol, may affect the detailed changes in petal color.

2.2 Known pathways and genes influencing pigment biosynthesis

The color change of rapeseed flowers is related to the synthesis of pigments in the body, mainly including two metabolic pathways: flavonoids and carotenoids. Hao et al. (2022) demonstrated in their research that genes like *BnaANS* and *BnaDFR* are involved in the synthesis of anthocyanins, which are crucial for the formation of red or purple petals. Li et al. (2023) discovered that the role of the *BnaF3'H* gene is to add hydroxyl groups to flavonoid molecules, influencing the color transition of petals from yellow to purple. The synthesis of carotenoids is controlled by the *BnaCRTISO* gene, which can balance the contents of lycopene and beta-carotene and regulate whether flowers turn yellow or orange (Li et al., 2022).

2.3 Regulatory networks involved in flower color formation

Transcription factors such as MYB and bHLH (for example, *BnaPAP2* and *BnaGL3*) are crucial for the synthesis of anthocyanins. They usually combine into a complex, turning on the switch of the related genes. Some hormones, such as jasmonic acid, also help activate these synthetic pathways to increase pigments when plants are under stress (Luo et al., 2021). External conditions such as light and temperature can also affect the expression of pigment-related genes. These factors combined make the color changes of rapeseed flowers more complex (Zeng et al., 2023).

3 Regulation and Expression of Flower Color Genes

3.1 Spatiotemporal expression patterns of key genes

In rapeseed, genes such as *BnaANS* (anthocyanin synthase) and *BnaF3'H* (flavonoid 3' -hydroxylase) are expressed differently in the petals, which can cause variations in the depth and hue of the flower color (Hao et al., 2022). Li et al. 's research in 2020 also found that the expression sites of transcription factors such as MYB and bHLH in related plants are relatively limited. They only function in specific regions, influencing where pigments accumulate and ultimately making the color distribution of flowers look very special.

3.2 Epigenetic regulation and its impact on flower color

Yang et al. (2015) found in *Arabidopsis thaliana* and *Brassica* plants that changes in methylation levels on promoters would affect the activity of these synthetic genes during the development of flowers. Wu et al. 's research in 2020 suggests that modifications to histones and changes in chromatin structure also precisely regulate the expression of these key genes, enabling them to respond to environmental changes or developmental stages.

3.3 Environmental influences on gene expression

In rapeseed, different light rays can change the activity of photosensitive pigment interaction factors (PIFs), and these factors will further regulate the synthesis pathway of pigments (Li et al., 2021). When the temperature changes, regulatory factors such as MYB and bHLH are also affected, thereby altering the accumulation of anthocyanins. Luo et al. (2021) hold that this indicates that the expression of flower color genes can respond to changes in the external environment.

4 Evolutionary Perspective on Flower Color Genes

4.1 Evolution of pigmentation genes in the *Brassica* genus

whole-genome triplication (WGT) has led to the duplication of some genes, laying the foundation for their subsequent different divisions of labor. The BnaZEP gene family related to carotenoid synthesis shows functional division of labor in different tissues. Some homologous genes are mainly expressed in petals, while others are more active in leaves. Liu et al. (2020) hold that this indicates that after gene duplication, the way of pigment synthesis becomes more flexible, which is helpful for plants to play a better role in reproduction and ecology. Mutations on some regulatory genes, such as changes in the promoter of flavonoid synthesis genes, also indicate that evolution is very important for the regulation of pigments in *Brassica* plants.

4.2 Comparative genomics of flower color traits across related species

There is a study conducted genomic comparisons of rapeseed and its two diploid ancestors - *Brassica rapa* and *Brassica oleracea*, and found that they have similarities as well as differences in flower color genetics. Some key genes in anthocyanin synthesis are conconservative in these species, indicating that their functions remain basically unchanged. However, the expression patterns of these genes have changed due to different regulatory mechanisms. Ye et al. 's research in 2022 demonstrated that the *BnaA07.PAP2* gene in rapeseed has variations in the promoter region, making it more prone to accumulating anthocyanins and forming apricot and pink petals, which are not common in its two ancestral species.

4.3 Adaptive significance of flower color variation in rapeseed

The bright petals are controlled by pigment genes like *BnaCRTISO*, which can better attract pollinating insects and are important for the reproduction of both wild and cultivated species. Li et al. (2022) found that some gene mutations related to carotenoid synthesis, such as the one that turns petals milky white, have been used to cultivate ornamental rapeseed varieties, making the use of rapeseed not only as grain and oil but also increasing its ornamental value. Flower color genes are beneficial for plants to adapt to the environment and have also played a role in artificial breeding, making rapeseed more important in both agriculture and ornamental plants.

5 Environmental and Physiological Influences on Flower Color

5.1 Role of temperature, light, and soil nutrients in pigment biosynthesis

Low temperatures can enhance the expression of genes like *BnaPAP1* and *BnaTT8*, causing more anthocyanins to accumulate and making the petal color purpler and brighter. Ye et al. 's research in 2022 found that the anthocyanin content in plants significantly increased in cold environments, indicating that these genes were activated. Li et al. (2022) hold that the type of light is also crucial. Red and blue light can activate the *BnaCRTISO* gene, facilitating the synthesis of carotenoids and making the petal color more distinct. Kumar et al. (2021) 's research indicates that soil nutrients such as nitrogen and sulfur also affect the generation process of anthocyanins and flavonoids, suggesting that these nutrients are also crucial for maintaining bright flower colors.

5.2 Interaction between genetic and environmental factors

Some variations in regulatory genes, such as changes in the promoter region of the *BnaA07.PAP2* gene, make it more sensitive to external conditions such as light and temperature, and it is easier for anthocyanins to accumulate in a suitable environment, resulting in brighter flower colors (Ye et al., 2022). Chen et al. (2022) 's transcriptome research found that environmental stresses such as drought and ultraviolet rays can enhance the expression of genes related to pigments, indicating that these genes have the ability to help plants cope with adverse environments.

5.3 Physiological changes affecting pigment stability and intensity

For anthocyanins and carotenoids to function properly, a stable state needs to be maintained inside the cells. Liu et al. (2020) found that the two genes, *BnaDFR* and *BnaANS*, regulate the pH of vacuoles and act together with some auxiliary pigments, which is beneficial for anthocyanins to maintain their color without fading easily and make the color appear brighter. Li et al. (2022) hold that the color of carotenoids also depends on the reduction of other metabolic pathways in the body, which can prevent the decomposition of pigments and make yellow or orange more prominent.

6 Case Studies of Flower Color Genes in Rapeseed

6.1 Identification and functional characterization of *BnaPAP1*

The BnaPAP1 gene is a “relative” of the *PAP1* gene in *Arabidopsis thaliana* and plays a very crucial regulatory role in the synthesis process of anthocyanins. This gene in rapeseed will produce different versions (called isomers) through “splicing”, and their functions are also different. *BnaPAP1-744* and some shorter variants have different effects on anthocyanin accumulation at the site of the flower. *BnaPAP1* in purple rapeseed (PR) causes a large accumulation of anthocyanins in the leaves, thus giving the leaves a bright purple color. Under the microscope, it can be seen that anthocyanins are mainly concentrated in vacuoles, which proves that *BnaPAP1* does play a role in anthocyanin synthesis (Figure 1). Chen et al. (2020) also found that *BnaPAP1* can initiate the expression of genes related to anthocyanin synthesis, which is why the petals of rapeseed can turn purple.

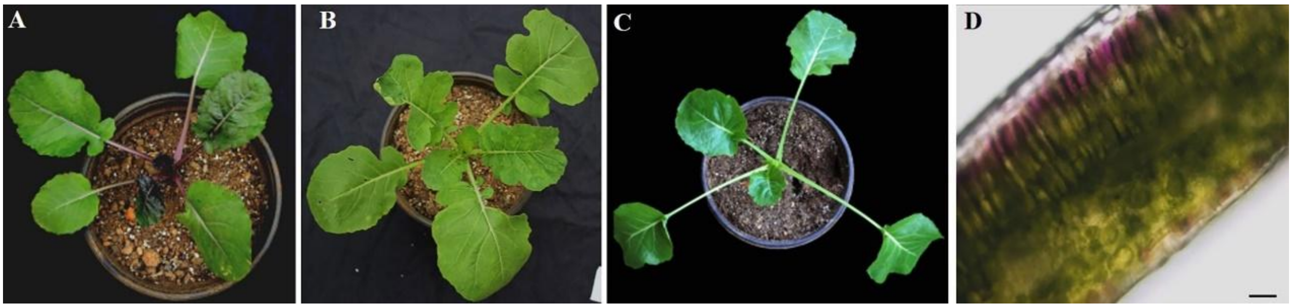

Figure 1 Characterization of anthocyanin accumulation in leaves of purple rapeseed (Adopted from Chen et al., 2020)

Image caption: (A-C) Different phenotype of young plant of PR (A) and ZS11 (B) planted outdoor and PR in the glass greenhouse (C). (D) Hand section of a young leaf of PR. Scale bar: 10 μm (Adopted from Chen et al., 2020)

6.2 Role of *BnaTTG1* in color modulation

BnaTTG1 is a homologous gene of the *TTG1* gene in *Arabidopsis thaliana*. It encodes something called the WD repeat protein and is an important part of regulating pigment synthesis. Research has found that *BnaTTG1* can cooperate with two types of transcription factors, MYB and bHLH, to form a complex and jointly initiate the synthesis process of anthocyanins. Among different rapeseed varieties, the depth of petal color varies, indicating that gene regulation also affects the accumulation of carotenoids. Although *BnaTTG1* is mainly responsible for regulating anthocyanins, it may also affect the stability of carotenoids and the overall coloring effect of petals through interactions with other regulatory pathways. The experimental data also show that the content of zeaxanthin and lutein, the two pigments, varies significantly among different varieties, indicating that the synthesis of these pigments is very complex (Figure 2). When the *BnaTTG1* gene mutates and loses its function, the pigment in the petals will significantly decrease, indicating that it is very important for the stability and intensity of the pigment (Liu et al., 2020).

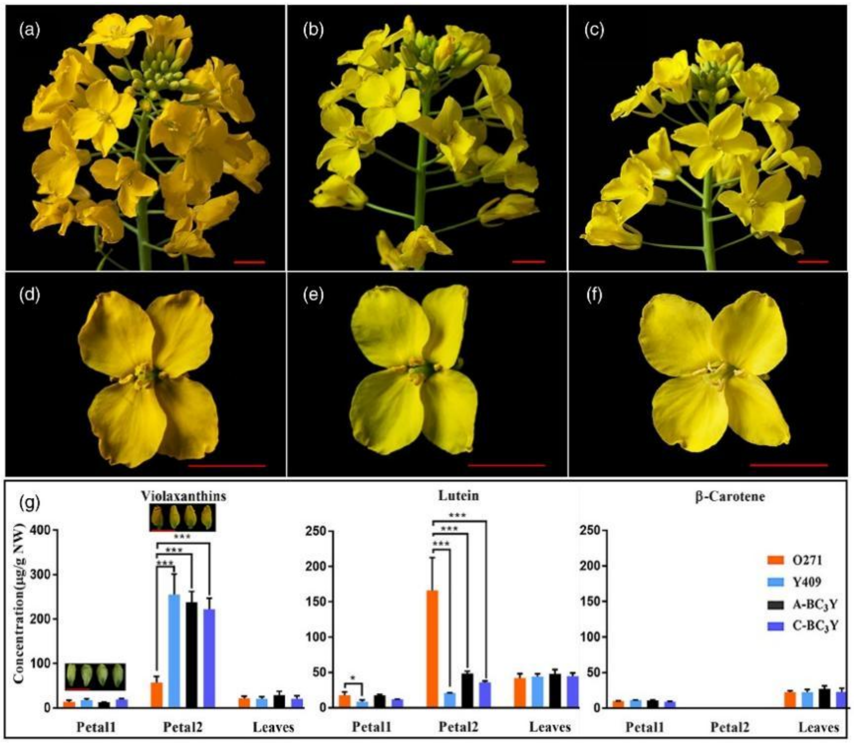

Figure 2 Petal color and carotenoid pigmentations of the parents and their progeny (Adopted from Liu et al., 2020)

Image caption: (a, b, c) An inflorescence from O271, Y409 and their F1 plant obtained with O271 as the female parent, respectively. (d, e, f) A flower from O271, Y409 and F1 plants, respectively. Scale bar = 1 cm. (g) Comparison of carotenoid contents in petals and leaves between Y409, O271 and yellow-flowered BC3 plants (C-BC3Y and A-BC3Y). Error bars represent the SDs from three measurements. Asterisks indicate significant differences: **P*<0.05 and ****P*<0.001 (Adopted from Liu et al., 2020)

6.3 Comparative analysis of orthologous genes in related species

By comparing the homologous genes related to pigments in rapeseed and its two diploid ancestors - *Brassica rapa* and *Brassica oleracea*, the study found that their regulatory networks have both similarities and many differences. *BnaPAP1* and *BnaTTG1* have similar genes in *B. rapa*. The functions of these genes are similar, but their expression patterns are also quite different due to different regulatory methods. He et al. (2021) found in their evolutionary research that after undergoing genomic polyploidization, rapeseed not only developed many repetitive genes but also underwent subfunctionalization. These changes have made its regulation of pigments in the flower organs more diverse.

7 Applications of Flower Color Research in Breeding

7.1 Development of rapeseed varieties with diverse flower colors

The research on anthocyanins is helpful for breeders to cultivate rapeseed petal varieties with diverse colors, enhancing the ornamental value of rapeseed and increasing economic benefits. By conducting directed mutations in the *BnaCRTISO* gene, a variety with milky white petals was bred. After improving the *BnaZEP* gene, rapeseed with orange petals was developed. These achievements have made the colors of rapeseed more rich and diverse (Liu et al., 2020; Li et al., 2022). Cultivating rapeseed varieties that are both practical and aesthetically pleasing, whether used as ornamental plants or in agriculture, has great potential for development.

7.2 Enhancing pollination efficiency through color variation

The color of flowers has a significant impact on attracting pollinating insects and can directly enhance the efficiency of pollination. In 2020, Chen et al. ’s research found that by modifying some key genes on the anthocyanin and carotenoid synthesis pathways, such as *BnaPAP1* and *BnaF3’H*, the color of flowers can be made brighter and more attractive to insects. In their 2022 study, Ye et al. demonstrated that apricot petals can attract more insects to visit, indicating that there is indeed a significant relationship between the color of a flower and the success of a plant's reproduction.

7.3 Integration of flower color traits into ornamental rapeseed breeding

The diversification of flower colors has also become an important goal in rapeseed breeding as people’s interest in ornamental plants is increasing. Sannikova (2020) holds that the application of gene editing technology and tools such as transcriptome analysis has made the pathways for modifying pigment synthesis more accurate, thereby cultivating rapeseed varieties with unique flower colors, which can be used in landscape design and eco-tourism. Raboanatahiry et al. (2021) found that an increasing number of breeding efforts have begun to take into account both practicality and aesthetics simultaneously, demonstrating the dual value of rapeseed as both an agricultural crop and an ornamental plant.

8 Challenges and Future Directions

8.1 Limitations in current genetic studies of flower color

Most current studies mainly focus on relatively clear genes and pathways such as carotenoids and flavonoids, while research on other factors that may affect flower color is still insufficient. Zhang et al. (2020) identified two gene loci related to white flowers, *Brwf1* and *Brwf2*, in *Brassica rapa* - but the complete regulatory network behind them has not yet been clarified. Liu et al. (2020) found that many studies only used relatively small sample populations, which would affect the effectiveness of statistical analysis methods like GWAS. The genomes of *Brassica* plants are polyploid, meaning they have many similar genes, which makes it more difficult to identify which genes are truly useful and which are merely repetitive auxiliary functions.

8.2 Opportunities with emerging genomic technologies

Combining high-resolution GWAS with large population segregation analysis (BSA) and whole-genome resequencing has achieved good results in identifying genes related to traits such as deep yellow petals (Yang et al., 2022). In their research in 2022, Ye et al. demonstrated that the combination of “multi-omics” methods such as transcriptomics, metabolomics, and proteomics has enabled researchers to gain a more comprehensive understanding of the process of pigment synthesis. The use of gene editing tools such as CRISPR/Cas9 makes it easy to precisely modify specific genes. Li et al. (2022) successfully changed the petal and leaf colors of rapeseed after modifying the *BnaCRTISO* gene.

8.3 Perspectives on functional gene editing for flower color traits

By precisely regulating gene regulatory factors such as *BnaPAP1* or *BnaTT8*, the target suit color can be stably expressed. Variations in regulatory regions such as *BnaA07.PAP2* have also been used to expand the variety of rapeseed flower colors because it can affect the accumulation of anthocyanins in petals (Ye et al., 2022). Epigenetic editing technology has also made progress, enabling the dynamic regulation of flower-related genes when encountering environmental stress. Although these new technologies have made breeding more precise and flexible, their use in agriculture has also raised some ethical and regulatory issues that need to be taken seriously.

9 Conclusion

This study introduces the main genetic mechanisms and regulatory methods influencing the flower color formation of rapeseed, with a focus on the roles of key genes such as *BnaPAP1*, *BnaTTG1* and *BnaCRTISO*. These genes are respectively involved in the synthesis of anthocyanins and carotenoids, which are an important basis for the diversification of rapeseed flower colors. With the continuous development of new technologies such as CRISPR-Cas9, high-resolution GWAS and the combination of multi-omics, researchers have made breakthrough progress in finding genes and studying their specific functions.

Future research needs to address some key issues in the recognition of flower color genes and make better use of these advanced tools available now. Combining multi-omics methods such as transcriptome, metabolome and epigenome is helpful for understanding how pigments are synthesized as a whole and how they regulate each other. Precise gene editing tools like CRISPR-Cas9 also offer brand-new possibilities for verifying key genes and regulating flower patterns. The dynamic interaction between genes and the environment is also a point worthy of attention, especially the role of factors such as the variation of cis-regulatory elements and epigenetic modifications. This is beneficial for a deeper understanding of how the color of petals changes and remains stable under different conditions.

By combining these new technologies and methods, researchers can more efficiently identify key genes and cultivate high-value rapeseed varieties with specific flower colors. This is useful for a deeper understanding of the basic principles of pigment synthesis and also opens up new development directions for rapeseed in agricultural production and ornamental applications.

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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.

References

Chen D., Liu Y., Yin S., Qiu J., Jin Q., King G.J., Wang J., Ge X., and Li Z., 2020, Alternatively spliced *BnaPAP2.A7* isoforms play opposing roles in anthocyanin biosynthesis of *Brassica napus* L., Frontiers in Plant Science, 11: 983.
https://doi.org/10.3389/fpls.2020.00983

Chen W., Miao Y., Ayyaz A., Hannan F., Huang Q., Ulhassan Z., Zhou Y., Islam F., Hong Z., Farooq M.A., and Zhou W., 2022, Purple stem *Brassica napus* exhibits higher photosynthetic efficiency, antioxidant potential and anthocyanin biosynthesis related genes expression against drought stress, Frontiers in Plant Science, 13: 936696.
https://doi.org/10.3389/fpls.2022.936696

Hao P., Liu H., Lin B., Ren Y., Huang L., Jiang L., and Hua S., 2022, *BnaA03.ANS* identified by metabolomics and RNA-seq partly played irreplaceable role in pigmentation of red rapeseed (*Brassica napus*) petal, Frontiers in Plant Science, 13: 940765.
https://doi.org/10.3389/fpls.2022.940765

He Z., Ji R., Havlickova L., Wang L., Li Y., Lee H.T., Song J., Koh C., Yang J., Zhang M., Parkin I.A.P., Wang X., Edwards D., King G.J., Zou J., Liu K., Snowdon R.J., Banga S.S., Machackova I., and Bancroft I., 2021, Genome structural evolution in *Brassica* crops, Nature Plants, 7: 757-765.
https://doi.org/10.1038/s41477-021-00928-8

Jia L., Wang J., Wang R., Duan M., Qiao C., Chen X., Ma G., Zhou X., Zhu M., Jing F., Zhang S., Qu C., and Li J., 2021, Comparative transcriptomic and metabolomic analyses of carotenoid biosynthesis reveal the basis of white petal color in *Brassica napus*, Planta, 253: 8.
https://doi.org/10.1007/s00425-020-03536-6

Kumar S., Seepaul R., Small I.M., George S., O'Brien G.K., Marois J.J., and Wright D.L., 2021, Interactive effects of nitrogen and sulfur nutrition on growth, development, and physiology of *Brassica carinata* A. Braun and *Brassica napus* L., Sustainability, 13(13): 7355.
https://doi.org/10.3390/su13137355

Li B.J., Zheng B.Q., Wang J.Y., Tsai W.C., Lu H.C., Zou L.H., Wan X., Zhang D.Y., Qiao H.J., Liu Z.J., and Wang Y., 2020, New insight into the molecular mechanism of colour differentiation among floral segments in orchids, Communications Biology, 3: 89.
https://doi.org/10.1038/s42003-020-0821-8

Li H., Yu K., Amoo O., Yu Y., Guo M., Deng S., Li M., Hu L., Wang J., Fan C., and Zhou Y., 2022, Site-directed mutagenesis of the carotenoid isomerase gene *BnaCRTISO* alters the color of petals and leaves in *Brassica napus* L., Frontiers in Plant Science, 13: 801456.
https://doi.org/10.3389/fpls.2022.801456

Li S., Li X., Wang X., Chang T., Peng Z., Guan C., and Guan M., 2023, Flavonoid synthesis-related genes determine the color of flower petals in *Brassica napus* L., International Journal of Molecular Sciences, 24(7): 6472.
https://doi.org/10.3390/ijms24076472

Li W., Liu Y., Wang W., Liu J., Yao M., Guan M., Guan C., and He X., 2021, Phytochrome-interacting factor (PIF) in rapeseed (*Brassica napus* L.): genome-wide identification, evolution and expression analyses during abiotic stress, light quality and vernalization, International Journal of Biological Macromolecules, 180: 14-27.
https://doi.org/10.1016/j.ijbiomac.2021.03.055

Liu Y., Ye S., Yuan G., Ma X., Heng S., Yi B., Ma C., Shen J., Tu J., Fu T., and Wen J., 2020, Gene silencing of *BnaA09.ZEP* and *BnaC09.ZEP* confers orange color in *Brassica napus* flowers, The Plant Journal, 104(4): 932-949.
https://doi.org/10.1111/tpj.14970

Luo Y., Teng S., Yin H., Zhang S., Tuo X., and Tran L.S.P., 2021, Transcriptome analysis reveals roles of anthocyanin-and jasmonic acid-biosynthetic pathways in rapeseed in response to high light stress, International Journal of Molecular Sciences, 22(23): 13027.
https://doi.org/10.3390/ijms222313027

Raboanatahiry N., Li H., Yu L., and Li M., 2021, Rapeseed (*Brassica napus*): processing, utilization, and genetic improvement, Agronomy, 11(9): 1776.
https://doi.org/10.3390/agronomy11091776

Sannikova V.Y., 2020, Genetic engineering as a way to obtain ornamental plants with a changed flower color, Plant Biotechnology and Breeding, 3(1): 40-45.
https://doi.org/10.30901/2658-6266-2020-1-o1

Wu J., Mohamed D., Dowhanik S., Petrella R., Gregis V., Li J., Wu L., and Gazzarrini S., 2020, Spatiotemporal restriction of *FUSCA3* expression by class I BPCs promotes ovule development and coordinates embryo and endosperm growth, The Plant Cell, 32(6): 1886-1904.
https://doi.org/10.1105/tpc.19.00764

Xiao M., Wang H., Li X., Mason A.S., and Fu D., 2021, Rapeseed as an ornamental, Horticulturae, 8(1): 27.
https://doi.org/10.3390/horticulturae8010027

Yang H., Chang F., You C., Cui J., Zhu G., Wang L., Zheng Y., Qi J., and Ma H., 2015, Whole - genome DNA methylation patterns and complex associations with gene structure and expression during flower development in Arabidopsis, The Plant Journal, 81(2): 268-281.
https://doi.org/10.1111/tpj.12726

Yang S., Liu H., Zhao Y., Su H., Wei X., Wang Z., Zhao X., Zhang X.W., and Yuan Y., 2022, Map-based cloning and characterization of *Br-dyp1*, a gene conferring dark yellow petal color trait in Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis*), Frontiers in Plant Science, 13: 841328.
https://doi.org/10.3389/fpls.2022.841328

Ye S., Hua S., Ma T., Ma X., Chen Y., Wu L., Zhao L., Yi B., Ma C., Tu J., Shen J., Fu T., and Wen J., 2022, Genetic and multi-omics analyses reveal *BnaA07.PAP2*$^{In\text{-}184\text{-}317}$ as the key gene conferring anthocyanin-based color in *Brassica napus* flowers, Journal of Experimental Botany, 73(19): 6630-6645.
https://doi.org/10.1093/jxb/erac312

Yin N.W., Wang S.X., Jia L.D., Zhu M.C., Yang J., Zhou B.J., Yin J.M., Lu K., Wang R., Li J.N., and Qu C.M., 2019, Identification and characterization of major constituents in different-colored rapeseed petals by UPLC–HESI-MS/MS, Journal of Agricultural and Food Chemistry, 67(40): 11053-11065.
https://doi.org/10.1021/acs.jafc.9b05046

Zeng H., Zheng T., Li Y., Chen Q., Xue Y., Tang Q., Xu H., and Chen M., 2023, Characterization variation of the differential coloring substances in rapeseed petals with different colors using UPLC-HESI-MS/MS, Molecules, 28(15): 5670.
https://doi.org/10.3390/molecules28155670

Zhang N., Chen L., Ma S., Wang R., He Q., Tian M., and Zhang L., 2020, Fine mapping and candidate gene analysis of the white flower gene *Brwf* in Chinese cabbage (*Brassica rapa* L.), Scientific Reports, 10: 6080.
https://doi.org/10.1038/s41598-020-63165-7