Proceedings of ICBioMed 2025 Symposium: AI for Healthcare: Advanced Medical Data Analytics and Smart Rehabilitation
DOI: 10.54254/2753-8818/2025.AU24446

# *Research Progress and Future Prospects of Anthocyanins in Flower Color Formation and Breeding of Chrysanthemums*

**Yixian Su**

*Aulin College, Northeast Forestry University, Harbin, China*
*suyixian@nefu.edu.cn*

***Abstract.*** Chrysanthemum, native to China, is an important horticultural plant. Its diverse flower colors play a crucial role in defining the plant's ornamental appeal and economic value. Metabolites play a crucial role in plant physiology as a bridge between genes, environment, and phenotype. Anthocyanin, a key plant secondary metabolite mainly distributed in flowers and also expressed in stems and leaves, is a core molecule involved in the molecular mechanism of flower color formation in chrysanthemums, and its type and accumulation level directly affects the color expression of petals. This article comprehensively reviews anthocyanin biosynthetic pathways, regulatory networks, and detection methods. By integrating metabolomics with multi-omics approaches, we highlight recent advances in chrysanthemum metabolomics research, and innovatively proposing a new strategy based on metabolic marker detection and metabolomics-assisted molecular breeding, aiming to improve the efficiency and precision of chrysanthemum breeding programs. The article also highlights the great potential for the application of anthocyanins in chrysanthemum breeding, suggesting that these pigments can play a key role in the development of new varieties with desirable floral characteristics. By utilizing the latest scientific insights and technological advances, this research could help to improve chrysanthemum breeding techniques, enhance their ornamental and commercial appeal, and bring economic benefits.

***Keywords:*** chrysanthemum, anthocyanin, metabolomics, breeding.

## 1. Introduction

Chrysanthemums (Chrysanthemum morifolium) are flowers native to China[1]. Through sustained horticultural development, the species has become one of the four major commercial cut flowers in international floriculture, with a global reputation[2]. Long-term artificial selection and cultivation breeding has facilitated the development of more than 30,000 varieties that exhibit significant phenotypic variation in flower shape, color characteristics, and aromatic scent[3]. Remarkably, flower color has evolved from the ancestral yellow phenotype to a wide range, including pink, red, white, green and purple. This color diversity is a key determinant of the ornamental and commercial value of chrysanthemum varieties in the contemporary horticultural market[4].

© 2025 The Authors. This is an open access article distributed under the terms of the Creative Commons Attribution License 4.0 (https://creativecommons.org/licenses/by/4.0/).

DOI: 10.54254/2753-8818/2025.AU24446

Flower color depends fundamentally on the biosynthesis and deposition of specific secondary metabolites. The development of color in plants depends primarily on three classes of pigments: flavonoids, carotenoids, and betalains. Anthocyanins are important members of the flavonoids that give chrysanthemums a wide range of color variations from yellow and red to purple and blue, and are the core metabolites that influence chrysanthemum flower color[5,6]. Contemporary anthocyanin-related research focuses on three interdisciplinary perspectives: (1) elucidating the biosynthetic pathways and regulatory networks, (2) analyzing the associated physiological functions and ecological adaptations, and (3) exploring commercial applications in the food, pharmaceutical, and cosmetic industries[7,8]. However, the mechanism of interaction between secondary metabolites represented by anthocyanins and phenotypic color polymorphisms is still not fully understood[9].

In this paper, we systematically summarize the known anthocyanin synthesis pathways, regulatory mechanisms and detection methods in chrysanthemums, combine metabolomics with multi-omics analysis methods to reveal the relationship between anthocyanins and chrysanthemum color expression, and innovatively propose a new strategy for metabolism marker-based detection and metabolomics-assisted molecular breeding. Compared with previous studies, this study deeply analyzed the patterns between key anthocyanin derivatives and flower color changes, and also provided new theoretical predictions for chrysanthemum flower color improvement breeding by analyzing the possibility of joint application of multi-omics.

## 2. Molecular basis and regulatory mechanism of flower color in chrysanthemums

### 2.1. The main influencing factors of chrysanthemum flower color

Park et al. demonstrated that petal color variation in chrysanthemums results from the combined accumulation and synergistic interactions of carotenoids and anthocyanins[5]. Carotenoids, a class of isoprenoid compounds consisting mainly of 40 carbon atoms and comprising mainly lutein, zeaxanthin, and β-carotene, have been identified as the key pigments conferring yellow, orange, and red coloration to floral tissues[10,11]. For example, quantitative analyses have shown that deep yellow chrysanthemum varieties exhibit relatively high concentrations of zeaxanthin and lutein in their petals[5].

Anthocyanin is a natural water-soluble pigment in plants and is a special product of the plant flavonoid metabolic pathway. These compounds act as the primary pigments responsible for the formation of a wide range of colors in chrysanthemum petals, including pink, red, purple, blue, and orange, through their distribution in the vesicles of the floral organs and the epidermis of the fruit[12].

Anthocyanins are characterized by instability, which is influenced by their own chemical structure, pH value, temperature, metal ions, etc[13]. For example, in acidic solutions with a pH of 2-7, the main forms of anthocyanins are flavonoid cations, which are red in color and fade with increasing pH. When the PH is 6-8, the amount of blue quinoline bases increases. When PH>8, chalcone is produced and is yellow in color[14]. Li revealed the effects of different metal ions on anthocyanins by studying petunia: Zn, Fe showed destructive interactions with petunia anthocyanins, Cu, Al and Na had minimal effects, whereas Ca enhanced the stability of anthocyanins and improved color fidelity[15]. The color variation of these anthocyanins with different factors is the biochemical basis for the different colors of chrysanthemums.

DOI: 10.54254/2753-8818/2025.AU24446

## 2.2. Anthocyanin species and color expression

The structural hallmark of anthocyanins resides in their conserved flavonoid aglycone core featuring a C6-C3-C6 configuration, which differentiate into six main structural derivatives - pelargonidin, cyanidin, delphinidin, peonidin, petunidin and malvidin - depending on the substituents on the B ring[9,16]. Pelargonidin gives fruits like strawberries a red or orange color[12], cyanidin and petunidin are the source of the deep purple color in fuchsia plants such as blackberries[17,18], and delphinidin and peonidin give an extra blue color[12]. Malvidin is also related to the formation of purple color[19].

## 2.3. The biosynthetic pathway of anthocyanins

The anthocyanin biosynthetic pathway in plants is well characterized and comprises five key stages: (1) Initial flavonoid metabolism: Phenylalanine is sequentially converted to p-coumaroyl-CoA via phenylalanine ammonia-lyase (PAL), cinnamic acid 4-hydroxylase (C4H), and 4-coumarate-CoA ligase (4CL)[20]. (2) Core flavonoid transformations: p-Coumaroyl-CoA condenses with malonyl-CoA (derived from acetyl-CoA) through chalcone synthase (CHS) to yield naringenin chalcone. Chalcone isomerase (CHI) isomerizes this intermediate to naringenin, which is hydroxylated by flavanone 3-hydroxylase (F3H) to dihydrokaempferol. Subsequent hydroxylation by flavonoid 3'-hydroxylase (F3'H) or flavonoid 3',5'-hydroxylase (F3'5'H) generates dihydroquercetin or dihydromyricetin, respectively[20,21]. (3) Anthocyanin synthesis: Dihydroflavonol-4-reductase (DFR) reduces dihydrokaempferol, dihydroquercetin, or dihydromyricetin to leucoanthocyanidins, which are oxidized by anthocyanidin synthase (ANS) to form colored anthocyanidins[21]. (4) Structural modifications: Anthocyanidins undergo stabilization via 3-O-glucosylation catalyzed by UDP-glucose flavonoid 3-O-glucosyltransferase (UF3GT), followed by potential glycosylation, methylation, and acylation[21,22]. (5) Transport and storage: Glutathione S-transferase (GST) facilitates vacuolar sequestration of modified anthocyanins from cytoplasmic or endoplasmic reticulum sites [20,22].

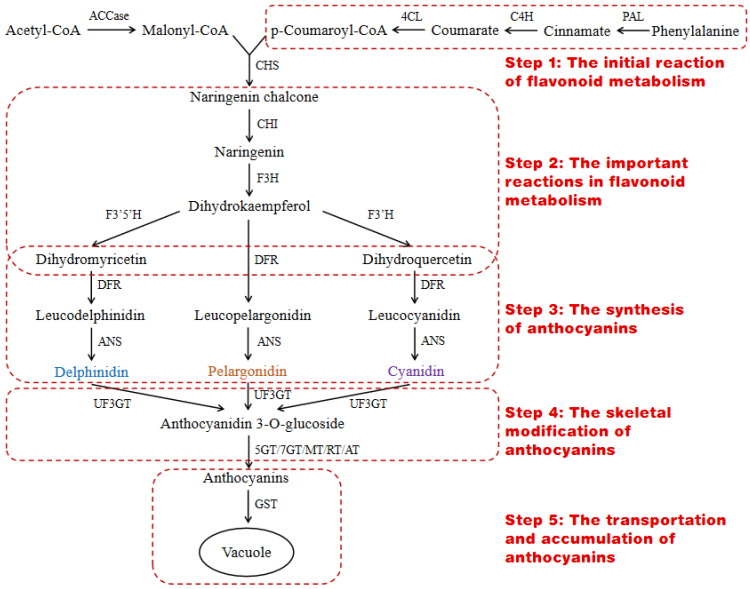


Figure 1: Anthocyanin biosynthesis pathway in chrysanthemum (key enzymes: PAL, CHS, etc.)

DOI: 10.54254/2753-8818/2025.AU24446

### 2.4. The regulatory network of anthocyanins

The anthocyanin biosynthesis pathway is conserved in plants and catalyzes specific biochemical transformations through coordinated enzymes, with key enzymes including CHS, F3H, F3'H, DFR, ANS, 3GT and 3MT. These biosynthetic genes are regulated by the MYB-bHLH-WD40 (MBW) ternary complex, in which proteins containing WD40 repeat sequences act as scaffolding proteins to maintain the structural integrity of the transcription complex[23,24].

As a superfamily of transcription factors with helix-loop-helix domains, bHLH proteins regulate anthocyanin biosynthesis in plants[23]. CmbHLH2 is the first bHLH transcription factor identified in chrysanthemums, and it exhibits conservatism across species. In colored varieties, there was a strong positive correlation between the expression of CmbHLH2 and the level of anthocyanin accumulation by the mechanism of co-activation of the CmDFR promoter by binding to CmMYB6 to form a classical MBW transcriptional regulatory module[25].

MYB transcriptional regulators constitute central molecules in the MBW regulatory network, coordinating anthocyanin biosynthesis through dynamic interactions with bHLH factors and other proteins. Most MYBs exhibit enhanced anthocyanin production. For example, CmMYB6 has been identified as an important gene that promotes anthocyanin accumulation in chrysanthemum[26,27]. Kee et al. ectopic expression of RsMYB1 in chrysanthemum varieties induced up-regulation of CmF3H, CmDFR, and CmANS transcripts and increased anthocyanin content[28]. In contrast, a fraction of MYB repressors (e.g., CmMYB#7) acted as negative regulatory elements to inhibit the expression of key enzymes for anthocyanin synthesis by competitively inhibiting the assembly of the MBW complex, in particular by disrupting the CmMYB6-CmbHLH2 heterodimerization through a spatial site-blocking mechanism[23,27].

Under the influence of various physical or chemical factors such as temperature, light, and pH, flowering plants such as chrysanthemums affect anthocyanin synthesis and accumulation by regulating the expression of structural genes through the above transcription factors[23].

## 3. Methods and advances in the study of anthocyanins and their derivatives

### 3.1. Detection of anthocyanins and their derivatives

Anthocyanins, secondary metabolites exclusive to higher plants, have been well characterized structurally and demonstrate significant industrial and biomedical potential. In food technology, they serve as natural colorants, while in pharmacology, they exhibit therapeutic properties including antioxidant, anti-inflammatory, anticancer, and cardiovascular-protective activities. Studies on crops and ornamental plants have established a comprehensive analytical framework for anthocyanin characterization and quantification[12].

Current anthocyanin analysis utilizes integrated analytical approaches combining ultraviolet-visible spectroscopy, nuclear magnetic resonance (NMR), and high-performance liquid chromatography (HPLC)[29]. NMR facilitates precise structural elucidation by determining the number, type, and spatial arrangement of specific atoms within anthocyanin molecules[30]. As the primary analytical tool, HPLC enables anthocyanin identification and quantification through characteristic retention times and spectral profiles under optimized chromatographic conditions[29,30]. Integration with advanced detection systems (e.g., liquid chromatography-mass spectrometry, LC-MS; electrospray ionization mass spectrometry, ESI-MS; quadrupole time-of-flight mass spectrometry, QTOF-MS) enhances resolution of anthocyanin subtypes and purity in complex matrices, establishing a systematic framework for plant metabolomics research[30,31].

DOI: 10.54254/2753-8818/2025.AU24446

The specific research methods for anthocyanin extraction[29,32], separation[32,33], identification[33,34]are summarized as follows.

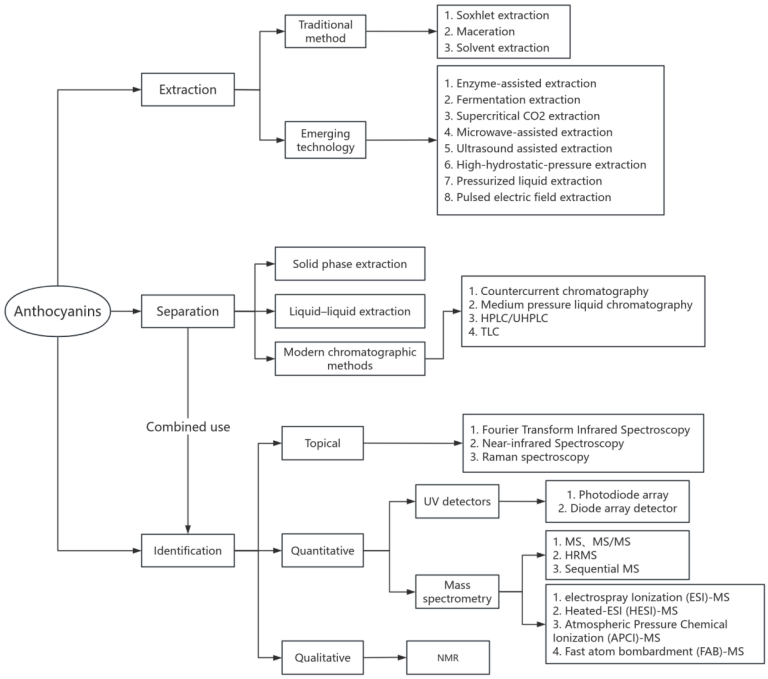


Figure 2: Anthocyanin extraction, separation, detection process and key methods

## 3.2. Research progress in chrysanthemum metabolomics

Metabolomics is used to analyze all metabolites in an organism and is able to measure all metabolites in a given biological system simultaneously, and is mainly classified into targeted metabolomics, non-targeted metabolomics, andwidely targeted metabolomics[35]. In recent years, metabolic diversity studies centered on metabolomics have been widely used in plants, especially in chrysanthemums[35,36].

Current metabolomics studies on chrysanthemums have focused on elucidating physiological and biochemical processes. For example, Chu et al. used integrated metabolomics-transcriptomics analysis to identify key regulatory genes in anthocyanin biosynthesis[36]; Zhao et al. revealed the effect of high temperature on anthocyanin metabolism of chrysanthemum petals during the flowering stage and its molecular mechanism through multi-omics analysis[37]; Wu et al. demonstrated the pattern of anthocyanin variation among different varieties by relating metabolic profiles to differences in gene expression during flower color formation[9]. As an ornamental plant with commercial value, comprehensive characterization of the molecular mechanisms controlling anthocyanin biosynthesis and flower color formation in chrysanthemum is of great significance for improving breeding efficiency[23]. However, the systematic implementation of a multi-omics integration strategy to identify key genetic determinants and metabolic biomarkers for accelerating flower color improvement in chrysanthemums still has limitations.

## 3.3. Exploration of early detection of seedling leaves

In addition to participating in flower color formation, anthocyanins are also present in the vacuoles of leaf epidermal cells and other cells, which can characterize the physiological state of

DOI: 10.54254/2753-8818/2025.AU24446

plants[38]. The extraction, detection and quantification of anthocyanins in leaves and the molecular mechanism of related gene expression regulation have also been deeply studied[38,39]. Hu's research confirmed that the key structural genes CHS, CHI, F3H, and F3'H were expressed in the stems and leaves of cineraria, while the expression of F3'5'H was only detected in the leaves of the blue variety. In chrysanthemums, CHS, CHI, F3H and F3'H are all expressed in the stems and leaves of the pink, red and purple color series[40]. This suggests that there is some potential connection between the accumulation of anthocyanins in leaves or the expression of related genes and flower color.

## 4. The application potential of anthocyanins in chrysanthemum breeding

### 4.1. Limitations and challenges of molecular marker breeding

Although traditional methods such as hybridization and mutation breeding still dominate chrysanthemum breeding, molecular breeding also shows great application potential[41]. Molecular breeding, or marker-assisted selection, employs genetic markers such as amplified fragment length polymorphism (AFLP), random amplified polymorphic DNA (RAPD), sequence-related amplified polymorphism (SRAP), simple sequence repeat (SSR), and single-nucleotide polymorphism (SNP) to screen chrysanthemum traits[23]. These markers are specifically associated with key phenotypic characteristics. Linkage maps, QTL mapping, genome-wide association studies (GWASs) and bulked segregant analysis have also provided technical support for chrysanthemum breeding[41]. However, chrysanthemums are allohexaploid, and their genomes are highly heterozygous, repetitive and large in size. It is extremely difficult to obtain complete genomic information, and it is hard to precisely locate the marked target genes in the genome, which has led to the slow progress of molecular marker-assisted breeding of chrysanthemum[1,23,41].

### 4.2. The advantages of metabolic marker-assisted breeding

Metabolites accumulate at specific sites or developmental stages in plants and are often regarded as a bridge between genes, environment and phenotype[35]. Metabolite detection and metabolomics can cover a large number of metabolites more quickly and easily than gene amplification or identification. Factors such as environmental stresses and gene mutations all cause changes in plant physiological status, which in turn cause changes in metabolite accumulation. By detecting relevant metabolic markers, metabolomics is emerging as a powerful tool for improved breeding[42]

Lu et al. identified cyanidin 3-O-(6″-O-malonyl-glucoside) and cyanidin 3-O-(3″,6″-O-dimalonyl-β-glucopyanoside) in pink, purple, orange-brown, and red varieties by analyzing the anthocyanin content of chrysanthemum flowers from several color families[6]. The research of Wu et al. also supports this view: Cyanidin 3-O-(6″-malonylglucoside) is the highest in red chrysanthemums, followed by pink ones, and has not been detected in yellow varieties. The content of pelargonidin 3-O-glucoside is relatively high in red chrysanthemums, but not detected in pink and yellow varieties[9]. These studies demonstrated that the accumulation of anthocyanins and their derivatives is closely related to the depth of flower color. In this regard, it is inferred that the flower color type of chrysanthemums can be predicted by detecting the content of the relevant anthocyanins, which provides an important reference for the breeding and genetic improvement of chrysanthemums.

DOI: 10.54254/2753-8818/2025.AU24446

### 4.3. Prospects for future research directions

The potential for the application of metabolites to assist chrysanthemum breeding is huge in the future. Combining metabolomics with other modern histological techniques is expected to do the following three things: (1) Metabolic marker breeding. Through a large number of sample testing, a specific anthocyanin and its derivatives can be associated with a specific flower color, and the flower color can be determined by detecting the content of this anthocyanin in seedling leaves or flower buds, which improves the breeding efficiency and brings economic benefits. (2) Assisting molecular breeding. Through metabolomics to identify new metabolites and metabolic pathways in response to new flower color or excellent traits such as resistance, cold resistance, to further enrich the understanding of the gene regulatory network of a trait; or through the metabolic assay to annotate gene function. (3) Risk assessment. Evaluate the differences between the new line and the wild type by detecting metabolite changes to prevent potential risks.

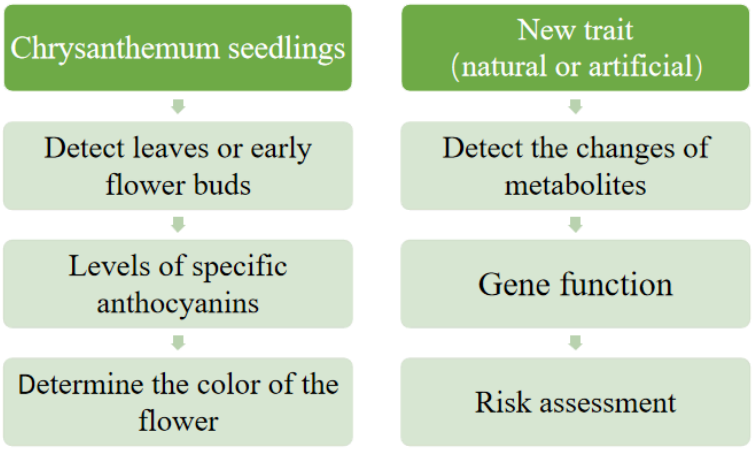


Figure 3: The key steps of molecular breeding of chrysanthemums assisted by metabolomics

## 5. Conclusion

Anthocyanins, distributed in stems, leaves, flowers, and fruits, play a central role in flower color formation of ornamental plants, particularly chrysanthemums. The types of existence and accumulated content directly affect the color of chrysanthemum petals. By combining various detection methods with metabolomics, it is expected that the content of anthocyanins or certain metabolites in chrysanthemum seedlings can be detected to predict flower color and achieve metabolic marker breeding. Meanwhile, integrating modern molecular breeding techniques with metabolomics can help understand gene functions and assess the risks of gene editing, which provides new research targets for future chrysanthemum breeding work.

## References

[1] Song, A. , Su, J. , Wang, H. , Zhang, Z. , Zhang, X. , Van de Peer, Y. , Chen, F. , Fang, W. , Guan, Z. , Zhang, F. , Wang, Z. , Wang, L. , Ding, B. , Zhao, S. , Ding, L. , Liu, Y. , Zhou, L. , He, J. , Jia, D. , & Zhang, J. (2023). Analyses of a chromosome-scale genome assembly reveal the origin and evolution of cultivated chrysanthemum. Nature Communications, 14, 2021. https://doi. org/10. 1038/s41467-023-37730-3

DOI: 10.54254/2753-8818/2025.AU24446

[2] Pan, B. , Du, Y. , Chen, Q. , Wang, Y. , Chen, L. , Li, H. , Huang, C. , & Gao, K. (2025). China's chrysanthemum in the global market: evaluating the international competitiveness and influencing factors. Frontiers in Sustainable Food Systems, 9. https://doi. org/10. 3389/fsufs. 2025. 1521709
[3] Dong, W. , Li, M. , Li, Z. , Li, S. , Zhu, Y. , Hongxu, & Wang, Z. (2020). Transcriptome analysis of the molecular mechanism of Chrysanthemum flower color change under short-day photoperiods. Plant Physiology and Biochemistry, 146, 315–328. https://doi. org/10. 1016/j. plaphy. 2019. 11. 027
[4] Wan, W. , Jia, F. , Liu, Z. , Sun, W. , Zhang, X. , Su, J. , Guan, Z. , Chen, F. , Zhang, F. , & Fang, W. (2024). Quantitative evaluation and genome-wide association studies of chrysanthemum flower color. Scientia Horticulturae, 338, 113561. https://doi. org/10. 1016/j. scienta. 2024. 113561
[5] Park, C. , Chae, S. , Park, S. -Y. , Kim, J. , Kim, Y. , Chung, S. , Arasu, M. , Al-Dhabi, N. , & Park, S. (2015). Anthocyanin and Carotenoid Contents in Different Cultivars of Chrysanthemum (Dendranthema grandiflorum Ramat. ) Flower. Molecules, 20(6), 11090–11102. https://doi. org/10. 3390/molecules200611090
[6] Lu, C. , Li, Y. , Wang, J. , Qu, J. , Chen, Y. , Chen, X. , Huang, H. , & Dai, S. (2021). Flower color classification and correlation between color space values with pigments in potted multiflora chrysanthemum. Scientia Horticulturae, 283, 110082. https://doi. org/10. 1016/j. scienta. 2021. 110082
[7] Zong, Y. , Zhao, Z. , Zhou, K. , Duan, X. , Han, B. , He, C. , Huang, H. , & Jiang, H. (2025). Metabolome and transcriptome analysis of anthocyanin biosynthesis reveal key metabolites and candidate genes in red-stemmed alfalfa (Medicago sativa). BMC Genomics, 26(1). https://doi. org/10. 1186/s12864-025-11529-6
[8] Sadowska-Bartosz, I. , & Bartosz, G. (2024). Antioxidant Activity of Anthocyanins and Anthocyanidins: A Critical Review. International Journal of Molecular Sciences, 25(22), 12001. https://doi. org/10. 3390/ijms252212001
[9] Wu, D. , Zhuang, F. , Wang, J. , Gao, R. , Zhang, Q. , Wang, X. , Zhang, G. , Fang, M. , Zhang, Y. , Li, Y. , Guan, L. , & Gao, Y. (2023). Metabolomics and Transcriptomics Revealed a Comprehensive Understanding of the Biochemical and Genetic Mechanisms Underlying the Color Variations in Chrysanthemums. Metabolites, 13(6), 742–742. https://doi. org/10. 3390/metabo13060742
[10] Nisar, N. , Li, L. , Lu, S. , Khin, N. , & Pogson, Barry J. (2015). Carotenoid Metabolism in Plants. Molecular Plant, 8(1), 68–82. https://doi. org/10. 1016/j. molp. 2014. 12. 007
[11] Lu, C. , Pu, Y. , Liu, Y. , Li, Y. , Qu, J. , Huang, H. , & Dai, S. (2019). Comparative transcriptomics and weighted gene co-expression correlation network analysis (WGCNA) reveal potential regulation mechanism of carotenoid accumulation in Chrysanthemum × morifolium. Plant Physiology and Biochemistry, 142, 415–428. https://doi. org/10. 1016/j. plaphy. 2019. 07. 023
[12] Lu, Z. , Wang, X. , Lin, X. , Mostafa, S. , Zou, H. , Wang, L. , & Jin, B. (2024). Plant anthocyanins: classification, biosynthesis, regulation, bioactivity, and health benefits. Plant Physiology and Biochemistry, 217, 109268–109268. https://doi. org/10. 1016/j. plaphy. 2024. 109268
[13] Enaru, B. , Drețcanu, G. , Pop, T. D. , Stănilă, A. , & Diaconeasa, Z. (2021). Anthocyanins: Factors Affecting Their Stability and Degradation. Antioxidants, 10(12), 1967. https://doi. org/10. 3390/antiox10121967
[14] Zhu, W. , Ma, Z. , Zhang, L. , Yang, C. , Xu, F. , & Yu, J. (2025). Natural anthocyanin-based wearable colorimetric pH indicator with high color fastness. Dyes and Pigments, 112789–112789. https://doi. org/10. 1016/j. dyepig. 2025. 112789
[15] Li, Y. (2019). Effects of Different Metal Ions on the Stability of Anthocyanins as Indicators. IOP Conference Series: Earth and Environmental Science, 300, 052015. https://doi. org/10. 1088/1755-1315/300/5/052015
[16] Zhao, D. , & Tao, J. (2015). Recent advances on the development and regulation of flower color in ornamental plants. Frontiers in Plant Science, 6. https://doi. org/10. 3389/fpls. 2015. 00261
[17] Zannou, O. , & Koca, I. (2022). Greener extraction of anthocyanins and antioxidant activity from blackberry (Rubus spp) using natural deep eutectic solvents. LWT, 158, 113184. https://doi. org/10. 1016/j. lwt. 2022. 113184
[18] Rajan, V. K. , Ragi, C. , & Muraleedharan, K. (2019). A computational exploration into the structure, antioxidant capacity, toxicity and drug-like activity of the anthocyanidin "Petunidin. " Heliyon, 5(7), e02115. https://doi. org/10. 1016/j. heliyon. 2019. e02115
[19] Xiao, P. , Zhang, H. , Liao, Q. , Zhu, N. , Chen, J. , Ma, L. , Zhang, M. , & Shen, S. (2023). Insight into the Molecular Mechanism of Flower Color Regulation in Rhododendron latoucheae Franch: A Multi-Omics Approach. Plants, 12(16), 2897–2897. https://doi. org/10. 3390/plants12162897
[20] Liu, S. , Zang, D. , Sun, Y. , Li, J. , & Zhao, H. Research advances on biosynthesis pathway of anthocyanins and relevant key enzymes. Soils and Crops, 2022, 11(3): 336-346. DOI: 10. 11689/j. issn. 2095-2961. 2022. 03. 011
[21] Mannino, G. , Gentile, C. , Ertani, A. , Serio, G. , & Bertea, C. M. (2021). Anthocyanins: Biosynthesis, Distribution, Ecological Role, and Use of Biostimulants to Increase Their Content in Plant Foods—A Review. Agriculture, 11(3), 212. https://doi. org/10. 3390/agriculture11030212

DOI: 10.54254/2753-8818/2025.AU24446

[22] Passeri, V. , Koes, R. , & Quattrocchio, F. M. (2016). New Challenges for the Design of High Value Plant Products: Stabilization of Anthocyanins in Plant Vacuoles. Frontiers in Plant Science, 7. https://doi. org/10. 3389/fpls. 2016. 00153

[23] Mekapogu, M. , Vasamsetti, B. M. K. , Kwon, O. -K. , Ahn, M. -S. , Lim, S. -H. , & Jung, J. -A. (2020). Anthocyanins in Floral Colors: Biosynthesis and Regulation in Chrysanthemum Flowers. International Journal of Molecular Sciences, 21(18), 6537. https://doi. org/10. 3390/ijms21186537

[24] Zhang, W. , Ye, Y. , Bao, Y. , Deng, X. , Yin, B. , Hong, Y. , Tian, S. , Wang, R. , Dong, L. , Zhang, W. , & Wu, K. (2025). The WD-40 repeat-containing protein CmRACK1 negatively regulates chrysanthemum flowering in response to photoperiod and gibberellin signaling. Environmental and Experimental Botany, 232, 106126. https://doi. org/10. 1016/j. envexpbot. 2025. 106126

[25] Xiang, L. , Liu, X. , Li, X. , Yin, X. , Grierson, D. , Li, F. , & Chen, K. (2015). A Novel bHLH Transcription Factor Involved in Regulating Anthocyanin Biosynthesis in Chrysanthemums (Chrysanthemum morifolium Ramat. ). PLOS ONE, 10(11), e0143892. https://doi. org/10. 1371/journal. pone. 0143892

[26] Liu, X. , Xiang, L. , Yin, X. , Grierson, D. , Li, F. , & Chen, K. (2015). The identification of a MYB transcription factor controlling anthocyanin biosynthesis regulation in Chrysanthemum flowers. Scientia Horticulturae, 194, 278–285. https://doi. org/10. 1016/j. scienta. 2015. 08. 018

[27] Li, C. , Yu, W. , Xu, J. , Lu, X. , & Liu, Y. (2022). Anthocyanin Biosynthesis Induced by MYB Transcription Factors in Plants. International Journal of Molecular Sciences, 23(19), 11701–11701. https://doi. org/10. 3390/ijms231911701

[28] Kee, E. S. , Naing, A. H. , Lim, S. H. , Han, J. S. , & Kim, C. K. (2016). MYB transcription factor isolated from Raphanus sativus enhances anthocyanin accumulation in chrysanthemum cultivars. 3 Biotech, 6(1). https://doi. org/10. 1007/s13205-016-0396-8

[29] Constantin, O. E. , & Istrati, D. I. (2022). Extraction, Quantification and Characterization Techniques for Anthocyanin Compounds in Various Food Matrices—A Review. Horticulturae, 8(11), 1084. https://doi. org/10. 3390/horticulturae8111084

[30] Teng, Z. , Jiang, X. , He, F. , & Bai, W. (2020). Corrigendum to “Qualitative and Quantitative Methods to Evaluate Anthocyanins” [eFood 1(5), October (2020) 339–346]. EFood, 1(6), 412–412. https://doi. org/10. 2991/efood. k. 210108. 001

[31] Chandra Singh, M. , Kelso, C. , Price, W. E. , & Probst, Y. (2020). Validated liquid chromatography separation methods for identification and quantification of anthocyanins in fruits and vegetables: A systematic review. Food Research International, 109754. https://doi. org/10. 1016/j. foodres. 2020. 109754

[32] Farooq, S. , Shah, M. A. , Siddiqui, M. W. , Dar, B. N. , Mir, S. A. , & Ali, A. (2020). Recent trends in extraction techniques of anthocyanins from plant materials. Journal of Food Measurement and Characterization, 14(6), 3508–3519. https://doi. org/10. 1007/s11694-020-00598-8

[33] Custodio-Mendoza, J. A. , Aktaş, H. , Zalewska, M. , Wyrwisz, J. , & Kurek, M. A. (2024). A Review of Quantitative and Topical Analysis of Anthocyanins in Food. Molecules, 29(8), 1735. https://doi. org/10. 3390/molecules29081735

[34] Garcia-Oliveira, P. , Pereira, A. G. , Fraga-Corral, M. , Lourenço-Lopes, C. , Chamorro, F. , Silva, A. , Garcia-Perez, P. , Barroso, F. , Barros, L. , Ferreira, I. C. F. R. , Simal-Gandara, J. , & Prieto, M. A. (2021). Identification, Quantification, and Method Validation of Anthocyanins. Chemistry Proceedings, 5(1), 43. https://doi. org/10. 3390/CSAC2021-10680

[35] Shen, S. , Zhan, C. , Yang, C. , Fernie, A. R. , & Luo, J. (2022). Metabolomics-centered mining of plant metabolic diversity and function: past decade and future perspectives. Molecular Plant, 16(1). https://doi. org/10. 1016/j. molp. 2022. 09. 007

[36] Chu, Z. , Xiong, R. , Peng, X. , Cui, G. , Dong, L. , & Li, W. (2024). Delineating Molecular Regulatory of Flavonoids Indicated by Transcriptomic and Metabolomics Analysis during Flower Development in Chrysanthemum morifolium “Boju. ” International Journal of Molecular Sciences, 25(19), 10261. https://doi. org/10. 3390/ijms251910261

[37] Zhao, G. , Li, Y. , Peng, J. , Li, X. , Xia, W. , Tian, Y. , Li, Y. , & Zhou, L. (2025). Anthocyanin Degradation Drives Heat-Induced Petal Fading in Chrysanthemum morifolium at Full Bloom: A Multi-Omics Analysis. Agriculture, 15(9), 950–950. https://doi. org/10. 3390/agriculture15090950

[38] Gitelson, A. A. , Chivkunova, O. B. , & Merzlyak, M. N. (2009). Nondestructive estimation of anthocyanins and chlorophylls in anthocyanic leaves. American Journal of Botany, 96(10), 1861–1868. https://doi. org/10. 3732/ajb. 0800395

[39] Zhu, X. , Wu, C. , & Hui, J. (2025). Effect of Light Intensity on Anthocyanin Synthesis Assessed Using Leaves of Aglaonema commutatum. Genes, 16(4), 375–375. https://doi. org/10. 3390/genes16040375

DOI: 10.54254/2753-8818/2025.AU24446

[40] Hu, K. (2010). Effects of structural gene expression in anthocyanin biosynthetic pathway on flower color in chrysanthemum and cineraria (Doctoral dissertation). Beijing Forestry University, Beijing, China.
[41] Su, J. , Jiang, J. , Zhang, F. , Liu, Y. , Ding, L. , Chen, S. , & Chen, F. (2019). Current achievements and future prospects in the genetic breeding of chrysanthemum: a review. Horticulture Research, 6(1), 1–19. https://doi. org/10. 1038/s41438-019-0193-8
[42] Razzaq, A. , Wishart, D. S. , Wani, S. H. , Hameed, M. K. , Mubin, M. , & Saleem, F. (2022). Advances in Metabolomics-Driven Diagnostic Breeding and Crop Improvement. Metabolites, 12(6), 511. https://doi. org/10. 3390/metabo12060511