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Functional Analysis and Molecular Improvement of Color-Related Genes in Pepper Fruit

Weiguo Lu, Deming Yu, Qishan Chen ✉
Modern Agricultural Research Center, Cuixi Academy of Biotechnology, Zhuji, 311800, China
✉ Corresponding email: qishan.chen@cuixi.org

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Abstract This study summarizes the main metabolic pathways, key genes and their regulatory methods involved in the color formation of peppers, introduces the latest progress of multi-omics technology in studying the mechanism of pigment accumulation, and proposes that in the future, the color of peppers can be improved through multi-omics integration, precise breeding and the construction of a color trait database to enhance the utilization rate of genetic resources. Research has found that there is mutual influence among different pigment metabolic pathways. The transcription factor network plays a major role in fruit development and ripening, determining the change in color. Environmental factors can also indirectly affect the synthesis of pigments by regulating transcription factors and signaling pathways. The combination of new technologies such as molecular marker-assisted selection, gene editing and metabolic engineering has opened up a new direction for the color improvement of peppers. This research aims to provide a theoretical basis and practical guidance for the molecular improvement and precise breeding of pepper color traits.

Keywords Pepper fruit color; Carotenoids and anthocyanins; Transcriptional regulation; Multi-omics integration; Genome editing and molecular breeding

1 Introduction

Pepper (*Capsicum* spp.) is one of the most widely grown and consumed vegetables in the world. Its fruit colors are very rich, including various types such as green, yellow, orange, red, purple, white and black (Feyera et al., 2024; Wei et al., 2025). This color difference makes peppers more ornamental and marketable, and also influences consumers' choices and breeding directions (Bhattarai et al., 2024). The pigments in fruits are also closely related to their nutritional value. Peppers are rich in components such as carotenoids, vitamin C and anthocyanins, which have positive effects on human health (Wang et al., 2023). The nutritional composition of peppers of different colors varies. For instance, the red varieties usually have higher contents of carotenoids and vitamin C (Moon et al., 2023).

The fruit color of peppers is mainly determined by three types of pigments: carotenoids, chlorophyll and anthocyanins (Wei et al., 2025). Carotenoids make mature fruits appear red, orange or yellow. The synthesis of these pigments is closely related to key enzyme genes (such as *PSY1*, *CC*S) (Jeong et al., 2018; Ro et al., 2024). Chlorophyll makes unripe fruits green, and its synthesis and degradation are regulated by various transcription factors (such as CaBBX10, CaRIN) (Wang et al., 2024; Song et al., 2025). Anthocyanins determine the formation of purple and black fruits and are regulated by transcription factors such as MYB and bHLH (Tang et al., 2020; Zhou et al., 2025). Multi-omics and genetic studies have shown that the process of pigment accumulation is regulated by multiple genes and is also affected by the environment (Liu et al., 2020; Shu et al., 2023).

This study summarizes the functions and molecular regulatory mechanisms of genes related to the color of peppers, introduces the synthesis and accumulation processes of carotenoids, chlorophyll and anthocyanins, analyzes their regulatory networks, and explores the application prospects of molecular breeding and gene editing techniques in the color improvement of peppers. This research aims to provide theoretical support and technical references for the cultivation of high-quality and diverse new pepper varieties.

2 Biochemical Pathways of Color Formation in Pepper Fruit

2.1 Overview of pigment biosynthetic pathways: carotenoid, flavonoid, and chlorophyll metabolism

The color of peppers is mainly determined by three types of pigments: carotenoids, flavonoids and chlorophyll. In the early stage of fruit development, chlorophyll is dominant and the color is green. As the fruit ripens, chlorophyll gradually decomposes, while carotenoids and flavonoids continuously accumulate, causing the fruit color to change to various tones such as yellow, orange or red (Figure 1) (Jang et al., 2022; Zhang et al., 2022). Chlorophyll a and b are synthesized in chloroplasts and they are important components for photosynthesis. The biosynthesis of chlorophyll starts with glutamic acid and is completed through multiple steps of reactions. During the fruit ripening process, these chlorophyll will gradually degrade, causing the green color to fade (Wang et al., 2023). The synthesis of carotenoids takes place in chloroplasts or pigment bodies, with GGPP as the starting substrate. Lycopene is formed under the catalysis of PSY enzyme, and then major pigments such as β -carotene, lutein and capsaicin are generated through cyclization and hydroxylation reactions (Song et al., 2022). The synthesis of flavonoids mainly occurs in the fruit epidermis, including compounds such as anthocyanins and flavonols. It uses phenylalanine as raw material and forms various derivatives under the action of enzymes such as CHS and C4H, thereby endowing the fruit with richer colors and antioxidant capacity (Wei et al., 2025).

Figure 1 Fruit color change during ripening of (A) “3501,” (B) “3509,” (C) “Long Sweet,” and (D) “AC2212.” FS, fruit set, MG, mature green, BK, breaker stage, FR, full red color fruit. White and black bars indicate 3 cm (Adopted from Jang et al., 2022)

2.2 Key enzymes involved in pigment synthesis and degradation

Genes such as *COX15* and *POR* promote the production of chlorophyll, while genes such as *PAO*, *PPH* and *RCCR* are responsible for degradation, causing the fruit color to transition from green to other tones (Wei et al., 2019; Jang et al., 2022). In the carotenoid pathway, PSY is the rate-limiting enzyme, and PDS, ZDS, LCYB and CCS, etc. successively catalyze the generation of lycopene, β -carotene and capsaicin. Especially CCS, which is a key enzyme in capsaicin synthesis and plays a decisive role in the final red color of the fruit (Berry et al., 2019; Wei et al., 2020; Villa-Rivera et al., 2022). The synthesis of flavonoids relies on the collaboration of multiple enzymes, including CHS, C4H, F5H, CCR and CAD, etc. These enzymes jointly regulate the accumulation of anthocyanins and flavonols, making the fruit color more layered and enhancing the antioxidant capacity (Zhang et al., 2022; Wang et al., 2023).

2.3 Cross-talk among pigment pathways and regulatory balance during fruit ripening

There are interactions and regulatory equilibria among different pigment metabolic pathways. The synthesis of chlorophyll and carotenoids both require GGPP as a precursor. Therefore, at fruit ripening, chlorophyll decomposition and carotenoid accumulation are usually negatively correlated (Jang et al., 2022; Song et al., 2022). The antioxidant function of flavonoids can also delay the degradation of chlorophyll and help fruits remain green (Wei et al., 2025). Meanwhile, multiple transcription factors such as CaBBX10, MADS-RIN and DIVARICATA1 can simultaneously regulate multiple pigment synthesis pathways, thereby maintaining the dynamic balance of fruit color changes (Song et al., 2023; Wang et al., 2024).

3 Functional Analysis of Color-Related Genes

3.1 Genetic and molecular characterization of structural genes controlling pigment accumulation

The carotenoid synthesis pathway contains a variety of key structural genes, such as *PSY*, *CCS*, *LCYB*, *ZEP*, etc. The expression levels and sequence changes of these genes will directly affect the types and contents of pigments in the fruit. Studies have found that the deletion or mutation of the *CCS* gene often leads to the fruit presenting yellow or orange, and the expression changes of genes such as *PSY*, *LCYB*, and *CRTZ* are also closely related to the pigment accumulation of different color types (Lee et al., 2021; Lv et al., 2023; Shen et al., 2024). In addition, genes such as *APRR2* and *GLK2* can regulate chlorophyll synthesis and play a decisive role in the green appearance of unripe fruits (Jeong et al., 2020; Wu et al., 2021; Sun et al., 2025). In terms of anthocyanin synthesis, the high expression of structural genes such as *PAL*, *C4H*, *CHI*, *DFR*, *ANS*, and *UFGT* promotes the formation of purple fruits (Tan et al., 2024).

3.2 Regulatory genes and transcription factors affecting color expression

Family members such as MYB, bHLH, WRKY, MADS-box and NAC are important in regulating capsaicin formation. MYB transcription factors can activate genes related to anthocyanin or carotenoid synthesis and promote pigment accumulation (Arce-Rodriguez et al., 2021; Zhou et al., 2025). Tang et al. (2024) and Wang et al. (2022) both found that bHLH and WRKY factors often work in synergy with MYB to regulate the anthocyanin synthesis pathway. WRKY6 can bind to the CCS promoter to enhance the synthesis of carotenoids. The MADS-box factor affects the color change during fruit ripening by regulating chlorophyll degradation and carotenoid metabolism (Song et al., 2023; Song et al., 2025). Meng et al. and Villa-Rivera et al. 's research in the same year, that is, in 2025, both indicated that members of the NAC family can regulate structural genes such as *PSY* to promote the accumulation of carotenoids.

3.3 Functional validation via transgenic approaches, gene silencing, and mutant studies

After VIGS silenced genes such as *CCS*, *PSY*, *LCYB*, and *ZEP*, the fruit color changed from red to yellow or orange, and the pigment content decreased significantly, proving that these genes are very important in pigment synthesis (Shen et al., 2024; Villa-Rivera et al., 2025). Overexpression or silencing of transcription factors such as MYB, bHLH, and WRKY can also change the expression levels of structural genes, directly affecting pigment accumulation and fruit color (Tang et al., 2024; Zhou et al., 2025). Jeong et al. (2020) and Lee et al. (2021) found that natural or artificially induced mutants provide valuable materials for studying the genetic basis of fruit color formation.

4 Omics Approaches to Elucidate Color Regulation

4.1 Transcriptomics and metabolomics profiling during fruit development

Researchers found that the flavonoid, propane and chlorophyll metabolic pathways are crucial in color formation by comparing the transcriptome and metabolome data of fruits at different developmental stages. In the comparison between dark green and light green pepper varieties, the metabolites such as quercetin, kaferferol-3-O-rhamnoside and cinnamic acid in dark green fruits increased significantly. These substances are related to stronger antioxidant activity and delayed chlorophyll degradation. Transcriptome analysis indicated that the chlorophyll synthesis gene and the light capture complex gene were upregulated in dark green fruits, and the expression of the chlorophyll degradation gene *PAO* also increased, suggesting that fruit color is jointly regulated by pigment synthesis and degradation (Lv et al., 2023; Sun et al., 2025; Wei et al., 2025). The accumulation of carotenoids and anthocyanins is closely related to the expression changes of their synthetic genes in different fruit colors, and presents specific expression patterns (Filyushin et al., 2020; Li et al., 2021; Xue et al., 2024).

4.2 Identification of key regulatory networks and co-expression modules

Researchers identified multiple gene modules closely related to pigment synthesis during the fruit development stage of peppers by using methods such as weighted gene co-expression network analysis (WGCNA). Some modules are positively correlated with the content of carotenoids and flavonoids, while others are correlated with the content of chlorophyll. Module analysis revealed that hub genes and transcription factors play a core role in pigment synthesis and transport (Li et al., 2021; Shen et al., 2024; Tan et al., 2024). Specific transcription factors can directly regulate the expression of structural genes, affect the accumulation of anthocyanins and carotenoids, and determine the final color of the fruit (Song et al., 2023; Tang et al., 2024; Song et al., 2025).

4.3 Integration of genomics, proteomics, and metabolomics for pigment pathway reconstruction

By integrating genomic mapping, proteomic identification and metabolomic quantitative analysis, researchers not only identified key structural genes but also depicted the hierarchical relationship of the regulatory network. Some studies have discovered a NAC domain gene related to anthocyanin synthesis by using GWAS combined with KASP typing technology, and verified its regulatory role through proteomic and transcriptomic analysis (Meng et al., 2025; Sun et al., 2025). The combined analysis of proteomics and metabolomics revealed the direct connection between the expression dynamics of pigment synthase and the accumulation of metabolites, providing a theoretical basis for molecular breeding and color improvement (Lv et al., 2023; Xue et al., 2024; Wei et al., 2025).

5 Molecular Breeding and Biotechnological Improvement

5.1 Marker-assisted selection (MAS) for color-related alleles in breeding populations

Through genome-wide association study (GWAS) and various molecular marker techniques, researchers can more accurately locate major genes and quantitative trait loci (QTL) related to fruit color. For instance, by using SLAF-seq technology, a total of 1 496 high-quality SNP markers were detected in 197 natural populations of peppers, which were further located to 30 significant SNP loci on chromosome 6. KASP classification technology and phenotypic analysis, the researchers identified a NAC domain structure of anthocyanin synthesis genes (*CA.PGAv.1.6.Scaffold919.44*), provides an important reference for molecular breeding peppers colour (Tong et al., 2022; Zakiyah et al., 2023; Meng et al., 2025). In addition, the molecular markers of the *CCS* gene have been successfully used to distinguish orange fruits from red ones. This marker is completely co-separated from the pigment composition and can be directly applied to the breeding of varieties of different colors.

5.2 CRISPR/Cas-based genome editing for targeted gene modification

Researchers targeted and edited key genes such as *CaPDS* in peppers through CRISPR/Cas9, achieving functional verification and trait improvement of the pigment synthesis pathway. After knocking out the *CaPDS* gene, Bulle et al. (2024) obtained mutants with a bleached phenotype, confirming the key role of this gene in carotenoid synthesis, with an editing efficiency as high as 62.5% (Figure 2). The DNA-free CRISPR/Cas RNP system has achieved efficient editing in *Capsicum* primortists without leaving exogenous DNA, providing a scientific basis for stable genetics and commercial breeding (Chen et al., 2019; Kim et al., 2020; Cardi et al., 2023) The multi-gene editing strategy has been successfully applied to the rapid directional improvement of multicolor fruits in Solanaceous crops such as tomatoes, providing an important reference for the molecular breeding of multicolor fruits in peppers (Xu et al., 2020; Yang et al., 2022).

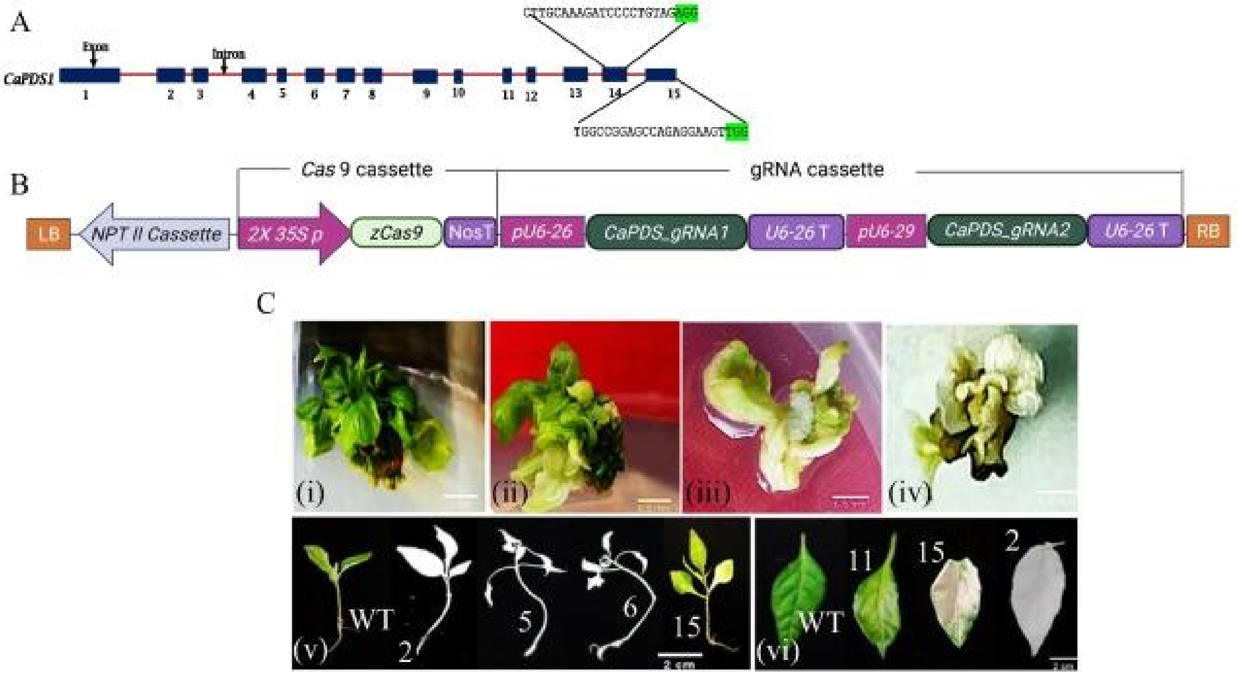

Figure 2 CRISPR/Cas9-mediated modification of *CaPDS* in Chilli pepper (*Capsicum annuum* L) (Adopted from Bulle et al., 2024)

5.3 Metabolic engineering to enhance pigment accumulation and color stability

Regulating the expression of key enzyme genes in the pigment synthesis pathway can increase the pigment content and color stability in fruits. Multi-omics studies have found that the synergistic regulation of flavonoid and chlorophyll metabolism is the main reason for the color differences of various green fruits. Wei et al. (2025) hold that the enrichment of key metabolites such as quercetin and apigenin-3-O-rhamnoside is closely related to the enhanced antioxidant capacity of fruits. In the carotenoid pathway, the expression levels of genes such as *PSY1*, *LCYB*, and *CCS* directly affect the accumulation of major pigments such as capsanthin (Wang et al., 2019; Wei et al., 2020). Gao et al. (2025) demonstrated in their research that exogenous melatonin treatment can activate the phenylpropane metabolic pathway, promote the synthesis of polyphenols and flavonoids, and enhance the color and stress resistance of fruits.

6 Case Study: Functional Characterization of a Key Color Gene in Pepper

6.1 Study background: identification of a novel gene affecting carotenoid or anthocyanin accumulation

The colors of peppers are diverse, mainly determined by the accumulation and metabolic regulation of carotenoids and anthocyanins. In recent years, scientists have identified a variety of key genes that affect pigment accumulation through population genetics, transcriptome and metabolome studies. The *CCS* gene is very important in the synthesis of carotenoids. When this gene is absent or its expression is decreased, the fruit color will change from red to orange or yellow (Li et al., 2021; Lv et al., 2023). Transcription factors such as NAC and MYB have also been proven to regulate anthocyanin synthesis and affect the degree to which the fruit appears purple or red (Liu et al., 2024; Tan et al., 2024; Meng et al., 2025).

6.2 Experimental approaches: gene cloning, expression profiling, and phenotypic validation

Gene cloning usually employs PCR amplification and sequencing methods to obtain the target gene, and analyzes its sequence differences to infer functional changes (Jeong et al., 2020; Liu et al., 2024). Li et al. (2021) and Lv et al. (2023) used qRT-PCR or transcriptome sequencing to compare materials at different developmental stages and fruit color types, and determine the expression pattern of the target gene during the pigment accumulation process. Phenotypic verification commonly employs methods such as VIGS (virus-induced gene silencing), gene overexpression, or CRISPR/Cas9 knockout to verify gene function. When *CCS* or *CaMYB113* was silenced, the contents of carotenoids or anthocyanins in the fruits decreased significantly and the color became lighter, thereby demonstrating the key role of these genes in fruit color formation (Liu et al., 2024; Zhou et al., 2025).

6.3 Key findings: molecular mechanism, breeding implications, and color phenotype outcomes

Li et al. (2021) and Lv et al. (2023) both found that the deletion or insufficient expression of the *CCS* gene would impede the synthesis of carotenoids, causing the fruit color to change from red to orange or yellow. Mutations in genes such as *PRR2* and *GLK2* can affect the formation and function of the pigment body, resulting in white or light-colored phenotypes in the fruit (Jeong et al., 2020; Lee et al., 2020). The synthesis of anthocyanins is regulated by transcription factors such as MYB and NAC. Mutations or expression changes of these genes can weaken or enhance the purple phenotype (Tan et al., 2024; Meng et al., 2025). Researchers can precisely improve the fruit color of peppers by using molecular marker-assisted selection (MAS) and gene editing techniques. Cultivating new germplasms with high pigment content or specific color types and enhancing the commercial value and nutritional quality of peppers can all be achieved through these methods (Sun et al., 2025). When the *CCS* gene is intact and highly expressed, the fruit appears bright red. When its expression is low or absent, the fruit turns orange or yellow. The loss of function of genes such as *MYB113* will cause the purple phenotype to disappear, while its overexpression can significantly increase the accumulation of anthocyanins, making the fruit appear deep purple or red-purple (Liu et al., 2024).

7 Environmental and Developmental Influences on Fruit Color

7.1 Temperature, light, and nutrient effects on pigment biosynthesis

Light exposure, especially UV-B radiation, can promote the increase in the expression of genes related to anthocyanin synthesis, making the fruit peel show a more obvious purple phenotype (Wang et al., 2022). The level of nitrogen fertilizer can also have a significant impact on the synthesis of carotenoids. Shen et al. ’s research in 2024 demonstrated that appropriately reducing the application of nitrogen fertilizer can increase the total content of carotenoids and capsaicin in fruits and enhance the activity of synthases such as PSY, LCYB, and CCS. The changes in temperature and photoperiod can also disrupt the balance between chlorophyll degradation and carotenoid accumulation, and alter the color of the fruit (Wang et al., 2023; Wei et al., 2025).

7.2 Developmental regulation of gene expression and color transition during ripening

During the fruit development process, the expression of genes related to pigment synthesis and degradation is staged. During the green ripening period, chlorophyll synthesis genes (such as *CaGLK2* and *CaAPRR2*) are highly expressed, keeping the fruit green. As the fruit ripens, chlorophyll degradation genes (such as *PAO*, *SGR*) and carotenoid synthesis genes (such as *PSY*, *CCS*) are gradually upregulated, promoting the color to change from green to red or yellow. MADS-box transcription factors (such as CaRIN) can regulate chlorophyll degradation-related genes (such as *CaLhcb-P4*), accelerate the decomposition of chlorophyll during the ripening period, and thereby promote fruit color changes (Song et al., 2023; Song et al., 2025). The accumulation amount of pigments and the expression patterns of related genes in different tissues (peel and pulp) are also different. This tissue difference further enriches the diversity of fruit color (Filyushin et al., 2020; Zhang et al., 2022).

7.3 Interaction between environmental cues and genetic control networks

Environmental signals can affect the expression of pigment synthesis and degradation genes by regulating transcription factors and non-coding RNAs, forming a complex regulatory network (Zuo et al., 2019; Tang et al., 2024). Abscisic acid (ABA) can promote chlorophyll degradation, while ethylene enhances carotenoid synthesis. The two jointly regulate fruit ripening and color change (Hou et al., 2018; Song et al., 2023). The key genes and metabolites in the pigment metabolism pathway interact in the co-expression network to jointly regulate fruit color formation (Wei et al., 2025). The interaction between environmental factors and genetic background is also an important reason for the color differences among different pepper varieties (Zhang et al., 2022; Sun et al., 2025).

8 Future Perspectives and Research Challenges

8.1 Need for multi-omics integration to map color regulation complexity

The color formation process of peppers involves multiple aspects such as pigment synthesis, metabolic regulation, and changes in cell structure. Single-omics studies often struggle to fully reveal this complexity. In recent years, researchers have begun to explore the molecular mechanism of pepper color formation through the joint analysis of multiple omics such as transcriptomics, metabolomics and genomics. There are synergistic changes in pigment accumulation and gene expression among different developmental stages or different varieties. These studies identified the key nodes and regulatory genes in metabolic pathways such as flavonoids, carotenoids and chlorophyll (Liu et al., 2020; Wei et al., 2025). The combination of multi-omics data is helpful for discovering new regulatory factors and gene networks, thereby promoting a systematic understanding of the regulatory mechanism of pepper color (Song et al., 2024). Lozada et al. (2022) indicated that future research requires further development of high-throughput, multi-dimensional omics techniques and the integration of epigenomic, proteomic and other data into integrated analysis to more comprehensively analyze the regulatory network of pepper fruit color.

8.2 Translational opportunities from molecular studies to precision breeding

A large number of studies have revealed the key genes and their variant types that affect the color of peppers, providing important theoretical basis and molecular tools for precision breeding. Shu et al. (2023) demonstrated that GWAS, QTL mapping, and candidate gene analysis have identified multiple major genes and regulatory factors, such as CCS, APRR2, PSY, and NAC, etc. These molecular markers and gene resources can be directly used for molecular marker-assisted selection (MAS) and gene editing to achieve efficient improvement of the target color traits (Meng et al., 2025). With the continuous accumulation of multi-omics data, researchers can predict complex traits more accurately and accelerate the process from gene discovery to the breeding of new varieties. Lozada et al. (2022) and Song et al. (2024) both hold that future work should place greater emphasis on the integration of molecular mechanisms and breeding practices, promoting the precise editing of color-related genes and the selection and breeding of new varieties.

8.3 Building genetic resources and color trait databases for *Capsicum* improvement

At present, diverse pepper core germplasm resource banks and MAGIC populations have been established globally, covering rich color phenotypes and genotype variations (Castaño et al., 2025; Ortega-Albero et al., 2025). The construction of a database based on high-throughput molecular markers and phenotypic data provides important support for genetic analysis and molecular breeding of pepper color traits (Lee et al., 2022; Moon et al., 2023). However, the existing databases still have deficiencies in aspects such as phenotypic standardization, molecular marker integration and data sharing. McLeod et al. (2023) proposed that in the future, the integration and unified standards of multi-source data should be strengthened, and an open and dynamically updated database of pepper color traits should be established to promote global resource sharing and collaborative scientific research innovation.

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Conflict of Interest Disclosure

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