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Review

Anthocyanins: Biosynthesis, Metabolism and Functions in Higher Plants

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Abstract: Anthocyanins, a class of water-soluble flavonoid pigments, are widely distributed in higher plants and are responsible for the red, blue, and purple coloration of many fruits, vegetables, and grains. In recent years, growing attention has been paid to their dual biological significance in plants and humans. In plants, anthocyanins play critical roles in photoprotection, stress resistance, and defense against pathogens. In humans, they exhibit potent antioxidant, anti-inflammatory, and metabolic regulatory activities, contributing to the prevention of chronic diseases such as cardiovascular disorders, diabetes, and cancer. These functions are largely mediated through the modulation of key cellular pathways, including NF-κB (Nuclear Factor kappa-light-chain-enhancer of activated B cells), MAPK (Mitogen-Activated Protein Kinase), and PPAR-γ (Peroxisome Proliferator-Activated Receptor gamma). Anthocyanin biosynthesis is tightly regulated by the MYB-bHLH-WD40 (MBW) transcriptional complex, in which R2R3-MYB proteins provide DNA-binding specificity, bHLH factors enhance transcriptional activation, and WD40 proteins serve as scaffolds to stabilize the complex. The activity of this MBW complex is further influenced by both genetic and environmental factors. However, the practical application of anthocyanins is limited by low stability and bioavailability. Emerging encapsulation technologies such as nano-formulation in biopolymer matrices have shown promise in overcoming these limitations. This review comprehensively summarizes recent advances in the biosynthesis, metabolic regulation, and physiological functions of anthocyanins in higher plants, with a particular focus on their molecular mechanisms and potential applications in health-promoting functional foods and plant breeding. Understanding the regulatory networks of anthocyanin biosynthesis and their functional implications provides valuable insight into the development of anthocyanin-enriched crops and nutraceuticals.

Keywords: anthocyanins; functions; biosynthesis; regulation

1. Introduction

Anthocyanins are a widely distributed class of plant pigments classified within the flavonoid family. Structurally, they are characterized by a 2-phenylbenzopyran backbone with diverse substituent groups and are commonly found in glycosylated forms [1]. The abundance and compositional profile of anthocyanins vary considerably among plant species and are influenced by the timing of harvest. Within individual plants, anthocyanins typically accumulate in substantial quantities across various tissues, including leaves, flowers, fruits, seeds, stems, epidermis, and other organs. There are over 600 types of anthocyanins in nature [2], which can be classified into many types based on modifications, such as substituent groups on the B ring, type and number of conjugated sugar and the presence or absence of an acyl group. Pelargonidin, cyanidin, delphinidin, peonidin, petunidin and malvidin are six main anthocyanins in higher plants. Peonidin is formed by the methylation of cyanidin, while petunia and malvidin are formed by the methylation of delphinidin with different degrees.

Anthocyanins are synthesized in the cytoplasm. The biosynthesis of anthocyanins goes through a series of complicated steps that contain many enzymes (PAL, CHS, CHI, F3'H, F3'5'H, DFR and ANS, et al.). Also, there are many factors that can affect this process, including transcription factors and environmental factors. The vacuoles of plants are the storage sites of anthocyanins, and anthocyanins are transported to vacuoles after biosynthesis in plant cells [3].

As the most abundant water-soluble pigments in the plant kingdom, anthocyanins are responsible for the vivid red, blue, and purple hues in many fruits, vegetables, and grains. Recent research has highlighted their significant health-promoting properties, including potent antioxidant, anti-inflammatory, antidiabetic, anti-obesity, and anticancer effects, which contribute to the prevention and management of chronic diseases such as cardiovascular disease, diabetes, neurodegenerative disorders, and certain cancers [4,5]. These benefits are largely attributed to their ability to modulate key cellular signaling pathways, such as NF-κB and Nrf2 (Nuclear factor erythroid 2–related factor 2), and to improve glucose and lipid metabolism by influencing gene expression, including upregulation of PPAR-γ [6].

In addition to their health effects in humans, anthocyanins play crucial physiological roles in plants, providing protection against oxidative stress, UV radiation, and pathogens, and contributing to plant adaptation and survival [5,7]. Their vibrant coloration and safety profile have led to widespread use as natural colorants in the food, pharmaceutical, and cosmetic industries, offering a safer alternative to synthetic dyes [4,8].

However, the practical application of anthocyanins is challenged by their structural instability and low bioavailability, prompting ongoing research into stabilization and encapsulation techniques to enhance their efficacy in functional foods and nutraceuticals [9,10]. Overall, anthocyanins represent a promising class of natural compounds with diverse applications and substantial potential for improving both human health and industrial product quality. Therefore, it is necessary for us to understand the functions of anthocyanins to improve human health by producing anthocyanin-rich food and medicine reasonably. To study anthocyanins biosynthesis and metabolism and comprehend the regulatory factors that influence anthocyanins content and the transport models of them can provide valuable information for the study of secondary metabolites and the breeding of pathogen- and insect-resistant varieties in higher plants.

2. Biosynthesis of Anthocyanins

2.1. Biosynthetic Pathway of Anthocyanins in Plants

Plant anthocyanins biosynthetic pathways and the involved enzymes were well characterized in many previous studies. They are produced in the cytoplasm (Figure 1). Phenylalanine experiences a series of enzymatic reactions, and then is modified by different glycosyltransferases, methyltransferase and acyltransferases and is transported to vacuoles in the end. The biosynthesis pathway can be divided into three stages according to the reaction process. The first stage is transformation of anthocyanins precursors; the second stage is flavonoid metabolism; the third stage is anthocyanins production.

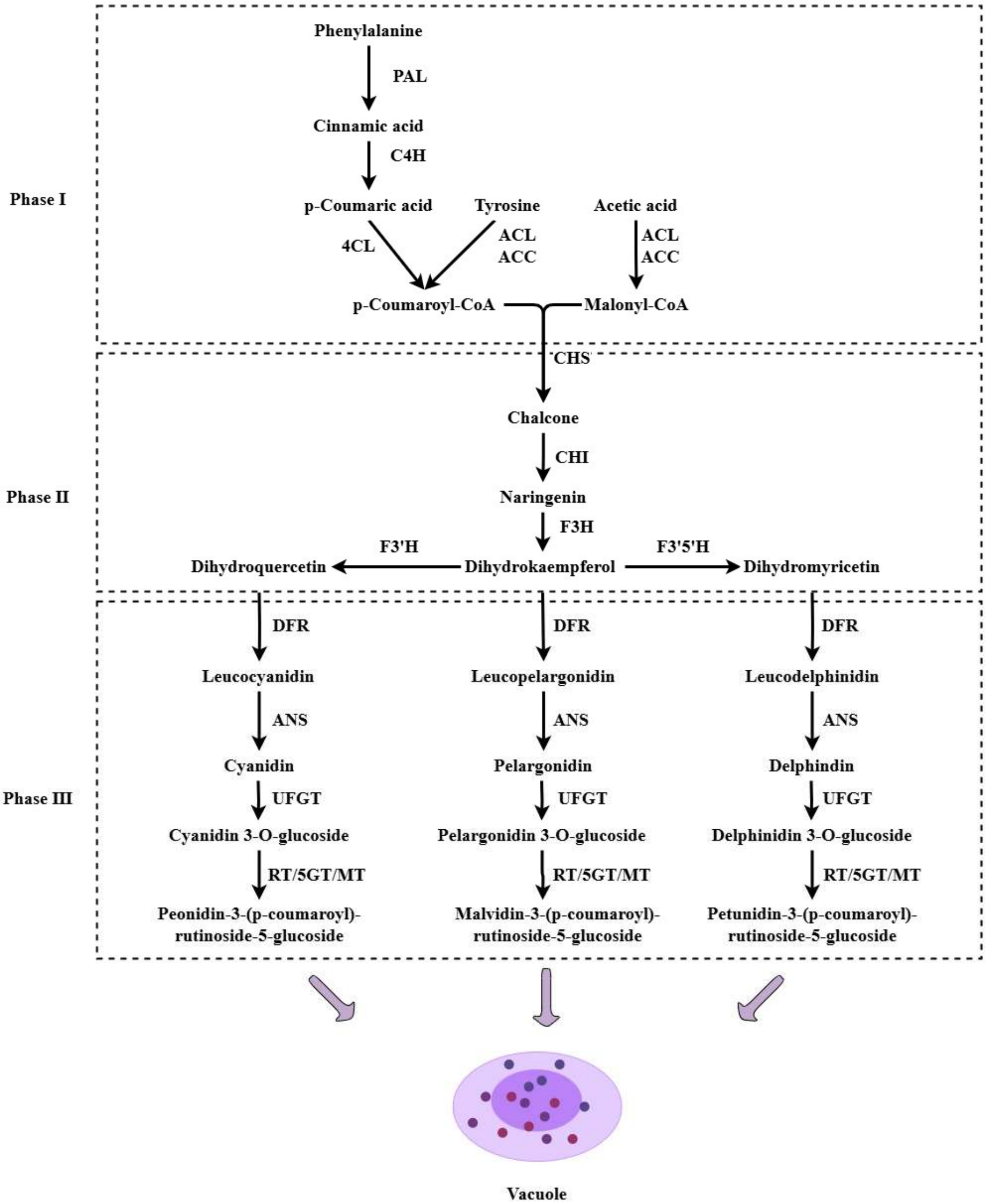

Figure 1. Anthocyanins biosynthesis pathway.

In the first stage, phenylalanine, which is the most important precursor of anthocyanin biosynthesis, is converted to trans-cinnamic acid by phenylalanine ammonia lyase (PAL) in the cytoplasm primarily. It is then hydroxylated to form p-coumaric acid to be p-coumaric acid by cinnamate 4-hydroxylase (C4H). Alternatively, in some plant species, tyrosine can be converted to p-coumaric acid by tyrosine ammonia lyase (TAL) [11]. Finally, p-coumaric acid is turned into p-coumaroyl-CoA by 4-coumarate-CoA ligase (4CL). Another, acetic acid is converted by acetyl-CoA ligase (ACL) and acetyl-CoA carboxylase (ACC) to malonyl-CoA [12].

The second stage is the condensation of three molecules of malonyl-CoA and one of p-coumaroyl-CoA to be chalcone, proceeds spontaneously at a low rate, but is accelerated by the chalcone synthase (CHS) [13]. Chalcone is then isomerized to naringenin by chalcone isomerase (CHI). Next, naringenin is converted to dihydrokaempferol (DHK) by flavanone 3-hydroxylase (F3H). Flavonoid-3'-hydroxylase (F3'H) and flavonoid-3'5'-hydroxylase (F3'5'H) hydroxylate at different sites of DHK to form dihydroquercetin (DHQ) and dihydromyricetin (DHM) [14]. Differences in the hydroxylation of the B-ring confer different colors of anthocyanins.

In the last stage, dihydrokaempferol (DHK), dihydroquercetin (DHQ) and dihydromyricetin (DHM) are reduced to colorless anthocyanins under the action of dihydroflavonol-4-reductase (DFR), and then transformed to colored anthocyanins: pelargonidin, cyanidin and delphinidin by anthocyanidin synthase [15–18]. However, anthocyanins structures are inherently unstable and they exist in the form of glycosylation. Pelargonidin, cyanidin and delphinidin usually combine with glucose to be pelargonidin 3-O-glucoside, cyanidin 3-O-glucoside and delphinidin 3-O-glucoside by flavonoid-3-O-glucosyltransferase (UFGT). Post biosynthesis, then they can be converted to the glucosides of malvidin, peonidin and petunidin respectively by flavonoid-5-O-glucosyltransferase (5GT), anthocyanidin-3-glucoside - rhamnosyltransferase, acyltransferase (AT) and methyltransferase (MT) [19]. Recent research demonstrates that glycosylation and acylation are not merely terminal steps but occur alongside anthocyanin production, often overlapping with transport and storage processes. These modifications are catalyzed by specific glycosyltransferases and acyltransferases, which act on anthocyanidins as soon as they are formed, rather than after the pathway is "complete" [20].

2.2. Functional Characterization of Key Structural Genes

The structural genes that encode key enzymes in the anthocyanins biosynthetic pathway include CHS, CHI, F3H, F3'H, F3'5'H, DFR, ANS and UFGT (Table 1). CHS is the first committed enzyme in the flavonoid pathway and is often induced by UV light, pathogens, or salicylic acid in plants such as Malaysian ginger [21,22]. CHS and CHI are pivotal early enzymes regulating anthocyanin accumulation and floral pigmentation. Functional studies in species like Malus crabapple and Petunia hybrida show that CHS expression levels correlate with flower color intensity [23,24]. CHS is often encoded by small gene families with tissue- and stage-specific expression.

Table 1. Key structural genes involved in anthocyanin biosynthesis and their biological functions

Gene name	Encoded Enzyme	Primary Function	Expression Characteristics	Example Species	Key References
CHS	Chalcone synthase	Catalyzes the initial step in flavonoid biosynthesis	UV- and pathogen-inducible	*Zingiber officinale* (Malaysian ginger), *Malus crabapple*, *Petunia hybrida*	[21–24]

CHI	Chalcone isomerase	Converts chalcone into naringenin	Highly active in early biosynthesis steps	*Clivia miniata*, *Hosta ventricose*, *Arabidopsis thaliana*	[25,26]
F3H	Flavanone 3-hydroxylase	Produces dihydroflavonols from flavanones	Expression reduction decreases pigments	*Fragaria* × *ananassa* (strawberry), *Centaurea cyanus*	[27–29]
DFR	Dihydroflavonol reductase	Converts dihydroflavonols into leucoanthocyanidins	High expression in red tissues	Wheat, *Centaurea cyanus*, poinsettia	[30–32]
ANS	Anthocyanidin synthase (LDOX)	Catalyzes the formation of colored anthocyanidins from leucoanthocyanidins	Mutation leads to pigment loss	Pomegranate, red currant	[12,33,34]
UFGT	UDP-glucosyltransferase	Stabilizes anthocyanins by glycosylation	Expression is tightly correlated with color	Red litchi pericarp	[35]

CHI catalyzes the stereospecific isomerization of chalcone into naringenin. Studies in Clivia miniata and Hosta ventricosa found multiple CHI isoforms, of which only certain types (e.g., type I) are catalytically active [25,26]. CHI expression is elevated in anthocyanin-rich tissues. Heterologous overexpression enhances pigmentation, and CHI can rescue anthocyanin biosynthesis in Arabidopsis thaliana mutants.

Further downstream, F3H hydroxylates the flavanone C-ring to form dihydroflavonols. F3'H and F3'5'H hydroxylate flavanones/flavanols on the B-ring, producing DHQ and DHM. F3H typically encodes 350–380 amino acids in two exons [27]. RNAi-mediated silencing of F3H in strawberry suppressed expression by 70% and significantly reduced anthocyanin levels [28]. In Centaurea cyanus, low F3H activity explains white petal coloration [29].

DFR reduces dihydroflavonols to leucoanthocyanidins. In Arabidopsis, overexpression of TaDFR (wheat) restores pigmentation in dfr mutants [30]. FpDFR expression is higher in red fruits than white in Fragaria pentaphylla [31]. In poinsettia, DFR expression is upregulated in red versus green bracts, and its overexpression increases anthocyanin levels in Arabidopsis [32].

ANS (also called LDOX) catalyzes the final oxidation step to generate anthocyanidins. It is a 2-ketoglutarate-dependent oxygenase [12]. In pomegranate, lack of ANS (PgLDOX) transcript correlates with absence of anthocyanins[33]. In red currant, pink/white coloration results from low ANS expression [34].

UFGT stabilizes anthocyanidins via glycosylation. Its expression strongly correlates with anthocyanin content in red litchi pericarp, according to RT-PCR analysis [35]. Glycosylation increases anthocyanin water solubility and chemical stability, especially at neutral pH and during storage or processing. Glycosylated anthocyanins are more resistant to degradation than aglycones, and the position/type of glycosylation (e.g., C3 vs. C5) can further modulate stability and color expression

[36–38]. Another structure, acylated anthocyanin dramatically enhances anthocyanin stability against heat, light, pH changes, and oxidation. Acylated anthocyanins show increased color retention, especially blue hues, due to intramolecular co-pigmentation and π–π stacking, which protect the chromophore from hydration and chemical breakdown [37,39,40]. The addition of acyl groups (e.g., malonyl, sinapoyl) to anthocyanins is common in purple corn and other pigmented crops, which dramatically increases pigment stability. Acylated anthocyanins form intramolecular "sandwich-type" stacking, which protects the chromophore from hydration and chemical breakdown, resulting in improved color retention under varying pH, light, and temperature conditions [37,38,41,42].

Structural modifications (especially acylation and glycosylation) are being harnessed to develop more stable, natural colorants and functional foods. These modifications improve anthocyanin retention during processing, storage, and digestion, expanding their use in food packaging, intelligent indicators, and health-promoting products [39,41]. While glycosylation generally improves stability and absorption, acylation can sometimes reduce intestinal uptake, potentially limiting systemic bioactivity. However, both modifications help preserve antioxidant and anti-inflammatory functions in the gut [37,38]. Most clinical studies use anthocyanin-rich foods or extracts, but few directly compare structural variants. The low stability and bioavailability of non-modified anthocyanins have limited their clinical translation. Advances in structural modification and encapsulation are expected to improve efficacy in future trials [37,38,43].

3. Transport Mechanisms of Anthocyanins

After biosynthesis in the cytoplasm, anthocyanins are transported into vacuoles for storage, where they contribute to pigmentation, stress responses, and stability. Current research has identified two major mechanisms underlying anthocyanin sequestration: protein-mediated transport and vesicle-mediated trafficking.

3.1. Protein-Mediated Transport: GSTs, ABC, and MATE Transporters

One of the most extensively studied mechanisms for anthocyanin sequestration involves the coordinated function of cytosolic glutathione S-transferases (GSTs) and ATP-binding cassette (ABC) transporters, particularly those of the ABCC subfamily. In this model, GSTs are proposed to bind anthocyanin glycosides in the cytosol and facilitate their recognition by tonoplast-localized ABCC transporters [44,45]. These transporters, such as AtABCC2 in Arabidopsis thaliana and VvABCC1 in Vitis vinifera, mediate the ATP-dependent translocation of anthocyanins like cyanidin 3-O-glucoside into the vacuole. This process is often enhanced by the presence of reduced glutathione (GSH), which may act as a co-substrate or contribute to transport efficiency [46,47].

Functional studies across various plant species have supported this mechanism. In cotton (Gossypium hirsutum), apple (Malus domestica), and tree peony (Paeonia suffruticosa), specific phi-class GSTs (e.g., GhGSTF12, MdGSTF6, PsGSTF3) have been identified as essential for anthocyanin accumulation. Gene silencing or mutation leads to reduced pigment deposition, while transgenic overexpression enhances pigmentation, indicating a conserved transport mechanism [48–51]. Additionally, transcriptome and phylogenetic analyses in Vitis vinifera and Paeonia suffruticosa show that GST expression correlates with anthocyanin content and developmental stage, contributing to tissue-specific pigmentation [50,51]. Ligand docking and mutagenesis studies show that anthocyanin and GSH bind closely within the transporter, mutually enhancing each other's binding. The GST may deliver anthocyanin (possibly as a non-covalent complex) to the ABC transporter, which then co-transports anthocyanin and GSH into the vacuole[46,52–54]. While direct physical interaction between GSTs and ABC transporters in vivo remains to be visualized, functional studies strongly support a sequential handoff mechanism.

Another protein family involved in anthocyanin transport is the multidrug and toxic compound extrusion (MATE) transporter family. MATE proteins typically use the electrochemical proton (H^+) or sodium (Na^+) gradients across the tonoplast to facilitate anthocyanin uptake [55]. In grape (Vitis vinifera), VvAM1 and VvAM3 are fruit-specific MATE transporters responsible for transporting partially acylated anthocyanins [56]. Ectopic expression of VvAM3 in the Arabidopsis mutant pab1 restored wild-type pigmentation, and immunofluorescence analyses showed its colocalization with anthocyanin-containing vesicles [57]. Further evidence comes from carrot (Daucus carota), where DcMATE21 expression strongly correlates with anthocyanin accumulation under various cultivars and stress conditions. Functional assays confirm that DcMATE21 specifically binds and transports C3G [58,59]. Similarly, OsMATE34 in black rice and PhMATE1 in Petunia hybrida have been shown to regulate anthocyanin accumulation in reproductive organs, further validating the conserved role of MATE transporters [60,61].

3.2. Vesicle-Mediated Trafficking and Anthocyanic Vacuolar Inclusions

In addition to transporter-dependent mechanisms, vesicle-mediated trafficking provides an alternative route for anthocyanin sequestration. In this model, anthocyanins are first packaged into anthocyanin-containing vesicles (ACVs) in the cytoplasm. These vesicles are then directed to perivacuolar compartments (PVCs) or protein storage vacuoles (PSVs), with eventual fusion to the central vacuole via Golgi-mediated trafficking [62]. Upon fusion, the vesicles may rupture, forming irregular, membrane-less bodies known as anthocyanic vacuolar inclusions (AVIs), which are considered essential for anthocyanin stabilization and compartmentalization [63].

4. The Regulation of Anthocyanin Biosynthesis

Transcription factors play a crucial role in the regulation of anthocyanin biosynthesis. Current studies have identified several key transcription factors involved in this process, including members of the MYB, MYC, bHLH, bZIP, and WD40 families. Among them, MYB, bHLH, and WD40 proteins can interact to form the MYB–bHLH–WD40 (MBW) transcriptional complex, which either activates or represses the expression of structural genes, thereby regulating anthocyanin accumulation in higher plants [64–67]. In addition to genetic regulation, environmental factors also significantly influence anthocyanin biosynthesis [68]. Numerous studies have demonstrated that external stimuli can modulate anthocyanin production by affecting enzyme activities and altering the expression of biosynthetic and regulatory genes. Table 2 shows major transcription factors regulating anthocyanin biosynthesis.

Table 2. Major transcription factors regulating anthocyanin biosynthesis

TF Family	Representative Genes/Proteins	Regulatory Role	Mechanism of Action	Example Species	Key References
MYB	*MdMYB1*, *PsMYB1*	Activator or repressor	Forms MBW complex with bHLH and WD40; regulates structural gene expression	*Primulina swinglei, Fagopyrum esculentum, Zinnia elegans, Brassica rapa, Litchi chinensis*	[68–72]
bHLH	*MdbHLH3*, *DcTT8*	Positive regulator	Enhances MYB activity and co-activates biosynthetic gene promoters	*Malus domestica, Dendrobium candidum*	[73,74]
WD40	*RsTTG1*, *MdTTG1*	Stabilizing co-factor	Stabilizes MBW complex, essential for efficient pigment accumulation	*Raphanus sativus, Platanus acerifolia,* apple, *Myrica rubra,* pomegranate	[75–79]
bZIP	*HY5*, *FvHY5*	Light-responsive activator	Modulates MYB expression and/or directly binds to structural gene promoters under light	*Arabidopsis thaliana, Fragaria vesca*	[80]

4.1. The Major Transcription Factors of Anthocyanin Biosynthesis

Anthocyanin biosynthesis in plants is primarily regulated by a conserved transcriptional complex consisting of R2R3-MYB, basic helix–loop–helix (bHLH), and WD40-repeat (WDR) proteins, commonly referred to as the MBW complex. These factors coordinate the spatiotemporal expression of structural genes in the anthocyanin biosynthetic pathway, thereby controlling pigment accumulation in plant tissues.

4.1.1. MYB Transcription Factors

R2R3-MYB transcription factors are key regulators of anthocyanin biosynthesis and act as either activators or repressors. For instance, in Primulina swinglei, PsMYB1 has been identified as a positive regulator that activates anthocyanidin synthase (ANS) expression and induces pigmentation in Nicotiana benthamiana leaves, especially when co-expressed with a bHLH partner [69]. Similarly, FeR2R3-MYB from Fagopyrum esculentum activates anthocyanin biosynthesis and also confers drought tolerance, revealing its dual functional role [70]. Conversely, repressive MYBs such as ZeMYB32 in Zinnia elegans suppress anthocyanin accumulation by disrupting activator complexes [71]. In Brassica rapa, the R3-MYB BrMYBL2.1 interferes with MBW complex formation, and allelic variation in this gene contributes to pigmentation differences among cultivars [72]. Likewise, LcMYBx in Litchi chinensis represses anthocyanin biosynthesis by competitively binding to bHLH partners [73].

4.1.2. bHLH Transcription Factors

bHLH transcription factors serve as crucial cofactors in the MBW complex, typically partnering with MYBs to activate gene expression. Though bHLHs are often broadly expressed, they are indispensable for efficient anthocyanin accumulation. In apple (Malus domestica), MdbHLH3 enhances anthocyanin content at low temperatures by activating MdDFR, MdUFGT, and MdMYB1 expression [74]. In Dendrobium candidum, DcTT8 directly activates late biosynthetic genes, promoting pigment accumulation [75].

4.1.3. WD40-Repeat Proteins

WD40 proteins provide structural support within the MBW complex. In radish (Raphanus sativus), RsTTG1 interacts with RsTT8 and RsMYB1 to activate CHS and DFR promoters [76]. In Platanus acerifolia, PaTTG1.1 and PaTTG1.2 restore anthocyanin production in Arabidopsis thaliana ttg1 mutants and promote expression of flavonoid biosynthetic genes [77]. In apple, MdTTG1 promotes anthocyanin accumulation [78]; MrWD40-1 in Myrica rubra and PgWD40 in pomegranate also interact with MYB and bHLH proteins to regulate pigment biosynthesis [79,81].

4.1.4. MBW Complex in Diverse Species

The MBW complex operates across various species: In Actinidia chinensis (kiwifruit), AcMYBF110, AcbHLH1, and AcWDR1 co-regulate late biosynthetic genes, leading to increased anthocyanin accumulation [82]. In Hordeum vulgare (barley), HvWD40-140, HvANT1 (MYB), and HvANT2 (bHLH) activate DFR expression, confirmed by transient expression and yeast two-hybrid assays [83]. In strawberry (Fragaria × ananassa), FaMYB5, FaEGL3, and FaLWD1 co-activate both anthocyanin and proanthocyanidin biosynthetic genes [67].

These examples illustrate the conserved role of the MBW complex across species. However, some species exhibit unique variations or regulatory mechanisms, highlighting functional divergence within this conserved architecture. In Freesia hybrida (a monocot), the MYB regulator FhPAP1 forms a canonical MBW complex but displays much higher transactivation capacity than its eudicot homologs, contributing to intense flower pigmentation and rapid domestication-driven color evolution. This highlights functional divergence even within conserved MBW architecture [84]. In eggplant, a novel R3-MYB repressor (SmelMYBL1) was identified that inhibits anthocyanin accumulation by competing with MYB activators for bHLH binding, suggesting species-specific repressor integration into the MBW complex [80].

4.1.5. bZIP Transcription Factors and Light Signaling

Besides MBW components, bZIP transcription factors like ELONGATED HYPOCOTYL 5 (HY5) also modulate anthocyanin biosynthesis. In Arabidopsis thaliana, HY5 binds flavonoid gene promoters and interacts with MBW proteins in light signaling [85]. In Fragaria vesca, FvHY5 heterodimerizes with FvbHLH9 to co-activate DFR expression, integrating environmental cues with pigment regulation [85].

4.2. The Major Environmental Factors of Anthocyanin Biosynthesis

Anthocyanin accumulation in plants is tightly regulated by environmental factors, including temperature, light, UV radiation, soil conditions, water availability, and nutrient status. These abiotic cues influence anthocyanin biosynthesis at both physiological and molecular levels, thereby affecting not only pigmentation but also the nutritional quality and market value of fruits, vegetables, and ornamental plants.

4.2.1. Temperature-Mediated Regulation

Temperature is a key determinant of anthocyanin biosynthesis. Elevated temperatures generally inhibit pigment accumulation by suppressing the transcription of structural and regulatory genes in the anthocyanin pathway, whereas low temperatures enhance their expression. In Olea europaea (olive), low-temperature conditions, particularly those associated with high-altitude environments, significantly increased both anthocyanin content and the expression of biosynthetic genes, indicating a positive correlation between cool climates and pigment biosynthesis [86]. Similarly, in Vaccinium myrtillus (bilberry), ecotypes from high-altitude regions exhibited substantially higher anthocyanin concentrations, which was attributed to the combined effects of reduced temperature and elevated UV exposure [87].

4.2.2. Light and UV Radiation

Light acts as a primary positive regulator of anthocyanin biosynthesis, often functioning through light-responsive transcription factors such as HY5 and members of the MYB and bHLH families. In Malus domestica (apple), light exposure significantly induced the expression of anthocyanin biosynthetic genes such as MdCHS, MdANS, and MdUFGT1, resulting in elevated pigment accumulation compared to shaded fruit [88]. Moreover, in Lycium ruthenicum, UV-B radiation exposure led to a twofold increase in anthocyanin levels in leaves and upregulated the expression of 24 structural genes. This response was largely mediated by the activation of MYB and bHLH transcription factors, underscoring the importance of UV signaling in secondary metabolite regulation [89].

4.2.3. Soil Properties, Water Availability, and Nutrient Effects

Soil physicochemical characteristics and water regimes also exert significant influences on anthocyanin biosynthesis. Soil characteristics can affect anthocyanin biosynthesis in plants through both direct and indirect mechanisms, primarily by modulating environmental stress responses, nutrient availability, and signaling pathways that ultimately impact gene expression and enzyme activity in the anthocyanin pathway. Soil nutrient composition, especially levels of nitrogen, phosphorus, potassium, and micronutrients (like magnesium and iron), can directly influence the expression of genes encoding enzymes in the anthocyanin biosynthetic pathway. For example, nutrient stress can upregulate anthocyanin biosynthetic genes as a protective response, mediated by transcription factors such as MYB, bHLH, and WD40 [64,90]. Soil pH can affect the internal pH of plant tissues, which not only influences anthocyanin stability and color but may also modulate the activity of biosynthetic enzymes and the expression of regulatory genes [64]. In Lycium ruthenicum, anthocyanin accumulation was positively associated with soil electrical conductivity and microbial biomass carbon, while high soil nitrogen content and excessive moisture exerted inhibitory effects in a specific ecological context [91]. These findings suggest that precise modulation of soil nutrient composition and water availability can be employed as agronomic strategies to enhance anthocyanin content in economically important crops.

4.2.4. Hormonal Regulation

Phytohormones such as ethylene, abscisic acid (ABA), auxin, gibberellins (GA), and jasmonates (JA) play integral roles in modulating anthocyanin biosynthesis by linking developmental signals with environmental stimuli.

Ethylene: Ethylene has been shown to promote anthocyanin biosynthesis. In Vitis vinifera cell cultures, ethephon (an ethylene-releasing compound) stimulated anthocyanin production, and when combined with pulsed electric field treatment, anthocyanin content increased by 2.5-fold compared to controls [92]. Phytohormones play integral roles in modulating anthocyanin biosynthesis by coordinating developmental cues and environmental stimuli. Among them, abscisic acid (ABA), auxin, gibberellins (GA), and jasmonates (JA) exhibit distinct regulatory effects, either promoting or repressing anthocyanin accumulation in various plant species.

Abscisic Acid (ABA): ABA is widely recognized as a key positive regulator of anthocyanin biosynthesis, particularly during fruit ripening and stress responses. In Vaccinium corymbosum (blueberry), exogenous ABA application significantly enhanced anthocyanin accumulation in leaves, as supported by transcriptomic evidence showing upregulation of phenylpropanoid and flavonoid biosynthetic genes, MYB transcription factors, and ABRE-binding proteins. These findings suggest a coordinated regulatory network involving ABA-responsive elements driving pigment biosynthesis [93]. Similarly, in Lycium species, endogenous ABA levels were closely correlated with anthocyanin accumulation during fruit ripening. Silencing of LbNCED1, a key ABA biosynthesis gene, resulted in substantial reductions in both ABA and anthocyanin content, underscoring the hormone's central role in activating the MBW transcriptional complex and downstream biosynthetic genes [94]. In Prunus avium (sweet cherry), ABA and light signals were found to synergistically enhance anthocyanin accumulation. B-box proteins PavBBX6 and PavBBX9 were shown to directly activate the promoters of both ABA and anthocyanin biosynthetic genes, indicating a convergence of hormonal and photomorphogenic pathways in the regulation of pigment biosynthesis [95].

Auxin and Gibberellins (GA): Auxin's influence on anthocyanin biosynthesis is context-dependent and appears to interact with other hormonal signals. In Malus domestica (apple), both indole-3-acetic acid (IAA) and ABA positively regulated anthocyanin accumulation. Comparative transcriptome analyses of red-fleshed mutants revealed enhanced expression of auxin-responsive genes (AUX1, SAUR) as well as ABA signaling components (PP2C, SnRK2), suggesting a cooperative effect of auxin and ABA in modulating the anthocyanin pathway under specific genetic backgrounds [96]. In contrast, gibberellins (GAs) tend to negatively regulate anthocyanin biosynthesis, potentially through antagonistic interactions with ABA or via suppression of key transcription factors and biosynthetic enzymes.

Jasmonates (JA): Jasmonates also act as positive regulators of anthocyanin biosynthesis, though their effects can be dose- and context-dependent. In tulip (Tulipa gesneriana), foliar application of methyl jasmonate significantly increased total anthocyanin content, particularly when applied in combination with sucrose or ABA, pointing to a synergistic mechanism involving multiple signaling pathways [97]. However, excessive JA or deregulation of JA signaling can lead to adverse effects. In Brassica napus (rapeseed), suppression of JAZ proteins—negative regulators of JA signaling—was associated with premature flower color fading, indicating that a balanced JA signaling network is critical for maintaining stable anthocyanin levels [98].

Plant hormones interact in complex networks to regulate anthocyanin biosynthesis. Recent studies reveal extensive crosstalk, with no strict hierarchy but rather context-dependent dominance and integration at both transcriptional and post-translational levels. Key transcription factors and repressors serve as integration nodes. For example, in apple, the zinc finger protein MdZFP7 integrates JA and GA signals by interacting with the JA repressor MdJAZ2 and the GA repressor MdRGL3a, modulating anthocyanin biosynthetic gene expression. The E3 ligase MdBRG3 further regulates MdZFP7 stability, adding a post-translational layer [99]. JA and GA often have antagonistic effects, with repressors from one pathway (e.g., MdJAZ2 for JA, MdRGL2a for GA) modulating the activity of repressors or activators from the other, as seen with MdbHLH162 in apple, which integrates both signals to fine-tune anthocyanin production. Similarly, SL and GA crosstalk is mediated by the SMXL8-AGL9 module, where GA disrupts SL-mediated repression of anthocyanin biosynthesis [100]. In Arabidopsis and pear, JA and ET signaling converge on ERF transcription factors (e.g., PbERF22), which respond to both hormones and enhance the activation of anthocyanin biosynthetic genes by MYB factors [101,102].

Anthocyanin content directly affects fruit coloration, nutritional value, and consumer appeal [103]. Environmental and hormonal regulation can be harnessed to optimize fruit color and quality, as seen in apples, grapes, and other fruit crops [104]. This has direct implications for breeding programs and post-harvest management to maximize commercial value.

5. Functions of Anthocyanins

The multifunctional roles of anthocyanins in higher plants and humans are graphically summarized in Figure 2. In plant systems, anthocyanins contribute to pigmentation and signal attraction, enhance abiotic stress resistance, and provide photoprotective and antioxidant defenses. These physiological roles are closely linked to their ability to scavenge reactive oxygen species and filter excessive light, particularly under environmental stress such as high irradiance, drought, and low temperatures.

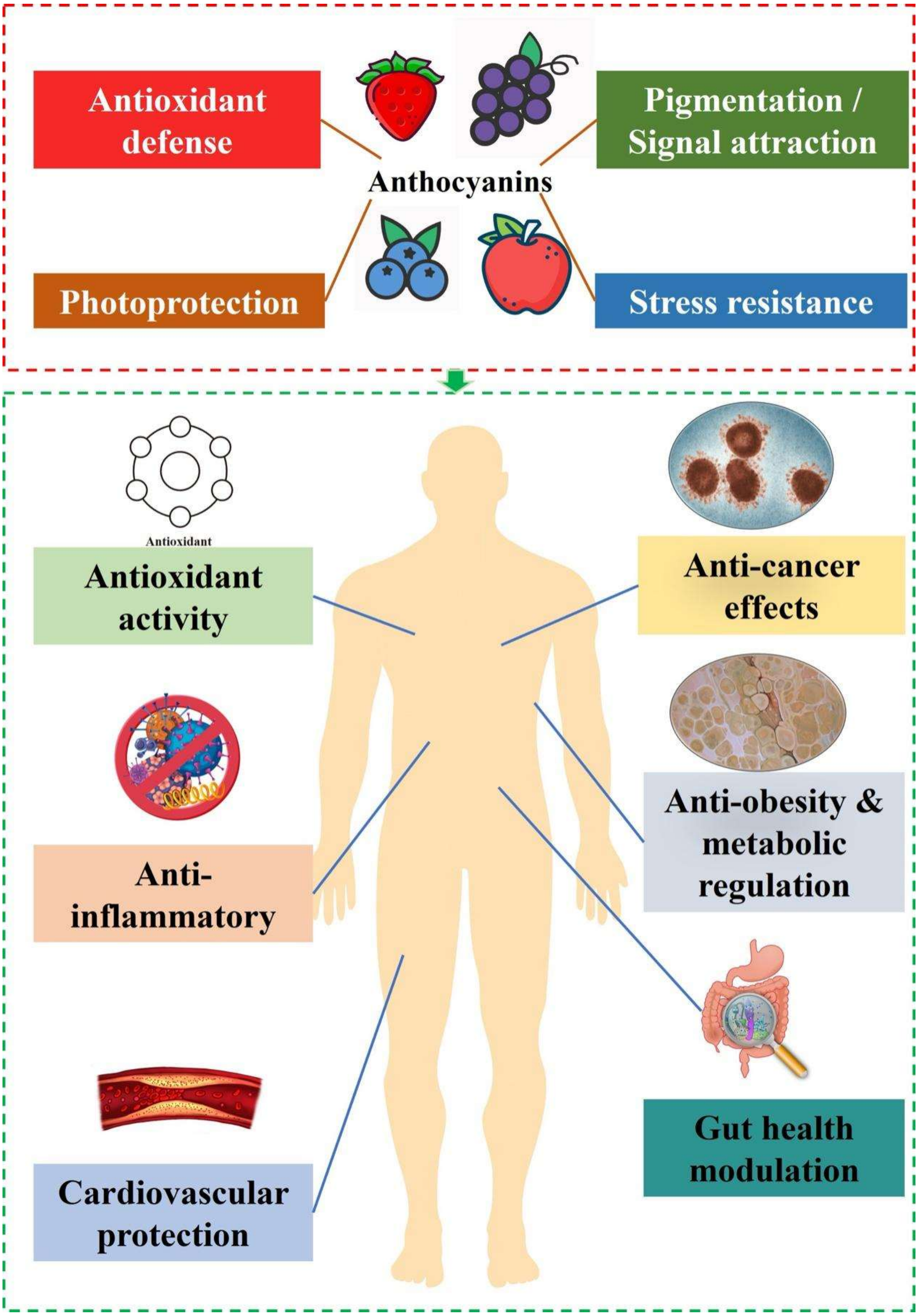

Figure 2. The multifunctional roles of anthocyanins in higher plants and human health.

In human health, anthocyanins exert pleiotropic biological effects, including antioxidant, anti-inflammatory, and anti-cancer activities. They have also been associated with cardiovascular protection, metabolic regulation, and gut microbiota modulation. These effects are mediated through multiple cellular pathways, such as suppression of oxidative stress and inflammation, regulation of lipid metabolism, and maintenance of intestinal barrier integrity. Collectively, these findings underscore the conserved and systemic significance of anthocyanins across biological kingdoms, highlighting their relevance as both functional phytochemicals and nutritional therapeutics.

5.1. Biological Functions of Anthocyanins in Higher Plants

5.1.1. Anthocyanins in Abiotic Stress Tolerance

As a class of flavonoid pigments widely distributed in higher plants, anthocyanins have been extensively implicated in modulating plant growth and enhancing tolerance to abiotic stress. A comprehensive meta-analysis encompassing over 100 studies revealed that anthocyanin accumulation is significantly induced under a range of abiotic stress conditions, including exposure to heavy metals, drought, and ultraviolet (UV) radiation [105]. The elevated levels of anthocyanins are strongly correlated with enhanced stress resistance in plants, particularly in genetically modified lines overexpressing key anthocyanin biosynthetic regulators, such as R2R3-MYB transcription factors. These transgenic plants exhibited up to a 5.8-fold increase in anthocyanin content, accompanied by improved tolerance to oxidative stress through upregulation of protective compounds such as glutathione and proline, both essential for maintaining redox homeostasis and cellular integrity [105].

The primary mechanism underlying anthocyanin-mediated stress tolerance involves reactive oxygen species (ROS) homeostasis. Field-grown plants frequently encounter multiple abiotic stressors that induce ROS production. While moderate ROS levels serve as signaling molecules activating stress-tolerance pathways, excessive accumulation causes oxidative cellular damage. Plants respond by upregulating anthocyanin biosynthesis genes through ROS signaling cascades, with the resulting anthocyanins functioning as potent antioxidants that neutralize excess ROS and restore cellular redox balance [106].

This antioxidant capacity has been validated across diverse stress conditions and plant species. Under low-temperature stress, Mikania micrantha exhibited enhanced antioxidant capability and cold tolerance, with red leaves and stems containing higher anthocyanin concentrations demonstrating superior antioxidant activity [107]. Similarly, in vitro and in vivo studies using anthocyanins from black chokeberry (Aronia melanocarpa) and purple potato (Solanum tuberosum cv. 'Purple Majesty') consistently showed superior antioxidant properties compared to conventional antioxidant compounds [108,109]. These findings underscore the multifunctional role of anthocyanins in enhancing plant growth and resilience under abiotic stress. Their combined effects in ROS detoxification and photoprotection render anthocyanin biosynthetic pathways promising targets for genetic manipulation aimed at improving crop stress tolerance and productivity.

Recent studies confirm that while genetic manipulation of anthocyanin pathways is feasible, field-level stability [110], environmental sensitivity [111], metabolic trade-offs [112], and regulatory hurdles [111] remain major obstacles. Translational research and improved biotechnological strategies are needed before widespread agricultural application is possible.

5.1.2. Anthocyanin-Mediated Photoprotection

Additionally, mechanistic studies in Arabidopsis thaliana have revealed the dual protective roles of anthocyanins. On one hand, their strong radical-scavenging activity contributes to the alleviation of oxidative stress. On the other hand, under high light conditions, their primary photoprotective function is mainly attributed to their capacity to attenuate excessive light, rather than solely to their antioxidant properties. Notably, plants exhibiting enhanced anthocyanin-mediated light absorption showed substantial resistance to photooxidative damage, even when the intrinsic antioxidant system alone was insufficient to prevent cellular injury [113].

Anthocyanins accumulate within the vacuoles of epidermal and sub-epidermal leaf cells, where they effectively absorb visible light wavelengths, particularly green and blue light, as well as portions of ultraviolet radiation. This selective light absorption reduces excess photon penetration into mesophyll cells, thereby alleviating excitation pressure on photosystem II and preventing photoinhibition and photobleaching phenomena. This "light-screening" mechanism is widely recognized as the primary photoprotective function of anthocyanins in plant tissues [114].

Photoreceptors such as UVR8, phytochromes, and cryptochromes perceive wavelength-specific light signals and activate transcription factors (e.g., HY5, MYB, and bHLH). These regulators then upregulate anthocyanin biosynthetic genes, promoting anthocyanin accumulation and enhancing plant adaptation to high-light conditions [115,116].

Anthocyanins are predominantly accumulated in the epidermal cells of plant tissues. Based on their distribution, it is widely believed that anthocyanins function as filters of visible and ultraviolet light, thereby alleviating light-induced stress in plants. For example, in Castanopsis fissa, anthocyanins were found in the trichomes of young leaves, forming a red coating that helped protect the leaves from severe light-induced photoinhibition [117]. Anthocyanins exhibit two characteristic absorption peaks: one in the ultraviolet region (270–290 nm) and another in the visible region (500–550 nm), confirming their capacity to absorb both UV and visible light. In many plant species, the accumulation of anthocyanins in young leaves has been proposed as a frontline defense mechanism against excess light exposure [118–120].

Recent experimental studies have advanced the understanding of anthocyanin-mediated photoprotection in woody plant leaves, particularly under low temperature and high light conditions. In transgenic apple plants overexpressing the MdMYB10 gene, enhanced anthocyanin accumulation in leaves led to increased absorption of visible light, especially in the green region, effectively reducing photoinhibition under intense light exposure. However, this photoprotection came at the cost of reduced photosynthetic capacity, indicating a trade-off between light shielding and carbon assimilation [114].

In Arabidopsis thaliana, physiological and biochemical analyses of lines with varying anthocyanin content demonstrated that the light-attenuating function of anthocyanins is more critical for photoprotection under prolonged high light than their antioxidant capacity. Mutants deficient in anthocyanin biosynthesis (ANS-deficient) exhibited greater sensitivity to high light, with lower chlorophyll content, reduced F_v/F_m ratios, and increased oxidative damage, despite elevated antioxidant activity. This suggests that anthocyanins primarily protect the photosynthetic apparatus by filtering excess light when non-photochemical quenching (NPQ) is insufficient [113, 121].

Seasonal studies in subtropical tree species further revealed that anthocyanin accumulation in young leaves during winter compensates for limited NPQ, providing an alternative photoprotective mechanism. Red leaves with high anthocyanin content showed improved recovery of photosynthetic efficiency after high-light stress compared to green leaves, supporting the functional advantage of anthocyanin-mediated light attenuation under cold, high-irradiance conditions [122].

In addition to their role in leaves, anthocyanins have also been shown to protect fruit tissues. For instance, in harvested pears, light stress treatments revealed that higher anthocyanin content in the peel was associated with reduced light-induced inhibition [123].

5.1.3. Anthocyanins in Biotic Stress Resistance

Anthocyanins contribute to biotic stress resistance at multiple levels, including herbivore defense, postharvest protection, and plant–microbiome interactions.

Anthocyanins have been shown to play a role in disease and pest resistance in higher plants. As early as 2006, Karageorgou and Manetas found that anthocyanins might protect red leaves either by making them less visible to herbivorous insects or by making the herbivores feeding on them more visible to predators. One possible mechanism is that the accumulation of anthocyanins masks the strong green reflectance of chlorophyll, thereby altering insect perception [124].

In postharvest fruits, anthocyanins have demonstrated benefits for storage and shelf life. Tomatoes are known to decay easily due to over-ripening and susceptibility to pathogens [125]. Anthocyanins, as a subclass of flavonoids with potent antioxidant and antimicrobial properties, have emerged as key metabolites in plant defense against biotic and abiotic stresses during the postharvest stage. Their accumulation in various crop species has been closely associated with enhanced resistance to pathogenic infections, low-temperature injury, and insect herbivory, thereby contributing significantly to the maintenance of food quality and the extension of shelf life.

Besides, recent metagenomic and 16S rRNA sequencing studies provide direct evidence that anthocyanin accumulation in plants can alter the composition of associated microbial communities: In Medicago truncatula, a mutant with elevated anthocyanin levels (purple leaves) showed a significant increase in the abundance of endophytic lactic acid bacteria in the phyllosphere. This shift was confirmed by 16S rRNA amplicon sequencing [126]. Mechanistically, anthocyanin accumulation reduced reactive oxygen species (ROS) in plant tissues, creating a more favorable environment for facultative anaerobic bacteria such as lactic acid bacteria. In vitro experiments further demonstrated that anthocyanins directly promoted the growth of these bacteria under anaerobic conditions [126].

5.1.4. Genetic Manipulation of Anthocyanin Biosynthesis

In Camellia sinensis (tea plant), infection by Colletotrichum spp. (the causal agent of anthracnose) induces the biosynthesis of anthocyanin-3-O-galactoside, which accumulates visibly as a “pink ring” around necrotic lesions. This metabolite functions as a phytoalexin, and its production is regulated by a set of structural and regulatory genes, including CsF3Ha, CsANSa, and CsMYB113. Functional studies have confirmed that manipulation of these genes can significantly enhance resistance to anthracnose, underscoring the defensive role of inducible anthocyanin biosynthesis pathways [127]. In Malus spp. (apple), ectopic expression of transcription factors MpERF105 and MpNAC72 has been shown to activate the anthocyanin regulatory gene MpMYB10b, resulting in increased anthocyanin accumulation in leaves and improved resistance to rust disease. These findings demonstrate the efficacy of transcription factor-based genetic engineering strategies for augmenting anthocyanin-mediated disease resistance [128]. Lettuce (Lactuca sativa) provides further evidence of this relationship. Genome-wide association studies (GWAS) have revealed that red and dark red cultivars, characterized by elevated anthocyanin content, exhibit a markedly lower incidence of Sclerotinia minor infection. Notably, resistance-associated QTLs frequently co-localize with anthocyanin biosynthetic loci such as RLL2 and ANS, suggesting pleiotropic or tightly linked genetic control of both traits [129]. Similar patterns have been observed in Brassica juncea (Indian mustard), where anthocyanin-rich genotypes and mutants display earlier and more robust antioxidant responses upon infection with Sclerotinia sclerotiorum. These lines show reduced lesion expansion and lower levels of lipid peroxidation, compared to anthocyanin-deficient controls, indicating that anthocyanin-mediated oxidative buffering plays a key role in restricting pathogen spread [130].

5.2. Physiological Functions of Anthocyanins

5.2.1. Antioxidant Activity and Bioavailability Enhancement

Anthocyanins exhibit strong antioxidant activity in both in vitro and in vivo systems, making them promising candidates for application in functional foods and nutraceutical formulations. A growing body of evidence has confirmed their efficacy in scavenging free radicals, mitigating oxidative stress, and conferring protection against inflammation and neurodegenerative processes.

Petunidin-3,5-O-diglucoside, the predominant anthocyanin identified in Lycium ruthenicum Murr. fruit, has demonstrated significant free radical scavenging activity as assessed by DPPH and ABTS assays. Beyond its in vitro antioxidant capacity, this compound effectively attenuated oxidative damage and neuroinflammatory responses in neuronal cell models and aged mice, leading to improved cognitive performance. These findings underscore its dual role as both an antioxidant and a neuroprotective agent [131].

Anthocyanins derived from purple potato (Solanum tuberosum cv. 'Purple Majesty') have similarly shown high DPPH radical scavenging ability and lipid peroxidation inhibition. Mechanistic analyses revealed their capacity to donate hydrogen atoms and stabilize reactive radical species, confirming their molecular basis of antioxidant action [109]. In vivo administration of blueberry anthocyanin extracts to murine models resulted in enhanced systemic antioxidant defenses, as evidenced by elevated total antioxidant capacity, increased activities of superoxide dismutase (SOD) and glutathione peroxidase (GPX), and reduced malondialdehyde (MDA) concentrations—an indicator of lipid peroxidation [132].

Advances in food processing technologies have further improved the functional properties of anthocyanins. Nanoencapsulation of black carrot anthocyanins within chitosan nanoparticles has been shown to enhance their bioavailability and stability, thereby increasing their in vivo antioxidant efficacy compared to non-encapsulated counterparts [133]. In addition, microencapsulation techniques utilizing fructooligosaccharides and whey protein matrices have been successfully applied to anthocyanins from black soybean seed coats. These encapsulated forms exhibited superior digestive stability and antioxidant activity, while also promoting beneficial shifts in gut microbiota composition under simulated gastrointestinal conditions [134].

5.2.2. Cardiovascular Protection

Anthocyanins have demonstrated potential in the prevention and treatment of cardiovascular diseases (CVDs), which remain a leading cause of death and a major threat to global public health. Atherosclerosis is a key pathological process underlying many forms of CVD, including hypertension, coronary artery disease, hyperlipidemia, and myocarditis. The cardioprotective effects of anthocyanins are largely attributed to their antioxidant properties. Wallace et al. [135] reported that anthocyanins may influence cardiovascular health through several mechanisms: (1) modulating nitric oxide (NO) signaling pathways; (2) inhibiting tumor necrosis factor-alpha (TNF-α)-induced monocyte chemoattractant protein-1 (MCP-1) secretion; (3) reducing monocyte adhesion to endothelial cells; and (4) lowering circulating levels of C-reactive protein (CRP), a key marker of inflammation. A systematic review and meta-analysis of randomized controlled trials further confirmed that anthocyanins, whether consumed through food or as purified extracts, significantly improved vascular function. Specifically, they enhanced flow-mediated dilation (FMD) and reduced arterial stiffness, as measured by pulse wave velocity (PWV) [136]. Mechanistically, black currant fruit extracts have been shown to activate endothelial nitric oxide synthase (eNOS) via a redox-sensitive PI3K/Akt signaling pathway. This activation promotes the biosynthesis of nitric oxide (NO), a potent vasodilator that plays a critical role in ameliorating endothelial dysfunction [137]. These findings support the role of anthocyanins as natural agents for cardiovascular protection and highlight their potential in functional foods or nutraceutical interventions aimed at reducing CVD risk.

5.2.3. Anti-inflammatory Effects and Immune Modulation

Anthocyanins, beyond their antioxidant properties, have been increasingly recognized for their anti-inflammatory potential, which is mediated through multiple molecular pathways. Accumulating clinical and experimental evidence supports their application as bioactive compounds in functional foods for the prevention and management of chronic inflammation-related diseases.

Clinical trials have demonstrated that anthocyanin supplementation in individuals with dyslipidemia and metabolic syndrome elicits significant reductions in systemic inflammatory markers, including interleukin-6 (IL-6), tumor necrosis factor-α (TNF-α), and C-reactive protein (CRP), as well as oxidative stress biomarkers such as malondialdehyde (MDA) and 8-iso-prostaglandin F2α. These improvements are accompanied by enhanced activities of endogenous antioxidant enzymes and favorable modulation of lipid metabolism [138,139].

At the molecular level, anthocyanins exert anti-inflammatory effects primarily through inhibition of the nuclear factor-kappaB (NF-κB) signaling pathway. This leads to downregulation of key pro-inflammatory genes, including those encoding cyclooxygenase-2 (COX-2) and inducible nitric oxide synthase (iNOS), at both mRNA and protein levels. In vitro experiments using macrophage and intestinal epithelial cell models have revealed that anthocyanin-rich extracts from red clover, purple vegetables, and banana bract effectively attenuate nitric oxide (NO) production, suppress prostaglandin E2 (PGE2) biosynthesis, and reduce the secretion of pro-inflammatory cytokines by modulating NF-κB and mitogen-activated protein kinase (MAPK) signaling cascades [140–142].

In addition to these direct effects on inflammatory mediators, anthocyanins influence the gut environment by modulating the composition of gut microbiota and enhancing intestinal barrier integrity. These effects contribute to systemic anti-inflammatory responses and underscore the role of gut–immune interactions in mediating the bioactivity of anthocyanins [143].

Experimental evidence further supports these findings. Anthocyanins from purple sweet potato were shown to suppress the expression of inflammatory cytokine mRNAs, thereby exerting anti-inflammatory effects. In black soybean seed coats, anthocyanins inhibited lipopolysaccharide (LPS)-induced production of pro-inflammatory mediators in BV2 microglial cells by downregulating the overexpression of relevant enzymes [144].

Moreover, petunidin glucosides isolated from Lycium ruthenicum were found to alleviate dextran sulfate sodium (DSS)-induced colitis in mice by blocking pro-inflammatory cytokines, enhancing the expression of tight junction proteins, and modulating gut microbiota composition [145]. These results underscore the therapeutic potential of anthocyanins, particularly in the form of purified monomeric compounds, for managing inflammatory conditions.

5.2.4. Anti-obesity and Metabolic Regulation

Obesity is a serious health concern and a major risk factor for cardiovascular diseases, cancer, and respiratory disorders. It has been extensively documented that anthocyanins combat obesity by reducing body fat accumulation and modulating lipid metabolism.

For example, anthocyanins extracted from purple sweet potato were found to inhibit fat formation and promote lipolysis. Studies demonstrated that these compounds suppressed the growth of lipid droplets by decreasing leptin secretion, reducing adipocyte size, and lowering the accumulation of free fatty acids. They also downregulated the expression of lipogenic genes, including fatty acid synthase (FAS), lipoprotein lipase (LPL), and acetyl-CoA synthetase, while enhancing lipolytic activity [146].

In another study, four-week-old C57BL/6 mice fed a high-fat diet and supplemented with blueberry and mulberry juice for 12 weeks exhibited reduced body weight gain, attenuated lipid accumulation, and decreased serum cholesterol levels. These effects were associated with the downregulation of fatty acid biosynthesis-related genes such as PPARγ and FAS, and upregulation of β-oxidation–related genes like CPT1 [147].

Anthocyanins have garnered considerable attention for their potential to combat obesity and prevent cancer through multifaceted mechanisms involving metabolic regulation, inflammatory suppression, and modulation of gut microbiota. Recent advances in both in vitro and in vivo studies support their efficacy as bioactive constituents in functional foods aimed at preventing metabolic disorders and tumorigenesis. In obesity models, anthocyanin-rich extracts derived from pigmented crops such as Cheongchunchal corn and color-fleshed sweet potatoes have been shown to inhibit adipocyte differentiation and lipid accumulation in 3T3-L1 preadipocytes. These extracts also attenuate body weight gain and improve serum lipid profiles in high-fat diet (HFD)-induced obese mice. These physiological benefits are associated with enhanced phosphorylation of AMP-activated protein kinase (AMPK) and suppression of key adipogenic transcription factors, including peroxisome proliferator-activated receptor-γ (PPARγ) and CCAAT/enhancer-binding proteins (C/EBPs), suggesting a conserved mechanism of anthocyanin-mediated metabolic control [148,149]. Beyond direct metabolic effects, anthocyanins also modulate the composition and activity of the gut microbiota, which plays a critical role in obesity pathogenesis. Animal studies have demonstrated that anthocyanin supplementation reduces obesity-associated dysbiosis and chronic low-grade inflammation, while improving gut barrier function and systemic energy balance. These observations support the emerging view of anthocyanins as prebiotic-like agents that contribute to metabolic homeostasis through host–microbe interactions [150,151]. In addition, anthocyanins have been reported to modulate key signaling pathways involved in lipid and glucose metabolism, such as Wnt/PPAR and PI3K/Akt, which further contribute to their anti-obesity and metabolic regulatory effects [152,153].

5.2.5. Anti-cancer Properties and Mechanistic Insights

In the context of cancer prevention, particularly colorectal cancer, anthocyanins exhibit chemopreventive effects by targeting pathways involved in cell cycle regulation, apoptosis induction, and inflammatory signaling. Diets enriched with anthocyanin-containing fruits and vegetables have been shown to suppress tumor formation and progression in experimental models. Mechanistically, these effects are attributed to the modulation of key molecular targets such as NF-κB, COX-2, and caspases, which govern inflammatory responses and programmed cell death [154].

These compounds exert their anti-carcinogenic effects by promoting apoptosis, arresting the cell cycle, inhibiting abnormal epithelial proliferation, and suppressing inflammation and oxidative stress pathways. In addition, anthocyanins from strawberries have been shown to inhibit the proliferation and metastasis of breast cancer cells, ultimately inducing apoptosis [155]. The anti-cancer potential of anthocyanins and their structural derivatives has become a focal point in phytochemical and functional food research, with mounting evidence supporting their efficacy against various malignancies, including cervical cancer. Comparative analyses of different anthocyanin derivatives have revealed distinct variations in bioactivity and chemical stability, highlighting the importance of structural optimization for therapeutic applications.

A study investigating the anti-cancer properties of blueberry-derived anthocyanins (glycosides), anthocyanidins (aglycones), and pyranoanthocyanidins (structurally modified derivatives) in HeLa cervical cancer cells demonstrated that anthocyanidins exhibit the most potent cytotoxic effects among the three pigment types [6]. These compounds significantly inhibited cancer cell proliferation, induced cell cycle arrest at the G2/M phase, and promoted late-stage apoptosis. These cellular responses were accompanied by an upregulation of the tumor suppressor protein p53 and were mechanistically linked to the activation of the p38 mitogen-activated protein kinase (MAPK)/p53 signaling pathway. Notably, pyranoanthocyanidins exhibited superior structural stability across a broad pH range, underscoring their potential as food-grade anti-cancer agents with enhanced physicochemical robustness [156].

Expanding beyond cervical cancer models, numerous in vitro and in vivo studies have demonstrated that anthocyanins and their derivatives impede tumorigenesis by suppressing cellular proliferation, inhibiting migration and invasion, and inducing apoptosis through modulation of key intracellular pathways, including MAPK and PI3K/Akt [157]. These compounds can downregulate oncogenes and simultaneously enhance the expression of tumor suppressor genes, thereby exerting a dual regulatory effect on cancer progression.

5.2.6 Gut Microbiota Metabolites in Regulating the Health Benefits of Anthocyanins

Recent studies indicate that gut microbiota-derived metabolites act as critical mediators of the health-promoting effects of anthocyanins. Since anthocyanins are largely unabsorbed in the upper gastrointestinal tract, they undergo extensive microbial metabolism in the colon, generating a range of bioactive compounds, including short-chain fatty acids (SCFAs), bile acids, indoles, and phenolic acids [134,158,159]. SCFAs such as acetate, propionate, and butyrate contribute to intestinal barrier maintenance, immune modulation, and systemic metabolic regulation, and have been linked to protection against obesity, diabetes, and cardiovascular disease [158,159]. Alterations in bile acid metabolism induced by anthocyanin-mediated changes in gut microbial composition further influence lipid and glucose homeostasis as well as inflammatory processes [158]. In addition, shifts in tryptophan metabolism can enhance the production of indole derivatives, which support barrier function, regulate host immunity, and exert potential neuroprotective effects via the gut–brain axis [159]. Collectively, these findings support the concept of an anthocyanin–microbiota–metabolite axis, in which anthocyanins reshape microbial communities (e.g., enrichment of Bifidobacterium and Lactobacillus) while microbial metabolism enhances the bioavailability and biological activity of anthocyanin-derived metabolites [134,158–160]. This bidirectional interaction highlights that many of the physiological effects attributed to anthocyanins may, in fact, be mediated by their microbial metabolites rather than the parent compounds [159–162].

6. Conclusions

Anthocyanins are multifunctional secondary metabolites that play critical roles in plant physiology and offer considerable health benefits in humans. Extensive studies have elucidated their biosynthetic pathways, transport mechanisms, regulatory networks, and bioactivities, highlighting their involvement in stress tolerance, pigmentation, and disease resistance. In humans, anthocyanins have demonstrated potent antioxidant, anti-inflammatory, cardioprotective, antidiabetic, and anticancer properties, supporting their application in functional foods and pharmaceuticals. Despite substantial progress, gaps remain in our understanding of their intracellular trafficking, environmental responsiveness, and molecular regulation. Continued exploration of these mechanisms, alongside the application of advanced biotechnological tools, will enable more precise manipulation of anthocyanin pathways for crop improvement and the development of anthocyanin-enriched nutraceuticals.

7. Perspective

Anthocyanins are bioactive compounds that contribute significantly to plant growth and development, while also offering considerable health benefits to humans and animals. Although the antioxidant structure of anthocyanins has been well characterized, the precise molecular mechanisms underlying their antioxidant functions in plants remain largely unknown. Current studies have primarily focused on anthocyanins extracted from plant tissues or applied exogenously to model systems. However, in vivo functions of anthocyanins are often influenced by other physiological and environmental factors, and their broader biological roles in promoting plant adaptation and survival under natural conditions warrant further investigation.

Anthocyanins are widely recognized as important dietary antioxidants, and numerous studies have explored their clinical potential. Despite the identification of multiple pharmacological effects, the molecular signaling pathways responsible for these functions are still poorly understood. Therefore, elucidating how to effectively harness and enhance the bioactivity of anthocyanins remains an important research challenge.

Although the biosynthetic pathway of anthocyanins has been extensively studied, the process is highly complex and not yet fully understood. Investigations into anthocyanin transport and transcriptional regulation are still in their early stages. While it is established that anthocyanins are synthesized in the cytoplasm and transported to the vacuole, little is known about their transport dynamics beyond this step—such as efflux from vacuoles, intercellular movement, and trafficking to specific subcellular compartments like the nucleus or chloroplast. Moreover, long-distance transport mechanisms of anthocyanins within the plant are still largely unexplored.

The accumulation of anthocyanins is regulated not only by intrinsic genetic factors but also by environmental cues such as temperature, light intensity, and sugar availability. However, the molecular mechanisms by which these external factors influence anthocyanin biosynthesis are not well characterized. It also remains unclear whether other, yet unidentified, environmental stimuli may affect anthocyanin production. Therefore, future studies should focus on the integrated regulation of anthocyanin biosynthesis by both internal and external factors, as well as the crosstalk between them.

Furthermore, research on anthocyanin stability and degradation is limited, and the regulatory mechanisms governing anthocyanin-degrading genes are poorly understood. Modern biotechnological tools such as genome editing, high-throughput sequencing, transcriptomics, and proteomics should be employed to advance this field. A comprehensive understanding of anthocyanin biosynthesis, modification, transport, and degradation, as well as its interaction with other metabolic pathways and environmental stimuli, will provide a theoretical basis for the genetic improvement of anthocyanin-rich plant varieties and promote their application in agriculture and health-related industries.

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