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Field Performance of Heat-Tolerant Traits in Tea and Cultivation Factors Affecting Summer Leaf Functional Stability

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Abstract This study mainly reviewed the performance of tea trees in the face of high temperatures, compared the field performance of different tea tree varieties under high temperatures, analyzed the genetic reasons behind them, and also examined how planting methods such as shading and increasing watering frequency help tea trees maintain leaf activity, increase yield and quality in summer. It emphasized that to ensure tea trees grow well even in hot weather, choosing the right variety is as important as doing a good job in field management. It also summarizes some tea garden management methods suitable for high-temperature summer weather, as well as several key criteria for judging whether a tea tree variety is heat-tolerant. This study aims to provide some theoretical basis and technical references for the breeding of more heat-tolerant tea tree varieties and the establishment of an efficient planting system suitable for summer.
Keywords Tea plant; Heat tolerance; Summer cultivation; Leaf stability; Climate adaptation

1 Introduction

The global temperature is constantly rising, and extreme high-temperature weather is becoming increasingly common, which has a significant impact on the yield of tea trees and the quality of tea (Huang and Chen, 2024). High temperatures can make the leaves of tea plants more prone to water loss, reduce chlorophyll, weaken antioxidant capacity, and damage cell membranes more easily, thereby affecting the normal functions of tea plants and the economic value of tea leaves (Seth et al., 2021). In addition, high temperatures will also slow down the energy metabolism of tea plants and increase reactive oxygen species in their bodies, which will further undermine the stability of leaves (Huang et al., 2024).

In recent years, many studies have employed molecular biology and omics methods to identify numerous genes and metabolites related to heat resistance. For instance, substances like heat shock proteins (HSPs) and heat shock transcription factors (HSFs) play a crucial role in helping tea plants tolerate heat. At high temperatures, those heat-resistant tea tree varieties exhibit stronger antioxidant capacity and accumulate more flavonoids in their bodies. Some related genes, such as *FLS*, *HSP90* and *HSP70*, are expressed earlier or more strongly in heat-tolerant varieties (Shen et al., 2019; Seth et al., 2021). These findings provide us with a theoretical basis for screening and cultivating heat-resistant tea trees.

In daily planting and management, methods such as reasonable watering, shading and fertilization can also protect tea trees in high-temperature weather. These practices can help tea plants better retain water and balance nutrients, enhance resistance to high temperatures, and also promote the accumulation of some protective metabolites in tea plants, thereby maintaining the activity and stability of leaves (Seth et al., 2021; Huang et al., 2024).

This study mainly observed the performance of different tea plants under high temperatures, analyzed the impact of various field management methods on leaf function in summer, and also explored how genes, metabolites and management measures work together. This study hopes to provide some theoretical support and practical experience for the screening of heat-resistant tea trees and scientific planting in summer.

2 Physiological Effects of Heat Stress on Tea Plants

2.1 Imbalance in photosynthesis and stomatal regulation

High temperatures can deteriorate the photosynthesis of tea plants. The most obvious manifestation is the decline in the carboxylation rate of Rubisco enzyme and the regeneration rate of RuBP. When it is hot, both the optical system II (PSII) and the optical System I (PSI) will be damaged. Among them, PSII is more prone to problems. At this time, photosynthetic parameters such as Fv/Fm, Y(I), Y(II) will decrease, while Y(NO), Y(NA) will increase instead, indicating that electron transfer slows down. In addition, high temperatures can also interfere with the opening and closing of stomata, making it more difficult for tea plants to carry out effective photosynthesis (Huang et al., 2024).

2.2 Enhanced oxidative stress and membrane damage

When the temperature rises, reactive oxygen species (ROS) in tea plants accumulate rapidly, such as an increase in H_2O_2 and O_2^-. This can cause lipid peroxidation, and malondialdehyde (MDA) will also increase, making the cell membrane unstable (Seth et al., 2021). In heat-resistant varieties, the activities of some antioxidant enzymes, such as SOD and POD, are enhanced, which can help eliminate ROS and reduce oxidative damage (Huang et al., 2024; Zheng et al., 2024). However, for varieties that are more sensitive to high temperatures, the activity of antioxidant enzymes will decrease instead, and cell membranes are more prone to damage.

2.3 Disruption of secondary metabolite biosynthesis

High temperatures can affect some secondary metabolites in tea plants. Research has found that substances such as polyphenols and catechins change their accumulation patterns at high temperatures. Some heat-tolerant tea tree varieties can enhance their resistance by activating genes like *FLS* to increase flavonoids in their bodies (Figure 1) (Huang et al., 2024). However, some genes, such as *CsUGT75C1* which controls anthocyanin synthesis, are expressed less at high temperatures, resulting in a decrease in anthocyanins (Shen et al., 2019). If exogenous GABA is applied to tea plants, the contents of polyphenols and catechins can increase, and the activities of related enzymes will also improve, thereby enhancing the antioxidant capacity (Ren et al., 2021).

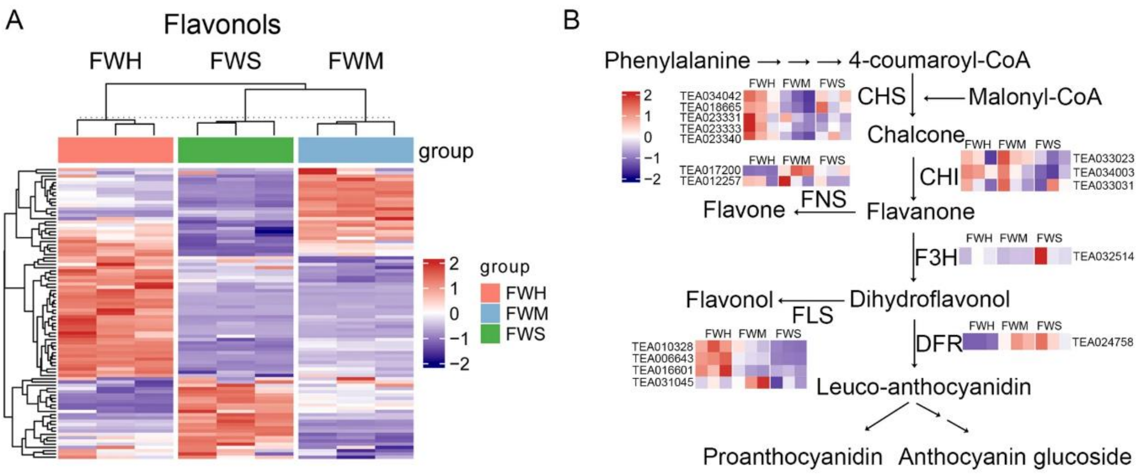

Figure 1 Identification of DEGs involved in flavonoids biosynthesis (Adopted from Huang et al., 2024)

Image caption: (A) The heat map of differentially accumulated flavinols in 'FWH', 'FWM' and 'FWS' varieties; (B) the DEGs in flavonoids biosynthesis pathway. *CHS* chalcone synthase, *CHI* chalcone flavanone isomerase, *F3H* flavanone 3P-hydroxylase, *DFR* dihydroflavonol 4-reductase, *FLS* flavonol synthase, *FNS* flavone synthase (Adopted from Huang et al., 2024)

3 Heat-Tolerant Traits in Tea

3.1 Morphological traits: leaf thickness, pubescence, leaf angle

Heat-resistant tea trees usually have some distinct physical features. Their leaves are relatively thick, covered with a lot of downy hairs, and the Angle of the leaves is also quite moderate. Thick leaves can reduce water evaporation and help tea trees retain moisture in drought and high temperatures. The pubescence on the leaves can reflect sunlight, reduce the temperature of the leaves and prevent sunburn. The angle of the leaf can affect sunlight exposure and air circulation, and also help regulate leaf temperature (Huang et al., 2024).

3.2 Physiological traits: chlorophyll fluorescence, water retention, antioxidant activity

Physiologically, the chlorophyll fluorescence values of heat-tolerant tea plants are generally high, indicating that their photosynthetic systems can still function normally in hot weather. The leaves of this type of tea tree have a strong water retention capacity, which can reduce water loss and also prevent the cell membrane from being damaged by high temperatures. Their antioxidant enzyme activities, such as POD and SOD, are also higher than those of common tea plants, which can eliminate reactive oxygen species produced at high temperatures and reduce cell damage (Seth et al., 2021; Huang et al., 2024). In addition, more regulatory substances like proline accumulate in the leaves of these tea plants, helping cells maintain a stable state.

3.3 Genetic basis and heritability of heat-tolerant traits

Heat resistance is also related to genes. Research has found that under high-temperature conditions, heat-tolerant tea trees will activate some “emergency” genes, such as *HSP90*, *HSP70* and *HSP18.1*, as well as the transcription factor HSFA2 that regulates them. These genes can regulate the heat stress response and help tea plants adapt to high temperatures (Seth et al., 2021). There are also some genes, such as *FLS*, which can promote flavonoid synthesis and enhance the antioxidant capacity of tea plants (Huang et al., 2024). The expression differences of these genes are the key to improving the heat tolerance of tea plants. Studies have also found that the heat tolerance traits of different tea tree varieties vary greatly and have relatively strong heritability, which provides a theoretical basis for the subsequent breeding of heat-tolerant tea trees (Driedonks et al., 2016).

4 Field Performance of Heat-Tolerant Tea Cultivars

4.1 Evaluation indicators and experimental methods

When evaluating heat-tolerant tea trees in the field, researchers usually look at three aspects of indicators: physiological, biochemical and molecular levels. The commonly observed physiological aspects include leaf water content, chlorophyll content, whether the cell membrane is damaged, and the level of photosynthetic pigments (Figure 2) (Seth et al., 2021; Huang et al., 2024). The biochemical aspects mainly include the activities of antioxidant enzymes (such as SOD, APX and POX), regulatory substances like proline and betaine, and the accumulation of reactive oxygen species (H_2O_2, O_2^-) in the body (Nalina et al., 2021). At the molecular level, we look at the expression of some key genes, such as heat shock proteins (HSPs) and heat shock transcription factors (HSFs) (Seth et al., 2021). Usually, when conducting such experiments, field treatment is carried out in a high-temperature environment, and then leaves are taken for physiological, biochemical, transcriptomic and metabolomic analyses (Shen et al., 2019).

4.2 Yield and quality maintenance under heat stress

High temperatures can affect the yield and quality of tea trees. However, heat-resistant varieties will perform better. When it is hot, their leaves can retain more water, chlorophyll is less likely to decline, and cell membranes are relatively stable, so the yield is relatively stable (Seth et al., 2021). In terms of quality, heat-tolerant tea trees can accumulate more flavonoids and antioxidants, which can reduce the influence of high temperature on the flavor and composition of tea (Huang et al., 2024). Also, these tea plants activate more heat shock proteins and chaperone proteins when they are hot, which helps maintain protein stability and also helps protect cells, thereby ensuring the quality and yield of tea (Shen et al., 2019).

4.3 Effects of genotype × environment × management (G×E×M) interactions

The heat tolerance of tea plants is also jointly influenced by variety, environment and management methods. Different varieties of tea trees react differently under the same high temperature. Some heat-resistant varieties can reduce tropical damage through more effective antioxidant and regulatory mechanisms. Environmental factors such as soil moisture content and temperature changes can also affect the expression of heat-tolerant genes and the accumulation of substances (Huang et al., 2024). If combined with reasonable management measures, such as irrigation or shading, it can also help tea plants better cope with high temperatures, maintain leaf function and improve field performance (Nalina et al., 2021). Therefore, for tea plants to grow well in summer with stable leaves and high yield, a good combination of variety, environment and management is the key.

5 Summer Leaf Functional Stability

5.1 Definition and importance of functional stability in summer leaves

Leaf functional stability means that the leaves of tea plants can still function normally during hot or dry summers, such as continuing photosynthesis, transpiration and maintaining cellular moisture. This ability is extremely important because it ensures that the tea plants are still growing leaves when it is hot and can still be picked. High temperature and water shortage can damage leaves, deteriorate photosynthesis, potentially damage cells, and make leaves prone to premature aging, ultimately affecting yield and quality (Peguero-Pina et al., 2020; Cao et al., 2024).

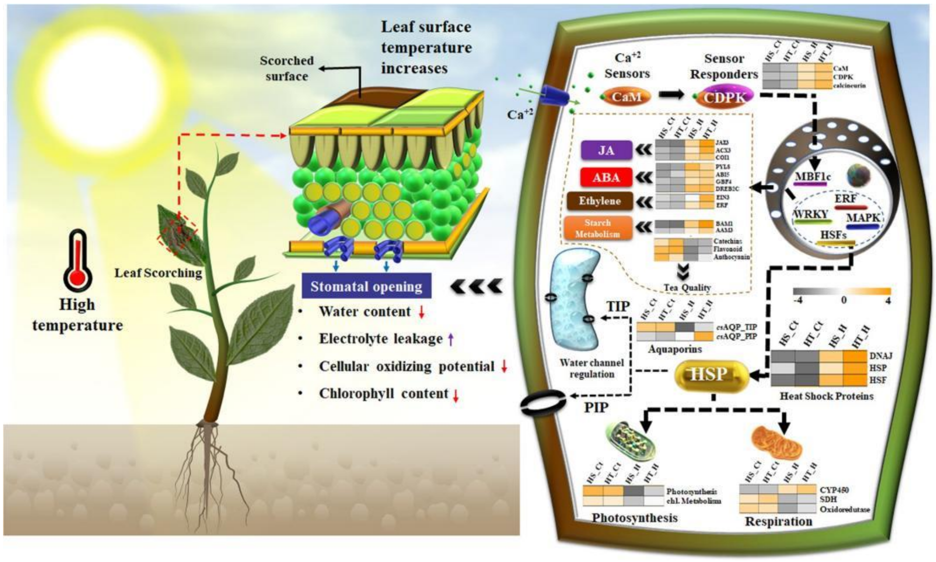

Figure 2 Summarized illustration of physiological and molecular insights underlying heat stress associated thermotolerance in tea (Adopted from Seth et al., 2021)

Image caption: The higher temperature leads to an increase in leaf surface temperature with decreased water content, cellular oxidizing ability, and chlorophyll content, while an increase in the membrane damage due to high electrolyte leakage. The heatmap represents gene enrichment in heat sensitive (HS) and tolerant (HT) cultivars under control (HS_Ct; HT_Ct) and under heat treatment (HS_H; HT_H) (Adopted from Seth et al., 2021)

5.2 Key evaluation indicators: SPAD, leaf temperature, turgor regulation

The SPAD value can reflect the amount of chlorophyll and is an indicator for judging the photosynthetic capacity and health status of leaves. When the weather is hot, if the SPAD value can still remain stable, it indicates that the leaves can still retain chlorophyll, which is conducive to maintaining photosynthetic efficiency and heat resistance (Gao et al., 2025; Hočevar et al., 2025). In addition, the temperature of the blades is also very crucial. When the temperature is high, the temperature of the leaves will also rise. If the leaves can dissipate heat through transpiration, they can be maintained at a relatively suitable temperature, which also indicates that it has a certain heat resistance capacity (Peguero-Pina et al., 2020; Cao et al., 2024). The turgor pressure loss point (πtlp) is an indicator used to determine whether leaves can retain cellular moisture when they are dry. The better this value is, the more drought-resistant the leaves will be. If the turgor pressure regulation ability of the leaves of a tea plant is strong, it is not easy to wither in the dry and hot summer, and the cell function can also be maintained better (Zhu et al., 2018; Trueba et al., 2019).

5.3 Relationship between functional stability, plucking quality, and economic return

Those tea trees with good stability in leaf function can still continuously grow high-quality fresh leaves in summer. Even if the weather is very hot, it is not easy for the leaves to get injured or for their quality to deteriorate. In this way, not only can the quality of the picked tea be guaranteed, but also better economic benefits can be brought (Zhu et al., 2018; Peguero-Pina et al., 2020; Cao et al., 2024; Gao et al., 2025). This stability mainly depends on several aspects: for instance, if the SPAD value remains high, it indicates that the chlorophyll in the leaves has not dropped too much; If the temperature of the leaves is well controlled, the cells are less likely to go bad. Another point is that if the blades can maintain turgor pressure, they are less likely to shrivel. With these indicators, the leaves of tea plants can continue photosynthesis, cells can function normally, the picking period can be prolonged, and the yield and grade of tea leaves will naturally increase. Moreover, in some extreme climates, such as extremely hot or dry conditions, these tea tree varieties also perform more stably, have lower planting risks, and are suitable for long-term development.

6 Effects of Cultivation Management on Functional Stability

6.1 Irrigation timing and water management techniques

Drought will cause the photosynthesis of tea plant leaves to deteriorate, reduce chlorophyll, and slow down the growth of new shoots. Eventually, it will affect the yield and quality of tea. To alleviate this situation, watering in a timely manner is very useful. Reasonable irrigation can help tea plants resume growth, especially during hot and dry summer days, which is conducive to maintaining the normal function of leaves and stabilizing the yield (Hasan et al., 2023). Therefore, mastering when to water and how to water is the key to managing tea gardens in summer.

6.2 Shade regulation and canopy structure optimization

Shading planting can control the intensity of light, help tea trees adjust the shape and internal composition of their leaves, and sometimes even increase the content of amino acids and caffeine in tea leaves. However, if too much is covered, the photosynthesis of the leaves will decline, the synthesis of sugar will decrease, and the leaf temperature may increase instead. This will instead make the tea plant more heat-sensitive (Sano et al., 2018; Yamashita et al., 2020). By adjusting the canopy of tea trees, such as using the method of umbrella-shaped pruning, the environment of the tea garden can be improved, the activity of soil enzymes and the types of beneficial microorganisms can be increased, making tea trees more adaptable to high temperatures and also increasing the content of some useful components (Jiang et al., 2023).

6.3 Role of nutrient management in heat resistance

Nutrient management is also very important, especially the proper combination of elements such as nitrogen, phosphorus, potassium and magnesium. Organic fertilizer substitution can also help improve the health of the soil and tea trees. When the nutrient supply is sufficient, substances such as amino acids and polyphenols in tea leaves will increase, and tea trees will be more heat-resistant (Tang et al., 2022; Zhou et al., 2022; Zhu et al., 2024). Adjusting soil pH and using organic farming methods can improve the soil environment, increase the utilization rate of fertilizers, and also enhance the quality of tea (Jia et al., 2024; Liu et al., 2025). Furthermore, some new types of foliar fertilizers or bio-fertilizers can also activate the self-protection ability of tea plants, enabling the leaves to function more stably at high temperatures (Lagoshina et al., 2021a; Lagoshina et al., 2021b).

7 Modulating Effects of Environmental and Soil Factors on Field Response

7.1 Influence of altitude, slope, and topographic conditions

The higher the altitude, the lower the temperature and the greater the air humidity. Such an environment helps increase the amino acid content in tea, making the flavor of the tea better. Studies have found that with the increase of altitude, the amino acids in tea will gradually increase, but the change of catechins is to decrease first and then increase, the change trend of phenolic acids is similar, and the content of flavonol glycosides basically does not change much (Ran et al., 2023). In addition, the slope and terrain can also affect the growth of tea trees. Water on sloping land is prone to flow away, especially after rain, when soil moisture and nutrients fluctuate greatly, and the root environment is also easily affected. In order for the leaves to grow well, the management methods need to be adjusted according to the terrain (Ye et al., 2024).

7.2 Soil type and water-holding capacity in regulating rhizosphere conditions

The type of soil also has a significant impact on the taste and composition of tea. For instance, there are more aromatic substances (such as linalool and phenylethanol) in paddy soil, but the content of amino acids is lower than that in red soil and yellow soil, while catechins and flavonoid glycosides are actually higher (Ran et al., 2023). The organic matter, pH level and water retention capacity in the soil can affect the environment around the roots, such as nutrient supply and the types of microorganisms. These factors will all affect the resistance of tea plants and the stable performance of leaves (Han et al., 2022; Feng et al., 2024). Soil with abundant organic matter and moderate pH can help increase yield and quality, while soil with good water retention can better resist drought and high temperature (Wen et al., 2021; Giannitsopoulos et al., 2023).

7.3 Interactions between rainfall patterns and heatwave timing

The intensity and distribution time of rainfall, as well as when heat waves arrive, have a significant impact on the moisture state and nutrient loss of tea trees. If it rains heavily, the nitrogen in the sloping tea garden is prone to be washed away, which will affect the yield and tea quality (Ye et al., 2024). During heat waves, if there is not enough rainfall, tea trees are also prone to water shortage, and their leaves are likely to be damaged. Simulation experiments have found that rainfall, soil water-conducting capacity and fertilization interact with each other, all of which affect nitrogen loss and tea yield. By rationally arranging fertilization and watering, the adverse effects brought by extreme weather on tea gardens can be reduced (Ahmed et al., 2019).

8 Technologies for Field Monitoring and Evaluation

8.1 Remote sensing and non-invasive monitoring tools

Nowadays, with remote sensing and hyperspectral imaging technology, it is possible to monitor the heat tolerance of tea plants more quickly and easily. By taking hyperspectral images of tea tree leaves and combining them with physiological indicators such as malondialdehyde, soluble sugar, and polyphenols, tea trees with strong heat resistance can be quickly screened out. If these image data are combined with machine learning methods (such as support vector machine, random forest, partial least squares regression), accurate prediction of the stress resistance of tea plants can be made, and large-scale field detection can be carried out without damaging the leaves (Chen et al., 2022).

8.2 Field phenotyping instruments

Some commonly used tools for measuring the heat resistance of tea plants in the field include portable chlorophyll meters, photosynthesis measurement instruments, biochemical detection equipment and automatic sampling systems. These instruments can help us understand in real time the key physiological responses such as chlorophyll level, water retention capacity and antioxidant enzyme activity of tea plants under high temperature, and thereby determine whether a variety is heat-resistant (Rahimi et al., 2018; Huang et al., 2024). Furthermore, if transcriptome and metabolome analyses are added, the internal regulatory mechanisms of heat-tolerant tea plants can be further understood at the molecular level, providing more data support for the analysis of field performance (Shen et al., 2019).

8.3 AI- and data-based models for adaptive trait evaluation

Artificial intelligence and data models are also very useful in the selection and breeding of tea trees. By integrating data from different sources such as high-throughput phenotypes, transcriptomes, and metabolomics, we can establish predictive models to more accurately determine which tea trees are more heat-tolerant. For instance, Tea-DTC is an AI model that uses hyperspectral data to predict the drought resistance of Tea plants and performs well (Chen et al., 2022). In addition, the combined analysis of transcriptome and metabolome also revealed some key regulatory pathways and gene networks at the molecular level of heat-tolerant varieties, providing a lot of valuable information for AI models (Seth et al., 2021; Huang et al., 2024).

9 Case Study: Field Performance of Heat-Tolerant Tea Varieties in Mississippi and Zhejiang

9.1 Regional background and ecological conditions

In subtropical humid climate zones like Mississippi in the United States, the hot summer weather and strong sunlight are the main problems affecting the growth of tea trees and the health of their leaves. It is often hot and rainy in summer here, and sometimes low temperature occurs in winter. Therefore, tea trees must have a stronger heat tolerance to adapt (Zhang et al., 2020; Zhang et al., 2022). Some tea-growing areas in China, such as Zhejiang, also encounter the situation of continuous high temperatures in summer, which will affect the output and quality of tea (Yang et al., 2023).

9.2 Cultivar selection and experimental design

In the fields of Mississippi, researchers selected nine different tea tree varieties, including 'BL1', 'BL2', 'Black Sea', 'Christine's Choice', etc. To test their growth conditions, leaf morphology, composition changes and heat tolerance performance under the local climate (Zhang et al., 2020). In Zhejiang Province, local tea trees that are relatively heat-sensitive, such as 'Longjing 43', were used in combination with exogenous treatments like AMHA to conduct experiments on improving heat tolerance (Yang et al., 2023). These experiments usually set up control groups and treatment groups to compare the physiological changes of leaves, yield and tea quality.

9.3 Leaf functional and yield performance under heat stress

Experiments have found that for those varieties that are relatively heat-tolerant, under high-temperature weather conditions, the activities of antioxidant enzymes (such as POD, CAT, SOD) are higher, substances such as amino acids and sugars accumulate more in the leaves, and at the same time, the photosynthetic capacity is stronger and the leaf state is more stable (Huang et al., 2024). For example, after treatment with AMHA, the net photosynthetic rate and stomatal conductance of tea plants will increase, the damage to leaf cell membranes will be alleviated, and the growth recovery will be faster (Yang et al., 2023). In experiments conducted in the United States, different tea tree varieties performed differently in summer. Some varieties can maintain good yield and quality even at high temperatures, and the levels of substances such as polyphenols, amino acids and theanine are not low (Zhang et al., 2020). In addition, the use of black, blue or red shading nets can effectively reduce leaf temperature, improve the photosynthetic efficiency and growth rate of tea plants, and thereby maintain leaf function.

9.4 Farmer feedback and technology promotion potential

These experiments demonstrate that planting heat-tolerant varieties, along with appropriate cultivation measures such as shading, spraying inducers or using new types of fertilizers, can indeed reduce the damage to tea trees caused by high summer temperatures, and also increase yield and the stability of tea quality (Lagoshina et al., 2021b). Local farmers also reported that practices such as shading and scientific fertilization are not difficult to operate and have good effects, and are suitable for promotion (Zhang et al., 2022). Furthermore, the selection and use of these heat-tolerant tea trees also provide a technical basis for emerging tea-growing areas like the southern United States (Zhang et al., 2020).

10 Concluding Remarks

The heat tolerance of tea plants is mainly reflected in three aspects: gene regulation, metabolic response and physiological manifestation. From the perspective of molecular mechanisms, some heat shock proteins (such as HSP90, HSP70, HSP17.6 and HSP101) and their transcription factors (such as HSFA2) play a core role in tea plants' response to high temperatures. They can help leaves retain water, maintain chlorophyll synthesis, stabilize cell membranes, and at the same time participate in signal transduction processes such as calcium and ethylene, thereby enhancing heat resistance. In terms of metabolism, heat-resistant varieties usually exhibit higher antioxidant enzyme activity at high temperatures and can accumulate more flavonoids, flavonols and other substances, which helps to eliminate reactive oxygen species in the body and reduce the damage caused by heat stress. Some tea tree varieties also have relatively obvious structural advantages in their leaves, such as a higher leaf mass per area (LMA). Such blades are less likely to be damaged in high temperatures and have more stable functions. From the perspective of field management, choosing the right variety, combined with reasonable irrigation, appropriate shading and scientific fertilization, can also significantly enhance the stability of leaf function of tea plants in summer and reduce the impact of high temperatures on growth and tea quality.

However, most of the current research is focused on laboratories, and there is still insufficient understanding of the long-term effects in real fields and stability under different environments. Many experiments were conducted in greenhouses or under controlled conditions, failing to systematically analyze the interactions between different cultivation and management methods and tea tree varieties. Moreover, there is still not much data available to make a clear judgment on the direct relationship between the heat resistance of tea tree leaves and the final yield and quality.

Future research should be carried out more in actual tea gardens, and it is best to verify it at multiple locations and in different years. At the same time, by integrating molecular marker technology, the breeding work of heat-resistant varieties is promoted. It is suggested that molecular breeding be combined with precision agriculture technologies, such as intelligent irrigation, adjustable shading and nutrient management, to jointly evaluate their effects on enhancing the functional stability of leaves. It is also necessary to pay attention to the relationship between the heat tolerance of leaves, yield and tea quality, and establish a multi-dimensional evaluation method. Finally, if different disciplines such as molecular biology, ecology and agronomy can be combined, there will be greater hope in the future to address the challenges brought by climate change and make tea production more stable and sustainable.

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Conflict of Interest Disclosure
The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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