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Review

Advances in the knowledge of adaptive mechanisms mediating abiotic stress responses in *Camellia sinensis*

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1. Abstract

Abiotic stresses are wide-ranging environmental factors that adversely affect the yield and quality of tea plants (*Camellia sinensis*). As perennial woody economic plants, various environmental factors affect its growth and development. To survive under stress conditions, plants adapt to or withstand these adverse external environments by regulating their growth and morphological structure. Recently, there have been knowledges regarding the significant progress in the mechanisms of abiotic stresses (including cold and heat, drought, salt and heavy metal stresses) tolerance in tea plants. Many evidences suggest that several phytohormones are in response to various environmental stresses, and regulate plant stress adaptation. However, the regulatory mechanisms of plant abiotic stress responses and resistance remain unclear. In this review, we mainly summarize the studies on the adaptive physiological and molecular mechanisms of tea plants under abiotic stress, and discuss the direction for tea plant resistance and breeding strategies.

2. Introduction

Tea plant (*Camellia sinensis* (L.) O. Kuntze), as an important economic plant, is popularly and widely cultivated in the world because of the tea leaves used for making a beverage. In tandem with the light-demanding, dampness and shade characteristics of tea plants, it generally grows in warm and humid hills, mountains and plains. As perennial evergreen woody plants, its development and growth are severely affected by various environmental factors such as extreme temperature, drought, salinity, heavy metal pollution. In addition, biotic stress such as pests and diseases are also known to affect its yield and quality [1–3]. With the rapid development of industrial modernization and the increase of human activities in recent years, unfavorable external factors around the plants become more serious and frequent in the face of environmental pollution and climate change. Hence, the study of the response mechanisms of tea plants to abiotic stresses not only to improve its stress resistance, but also increase yield and agronomic traits. In this article, we review the effects of abiotic stress on the growth and development of tea plants, and provide the references for further study on the molecular mechanisms of

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plant stress resistance. It also expands the relevant knowledge to develop superior stress resistance and high yield cultivar.

3. Abiotic stress

3.1 Effects of high temperature stress on the growth and development of tea plants

Extreme temperature, which has a periodic variation by season, includes high temperature, low temperature and frost. It is the most common environmental factor that affects tea plant's growth in nature. In recent years, with the increase in human activities and exacerbation of global climate change, tea plants are often subjected to extreme high or low temperature environment. The yield and quality of tea plants was seriously affected by these adverse conditions [4–6]. When tea plants are suffered from high temperature stress, its growth and development are significantly inhibited, which mainly shows in physiological responses and metabolic abnormalities. In the natural environments, high temperature weather is often accompanied by drought. It has previously been shown that the stomatal conductance, net photosynthetic rate and transpiration rate of tea leaves are significantly lower under the combined stress of high temperature and drought than shading conditions [7].

Photosynthesis is regarded as the most important physiological and biochemical reaction in plants, which is most vulnerable to environmental stresses. Investigations on tea leaves photosynthetic system has shown that high temperature stress can inhibit the activity of enzymes that affect the electron transmission and the structure of photosystem I and II [8]. High temperature also leads to the overproduction of reactive oxygen species (ROS) in leaves and cause serious damage to tea plants. This can damage the plant leaves during growth and photosynthesis process [9]. The *C. sinensis* sucrose non-fermenting-related protein kinase (CsSnRK) can be induced by high temperature stress [10]. The *C. sinensis* transcription factor CsRAV2 is present mainly in roots and its expression can be largely induced by high temperature stress [11]. The *C. sinensis* heat shock protein CsHSP17.2 is located in the cytoplasm and nucleus. The shock protein has also been found to be induced by high temperature, but it is not induced by cold temperature. Heterologous expression of CsHSP17.2 can enhance the tolerance of Escherichia coli and Saccharomycetes to high temperature stress [12]. The CsHSP17.2 can also function as a molecular chaperone to improve plant stress tolerance under high temperature stress [12]. It does this by maintaining high levels of photosynthesis and protein synthesis efficiency, eliminating ROS as well as inducing the expression of high temperature stress-related genes.

Indeed, the current research on tea plants response to high temperature is insufficient as there are only a few reports on the physiological, biochemical and gene expression of the plants under high temperature stress [7, 8]. Due to its long growth cycle, tea plants are exposed to complex and ever-changing external environments during its growing process. During the summer, it is also often suffered from joint stresses of high temperature and drought. Therefore, it is difficult to get an accurate reflection of its response mechanisms to adverse stresses in the natural environments by a single experimental condition. During the study of tea plants, the functions of several stress-related genes are achieved by heterologous expression in Arabidopsis or tobacco. However, the study of molecular biology and heritage is still lagging behind in other plant models. In conclusion, for the conduction of depth-exploration of the molecular regulatory mechanisms of tea plants response to high temperature stress, further research is needed.

3.2 Effects of low temperature stress on the growth development of tea plants

Low temperature stress includes cold damage (above freezing point) and freeze injury (below freezing point) [13]. Tea trees thrive in a warm and humid climate, so the low temperature environment has become one of the main factors that affect their growth and development and restrict their geographical distribution. Cold damage or freeze injury caused by low temperature environment leads to the abnormality of cell membrane structures. Moreover, this results in reduction in enzyme activity and affects normal physiological response of tea plants, causing disorder of cell metabolism and eventually inhibition of the plant's growth [13, 14]. It has been found that the systems of enzyme protection, which includes peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD) etc., are involved in the cold resistance response [15]. The activities of POD, CAT and SOD are considerably higher in strong cold-resistant tea plants and lower in weak cold-resistant tea plants [16]. Soluble protein content is also remarkably higher in strong cold-resistant tea plants than those in weak cold-resistant tea plants [16]. Consequently, the activities of POD, CAT, SOD and soluble protein content can be used as the physiological evaluation indexes to identify the cold resistance of tea plants [15]. Under low temperature, it appeared to inhibit cellular respiration, reduce consumption of carbohydrate as well as increase content of soluble sugar and irreducible water. This thus contributes to enhancing the cold hardiness of tea plants [15, 17].

With the application of molecular biology and transcriptome technology, multiple genes related to tea plants response to cold stress have been identified. The *C. sinensis* cold-regulated gene *CsCOR1* is located in the cell wall [18]. Under low temperature or dehydration, the expression levels of *CsCOR1* in tea leaves are increased significantly [18]. The *C. sinensis* betaine aldehyde dehydragenase gene *CsBADH1* and choline monooxygenas gene *CsCMO* are key enzymes in the synthesis of betaine

[19, 20]. It has been found that low temperature induces the expression of both the enzymes. The *C. sinensis* transcription factor CsRAV2 is expressed in the roots, stems, leaves and flowers of tea plants. It is also found that the expression of *CsRAV2* is significantly up-regulated when tea plants are exposed to low temperature [11]. The transcription factors CsICE and CsCBF3 are related to low temperature stress of *C. sinensis* [21, 22]. CsICE is located in the nucleus while CsCBF3 is located in the nucleus and cell membrane and both the genes are detected in all tea organs. Low temperature can significantly induce the expression of CsICE and CsCBF3 (Fig. 1). In Arabidopsis, overexpression of CsICE and CsCBF3 can improve the tolerance of plants to low temperature [21, 22]. Further study has proved that CsCBF3 is involved in mediating the response of low temperature stress through regulation of the downstream gene-expression of AtCOR15a and AtCOR78 in the cold response pathway [22]. Zhao *et al*. [23] have reported that the expression of UGT91Q2 encoding a putative glucosyltransferase is strongly induced by cold stress. The glucosyltransferase UGT91Q2 specifically catalyzes and glycosylates the nerolidol. The glycosylated nerolidol exhibits significantly higher scavenging ability of ROS than dissociation state nerolidol. The down-regulation of UGT91Q2 expression reduces the accumulation of glucosides in tea plants as well as the scavenging capacity of ROS (Fig. 1). These eventually contribute to the increased tolerance of tea plants to cold stress [23].

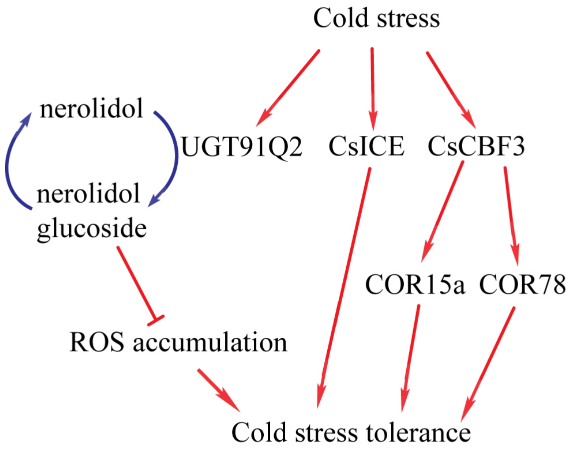

Fig. 1. A proposed model for UGT91Q2 and CsCBF3 involved in cold stress response.

Nerolidol, as the volatiles, which is synthesized and released from tea plants during cold stress. The expression of the glucosyltransferase UGT91Q2 is induced by cold stress. The plant cells can absorb nerolidol and convert it to the glucosylated nerolidol catalyzed by UGT91Q2. The nerolidol glucoside reduces the ROS accumulation and thus increases the cold tolerance of tea plants. The transcription factors CsICE and CsCBF3 are important cold responsive genes. The expression levels of *CsICE* and *CsCBF3* are induced by cold stress, CsCBF3 regulates the expressions of the cold-regulated gene COR15a and COR78 and improves the cold tolerance of plants. Abbreviations: UGT91Q2, sesquiterpene UDP-glucosyltransferase; ROS, reactive oxygen species.

So far, several genes related to the tea plants response to low temperature stress is mainly conducted for the cloning of tea plant genes into other plant models such as *Arabidopsis*, tobacco, etc. This is done so as to observe their expression and to verify the specific function of genes when tea plants are suffering from cold damage. However, there are few reports on transgenic researches about tea plants. Also, the in-depth research of molecular regulatory mechanisms is neither adequate nor systematic.

3.3 Effects of drought stress on the growth development of tea plants

Due to global warming and water shortage, drought stress has become one of the main limiting factors that affect tea plant production [1, 5]. Drought stress can seriously affect tea plant growth and yield, sometimes even causing death to the tea plants [24]. Some statistics have it that, in some major tea plant producing regions around the world, the losses of tea production caused by drought is about 17–33%. These stats also show that large regional differences exist as different geographical environment and tea plant varieties. For instance, the yield of tea plants tends to decrease during drought, by 17%–31% in some regions of India [25], by about 26% in some regions of Sri Lanka [26], and by about 33% in some regions of Tanzania [27]. Going on, in Yunnan, Guizhou provinces and other southern tea producing regions of China, the losses of tea production caused by drought has been found to be particularly frequent. In conclusion, due to global climate change, drought has become an important constraint for the growth and yield of tea plants.

Drought stress often leads to the morphological and physiological changes in tea plants. These changes include the accelerated senescence, yellowing of leaves, dropping of old leaves, and inhibited growth of new shoots. The abnormal growth resulted from drought stress is usually due to the imbalance of hormone metabolism, excessive accumulation of ROS, and weakening of photosynthesis in tea plants [28–31]. Different degrees of drought influence tea plants in various ways. First and foremost, under low drought stress, tea leaves, with decreasing photosynthetic capacity, change from green to yellow-green. Secondly, under high drought stress, tea leaves, which are curled and wilting, turn yellow or brown and fall off. Thirdly, the extreme and severe drought environment causes the tea plants to wither and die due to an acute lack of water.

There have been a series of recent researches in which tea plants response to drought stress are mainly focused on the analyses of physiology, biochemistry and gene

Table 1. Related genes of tea plant (*C. sinensis*) response to drought stress.

Gene	Genbank accession	Gene type	The subcellular location	References
CsINV10	KT359348	Neutral/alkaline invertase	Chloroplast	[33, 34]
CsMDHAR	MN402504	Monodehydroascobate reductase		[35]
CsGPX1		Glutathione peroxidase		[36]
CsGPX2	JQ247186	Glutathione peroxidase		[37]
CsSnRK2.1	*MG026837*	Sucrose non-fermenting-1-related protein kinase	Cytoskeleton	[10]
CsSnRK2.2	*MF662805*	Sucrose non-fermenting-1-related protein kinase	Cytoplasm	[10]
dr1	*BQ825883*	Drought responsive		[1]
dr2	*BQ825884*	Drought responsive		[1]
dr3	*BQ825885*	Drought responsive		[1]
CsCOR1	*GQ461357*	*Camellia sinensis* cold-regulated gene 1	Cell wall	[18]
CsLEA3		Late embryogenesis abundant protein		[38]
CsNAM-like protein	JQ619837	NAC family proteins	Nucleus	[39]
CsARF6		Auxin response factor	Nucleus	[40]
CsWRKY40		The WRKY transcription factor		[41]
CsWRKY57		The WRKY transcription factor		[41]

expression. To respond to drought stress, tea plants undergo signal transduction through signal perception, transmission and response. After that, it regulates the changes of gene expression, physiological response and morphological structure [32]. Presently, scientists have pin-pointed and identified multiple genes that participate in the response of tea plants to drought stress (Table 1, Ref. [1, 10, 18, 33–41]). These genes mainly contain transcription factors, with some genes related to stress resistance and metabolism [42–44]. In addition, some heat shock proteins, molecular chaperones, miRNAs, MYB protein families are believed to be related to tea plants response to drought stress [45, 46]. Wang *et al*. [47] have reported that the CsHis-H1 gene is involved in mediating the response of tea plants to drought stress. The heterologous expression of the nucleus-localized CsHis-H1 in tobacco can improve the tolerance to drought stress. Further researches have also reported that CsHis-H1 improves the resistance of tea plants by maintaining the photosynthetic efficiency of leaves [47].

Under drought stress, tea plants resist or adapt to adverse condition by activating the expression of drought-enduring genes and protein synthesis. This resistance involves multiple adaptive physiological responses in tea plants, including osmotic regulation, endo-hormone regulation, and antioxidant defense system regulation, etc. [48]. During drought, plant cells lose their water and thus give rise to cell turgor. As such, tea plants need to maintain the turgor pressure by synthesizing proline, soluble saccharide and proteins to ensure that photosynthesis and life activities are not being affected. Drought stress can also result in excessive production of ROS, oxidation and destruction of cell membrane structure, as well as impact the physiological and biochemical reactions [49]. Tea plants scavenge ROS mainly through the combination of catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), etc. [50, 51]. Tea plants can also reduce the ROS-induced injury by combining antioxidant substances such as ascorbic acid, glutathione and carotenoid [51, 52].

Furthermore, hormones are also involved in the regulation of the response of tea plants to drought stress. It has previously been indicated that salicylic Acid (SA) is involved in mediating the response of tea plants to drought stress by regulating the activities of SOD and POD. Abscisic Acid (ABA) can regulate stomata divergence degree and transpiration for alleviating adverse effects of drought on tea plants [53]. Over the years, the tea plants have established physiological adaptive response to drought stress by regulating gene expression, endogenous hormone level and stomatal switch [54]. This is to enhance its ability to resist and adapt to adverse stresses.

3.4 Effects of salt stress on the growth development of tea plants

Soil salinization is also a major limiting factor that affects the production of tea plants [55]. Tea plants grow well in acid soil, as it directly affects its growth development with changes in the pH value of the soil. High concentration of salt and alkali in the soil affects the absorption of mineral ions and water by plant roots, and then inhibits the growth of tea plants. When teat plants are subjected to high salt, the water absorption ability of the roots is significantly decreased. Also, excessive amounts of Na^+ and Cl^- entering tea plants can cause a prominent toxic effect. High salt stress can cause an excessive production of ROS, destruction of cell membrane structure, and reduction of protease activity [56, 57]. Chlorophyll content in tea leaves is significantly decreased while the ability of photosynthesis weakens visibly [51]. High salinity soil makes it difficult for roots to absorb water, which lead to low osmotic pressure of tea plant cells and affect their activities. Tea plants regulate and maintain cell osmotic pressure by synthesizing proline, soluble saccharide and proteins etc., to alleviate the damage of salt stress to cells [58, 59].

Under the stimulation by salt and alkali, plant cells can induce the expression of stress-inducible genes and protein synthesis through the perception, transduction and response of environmental signals. It involves an elaborative regulatory network to resist or adapt to adverse environmental conditions. Recently, scientists have cloned and highlighted some genes related to the response of tea plant to salt and alkali stress through molecular biological technology (Table 2, Ref. [10, 11, 19, 20, 33–35, 37, 39–41, 47, 60–67]). The Na^+/K^+ reverse transport protein gene *CsNHX6* is located in the Golgi apparatus, and its expression is considerably induced by high salt stress [64]. Heterologous expression of *CsNHX6* can significantly improve the tolerance of *Arabidopsis* mutants, yeast *GX3* and *AXT*. Also, the overexpression of *CsNHX6* in *Arabidopsis* can significantly improve the seed germination rate under salt stresses [64]. Further research has shown that *CsNHX6* had the transport activity of Na^+ and K^+ [64]. Cao *et al*. [19, 20, 66] have cloned three gens including *CsBADH1*, *CsCMO* and *CsMAPK3*, and analyzed their expression patterns under salt stress. The transcription factor CsRAV2 from tea plants is strongly expressed in the roots and NaCl treatment can induce up-regulation of the expression of *CsRAV2* [11]. The expression of the transcription factors *CsBZIP17* and *CsBZIP18* is also significantly induced by salt stress [60]. Qian *et al*. [33, 34] have cloned *CsINV10* and demonstrated that it can improve the alkali-resistance of tea plants. The expression of *CsSnRK2.1* and *CsSnRK2.2* from tea plants can be significantly induced by abiotic stress [10]. Overexpression of *CsCOR1* in tobacco can remarkably improve the tolerance of plants to both salt stress and dehydration stress [18]. Some genes with considerable response to salt and alkali stresses have been identified in tea plants, but their gene function is mostly investigated through heterologous expression in tobacco and *Arabidopsis*. As such, the gene function in tea plants needs be further verification. In future scientific research projects, the molecular regulatory mechanisms and gene regulatory networks of tea plants under salt and alkali stress need to be deeply studied.

The ABA-mediated signaling pathways have been shown to be the most critical regulatory pathways in the response of plants to salt and drought stress [34, 68]. In response to high salt stress, ABA mediates stomatal closure and the expression of stress-resistant genes, and weakens physiological activities related to tea plant growth, and enhances the ability of plants to resist salt stress [34, 68]. The expression of *CsNHX6* is induced by ABA, implying that *CsNHX6* can possibly participate in tea plant response to salt stress through the ABA-dependent signal pathway [64]. Li *et al*. [18] have reported that exogenous application of ABA can induce the expression of *CsCOR1*, and overexpression of *CsCOR1* in tobacco can significantly improve the tolerance of tea plants to salt stress. This indicates that the expression of *CsCOR1* may be activated by the ABA-dependent signaling pathway in the process of tea plants response to salt stress [18, 69, 70]. In addition, exogenous application of SA or hydrogen sulfide (H_2S) to tea leaves can also attenuate the damage caused by salt stress and improve the stress resistance of tea plants [51, 71]. Up until now, there has not been enough information concerning the hormone regulation of tea plants in response to salt stress, so its resistance mechanisms to salt stress remain very unclear.

3.5 Effects of heavy metal on the growth development of tea plants

Due to modern industrialization, massive exploitation of minerals, large scale use of pesticides and fertilizers, and discharge of sewage, the problem of environment contamination is increasingly becoming serious. The soil, containing heavy metals, not only has a serious impact on the growth of tea plants, but also affects the yield and quality of agricultural products. Heavy metal can be taken up by plants roots and accumulated in different plant organs, which leads to adverse effects on human health through the food chain. As a result, a vast majority of the research works is conducted on the basis of the impacts of heavy metal stress on the growth and development of tea plants. It has previously been shown that heavy metal with low concentration can promote the growth of tea plants. However, heavy metal with high concentration inhibits the growth of tea plant and reduces the yield and quality of tea plants [72]. High heavy metal content also changes the pH of soil and growing circumstance of rhizosphere microorganism. It not only affects the nutrient absorption by plant roots, but also leads to excessive absorption of heavy metal, consequently inhibiting the growth and development of the plants [72, 73]. Through evolution over the years, the plants have gradually developed multiple mechanisms for tolerance and avoidance of heavy metal stress. The avoidance mechanisms mainly refer to how root exudates mediate the activity of rhizosphere microorganism and mobility of heavy metals. It also highlights changes in the cell wall structure, so as to reduce the entry of heavy metals into plants [73, 74]. The tolerance mechanisms mainly refer to the physiological regulatory mechanisms of tea plants, such as osmotic regulation, antioxidant systems and chelation, so as to reduce the damage of heavy metals to the plants [74–77].

An investigation on hydrargyrum stress shows that mercury treatment can reduce the chlorophyll content in tea leaves and affect the photosynthesis of tea plants. It also highlights how the mercury treatment can cause a significant decrease in the content of proline and propylene glycol in tea leaves [78]. Xia and Lan [79] have conducted biophysical research on tea plants response to cadmium stress and found that low cadmium (Cd) concentration had no significant effect on the growth of tea plants. However, with increase in the Cd concentration, the damage degree is gradually increased, mainly manifested in the wilting, yellow-

Table 2. Related genes of tea plant (*C. sinensis*) response to salt and alkali stress.

Gene	Genbank accession	Gene type	The subcellular location	References
CsbZIP1	JX050148.1	The basic leucine zipper proteins	Nucleus	[60, 61]
CsbZIP4	AGD98702.1	The basic leucine zipper proteins	Nucleus	[62]
CsbZIP7	KC215406.1	The basic leucine zipper proteins	Nucleus	[60]
CsbZIP8	KC215415.1	The basic leucine zipper proteins	Nucleus	[60]
CsbZIP14	KR906062	The basic leucine zipper proteins	Nucleus	[60]
CsbZIP17	KR906065	The basic leucine zipper proteins	Nucleus	[60]
CsbZIP18	KR906066	The basic leucine zipper proteins	Nucleus	[60]
CsNHX1	MG722977	The Na^+/H^+ antiporter	Vacuolar membrane	[63]
CsNHX2	MG515211	The Na^+/H^+ antiporter	Vacuolar membrane	[63]
CsNHX6		The Na^+/H^+ antiporter	Golgi apparatus	[64]
CsWRKY40		The WRKY transcription factor		[41]
CsWRKY57		The WRKY transcription factor		[41]
CsSnRK2.1	MG026837	Sucrose non-fermenting-1-related protein kinase		[10]
CsSnRK2.2	MF662805	Sucrose non-fermenting-1-related protein kinase		[10]
CsARF1	JX307853	Auxin response factor	Cytoplasm	[40, 65]
CsARF6		Auxin response factor	Nucleus	[40]
CsARF16		Auxin response factor	Nucleus	[40]
CsMAPK3	MF034662	Mitogen-activated protein kinase	Cytoplasm and nucleus	[66]
CsGPX2	JQ247186	glutathione peroxidase 2	Chloroplast	[37]
CsNAM-like protein	JQ619837	NAC family proteins	Nucleus	[39]
CsERF-B3	GU393024	APETALA2/ethylene-responsive factor		[67]
CsMDHAR	MN402504	Monodehydroascobate reductase		[35]
CsINV10	KT359348	neutral/alkaline invertase	Chloroplast	[33, 34]
CsCMO	JX050146	Choline monooxygenase	Chloroplast	[20]
CsBADH1	JX050145	Betaine aldehyde dehydragenase		[19]
CsHis-H1	EU716314	H1 Histone gene	Nucleus	[47]
CsRAV2	GQ227992.1	CsRAV2 Transcription Factor		[11]

ing and abscission of leaves. When the Cd concentration reaches up to 60 mg/kg, tea plants start dying. After Cd treatment, the content of malondialdehyde and free proline in tea is increased, while the content of chlorophyll and soluble sugar exhibits opposite trends in different seasons [79]. During spring season, Cd treatment leads to significant increases in the content of chlorophyll and soluble sugar in leaves, but reduces the content of chlorophyll and soluble sugar in leaves in the summer season, indicating the temporal and spatial differences in response to Cd stress [79]. In addition, lead (Pb) and chromium (Cr) treatment are used to study the physiological and biochemical response of tea plants. It is observed that, when the concentration of Pb^{2+} and Cr^{3+} is increased, there is a corresponding decrease in the chlorophyll content, photosynthetic capacity, stomatal conductance and transpiration rate of tea plants, giving rise to visible harmful symptoms [80]. During zinc (Zn) treatment, excessive concentration of Zn^{2+} inhibits the tea plant's growth. As such, the yield and quality are significantly reduced [81]. Also, the research has shown that low aluminum (Al) concentration can promote the chlorophyll synthesis and photosynthesis of tea leaves, while high Al concentration can inhibit it [82]. However, our study on tea plants response to heavy metal stress is neither incisive nor systematic, lacking in gene regulation and signal pathway research. Hence, it can be concluded that the in-depth study of tea plant response to adverse stresses is not only necessary but also has a long way to go.

4. Conclusion and prospect

Tea plant, a perennial green plant, experiences multiple seasonal changes in its life cycle. Also, changes in external environments directly affect the growth development of the plant. In the natural environments, diverse stressful factors often adversely affect the performance of plant growth. With the frequent occurrence of abnormal weather and aggravation of environmental pollution, tea plant production is under huge threat by cold damage, high temperature, soil heavy metal pollution and soil salinization. In the process of tea plant growth, its development is often affected by multiple environmental factors at the same time. These stresses are important factors affecting the yield and quality of tea. As the AP2/ERF-B3 transcription factor, the expression of *CsERF-B3* was induced by high temperature stress, low temperature stress and salinity stress [67]. In the plants, the transcription factor of ERF subfamily is involved in the abiotic stresses by regulating the expression of stress-related genes. This implies CsERF-B3 play an important role in abiotic stress response and tolerance in tea plants. With the development of molecular biotechnology, the application of transcriptomics and transgenic technology has become an effective way to explore the regulatory mechanisms of tea plant adaptation to abiotic stress. In the future, we expect more genes that regulate plant stress adaptation to be discovered. Searching for important genes and exploring its molecular regulatory networks of tea plants response to abiotic stress will help us better understand the regulatory mechanism of plant resistance to adverse stress.

Previous studies mainly focus on single stress treatment but little study of tea plants response to a variety of stresses has been reported. Therefore, it is of great necessity to carry out the experiments of combining multiple stresses together, including high temperature, drought, salt-alkali and heavy metal to better explore the stress-resistance physiology of plants in the natural environments. The combination process is also important for the cultivation of excellent salt-tolerant, drought-tolerant and high temperature resistant tea varieties. Moreover, most of the previous reports about the stress resistance of tea plants focuses squarely on the phenotypic observation and the determination of physiological and biochemical indexes. The researches on the molecular regulatory mechanism of teat plants response to abiotic stress is still far behind other model plants such as *Arabidopsis*, rice, corn and soybean. Thus, it is very important to unravel the molecular mechanisms of stress resistance in tea plants by applying the physiological, biochemical and molecular analyses, so as to improve the plant's stress resistance ability and to increase its yield.

5. Author contributions

YS is the main author of the thesis; YS, JZ and JG participate in the writing and revision of the thesis.

6. Ethics approval and consent to participate

Not applicable.

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9. Conflict of interest

The authors declare no conflict of interest.

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Abbreviations: CsSnRK, *Camellia sinensis* Sucrose non-fermenting-Related protein Kinase; POD, peroxidase; CAT, catalase; SOD, superoxide dismutase; CsBADH1, *Camellia sinensis* Betaine Aldehyde Dehydragenase; CsCMO, *Camellia sinensis* Choline Monooxygenas; SA, Salicylic Acid; ABA, Abscisic Acid; H_2S, Hydrogen Sulfide.

Keywords: *Camellia sinensis*; Abiotic stress; Regulatory mechanism

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