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### Molecular and Metabolic Changes under Environmental Stresses: The Biosynthesis of Quality Components in Preharvest Tea Shoots

Jianjun Liu, Beibei Wen, Xiaobo Liu, Yun Yang, Meifeng Li \* and Xiaojing Wang \*

College of Tea Science, Guizhou University, Guiyang 550025, China; jjliu3@gzu.edu.cn (J.L.); jdllqcclfc@163.com (B.W.); xbliu@gzu.edu.cn (X.L.); 17585113068@163.com (Y.Y.) \* Correspondence: mfli3@gzu.edu.cn (M.L.); xjwang8@gzu.edu.cn (X.W.)

**Abstract:** Severe environments impose various abiotic stresses on tea plants. Although much is known about the physiological and biochemical responses of tea (*Camellia sinensis* L.) shoots under environmental stresses, little is known about how these stresses impact the biosynthesis of quality components. This review summarizes and analyzes the changes in molecular and quality components in tea shoots subjected to major environmental stresses during the past 20 years, including light (shade, blue light, green light, and UV-B), drought, high/low temperature, CO<sub>2</sub>, and salinity. These studies reveal that carbon and nitrogen metabolism is critical to the downstream biosynthesis of quality components. Based on the molecular responses of tea plants to stresses, a series of artificial methods have been suggested to treat the pre-harvest tea plants that are exposed to inhospitable environments to improve the quality components in shoots. Furthermore, many pleiotropic genes that are up- or down-regulated under both single and concurrent stresses were analyzed as the most effective genes for regulating multi-resistance and quality components. These findings deepen our understanding of how environmental stresses affect the quality components of tea, providing novel insights into strategies for balancing plant resistance, growth, and quality components in field-based cultivation and for breeding plants using pleiotropic genes.

**Keywords:** *Camellia sinensis;* environmental stresses; quality components; molecular mechanisms; preharvest treatment; multifunctional genes; breeding

### 1. Introduction

Tea tree (*Camellia sinensis* L.) is an important worldwide cash crop. Tea, which is made from its tender shoots, is one of the most important beverages in the world, and its value is heavily dependent on its sensory qualities and health benefits. Primary metabolites, such as amino acids and lipids, and secondary metabolites, such as catechins, flavonoids, anthocyanins, terpenes, carotenoids, and caffeine, are important contributors to the sensory quality and health benefits of tea. The quality components are generally produced from the following pathways: amino acid metabolism, caffeine metabolism,  $\alpha$ -linolenic and linoleic acid degradation, flavonoid biosynthesis, and terpenoid biosynthesis. Tea shoots that are rich in those metabolites (quality components) and their corresponding precursors are recognized as high-grade materials. However, the contents and proportions of quality components are seriously influenced by agro-climatic conditions [1,2].

Global warming has triggered drastic environmental changes and a series of extreme climate events, according to the Intergovernmental Panel on Climate Change (IPCC) (https://www.ipcc.ch/srccl/chapter/summary-for-policymakers/, accessed on 21 Semptember 2021) [3]. Environmental stresses, such as light, drought, cold, high temperature, and high salinity, among others, threaten the growth of food and cash crops [4]. To survive, plants have developed mechanisms for stress perception, signal transduction, and genetic and metabolic reprogramming [5–7]. This reprogramming, which is based on defense responses,



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**Copyright:** © 2022 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/). often impacts the crop composition and the origin of the nutritional value, flavor, color, and aroma [8].

In view of the importance of the quality components in tea shoots to the quality of tea, the effects of environmental stresses on tea quality components have garnered significant attention in recent years. When the tea tree recognizes threat signals, it will adjust the metabolism of its primary and secondary pathways to improve its resistance and mitigate the impact of environmental stresses, such as drought, high temperature, cold, and UV light [2,9–11]. In plants, the primary and secondary biosynthetic pathways are dependent, and the secondary biosynthetic pathways are initiated from the primary biosynthetic ones, and thus, originate from carbon and nitrogen metabolism [12]. Stress unbalances the metabolism of carbon and nitrogen and redistributes the metabolic flux in primary and secondary biosynthetic pathways, which subsequently changes the accumulation of quality components. Subsequently, the quality components, including volatile and non-volatile compounds, differentially accumulate in the tea shoots, which will affect the final quality of tea products. Many factors in plants ranging from stress perception to the synthesis of metabolites play important roles in this course, including signal receptors, signaling factors, transcription factors (TFs), and synthetic genes among others [13–15]. The accumulation of quality components in those pathways greatly depends on the stress conditions, which finally improve or degrade the quality of tea. However, although the relationship between environmental stresses and tea quality has been studied, there is a substantial lack of a review that summarizes previous studies. First, how these stresses impact the quality components in tea shoots is still not clearly understood. Secondly, the effects that these stresses have on the final product in terms of sensory qualities and nutrition remain unclear, and third, the methods required to manage stresses when considering plant growth and quality have yet to be established.

In this review, we focus on the changes in quality components in tea shoots under the main environmental stresses, including light (shade, blue light, green light, and UV-B), drought, high temperature, low temperature, CO<sub>2</sub>, and salinity, and we review how the components are affected by these stresses. In addition, we also consider the current strategies for tea cultivation and processing and the prospects for tea breeding.

### 2. Quality Components and Their Metabolic Pathways in Tea Shoots

### 2.1. Taste Contributors and Their Biosynthetic Pathways in Tea Shoots

The flavor of tea primarily consists of properties that affect its taste. These are the most substantial contributors to quality. Amino acids, polyphenols, and caffeine are generally the most important contributors to taste, and their de novo biosynthesis has been well studied.

Amino acids provide the taste of umami and are easily converted into aroma compounds during the baking process. Theanine is a unique and abundant amino acid that comprises >50% of the total free amino acids in tea. Its consumption has a calming effect, is neuroprotective, and enhances memory. Theanine is primarily synthesized in tea roots and is subsequently transported to young shoots by amino acid permease family members [16]. During the biosynthethic process, L-glutamine serves as the precursor of L-glutamate via glutamine synthetase (GS) and glutamate synthase (GOGAT), whereas ethylamine is formed from L-alanine by arginine decarboxylase (ADC) [17]. L-glutamic acid and ethylamine are then provided as precursors to synthesize theanine via theanine synthase [17]. However, a recent study reported that L-alanine is not a direct precursor of ethylamine, but instead serves as a precursor of L-glutamate, which is involved in the biosynthesis of L-theanine in tea [18]. Theanine in the tea plant is considered to store nitrogen [19] and enhances the growth and stress tolerance of tea plants [20].

Polyphenols are described as bitter and astringent taste contributors that function as antioxidants. Tea polyphenols are primarily composed of catechins (epicatechin [EC], epigallocatechin [EGC], epicatechin gallate [ECG], epigallocatechin gallate [EGCG], catechin [C], gallocatechin [GC], catechin gallate [CG], and gallocatechin gallate [GCG], respectively, which comprise 12–16% of the dry weight in tea shoots. Catechin is synthesized in the flavonoid pathway, and is regulated by several key rate-limiting enzymes, including phenylalanine ammonia lyase (PAL), cinnamate 4-hydroxylase (C4H), 4-coumaroyl-CoA ligase (4CL), chalcone synthase (CHS), chalcone isomerase (CHI), flavanone 3'-hydroxylase (F3'H), flavanone 3',5'-hydroxylase (F3'5'H), flavanone 3-hydroxylase (F3H), flavonol synthase (FLS), dihydroflavonol 4-reductase (DFR), leucoanthocyanidin reductase (LAR), anthocyanidin synthase (ANS), anthocyanidin reductase (ANR), flavonoid-3-O glycosyltransferases (F3GT), isoflavone 2-hydroxylase (I2'H), UDPG flavonoid glucosyltransferase (UFGT), and hydroxycinnamoyl transferase (HCT) [21] (Figure 1b). The expression of these structural genes is closely related to the level of catechin and often affected by multiple environmental factors and seasonal variation [22,23].

Caffeine, 1,3,7-trimethylxanthine, is an important purine alkaloid present in tea plants. This alkaloid has a bitter taste, antibacterial functions and excites the central nervous system. Caffeine primarily accumulates in tender tissues (20–50 mg g<sup>-1</sup>) and seeds [24]. The metabolism of caffeine begins with S-adenosyl methionine, which provides the CH<sub>3</sub><sup>+</sup> moiety for the formation of 7-methylxanthosine, 7-methylxanthine, theobromine, paraxanthine, and caffeine from xanthosine. The enzymes 7-methylxanthosine synthase (XMT), N-MeNase, theobromine synthase (MXMT), 3,7-dimethylxanthine N-methyltransferase (DXMT), and caffeine synthase (TCS) are important in caffeine synthesis [17] (Figure 1a). However, the high level of expression of TCS synthase and its genes is what determines the level of caffeine in the tea trees, as well as the expression of related enzymes and genes in the degradative pathways [24]. Furthermore, the content of caffeine is significantly affected by seasonal variation, such as pre-monsoon, monsoon, and autumn [25]. Thus, it is apparent that tissue development and environmental factors can significantly affect the biosynthesis of caffeine in tea.



Figure 1. Cont.



Figure 1. Biosynthetic pathways of the main quality components in tea. The biosynthetic pathways of theanine, caffeine, green leaf volatiles (GLV), volatile terpenes (VT), and carotenoids (a), and the biosynthetic pathways of volatile phenylpropanoids/benzenoids (VPBs) and catechins (b). AAAT, aromatic amino acid aminotransferases; ACAT, Acetoacetyl-CoA; ADC, arginine decarboxylase; ADH, Alcohol dehydrogenase; AIM1, abnormal inflorescence meristem1; ANR, anthocyanidin reductase; ANS, anthocyanidin synthase; BA2H, benzoic acid 2-hydroxylase; BALDH, benzaldehyde dehydrogenase; BMST, salicylic acid carboxyl methyltransferase; BPBT, benzoyl-CoA:benzylalcohol/2phenylethanol benzoyl transferase; CHI, chalcone isomerase; CHS, chalcone synthase; CM, chorismate mutase; DFR, dihydroflavonol 4-reductase; DXR, 1-deoxy-D-xylulose 5-phosphate reductoisomerase; DXS, 1-deoxy-D-xylulose-5-phosphate synthase; EPS1, ENHANCED PSEUDOMONAS SUSCEPTI-BILITY 1; FDPS, farnesyl diphosphate synthase; F3H, flavanone-3-hydroxylase; F3'5'H, flavonoid 3',5'-hydroxylase; GGPPS, geranylgeranyl pyrophosphate synthase; GOGAT, glutamate synthase; GS, glutamine synthetase; HMGR, 3-hydroxy-3-methylglutaryl-coenzyme A reductase; HMGS, hydroxymethyl glutaryl-CoA synthase; HPL, hydroperoxide lyase; ICS, isochorismate synthase; IDI, isopentenyl-diphosphate Delta-isomerase; LAR, leucoanthocyanidin reductase; LOX, lipoxygenase; LYC, lycopene beta cyclase; MXMT, theobromine synthase; PAAS, phenylacetaldehyde synthase; PAL, phenylalanine ammonia lyase; PAR, phenylacetaldehyde reductase; PBS3, avrPphB SUSCEPTIBLE3; PDS, phytoene desaturase; PSY, phytoene synthase; SCPL1A, type 1A serine carboxypeptidase-like acyltransferases; TCS, caffeine synthase; TS, Theanine synthase; XMT, 7-methylxanthosine synthase; ZDS, carotene desaturase; 1PES, 1-Phenylethanol synthetase. Green represents the metabolic pathways of volatile components, while brown represents the metabolic pathways of non-volatile quality components.

### 2.2. Aroma Contributors and Their Biosynthetic Pathways

Tea aroma, the second most important contributing factor to sensory quality, primarily originates from volatile compounds that are dominated by green leaf volatiles (GLVs), volatile terpenes (VTs), and volatile phenylpropanoids/benzenoids (VPBs). Tea shoots with rich volatile compounds and their precursors are considered high-grade raw materials for elite tea.

GLVs, 6- to 10-carbon aroma compounds, are mostly derived from the degradation of unsaturated fatty acids, including  $\alpha$ -linolenic, linoleic, oleic, and palmitoleic acids. The degradation of  $\alpha$ -linolenic acid is the principal pathway that produces GLVs. Lipoxygenase (LOX) and hydroperoxide lyase (HPL) play major roles in the oxidation and lipolysis of unsaturated fatty acids during the degradation process. Six-carbon GLVs that are derived from  $\alpha$ -linolenic acid, such as (E)-2-hexanal, (E)-2-hexanol, and (Z)-3-hexanol, contribute to the fresh and greenish odors, whereas GLVs with longer carbon chain, including nonenal, nonenol, and nonadienal, contribute to the pleasant odors in tea [26,27] (Figure 1a).

VTs possess floral, fruity, and sweet odorants and comprise the major fraction of tea aroma. Their constitution and quantity are vital to the sensory evaluation of teas. Terpenes have a wide range of medicinal uses, such as antiplasmodial and antiviral activities, along with their use as anticancer and antidiabetic reagents [28]. The terpenoid backbone and carotenoid biosynthesis are the principal sources of volatile terpenes, including monoterpenes, sesquiterpenes,  $\beta$ -ionone,  $\beta$ -damascone, and the aspirone among others [29]. Two pathways are involved in the biosynthesis of terpenoid backbone. The mevalonate pathway (MVA pathway) and the methylerythritol 4-phosphate pathway (MEP pathway), and 3-hydroxy-3-methylglutaryl-coenzyme A reductase (HMGR), 1-deoxy-D-xylulose-5phosphate synthase (DXS), and 1-deoxy-D-xylulose-5-phosphate reductoisomerase (DXR) are the rate-limiting enzymes of these two pathways. Farnesyl diphosphate synthase (FPPS) and geranylgeranyl pyrophosphate synthase (GGPPS) play substantial roles in the biosynthesis of geranyl diphosphate, farnesyl diphosphate, and geranylgeranyl diphosphate, which are converted into several monoterpenes, sesquiterpene, and carotenoids, respectively. In carotenoid biosynthesis, a series of enzymes, including phytoene synthase (PSY), phytoene desaturase (PDS), carotene desaturase (ZDS), and lycopene  $\beta$ -cyclase (LYC), are crucial for synthesizing diverse aroma precursors that primarily include  $\alpha$ -carotene,  $\beta$ -carotene,  $\gamma$ -carotene, lycopene, phytofluene, lutein, cryptoxanthin, zeaxanthin, and neoxanthin (Figure 1a). These precursors can be converted to 13 carbon cyclic aroma compounds, including  $\alpha$ -ionone,  $\beta$ -ionone, linalool,  $\beta$ -damascenone, and the aspirone, among others, by both enzymatic oxidative degradation during fermentation and nonenzymatic degradation, such as photo-oxidation (solar withering and solar drying), auto-oxidation, and thermal degradation (steaming, pan-firing, rolling, and drying) [17]. In general, volatile terpenes are most abundant in the first leaves, followed by flowers, buds, mature leaves, and old leaves [30], and can be significantly induced by abiotic and biotic stresses [31].

VPBs, including benzaldehyde, benzyl alcohol, phenylacetaldehyde, phenethyl alcohol, and methyl salicylate, are important aroma components derived from the metabolism of phenylalanine (Figure 1b). Benzaldehyde has an almond flavor, and methyl salicylate has the characteristic odor of wintergreen oil, while benzyl alcohol, phenylacetaldehyde, and phenethyl alcohol have floral, fruity, sweet, and honey-like aromas, respectively. In Ca. sinensis, shikimic acid, prephenic acid, and phenylpyruvic acid are the upstream substrates of VPBs [32]. The enzymes phenylacetaldehyde synthase (PAAS), aromatic amino acid aminotransferases (AAAT), phenylacetaldehyde reductase (PAR), and 1-phenylethanol synthetase (1PES) have been identified as playing key roles in the production of phenylacetaldehyde and phenethyl alcohol [32] (Figure 1b), and 21 short-chain dehydrogenases are functionally responsible for the specific synthesis of (R)- and (S)-1-phenylethanol [33]. Benzaldehyde, benzyl alcohol, benzoic acid, benzylbenzoate, and methyl salicylate (MeSA) are derived from the *trans*-cinnamic acid branch by phenylalanine ammonia lyase (PAL), benzaldehyde dehydrogenase (BALDH), and abnormal inflorescence meristem1 (AIM1) among others. [34,35]. Recently, several enzymes in the isochorismate pathway, which is the major route for the biosynthesis of salicylic acid (SA) and MeSA, were identified in Arabidopsis. These included isochorismate synthase (ICS), avrPphB Susceptible3 (PBS3), and Enhanced Pseudomonas Susceptibility1 (EPS1) [36,37]. VPBs have been investigated in tea flowers and leaves [38], and 1-phenylethanol (1PE) is particularly predominant in tea flowers [38].

Aromas form the major constituent of essential oils from plants. These natural products are not only important contributors to the quality of tea, but also provide defensive benefits for an organism. For tea plants, these aromatic compounds are involved in the chemical resistance against biotic and/or abiotic stresses. Understanding the biosynthetic pathways of aromatic compounds in tea will provide insights into the level of changes of aroma substances and the quality changes in fresh tea shoots that are affected by environmental changes.

#### 3. Molecular and Metabolic Responses of Tea Shoots to Environmental Stresses

3.1. Changes of Quality Components in Tea Shoots under Light Stress and the Associated Molecular Mechanisms

Light is an important environmental factor that regulates plant growth and metabolism. Photosynthesis and carbon and nitrogen fixation are essential to establishing metabolic reactions and creating energy sources for all organisms [39]. However, shade, excessive light, and ultraviolet (UV) radiation can induce stress responses in plants, resulting in remodeled metabolic pathways in tea.

Shade decreases the photosynthetic efficiency of plants and impacts their carbon and nitrogen metabolism. It has been reported that many genes involved in flavonoid and catechin biosynthesis, such as R2R3MYBs of MYB4, MYB12, MYB14, MYB111, MYBT1 and MYBT2, and the structural genes PAL, CHS, 4CL, F3H, F3'H, DFR, ANR1, LAR and ANS, are down-regulated by shade, resulting in reduced amounts of total catechins and glycosylflavonoids [22,40,41]. Simultaneously, shade induces the proteolysis of chloroplast proteins through an ATP-dependent Clp protease proteolytic subunit 3 (CLPP3) and protease Do-like 2 (DEGP2), while causing the up-regulation of theanine synthetase (TS), leading to increases in the contents of total amino acids and theanine [42,43]. These genes and proteases result in increased levels of amino acids, and decreased levels of total flavonoids and total polyphenols, which lead to a lowered TP/AA ratio, an important index for green tea (Figure 2a). Furthermore, shade significantly increases levels of volatiles of GLVs, VPBs, VTs [32] (Figure 2a). High-quality green tea is produced from buds and young leaves grown by a covering-culture method, which involves growing *Ca. sinensis* in the shade [44]. Additionally, tea grown under artificial shade in Kenya produced black tea with a better flavor index and evaluation by tasters than tea grown in the sun [45].



**Figure 2.** Effects of shade (**a**), blue and green light (**b**), and UV-B (**c**) on tea metabolites. CLPP3, ATPdependent Clp protease proteolytic subunit 3; COP1, CONSTITUTIVE PHOTOMORPHOGENIC 1; CRY, cryptochrome; CUL4, CULLIN4; DDB1, DET1-Damaged DNA Binding Protein 1; DEGP2, protease Do-like 2; HY5, ELONGATED HYPOCOTYL 5; SPA, SUPPRESSOR OF PHYA; UVR8, UV RESISTANCE LOCUS 8.

Single wavelength light radiation has been found to regulate the compounds responsible for aroma and flavor in tea shoots in recent years (Figure 2b). Blue and red light have been reported to induce GLVs, VPBs, and VTs by up-regulating the expression of 9/13-LOX, PAL, and terpene synthase (TPS) [46]. Blue light facilitates the accumulation of anthocyanins and catechins by up-regulating several R2R3-MYBs, including *MYB12*, *MYB44*, *TT2*, and anthocyanin regulatory C1 (*C1*) and most of the genes in flavonoid biosynthetic pathway, including *4CL*, *CHS*, *C4H*, *CHI*, *F3H*, *F3'H*, *F3',5'H*, *ANR*, and flavonol synthase (*FLS*) [47]. Green light inhibits the accumulation of catechins by tempering their TFs and structural genes [47]. However, blue combined with green light enhances anthocyanin but reduces catechins by increasing the levels of expression of *CHS*, *F3'H*, *DFR*, and *ANR* and decreasing the levels of expression of *CHI*, *F3H*, *F3',5'H*, *FLS* and *UFGT* [31]. In addition, high-intensity blue light (200 µmol m<sup>-2</sup> s<sup>-1</sup>) has been shown to inhibit the photosynthetic, lipid metabolic, and flavonoid synthetic pathways [48]. Ultraviolet B inhibits plant growth

but increases the accumulation of certain compounds, such as phenol, chalcomoracin, and its precursor moracin N [9,49,50]. Following exposure to UV-B, total flavonoids and total catechins were significantly accumulated in *Ca. sinensis* owing to the marked up-regulation of *MYB4*, *MYB12*, *bHLH62*, and the structural genes of 4CL, *DFR-4*, *ANR-2*, *CHI*, *FLS1*, *ANS*, and *LAR-1~3* in flavonoid biosynthesis [51] (Figure 2c). UV-B also promotes diterpenoid biosynthesis but inhibits that of monoterpenoids following 2 h and 8 h of exposure, resulting in a reduction in VTs [51]. In the variety Ziyan, which is rich in anthocyanins, all UV treatments (UV-A, UV-B, and UV-AB) induced the accumulation of anthocyanins by up-regulating *ANS* and UDP-glucose:flavonoid 3-O-glucosyltransferase (*UFGT*) in anthocyanin biosynthesis but reduced the amounts of catechins by down-regulating *LAR* and *ANR* in catechin biosynthesis, resulting in a different type of regulation for catechin biosynthesis between Ziyan and other green-leaf varieties [52].

During the light-induced changes in plant metabolism, the coordination of light-signal modulators, composed of ELONGATED HYPOCOTYL 5 (HY5), CONSTITUTIVE PHO-TOMORPHOGENIC 1 (COP1), SUPPRESSOR OF PHYA (SPA), CULLIN4 (CUL4), and DET1-Damaged DNA Binding Protein 1 (DDB1), plays a vital part in the regulation of quality components in tea shoots. In darkness, the COP1–SPA complex acts in concert with the CUL4–DDB1 complex to target photomorphogenesis-promoting TFs, such as HY5, for ubiquitin-proteasome system-mediated degradation and to repress the traditional photomorphogenesis triggered by far-red and visible light [13]. When exposed to light, cryptochrome (CRY) and phytochrome (PHY) photoreceptors interact with SPA1 to inhibit the formation of the COP1-SPA complex, thereby stabilizing substrate transcription factors, including HY5, and promoting photomorphogenesis [53,54]. The COP1–SPA complex disassociates with CUL4-DDB1 in seedlings treated with UV-B and recruits UV RESISTANCE LOCUS 8 (UVR8) to establish a UVR8–COP1–SPA complex to facilitate HY5 stability and activity [13]. Similarly, shade decreases the expression of several photoreceptors in Ca. sinensis, including UVR8, HY5, COP1, and the WD repeat-containing protein RUP1/2 (RUP1/2), leading to the down-regulation of TFs and structural genes in flavonoid biosynthesis [40]. Blue light significantly induces SPA, HY5 and CRY2/3 to regulate downstream R2R3-MYBs to promote the biosynthesis of flavonoids, anthocyanins, and catechins [47]. Moreover, green light significantly decreases the level of expression of SPA and CRY2/3 to cancel the effect of blue light on the accumulation of metabolites [47]. Finally, as concluded in Figure 2, the coordination of light-signal modulators mediated the metabolic reprogramming of the biosynthesis of flavonoids, anthocyanins, and catechins through transcriptional regulatory networks, the ubiquitin-proteasome system and other regulatory mechanisms when responding to different light stresses. These findings revealed that the coordination of light-signal modulators is critically important to regulate the metabolic responses under different light conditions, and the application of light radiation could be an important research field in tea quality formation and regulation in the future.

## 3.2. Changes in the Quality Components in Tea Shoots under Drought Stress and Their Associated Molecular Mechanisms

Drought is considered to be one of the most significant environmental stresses that inhibits cell proliferation and expansion, while preventing plant growth and reducing yields. To ensure cell survival, plants modulate osmotic substances and antioxidants, such as free amino acids, total soluble sugars, flavonoids, and catechins, among others, to resist drought stress [55,56]. In tea plants, photosynthesis, glycolysis, and starch and sucrose metabolism have been revealed to respond to drought and provide various intermediates for primary and secondary metabolism [15,57].

Drought significantly impacts starch and sucrose metabolism. Sucrose, particularly soluble sugars, monosaccharides, and disaccharides, contribute to the sweetness of tea. Both sucrose and the hydrolyzed products of starch have this effect. Under drought stress, sucrose synthesis-related genes, such as sucrose-phosphate synthase 2/3/4 (*SPS2/3/4*), are up-regulated [57]. Moreover, many genes related to starch synthesis are repressed,

including glucose-6-phosphate isomerase 1 (*PGI1*), soluble starch synthase 1 (*SSI1*), granulebound starch synthase 2 (*SS2*), glucose-1-phosphate adenylyl transferase large subunit 1 (*ADG2*), and glucose-1-phosphate adenylyl transferase large subunit (*AGPS1/3*). However, the genes involved in starch degradation are up-regulated and include  $\alpha$ -amylase 1/1.1 (*AMY1/1.1*) and  $\beta$ -amylase  $\frac{1}{2}/3/7$  (*BAM1/2/3/7*) [57]. These molecular changes in starch and sucrose metabolism increase the levels of soluble sugars, and therefore improve the osmotic stress dynamics in tea plants, while contributing to the sweetness of tea flavor.

Drought stress also changes the carbon flux in the flavonoid pathway. Previous studies have indicated that flavonoids typically accumulate, but the levels of catechin are reduced [15,58,59]. Compared with the control, mild, severe, and moderate drought can benefit the accumulation of glycosylflavonoids and isoflavonoids by significantly upregulating the levels of expression of *CHS*, Type III polyketide synthase B (*PKSB*), FLS, flavone synthase (*FNS*), *F3H*, *F3'5'H*, and glycosyltransferases (*UGT94P1* and *UFGT*) but inhibit the accumulation of catechin and anthocyanin by significantly repressing the levels of expression of *DFR*, *ANS*, *LAR*, and *ANR* [15]. Moreover, *MYB16-like* and *MYB108-like*, negative regulators of flavonoid biosynthesis, are repressed by moderate drought [15]. This study revealed that moderate drought promoted the biosynthesis of glycosylflavonoids and isoflavonoids, which increase the solubility of flavonoids to enhance the absorptivity of beneficial compounds by the human body.

Most amino acids are derived from the intermediates produced by the TCA cycle. Drought significantly enhances the activity of TCA cycle and amino acid metabolism [14,15]. Total amino acids increase under moderate drought but decrease under severe drought [2,15]. Other studies have noted that theanine accumulates under mild drought but is then reduced under moderate and severe drought [15,60]. However, PEG6000 resulted in a decrease in the levels of theanine via the down-regulation of *GOGAT*, glutamate dehydrogenase (*GDH*), alanine aminotransferase (*ALT*), *ADC*, and *TS* [59]. These studies showed that drought stress can significantly increase the levels of total amino acids, thereby enhancing the sweetness and umami taste of tea infusions.

Caffeine is a chemical defense substance with a bitter taste that is derived from purine metabolism. It protects plants from various abiotic and biotic stresses, such as the fungus *Colletotrichum gloeosporioides* [61]. Mild drought increases the level of caffeine, while severe drought decreases it in most tea cultivars under field conditions [1,60,62]. However, PEG treatment continues to reduce the contents of caffeine owing to the down-regulation of TCS [63]. The evidence suggests that the metabolism of caffeine is closely associated with the treatment and intensity of drought, which provides a strategy to reduce the bitterness of caffeine by means of drought stress.

Drought induces the emission of isoprene, monoterpenes, fatty acid derivatives, amino acid derivatives, and phenylpropanoids in many ligneous and herbaceous plants [64,65]. Spice plants in semiarid areas, such as the Mediterranean region, often produce more secondary metabolites than identical plants of the same species cultivated in moderate climates [66]. Tea farmers have long observed that the characteristic flavors and aromas of tea are enhanced by dry weather in the traditional tea-growing regions of the Kangra Valley, Darjeeling, Sri Lankan, and Yunnan Provinces [1,67]. Further investigation showed that drought stress increases the amounts of GLVs and VPBs by up-regulating the levels of expression of *LOXs*, *HPL*, *ADH*, hexenal isomerase (*HI*), and *BSMT1* but decreases VTs by down-regulating the level of expression of *TPSs* [14,57,60,68,69]. However, carotenoid biosynthesis, a process that provides precursors of carotenoid-derived aroma compounds, is significantly up-regulated under drought conditions to defend tea plants from oxidative damage and produce aroma precursors in preharvest tea shoots [57]. As revealed in previous studies, drought stress induced the levels of GLVs and VPBs, while increasing carotenoid biosynthesis, which all improved the aroma of tea.

Carbon metabolism, such as photosynthesis, glycolysis, starch and sucrose metabolism, has been revealed to provide intermediates into primary and secondary metabolism to participate in the drought response [57]. Drought promotes glycolysis and starch and

sucrose metabolism; however, it inhibits photosynthesis [57]. It has been hypothesized that the inhibition of photosynthesis, with decreased uptake and fixation of CO<sub>2</sub> under drought conditions, is compensated for by altered carbon allocation to maintain or increase secondary metabolism and protect the plants faced with stress [65]. This hypothesis explained the findings that amino acids, flavonoids, phenylpropanoids, GLVs, VPBs, and carotenoids accumulated, whereas the levels of catechins were reduced under drought stress (Figure 3a). Furthermore, the allocation of carbon explains the accurate regulation over quality compounds of tea in the future.





# 3.3. Changes in the Quality Components in Tea Shoots under Temperature Stress and the Associated Molecular Mechanisms

The growth and development of plants require certain temperature conditions. When the environmental temperature is not optimal, i.e., high temperature or low temperature (cold), for some time, plants can suffer heat or freezing damage. The plants initiate the reprogramming of their transcriptome, proteome, and metabolome to maintain cellular homeostasis and counteract the negative effects of extreme temperatures. Owing to differences in the symptoms and mechanisms of damage under high and low temperature, we separately summarized and analyzed the effects of two extreme temperatures on the metabolism of tea shoots.

High temperature inhibits the photosynthesis of higher plants and damages the antioxidant system. In response to heat stress, citrus accumulates many primary and secondary metabolites, such as sucrose, flavonol, coumarin scopoletin, scopolin, and sinapic acid, that serve as osmotic compounds and scavenge free radicals [70]. In wheat (*Triticum aestivum*) grains, phenolic acids and total flavonoids increase as the temperature increases from 20 °C to 30 °C, but unsaturated fatty acids such as linoleic acid and linolenic acid decrease [71]. In *Ca. sinensis* cv. 'Suchazao', moderate-high temperatures (MH, day/night, 30 °C/27 °C, 2 days) increased the levels of proteins related to photosynthesis, oxidation, and osmotic resistance to improve resistance; severe high temperatures (SH, day/night, 39 °C/32 °C, 2 days) enhance carbon metabolism, the glycolysis/gluconeogenesis pathway, starch and sucrose metabolism, and amino acid metabolism to maintain the survival of plant [72]. Anthocyanins notably accumulated in MH. However, they decreased in SH owing to the down-regulation of genes for enzymes in the flavonoid and anthocyanin pathway in SH, including PAL, C4H/CYP73A, 4CL, CHS, CHI, DFR, F3H, FLS, F3'H, F3'5'H/CYP75A, LAR, ANR, ANS, UGT75C1 and UGFT, whereas the genes for enzymes C4H, F3H, LAR and ANS were up-regulated during MH stress [72]. In addition, most of the amino acids, lipid fatty acids and lipid glycerophospholipids increased during SH [72]. Other studies found that MH increases the levels of total polyphenols, catechins (C, EC, GC, EGC, ECG, and EGCG), and caffeine by up-regulating the levels of expression of C4H, F3H, DFR, and ANR in flavonoid biosynthesis and the level of expression of inosine 5'-monophosphate dehydrogenase (TIDH) and TCP1 in caffeine metabolism, respectively; however, the accumulation of theanine decreased by repressing the levels of expression of ADC, GS, GOGAT, and TS [10,73]. This suggests that MH positively affects the accumulation of quality components that include amino acid, caffeine, catechins, anthocyanins and soluble sugars. In contrast, SH negatively affects the accumulation of anthocyanins. This discovery is consistent with the common observation that tea made in the summer is inferior and strongly bitter and astringent owing to the significant increase in total polyphenols and the TP/AA ratio. However, the metabolic changes during SH are different from those during MH, which merits further study in the aspects of the correlation of flavor with metabolites.

Low temperature stress affects enzyme activity, membrane systems, and cell dehydration in plants, leading to metabolic disturbance and even cell death. In many plants, soluble sugars and flavonoids are regarded as substantial metabolites that play key roles in facilitating the stability of cell membranes under cold conditions [74,75]. The same is true in *Ca. sinensis*. Low temperatures extensively influence the types of metabolism or pathways of tea plants, including carbon metabolism, the glycolysis/gluconeogenesis pathway, lipid metabolism, terpenoid backbone biosynthesis, carotenoid biosynthesis, and terpene biosynthesis among others [57,72,76]. The concentrations of soluble sugars, such as sucrose, raffinose, maltose, glucose, and fructose, are increased by dramatic starch degradation to provide energy for cold tolerance and subsistence [76,77]. During this process, the genes involved in starch hydrolysis, including AMY, BAM, glucan water dikinase (GWD), maltose transporter (MEX1), and disproportionate enzyme 2 (DPE2), are intensively induced, whereas the genes for starch synthesis, such as SS1/2, PGI1, ADG2, and AGPS1/3, are repressed [57,76]. Low temperatures increase the levels of anthocyanin by up-regulating the levels of expression of C4H, CHI, CHS, F3',5'H, F3H, FLS, leucoanthocyanidin oxidase (LDOX), UDP-glucose:anthocyanin 5-O-glucosyl transferase (UGT75C1), and UFGT but decreasing the concentrations of catechin and total polyphenols by downregulating the levels of expression of *LAR*, while changing the shoot color phenotype from green to purple [57,72]. Cold increases the glycosylation of eugenol, quercetin, kaempferol, and nerolidol by up-regulating the levels of expression of UGT78A15, UGT91Q2, and UGT78A14 [11,78,79]. However, a -5 °C freezing treatment significantly increased the concentration of total polyphenols, indicating a different mechanism that responds under freezing conditions compared with low temperatures [80]. Cold down-regulates theanine metabolism, such as GS and GOGAT, but causes the accumulation of total amino acids to adjust the osmotic regulation, with higher contents present in cold-tolerant varieties than in sensitive ones [57,72,81]. However, under conditions of -5 °C, the levels of total amino acid accumulation decreased to as low as 39.5%, resulting in an increase of the TP/AA ratio to 86.3% and a corresponding deterioration in quality [80]. These studies showed that a low temperature threshold that is related to cold resistance is crucial for tea quality (improved or deteriorated), while moderate low temperatures induce osmotic and antioxidant substances, such as soluble sugars, amino acids, and total polyphenols in tea shoots, that not only remodel the cold resistance of tea plants but also increase water extracts and decrease the TP/AA ratio to improve their quality.

Because both severe heat and freezing conditions are lethal, a discussion of the metabolic processes that occur under such conditions is not merited. Therefore, in this review, we only discuss the molecular and metabolic responses of tea plants under stresses that enable the plant to survive. Although the molecular mechanisms induced by high and low temperatures differ, several fundamental metabolic pathways, including starch and sucrose metabolism, amino acid metabolism, theanine metabolism, and flavonoid biosynthesis, are co-regulated to resist plant stresses, playing roles in free radical scavenging, lipid peroxidation inhibition, and cellular homeostasis (Figure 3b). However, there are specific pathways induced by these two different stresses. High temperature stress leads to the significant accumulation of caffeine, catechins, and total polyphenols via enhanced caffeine metabolism and catechin biosynthesis, while low temperature stress increases the levels of flavonoids and anthocyanins by enhancing the glycosylation of flavonoids and anthocyanin biosynthesis but decreasing the accumulation of catechins and total polyphenols by the repression of catechin biosynthesis. A better understanding of these shared and specific molecular and metabolic changes in tea shoots can provide a reference for improving the resistance of tea plants and quality components of tea shoots under low and high temperatures in the future.

## 3.4. Changes in the Quality Components in Tea Shoots under Elevated Levles of Carbon Dioxide and Their Associated Molecular Mechanisms

The elevated concentration of CO<sub>2</sub> in the atmosphere fertilizes terrestrial vegetation by stimulating photosynthetic rates and suppressing respiration [82]. In non-leguminous plants, elevated CO<sub>2</sub> increases the levels of carbohydrates while decreasing the levels of proteins and amino acids in plant leaves, probably owing to the increases in production of sugar and starch and a decrease in the allocation of nitrogen at the whole plant level [83,84]. These macronutrient changes are not only owing to the up-regulation of level of expression of sucrose phosphate synthase (SPS) and sucrose synthase (SUS), which determine the sink activity, but also to the down-regulated expression of the proteins involved in nitrogen uptake, deamination and assimilation, and nitrate transport, such as GDH1, aspartate synthetase (ASN1), ferredoxin-nitrate reductase (NiR), and low-affinity nitrate transporter (NRT1.5B) [84,85].

In tea plants, elevated levels of  $CO_2$  increase the rates of net photosynthesis and the rates of total respiration, salicyl hydroxamic acid (SHAM)-resistant respiration, and CN-resistant respiration [86]. Photosynthesis and respiration play fundamental roles in photoassimilate synthesis, C-skeleton intermediate generation, and energy supply. Enhanced photosynthesis and respiration promote the production of soluble saccharides, starch, and polyphenols, but repress the production of total nitrogen, caffeine, and free fatty acids, resulting in a higher C/N ratio [86,87]. This high C/N ratio favors the accumulation of carbon-based secondary metabolites, such as flavonoids, catechins, caffeic acid, carotenoids, and soluble sugars among others [86–89] (Figure 4a). The structural genes PAL, C4H, 4CL, CHS, CHI, DFR, ANS, ANR, and UFGT, which are controlled by CO<sub>2</sub>-dependent salicylic acid (SA) and nitric oxide (NO), are up-regulated to accumulate flavonoids and catechins [87,90]. The decrease in amino acids and theanine at elevated levels of  $CO_2$  is higher in the spring than in the summer and autumn [91]. Conversely, Li et al. [86] found that free amino acids and theanine increased with elevated CO<sub>2</sub>. The caffeine in tea shoots decreased with the down-regulated expression of TIDH, S-adenosyl-L-methionine synthase (SAMS), and TCS1 in caffeine metabolism under elevated levels of CO<sub>2</sub> [86,87].



**Figure 4.** Metabolic changes of tea plants under elevated levels of  $CO_2$  (**a**) and salt stress (**b**). Pink indicates up-regulated metabolic activity or increased quality components, while green indicates the down-regulation of metabolic activity or a decrease in quality components.

The effect of elevated  $CO_2$  on the quality of agricultural products has been widely investigated. Elevated  $CO_2$  is reported to decrease protein concentrations but improve the palatability of cooked rice [92]. The treatment of tomato fruit with elevated  $CO_2$  improves their flavor owing to an increase in the soluble sugar, lycopene, and carotenoid contents and decrease in the content of nitrate [93]. In *Ca. sinensis*, enrichment with  $CO_2$  results in the accumulation of quality components, such as soluble sugars, sucrose and starch, total polyphenols, and catechins, while diminishing nitrogen metabolism to decrease the amounts of proteins. Since amino acid and theanine metabolism are downstream pathways of both carbon and nitrogen metabolism, supplementation with a nitrogen source can compensate for the diminishing levels of amino acids and theanine caused by the inhibition of nitrogen metabolism, which is triggered by elevated  $CO_2$ . Therefore, the content of nitrogen in soil has been hypothesized to be the critical factor that determines the metabolic regulation of amino acids and theanine. However, in both cases, the TP/AA ratio increases in tea shoots, which suggests that elevated  $CO_2$  could help process black tea but not green tea.

# 3.5. Changes in the Quality Components in Tea Shoots under Salt Stress and Their Associated Molecular Mechanisms

Salinity is one of the major impediments to crop production throughout the world. Salinity causes ion toxicity and physiological drought, destroys fundamental carbon and nitrogen metabolic processes, and further disturbs the balance of secondary metabolites [94,95]. The transcriptome analysis showed that salt stress in *Ca. sinensis* interferes with photosynthesis, carbon metabolism, nitrogen metabolism, and the primary and secondary pathways for the biosynthesis of soluble sugars, amino acids, alkaloids, and phenylpropanoid and flavonoids among others [63] (Figure 4b). Salt stress up-regulates most biosynthetic genes involved in amino acid and carbohydrate metabolism but downregulates the genes involved in caffeine metabolism [63]. In response to salt stress, F3H is up-regulated to catalyze the biosynthesis of flavan-3-ols [96], while most terpene synthase genes decrease first and then recover slightly to differentially release VTs [69]. Under higher concentrations (100 and 150 mM NaCl), salt stress increases the levels of polyphenols, total amino acids, and theanine through the promotion of GS and TS activities [97,98]. Under lower concentrations (40 and 50 mM NaCl), salt stress decreases the levels of total polyphenols, amino acids, and caffeine, while increasing the TP/AA ratio [98,99]. Because there are few studies on the effect of salt stress on the accumulation of quality components in tea, how salt stress affects the molecular mechanisms from carbon and nitrogen metabolism to secondary metabolic synthesis is still poorly understood. Anyhow, these studies clearly indicate that salt stress extensively affects primary and secondary metabolism in tea plants, depending on the salt concentration and duration of exposure.

#### 4. Discussion and Prospects

# 4.1. Changes in Carbon and Nitrogen Metabolism Are Critical to the Levels of Quality Components in Tea Shoots

The biosynthesis of plant macromolecules requires C and N metabolites, and carbon and nitrogen metabolism are critical to the growth and productivity of plants [100]. Carbon and nitrogen metabolism is not only always affected by photosynthetic capacity and glycolysis [100,101], but also disturbed by many types of stresses, including drought and salt [100]. After an analysis of the molecular responses under different types of environmental stress, we discovered that changes in the level of quality components are closely related to carbon and nitrogen metabolism in tea shoots. For example, changes in the levels of quality components under light stress are regulated through R2R3MYBs that are induced by different combinations of light-signal modulators (Figure 3). These modulators, such as HY5, COP1, and SPA, coordinate the acquisition of carbon and nitrogen [102,103]. Drought, temperature, and salt stress, and elevated  $CO_2$  have a substantial impact on photosynthesis, and subsequently impact carbon and nitrogen metabolism, including starch and sucrose metabolism, glycolysis, nucleotide metabolism, amino acid metabolism, and many types of secondary metabolism (Figures 3 and 4), which is consistent with the conclusions of previous studies [94]. This suggests that the disturbance of carbon and nitrogen metabolism is the major factor that leads to changes in the levels of quality components in tea shoots.

# 4.2. Artificial Environments Could Be Created to Affect the Metabolic Biosyntheis of Preharvest Tea Shoots

With their high level of experience in tea planting and tea making, tea farmers in China have long realized that certain stresses aid in the formation of flavors and aromas during tea processing. Wound stresses, such as "tossing" for oolong tea and "heavy rolling" for black tea, are important for generating the typical floral aroma and thick and refreshing taste of oolong tea and the sweet and honey aroma and mellow taste of black tea. Different types of light radiation and light-wave bands have been used for withering to improve the overall quality of tea [104,105]. This suggests that endogenous metabolites in picked fresh leaves changed even when isolated from the branches over a period. Thus, many researchers have focused on increasing the levels of expression of functional genes during the spreading out process to improve tea quality before deactivating the enzymes [106,107]. However, during the withering process of postharvest tea shoots, the metabolic changes are likely to depend more on hydrolysis or enhanced enzymatic activities caused by dehydration than to the de novo biosynthesis of enzymes owing to the relatively long time needed to go from the expression of genes to enzymatic biosynthesis and functionating. This indicates that pretreatment of the preharvest tea shoots in field conditions may have to be more effective at improving the components of tea quality compared with postharvest treatment.

Specific environmental stresses have been found to benefit tea flavor and aroma. For example, dry and cool environments result in tea with better taste and aroma [1,2,15], and shading improves the flavor and aroma of matcha [22,32,42]. Pre-treating preharvest tea shoots with cold and shade enhances the "umami" and "sweet" flavors of green tea and white tea, respectively, by leading to the accumulation of amino acids and soluble sugars [72,79,108]. In terms of tea quality, the grade of tea materials is crucial to the sensory flavor of the tea product. However, unfavorable environments always have side effects on the metabolism of tea plants that result in a deterioration in sensory quality. Herein, we proposed preliminary plans to avoid the material degradation caused by the severe environments by using appropriate artificial methods. We used several examples to demonstrate this. Waterlogging represses the activity of PAL enzyme in the flavonoid pathway, which leads to a significant reduction in the content of catechins and caffeine [109]. The addition of drainage and the use of canopies can be used to reduce the soil water content and alleviate water-logging on tea trees, and the addition of blue and/or violet light can induce the level of expression of many genes involved in the flavonoid biosynthesis and

subsequently increase the content of flavonoids and catechins [47,51]. The strong UV-B rays in high-altitude areas cause the anthocyanin to precipitate in the tea leaves and reduces the production of monoterpenes [51], while artificial shading can be used to induce a green-revertible leaf phenotype and increase the levels of GLVs, VPBs, VTs, and amino acids [17]. In areas with little sunshine, the primary and secondary metabolic activities of tea plants can be enhanced by elevating  $CO_2$  concentration. It is worth noting that the developmental stage of tea shoot and the intensity of artificial stresses on tea plants are important for both the quality components and yields of tea shoots [15]. Therefore, to establish more effective stress management methods, the next step is to understand the impact of frequency and intensity of each stress and the optimal stage of tea shoots when stresses are applied to tea plants.

## 4.3. The Prospects of Studying the Co-Regulated Genes to Improve Quality Components and Multiresistance in Breeding and Field Cultivation

As is often the case, plants are subjected to concurrent environmental stresses because of their sessile nature. For example, tea plants often face high temperature and drought stresses in the summer and cold and drought stresses in the winter [57,110]. The molecular changes under multiple stresses are much more complicated than those that occur under a single stress, but many genes have shown trends of the co-up/down-regulation in this case [47,57]. These genes are increasingly being valued by researchers in the areas of plant resistance and nutrient reprogramming. First, these co-expressed genes are found to be multifunctional when faced with different stresses. For example, the blue-green lightspecific genes ZAT10, RBCS1A, CRPK1, TIL, VTC2, FBS1, WRKY33, MPK1, PTI5, RAV1, and *PR1B1* are also involved in biotic and abiotic stress responses to viruses, bacteria, cold, water deprivation, hydrogen peroxide, and phytoalexin biosynthetic processes [47]. Secondly, many co-up/down-regulated genes play substantial roles in regulating both primary and secondary metabolic biosynthesis. For example, a set of up-regulated genes under cold and drought stress play regulatory roles in carbohydrate metabolism, starch and sucrose metabolism, photosynthesis, and secondary metabolite biosynthesis [57]. Third, many genes are found to be involved in both plant resistance and metabolic biosynthesis. For example, phospholipid: diacylglycerol acyltransferase 1 (PDAT1), HMG2/R1/R2, aminotransferase ACS10 (ACS10), and LOX2.1/1.5 are induced by cold, drought, and colddrought conditions to delay leaf senescence, but PDAT1 and HMG2/R1/R2 also regulate lipid metabolism and terpenoid biosynthesis, while ACS10 and LOX2.1/1.5 play crucial roles in the accumulation of amino acids and the biosynthesis of GLV [57]. COP1 and HY5 improve the resistance of tea tree under various light stresses, and they are also important in regulating the biosynthesis of flavonoids and anthocyanins [47,111]. In addition, the co-up-regulation of MYB4, MYB12, and bHLH62 play important roles in both flavonoid biosynthesis and various types of abiotic and biotic resistance [15,51,112].

As the Earth warms, crop production is threatened by climate change in complex ways in the incidence of environmental stresses, pests, and pathogens [4,113]. Improving crop yield and composition per se and making it more resilient to stress will be crucial to ensuring food security in the coming decades [8]. There is increasing evidence suggesting that defensive genes serve as important regulators for the biosynthesis of primary and secondary metabolites [15,47,51,57,111,112]. Among these genes, those co-expressed genes described are recognized as being the most effective at regulating multi-resistance and metabolism, owing to constraints in resources. These types of pleiotropic genes have been explored in many studies to enhance agronomic prosperity. To activate the reprogramming of pleiotropic genes, the artificial environmental changes seem effective and sustainable during planting. For example, phytochrome-interacting factor 3 (*PIF3*, a TF in light signaling under UV-B stress) regulates the terpene synthase genes and terpenoid biosynthesis [114], and the induction of this pleiotropic gene using monochrome LED light was found to retard the development of the begomovirus and its vector whitefly [115]. In addition, genetic transformation of pleiotropic genes into crops using transgenic technology is considered to

be very effective. For example, maize (*Zea mays*) that overexpresses *LOX* not only possess enhanced resistance to osmotic pressures, drought, high salinity, and insect attack, it also has increased contents of GLVs, jasmonate, and herbivore-induced plant volatiles [116,117]. Previous studies have indicated that the co-regulated genes under various environmental stresses may be a key solution in the breeding and field cultivation of multi-resistant and quality-improved crops, which will be the focus of future research.

#### 5. Conclusions

With the increase in global warming, deteriorated environments and extreme climates are becoming more frequent, which impacts the nutrition of crops worldwide. Tea is the most consumed beverage crop in the world. However, the quality components that provide the material basis for the flavor and healthy benefits are significantly impacted by environmental stresses. In this review, we elucidated the metabolic changes and underlying molecular mechanisms in tea shoots under environmental stresses as much as possible. We discovered that the levels of quality components depend on the type and intensity of the environmental stress. Furthermore, we established a method for managing the stresses on tea plants when faced with inhospitable environments that can improve the quality and nutrition of tea to meet consumer needs and avoid inhibition in growth. In addition, pleiotropic genes have been found to be involved in multiple stresses and metabolic regulation. Since tea yields and quality components are both important for the tea industry, it has been proposed that future research be focused on the balance of the growth, resistance, and quality components in tea shoots when stresses are applied to tea plants and when pleiotropic genes should be used to enhance the quality of tea.

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