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Case Study **Open Access**

Comparative Molecular Analysis of Anthocyanin Accumulation between Contrasting Purple Cabbage Lines

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Abstract This study compared the main characteristics of different purple intensity cabbage lines, summarized the expression differences of multiple key structural genes and regulatory genes in the anthocyanin synthesis pathway among different strains, and pointed out that the MBW complex plays a core role in regulating the entire pathway. It also sorted out the interaction mode between environmental signals and molecular regulatory networks It explains how external factors such as light and low temperature affect the expression of related genes. Through the joint analysis of metabolomics and transcriptomics, the key links influencing the anthocyanin pathway flux were identified, and the main molecular reasons for the differences in purple intensity were explained. The possible applications of technologies such as molecular marker-assisted selection, CRISPR/Cas gene editing and nutritional fortification in the breeding of high-anthocyanin cabbage were also discussed. This study aims to provide reference and theoretical support for the color improvement and nutritional enhancement of cruciferous vegetables.

Keywords Purple cabbage; Anthocyanin accumulation; Molecular regulatory networks; Multi-omics analysis; Molecular breeding

1 Introduction

Anthocyanins are a very common type of secondary metabolites in plants and belong to the category of flavonoids. It is synthesized through the phenylpropane pathway and is the main pigment for forming colors such as red, purple and blue in plants (Tian et al., 2023). In Brassica oleracea and its related species, the synthesis of anthocyanins depends on a series of structural genes, such as PAL, C4H, CHS, CHI, F3H, DFR, ANS, UFGT and GST, etc. Meanwhile, there are also some regulatory genes such as MYB, bHLH and WD40 involved in regulating this pathway (Liu et al., 2022). The expression of these genes will directly affect the amount and distribution location of anthocyanins, thereby determining the depth of color of cabbage leaves (Jin et al., 2018; Tian et al., 2023). Furthermore, anthocyanins not only determine the purple appearance of cabbage, but also provide functions such as antioxidation, stress resistance and health care (Song et al., 2018; Liu et al., 2022).

There are obvious differences in the depth of purple among different lines of cabbage. This is mainly because they differ in anthocyanin content and the expression of genes related to synthesis. Studies have found that lines with a darker purple color usually have higher levels of expression of key structural genes and regulatory genes in the anthocyanin synthesis pathway, resulting in a large accumulation of anthocyanins (Jin et al., 2018; Liu et al., 2022). For instance, BoMYBL2-1 is a negative regulatory factor. When it is absent or expressed at a very low level, the inhibition of anthocyanins weakens, and the leaves are more likely to turn purple. In addition, low temperatures can also induce an increase in the expression of these genes, making the purple color more prominent. Genetic variations between strains, such as mutations or insertions and deletions, can also cause more differences in the degree of purple (Song et al., 2018; Song et al., 2020).

This study selected two cabbage lines with significant differences in purple color and analyzed the different reasons for anthocyanin accumulation through molecular-level comparisons. The focus was on comparing the expression patterns of anthocyanin synthesis and regulatory genes in different varieties, and the key molecular factors leading to different purple intensities were identified. This study aims to provide a reference basis for molecular breeding and color improvement of cabbage and other vegetables.

2 Phenotypic and Biochemical Differences in Anthocyanin Accumulation

2.1 Comparative pigment profiles between dark-purple and light-purple cabbage lines

The anthocyanin content in the leaves of the deep purple cabbage lines, especially the inner young leaves, is much higher than that of the light purple or white lines. Take ornamental cabbage as an example. The total amount of anthocyanins in the young leaves of the purple lines is approximately 2.5 times that of the middle-aged leaves and is more than 10 times higher than that in the leaves of the white lines at any stage. As the leaves gradually grow larger, the purple color spreads to the outer leaves, but the anthocyanin content in the outer old leaves decreases, so they appear greener (Jin et al., 2018). In contrast, the anthocyanin levels of the light purple or white lines changed little at different developmental stages, and the overall content was very low. The anthocyanins of the deep purple lines are mostly concentrated in the epidermis and the near-epidermal cell layer. This distribution pattern also makes the leaf surface present a more obvious purple color.

2.2 Differences in anthocyanin composition and metabolic intermediates

The deep purple variety not only has a high anthocyanin content but also offers a greater variety of anthocyanins. Studies have shown that the main anthocyanins in purple cabbage include cyanidin-3,5-O-diglucoside, cyanidin-3-O-glucoside and paeonidin-3-O-β-D-glucoside, etc. (He et al., 2022). The purple lines also contains some specific anthocyanin metabolites, while the light purple or green lines mainly contain chlorophyll and carotenoids, with very few types and contents of anthocyanins (Zhao et al., 2022). Metabolomics studies have also found that genes related to the anthocyanin synthesis pathway, such as BrMYB2, BrTT8, BrF3'H, BrDFR1, etc. in the purple lines are significantly upregulated, promoting the synthesis and accumulation of anthocyanins (Park et al., 2021; Kim et al., 2022; Tang et al., 2022).

2.3 Physiological traits associated with pigmentation levels

The accumulation of anthocyanins is also related to other physiological characteristics of leaves. The contents of chlorophyll and carotenoids in deep purple lines are generally lower than those in light purple or green lines, and there is a significant negative correlation between the two (Jin et al., 2018). Anthocyanins not only make leaves purple, but also protect the photosynthetic system and enhance the stress resistance of plants (Zhao et al., 2022). Under stress conditions such as low temperature, the accumulation of anthocyanins in the purple lines is more obvious. At this time, the expression of positive regulatory genes such as BrMYB2 and BrTT8 is enhanced, while the expression of negative regulatory factors such as BrMYBL2.1 is decreased, thereby further promoting the increase of anthocyanins (Figure 1) (Kim et al., 2022).

3 Molecular Basis of Anthocyanin Biosynthesis

3.1 Structural genes involved in anthocyanin biosynthetic pathways

The synthesis of anthocyanins requires the joint work of multiple structural genes. The main genes include CHS, DFR, ANS and UFGT, which are respectively responsible for the key steps in the anthocyanin synthesis pathway (Liu et al., 2022). In purple cabbage and related species, these genes are usually strongly upregulated, and their expression levels are basically consistent with the accumulation of anthocyanins. Many studies have found that the purple line maintains high expression of CHS, DFR, ANS and UFGT at different developmental stages, and the changes of these genes are highly correlated with anthocyanin content (Rameneni et al., 2020). For instance, BcDFR is particularly high in the upper epidermis of purple non-heading Chinese cabbage, directly promoting anthocyanin synthesis (Zhou et al., 2024). Meanwhile, homologous genes such as UFGT and UGT75C1 are also very important for the glycosylation and stable accumulation of anthocyanins (Zhao et al., 2022; Tang et al., 2024).

3.2 Regulatory genes and transcription factors

The expression of these structural genes is regulated by multiple transcription factors, among which MYB, bHLH and WD40 are the three most important types. They can combine to form MBW complexes to jointly activate late-stage structural genes, such as DFR, ANS and UFGT (Yan et al., 2021; Yang et al., 2022; Zhao et al., 2022). In purple cabbage and its related species, R2R3-MYB is a core positive regulatory factor, such as BrMYB2, BrMYB75, BrMYB90 and BrMYB114, which can directly initiate the expression of structural genes (Rameneni et al., 2020; Fu et al., 2023). bHLH (such as TT8) often works in synergy with MYB to enhance the regulatory effect (Tang et al., 2022; Xu et al., 2024). WD40 (such as TTG1) acts as a platform protein to stabilize the entire complex (Rameneni et al., 2020; Liu et al., 2022; Fu et al., 2023). Furthermore, R3-MYB like MYBL2 belongs to negative regulatory factors, which reduce anthocyanin synthesis by inhibiting the activity of MBW (Chen et al., 2019; Zhou et al., 2024). A common situation in the purple lines is that the expression of positive regulatory factors of MYB is very high, while the expression of negative regulatory factors is low or their functions are impaired. This also leads to the easy accumulation of anthocyanins in large quantities (Song et al., 2018; Kim et al., 2022).

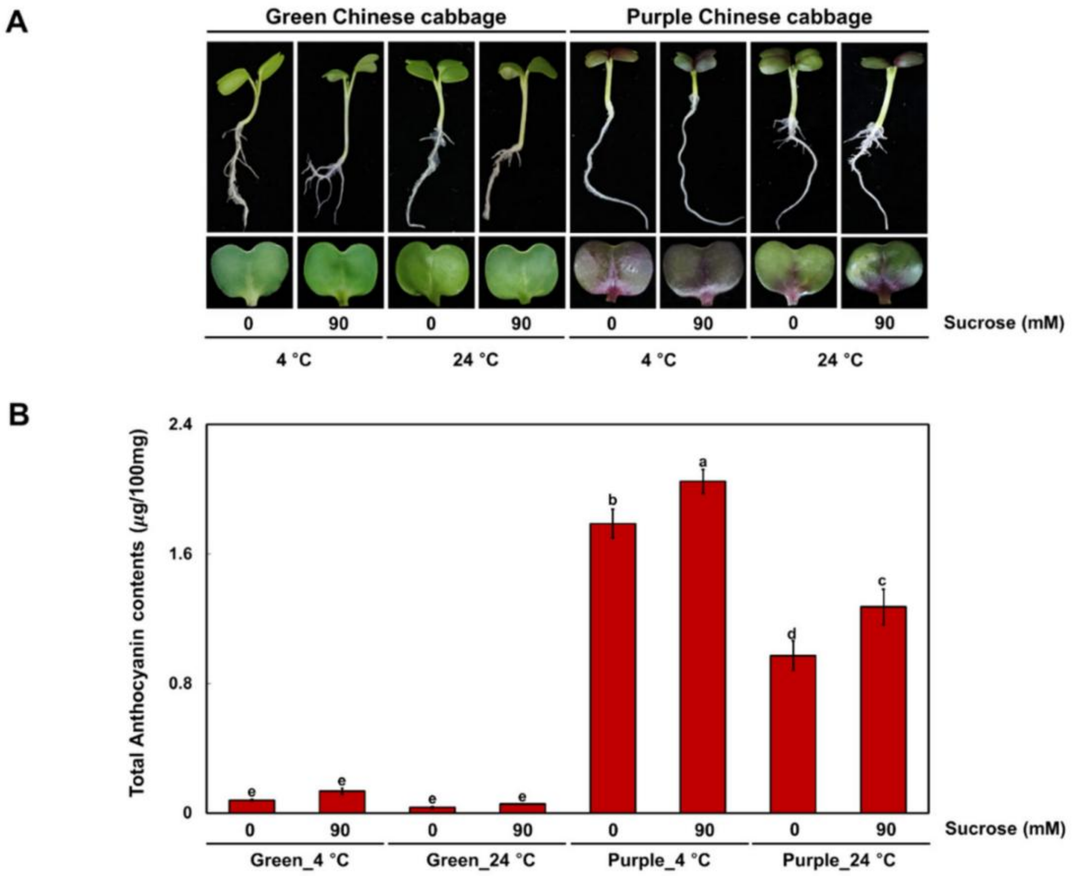

Figure 1 Phenotype and anthocyanin contents of green and purple Chinese cabbage under various cultivation conditions (Adopted from Kim et al., 2022)

Image caption: (A) Phenotypes of seedlings from two Chinese cabbage cultivars were grown under low temperature or an optimal temperature, with or without 90 mM sucrose. (B) Mean anthocyanin contents of seedlings from green and purple Chinese cabbage cultivars. Results represent the mean values ± standard deviation (SD). Three independent biological replicates were performed. Different letters indicate significantly different values ($p < 0.01$), as determined by two-way ANOVA followed by Duncan's multiple range tests (Adopted from Kim et al., 2022)

3.3 Transport, sequestration, and vacuolar modification factors

Anthocyanins need to be transported to the vacuole after synthesis, and this step is also involved by multiple proteins. The related genes include GST, MATE and ABC class transporters, which usually have higher expression levels in purple cabbage (Liu et al., 2022; Zhao et al., 2022). Among them, GSTS, such as BrGST1, BrGST2 and BoGSTF12, are regarded as key proteins. They can combine with anthocyanins and deliver them into vacuoles, thereby helping anthocyanins accumulate stably (Tang et al., 2024). After entering the vacuum, some modification enzymes (such as UFGT, AT, 5MAT, etc.) will perform glycosylation or acylation modification on anthocyanins to improve their stability and also make the color of anthocyanins more diverse (Rameneni et al., 2020; Liu et al., 2022). These transportation and modification processes jointly determine the distribution and final accumulation of anthocyanins in cells.

4 Comparative Genomic and Transcriptomic Insights

4.1 Genetic variation between contrasting purple cabbage lines

The accumulation of anthocyanins in purple cabbage lines is directly related to structural variations in some key regulatory genes. For instance, the length of the first intron of BrMYB2 varies, which determines whether the cabbage is purple or white. Purple lines (such as 11S91) with short introns of gBrMYB2 are more likely to promote the synthesis of anthocyanins. The white lines usually contains gBrmyb2 with long introns, which can inhibit the accumulation of anthocyanins. Furthermore, the deletion of BoMYBL2-1 or the mutation of its promoter can render this negative regulatory gene inactive and also cause the plant to turn purple (Song et al., 2018). The insertion mutation of BoLBD37L also affects its inhibitory effect, thereby influencing the expression of downstream BoMYB114L and BoTT8, and ultimately resulting in different anthocyanin contents. It is precisely these genetic variations that provide useful markers and theoretical basis for the molecular breeding of purple traits.

4.2 Differential expression patterns of key biosynthetic and regulatory genes

Transcriptome analysis indicated that structural genes of the anthocyanin synthesis pathway in the purple lines, such as PAL, C4H, CHS, CHI, F3H, DFR, ANS, UFGT, GST, etc., all showed a significant high expression trend and were highly correlated with the actual content of anthocyanins (Jin et al., 2018; Rameneni et al., 2020). In terms of regulating genes, positive regulatory factors such as R2R3-MYB (such as BrMYB2, BrMYB75, BrMYB90), bHLH (such as BrTT8), and WD40 have high expression levels in purple lines. Negative regulatory factors (such as BrMYBL2.1, BoMYBL2-1) were expressed more in green or white lines (Song et al., 2018; Kim et al., 2022). Some other MYB genes, such as BrMYB114 and BrPAP2, also show high expression in specific tissues or at certain developmental stages (Fu et al., 2023; Xu et al., 2024; Zhu et al., 2025). These expression differences jointly promoted the high accumulation of anthocyanins in the purple lines.

4.3 Co-expression networks related to anthocyanin pathway activation

Co-expression network analysis revealed a strong positive correlation and interaction between regulatory factors such as MYB and bHLH and the structural genes of anthocyanin synthesis. For instance, MYB75, MYB90, MYBL2, etc. have formed tight regulatory networks with key structural genes such as BrDFR, BrLDOX, BrUF3GT (Rameneni et al., 2020). WGCNA analysis also demonstrated that the expressions of genes such as PAP2, TT8, and MYBL2 were highly coordinated with those related to the anthocyanin pathway, and they jointly regulated the generation and accumulation of anthocyanins (Xu et al., 2024). Furthermore, new regulatory factors can also be introduced through the introduction of exogenous genes or hybrid breeding, thereby further enhancing the overall activity of the anthocyanin pathway. These network-level pieces of evidence contribute to a more comprehensive understanding of the molecular basis behind the formation of the purple trait.

5 Metabolic Regulation and Environmental Influences

5.1 Metabolomics-based comparison of pathway flux and metabolite abundance

The combined analysis of metabolomics and transcriptomics indicates that the accumulation of anthocyanins in purple cabbage and its related vegetables is closely related to the high expression of key genes in the anthocyanin biosynthesis pathway. In the purple lines, the expression levels of genes such as PAL, C4H, CHS, CHI, F3H, DFR, ANS, and UFGT were significantly higher than those in the green lines, which would directly increase the abundance of anthocyanin precursors and final products (Park et al., 2021). For instance, the content of anthocyanins and their derivatives (such as cyanidin-3, 5-o-diglucoside) in purple non-heading Chinese cabbage and purple-stem Chinese kale is much higher than that in green lines, and the changes of these metabolites are highly consistent with the expression of related genes (Zhao et al., 2022). In addition, transporters such as BoGSTF12 have also been shown to affect the accumulation and intracellular distribution of anthocyanins, which are very important for color formation (Tang et al., 2024).

5.2 Light, temperature, and other environmental factors affecting pigmentation

Light and temperature are important environmental factors regulating the accumulation of anthocyanins. Strong light can significantly increase the expression of genes in the anthocyanin synthesis pathway, while shading can down-regulate structural genes such as PAL, CHS, and DFR, resulting in a decrease in anthocyanin content (Ma et al., 2021). Some light signal factors, such as CRY3, HY5, and transcription factors such as BoMYB6, BoTT8, play a core role in light-induced anthocyanin synthesis (Liu et al., 2020; Tian et al., 2023). Low temperatures can also promote the accumulation of anthocyanins in purple cabbage and purple Chinese cabbage. Under low-temperature conditions, positive regulatory genes such as BrMYB2 and BrTT8 are upregulated, while in the white lines, BrMYBL2.1 increases, thereby inhibiting anthocyanin synthesis (Song et al., 2018; Dai et al., 2022). If exposed to a weak light environment for a long time, the activity of anthocyanin synthase will decrease and the color will gradually fade.

5.3 Interaction of environmental cues with molecular regulatory networks

Environmental signals form a relatively complex regulatory network by regulating transcription factors such as MYB, bHLH, and WD40 and their downstream structural genes. Factors such as light and temperature can affect the composition and activity of the MYB-bHLH-WD40 complex, thereby altering the synthetic efficiency of anthocyanins (Ma et al., 2021; Yan et al., 2021; Tian et al., 2023). For instance, light exposure can induce signal factors such as HY5 to activate the MYB gene, and subsequently upregulate the expression of structural genes. Low temperature promotes anthocyanin accumulation by increasing the expression of positive regulatory factors such as BrMYB2 and BrTT8 (Dai et al., 2022; Yang et al., 2022). In addition, hormones such as ABA, ethylene, and IAA also regulate anthocyanin synthesis together with light and temperature signals (Liu et al., 2020). Negative regulatory factors such as MYBL2 are more expressed in white or green lines, which can inhibit anthocyanin synthesis, thereby causing significant color differences (Song et al., 2018; Xu et al., 2024).

6 Case Study: Molecular Characterization of Anthocyanin Differences in Two Purple Cabbage Lines

6.1 Study background and selection of contrasting purple lines

Purple cabbage (Brassica oleracea) and its related species have attracted attention due to their high anthocyanin content. Anthocyanins give cabbage its purple appearance and also enhance its nutritional value and antioxidant capacity. With the development of molecular breeding and genomics, researchers began to systematically compare the differences between purple and green (or white) cabbages. The comparison materials are generally selected from lines with obvious differences in appearance but similar genetic backgrounds, such as purple-leaf and green-leaf, purple-head and white-head, or purple and white inner leaves, to ensure that the comparison focus is concentrated on anthocyanin-related traits (Jin et al., 2018; Liu et al., 2022).

6.2 Integrated analysis: phenotyping, metabolomics, and transcriptomics

Phenotypic analysis indicated that the anthocyanin content of the purple lines was higher at the young leaf or inner leaf stage, and the anthocyanins were mainly concentrated in the leaf epidermis and near-epidermal cell layer (Zhou et al., 2024). Metabolomic analysis detected many anthocyanin derivatives specific to purple lines, such as cyanidin and pelargonidin modifications. The content of these compounds in purple lines was much higher than that in green or white materials (Jin et al., 2018; Zhao et al., 2022). Transcriptome studies have also found that structural genes and regulatory genes in the anthocyanin synthesis pathway of purple lines are generally upregulated (Rameneni et al., 2020; Park et al., 2021). Some negative regulatory genes (such as BrMYBL2.1) are expressed more in non-purple lines, thereby inhibiting anthocyanin formation (Kim et al., 2022). In addition, hybridization or exogenous gene insertion (such as *Dark_Pur* gene) can also significantly enhance the purple phenotype and upregulate the expression of related genes (Figure 2) (Liu et al., 2022).

6.3 Key findings and implications for breeding high-pigment cabbage varieties

The anthocyanin accumulation in purple cabbage is closely related to the co-high expression of structural genes and regulatory genes. Among them, genes such as BrMYB2 and BrTT8 play the most obvious role in regulation (Park et al., 2021; Liu et al., 2022). The decreased expression or loss of function of negative regulatory factors (such as BrMYBL2.1) will weaken the inhibition of anthocyanin synthesis (Kim et al., 2022). Hybrid breeding or the introduction of exogenous genes (such as Dark_Pur) can also enable the stable inheritance of purple traits, thus becoming a key strategy in molecular breeding (Liu et al., 2022). Meanwhile, the combined analysis of metabolomics and transcriptomics can also help screen high anthocyanin lines and be used for marker-assisted selection (Rameneni et al., 2020; Zhao et al., 2022). These research results provide important targets for the design and breeding of new lines of cabbage with high anthocyanins, and also help improve the nutritional quality and market value of cabbage.

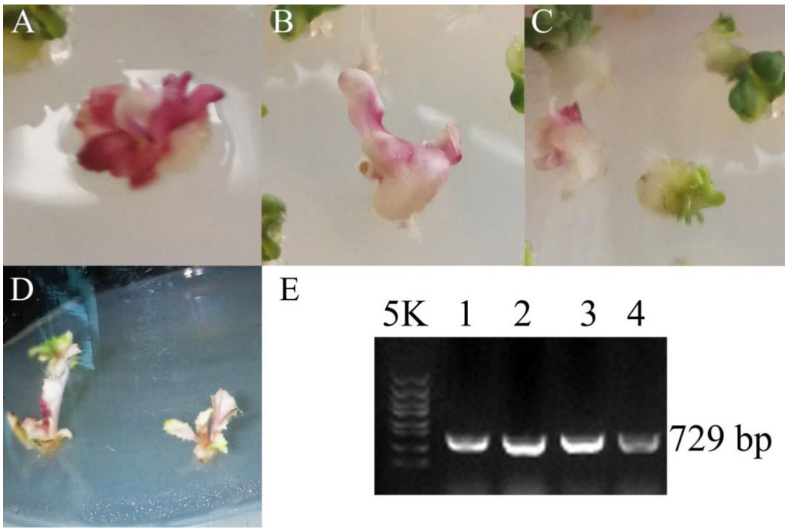

Figure 2 *Dark_Pur* gene transformation in *B. rapa*. (A-D): The different periods of the T0 transgenic *B. rapa*. (E) 1-4 represent the PCR product in T0 transgenic *B. rapa*, and the product length is 729 bp (Adopted from Liu et al., 2022)

7 Breeding and Genetic Improvement Implications

7.1 Marker-assisted selection for high-anthocyanin traits

The accumulation of anthocyanins is mainly determined by transcription factors such as MYB and bHLH and the structural genes they control. Studies have shown that mutations or expression changes in genes such as BoMYBL2-1, BrMYB2, and Bol012528 can directly affect whether cabbage appears purple (Song et al., 2018; Zhu et al., 2023). Based on these genes, molecular markers capable of distinguishing purple from green cabbage have been developed, which can be used to rapidly screen high anthocyanin materials and also accelerate breeding progress. They are particularly suitable for hybrid breeding and functional food development. Meanwhile, if the markers of multiple genes such as BoRVE5 and BoDFR1 are used together, the accuracy of molecular selection can be further improved.

7.2 Potential applications of CRISPR/Cas for modifying pathway genes

Gene editing techniques such as CRISPR/Cas9 have been proven to effectively knockout or regulate key genes in the anthocyanin synthesis pathway, such as MYBL2, DFR, F3H, etc., thereby achieving precise regulation of anthocyanin content (Mackon et al., 2023). For instance, knocking out BoNA1 or MYBL2 can yield cabbage materials with high anthocyanins or no anthocyanins, and new technologies such as HI-Edit can also achieve rapid breeding "without transgenic traces" (Yuan et al., 2023; Li et al., 2025). Furthermore, point mutations of key genes or editing of regulatory elements also provide more possibilities for creating new functional varieties (Khusnutdinov et al., 2021; Khusnutdinov et al., 2022).

7.3 Prospects for enhancing nutritional value via pigment biofortification

Anthocyanins not only give vegetables their bright colors but also have health values such as antioxidation and anti-inflammation. Through molecular breeding, gene editing and environmental regulation (such as low temperature or enhanced light), the anthocyanin content of vegetables like cabbage can be significantly increased, thereby improving their nutritional quality (Haghighi et al., 2022; Lee et al., 2024). The methods of biofortification include regulating the expression of key genes such as PAL, MYB, and DFR, or promoting the accumulation of anthocyanins and other secondary metabolites through treatment with exogenous amino acids, selenium and other nutritional elements (Tian et al., 2023; Yu et al., 2023). These methods provide important tools for developing high-nutrition and functional vegetables and also help meet the demands of healthy consumption.

8 Challenges and Future Directions

8.1 Complexity of multi-level regulation in anthocyanin biosynthesis

The biosynthesis of anthocyanins requires the joint regulation of multiple genes. Structural genes, such as PAL, CHS, DFR, ANS, UFGT, etc., are responsible for the main synthesis steps of anthocyanins; transcription factors such as MYB, bHLH and WD40 regulate the expression of these structural genes. The balance of positive and negative regulatory factors has a significant impact on anthocyanin accumulation. For instance, when positive regulatory factors such as BrMYB2 and TT8 are upregulated, they will promote the production of anthocyanins. However, when the expression of MYBL2, a negative regulatory factor, increases, it inhibits the accumulation of anthocyanins (Yan et al., 2021). Environmental factors such as light, low temperature and hormones can also affect the expression of these genes, making the regulatory network more complex (Liu et al., 2020; Dai et al., 2022). There are also obvious differences among different tissues, different developmental stages and even different lines. Therefore, it is still quite difficult to fully understand the molecular mechanism of anthocyanin accumulation (Jin et al., 2018). At present, there is still much to be further studied regarding the interaction patterns of positive and negative regulatory factors, feedback regulation, and their roles in different genetic contexts (Kim et al., 2022; Wang et al., 2025).

8.2 Need for multi-omics integration and high-resolution comparative datasets

Although single-omics such as transcriptomics and metabolomics have helped identify some key genes and metabolites, the complete picture of anthocyanin accumulation remains unclear. Combining multi-omics technologies such as genomics, transcriptomics, metabolomics and proteomics can more systematically analyze regulatory networks, signaling pathways and metabolic flows (Rameneni et al., 2020). For instance, the combined analysis of the transcriptome and metabolome has been used to identify key genes that regulate anthocyanin synthesis and transport, such as BjMYB90 and BjGSTF12 (Karamat et al., 2025). However, at present, high-quality multi-omics data across varieties and developmental stages are still scarce, and the methods of data standardization and integration also need to be improved (Jin et al., 2018). In the future, it is necessary to establish large-scale and systematic multi-omics databases and develop efficient data integration and visualization tools to better analyze complex traits and be more conducive to precise breeding.

8.3 Future prospects for precision improvement in Brassica pigmentation

With the development of molecular markers, gene editing and multi-omics, new opportunities have emerged for pigment improvement in cruciferous vegetables such as purple cabbage. The discovered key regulatory genes, such as BrMYB2, BoMYBL2-1, TT8, etc., and their molecular markers, can all be used for molecular-assisted selection, laying the foundation for precision breeding (Li et al., 2019). In the future, technologies such as CRISPR/Cas can be utilized to directly regulate these positive and negative regulatory factors, thereby achieving targeted increase in anthocyanin content and distribution (Song et al., 2018; Wang et al., 2025). Meanwhile, in-depth exploration of environmentally sensitive regulatory elements and establishment of a high-throughput phenotypic platform can also accelerate the screening of high-quality purple cabbage materials (Jin et al., 2018). However, while improving anthocyanins, traits such as plant growth and stress resistance should also be considered, because anthocyanin accumulation may have complex associations with multiple traits (Dai et al., 2022; Tian et al., 2023).

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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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