

Anjarsari IRD · Suminar E · Wiharti NR

A review on detection of drought stress in tea plants through morphological, physiological, and biochemical approaches

Abstract. Tea plants (*Camellia sinensis*) are important commodities with high economic value, but their production is greatly affected by environmental stresses such as drought and extreme temperatures. Global warming in recent years has led to extreme weather events and an increase in the earth's temperature, which also causes drought. Drought stress is one of the most significant abiotic factors affecting crop productivity. However, despite significant progress, there remains a notable gap in research, particularly the lack of integrated studies that combine morphological, physiological, and biochemical indicators for early and precise detection of drought stress in tea plants. To identify and mitigate the impact of this stress, a comprehensive approach is needed that includes morphological, physiological, and biochemical aspects. The morphological approach includes changes in leaf structure, stomatal size and number, and root growth patterns. From a physiological perspective, plant response to drought can be seen through measurements of transpiration rate, leaf water potential, and photosynthetic capacity. On the biochemical side, the accumulation of compounds such as proline, antioxidant enzymes, and stress-related hormones, such as abscisic acid, plays a crucial role in plant adaptation to drought conditions. This review summarizes the latest findings related to these indicators by analyzing relevant articles published between 2007 and 2024, obtained through reference searches on Google Scholar and academic databases such as Scopus, EBSCO, and Clarivate. The articles were further analyzed using descriptive methods. This review aims to summarize the latest findings related to these indicators and identify the most effective methods for detecting drought stress in tea plants. A deeper understanding of the tea plant's response to drought through these three approaches is expected to provide a solid basis for developing better drought management strategies to maintain tea plant productivity amid increasingly extreme climate change

Keywords: Abiotic stress · Antioxidant · Climate change · Global warming · Tea

Submitted: 9 January 2025, Accepted: 30 April 2025, Published: 30 April 2025

DOI: <https://doi.org/10.24198/kultivasi.v24i1.62127>

Anjarsari IRD^{1*} · Suminar E¹ · Wiharti NR²

¹ Department of Agronomy, Faculty of Agriculture, Universitas Padjadjaran, Jl. Raya Bandung-Sumedang KM 21 Jatinangor Jawa Barat 45363

² Undergraduate Student of Agrotechnology Study Program, Faculty of Agriculture, Universitas Padjadjaran, Jl. Raya Bandung-Sumedang KM 21 Jatinangor Jawa Barat 45363

*Correspondence : intan.ratna@unpad.ac.id

Introduction

Drought is a climate disaster that occurs under most climatic conditions and can have considerable economic, social, and environmental impacts (Meng et al., 2023). In recent decades, drought caused by rapid warming has deeply affected the global climate. Global climate change will lead to new combinations of temperature and precipitation patterns. Extreme precipitation events become more common by the late 21st century due to anthropogenic warming, particularly in high altitudes; however, the specific responses of high-altitude species are mostly unknown (Zhu et al., 2020), especially for tea.

Tea plants, as evergreen crops, are highly sensitive to drought stress, which negatively impacts their growth, yield, and quality. According to a report from the International Tea Committee (International Tea Committee (ITC), 2024)), some tea-producing countries experience a 15-30% drop in yield during extreme drought seasons. In India, for example, tea production in Assam and Darjeeling fell by almost 20% in the summer of 2021 due to extreme weather (Food Agricultural Organization, 2022). Climate change is also causing some previously suitable lands for tea cultivation to become unsuitable. A study conducted by Ahmed et al. (2020) shows that in Kenya, it is estimated that about 26% of tea plantation areas will lose their suitability for high-quality tea cultivation by 2050. Similarly, climate model simulations in Indonesia project a reduction in the optimal area of tea cultivation in West Java by 12-18% if temperatures continue to increase by more than 2°C (Fatawa et al., 2024). Climate change is also causing shifts and uncertainty in harvest seasons. For example, green and black tea production experienced significant harvest irregularities in Sri Lanka, making production planning and marketing difficult (Srilanka Teaboard, 2023). A similar situation was reported in some (Food Agricultural Organization, 2022) tea plantations in West Java, where the timing of young leaf flush became erratic, resulting in supply irregularities (Badan Litbang Pertanian., 2022). Furthermore, changes in temperature and humidity affect the content of secondary metabolites such as catechins, teaflavins, and tearubigins that determine the flavor and aroma of tea. Research by (Han et al., 2018) showed that high temperatures and drought can reduce catechin

levels by up to 25%, leading to a decrease in the sensory quality and selling value of tea.

This review summarizes recent research on physiological, biochemical, and molecular responses of tea plants to drought stress. Tea plants are susceptible to changes in environmental conditions, such as fluctuations in temperature, humidity, light intensity, and water availability. Non-optimal environmental conditions can cause stress to the plant, which in turn affects its growth, development, and productivity. Environmental stresses can be divided into several types, including abiotic stresses (such as drought, salinity, extreme temperatures, and light) and biotic stresses (such as pathogen and pest attacks). Each type of stress can trigger specific responses in plants, either morphologically, physiologically, or biochemically. One of the stresses that often hits tea plantations is drought stress, which can cause a decrease in water content in plant tissues, changes in leaf structure, and accumulation of osmoregulatory compounds (Qian et al., 2018).

Drought stresses can be characterized by extreme temperatures, such as high temperatures, which affect key enzymes in the photosynthetic process (Sun et al., 2022). Increased light intensity causes a decrease in chlorophyll and the yellowing of tea leaves (Zhang et al., 2023). Plants adapt to drought stress in their environment through drought escape, drought avoidance, drought tolerance strategies, or a combination of all three (Yadav & Sharma, 2016). By plants, these strategies are packaged in various forms of morphological, physiological, biochemical, and molecular adaptations as a unified plant adaptation system in response to water deficits in the environment (Zlatev, 2012).

Drought stress is the inevitable factor that exists in various environments without recognizing borders and with no clear warning, thereby hampering plant biomass production, quality, and energy. It is a key important environmental stress that occurs due to temperature dynamics, light intensity, and low rainfall (Seleiman et al., 2021). Drought is a serious threat to tea plantations, significantly affecting tea shoot production. The negative impact of these factors will cause a decrease in the water potential of plant cells, resulting in osmotic stress. Osmotic stress causes oxidative damage and involves the formation of reactive oxygen species (ROS) in plant cells, which then causes membrane damage (Nour et al., 2024). The

production of ROS in plant cells displays both detrimental and beneficial effects. However, the exact pathways of ROS-mediated stress alleviation are yet to be fully elucidated (Sachdev et al., 2021)

Plants can respond to stress morphologically, physiologically, and biochemically. Tea plants can adapt to a variety of stresses, but tolerance levels vary by cultivar. A deep understanding of how tea plants respond to various drought stresses is essential for developing adaptation and mitigation strategies. Morphological, physiological, and biochemical analysis methods provide effective tools to study plant responses holistically. Morphological analysis involves visual observations and physical measurements of plant parts such as leaves, stems, and roots. Physiological analysis involves the study of vital plant functions, including the processes of photosynthesis, respiration, and transpiration. Meanwhile, biochemical analysis focuses on the identification and quantification of important compounds in the plant that play a role in adaptation and defense mechanisms. Therefore, the objective of this review is to critically analyze current methods used to detect drought stress in tea plants across morphological, physiological, and biochemical domains, highlight their advantages and limitations, and propose an integrated framework for more accurate and early detection.

Materials and Methods

The reference search of this review was conducted through Google Scholar and academic websites such as Scopus, Ebsco, and Clarivate using the keywords “drought stress,” “*Camellia sinensis*,” “climate change,” and “morphological, biochemical adaptation”. The articles obtained are relevant for further analysis using descriptive methods. Articles published between 2007 and 2024 were considered to ensure the inclusion of recent and appropriate findings. A total of approximately 54 articles were initially retrieved. Inclusion criteria comprised original research articles, review papers, and book chapters that addressed drought stress detection in tea plants through morphological, physiological, or biochemical approaches. Studies focusing on general drought stress in other crops were included only if they provided comparative insights applicable to tea plants.

Results and Discussion

Morphological Responses of Tea Plants under Drought Stress

Drought stress reduces plant height, decreases the number and area of leaves, reduces the fresh and dry weights of the leaves, significantly reduces root length and weight, and reduces the content of leaf photosynthetic pigments (Shil & Dewanjee, 2022). Tea plants exhibit various morphological adaptations to cope with drought stress, which are crucial for maintaining their growth and productivity. These adaptations include changes in leaf structure, root development, and overall plant architecture.

Leaf Morphology and Anatomy. Under drought stress, tea plants exhibit smaller leaves, thicker cuticles, and reduced stomatal conductance to minimize water loss. In tea plants, which are cultivated in tropical and subtropical regions with seasonal rainfall, the ability to maintain high water content during drought periods is an important physiological feature in abiotic stress resistance. The cuticle layer becomes thicker, enhancing the leaf's ability to retain moisture. Additionally, there is an increase in trichome (leaf hair) density, which reflects sunlight and reduces leaf temperature, further conserving water. Stomatal density may also decrease, leading to reduced transpiration rates. These modifications collectively enhance the plant's drought tolerance (Qian et al., 2018).

Relative water content (RWC) decreases significantly during drought but recovers partially upon rehydration (Shen et al., 2022). RWC is a physiological parameter that reflects the water status of plant tissues, particularly their hydration level relative to their maximum water-holding capacity. Relative water content is a direct measure of the dehydration state of plant organs and is tightly linked with cell volume and turgor under most biologically relevant circumstances, and these are likely to be the key drought stress signals to which most plant biochemical systems respond (Sack et al., 2018).

Root System Adaptations. Drought stress is a major environmental constraint that limits water availability for tea plants. One of the key adaptive responses to this stress is modification of root system architecture (RSA)—particularly an increase in root depth, length, and biomass to improve water acquisition from deeper soil layers. Drought is one of these stresses (Gupta et

al., 2020) (Gupta et al., 2020), and roots have evolutionarily become the first organ that senses the changes in soil moisture and adapts to them at morphological, anatomical, and molecular scales (Zahedi et al., 2024) (Amtmann et al., 2022). Fresh water availability is projected to decline by 50% owing to climate change, whereas water demand for agriculture is expected to double by 2050 (Gupta et al., 2020). Temperature extremes, whether too hot or too cold, can damage plant tissues, disrupt physiological processes, and reduce the quality and quantity of tea production. In addition to the changes already mentioned, tea plants may also undergo modifications to the root system in response to environmental stress. For example, plants may develop deeper roots or increase the production of lateral roots to enhance the uptake of water and nutrients from the soil, which may become more difficult to access due to unfavorable environmental conditions. Tea plants subjected to drought stress often develop deeper and more extensive root systems. This adaptation allows them to access water from deeper soil layers, improving their ability to withstand prolonged dry periods.

Drought rhizogenesis, where new roots form under drought conditions, has been observed in some plant species, enabling rapid water uptake upon rehydration (Thiep et al., 2015). Root system architecture (RSA) is the spatial distribution of roots in the soil profile (Pandey & Bennett, 2019) and it is primarily shaped by length, branching, angle, and thickness. Root System Architecture is characterized by a series of traits including rooting depth, root growth angle, root-to-shoot ratio, root diameter, root length density, root surface area, root volume, root distribution, root tip frequency, and root hair development (Germon et al., 2020). Roots have developed the ability to change the RSA traits in response to water stress ('plasticity') (Kang et al., 2022). A review showed that drought decreased total root length and tip frequency, increased rooting depth, and had no effect on root branching in tree species (Brunner et al., 2015). According to Xiao et al., (2020) the root system configurations, such as root hair, root branches, and root density, can significantly affect the water deficiency of plants. According to (Zhou et al., 2018) found that tea seedlings exposed to progressive drought for 21 days had a 46% increase in root mass fraction and a significant increase in specific root length

(SRL), allowing the plant to exploit a larger soil volume for water absorption. Furthermore, according to (Wang et al., 2020) that root scanning and 3D modeling demonstrated that tea plants under drought conditions increase vertical root penetration by an average of 12.4 cm deeper compared to control plants. The study emphasized that drought-stressed plants showed a shift toward fewer but thicker roots in upper layers and denser root networks in deeper soil strata (>30 cm depth).

Stem and Branch Modifications. Drought stress can lead to reduced stem elongation and altered branching patterns in tea plants (Rokhmah et al., 2022). These changes result in a more compact plant architecture, which reduces the overall water requirement and exposure to sunlight, thereby minimizing water loss. Drought stress can reduce cell division and expansion, nutrient uptake and transport, and alter phytohormone metabolism and signaling, as well as general metabolism in plants (Xiao et al., 2020). Reductions in stem elongation and photosynthetic rates can result from acclimation and can intensify with increasing stress (Xu et al., 1997). The reduction in stem elongation under drought stress may result from a reduction in cell division, expansion, or both. Cell expansion, an increase in cell volume, is very sensitive to drought stress. Reduced cell size is often observed across a range of drought severities (Zhao et al., 2011). Loosening of the cell wall to increase plasticity and the presence of adequate turgor pressure are key factors that facilitate cell expansion (Cosgrove, 2015). Cell wall extensibility is affected by multiple enzymes, including expansins. Expansins increase loosening of the cell wall, potentially by breaking bonds among cellulose microfibrils and/or hemicelluloses, thereby allowing turgor pressure to expand the cell (Cosgrove, 2015).

In addition, drought stress often triggers stomatal closure in tea leaves to reduce water loss, which limits CO₂ intake and inhibits photosynthesis. As a result, the growth rate is reduced, and the formation of new leaves is inhibited. Extreme temperatures, such as heat waves, can cause thermal stress that damages proteins and cell membranes, while low temperatures can freeze plant tissues. All these factors result in reduced yield and quality of tea production. Proper agronomic management, including efficient irrigation, plant protection, and selection of stress-resistant varieties, is

essential to reduce the negative impact of environmental stress on tea plants (Samarina et al., 2020).

Physiological Responses of Tea Plants under Drought Stress

Photosynthesis Performance. Environmental stresses such as drought extremes significantly impact tea plants' growth and morphological development. Drought causes water stress that inhibits photosynthesis, reduces leaf growth, and affects water use efficiency. Excess or lack of water can also cause stress conditions, as water is a core environmental factor affecting plant growth and development (Rezamela et al., 2020).

Photosynthesis is the essential metabolic activity that produces energy and carbohydrates for the growth and development of tea plants. Drought reduces photosynthesis due to stomatal closure, limiting CO₂ uptake (Ding & Jiang, 2022). This leads to decreased carbohydrate synthesis and overall energy production (Gu et al., 2020). The foliar photosynthetic rate is decreased with the decrease of relative water content (RWC) and water potential under drought stress (Qian et al., 2018).

Tea plants regulate their growth and development under temperature stress through physiological and biochemical adaptations, such as adjusting their photosynthetic machinery, activating stress-responsive genes, and accumulating compatible solutes to maintain cellular osmotic balance. Drought stress reduces the availability of water for tea plants, leading to stomatal closure, decreased photosynthesis, and ultimately, reduced growth. Tea plants respond to drought stress by closing stomata to minimize water loss, developing a deeper root system to access deeper soil moisture, and synthesizing protective compounds like proline and antioxidants to mitigate oxidative damage caused by drought-induced reactive oxygen species (Morris, 2023).

When exposed to drought stress, physiological changes in tea plants include various complex responses that affect overall plant growth and development. In addition, drought stress can affect the photosynthesis process of tea plants. Decreased photosynthesis can occur due to disruption in the carbon dioxide uptake process or damage to photosynthetic pigments due to oxidative stress. Plant cells may also change the cell membrane's structure and composition, affecting the cell's permeability to

water and nutrients. As a result, the tea plant may experience a decrease in its uptake of water or essential nutrients from the soil, which may hinder its growth and development (Maritim et al., 2015).

Prolonged drought stress can also lead to chronic stress conditions that inhibit the overall growth and productivity of the tea plant. One of the main changes occurs in the chlorophyll content, a pigment that plays an important role in photosynthesis. Drought stress and extreme temperatures often lead to a decrease in chlorophyll content, which impacts photosynthetic efficiency and plant growth (Li et al., 2024).

Nutrient Use Efficiency. Nutrient use efficiency (NUE) refers to the ability of plants to absorb, translocate, and utilize nutrients efficiently for growth, development, and yield production. Under drought stress, NUE becomes a critical factor as water scarcity directly affects nutrient availability, uptake, and metabolism in plants. This is particularly important in tea plants which are often grown in regions prone to periodic drought. Mineral nutrients play electrochemical, structural, and catalytic roles in all biological organisms and are essential for the completion of the plant life cycle (Lopez et al., 2023). Abiotic stresses and nutrient deficiency severely impact the growth, development, and productivity of plants (Shikha et al., 2023). Environmental changes cause abiotic stress in plants primarily by altering the uptake and utilization of the nutrients. Maintaining nutrient use efficiency under abiotic stress is an effective means of increasing plant stress resistance. Thus, the intensification of abiotic stresses will require the development of plants with high nutrient use efficiency (Liang et al., 2023). For tea plants, maintaining NUE under drought stress is vital for sustaining yield and quality. Strategies to enhance NUE include:

Breeding for Drought-Resilient Varieties: Developing tea cultivars with traits such as deeper root systems or higher water use efficiency (WUE) can improve Nutrient Use Efficiency under drought conditions. WUE is an important parameter in assessing how efficiently plants use water to produce biomass or photosynthetic products. Under drought stress conditions, WUE is very relevant because it reflects the ability of plants to adapt to water limitation to improve the production of adapted varieties, future breeding programs must

combine desirable plant traits that complement climate, soil, and management practices (e.g., sowing dates, fertilization, plant density, etc.) in target production systems (Varshney et al., 2021).

Optimized Fertilization Practices:

Fertilization optimization is one of the important strategies in managing drought stress in tea plants especially in the context of climate change, which increases the frequency and intensity of droughts in plantation areas. Tea plants are very sensitive to water availability, and a lack of water can inhibit physiological processes such as photosynthesis, nutrient uptake, and the formation of secondary metabolites that determine yield quality. Therefore, proper application of fertilizers in terms of type, dosage, timing, and application method can help improve water use efficiency (WUE), stimulate root growth, and strengthen the plant's defense system against drought stress (Zerfu, 2018). Fertilizer management enhances WUE by promoting stomatal regulation, osmotic adjustment, and the maintenance of leaf turgor pressure under water-limited conditions (Farooq et al., 2009). Adequate nitrogen and potassium supply, for example, supports deeper and more extensive root development, improving water and nutrient acquisition from the soil (Xu et al., 2010). Moreover, balanced fertilization can upregulate the synthesis of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT), which protect plant cells against oxidative damage caused by drought-induced reactive oxygen species (ROS) (Ashraf, 2010).

Nutrients such as nitrogen (N), phosphorus (P), and potassium (K) play a crucial role in enhancing the drought resistance of tea plants. Nitrogen supports the synthesis of proteins and chlorophyll that are important in maintaining photosynthetic activity, while phosphorus strengthens root growth, thereby increasing the plant's ability to absorb water. Potassium has a special role in regulating stomatal aperture and maintaining osmotic balance, which is important in maintaining cell turgor in times of water deficit (Taiz and Zeiger, 2015). The nutrient supply is crucial to improving tea plant health and productivity. Fertilizer optimization is a key strategy to manage drought stress in tea by improving water use efficiency, enhancing root development, and supporting physiological resilience (Que & Zhao, 2024). Balanced application of nitrogen, phosphorus, and especially potassium helps maintain

photosynthesis, regulate stomatal function, and promote osmotic adjustment under water deficit. The increased uptake of nutrients from soil due to the application of chemical nutrients or biofertilizers might have produced enough carbohydrate in leaves for translocation to the sink for maximum productivity (Easwaran et al., 2023). Biofertilizers such as mycorrhizae and phosphate-solubilizing bacteria can enhance nutrient uptake and root health, increasing the plant's ability to access moisture during drought. Integrating organic and inorganic fertilizers improves drought tolerance and tea yield by supporting antioxidant defense and metabolic stability. The integration of organic and inorganic fertilizers enhances drought tolerance in tea by improving soil structure and water-holding capacity (via organic inputs), while ensuring immediate nutrient availability (via inorganic sources). This synergy promotes root development, osmotic adjustment (e.g., proline and soluble sugars), and activates antioxidant enzymes, thereby stabilizing cellular metabolism under drought stress. The improved nutrient balance also supports chlorophyll maintenance and secondary metabolite production, contributing to sustained yield and quality under water-limited conditions (Manzoor et al., 2024). Thus, targeted fertilization not only mitigates drought impacts but also sustains tea productivity under climate stress (Easwaran et al., 2023). Integrated fertilization improved the soil nutrient status, which is associated with the improvement of tea growth and quality (Manzoor et al., 2024).

Soil Moisture Conservation Techniques: The scarcity of water caused by rising temperatures and unpredictable rainfall patterns is responsible for the limited crop yields in arid and semi-arid regions (Li et al., 2018). Hence, it is crucial to manage water usage on farmland to preserve water resources in agricultural areas. Implementing mulching or other soil moisture retention practices can mitigate the effects of drought, thereby supporting consistent nutrient availability and uptake (Demo & Bogale, 2024). Mulching helps conserve water resources, reduce soil erosion, and minimize nutrient runoff, which can improve water quality (Blaise et al., 2021). Among the reviewed strategies, optimized fertilization practices emerge as one of the most directly effective methods to enhance NUE under drought stress. The reason is that targeted nutrient management immediately addresses the

nutrient imbalance caused by limited water availability. Overall, a combination of optimized fertilization practices with soil moisture conservation offers a practical and immediately implementable solution, while breeding for drought-resilient varieties is crucial for long-term resilience. The following table summarizes the comparison of NUE strategies under drought stress:

Table 1. Summarizes the comparison of nutrient use efficiency (NUE) strategies under drought stress

| Strategy | Mechanism | Strength |
|--|---|--|
| Breeding for drought-resilient varieties | Develops traits like deep roots and higher WUE | Sustainable long-term solution, genetic improvement |
| Optimized fertilization practices | Enhances nutrient availability and uptake | Immediate effect: improves physiological resilience |
| integrated fertilization (chemical + biofertilizers) | Enhances nutrient absorption and soil health | Improves drought tolerance, boosts antioxidant systems |
| Soil moisture conservation techniques (e.g., mulching) | Retains soil water, supports consistent nutrient uptake | Easy to implement, cost-effective |

Biochemical Responses of Tea Plants to Drought Stress

Tea plants exhibit various biochemical responses to mitigate the adverse effects of drought stress. These responses are crucial for maintaining cellular homeostasis and ensuring plant survival under water-deficient conditions.

Phytohormone. Plants accumulate hormones [e.g., abscisic acid (ABA) or salicylic acid (SA), or methyl jasmonate (MJ) under abiotic stress conditions and pathogen attack. Among the hormones, Abscicic acid is involved in several abiotic and biotic stress conditions and is therefore considered an essential and versatile compound. In contrast, SA, MJ, and ethylene (ET) help in resistance against biotic stress (Bharath et al., 2021). Abscicic acid (ABA) is a stress hormone that accumulates under different abiotic and biotic stresses. A typical effect of ABA on leaves

is to reduce transpirational water loss by closing stomata and simultaneously defending against microbes by restricting their entry through stomatal pores (Bharath et al., 2021). When plants were exposed to water stress (drought), an increase in ABA was typical due to either synthesis or degradation of ABA or both (Chen et al., 2020)(Ma et al., 2018); (Gietler et al., 2020)). The soil-water deficit could be perceived as a signal by roots to trigger ABA's de novo synthesis (Qi et al., 2018). Salicylic acid (SA) is an endogenous growth regulator naturally produced by plants and belongs to the group of phenolic acids. It plays an important role in regulating plant growth, development, and physiological processes such as photosynthesis and metabolism. SA also enhances plant resistance to biotic and abiotic stresses (Damayanthi et al., 2023).

Under drought-stress conditions, ABA and Salicylic Acid (SA) contents rapidly accumulated in the cells of tea plants, and drought-resistance tea cultivars showed higher ABA and SA contents than drought-susceptible tea cultivars (Liu et al., 2015). ABA is generally emphasized and regarded as a key drought-sense signal from root to shoot. Stomatal closure can also result from direct evaporation of water from guard cells through an active metabolic process involving the reversal of ion fluxes responsible for stomatal opening. This process is regulated by ABA, which mediates signaling between shoots and roots (Sharma et al., 2023). ABA limits transpiration water loss and gas exchange by inducing stomatal closure (Kishor et al., 2022).

Secondary Plant Metabolites. Drought negatively impacts the quality of active ingredients in medicinal and aromatic plants (Emami et al., 2024). Water availability is a crucial environmental factor influencing the growth, development, and synthesis of medicinal plant constituents. Drought stress can influence the biosynthesis of secondary metabolites in tea plants, such as flavonoids and tannins. These compounds have antioxidant properties and may play roles in mitigating oxidative stress. Changes in secondary metabolite profiles can also affect the quality attributes of tea, including flavor and aroma. Water stress causes a reduction in plant size, reduces plant leaf area, decreases whole biomass, and not only alters the plant structurally and anatomically but also leads to fluctuation of their secondary chemical constituents. Secondary plant metabolites (SPMs) are useful to assess the

quality and quantity of the therapeutic ingredients, and such metabolites synthesized by the plant help to cope with the negative effects of stress for adaptation and defence (Shil & Dewanjee, 2022).

On the other hand, under drought conditions, tea plants can synthesize a wide variety of flavonoids, including anthocyanins, flavonones, flavonols, and flavanols. As important secondary metabolites in tea plants, flavonoids not only play a role in the stress response of tea plants but also have a significant impact on tea quality (Dong et al., 2019). Flavonoids are responsible for the bitter taste of tea infusions by activating bitter receptors in humans. Flavonoid glycosides are also the main pigments in green tea infusions that determine the appearance and quality of green tea (Li et al., 2023). These secondary metabolites not only serve as defense agents against pathogens and pests but also have important roles as antioxidants that help reduce drought damage. Under the influence of environmental stresses such as drought and temperature extremes, the biochemistry of tea plants undergoes significant changes that reflect adaptation and stress response. One common response is the increased production of antioxidant compounds such as polyphenols and flavonoids. Tea plants produce these compounds as a defense mechanism against environmental stress, such as excessive UV exposure or extreme temperatures.

Proline. Proline degradation is equally essential for supplying energy under long-term

stress and when the plants are relieved from stress. Proline is synthesized in chloroplasts/cytoplasm but transported through proline porters to the root and shoot tips, where it supplies energy by oxidation in mitochondria (Kishor et al., 2022). In addition, under environmental stress conditions, such as drought or excess water, tea plants can show an increase in the production of osmotic compounds such as proline, which help maintain osmotic pressure and water balance in their cells.

Drought spur the formation of proline. Proline is one of several small molecules classified as osmolytes or osmoprotectants (X. Liang et al., 2013). Proline is one of the amino acids produced by plants when experiencing abiotic stress. One of the abiotic stresses in question is drought stress. Plants that experience drought stress will usually try to make physiological adaptations. One form of physiological adaptation is to produce proline.

Proline is synthesized as a compound that helps the plant maintain cell turgor. Proline content in drought-tolerant plants is seen to increase in accumulation compared to drought-sensitive plants (Masheva et al., 2022). Proline levels can be used as an indicator of drought resistance (Khan et al., 2025), but not all plants produce it, including even drought-resistant species. The following illustrates the potential function of proline and proline metabolism in stress protection (Fig. 1).

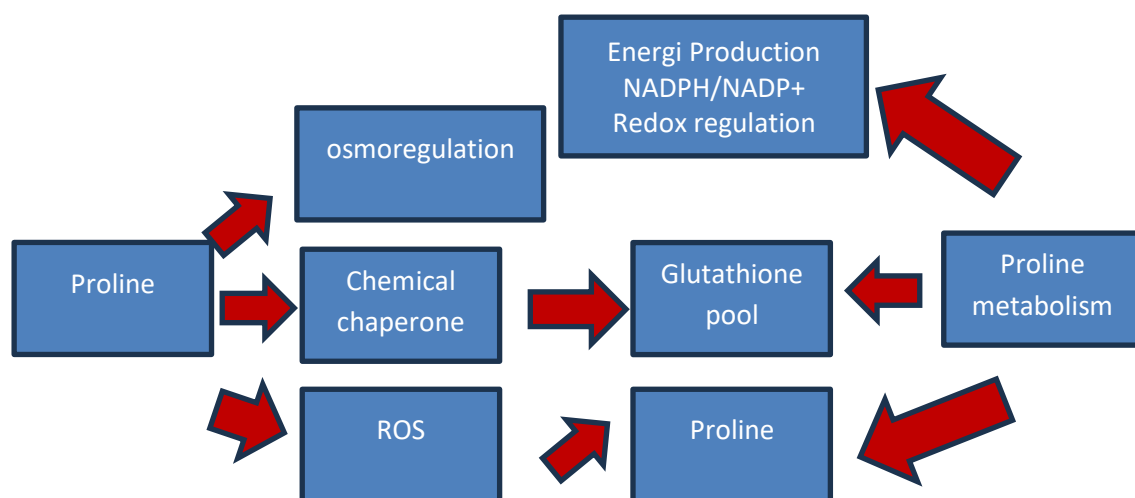


Figure 1. Potential functions of proline and proline metabolism in stress protection (Liang et al., 2013)

The figure shows changes in proline and total sugar levels in tea clones, along with the duration of drought stress. The increase in proline content is a characteristic of plants in acclimatizing to stress. Proline accumulation was highest in clone 276 (50.13%) after 40 days of drought stress, while clone 278 (1.54%) showed the smallest increase compared to control plants. Proline acts as an osmoprotectant during drought stress; high proline accumulation in clone 276 indicates that this clone has genotypic tolerance to drought. Proline accumulation helps maintain water balance and prevent membrane distortion. Under water stress conditions, resistant and tolerant cultivars accumulate higher proline levels than susceptible cultivars (Masheva et al., 2022). Total sugar content increased after 40 days of drought stress by 52.20% and 52.08% for clones 285 and 399, respectively, compared to the control (Chaeikar et al., 2020). During drought stress, especially severe or prolonged, plants utilize soluble sugars optimally to maintain growth.

An increase in total sugar content under drought conditions is a positive characteristic of drought-tolerant plants. Activation of the ROS system helps protect proline and soluble sugars against oxidant stress. Abiotic stress leads to increased accumulation of proline, which acts as an osmolyte. Proline helps stabilize antioxidant proteins and enzymes, scavenge ROS, restore intracellular redox balance, and trigger cellular signaling (M. J. Zhang et al., 2020). Environmental stress also affects enzyme activity and secondary metabolite production. Antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) have increased activity in response to stress-induced oxidative stress (X. Zhang et al., 2023). Reactive oxygen compounds (ROS) produced in response to stress can damage cells, so an increase in antioxidant enzyme activity helps protect plant cells from oxidative damage (Han & Wang, 2023).

Conclusion

Detection of drought stress in tea plants through morphological, physiological, and biochemical approaches provides a comprehensive picture of plant responses to water deficit. Changes in leaf structure, decreased photosynthetic activity, and accumulation of proline, ABA, and secondary metabolites are important indicators that can be

utilized. NUE also plays an important role in strengthening the plant's adaptive response to drought. The integration of these three approaches allows for more accurate identification of stress and supports the development of adaptation strategies to enhance tea plant resilience under climate change. Future research should focus on field experiments evaluating the combined effects of optimized fertilization, biofertilizer application, and soil moisture conservation techniques across different environments would provide practical insights. Exploring the role of microbial inoculants and biostimulants in enhancing physiological and biochemical responses under drought conditions is also recommended. Developing predictive models that link morphological, physiological, biochemical, and environmental data will further support precision management strategies in tea cultivation under climate change.

References

- Amtmann A, Bennett MJ, Henry A. 2022. Root phenotypes for the future. *Plant Cell Environ.*, 45(3): 595–601. <https://doi.org/10.1111/pce.14269>
- Ashraf M. 2010. Inducing drought tolerance in plants: Recent advances. *Biotechnology Advances*, 8(1): 169–183. <https://doi.org/https://doi.org/10.1016/j.biotechadv.2009.11.005>
- Badan Litbang Pertanian. 2022. Laporan Tahunan Riset Teh dan Kina Indonesia. Balai.
- Bharath P, Gahir S, Raghavendra AS. 2021. Absciscic acid-induced stomatal closure : An important component of plant defense against abiotic and biotic stress. *Front Plant Sci.*, 12(March): 1–18. <https://doi.org/10.3389/fpls.2021.615114>
- Blaise D, Manikandan A, Desouza ND, Bhargavi B, Somasundaram J. 2021. Intercropping and mulching in rain-dependent cotton can improve soil structure and reduce erosion. *Environmental Advances*, 4(April): 100068. <https://doi.org/10.1016/j.envadv.2021.100068>
- Brunner I, Herzog C, Dawes MA, Arend M, Sperise C. 2015. How tree roots respond to drought. *Frontiers in Plant Science*, 6(July): 1–16.

- <https://doi.org/10.3389/fpls.2015.00547>
Chaeikar SS, Marzvan S, Khiavi SJ, Rahimi M. 2020. Changes in growth, biochemical, and chemical characteristics and alteration of the antioxidant defense system in the leaves of tea clones (*Camellia sinensis* L.) under drought stress. *Scientia Horticulturae*, 265: 109–257.
<https://doi.org/10.1016/j.scienta.2020.109257>
- Chen K, Li G, Bressan R, Song C, Zhu J, Zhao Y. 2020. Abscissic acid dynamics, signaling, and functions in plants. *J. Integr. Plant Biol.*, 62: 25–54.
<https://doi.org/10.1111/jipb.12899>
- Cosgrove DJ. 2015. Plant expansins: Diversity and interactions with plant cell walls. *Curr. Opin. Plant Biol.*, 25: 162–172.
<https://doi.org/10.1016/j.pbi.2015.05.014>
- Damayanthi MMN, Wijeratne TL, Damunupola JW. 2023. Exogenous salicylic acid induced drought stress tolerance in immature tea tropical agricultural research exogenous salicylic acid induced drought stress tolerance in immature tea (*Camellia sinensis* L.) *Plants. Tropical Agricultural Research*, 34(3): 237–253.
<https://doi.org/10.4038/tar.v34i3.8649>
- Demo AH, Bogale GA. 2024. Enhancing crop yield and conserving soil moisture through mulching practices in dryland agriculture. *Front. Agron.*, 6: 1361697.(May).
<https://doi.org/10.3389/fagro.2024.1361697>
- Ding Z, Jiang C. 2022. Transcriptome profiling to the effects of drought stress on different propagation modes of tea plant (*Camellia sinensis*). *Frontiers in Genetics*, 13(August): 1–13.
<https://doi.org/10.3389/fgene.2022.907026>
- Dong F, Hu J, Shi Y, Liu M, Zhang Q, Ruan J. 2019. Effects of nitrogen supply on flavonol glycoside biosynthesis and accumulation in tea leaves (*Camellia sinensis*). *Plant Physiology and Biochemistry*, 138: 48–57.
<https://doi.org/10.1016/j.plaphy.2019.02.017>
- Easwaran S, Marimuthu M, Guhan V. 2023. Studies on the effect of integrated nutrient management on drought influenced parameters in tea (*Camellia* sp .). *International Journal of Environment and Climate Change*, 13(3): 257–261.
<https://doi.org/10.9734/IJECC/2023/v13i32075>
- Emami Z, Barker AV & Hashemi M. 2024. Physiology of medicinal and aromatic plants under drought stress. *The Crop Journal*, 12(2): 330–339.
<https://doi.org/10.1016/j.cj.2023.12.003>
- Farooq M, Wahid A, Kobayashi N, D Fujita, Basra SMA. 2009. Plant drought stress: effects, mechanisms and management: Review article. *Agronomy for Sustainable Development*, 29(1): 185–212.
- Fatawa MI, Santosa E, Hapsari DP. 2024. Climate change and its adaptation strategies on tea plantation in West Java , Changing rainfall and its adaptation strategies on tea plantation in West Java, Indonesia. *Indonesian Journal of Agronomy*, 51(2): 257–268.
<https://doi.org/10.24831/ija.v51i2.47081>
- Food Agricultural Organization. 2022. Market and Trade of Tea.
<https://www.fao.org/markets-and-trade/commodities-overview/beverages/tea/en>
- Germon A, Laclau JP, Robin A, Jourdan C. 2020. Tamm review: Deep fine roots in forest ecosystem. *Forest Ecology and Management*, 466: 118–135.
<https://doi.org/10.1016/j.foreco.2020.118135>
- Gietler M, Fidler J, Labudda M. 2020. Abscissic acid – Enemy or savior in the response of cereals to abiotic and biotic stresses? *Int. J. Mol. Sci.*, 21(4607): 1–28.
- Gu H, Wan, Y, Xie H, Qiu, C, Zhang S, Xiao J, Li H, Chen L, Li X, Ding Z 2020. Drought stress triggers proteomic changes involving lignin, flavonoids and fatty acids in tea plants. *Scientific Reports*, 10: 1–11.
<https://doi.org/10.1038/s41598-020-72596-1>
- Gupta A, Andrés Rico-Medina, Caño-Delgado AI. 2020. The physiology of plant responses to drought. *Science*, 368(6488): 266–269.
<https://doi.org/10.1126/science.aaz7614>
- Han C, Wang P. 2023. Reactive oxygen species: Multidimensional regulators of plant adaptation to abiotic stress and development. *Journal of Integrative Plant Biology*, 66(3): 301–631.
<https://doi.org/10.1111/jipb.13601>
- Han WY, Li X, Yan P, Zhang L, Golam Jalal A.

2018. Tea cultivation under changing climatic conditions. In *Global tea science*. Burleigh Dodds Science Publishing. <https://doi.org/http://dx.doi.org/10.19103/AS.2017.0036.19>
- International Tea Committee (ITC). 2024. The Global Tea Report 2024. Tea and Coffee Trade Journal. <https://www.teaandcoffee.net/organisation/international-tea-committee-itc/>
- Kang J, Peng Y, Xu W. 2022. Crop root responses to drought stress: Molecular mechanisms, nutrient regulations, and interactions with microorganisms in the rhizosphere. *Int. J. Mol. Sci.*, 23(9310): 1–26. <https://doi.org/https://doi.org/10.3390/ijms23169310>
- Khan P, Abdelbacki AMM, Albaqam M, Jan R, Kim K. 2025. Proline promotes drought tolerance in maize. *Biology*, 14(1): 41.
- Kishor PBK, Suravajhala P, Rathnagiri P, Sreenivasulu N. 2022. Intriguing role of proline in redox potential conferring high temperature stress tolerance. *Front. Plant Sci.*, 13(June): 1–16. <https://doi.org/10.3389/fpls.2022.867531>
- Li J, Bai, X, Ran F, Zhang, Yan Y, Li P, Chen H. 2024. Effects of combined extreme cold and drought stress on growth, photosynthesis, and physiological characteristics of cool-season grasses. *Scientific Reports*, 14(0123456789): 1–19. <https://doi.org/10.1038/s41598-023-49531-1>
- Li Q, Li H, Zhang L, Zhang S, Chen Y. 2018. Mulching improves yield and water-use efficiency of potato cropping in China: A meta-analysis. *Field Crops Res.*, 221: 50–60. <https://doi.org/10.1016/j.fcr.2018.02.017>
- Li Y, Chen Y, Chen, Shen C. 2023. Flavonoid metabolites in tea plant (*Camellia sinensis*) stress response: Insights from bibliometric analysis. *Plant Physiology and Biochemistry*, 202(107934). <https://doi.org/https://doi.org/10.1016/j.plaphy.2023.107934>
- Liang B, Li C, Bai T, Wang P. 2023. Editorial: Nutrient use efficiency of plants under abiotic stress. *Front Plant Sci.*, 14(11798): 10–12. <https://doi.org/10.3389/fpls.2023.1179842>
- Liang X, Zhang, Natarajan SK, Becker D F. 2013. Proline mechanisms of stress survival. *Antioxidants and Redox Signaling*, 19(9): 998–1011. <https://doi.org/10.1089/ars.2012.5074>
- Liu S, Yao, Ma C., Jin J, Ma J, Li C, Chen L. 2015. Physiological changes and differential gene expression of tea plant under dehydration and rehydration conditions. *Sci. Hortic.*, (184): 129–141. <https://doi.org/10.1016/j.scienta.2014.12.036>
- Lopez G, Ahmadi SH, Amelun W, Athmann M, Ewert F, Gaiser T, Gocke MI, Kautz T, Postma J, Stoschus A, Watt M, Yu P, Seidel SJ. 2023. Nutrient deficiency effects on root architecture and root-to-shoot ratio in arable crops. *Front Plant Sci.*, 13(1067498): 1–18. <https://doi.org/10.3389/fpls.2022.1067498>
- Ma Y, Cao J, He J, Chen Q, Li X, Yang Y. 2018. Molecular mechanism for the regulation of ABA homeostasis during plant development and stress responses. *Int. J. Mol. Sci.*, 2(19): 1–14. <https://doi.org/10.3390/ijms19113643>
- Manzoor ML, Ni K, Ruan J. 2024. Influence of organic and inorganic fertilizers on tea growth and quality and soil properties of tea orchards' top. *Plants*, 13(207): 1–22. <https://doi.org/Plan> <https://doi.org/10.3390/plants13020207>
- Maritim TK, Kamunya SM, Mirej P, Mwendia C, Muoki RC, Cheruiyot EK, Wachira FN, Breeding T, Africa C. 2015. Physiological and biochemical response of tea [*Camellia sinensis* (L.) O. Kuntze]. *Journal of Horticultural Science & Biotechnology*, 90(4): 395–400. <https://doi.org/https://doi.org/10.1016/j.cj.2023.12.003>
- Masheva V, Spasova-apostolova V, Aziz S, Tomlekova N. 2022. Variations in proline accumulation and relative water content under water stress characterize bean mutant lines (*P. vulgaris* L.). *Bulgarian Journal of Agricultural Science*, 28(3): 430–436.
- Meng F, Zhang T, Yin D. 2023. The effects of soil drought stress on growth characteristics, root system, and tissue anatomy of *Pinus sylvestris* var. *mongolica*. *PerrJ*, 11(14578): 1–19. <https://doi.org/10.7717/peerj.14578>
- Morris J. 2023. Regulation of growth and development of *camellia sinensis* (tea plant) under abiotic and biotic stress. *J Biotech and Phytochem*, 7(3): 1–2. <https://doi.org/10.35841/ajbp-7.3.148>
- Nour MM, Aljabi HR, Al-huqail AA, Horneburg

- B. 2024. Drought responses and adaptation in plants differing in life-form. *Frontiers in Ecology and Evolution*, 11: 1–14. <https://doi.org/10.3389/fevo.2024.1452427>
- Pandey BK, Bennett MJ. 2019. A new angle on how roots acclimate to sporadic rainfall. *Cell*, 178(2): 269–271. <https://doi.org/10.1016/j.cell.2019.06.018>
- Qi, J, Song, C, Wang, B, Zhou, J, Zhu J, Gong Z. 2018. Reactive oxygen species signaling and stomatal movement in plant responses to drought stress and pathogen attack. *Journal of Integrative Plant Biology*, 60(9): 805–826. <https://doi.org/10.1111/jipb.12654>
- Qian W, Hu J, Zhang X, Zhao L, Wang Y. 2018. Response of Tea Plants to Drought Stress. In *Stress Physiology of Tea in the Face of Climate Change*. Springer Nature Singapore Pte Ltd. <https://doi.org/10.1007/978-981-13-2140-5>
- Que Y, Zhao Q. 2024. High-yield tea plant cultivation: Ecological and agronomic insights. *Journal of Tea Science Research*, 14(4): 215–224. <https://doi.org/10.5376/jtsr.2024.14.0020>
- Rezamela, Rosniawaty S, Suherman C. 2020. Respons pertumbuhan bibit setek teh (*Camellia sinensis* (L .) O . Kuntze) Klon GMB 7 pada berbagai interval penyiraman. *Agrikultura*, 31(3): 263–272.
- Rokhmah DN, Astutik D, Supriandi H. 2022. Cultivation technology for drought stress mitigation in tea plants: A review. *IOP Conference Series Earth and Environmental Science*, 1038(1): 012015. <https://doi.org/10.1088/1755-1315/1038/1/012015>
- Sachdev S, Ansari SA, Ansari MI, Fujit M. 2021. Abiotic stress and reactive oxygen species: generation, signaling, and defense mechanisms. *Antioxidants*, 10(277): 1–37. <https://doi.org/https://doi.org/10.3390/antiox10020277>
- Sack L, John GP, Buckley TN. 2018. ABA accumulation in dehydrating leaves is associated with decline in cell volume, not turgor pressure. *Plant Physiology*, 176(1): 489–493. <https://doi.org/10.1104/pp.17.01097>
- Samarina LS, Malyukova LS, Efremov AM, Simonyan TA, Matskiv AO, Koninskaya NG, Rakhmangulov RS, Gvasaliya MV, Malyarovskaya VI, Ryndin AV, Orlov YL, Tong W, & Hanke MV. 2020. Physiological, biochemical, and genetic responses of Caucasian tea (*Camellia sinensis* (L.) Kuntze) genotypes under cold and frost stress. *PeerJ*, (8): 1–23. <https://doi.org/10.7717/peerj.9787>
- Seleiman MF, Al-Suhaibani N, Ali N, Akmal M, Alotaibi M, Refay Y, Dindaroglu T, Abdul-Wajid HH, Battaglia ML. 2021. Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants*, 10(2): 1–25. <https://doi.org/10.3390/plants10020259>
- Sharma A, Gupta A, Ramakrishnan M, Van HC, Zheng B, Bhardwaj M, Tra, LSP. 2023. Roles of abscisic acid and auxin in plants during drought: A molecular point of view. *Plant Physiology and Biochemistry*, (204): 108129. <https://doi.org/https://doi.org/10.1016/j.plaphy.2023.108129>
- Shen J, Wang S, Sun L, Wang Y, Fan K, Li C, Wang H, Bi C, Zhang F, Ding Z. 2022. Dynamic changes in metabolic and lipidomic profiles of tea plants during drought stress and re-watering. *Front. Plant Sci.*, 13(9): 1–16. <https://doi.org/10.3389/fpls.2022.978531>
- Shikha D, Jakhar P, Satbhai SB. 2023. Role of jasmonate signaling in the regulation of plant responses to nutrient deficiency. *J. Exp. Bot.*, 74:1221–1243. <https://doi.org/10.1093/jxb/erac387>
- Shil S, Dewanjee S. 2022. Impact of drought stress signals on growth and secondary metabolites (SMs) in medicinal plants. *The Journal of Phytopharmacology*, 11(5): 371–376. <https://doi.org/10.31254/phyto.2022.11511>
- Sri Lanka Teaboard. 2023. Tea Production For the October 2023. Tea Production. <https://srilankateaboard.lk/production-volume/>
- Sun W, Wei J, Wu G, Xu H, Chen Y, Yao M, ... Li Q. 2022. CqZF-HD14 enhances drought tolerance in quinoa seedlings through interaction with CqHIPP34 and CqNAC79. *Plant Science*, 323(111406): 1–6.
- Taiz L, Zeiger E. 2015. *Plant physiology and Development* (3rd Edition). Sinauer Associates, Inc., Publishers.
- Thiep NV, Thi N, Ha T, Thi T, My K. 2015. Evaluating characteristics related to drought tolerance in tea genetic resources as the basis to select new tea clone with drought resistance. *Journal of Agricultural*

- Technology, 11(4): 2239–2248.
- Varshney RK, Kholova J, Tuberosa R, Tardieu F, Siddique KHM, Reynolds MP. 2021. Breeding custom-designed crops for improved drought adaptation. *Advanced Genetics*, 2: 1–15. <https://doi.org/10.1002/ggn2.202100017>
- Wang L, Lee M, Ye B, Yue GH. 2020. Genes, pathways and networks responding to drought stress in oil palm roots. *Scientific Reports*, 10(21303): 1–13. <https://doi.org/10.1038/s41598-020-78297-z>
- Xiao S, Liu, L, Sun YZH, Zhang K, Bai Z, Li C, Dong H. 2020. Fine root and root hair morphology of cotton under drought stress revealed with RhizoPot. *J. Agron. Crop Sci.*, 14(16): 679–693. <https://doi.org/https://doi.org/10.1111/jac.12429>
- Xu Z, Zhou G, Shimizu H. 2010. Plant responses to drought and rewatering. *Plant Signaling & Behavior*, 5(6): 649–654.
- Yadav S, Sharm KD. 2016. Molecular and Morphophysiological Analysis of Drought Stress in Plants. In Everlon Cid Rigobelo (Ed.), *Plant Growth*. IntchOpen. <https://doi.org/DOI: 10.5772/65246>
- Zahedi SM, Karimi M, Venditti A, Zahra N, Siddique KHM, Farooq M. 2024. Plant Adaptation to Drought Stress: The Role of Anatomical and Morphological Characteristics in Maintaining the Water Status. *Journal of Soil Science and Plant Nutrition*, 25: 409–427. <https://doi.org/DOI:10.1007/s42729-024-02141-w>
- Zerfu A. 2018. Review on integrated nutrient management of tea (*Camellia sinensis* L.). *Cogent Food & Agriculture*, 4(1): 1–12. <https://doi.org/10.1080/23311932.2018.1543536>
- Zhang MJ, Zhang XS, Gao X. 2020. ROS in the male – female interactions during pollination: Function and Regulation. *Frontiers in Plant Science*, 11(2): 1–8. <https://doi.org/10.3389/fpls.2020.00177>
- Zhang X, Liu K, Tang Q, Zeng, Wu Z. 2023. Light intensity regulates low-temperature adaptability of tea plant through ROS stress and developmental programs. *International Journal of Molecular Sciences*, 24(12). <https://doi.org/10.3390/ijms24129852>
- Zhao ML, Fang Y, Gao Q, Wang W. 2011. Expansin-regulated cell elongation is involved in the drought tolerance in wheat. *Protoplasma*, 248(2): 313–323. <https://doi.org/DOI:10.1007/s00709-010-0172-2>
- Zhou G, Zhou X, Zhou L, Shao J, Fu Y, Nie Y, Hosseini S, Cheng W, Wang J, Hu F. 2018. Drought - induced changes in root biomass largely result from altered root morphological traits: Evidence from a synthesis of global field trials. *Plant Cell Environ.*, 41: 2589–2599. <https://doi.org/10.1111/pce.13356>
- Zhu M, Li N, Zhou F, Ouyang J, Lu D, Xu W, Li J, Lin H, Zhang Z, Xiao J, Wang K, Huang J, Liu Z, Wu J. 2020. Microbial bioconversion of the chemical components in dark tea. *Food Chemistry*, 312(126043): 1–5. <https://doi.org/https://doi.org/10.1016/j.foodchem.2019.126043>
- Zlatev Z. 2012. An overview on drought induced changes in plant growth, water relations and photosynthesis. *Emirates Journal of Food and Agriculture*, 23(1): 56–72. <https://doi.org/10.9755/ejfa.v24i1.10599>