



Review

Advances in Purple Tea Research: Chemical Compositions, Anthocyanin Synthesis and Regulation, Processing, and Health Benefits

Meihong Yan ^{1,2,†}, Xiangxiang Huang ^{1,2,†}, Nianci Xie ^{1,2}, Tiyue Zhao ^{1,2}, Mingzhi Zhu ^{1,2} , Juan Li ^{1,2,*} and Kunbo Wang ^{1,2,3,*}

¹ National Research Center of Engineering and Technology for Utilization of Botanical Functional Ingredients & Co-Innovation Center of Education Ministry for Utilization of Botanical Functional Ingredients, Hunan Agricultural University, Changsha 410128, China; yan1446293914@163.com (M.Y.); xiangxianghuang111@163.com (X.H.); xienc2020@163.com (N.X.); zhaotiyue@gmail.com (T.Z.); mzzhucn@hotmail.com (M.Z.)

² Key Laboratory of Tea Science of Ministry of Education, Hunan Agricultural University, Changsha 410128, China

³ Key Laboratory for Evaluation and Utilization of Gene Resources of Horticultural Crops, Changsha 410125, China

* Correspondence: xixi_lj@126.com (J.L.); wangkunbo@hunau.edu.cn (K.W.)

† These authors contributed equally to this work.

Abstract: Purple tea, renowned for its anthocyanin content and distinctive purple hue, has gained prominence. The anthocyanin content in purple tea can exceed three times that of traditional green-leaf tea. Purple tea harbors various anthocyanins, implicating intricate pathways of biosynthesis and transcriptional regulation. Concurrently, owing to its distinctive chemical composition, the processing of purple tea may be constrained, potentially influencing the sensory attributes and flavor profile of the tea. The richness of anthocyanins in purple tea has yielded potential health benefits, including antioxidative and anti-cancer properties, rendering purple tea a sought-after commodity in the tea market. However, current research on purple tea remains incomplete, including indistinct networks of anthocyanin biosynthesis and regulatory mechanisms, incomplete chemical characterization, and a need for comprehensive investigations into its biological activities. The limited research foundation has greatly reduced the popularity and consumption of purple tea. This paper aims to provide an overview of recent advancements in the biosynthesis and regulation of anthocyanins, as well as the chemical compositions, processing, and health benefits of purple tea. This review will provide the groundwork for future efforts in the selection and innovation of purple tea germplasm, purple tea processing, and the expansion of the market for purple tea consumption.

Keywords: purple tea; anthocyanins; chemical compositions; processing; health benefit



Citation: Yan, M.; Huang, X.; Xie, N.; Zhao, T.; Zhu, M.; Li, J.; Wang, K. Advances in Purple Tea Research: Chemical Compositions, Anthocyanin Synthesis and Regulation, Processing, and Health Benefits. *Horticulturae* **2024**, *10*, 50. <https://doi.org/10.3390/horticulturae10010050>

Academic Editor: Jianyun Ruan

Received: 10 November 2023

Revised: 18 December 2023

Accepted: 20 December 2023

Published: 4 January 2024



Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Tea, one of the world's top three non-alcoholic beverages, holds a significant place as a cash crop [1]. Tea plants possess a wealth of germplasm resources. In recent years, the discovery of a unique tea plant variety known as purple tea has captured the attention of numerous scientists. Purple tea stands out due to its striking purple appearance and high anthocyanin content, making it noteworthy for both ornamental and health-related purposes. Anthocyanins are widely present in tea plants, with the highest accumulation observed in purple tea, directly proportional to the intensity of its purple color [2]. The purple transformation of tea plants can be attributed to two primary factors. Firstly, the accumulation of anthocyanins in the bud and leaf tissues occurs as a response to adverse environmental conditions such as strong light and low temperatures. Secondly, a genetic factor leads to the accumulation of substantial amounts of anthocyanins, resulting in the

red–purple coloration characteristic of high-anthocyanin germplasm like Zijuan [3]. The characteristics of purple tea involve the deep purple coloration of the buds and the first three young leaves, while the fourth and fifth young leaves exhibit a lighter shade of purple. The older leaves beneath gradually transition to green, resembling other green-leaf varieties [4]. Moreover, the degree of purple pigmentation in purple tea is intricately linked to environmental factors. During spring, the purple buds exhibit a light purple hue, but as summer advances, accompanied by heightened ultraviolet radiation, most purple tea leaves acquire a deeper purple color. In autumn, the intensity of purple diminishes due to reduced or halted anthocyanin biosynthesis and the extent of anthocyanin degradation.

China, Japan, and Kenya have achieved significant research and promotion results in purple tea. Currently, widely cultivated purple tea varieties include TRFK306 [5], Sunrouge [6], Zijuan, and Ziyun [7], among others. The process of selecting and breeding high anthocyanin tea tree varieties continues to advance. Recent years have witnessed the identification of several exceptional purple tea cultivars, including Hongyafoshou [8], Jinmingzao [9], and Wuyiqizhong [10] from Fujian, Zikui [11] and Dachang P113 [12] from Guizhou, Self-selected 9803 [13] from Hunan, Zixin [14] from Shandong, Benibana-cha [15] from Japan, ACNs [16] from Kenya, and various unnamed high anthocyanin tea plant varieties were discovered across diverse geographical regions. These cultivars have been investigated to offer an expanded scope for comprehensive research into the realm of purple tea.

With the advancement of biotechnology, purple tea has become a prominent focus of economic plant research. Numerous studies have delved into the metabolic, genomic, and transcriptomic functions of compounds in purple tea. Additionally, the metabolism and differential regulation of anthocyanins in tea plants have been thoroughly reviewed [17]. However, limited attention has been paid to exploring the bioactivity of purple tea. Furthermore, the unique bitter taste of anthocyanins has a great adverse effect on purple tea products, so traditional tea-making processes do not adequately enhance the quality of purple tea or tailor its varieties to meet consumer preferences. As a result, there is a shortage of popular purple tea products in the market, hindering its promotion. Therefore, it is necessary to have a comprehensive understanding of the characteristics of purple tea. In this paper, the existing research on purple tea was summarized for the first time, including the differences in chemical compositions of purple tea, the synthesis and regulation of anthocyanins in purple tea, and the biological activity of purple tea. Additionally, a comparative analysis of various teas derived from purple tea has been conducted, encompassing aspects of flavor and consumer preferences. This review contributes to the formulation of strategies aimed at enhancing the diversity of purple tea varieties and establishing a theoretical framework for advancing the economic prospects of purple tea within the market.

2. The Chemical Compositions of Purple Tea

The chemical compositions within the tea plant exhibit a consistent similarity, yet what distinguishes the various purple tea varieties prominently is the anthocyanin levels. Purple tea has numerous varieties of anthocyanins, each imparting a distinct hue. Current analytical and identification techniques have demonstrated proficiency in the successful isolation of anthocyanins from tea plants. Furthermore, shifts in the concentrations of other chemical constituents, such as fluctuations in flavonoid levels triggered by variations in anthocyanin content and variations in amino acid content influencing tea flavor, have garnered the scientific community's attention.

2.1. Anthocyanins in Purple Tea

Anthocyanins are widely present in tea plants, with purple tea exhibiting three times higher anthocyanin content than conventional tea plant varieties [18]. The types of anthocyanin glycosides in tea plants vary significantly depending on the tea plant cultivar, and the content of anthocyanin glycosides also differs considerably based on the maturity level of the fresh leaves. In high-anthocyanin tea plants, the main anthocyanins consist

of delphinidin, cyanidin, pelargonidin, and their glycosides [19,20]. Recently, petunidin has been identified as the fourth major anthocyanin in tea plants [21]. Multiple regulatory mechanisms contribute to anthocyanin accumulation, including variations in precursor levels, expression of structural genes, and transcription factor genes. Furthermore, anthocyanin content varies significantly among different tea plant cultivars due to varietal characteristics and environmental factors [22], which accounts for the observed differences in anthocyanin pigmentation in tea buds and leaves.

The currently promoted purple tea cultivars exhibit significant variations in the proportions of different anthocyanins [23]. Four anthocyanins (delphinidin-3-O-β-D-galactoside, cyanidin-3-O-β-D-galactoside, delphinidin-3-O-β-D-(6-(E)-p-coumaroyl) galactopyranoside, and cyanidin-3-O-β-D-(6-(E)-p-coumaroyl) galactopyranoside) were isolated from Zijuan tea [19]. Studies conducted by Lai et al. [20] have indicated that delphinidin, cyanidin, and pelargonidin, but no other anthocyanin pigments were detected in Ziyan, and delphinidin was particularly predominant. In Kenyan purple tea TPFK306, malvidin exhibited the highest accumulation [5]. Saito et al. [6] used chromatography, LC-MS/MS, and NMR techniques to analyze and identify six anthocyanins from Japanese red-leaf tea “Sunrouge”: delphinidin-3-O-β-D-(6-(E)-p-coumaroyl) galactopyranoside; delphinidin-3-O-β-D-(6-(E)-p-coumaroyl) glucopyranoside; cyanidin-3-O-β-D-(6-(E)-p-coumaroyl) galactopyranoside; cyanidin-3-O-β-D-(6-(E)-p-coumaroyl) glucopyranoside; delphinidin-(Z)-p-coumaroylgalactopyranoside; and petunidin-(E)-p-coumaroylgalactopyranoside. Tan et al. [24] found that delphinidin was the main pigment responsible for the seasonal differences in anthocyanins and a major component responding to environmental changes. Table 1 lists the anthocyanin components measured by different detection methods in recent years. In light of the present investigation, it is evident that the methodologies for isolating anthocyanins from purple tea have become more diverse and efficacious. Concurrently, enhancements in the identification of anthocyanin compounds have been achieved. Nevertheless, the underlying factors contributing to the divergent distribution of anthocyanins necessitate further exploration, particularly through transcriptional regulatory analysis.

Table 1. Anthocyanin compounds of purple tea.

Samples	Detection Method	Anthocyanin Compounds	References
Zijuan from Yunnan Province	HPLC, LC-ESI-MS	Delphinidin-3-O-β-D-galactoside, Cyanidin-3-O-β-D-galactoside, Delphinidin-3-O-β-D-(6-(E)-p-coumaroyl) galactopyranoside, Cyanidin-3-O-β-D-(6-(E)-p-coumaroyl) galactopyranoside	[19]
Zijuan from Yunnan Province	HPLC and LC-MS	Pelargonidin-3,5-diglucoside, Cyanidin-3-O-galactoside, Cyanidin-3-O-glucoside, Delphinidin, Cyanidin, Pelargonidin, Peonidin, Malvidin	[25]
Zijuan from different provinces of China (Yunnan, Qijiang, and Ersheng)	UPLC-ESI-MS/MS	Delphinidin-3-O-sambubioside-5-O-glucoside, Delphinidin-3-O-(6-O-malonyl-beta-D-glucoside), Delphinidin-3-O-(6-O-p-coumaroyl)-glucoside, Delphinidin-3-O-galactoside, Delphinidin-3-O-glucoside, Delphinidin-3-O-rutinoside, Delphinidin-3,5-O-diglucoside, Delphinidin-3-O-rutinoside-5-O-glucoside, Delphinidin-3-O-sophoroside, Delphinidin, Cyanidin-3-(6-O-p-caffeoyl)-glucoside, Cyanidin-3-O-xyloside, Cyanidin-3-O-rutinoside, Cyanidin-3-O-(6-O-p-coumaroyl)-glucoside, Cyanidin-3-O-galactoside, Cyanidin-3-O-arabioside, Cyanidin-3-O-glucoside, Pelargonidin-3-O-(6-O-p-coumaroyl)-glucoside, Pelargonidin-3-O-arabioside, Pelargonidin-3,5-O-diglucoside, Pelargonidin-3-sophoroside-5-glucoside, Pelargonidin-3-O-galactoside, Pelargonidin-3-O-rutinoside, Pelargonidin-3-O-sambubioside-5-O-glucoside, Peonidin-3-O-(6-O-p-coumaroyl)-glucoside, Peonidin-3-O-rutinoside, Peonidin-3-O-arabioside, Peonidin-3,5-O-diglucoside, Petunidin-3-O-sambubioside-5-O-glucoside, Petunidin-3-O-arabioside, Petunidin-3-O-glucoside, Petunidin-3-O-sambubioside, Petunidin-3-O-galactoside, Malvidin-3-O-galactoside	[26]

Table 1. Cont.

Samples	Detection Method	Anthocyanin Compounds	References
Ziyan from Sichuan Province	HPLC	Delphinidin, Cyanidin, Pelargonidin	[20]
Chuanzi 3 (ZZ), Zijuan, Ziyan from Sichuan Province	UPLC-ESI-MS/MS	Cyanidin-3-(6- <i>O</i> - <i>p</i> -caffeoyl)-glucoside, Cyanidin-3,5- <i>O</i> -diglucoside, Cyanidin-3- <i>O</i> -arabinoside, Cyanidin-3- <i>O</i> -galactoside, Cyanidin-3- <i>O</i> -glucoside, Cyanidin-3- <i>O</i> -rutinoside, Delphinidin, Delphinidin-3,5- <i>O</i> -diglucoside, Delphinidin-3- <i>O</i> -(6- <i>O</i> - <i>p</i> -coumaroyl)-galactoside, Delphinidin-3- <i>O</i> -5- <i>O</i> -(6- <i>O</i> -coumaroyl)-diglucoside, Delphinidin-3- <i>O</i> -galactoside, Delphinidin-3- <i>O</i> -glucoside, Delphinidin-3- <i>O</i> -sophoroside, Pelargonidin-3- <i>O</i> -(6- <i>O</i> - <i>p</i> -coumaroyl)-galactoside, Pelargonidin-3- <i>O</i> -arabinoside, Pelargonidin-3- <i>O</i> -galactoside, Pelargonidin-3- <i>O</i> -glucoside, Peonidin-3- <i>O</i> -(6- <i>O</i> - <i>p</i> -coumaroyl)-glucoside, Peonidin-3- <i>O</i> -galactoside, Petunidin-3- <i>O</i> -arabinoside, Petunidin-3- <i>O</i> -glucoside	[27]
Zikui from Guizhou	UPLC MS/MS ESI-QTRAP-MS/MS	Petunidin 3- <i>O</i> -glucoside, Cyanidin 3- <i>O</i> -galactoside, Cyanidin 3- <i>O</i> -glucosid	[11]
Purple-leaf tea cultivars from Jiangsu Province	UPLC-ESI-MS/MS	Cyanidin 3- <i>O</i> -(6- <i>O</i> -malonyl-beta-D-glucoside), Cyanidin 3- <i>O</i> -arabinoside, Cyanidin 3- <i>O</i> -galactoside, Cyanidin 3- <i>O</i> -glucoside, Delphinidin 3,5- <i>O</i> -diglucoside, Delphinidin 3- <i>O</i> -(6''- <i>O</i> -malonyl)-beta-D-glucoside, Delphinidin 3- <i>O</i> -arabinoside, Delphinidin 3- <i>O</i> -galactoside, Delphinidin 3- <i>O</i> -glucoside, Malvidin 3- <i>O</i> -arabinoside, Malvidin 3- <i>O</i> -galactoside, Malvidin 3- <i>O</i> -glucoside, Pelargonidin 3- <i>O</i> -(6- <i>O</i> -malonyl-beta-D-glucoside), Pelargonidin 3- <i>O</i> -arabinoside, Pelargonidin 3- <i>O</i> -galactoside, Pelargonidin 3- <i>O</i> -glucoside, Pelargonidin 3- <i>O</i> -rutinoside, Peonidin 3- <i>O</i> -glucoside, Peonidin 3- <i>O</i> -arabinoside, Peonidin 3- <i>O</i> -galactoside, Petunidin 3,5-diglucoside, Petunidin 3- <i>O</i> -arabinoside, Petunidin 3- <i>O</i> -galactoside, Petunidin 3- <i>O</i> -glucoside	[28]
Hongyecha, Zijuan, 9803, Hongyafoshou from Hunan Province	(UPLC-DAD-QTOF-MS)	Delphinidin 3- <i>O</i> -galactoside, Cyanidin 3- <i>O</i> -galactoside, Pelargonidin- <i>O</i> -hexose, Pelargonidin- <i>O</i> -dihexose, Delphinidin-(<i>Z</i>)- <i>p</i> -coumaroylgalactoside, Delphinidin-(<i>E</i>)- <i>p</i> -coumaroylgalactoside, Cyanidin-(<i>Z</i>)- <i>p</i> -coumaroylgalactoside	[29]
Jinmingzao from Fujian Province	LC-ESI-MS/MS	Cyanidin 3- <i>O</i> -glucoside, Delphinidin 3- <i>O</i> -glucoside, Peonidin 3- <i>O</i> -glucoside chloride, Cyanidin 3-rutinoside, Cyanidin 3- <i>O</i> -galactoside	[30]
Purple tea leaves from Asilia Inc.	LC-MS/MS	Delphinidin-3-galactoside, Delphinidin-3-glucoside, Cyanidin-3-galactoside, Cyanidin-3-glucoside, Delphinidin-coumaroyl-hexoside isomers 1, 2, and 3, Cyanidin-coumaroyl-hexoside isomers 1 and 2, Petunidin-coumaroyl-hexoside	[21]
Zijuan from Yunnan, Puer TRFK 306 from Kenya	LC-ESI-MS/MS HPLC	Cyanidin 3- <i>O</i> -galactoside, Cyanidin 3- <i>O</i> -glucoside, Delphinidin 3- <i>O</i> -glucoside, Petunidin 3- <i>O</i> -glucoside, Pelargonidin 3- <i>O</i> -glucoside Cyanidin-3- <i>O</i> -galactoside, Cyanidin-3- <i>O</i> -glucoside, Delphinidin, Cyanidin, Pelargonidin, Peonidin, Malvidin	[31] [16]
Purple-colored tea cultivars from Kenya	HPLC-UV-Visible	Delphinidin, Cyanidin, Pelargonidin, Peonidin, Malvidin, Cyanidin-3- <i>O</i> -galactoside, Cyanidin-3- <i>O</i> -glucoside	[5]
Sunrouge from Japan	HPLC, LC/MS/MS, and NMR	Delphinidin-3- <i>O</i> -β-D-(6- <i>E</i>)- <i>p</i> -coumaroyl)galactopyranoside, Delphinidin-3- <i>O</i> -β-D-(6- <i>E</i>)- <i>p</i> -coumaroyl)glucopyranoside, Cyanidin-3- <i>O</i> -β-D-(6- <i>E</i>)- <i>p</i> -coumaroyl)galactopyranoside, Cyanidin-3- <i>O</i> -β-D-(6- <i>E</i>)- <i>p</i> -coumaroyl)glucopyranoside, Delphinidin-(<i>Z</i>)- <i>p</i> -coumaroyl)galactopyranoside, Petunidin-(<i>E</i>)- <i>p</i> -coumaroyl)galactopyranoside	[6]

2.2. Flavonoids in Purple Tea

Tea plant boasts a substantial reservoir of flavonoids. Anthocyanins, catechins, and flavonols represent distinct branches of the flavonoid biosynthetic pathway. Notably, the biosynthesis of these compounds in purple tea exhibits a strong correlation with external

environmental factors, encompassing light exposure, temperature fluctuations, and abiotic stressors, resulting in a dynamic profile of flavonoid distribution. Among them, the metabolism of flavonoids and flavonols in purple tea exhibits remarkable instability. This phenomenon may be attributed, in part, to competitive substrate utilization and differential responses in biological activity in reaction to environmental cues [31].

Flavonoids seem to accumulate more abundantly in purple tea than in other teas. It has been demonstrated that there is a notably augmented presence of proanthocyanidins and total flavonoids in Zijuan when juxtaposed with YunKang10 [31]. In an investigation conducted by Zhang et al., an enriching of anthocyanins, proanthocyanidins, and flavonol glycosides was evident in the purple tea leaves when analyzing secondary metabolites in both the green and purple leaf variants of Longjing 43 [32]. This phenomenon is closely linked to the heightened expression of enzymes involved in flavonoid biosynthesis and the influence of environmental factors.

Catechins are the main components of substances in tea, which have an important influence on the formation of color, aroma, and flavor of tea. In our exploration of the molecular mechanisms underlying anthocyanin synthesis, we examined the dynamics of substrate competition between anthocyanins and catechins (see Section 3.1 for details). However, extant metabolic research has failed to reveal a pronounced trend in catechin accumulation within purple tea. Shi et al. [28], in their comprehensive investigation of flavonoids across nine distinct purple tea cultivars, reported that a notable disparity in the total catechin content of purple tea was significantly higher than that of green tea varieties, and the EGCG3'-Me of purple tea accumulation was higher. In a parallel study, Tang et al. [33] conducted a transcriptomic and metabolomic analysis encompassing nine local tea varieties, including three purple tea cultivars from Huizhou City, Guangdong Province. Their findings revealed that the disparities in total catechin content among these nine varieties were statistically insignificant, aligning with the results reported by Li et al. [2]. However, the catechin contents of the same batch of purple and green teas determined by El-Sayed M. Abdel-Aal et al. [21] were 140–148 mg/g and 259–311 mg/g, respectively, and the catechin content of green tea was significantly higher than that of purple tea. In a related investigation conducted by Zhu et al. [29], which focused on flavonoid levels within identical batches of purple and green teas harvested in Hunan Province, the results revealed that the EGCG content and the total content of certain monomeric catechin derivatives in purple tea were lower than their counterparts in green tea. However, the content of most polymerized catechin derivatives displayed an intriguing pattern, wherein purple tea exhibited higher levels than green tea. This observation suggests that elevated anthocyanin levels might lead to reduced levels of monomeric catechin derivatives in tea. This phenomenon underscores that, even within the confines of the flavonoid biosynthetic pathway, catechin content does not consistently decrease as a consequence of heightened anthocyanin production. Such variability may be attributed to the ample substrate availability resulting from the robust flavonoid production in purple tea. Simultaneously, the influence of diverse tea varieties, as well as the effects of light exposure, temperature fluctuations, and abiotic stressors, contribute to fluctuations in catechin content. Nevertheless, the overall catechin content remains sufficiently robust, resulting in the distinctive characteristic of purple tea boasting both high anthocyanin and catechin levels, thus enhancing its potential health benefits.

2.3. Other Compounds in Purple Tea

In addition to these principal influential compounds, several minor constituents in purple tea have been explored in limited quantities, including amino acids, organic acids, and a variety of sugars. Amino acids predominantly contribute to the fresh and refreshing taste of tea and play a crucial role in shaping both its taste profile and associated health benefits. Numerous studies have consistently reported a substantial reduction in amino acid content in purple tea relative to green tea. This deficiency in amino acids is an additional contributing factor to the less favorable flavor outcomes observed in purple tea production.

Furthermore, the organic acid content in purple tea is also markedly diminished [21,32]. Conversely, the concentration of carbohydrates and sugars, among other constituents, surpasses that of green-leaf tea by more than twofold. It is evident that, among the constituents analyzed, flavonoids remain the most influential and dynamic compounds in purple tea, while the content of other compounds exhibits distinct characteristics dependent on the tea varieties under investigation.

3. Biosynthesis and Regulation of Anthocyanins in Purple Tea

Extensive research has been conducted on the biosynthetic pathway of anthocyanins in plants, as these compounds represent the final products of flavonoid biosynthesis. The anthocyanin synthesis pathway in tea plants closely resembles that of other plants. However, there is a notable difference: anthocyanin synthesis in tea plants diverges from the synthesis of catechins, representing two distinct branches within the flavonoid biosynthesis pathway. Consequently, there is a competitive relationship, to some extent, between anthocyanins and catechins [34]. The synthesis of anthocyanins is predominantly controlled by two categories of genes: structural genes that encode the enzymes responsible for the anthocyanin biosynthesis pathway; the EBGs (the early biosynthesis genes such as CHS, CHI, F3H, F3'H, and F3'5'H) and LBGs (the late biosynthesis genes such as DFR, LDOX/ANS, and UFGT); and regulatory genes consisting of three types of transcription factors (TFs): MYB (*v-myb* avian myeloblastosis viral oncogene homolog) proteins, bHLH (basic helix–loop–helix) proteins, and WD40 (WD40 repeat protein with a scaffolding function) proteins [35].

3.1. Biosynthetic Pathway of Anthocyanin in Purple Tea

The biosynthesis of anthocyanins in tea plants closely resembles that of other plants. It occurs in the cytoplasm and involves both the phenylpropanoid pathway and the flavonoid pathway. The primary metabolic pathways responsible for anthocyanin production in tea plants are depicted in Figure 1. The process of anthocyanin biosynthesis is regulated by a diverse range of enzymes.

Phenylalanine, serving as a substrate, is catalyzed by phenylalanine ammonia-lyase (PAL), cinnamate 4-hydroxylase (C4H), and 4-cinnamate-CoA ligase (4CL) enzymes to accomplish the phenylpropyl pathway, yielding 4-coumarin CoA, and subsequently entering the flavonoid synthesis pathway, which plays a crucial role in anthocyanin synthesis. Afterward, 4-coumarin CoA undergoes catalysis by chalcone synthase (CHS) to synthesize naringenin chalcone [36]. Further enzymatic actions by chalcone isomerase (CHI) and flavanone 3-hydroxylase (F3H) generate naringenin and dihydrokaempferol (DHK). DHK can be converted into Dihydromyricetin (DHQ) or dihydroquercetin (DHM) through the enzymatic activity of flavanone 3'-hydroxylase (F3'H) or flavanone 3'5'-hydroxylase (F3'5'H), respectively. F3'H and F3'5'H play pivotal roles in the anthocyanin biosynthesis pathway, as they determine the hydroxylation pattern of the anthocyanin B-ring, thus influencing the type of anthocyanin produced. Subsequently, dihydroflavonols serve as substrates for dihydroflavonol 4-reductase (DFR), facilitating the synthesis of colorless anthocyanidins, which form the fundamental backbone of both flavonoids and anthocyanidins [37]. Anthocyanidin synthase (ANS) then converts the colorless anthocyanidins into pigmented anthocyanins: pelargonidin; cyanidin; and delphinidin [38,39]. The next step is the mono- or demethylation of pelargonidin, cyanidin, and delphinidin to peonidin, petunidin, and malvidin. In the presence of flavonoid 3-O-glucosyltransferase (UFGT), anthocyanins form disaccharide glycosides by linking the hydroxyl group of a monosaccharide molecule's hemiacetal with the hydroxyl group of another monosaccharide molecule, which is mainly hexoses (glucose and galactose) or pentoses (arabinose, rhamnose, and xylose), and the disaccharide glycosides can then be further modified to form acylated anthocyanins. Acyltransferases (ATs) can then catalyze the addition of acyl groups, such as aliphatic groups, to the glycosylated molecules in the disaccharide glycosides to create acylated anthocyanins [27,40]. Anthocyanin stability and color function are impacted by

side-chain modifications [41,42]. Finally, glutathione S-transferases (GST), ATP-binding cassette transporters (ABC), and multidrug and toxic extrusion transporter (MATE) facilitate the transfer of the synthesized anthocyanins into vesicles for storage [43,44].

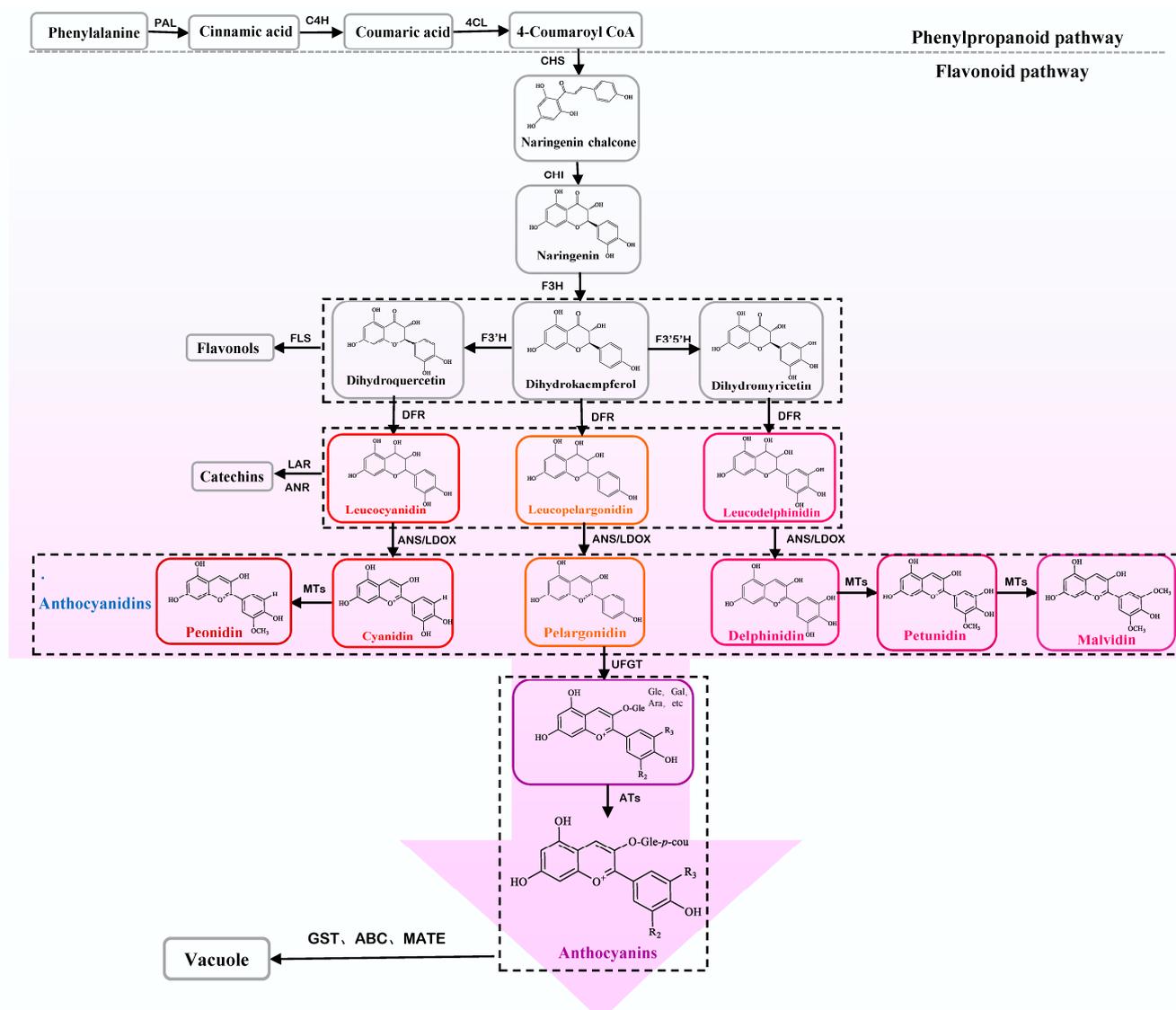


Figure 1. Tea plant anthocyanin synthesis pathway. PAL: phenylalanine ammonia-lyase; C4H: cinnamate 4hydroxylase; 4CL: p-coumaroyl coenzyme A ligase; CHS: chalcone synthase; CHI: chalcone isomerase; F3H: flavanone 3-hydroxylase; F3'H: flavanone 3'-hydroxylase; F3'5'H: flavanone 3'/5'-hydroxylase; FLS: flavonol synthase; DFR: dihydroflavonol 4-reductase; LAR: leucoanthocyanidin reductase; ANR: anthocyanidin reductase; ANS/LDOX: anthocyanidin synthase/Leucoanthocyanidin dioxygenase; UFGT: UDP-glucose: flavonoid 3-O-glucosyltransferase; MTs: methyltransferases; ATs: acyltransferases; GST: glutathione S-transferases; ABC: ATP-binding cassette transporters; MATE: multidrug and toxic extrusion transporter.

The biosynthetic enzymes and transporters responsible for anthocyanins have a direct impact on the synthesis and accumulation of anthocyanidins. It is worth noting that several common genes, including *CsANS* and *CsUGT*, are responsible for the substantial accumulation of anthocyanins in numerous purple-leaf tea germplasm [45]. *Cs4CL*, *CsANS*, and *CsUGT* have been identified as crucial regulatory genes that contribute to the high anthocyanin content in certain CSA (*Camellia sinensis* var. *assamica*) and CSS (*Camellia sinensis* var. *sinensis*) purple tea germplasm [29]. Moreover, the elevated expression of

CsCHI and *CsCHS* in the purple-leaf cultivar Wuyiqizong 18 promotes the accumulation of anthocyanins [46]. *CsUGT78A15* was identified in tea plants and demonstrated its ability to facilitate the biosynthesis of cyanidin 3-O-galactoside and delphinidin 3-O-galactoside by utilizing UDP-galactose as a glycosyl donor [47]. The hybrid variety Chuanzi 3 (ZZ), derived from the cross between Zijuan and Ziyan, exhibits a total anthocyanin content that surpasses the sum of its parental lines. Analysis of the expression of anthocyanin biosynthetic enzymes in ZZ revealed that *CsF3'5'H* was highly expressed, which might significantly contribute to the synthesis of delphinidin. Additionally, *CsANS* is significantly upregulated in ZZ, while *CsLARs* and *CsANRs* exhibit a significant down-regulation trend, consistent with the increase in anthocyanin content and decrease in catechin content [27]. This research indicates that these biosynthetic enzymes at different stages of synthesis play unique roles in the growth of purple tea during different periods within the same variety or across different varieties.

Transporter proteins are responsible for transporting stabilized anthocyanins to the vacuole for storage. In this study focusing on the seasonal variations in anthocyanins, the deposition of anthocyanin pigments was categorized into three stages: reddish–purple (S1-RP); deep gray–purple (S2-GP); and medium olive–green (S3-GP). Among these stages, S2-GP displayed the highest levels of anthocyanin glycosides. Studies of protein expression levels at three stages found that differential expression of 26 candidate genes involved in anthocyanin transport, including 10 ABC transporters, 9 MATE transporters, and 7 GST transporters, was observed, with most of them showing upregulation in S2-GP [48]. This suggests a crucial role of transport proteins in regulating anthocyanin biosynthesis. Interestingly, the upregulation of key transport proteins showed a strong positive correlation with the accumulation of total anthocyanins, indicating their involvement in the accumulation of anthocyanins in tea leaves. Among the transport proteins, GST is the most extensively studied in the context of anthocyanin transport. Compared to the green shoots of tea plants, purple shoots of tea plants showed relatively higher expression levels of late biosynthetic genes 3GT and ANS, as well as the transport-related gene *CsGSTF1*. This suggests a close relationship between anthocyanin accumulation in tea plants and the strength of late modification and transport capabilities. This association between *CsGSTF1* expression and the purple shoots trait was further validated by Wei et al. using metabolomics, transcriptomics, and QTL mapping methods. When *CsGSTF1* was overexpressed in the tt19-8 *Arabidopsis* mutant, which lacks *AtGSTF12*, it restored anthocyanin production while the seed coat remained transparent, indicating no effect on proanthocyanin accumulation. This underscores *CsGSTF1*'s significance as a key gene for anthocyanin accumulation, with its expression level directly impacting the anthocyanin content in tea leaves [49]. Furthermore, Liu et al. conducted in vitro recombinant experiments, demonstrating that among the three recombinant CsGSTs, only *CsGSTF1* exhibited a higher affinity for anthocyanins, underscoring the importance of this gene [50].

3.2. The Transcriptional Regulation of Anthocyanin in Purple Tea

The metabolism of anthocyanins is regulated by various transcription factors, including the MBW (MYB, bHLH, and WD40) ternary complex formed through the interaction of these regulatory proteins, as well as the b-ZIP, WRKY, and NAC families [40]. Extensive previous research has revealed that the regulation of anthocyanin synthesis involves both the control of individual transcription factors and the structural regulation within the anthocyanin biosynthetic network. The primary transcriptional regulators in anthocyanin synthesis are the MYB, bHLH, and WD40 protein classes. These three types of transcription factors, whether by regulating their unique structures or by forming the transcription activation complex MBW, bind to the promoters of structural genes responsible for anthocyanin biosynthesis. In doing so, they activate or inhibit the expression of different genes [51]. Among them, MYB transcription factors have been extensively studied in tea plants for their role in anthocyanin and catechin synthesis. They occupy a dominant position in the

regulatory network of anthocyanin biosynthesis and serve as the core transcription factors of the MBW complex, determining its specificity and functionality [52] (Table 2, Figure 2).

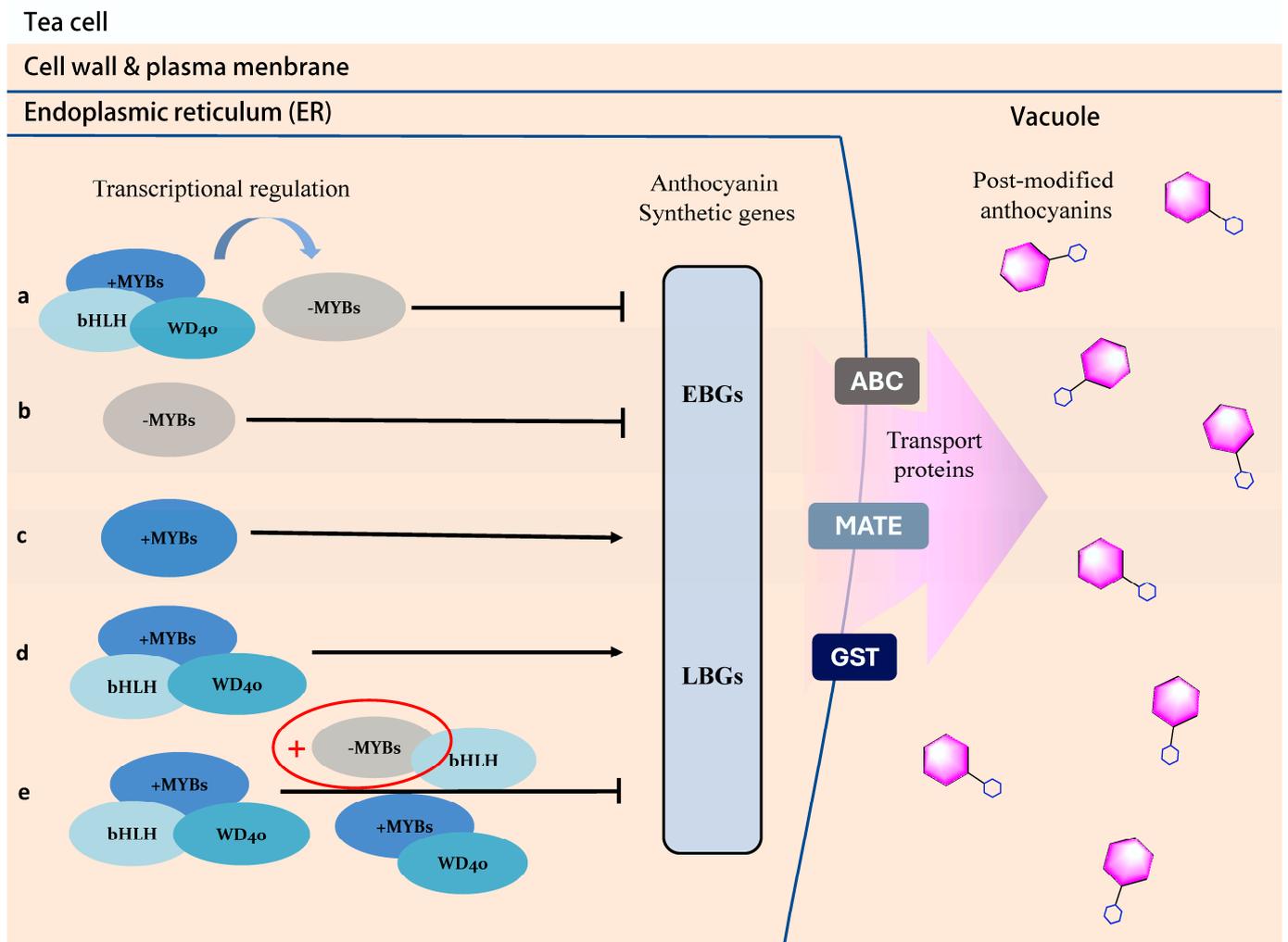


Figure 2. Molecular mechanisms underlying the dynamic anthocyanin accumulation. The synthesis of anthocyanins occurs in the endoplasmic reticulum, where transcription factors regulate the anthocyanin synthesis genes, thus affecting anthocyanin synthesis. The synthesized anthocyanins are transported to vacuoles for storage by transport proteins. Molecular mechanism of anthocyanin transcription regulation in tea plants: (a) MBW complex activates MYB-negatively regulated transcription factors and inhibits anthocyanin synthesis; (b) MYB-negative regulators inhibit anthocyanin synthesis by directly binding to anthocyanin synthesis genes; (c) MYB-positive regulators activate anthocyanin synthesis genes and promote anthocyanin synthesis; (d) MYB-positive regulators combine with bHLH and WD40 transcription factors to form the MBW complex, which activates structural gene expression and promotes anthocyanin synthesis; (e) MYB-negative regulators inhibit new MBW formation by binding to bHLH factors in the MBW complex, thereby reducing anthocyanin synthesis.

The MYB transcription factor family possesses highly conserved DNA-binding domains and can be classified into three categories based on the number of MYB functional domains: 1R-MYB; R2R3-MYB; and 3R-MYB. R2R3-MYBs and 3R-MYBs are particularly important as transcriptional regulatory factors in anthocyanin synthesis [53]. In studies on purple tea, the researchers have screened and studied several MYB transcription factors that positively regulate the biosynthesis and accumulation of anthocyanins in tea plants through transcriptome sequencing and other methods, such as *CsAN1/CsMYB75*, *CsMYB5a*,

CsMYB5b, *CsMYB6a*, and *CsMYB113*, and have conducted in-depth investigations into their functions.

The homologous transcription factor *CsAN1* in *Arabidopsis*, *AtMYB75*, positively regulates the expression of anthocyanin biosynthetic enzyme genes [54]. Activation of *CsAN1* leads to the specific upregulation of bHLH transcription factors (*CsGL3* and *LBGs*), resulting in ectopic accumulation of anthocyanins in purple tea. In addition, *CsAN1* forms a dimer with *CsGL3* and *CsEGL3* (bHLH TFs), then combines with *CsTTG1* (WD40) to form the MBW complex, which positively regulates the expression of the anthocyanin biosynthesis gene *CsLDOX*, promoting anthocyanin accumulation [55]. Simultaneously, the expression of *CsAN1* is epigenetically regulated, and its expression level is positively correlated with the low methylation level of the promoter. Transcriptome analysis by Wei et al. [49] on genetic populations related to leaf color differentiation in tea plants revealed that *CsMYB75* (also referred to as *CsAN1*) shares a high similarity with *AtPAP1* in *Arabidopsis*. *CsMYB75* was experimentally proven to act on the promoter of the anthocyanin transport gene *CsGSTF1*, thus promoting anthocyanin accumulation in vacuoles. Transactivation experiments demonstrated that *CsMYB75* upregulates the expression of *CsCHS* and *CsA3T* genes [56] and activates transient expression of *CsDFR*. Genetic studies found that *CsMYB75* co-localizes with QTLs, controlling shoot color in tea plants. Comparative analysis between purple shoot varieties (Zijuan, Ziyan, and their natural hybrid ZZ) and the normal green-leaf variety Fudingdabai (FD) revealed that *CsMYB75* expression levels in purple shoot varieties were approximately 15 times higher than in FD [27]. These studies indicate that *CsMYB75* is a crucial gene for anthocyanin transcriptional regulation in purple tea.

Other MYB-positive regulators promote anthocyanin synthesis to varying degrees. Overexpression analysis of the selected R2R3-MYB transcription factors *CsMYB5a* and *CsMYB5e* revealed that *CsMYB5a* conferred a distinct pink color to tobacco petals when overexpressed, while *CsMYB5e* overexpression did not result in noticeable anthocyanin changes but significantly increased the content of proanthocyanidins (PAs). Furthermore, most genes associated with PAs and anthocyanin biosynthesis pathways were significantly upregulated in the overexpressing flowers, indicating that *CsMYB5a* and *CsMYB5e* positively regulate the expression of anthocyanins and PAs, respectively [57]. Further identification of sucrose-controlled polyphenolic regulators led to the discovery of a sucrose-induced MYB transcription factor, *CsMYB5b*. Overexpression of *CsMYB5b* in tobacco and *Arabidopsis* experiments demonstrates that this gene induces PA accumulation by upregulating key structural genes *CsLAR* or *CsANRs*, and *CsMYB5b* interacts with *CsTT8* and *CsWD40* proteins to form the MBW complex [58]. Tobacco overexpression of *CsMYB6a* [56] and *CsMYB113* [59] activates the expression of *CsCHS* and *Cs3GT* genes and enhances the expression of synthesis genes *CsF3H*, *CsCHI*, *CsUF3G*, and *CsDFR* in different tissues, thereby promoting anthocyanin synthesis and accumulation.

In addition to these anthocyanin MYB activators, researchers have also identified several repressor factors, such as *CsMYB4a*, *CsMYBL2a*, and *CsMYBL2b*. These repressor factors reduce anthocyanin synthesis by directly inhibiting the activity of anthocyanin biosynthesis genes or inhibiting complex formation. An R2R3-MYB transcription factor, *CsMYB4a*, isolated from tea plants, suppresses the promoter activity of five synthesis factors (*CsC4H*, *Cs4CL*, *CsCHS*, *CsLAR*, and *CsANR*) in the phenylpropanoid pathway [60]. *Arabidopsis* *AtMYBL2* homologs, *CsMYBL2a* and *CsMYBL2b*, negatively regulate anthocyanin and proanthocyanidin synthesis in tea plants. Although they both physically interact with *CsTT8* or *CsGL3*, inhibiting the formation of *CsMYB75*-*CsTT8*/*CsGL3*-*CsTTG1* MBW complex, thus suppressing the transcription of *CsDFR* and *CsANR*, as well as the biosynthesis of anthocyanins and proanthocyanidins, *CsMYBL2b* exhibits stronger inhibitory activity than *CsMYBL2a*. In addition, the MBW complex can activate the promoter of *CsMYBL2a* to establish a negative feedback mechanism for fine-tuning the activity of the MBW complex [61].

Apart from the research on MYB transcription factors, there has been relatively limited investigation into bHLH and WD40 transcription factors in tea plants, but some understanding has been gained. The bHLH and WD40 proteins do not directly interact with structural genes involved in anthocyanin synthesis, but they exert their effects on these structural genes by forming complexes with MYB transcription factors. Therefore, the expression of these two protein classes also significantly influences anthocyanin synthesis. In tea plants, only one WD40 gene has been confirmed as a direct homolog of *Arabidopsis* AtTTG1. Ectopic expression of CsWD40 in tobacco resulted in a significant increase in anthocyanin content in transgenic petals. Not only were the structural genes *NtCHS*, *NtF3αH*, *NtDFR*, and *NtANS* upregulated in CsWD40 transgenic tobacco petals, but also the transcription factor genes *NtAN2*, and *NtANb1*. This suggests that CsWD40 may enhance the stability of certain MBW complexes or promote the formation of specific MBW complexes. These complexes can regulate the gene expression of certain transcription factors. Further yeast two-hybrid experiments verified that CsWD40 interacts with two bHLH TFs (CsGL3 and CsTT8) and two MYB TFs (CsAN2 and CsMYB5e) [62]. The regulation of anthocyanin biosynthesis by transcription factors is a complex network, of which the current study is only the tip of the iceberg, and more in-depth studies are needed to characterize it.

Table 2. Transcription factors have been studied in tea plants.

Function	Gene	Type	Impact Factors	Accession	References
positive	CsAN1/ CsMYB75	R2R3-MYB	CsGSTF1	CSS0010687	[49,54–56]
positive	CsMYB5a	R2R3-MYB	/	AT2G16720	[57]
positive	CsMYB5e	R2R3-MYB	/	AT3G13540	[57]
positive	CsMYB5b	R2R3-MYB	CsLAR, CsANR	AT1G22640	[58]
positive	CsMYB6a	R2R3-MYB	CsCHS, Cs3GT	AT1G56650	[56]
positive	CsMYB113	R2R3-MYB	CsF3H, CsCHI, CsUF3G and CsDFR	AT1G66370	[59]
negative	CsMYB4a	R2R3-MYB	CsC4H, Cs4CL, CsCHS, CsLAR, and CsANR	MN894521	[60]
negative	CsMYBL2a	R2R3-MYB	CsDFR, CsANR,	MW837257	[61]
negative	CsMYBL2b	R2R3-MYB	CsDFR, CsANR	MW837258	[61]
	CsTTG1	WD40	interacts with MYB TFs and bHLH TFs	XM_028248215	[62]
	CsGL3	bHLH	interacts with MYB TFs and WD40 TFs	AT5G41315	[61]
	CsEGL3	bHLH	interacts with MYB TFs and WD40 TFs	AT1G63650	[61]
	CsTT8	bHLH	interacts with MYB TFs and WD40 TFs	AT4G09820	[61]

3.3. Other Influencing Factors

Environmental factors, such as light and temperature, greatly influence the accumulation of anthocyanins [63,64] (Figure 3). They regulate the accumulation of flavonoid glycosides and organ coloring in tea plants, but the underlying mechanisms of this regulation are still unclear. It is well-known that purple tea, rich in anthocyanins, exhibits distinct changes in coloration between new and mature leaves, as well as across seasons. Zijuan, near the Himalayas, exhibits a rich repertoire of differentially expressed genes associated with stress, heat, and defense responses, indicating their relevance to environmental stressors [65]. Ultraviolet radiation within a specific range can stimulate the synthesis and buildup of anthocyanins [29]. Temperature variations also affect anthocyanin synthesis and accumulation. Under high-temperature stress, the production of anthocyanins and proanthocyanidins in tea plants is reduced [65].

Quantitative and qualitative alterations in plant anthocyanins can be induced by light stimuli [66]. Different light qualities have varying effects on the mechanisms of anthocyanin biosynthesis in tea plants. Total anthocyanin content and the levels of three major anthocyanin molecules, cyanidin, delphinidin, and pelargonidin, were significantly higher in leaves treated with ultraviolet-A (UV-A), ultraviolet-B (UV-B), and ultraviolet-AB (UV-AB) compared to those treated with white light alone. Among these treatments, UV-A resulted in the highest content of anthocyanins. Compared to white light treatment

alone, the activities of *CsCHS*, *CsF3'5H*, and *CsANS* significantly increased under UV treatments, whereas the activities of *CsLAR* and *CsANR* decreased [67]. The UV-B radiation treatment of hydroponically cultured young Zijuan tea plant seedlings in nutrient solution led to varying degrees of increased anthocyanin content. The expression of the UV-B signaling proteins ELONGATED HYPOCOTYL 5 (HY5) and UV RESISTANCE LOCUS 8 (UVR-8) increased concurrently. Additionally, while the expression of *CsMYBL2*, the antagonistic regulator of anthocyanin, was reduced, both the MBW complex and structural genes involved in anthocyanin production were activated. Because *CsHY5* may bind to the *CsMYB75* and *CsMYBL2a* promoters, it may activate *CsMYB75* expression or inhibit *CsMYBL2* expression, encouraging anthocyanin production and accumulation. In addition to HY5, another light-responsive protein, basic leucine zipper (bZIP), has also been shown to have an important effect on anthocyanin accumulation in tea plants. The transcript levels of the light-responsive proteins *CsbZIP1* and *CsMYB75* were significantly correlated, according to the integration of metabolomic profiling and qRT-PCR data. In contrast to the wild type and *athy5* mutants, the *CsbZIP1*-OE line of transgenic *Arabidopsis* overexpressing *CsbZIP1* demonstrated a higher accumulation of anthocyanin glycosides under high-light conditions because of the higher mRNA levels of *AtDFR*, *AtLDOX*, and *AtPAP1* [61]. Red light (630 nm) also produces higher anthocyanin formation than natural light (260 nm), increasing the flavor and quality of tea leaves [68]. It was discovered that blue light increased the expression of the genes *CsGSTF12* and *CsMYB75*, which, in turn, boosted the accumulation of anthocyanins in the leaf vacuole of tea plants [69].

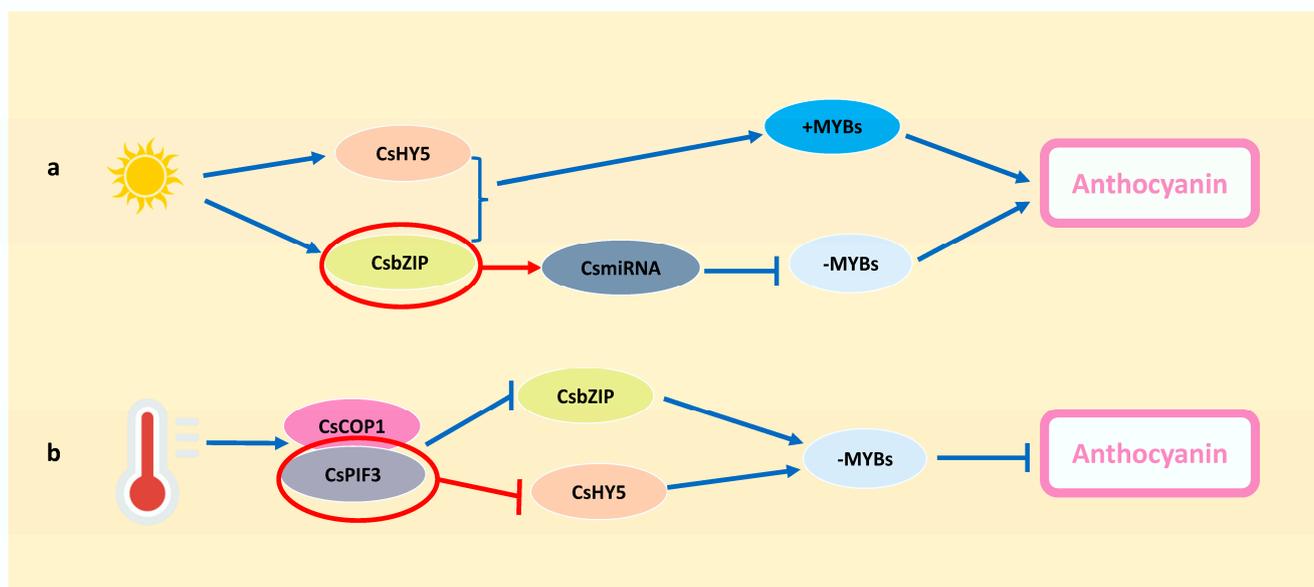


Figure 3. Influence of environmental factors on anthocyanin synthesis: (a) Strong light can promote the expression of HY5 and bZIP proteins in tea plants; *CsHY5* can promote anthocyanin accumulation by combining with MYB-positive regulators, and *CsbZIP* can promote *CsmiRNA* expression in tea trees, thereby targeting the inhibition of transcription levels of MYB-negative regulators and promoting anthocyanin synthesis; (b) High temperature promoted the expression of *CsCOP1* and *CsPIF3*, and *CsCOP1* protein decreased the stability of bZIP protein. *CsPIF3* could form a complex with bZIP, resulting in increased expression of MYB-negative regulators and inhibition of anthocyanin synthesis. HY5 and PIF3 can form a dimer, and the high expression of PIF3 at high temperatures leads to a decrease in HY5 expression, which weakens the ability to inhibit MYB-negative regulators and indirectly inhibits the production of anthocyanins.

Low temperatures and extended light exposure were shown to cause the *CsAN1* promoter to become demethylated in tobacco plants, overexpressing the gene. This promoted the formation of anthocyanins in the leaves [55]. The expression levels of *NtLAR*

and NtANS considerably increased in comparison to the control under low-temperature circumstances when tobacco plants overexpressing CsMYB5a and CsMYB5e were subjected to a low-temperature (10 °C) treatment. An increase in anthocyanins and PAs accumulation was the effect of this [57]. However, high temperature has a significant adverse effect on anthocyanin biosynthesis. The expression levels of CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) and PHYTOCHROME INTERACTING FACTOR 3 (PIF3) were found to be higher under the 28 °C condition compared to the 17 °C condition in an experiment looking at the effects of 17 °C and 28 °C on anthocyanin accumulation in Zijuan tea seedlings, while the expression of CsHY5 was inhibited at 28 °C. One of the factors that inhibit anthocyanin biosynthesis at high temperatures is the activation of CsCOP1 at high temperatures. CsCOP1 protein can degrade the stability of CsbZIP1 protein, resulting in increased expression of CsMYBL2, thereby inhibiting anthocyanin biosynthesis genes. On the other hand, high temperatures trigger an uptick in CsPIF3. CsPIF3 can interact with CsbZIP1 to form a complex, which weakens the inhibition of CsbZIP1 to CsMYBL2, thereby indirectly inhibiting anthocyanin biosynthesis. In summary, CsMYBL2 is a key regulatory target of high-temperature stress in anthocyanin biosynthesis. The yeast two-hybrid experiment proved that CsHY5 and CsPIF3 could interact to form dimers and reduce the activity of CsHY5 protein, which explained the reason for the decreased expression of CsHY5 at 28 °C. As mentioned in the light factor section above, HY5 can bind MYBL2 transcription factor and inhibit its activity, so at 28 °C, the expression of CSHY5 can be reduced. The expression of CsMYBL2 increased, which indirectly inhibited the production of anthocyanins. [61]. These findings suggest that whereas low temperature has a more beneficial effect on anthocyanin biosynthesis, high temperature inhibits anthocyanin biosynthesis in tea plants by decreasing the expression of genes involved in anthocyanin biosynthesis and transcriptional complexes.

Not only do light and low temperatures regulate the accumulation of anthocyanins, but miRNAs, plant hormones, and high sucrose stress also induce the activation of MYBs, regulating the biosynthetic network of anthocyanins [70]. Numerous miRNAs have been discovered in tea plants. For instance, CsmiRNA319 modulates the growth and development of tea plants via the regulation of TEOSINTE BRANCHED1, CYCLOIDEA, and PCF (TCP) family genes [71]. The functional role of CsmiR858 in tea was demonstrated by gene-specific interference with antisense oligodeoxynucleotide (AsODN) strategies. The results showed that inhibition of CsmiR858 expression in buds and young leaves could significantly reduce anthocyanin biosynthesis. Both CsMYBL2a and CsMYBL2b have CsmiR858a binding sites. The results indicated that CsmiR858a could target the CsMYBL2a/2b transcript and reduce its transcript levels. Under strong light conditions, CsbZIP1 promoted CsmiR858a expression and inhibited CsMYBL2 transcription in tea plants [57]. The other is the study of anthocyanin accumulation by hormones. Transcriptomic data from tea plant leaves treated with methyl jasmonate (MEJA) confirmed the activation of flavonoid biosynthesis in response to MEJA [34]. Treatment with the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) led to higher concentrations of total polyphenols, flavonoids, and anthocyanins [72]. There are few studies on anthocyanin accumulation in tea plants treated with high sucrose. In vitro, sucrose treatment of tea plants resulted in reddening of the stems in 9–14-day-old seedlings. Transcriptomic data revealed the upregulation of most structural genes, transcription factors, and transport proteins involved in polyphenol biosynthesis after 2 days of sucrose treatment. Metabolomic data indicated varying degrees of increase in polyphenolic substances in young tea plantlets following sucrose treatment [58].

The effects of environmental factors and abiotic stresses, such as those mentioned above on anthocyanin biosynthesis in tea plants, provide many directions for the subsequent cultivation of high anthocyanin germplasm, such as altering the light and temperature environment of purple tea cultivation through shading and promoting anthocyanin accumulation through exogenous hormones.

4. The Processing of Purple Tea

The water-soluble constituents present in tea leaves contribute to the development of a flavorful tea soup. Broadly speaking, various processing methods can be employed to transform fresh tea plant leaves into six distinct types of tea. However, owing to the inherent variations in chemical constituents among different tea plant varieties, the quality of the tea product exhibits substantial divergence. To fully harness the unique attributes of tea plant varieties, the concept of suitability has been introduced. Notably, purple tea germplasm exhibits a heightened concentration of anthocyanins and flavanols and a diminished amino acid content that imparts a less favorable taste to the tea products. Consequently, the challenge lies in mitigating and optimizing the impact of anthocyanins on the undesirable taste of purple tea, as well as investigating the suitability of purple tea varieties. This issue assumes significance as it necessitates resolution within the context of tea production and quality enhancement.

Presently, research endeavors pertaining to the processing of purple tea predominantly center on green tea and black tea (Figure 4). It was shown that the same batch of Zijuan fresh leaves was divided into two portions, one processed into non-fermented green tea and the other into fermented black tea. The results elucidated that the processing method for green tea had little impact on the content of anthocyanins, while the processing of black tea, especially during the rolling and fermentation stages, resulted in a significant loss of anthocyanins. The fermentation of black tea involves polyphenol oxidation [73]. During the fermentation, polyphenol oxidase (PPO) oxidizes and condenses the polyphenols in tea leaves into complex fermentation products such as theaflavins, thearubins, and theaflavins, and anthocyanins are a group of polyphenolic compounds. The oxidation of anthocyanins may be an important factor contributing to the decrease in total anthocyanin content during black tea processing. The antioxidant activity of green tea is significantly higher than that of black tea, indicating that the tea processing method has a substantial influence on the antioxidant activity of tea leaves rich in anthocyanins [74]. Making some new purple tea varieties and standard green bud varieties of tea grown in the Kangra Valley into black and green tea samples: black tea purple (BTP); black tea (BT); green tea purple (GTP); and green tea (GT) [75]. The heightened polyphenolic content found in purple buds resulted in black teas with augmented theaflavin levels and heightened concentrations of sweet floral compounds, including linalool, trans-linalool oxide, methyl salicylate, phenylethanol, and epoxyated linalool, which contributed to distinctive aromas and flavors in the GTP and BTP water extracts, distinguishing them from GT and BT. Notably, catechins and anthocyanins, being highly water-soluble, are promptly extractable from the tea liquid, resulting in a tea soup that is more astringent with enhanced taste and sweetness for GTP and BTP in comparison to GT and BT and have higher antioxidant values. It is evident that the anthocyanin content of purple tea undergoes variations during distinct processing methods, leading to discrepancies in antioxidant properties based on the specific processing techniques employed.

In addition to being processed into unfermented green tea and fully fermented black tea, purple tea has also been processed into lightly fermented white tea and post-fermented dark tea to further explore its flavor and antioxidant activity. When purple tea was processed into black tea, green tea, and white tea separately, the total polyphenols, total catechins, and antioxidant activity of green tea were significantly higher than those of black tea [76]. However, the antioxidant capacity of black tea can also reach 91%, mainly due to the conversion of catechins into theaflavins, which does not affect the free radical scavenging ability of dimeric products. The overall trend of antioxidant activity of purple tea product was green tea > white tea > black tea. Wang Q. et al. used purple tea of new varieties to process into green tea, black tea, and white tea, and the results show that purple buds made of green tea and white tea in the water leachate, tea polyphenols, soluble sugars, and caffeine are higher in catechins than the corresponding black tea, and anthocyanin content of the green tea is higher, in addition to the detection of traces of anthocyanins in the spring of white tea; the rest of the different seasons of the white tea and black tea are

not detected anthocyanins [77]. The sensory evaluation showed that the white tea made of purple tea in spring has an elegant aroma, rich floral and fruity fragrance, sweet and mellow taste, and no bitterness and astringency, which is very suitable for a class of purple tea; the black tea made of purple tea is generally characterized by the rich sweet aroma and sweet and mellow taste; the green tea made of purple tea has the typical chestnut aroma characteristics, and the color of the soup is reddish–purple with good visual ornamental properties. In addition to using Zijuan to make green tea and black tea, it is also processed into a mellow aroma and rich flavor of the Six Castles tea [78].

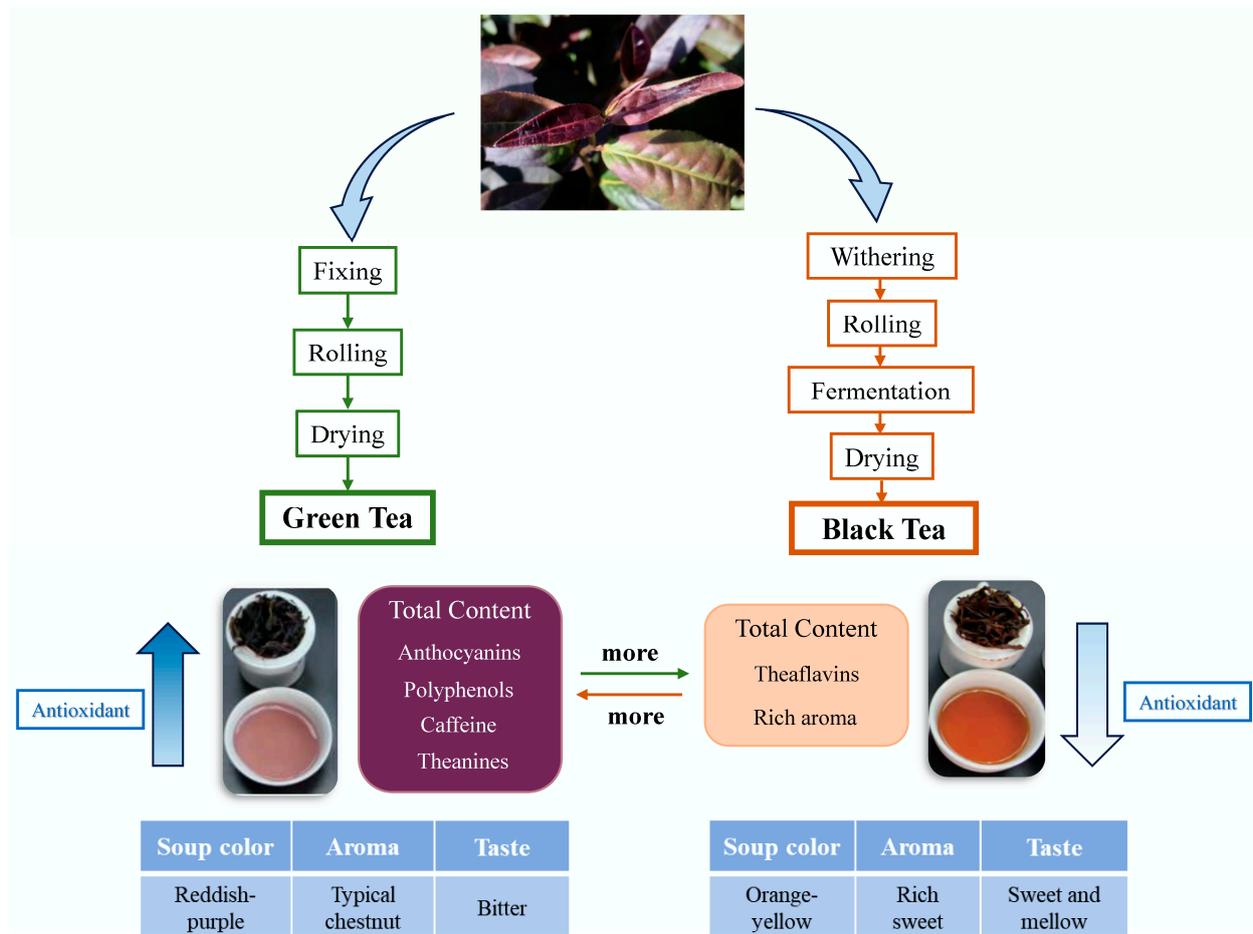


Figure 4. Changes in internal substances and quality characteristics of purple tea processed into green tea and black tea. Green tea: The fresh leaves of purple tea are made by fixing, rolling, and drying. The tea soup is purplish–red, with a typical chestnut aroma and bitter taste, but it has superior antioxidant properties and rich contents of anthocyanins, polyphenols, caffeine, and theanine. Black tea: Made by withering, rolling, fermentation, and drying, the tea is orange–yellow, has rich sweet aroma, and sweet and mellow taste. Its antioxidant properties are reduced during processing, but the content of theaflavins is rich.

Taken together, the general preference among the public leans toward the utilization of purple tea varieties for the production of either black tea or green tea. The green tea processing method preserves a higher content of anthocyanins in the purple bud raw material while also bestowing it with potent antioxidant properties. This approach effectively retains the distinctive composition and health-promoting attributes inherent to purple tea. Conversely, the black tea processing method results in a greater loss of anthocyanins, leading to comparatively lower antioxidant properties. However, it imparts a richer aroma compared to conventional black tea varieties.

Nonetheless, the flavor of tea soup is a complex mixture of various substances, and in the processing of purple tea, reducing other bitter substances (such as caffeine and catechins) and increasing the content of fresh (amino acids) and sweet (water-soluble sugars) substances can, to some extent, improve the taste of purple tea soup. Hence, in order to expand the consumer market for purple tea, it is imperative to enhance the processing methods employed for purple tea or refine the purple tea cultivars to align more closely with consumer preferences. Scientists have undertaken initial explorations in the realm of improving purple tea varieties. Zhou Q. et al. found that a high abundance of glutamine synthase (GS), an enzyme involved in the synthesis of theanine, could significantly improve the quality and flavor of purple tea [79]. Wang et al. used fresh leaves of Zijuan as raw material, analyzed them through inoculation with the endophytic strain *herbaspirillum* sp. ZNX111 wild type and its mutant, and observed that the wild type ZNX111 significantly decreased the content of theobromine and theanine, while the ACC deaminase mutant δ ACC significantly increased the content of theobromine, caffeine, and L-theanine, thus improving the freshness of purple tea [80]. Research on the breeding and improvement in purple tea plant varieties is currently scarce, and the study of improving the flavor of purple tea still has a long way to go.

5. Health Benefits of Purple Tea

Multiple studies have furnished compelling evidence bolstering the diverse health benefits linked to anthocyanins. These benefits encompass antioxidant activity, anti-cancer properties, amelioration of cardiovascular and neurodegenerative conditions, diabetes management, and enhancement of ocular health [81]. Tea, as one of the most widely consumed beverages globally, occupies a pivotal position in the context of health benefits conferred by water-soluble anthocyanins present in tea infusions. By incorporating tea infusions into their daily routines, individuals can conveniently access mild therapeutic effects, rendering it an expedient strategy for disease prevention. While the pharmacological potential of purple tea remains comparatively less explored in contrast to green leaf tea and other tea varieties, some research has already unveiled the noteworthy influence of anthocyanins within tea plants on human health (Figure 5).

5.1. Antioxidant and Anti-Inflammatory

Anthocyanins have demonstrated pronounced antioxidant and anti-inflammatory attributes in numerous scientific investigations. These findings have served as a foundation for advancing the examination of the antioxidant properties of purple tea. A research investigation into the antioxidative potential of Kenyan purple tea extract (PTE) in mice subjected to post-treatment reactive encephalopathy (PTRE) found that PTE significantly increased brain glutathione (GSH) levels, indicating for the first time that PTE from Kenyan purple tea can cross the blood–brain barrier (BBB) and enhance brain antioxidant capacity [16]. Additionally, PTE inhibits the expression of cyclooxygenase-2 (COX-2), an isoenzyme that undergoes significant upregulation in inflammatory cells and plays a crucial role in inflammatory processes. This inhibition occurs through the blockade of the mitogen-activated protein kinase (MAPK) pathway while simultaneously modulating the NF- κ B pathway and activator protein 1 (AP-1) [82]. Furthermore, PTE extracts have demonstrated their ability to reduce various inflammatory mediators, including inducible nitric oxide synthase (iNOS), tumor necrosis factor- α (TNF- α), (interleukin 1- β (IL-1 β), interleukin-6 (IL-6), and cytokine-induced neutrophil chemoattractant-1 (CINC-1), as observed in an ELISA-induced inflammatory mouse model [83]. Four anthocyanins (AN1-4: cyanidin-3-glucoside (AN1), cyanidin-3-O- β -D-(6-(E)-coumaroyl) glucopyranoside (AN2), delphinidin-3-O- β -D-(6-(E)-coumaroyl) glucopyranoside (AN3), cyanidin-3-O-(2-O- β -xylopyranosyl-6-O-acetyl)- β -glucopyranoside (AN4), and crude extract (AN5)) were isolated and characterized from the IHBT 269 clone (one of the purple colored tea shoot clones), with the highest total anthocyanin content by UPLC-ESI-QTOF-MS/MS analysis [84]. AN2 showed the highest in vitro antioxidant activity (IC₅₀ DPPH = 25.27 \pm 0.02 Ug/mL, IC₅₀ ABTS = 10.71 \pm 0.01 Ug/mL).

In vitro immunostimulatory activity of anthocyanins against human interleukins, as determined by a lymphocyte proliferation assay, revealed that AN1 at a concentration of 200 U μ g/mL had the greatest stimulatory effect on the growth of human monocytes in the presence and absence of mitogens (68.7% and 122.2%, respectively). In the absence of mitogens (PHA), anthocyanins AN1-4 and AN5 were not cytotoxic to cultured lymphocytes. The in vitro immunostimulatory activity of anthocyanins AN1-4 and AN5 on human monocytes suggests that anthocyanins have the potential to contribute to the field of immunotherapy. Purple green or black teas (PG and PB) and Taiwan Tea Experiment Station No.12 (TTES No. 12) green or black teas (TG and TB) extracted from the shoots of purple tea have shown varying degrees of antioxidant and anti-inflammatory effects. An experimental model of macrophage stimulation by lipopolysaccharide (LPS) showed strong inhibition of LPS-induced expression of cytokines monocyte chemoattractant protein-1 (MCP-1), IL-6, and TNF- α by PG through scavenging of free radicals and NO in a prophylactic model. Given the preventive effect of PG on lipopolysaccharide (LPS)-related inflammation, habitual consumption of PG can effectively scavenge reactive oxygen species (ROS) and, thus, regulate cytokine cascades, which can be used as a functional food for immunomodulation [85]. De Moura C. et al. maximized the extraction of bioactive compounds and antioxidant activity from green tea derived from purple leaves and optimized the extraction conditions. The optimized extracts of purple tea leaves (OEPL) were stable to pH changes, and lyophilized OEPL exhibited cytotoxicity and antiproliferative effects on cancer cells (A549 and HCT8) and antimicrobial activity against *Listeria monocytogenes* (ATCC 7644), *Staphylococcus aureus* (ATCC 13565), and *Staphylococcus epidermidis* (ATCC 12288). It also inhibits α -amylase and α -glucosidase and reduces the release of pro-inflammatory cytokines (TNF- α , CXCL2: C-X-C motif chemokine ligand 2/MIP-2; Macrophage Inflammatory Protein-2, and IL-6) in lipopolysaccharide-stimulated RAW 264.7 macrophages [86]. These results indicate that purple tea has a significant effect on antioxidant and anti-inflammatory activity, which also lays the foundation for exploring other biological activities.

5.2. Metabolic Syndrome Regulation

Metabolic syndrome (MS) represents a constellation of multiple metabolic disorders, and its intricate pathophysiological underpinnings have posed significant challenges in the quest to develop efficacious pharmaceutical interventions aimed at its prevention or amelioration [87]. Currently, the beneficial research on purple tea in this regard is reflected in various aspects. Notably, PTE has exhibited the capacity to regulate diet-induced weight gain by impeding fat absorption and enhancing hepatic fat metabolism, as evidenced in both murine and human studies [88]. Administration of purple tea extract (200 mg/kg) led to significant inhibitions in weight gain, liver mass, and abdominal fat accumulation, as well as reductions in serum and hepatic triglyceride levels. This was concomitant with an upregulation in the protein expression of carnitine palmitoyltransferase (CPT) 1A. Moreover, in murine models subjected to olive oil loading, PTE (100 mg/kg) and caffeine (25 mg/kg) effectively suppressed fat absorption. Further substantiating these findings, in humans, the consumption of a purple tea beverage over a span of four weeks yielded improvements in key obesity parameters, including body weight, body mass index (BMI), and body fat mass, when compared to baseline measurements.

Purple tea has demonstrated remarkable inhibitory effects on starch digestion and pancreatic α -amylase activity in comparison to aqueous extracts from various tea varieties. This substantiates its superior potential for postprandial hypoglycemic activity, which can be primarily attributed to the presence of deoxyhexosyl flavonols, notably cyanidin and delphinidin derivatives [89]. Purple tea exhibited greater sensitivity when contrasted with green tea. Notably, its sensitivity further increased following incubation with purple tea extract. The inhibition of triglyceride absorption appears to be a key contributing factor to the influence of purple tea on lipid metabolism. In this context, purple tea extract displayed significantly more potent inhibition of pancreatic lipase compared to analogous green tea

extracts. This pronounced inhibition signifies a specific targeting of triglyceride digestion by purple tea extract. Consequently, these findings suggest a potential positive role for purple tea extract in the management of obesity and diabetes [90]. Furthermore, purple tea has been found to modulate the gut microbiota in murine models by augmenting microbial diversity and the Firmicutes-to-Bacteroidetes ratio. This modulation contributes to the amelioration of metabolic disorders associated with a high-fat diet, thereby participating in the regulation of insulin resistance, liver diseases, and susceptibility to obesity linked with a high-fat dietary regimen [91].

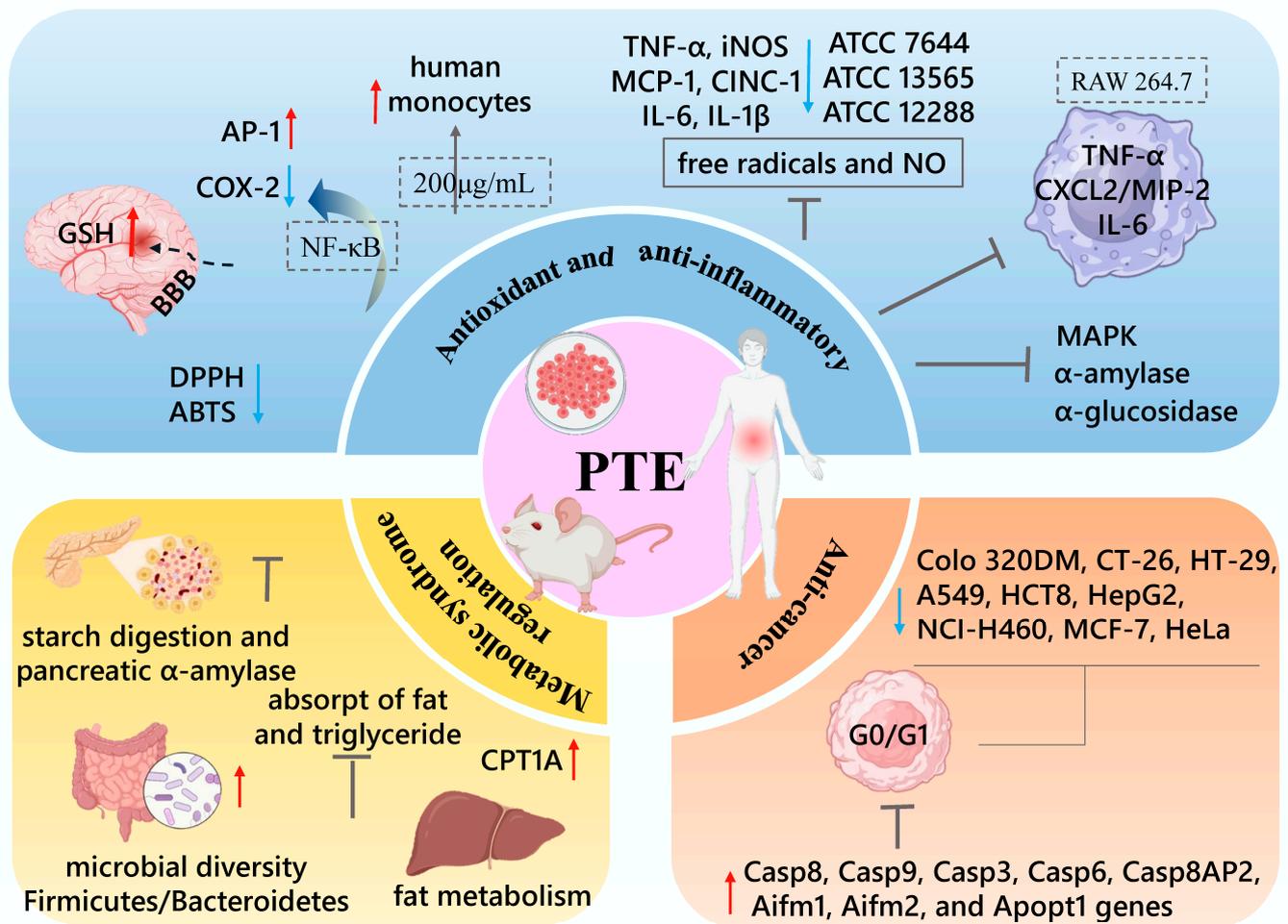


Figure 5. Research on the mechanism of health effects of purple tea.

5.3. Anti-Cancer

Anthocyanins are acknowledged as potential inhibitors of cancer cell proliferation [83]. Prior investigations have elucidated the significant role of anthocyanins in the prevention of specific cancers, with preliminary findings supporting the anti-cancer properties of purple tea. An experiment assessing growth inhibition in A549 cells and the C-6 cancer cell line using anthocyanins AN5 and AN1-4, AN4, and AN5 demonstrated substantial anti-cancer activity against C-6 cells. Furthermore, AN5 hindered the proliferation of CoLo 320DM ($IC_{50} = 64.9 \text{ Ug/mL}$) and HT-29 ($IC_{50} = 55.2 \text{ Ug/mL}$) by impeding cell cycle progression within the G0/G1 phase and inducing apoptosis [88]. To evaluate cytotoxicity and explore differentially expressed genes, 4TI cancer cell suspensions underwent in vitro incubation with various concentrations of green, black, and purple tea infusions. The outcomes revealed a noteworthy upregulation of Casp8, Casp9, Casp3, Casp6, Casp8AP2, Aifm1, Aifm2, and Apopt1 genes, indicative of the initiation and execution of apoptosis. Furthermore, this study posits that the heightened antioxidant activity observed in anthocyanin-rich teas

with purple leaf pigmentation may be ascribed to the catechin–anthocyanin complexes containing additional hydroxyl groups crucial for effective free radical scavenging. This antioxidative property of polyphenols present in purple tea provides a plausible rationale for its efficacy against 4T1 cancer cells [92]. The aqueous extract derived from purple tea exerts an inhibitory effect on the proliferation of colorectal cancer cells through the blockade of the G0/G1 cell cycle progression and the induction of apoptosis. These findings underscore the potential anti-tumor activity of anthocyanins in suppressing the growth of colon cancer cells and inhibiting tumor angiogenesis. Furthermore, the aqueous extract of purple tea demonstrates notable inhibitory effects on the proliferation of two distinct colon cancer cell lines, exhibiting superior efficacy compared to conventional green tea in Taiwan [93]. Antiproliferative investigations conducted on HT-29, Colo 320DM, and CT-26 cell lines reveal that the antioxidant properties inherent to purple tea substantially impede their proliferation. Cell cycle assessments confirm the capacity of purple tea to arrest colon cancer cells in the G0/G1 phase. The substantial content of anthocyanins and anthocyanidins within purple tea may contribute to the enhancement of cytotoxicity and the induction of apoptosis post-irradiation [94]. Lyophilized hydroalcoholic extract (LHE) concentrations were employed to evaluate the safeguarding effects on phospholipids, triacylglycerols, and proteins in egg yolks, as well as their susceptibility to non-enzymatic oxidation induced by ROS upon exposure to ferric ions. LHE demonstrates a reduction in cell viability of purple tea extracts across all tested cancer cell lines (A549: adenocarcinoma human alveolar basal epithelial cells, HCT 8: colon adenocarcinoma, HepG-2: hepatocellular carcinoma), including EA.hy926 (human endothelial cells) endothelial hybrid cells (IC_{50} values of 95.3 to 414.8 Yg QE/mL). Additionally, LHE exhibits cytotoxic effects (IC_{50} values ranging from 199.5 to >500 Yg QE/mL) and antiproliferative effects (GI_{50} values ranging from 18.5 to 222.2 Yg QE/mL) on both cancer cells and hybrid cells [95]. In a separate study, Khan F. et al. observed that an aqueous extract of purple tea significantly inhibited cell growth of three different cancer cells: NCI-H460 (lung cancer); MCF-7 (breast cancer); and HeLa (cervical cells) [96]. The above results clearly show that purple tea plays a significant role in inhibiting the proliferation of cancer cells, which has important implications for the health benefits of purple tea.

In addition to the aforementioned investigations, purple tea has been identified as having potential benefits for enhancing visual function and regulating blood pressure in healthy adults. An experiment under controlled conditions was conducted by Maeda-Yamamoto et al., employing the Japanese anthocyanin-rich tea cultivar “Sunrouge.” The findings of this study revealed that the sustained consumption of “Sunrouge” tea extract led to a notable enhancement in ocular adaptation, a reduction in visual fatigue, and an improvement in blood pressure regulation [97].

6. Conclusions and Prospect

Anthocyanins, an essential component of flavonoids, are abundantly present in tea plants and have attracted substantial attention due to their distinctive physiological functions and potential health benefits. The biosynthesis of tea anthocyanins is a complex process involving the regulation of numerous genes, including biosynthetic and transcription factors. Additionally, both inherent genetic traits and external environmental factors influence the synthesis of anthocyanins in tea plants. Currently, the general mechanisms of MYB transcription factors and MBW complexes in regulating tea anthocyanin synthesis have been elucidated, and preliminary identification of factors influencing anthocyanin synthesis under light, temperature, and other biotic and abiotic stresses has been achieved. This provides an important foundation for understanding the mechanisms underlying anthocyanin biosynthesis and accumulation in purple tea plants. Moreover, research on the health benefits of purple tea has also gained significant attention from scientists and consumers alike.

This paper systematically reviewed the biosynthesis and regulation of anthocyanins, as well as the chemical compositions, processing, and health benefits of purple tea. Never-

theless, it is worth noting that specific, undiscovered biosynthesis regulatory mechanisms of anthocyanins may exist in tea plants due to distinctive genetic traits. Further research should prioritize the investigation of the synergistic regulatory effects exerted by different transcription factors and candidate genes on tea tree anthocyanin biosynthesis based on a large amount of transcriptome data. The establishment of an efficient genetic transformation system for tea plants, coupled with the application of multi-omics analysis technologies, is of paramount importance for the comprehensive elucidation of the anthocyanin biosynthesis regulatory system in tea plants. Additionally, the characteristics of finished purple tea, along with its potential health benefits and the latest advancements in the variety selection of purple tea, were also introduced briefly in this article. In furtherance of this, promoting the development of new purple tea varieties and fostering innovation in tea-making processes are essential steps for enhancing the final tea product's sensory attributes and quality characteristics. Moreover, it is imperative to elucidate the mechanism underlying the interaction of secondary metabolites in purple tea and their influence on its health benefits. Such research will establish a solid theoretical foundation for the comprehensive development of purple tea products.

Author Contributions: M.Y., investigation, writing—original draft; X.H., supervision and writing—review and editing; N.X., writing—review and editing; T.Z., writing—review and editing; M.Z., project administration, conceptualization, and writing—review and editing; J.L., supervision and conceptualization; K.W., project administration, supervision, and writing—review and editing. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the National Key Research and Development Program of China (2022YFD2101102), the National Natural Science Foundation of China (U19A2030, 32072629), the Natural Science Foundation of Hunan Province for Outstanding Young Scholars (2022JJ20028), Yunnan Province Key Research and Development Program of China (202202AE090030), and Xiangxi Zhou Key Research and Development Program (2022JBGS0007).

Data Availability Statement: No new data were created or analyzed in this study.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Hazra, A.; Dasgupta, N.; Sengupta, C.; Das, S. Next generation crop improvement program: Progress and prospect in tea (*Camellia sinensis* (L.) O. Kuntze). *Ann. Agrar. Sci.* **2018**, *16*, 128–135. [[CrossRef](#)]
2. Li, M.; Liu, Y.; Yang, Y.; An, S.; Guo, X.; Xu, T.; Hao, Q. Research advance in chemical constituents and pharmacological activities of Zijuan tea. *J. Food Saf. Qual.* **2019**, *10*, 2293–2299.
3. Zhang, K.; Su, H.; Lin, Y.; Zhang, L. Research progress on the mechanism of color generation and anthocyanin accumulation in anthocyanin-rich tea. *J. Food Saf. Qual.* **2022**, *13*, 3585–3592.
4. Wang, X.; Liu, B.-Y.; Zhao, Q.; Sun, X.; Li, Y.; Duan, Z.; Miao, X.; Luo, S.; Li, J. Genomic variance and transcriptional comparisons reveal the mechanisms of leaf color affecting palatability and stressed defense in tea plant. *Genes* **2019**, *10*, 929. [[CrossRef](#)] [[PubMed](#)]
5. Kerio, L.C.; Wachira, F.N.; Wanyoko, J.K.; Rotich, M.K. Characterization of anthocyanins in Kenyan teas: Extraction and identification. *Food Chem.* **2012**, *131*, 31–38. [[CrossRef](#)]
6. Saito, T.; Honma, D.; Tagashira, M.; Kanda, T.; Nesumi, A.; Maeda-Yamamoto, M. Anthocyanins from new red leaf tea 'Sunrouge'. *J. Agric. Food Chem.* **2011**, *59*, 4779–4782. [[CrossRef](#)]
7. Tian, Y.; Yin, Z.; Tang, Q. Water extraction process of anthocyanins from "Ziyan" tea and the antitumor activity of its extracts. *J. Anhui Agric. Univ.* **2019**, *46*, 1–7.
8. Lin, Y.; Yu, W.; Li, X.; Zheng, Y.; Ye, N. Analysis on the protection status and characteristics of geographical indication products of oolong tea in Fujian province. *Tea Fujian* **2018**, *40*, 1–2.
9. Wei, M.; Lu, M.; Chen, X.; Xu, B.; Lin, C.; Chen, X.; Wang, P.; Ye, N. Biological traits of three new tea tree lines including JinMingzhao survey. *Tea Fujian* **2021**, *43*, 30–32.
10. Tang, X.; Sun, W.; Hong, Y.; Xie, F.; Chen, J.; Chen, Z. Differential expression of genes associated with anthocyanin synthesis in *Camellia sinensis* varieties with different leaf colors. *J. Fujian Agric. For. Univ. Nat. Sci. Ed.* **2019**, *48*, 742–745.
11. Cai, J.; Lv, L.; Zeng, X.; Zhang, F.; Chen, Y.; Tian, W.; Li, J.; Li, X.; Li, Y. Integrative analysis of metabolomics and transcriptomics reveals molecular mechanisms of anthocyanin metabolism in the Zikui tea plant (*Camellia sinensis* cv. Zikui). *Int. J. Mol. Sci.* **2022**, *23*, 4780. [[CrossRef](#)] [[PubMed](#)]

12. Li, F.; Deng, X.; Huang, Z.; Zhao, Z.; Li, C.; Song, Q.; He, Y.; Niu, S. Integrated transcriptome and metabolome provide insights into flavonoid biosynthesis in 'P113', a new purple tea of *Camellia tachangensis*. *Beverage Plant Res.* **2023**, *3*, 1–11. [[CrossRef](#)]
13. Wu, H.; Qiao, X.; Li, J.; Chen, D.; He, Y.; Huang, H.; Liu, J.; Guan, M. Biological characters of new tea germplasms with reddishviolet shoots. *Chin. J. Trop. Crops* **2011**, *32*, 1009–1015.
14. Shen, J.; Zou, Z.; Zhang, X.; Zhou, L.; Wang, Y.; Fang, W.; Zhu, X. Metabolic analyses reveal different mechanisms of leaf color change in two purple-leaf tea plant (*Camellia sinensis* L.) cultivars. *Hortic. Res.* **2018**, *5*, 7. [[CrossRef](#)] [[PubMed](#)]
15. Terahara, N.; Takeda, Y.; Nesumi, A.; Honda, T. Anthocyanins from red flower tea (Benibana-cha), *Camellia sinensis*. *Phytochemistry* **2001**, *56*, 359–361. [[CrossRef](#)] [[PubMed](#)]
16. Rashid, K.; Wachira, F.N.; Nyabuga, J.N.; Wanyonyi, B.; Murilla, G.; Isaac, A.O. Kenyan purple tea anthocyanins ability to cross the blood brain barrier and reinforce brain antioxidant capacity in mice. *Nutr. Neurosci.* **2014**, *17*, 178–185. [[CrossRef](#)] [[PubMed](#)]
17. Li, X.; Li, Z.; Zhu, W.; Wang, Y.; Liang, Y.; Wang, K.; Ye, J.; Lu, J.; Zheng, X. Anthocyanin metabolism and its differential regulation in purple tea (*Camellia sinensis*). *Plant Physiol. Biochem.* **2023**, *201*, 107875. [[CrossRef](#)]
18. Wei, K.; Zhang, Y.; Wu, L.; Li, H.; Ruan, L.; Bai, P.; Zhang, C.; Zhang, F.; Xu, L.; Wang, L. Gene expression analysis of bud and leaf color in tea. *Plant Physiol. Biochem.* **2016**, *107*, 310–318. [[CrossRef](#)]
19. Jiang, L.; Shen, X.; Shoji, T.; Kanda, T.; Zhou, J.; Zhao, L. Characterization and Activity of Anthocyanins in Zijuan Tea (*Camellia sinensis* var. *kitamura*). *J. Agric. Food Chem.* **2013**, *61*, 3306–3310. [[CrossRef](#)]
20. Lai, Y.; Li, S.; Tang, Q.; Li, H.; Chen, S.; Li, P.; Xu, J.; Xu, Y.; Guo, X. The dark-purple tea cultivar 'Ziyan' accumulates a large amount of delphinidin-related anthocyanins. *J. Agric. Food Chem.* **2016**, *64*, 2719–2726. [[CrossRef](#)]
21. Abdel-Aal, E.-S.M.; Rabalski, I.; Mats, L.; Rai, I. Identification and quantification of anthocyanin and catechin compounds in purple tea leaves and flakes. *Molecules* **2022**, *27*, 6676. [[CrossRef](#)] [[PubMed](#)]
22. Mei, Y.; Xie, H.; Liu, S.; Zhu, J.; Zhao, S.; Wei, C. Metabolites and transcriptional profiling analysis reveal the molecular mechanisms of the anthocyanin metabolism in the "Zijuan" tea plant (*Camellia sinensis* var. *assamica*). *J. Agric. Food Chem.* **2021**, *69*, 414–427. [[CrossRef](#)] [[PubMed](#)]
23. Yang, X.; Yi, B.; Li, Y.; Jiang, H.; Duan, Z.; Shang, W.; Yang, Y.; Yang, S.; Liu, B. Analysis on differences of major biochemical components of purple-bud tea tree germplasm resources. *Shandong Agric. Sci.* **2015**, *47*, 14–19.
24. Tan, X.; Li, W.; Wang, C.; Huang, J.; Yang, Y.; Tang, Q. Seasonal changes of anthocyanins and main biochemical components in 'Ziyan' and 'Zijuan' tea plants. *Chin. J. Trop. Crops* **2021**, *42*, 168–174.
25. Lv, H.; Dai, W.; Tan, J.; Guo, L.; Zhu, Y.; Lin, Z. Identification of the anthocyanins from the purple leaf coloured tea cultivar Zijuan (*Camellia sinensis* var. *assamica*) and characterization of their antioxidant activities. *J. Funct. Foods* **2015**, *17*, 449–458. [[CrossRef](#)]
26. Chen, Y.; Yang, J.; Meng, Q.; Tong, H. Non-volatile metabolites profiling analysis reveals the tea flavor of "Zijuan" in different tea plantations. *Food Chem.* **2023**, *412*, 135534. [[CrossRef](#)] [[PubMed](#)]
27. Tan, L.; Zhang, P.; Cui, D.; Yang, X.; Zhang, D.; Yang, Y.; Chen, W.; Tang, D.; Tang, Q.; Li, P. Multi-omics analysis revealed anthocyanin accumulation differences in purple tea plants 'Ziyan', 'Zijuan' and their dark-purple hybrid. *Sci. Hortic.* **2023**, *321*, 112275. [[CrossRef](#)]
28. Shi, J.; Simal-Gandara, J.; Mei, J.; Ma, W.; Peng, Q.; Shi, Y.; Xu, Q.; Lin, Z.; Lv, H. Insight into the pigmented anthocyanins and the major potential co-pigmented flavonoids in purple-coloured leaf teas. *Food Chem.* **2021**, *363*, 130278. [[CrossRef](#)]
29. Zhu, M.; Zhou, F.; Ran, L.; Li, Y.; Tan, B.; Wang, K.; Huang, J.; Liu, Z. Metabolic profiling and gene expression analyses of purple-leaf formation in tea cultivars (*Camellia sinensis* var. *sinensis* and var. *assamica*). *Front. Plant Sci.* **2021**, *12*, 606962. [[CrossRef](#)]
30. Chen, X.; Wang, P.; Zheng, Y.; Gu, M.; Lin, X.; Wang, S.; Jin, S.; Ye, N. Comparison of metabolome and transcriptome of flavonoid biosynthesis pathway in a purple-leaf tea germplasm Jinmingzao and a green-leaf tea germplasm Huangdan reveals their relationship with genetic mechanisms of color formation. *Int. J. Mol. Sci.* **2020**, *21*, 4167. [[CrossRef](#)]
31. Liu, Z.; Shi, X.; Duan, S.; Nian, B.; Chen, L.; Zhang, G.; Lv, C.; Ma, Y.; Zhao, M. Multiomics analysis of the mechanisms behind flavonoid differences between purple and green tender shoots of *Camellia sinensis* var. *assamica*. *G3* **2022**, *13*, jkac297. [[CrossRef](#)] [[PubMed](#)]
32. Zhang, Q.; Hu, J.; Liu, M.; Shi, Y.; De Vos, R.C.H.; Ruan, J. Stimulated biosynthesis of delphinidin-related anthocyanins in tea shoots reducing the quality of green tea in summer. *J. Sci. Food Agric.* **2020**, *100*, 1505–1514. [[CrossRef](#)] [[PubMed](#)]
33. Tang, H.; Zhang, M.; Liu, J.; Cai, J. Metabolomic and transcriptomic analyses reveal the characteristics of tea flavonoids and caffeine accumulation and regulation between Chinese varieties (*Camellia sinensis* var. *sinensis*) and Assam varieties (*C. sinensis* var. *assamica*). *Genes* **2022**, *13*, 1994. [[CrossRef](#)] [[PubMed](#)]
34. Li, P.; Xia, E.; Fu, J.; Xu, Y.; Zhao, X.; Tong, W.; Tang, Q.; Tadege, M.; Fernie, A.R.; Zhao, J. Diverse roles of MYB transcription factors in regulating secondary metabolite biosynthesis, shoot development, and stress responses in tea plants (*Camellia sinensis*). *Plant J.* **2022**, *110*, 1144–1165. [[CrossRef](#)] [[PubMed](#)]
35. Wang, X.; Wu, J.; Guan, M.; Zhao, C.; Geng, P.; Zhao, Q. *Arabidopsis* MYB4 plays dual roles in flavonoid biosynthesis. *Plant J.* **2020**, *101*, 637–652. [[CrossRef](#)] [[PubMed](#)]
36. Schäffner, A.R. Flavonoid biosynthesis and *Arabidopsis* genetics: More good music. *J. Exp. Bot.* **2016**, *67*, 1203–1204. [[CrossRef](#)] [[PubMed](#)]
37. Schwinn, K.; Miosic, S.; Davies, K.; Thill, J.; Gotame, T.P.; Stich, K.; Halbwirth, H. The B-ring hydroxylation pattern of anthocyanins can be determined through activity of the flavonoid 3'-hydroxylase on leucoanthocyanidins. *Planta* **2014**, *240*, 1003–1010. [[CrossRef](#)]

38. Krol, A.R.V.D.; Mur, L.A.; Lange, P.D.; Mol, J.N.M.; Stuitje, A.R. Inhibition of flower pigmentation by antisense CHS genes: Promoter and minimal sequence requirements for the antisense effect. *Plant Mol. Biol.* **1990**, *14*, 457–466. [[CrossRef](#)]
39. Kobayashi, S.; Ishimaru, M.; Hiraoka, K.; Honda, C. Myb-related genes of the Kyoho grape (*Vitis labruscana*) regulate anthocyanin biosynthesis. *Planta* **2002**, *215*, 924–933. [[CrossRef](#)]
40. Sun, L.; Huo, J.; Liu, J.; Yu, J.; Zhou, J.; Sun, C.; Wang, Y.; Leng, F. Anthocyanins distribution, transcriptional regulation, epigenetic and post-translational modification in fruits. *Food Chem.* **2023**, *411*, 135540. [[CrossRef](#)]
41. Zhang, Y.; Butelli, E.; Martin, C. Engineering anthocyanin biosynthesis in plants. *Curr. Opin. Plant Biol.* **2014**, *19*, 81–90. [[CrossRef](#)] [[PubMed](#)]
42. Provenzano, S.; Spelt, C.; Hosokawa, S.; Nakamura, N.; Brugliera, F.; Demelis, L.; Geerke, D.P.; Schubert, A.; Tanaka, Y.; Quattrocchio, F.; et al. Genetic control and evolution of anthocyanin methylation. *Plant Physiol.* **2014**, *165*, 962–977. [[CrossRef](#)] [[PubMed](#)]
43. Broun, P. Transcriptional control of flavonoid biosynthesis: A complex network of conserved regulators involved in multiple aspects of differentiation in *Arabidopsis*. *Curr. Opin. Plant Biol.* **2005**, *8*, 272–279. [[CrossRef](#)] [[PubMed](#)]
44. Alfenito, M.R.; Souer, E.; Goodman, C.D.; Buell, R.; Mol, J.; Koes, R.; Walbot, V. Functional complementation of anthocyanin sequestration in the vacuole by widely divergent glutathione S-transferases. *Plant Cell* **1998**, *10*, 1135–1149. [[CrossRef](#)] [[PubMed](#)]
45. Li, J.; Xiao, Y.; Zhou, X.; Liao, Y.; Wu, S.; Chen, J.; Qian, J.; Yan, Y.; Tang, J.; Zeng, L. Characterizing the cultivar-specific mechanisms underlying the accumulation of quality-related metabolites in specific Chinese tea (*Camellia sinensis*) germplasms to diversify tea products. *Food Res. Int.* **2022**, *161*, 111824. [[CrossRef](#)] [[PubMed](#)]
46. Zhou, Q.; Sun, W.; Lai, Z. Differential expression of genes in purple-shoot tea tender leaves and mature leaves during leaf growth. *J. Sci. Food Agric.* **2016**, *96*, 1982–1989. [[CrossRef](#)] [[PubMed](#)]
47. He, X.; Huang, R.; Liu, L.; Li, Y.; Wang, W.; Xu, Q.; Yu, Y.; Zhou, T. CsUGT78A15 catalyzes the anthocyanidin 3-O-galactoside biosynthesis in tea plants. *Plant Physiol. Biochem.* **2021**, *166*, 738–749. [[CrossRef](#)]
48. Maritim, T.K.; Masand, M.; Seth, R.; Sharma, R.K. Transcriptional analysis reveals key insights into seasonal induced anthocyanin degradation and leaf color transition in purple tea (*Camellia sinensis* (L.) O. Kuntze). *Sci. Rep.* **2021**, *11*, 1244. [[CrossRef](#)]
49. Wei, K.; Wang, L.; Zhang, Y.; Ruan, L.; Li, H.; Wu, L.; Xu, L.; Zhang, C.; Zhou, X.; Cheng, H.; et al. A coupled role for CsMYB75 and CsGSTF1 in anthocyanin hyperaccumulation in purple tea. *Plant J.* **2019**, *97*, 825–840. [[CrossRef](#)]
50. Liu, Y.; Jiang, H.; Zhao, Y.; Li, X.; Xia, T. Three *Camellia sinensis* glutathione S-transferases are involved in the storage of anthocyanins, flavonols, and proanthocyanidins. *Planta* **2019**, *250*, 1163–1175. [[CrossRef](#)]
51. Stracke, R.; Ishihara, H.; Huep, G.; Barsch, A.; Weisshaar, B. Differential regulation of closely related R2R3-MYB transcription factors controls flavonol accumulation in different parts of the *Arabidopsis thaliana* seedling. *Plant J.* **2010**, *50*, 660–677. [[CrossRef](#)] [[PubMed](#)]
52. Chen, L.; Hu, B.; Qin, Y.; Hu, G.; Zhao, J. Advance of the negative regulation of anthocyanin biosynthesis by MYB transcription factors. *Plant Physiol. Biochem.* **2019**, *136*, 178–187. [[CrossRef](#)] [[PubMed](#)]
53. Chagné, D.; Wang, K.; Espley, R.V.; Volz, R.K.; How, N.M.; Rouse, S.; Brendolise, C.; Carlisle, C.M.; Kumar, S.; De Silva, N.; et al. An ancient duplication of apple MYB transcription factors is responsible for novel red fruit-flesh phenotypes. *Plant Physiol.* **2012**, *161*, 225–239. [[CrossRef](#)] [[PubMed](#)]
54. Huang, F.; Duan, J.; Lei, Y.; Kang, Y.; Luo, Y.; Chen, Y.; Ding, D.; Li, S. Metabolomic and transcriptomic analyses reveal a MYB gene, CsAN1, involved in anthocyanins accumulation separation in F1 between ‘Zijuan’ (*Camellia sinensis* var. *assamica*) and ‘Fudingdabaicha’ (*C. sinensis* var. *sinensis*) tea plants. *Front. Plant Sci.* **2022**, *13*, 1008588. [[CrossRef](#)] [[PubMed](#)]
55. Sun, B.; Zhu, Z.; Cao, P.; Chen, H.; Chen, C.; Zhou, X.; Mao, Y.; Lei, J.; Jiang, Y.; Meng, W.; et al. Purple foliage coloration in tea (*Camellia sinensis* L.) arises from activation of the R2R3-MYB transcription factor CsAN1. *Sci. Rep.* **2016**, *6*, 32534. [[CrossRef](#)] [[PubMed](#)]
56. He, X.; Zhao, X.; Gao, L.; Shi, X.; Dai, X.; Liu, Y.; Xia, T.; Wang, Y. Isolation and characterization of key genes that promote flavonoid accumulation in purple-leaf tea (*Camellia sinensis* L.). *Sci. Rep.* **2018**, *8*, 130. [[CrossRef](#)] [[PubMed](#)]
57. Jiang, X.; Huang, K.; Zheng, G.; Hou, H.; Wang, P.; Jiang, H.; Zhao, X.; Li, M.; Zhang, S.; Liu, Y. CsMYB5a and CsMYB5e from *Camellia sinensis* differentially regulate anthocyanin and proanthocyanidin biosynthesis. *Plant Sci.* **2018**, *270*, 209–220. [[CrossRef](#)]
58. Wang, P.; Ma, G.; Zhang, L.; Li, Y.; Fu, Z.; Kan, X.; Han, Y.; Wang, H.; Jiang, X.; Liu, Y. A sucrose-induced MYB (SIMYB) transcription factor promoting proanthocyanidin accumulation in the tea plant (*Camellia sinensis*). *J. Agric. Food Chem.* **2019**, *67*, 1418–1428. [[CrossRef](#)]
59. Shui, L.; Li, W.; Yan, M.; Li, H.; Guo, F. Characterization of the R2R3-MYB transcription factor CsMYB113 regulates anthocyanin biosynthesis in tea plants (*Camellia sinensis*). *Plant Mol. Biol. Rep.* **2022**, *41*, 46–58. [[CrossRef](#)]
60. Li, M.; Li, Y.; Guo, L.; Gong, N.; Pang, Y.; Jiang, W.; Liu, Y.; Jiang, X.; Zhao, L.; Wang, Y.; et al. Functional characterization of tea (*Camellia sinensis*) MYB4a transcription factor using an integrative approach. *Front. Plant Sci.* **2017**, *8*, 00943. [[CrossRef](#)]
61. Zhao, X.; Li, P.; Zuo, H.; Peng, A.; Lin, J.; Li, P.; Wang, K.; Tang, Q.; Tadege, M.; Liu, Z.; et al. CsMYBL2 homologs modulate the light and temperature stress-regulated anthocyanin and catechins biosynthesis in tea plants (*Camellia sinensis*). *Plant J.* **2023**, *115*, 1051–1070. [[CrossRef](#)] [[PubMed](#)]
62. Liu, Y.; Hou, H.; Jiang, X.; Wang, P.; Dai, X.; Chen, W.; Gao, L.; Xia, T. A WD40 repeat protein from *Camellia sinensis* regulates anthocyanin and proanthocyanidin accumulation through the formation of MYB–bHLH–WD40 ternary complexes. *Int. J. Mol. Sci.* **2018**, *19*, 1686. [[CrossRef](#)] [[PubMed](#)]

63. Lee, W.J.; Jeong, C.Y.; Kwon, J.; Van Kien, V.; Lee, D.; Hong, S.-W.; Lee, H. Drastic anthocyanin increase in response to PAP1 overexpression in fls1 knockout mutant confers enhanced osmotic stress tolerance in *Arabidopsis thaliana*. *Plant Cell Rep.* **2016**, *35*, 2369–2379. [[CrossRef](#)] [[PubMed](#)]
64. Wang, Y.; Zhang, X.; Zhao, Y.; Yang, J.; He, Y.; Li, G.; Ma, W.; Huang, X.; Su, J. Transcription factor PyHY5 binds to the promoters of PyWD40 and PyMYB10 and regulates its expression in red pear ‘Yunhongli No. 1’. *Plant Physiol. Biochem.* **2020**, *154*, 665–674. [[CrossRef](#)] [[PubMed](#)]
65. Li, X.; Ahammed, G.J.; Li, Z.; Zhang, L.; Wei, J.; Shen, C.; Yan, P.; Zhang, L.; Han, W. Brassinosteroids improve quality of summer tea (*Camellia sinensis* L.) by balancing biosynthesis of polyphenols and amino acids. *Front. Plant Sci.* **2016**, *7*, 01304. [[CrossRef](#)] [[PubMed](#)]
66. Zhang, Y.; Jiang, L.; Li, Y.; Chen, Q.; Ye, Y.; Zhang, Y.; Luo, Y.; Sun, B.; Wang, X.; Tang, H. Effect of red and blue light on anthocyanin accumulation and differential gene expression in strawberry (*Fragaria × ananassa*). *Molecules* **2018**, *23*, 820. [[CrossRef](#)]
67. Wang, L.; Pan, D.; Liang, M.; Abubakar, Y.S.; Li, J.; Lin, J.; Chen, S.; Chen, W. Regulation of Anthocyanin Biosynthesis in Purple Leaves of Zijuan Tea (*Camellia sinensis* var. *kitamura*). *Int. J. Mol. Sci.* **2017**, *18*, 833. [[CrossRef](#)]
68. Lin, J.; Liu, F.; Zhou, X.; Tu, Z.; Chen, L.; Wang, Y.; Yang, Y.; Wu, X.; Lv, H.; Zhu, H.; et al. Effect of red light on the composition of metabolites in tea leaves during the withering process using untargeted metabolomics. *J. Sci. Food Agric.* **2022**, *102*, 1628–1639. [[CrossRef](#)]
69. Shirin, A.; Zhang, Y.; Mao, P.; Lei, Y.; Bai, P.; Wang, Y.; Ruan, L.; Xun, H.; Wu, L.; Cheng, H.; et al. Responses of secondary metabolites and transcriptomes in the tea cultivar ‘Zhong Ming 6’ (*Camellia sinensis*) to blue light and red light. *Plant Growth Regul.* **2022**, *98*, 343–358. [[CrossRef](#)]
70. Zheng, T.; Tan, W.; Yang, H.; Zhang, L.; Li, T.; Liu, B.; Zhang, D.; Lin, H. Regulation of anthocyanin accumulation via MYB75/HAT1/TPL-mediated transcriptional repression. *PLoS Genet.* **2019**, *15*, e1007993. [[CrossRef](#)]
71. Yu, S.; Li, P.; Zhao, X.; Tan, M.; Ahmad, M.Z.; Xu, Y.; Tadege, M.; Zhao, J. CsTCPs regulate shoot tip development and catechin biosynthesis in tea plant (*Camellia sinensis*). *Hortic. Res.* **2021**, *8*, 104. [[CrossRef](#)] [[PubMed](#)]
72. Ke, S.-W.; Chen, G.; Chen, C.; Tzen, J.T.C.; Yang, C. Ethylene signaling modulates contents of catechin and ability of antioxidant in *Camellia sinensis*. *Bot. Stud.* **2018**, *59*, 11. [[CrossRef](#)] [[PubMed](#)]
73. Tang, M.; Zhang, S.; Xiong, L.; Zhou, J.; Huang, J.; Zhao, A.; Liu, Z.; Liu, A. A comprehensive review of polyphenol oxidase in tea (*Camellia sinensis*): Physiological characteristics, oxidation manufacturing, and biosynthesis of functional constituents. *Compr. Rev. Food Sci. Food Saf.* **2023**, *22*, 2267–2291. [[CrossRef](#)] [[PubMed](#)]
74. Hu, J.; Zhang, L.; Sheng, Y.; Wang, K.; Shi, Y.; Liang, Y.; Zheng, X. Screening tea hybrid with abundant anthocyanins and investigating the effect of tea processing on foliar anthocyanins in tea. *Folia Hort.* **2020**, *32*, 279–290. [[CrossRef](#)]
75. Joshi, R.; Rana, A.; Gulati, A. Studies on quality of orthodox teas made from anthocyanin-rich tea clones growing in Kangra valley, India. *Food Chem.* **2015**, *176*, 357–366. [[CrossRef](#)] [[PubMed](#)]
76. Kerio, L.C.; Wachira, F.N.; Wanyoko, J.K.; Rotich, M.K. Total polyphenols, catechin profiles and antioxidant activity of tea products from purple leaf coloured tea cultivars. *Food Chem.* **2013**, *136*, 1405–1413. [[CrossRef](#)] [[PubMed](#)]
77. Wang, Q.; Cao, B.; Wang, Q.; Qin, D.; Pan, C.; Li, B.; Li, H.; Fang, K.; Ni, E.; Jiang, X.; et al. Research on the suitability of teas made from fresh tea leaves of purple tea. *Sci. Technol. Food Ind.* **2022**, *43*, 279–288.
78. Wei, L.; Lai, Z.; Deng, H.; Luo, X.; Qiu, Y.; Zhuge, T.; Huang, J. Study on the suitability of different tea types of the tea tree species Zijuan. *Agric. Technol.* **2023**, *43*, 4–6.
79. Zhou, Q.; Chen, Z.; Lee, J.; Li, X.; Sun, W. Proteomic analysis of tea plants (*Camellia sinensis*) with purple young shoots during leaf development. *PLoS ONE* **2017**, *12*, 0177816. [[CrossRef](#)]
80. Wang, X.; Zeng, X.; Qin, C.; Yan, X.; Chen, X.; Zhang, L.; Zhou, Y. *Herbaspirillum* sp. ZXN111 colonization characters to different tea cultivars and the effects on tea metabolites profiling on Zijuan (*Camellia sinensis* var. *assamica*). *J. Agric. Food Chem.* **2023**, *71*, 5283–5292. [[CrossRef](#)]
81. Mohammed, H.A.; Khan, R.A. Anthocyanins: Traditional uses, structural and functional variations, approaches to increase yields and products’ quality, hepatoprotection, liver longevity, and commercial products. *Int. J. Mol. Sci.* **2022**, *23*, 2149. [[CrossRef](#)] [[PubMed](#)]
82. Hou, D.; Yanagita, T.; Uto, T.; Masuzaki, S.; Fujii, M. Anthocyanidins inhibit cyclooxygenase-2 expression in LPS-evoked macrophages: Structure–activity relationship and molecular mechanisms involved. *Biochem. Pharmacol.* **2005**, *70*, 417–425. [[CrossRef](#)] [[PubMed](#)]
83. Tsuda, T.; Horio, F.; Osawa, T. Cyanidin 3-O-β-D-glucoside Suppresses Nitric Oxide Production during a Zymosan Treatment in Rats. *J. Nutr. Sci. Vitaminol.* **2002**, *48*, 305–310. [[CrossRef](#)] [[PubMed](#)]
84. Joshi, R.; Rana, A.; Kumar, V.; Kumar, D.; Padwad, Y.S.; Yadav, S.K.; Gulati, A. Anthocyanins enriched purple tea exhibits antioxidant, immunostimulatory and anticancer activities. *J. Food Sci. Technol.* **2017**, *54*, 1953–1963. [[CrossRef](#)] [[PubMed](#)]
85. Lin, C.; Lin, H.; Chang, H.; Chuang, L.; Hsieh, C.; Lu, S.; Hung, C.; Chang, J. Prophylactic effects of purple shoot green tea on cytokine immunomodulation through scavenging free radicals and NO in LPS-stimulated macrophages. *Curr. Issues Mol. Biol.* **2022**, *44*, 3980–4000. [[CrossRef](#)] [[PubMed](#)]
86. de Moura, C.; Kabbas Junior, T.; Pedreira, F.R.d.O.; Azevedo, L.; Furtado, M.M.; Sant’Ana, A.S.; Franchin, M.; Gonzaga, V.R.; Cui, Y.; Wen, M.; et al. Purple tea (*Camellia sinensis* var. *assamica*) leaves as a potential functional ingredient: From extraction of phenolic compounds to cell-based antioxidant/biological activities. *Food Chem. Toxicol.* **2022**, *159*, 112668. [[CrossRef](#)]

87. van Zwieten, P.A.; Mancía, G. Background and treatment of metabolic syndrome: A therapeutic challenge. *Semin. Cardiothorac. Vasc. Anesth.* **2006**, *10*, 206–214. [[CrossRef](#)]
88. Shimoda, H.; Hitoie, H.; Nakamura, S.; Matsuda, H. Purple tea and its extract suppress diet-induced fat accumulation in mice and human subjects by inhibiting fat absorption and enhancing hepatic carnitine palmitoyltransferase expression. *Int. J. Biomed. Sci.* **2015**, *11*, 67–75. [[CrossRef](#)]
89. da Silva, T.B.V.; Castilho, P.A.; Sá-Nakanishi, A.B.d.; Seixas, F.A.V.; Dias, M.I.; Barros, L.; Ferreira, I.C.F.R.; Bracht, A.; Peralta, R.M. The inhibitory action of purple tea on in vivo starch digestion compared to other *Camellia sinensis* teas. *Food Res. Int.* **2021**, *150*, 110781. [[CrossRef](#)]
90. da Silva, T.B.V.; Dias, M.I.; Pereira, C.; Mandim, F.; Ivanov, M.; Soković, M.; Ferreira, I.; Barros, L.; Seixas, F.A.V.; Bracht, A.; et al. Purple tea: Chemical characterization and evaluation as inhibitor of pancreatic lipase and fat digestion in mice. *Food Funct.* **2023**, *14*, 1761–1772. [[CrossRef](#)]
91. Lin, Y.; Lu, H.; Chen, J.; Huang, H.; Chen, Y.; Su, Y.; Tung, C.; Huang, C. Purple-leaf tea (*Camellia sinensis* L.) ameliorates high-fat diet induced obesity and metabolic disorder through the modulation of the gut microbiota in mice. *BMC Complement. Med. Ther.* **2020**, *20*, 376. [[CrossRef](#)] [[PubMed](#)]
92. Mbuthia, K.S.; Mireji, P.O.; Ngure, R.M.; Stomeo, F.; Kyallo, M.; Muoki, C.; Wachira, F.N. Tea (*Camellia sinensis*) infusions ameliorate cancer in 4T1 metastatic breast cancer model. *BMC Complement. Altern. Med.* **2017**, *17*, 202. [[CrossRef](#)] [[PubMed](#)]
93. Hsu, C.; Shih, Y.; Lin, B.; Chiu, C.; Lin, C. Inhibitory Effect and Mechanisms of an Anthocyanins- and Anthocyanidins-Rich Extract from Purple-Shoot Tea on Colorectal Carcinoma Cell Proliferation. *J. Agric. Food Chem.* **2012**, *60*, 3686–3692. [[CrossRef](#)] [[PubMed](#)]
94. Lin, C.; Hsu, C.; Chen, C.; Liao, T.; Chiu, C.; Lien, L.P.J.; Shih, Y. Anti-proliferation and radiation-sensitizing effect of an anthocyanidin-rich extract from purple-shoot tea on colon cancer cells. *J. Food Drug Anal.* **2012**, *20*, 328–331. [[CrossRef](#)]
95. de Moura, C.; Kabbas, T.; Mendanha Cruz, T.; Boscacci Marques, M.; Araújo Vieira do Carmo, M.; Turnes Pasini Deolindo, C.; Dagher, H.; Azevedo, L.; Xu, Y.-Q.; Granato, D. Sustainable and effective approach to recover antioxidant compounds from purple tea (*Camellia sinensis* var. *assamica* cv. Zijuan) leaves. *Food Res. Int.* **2023**, *164*, 112402. [[CrossRef](#)]
96. Bashir, A.; Khan, F.; Al Mughairbi, F. Purple tea composition and inhibitory effect of anthocyanin-rich extract on cancer cell proliferation. *Front Hum. Neurosci.* **2019**, *229*, 00028. [[CrossRef](#)]
97. Maeda-Yamamoto, M.; Nishimura, M.; Kitaichi, N.; Nesumi, A.; Monobe, M.; Nomura, S.; Horie, Y.; Tachibana, H.; Nishihira, J. A randomized, placebo-controlled study on the safety and efficacy of daily ingestion of green tea (*Camellia sinensis* L.) cv. “Yabukita” and “Sunrouge” on eyestrain and blood pressure in healthy adults. *Nutrients* **2018**, *10*, 569. [[CrossRef](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.