

Research Report

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Synergistic Effects of Shading and Irrigation Frequency on Summer Bud Growth and Quality in Tea Plants

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Abstract This study mainly discusses how shading and irrigation frequency jointly affect the growth of tea plant buds and the quality of tea in summer. It summarizes the impact of shading on important substances in tea plants that affect tea quality, such as chlorophyll, amino acids, polyphenols, and aroma precursors. It also discusses the effects brought about by the combination of different shading materials and different irrigation cycles. Combined with the case of field experiments in Zhejiang tea gardens, it was examined whether these treatments were helpful for improving tea yield, quality and sustainable cultivation. This study aims to provide some ideas and methods for the management of tea plants in summer, hoping to help tea farmers grow better tea and also improve the efficiency of planting.

Keywords Irrigation frequency; Tea buds; Tea quality; Shading; Secondary metabolites

1 Introduction

Summer is an important period when tea plants grow relatively fast and sprout new buds. Whether the summer buds grow well or not will directly affect the yield and quality of the tea. Well-grown summer buds contain more beneficial components such as amino acids and chlorophyll, and can also make the taste of tea better and the color more beautiful (Zhang et al., 2022; Hu et al., 2024). Therefore, to make tea sell well, improving the quality of summer buds is extremely crucial.

However, the high temperatures, intense sunlight and lack of water in summer often affect the normal growth of tea plants. Too strong sunlight or too high temperature will increase the polyphenols in tea, making the tea bitter and less fresh and refreshing to drink (Elango et al., 2023). If there is a lack of water, tea buds cannot grow, the metabolism of tea plants will also be affected, and both yield and quality will decline (Ge et al., 2024). Current research shows that providing appropriate shade for tea plants is a good way to regulate light and temperature. This can not only improve the growth environment, but also enhance the quality of tea (Chen et al., 2022).

This study aims to explore how the combination of shading and watering frequency affects the bud growth and tea quality of tea plants in summer. Based on relevant field experiment cases and using some multi-omics methods, it will analyze the regulatory effects of different shading intensities and irrigation arrangements on the physiology, metabolism and quality of tea plants. This research aims to provide some scientific basis and practical suggestions for the management of tea gardens in summer, ensuring that there are both abundant and high-quality tea leaves.

2 Physiology of Summer Bud Development in Tea Plants

2.1 Developmental stages of summer buds

The process of tea plants sprouting in summer goes through several stages, including dormancy, activation, germination and growth. The size and shape of buds vary among different varieties and natural populations. These differences are influenced by both genes and the environment (Zhang et al., 2025b). The process by which buds go from dormancy to activation is extremely crucial, as it is related to the yield and quality of tea. This process involves many molecular-level regulations, such as transcription factors, hormone signals, and epigenetic mechanisms (Liu et al., 2019; Hao et al., 2024). Before the bud begins to germinate, the accumulation of sugar and a certain degree of oxidative stress will help the bud transition from the “resting” state to the “active” state (Tang et al., 2023).

2.2 Key metabolic pathways involved in bud formation

The formation and growth of buds rely on multiple metabolic pathways, among which plant hormones and secondary metabolism are the most important. Hormones such as auxin, gibberellin, abscisic acid, cytokinin and jasmonic acid jointly regulate the expression of related genes, thereby controlling the dormancy, activation and growth of buds (Hao et al., 2018). Among them, the regulatory genes of gibberellin and abscisic acid play a very important role in the process of bud transformation from dormant to active (Yue et al., 2018). Meanwhile, the synthesis of some secondary metabolites, such as gallic acid (GA) and tea polyphenols, is also regulated by hormones, and these substances can affect the quality and flavor of the buds (Shi et al., 2025). In addition, sugar metabolism, photosynthesis, and antioxidation-related metabolic activities also play a role in the growth of buds (Tong et al., 2018; Tang et al., 2023).

2.3 Environmental sensitivity of bud quality traits

The quality of buds, such as the content of amino acids, tea polyphenols and caffeine, is particularly sensitive to the environment. Changes in conditions such as light, temperature and moisture can affect hormone signaling, expression of transcription factors and various metabolic pathways, thereby altering the growth rate of buds and accumulation of quality components (Chen et al., 2023b; Liu et al., 2023). For instance, different shading and watering frequencies can cause changes in amino acids and secondary metabolites in buds, thereby affecting the flavor and economic value of tea (Zhang et al., 2025a). In addition, the quality of buds is also influenced by genetic factors. There will be differences among different varieties, and it is also affected by seasonal changes. That is to say, the final quality of tea buds is determined by both genes and the environment.

3 Role of Light and Shading in Tea Plant Physiology

3.1 Effects of light intensity on photosynthesis and secondary metabolites

The intensity of light directly affects the photosynthesis effect of tea plants and also influences the accumulation of various metabolites in tea leaves. Appropriate shading can increase the chlorophyll in the leaves, make the leaf color greener and improve the quality of tea (Figure 1) (Chen et al., 2021; Elango et al., 2023). Research has found that after shading, the content of amino acids (such as theanine) and caffeine in tea plants will increase, while polyphenols like epicatechin and epigallocatechin will decrease. This change is conducive to enhancing the freshness and flavor of tea (Liu et al., 2018; Kc et al., 2021; Kc et al., 2022). In addition, shading can also inhibit the synthesis of some substances such as flavonoids and lignin, thereby improving the taste of tea (Li et al., 2020; Teng et al., 2020; Zhang et al., 2020). Light changes can also affect many metabolic pathways and gene expressions, such as nitrogen metabolism, glucose metabolism and the synthesis of photosynthetic pigments.

3.2 Types of shading materials and their impacts

Different shading materials have different effects on tea plants. For instance, black nets, blue nets, red nets, straw nets, etc. have all been used. Studies have found that using double-layer shading nets (such as those 50 cm high) can significantly increase the amino acid content in tea, reduce polyphenols, and also improve the environment of tea gardens, such as cooling and maintaining soil moisture (Ge et al., 2024). The blue net and the red net have better effects than the black net in promoting bud quantity and yield, but they have similar effects in reducing bitter substances (Fang et al., 2022). Different shading materials can also change the quality of light, such as the ratio of red light to far-red light, which can also affect the physiological activities of tea plants.

3.3 Adaptive responses of tea plants to light reduction

Tea plants have many levels of responses to reduced light. Shading will increase the accumulation of chlorophyll and carotenoids, make the leaves greener and enhance the photosynthetic capacity (Chen et al., 2021; Yue et al., 2021). Shading also regulates the expression of some key genes, such as *CsPOR*, *CsHY5*, *CPOX* and *SGR*. These genes affect the synthesis and degradation of chlorophyll, and also change the distribution of amino acids and polyphenols (Chen et al., 2022; Han et al., 2023). In addition, shading can also cause changes in the structure of leaves, such as thinning of epidermal cells and reduction of downy hairs. At this time, the expression of some genes related to hair (such as *CsCPCs*) will increase, indicating that tea plants adapt to the weak light environment through both morphological and gene regulation (Jiang et al., 2020; Wang et al., 2023; Wakamatsu et al., 2024).

Shading also helps enhance the resistance of tea plants, such as increasing the activity of antioxidant enzymes, which helps tea plants resist sudden strong light damage (Sano et al., 2020; Zaman et al., 2023).

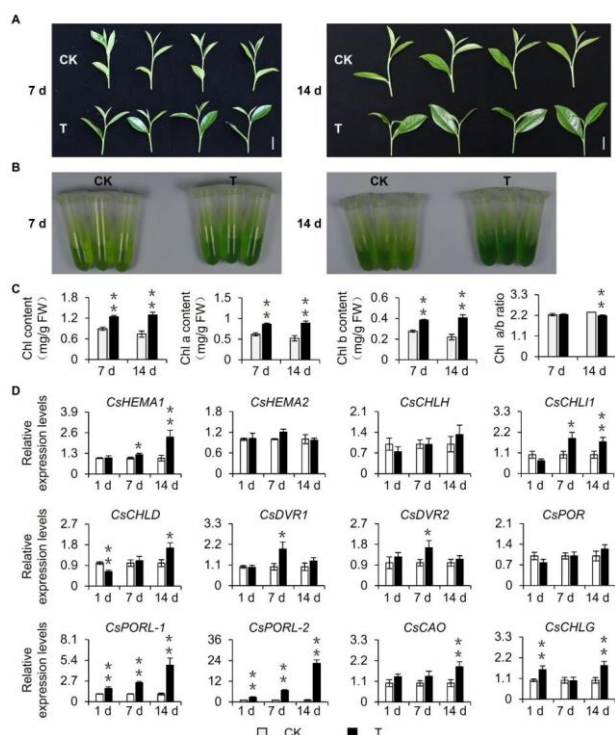


Figure 1 Effect of shading treatment on the chlorophyll content of tea leaves and the expression of related genes (Adopted from Chen et al., 2021)

Image caption: (A) The phenotype of new shoots after 7 day and 14 day shading treatment. Bar=2 cm. (B) The comparison of leaf pigments after 7 day and 14 day shading treatment. (C) The change of chlorophyll content after shading treatment. Chl: total chlorophyll; Chl a: chlorophyll a; Chl b: chlorophyll b; and FW: fresh weight. (D) The changes in the gene expression of chlorophyll synthesis pathway after shading treatment. CK: no shading treatment group (about 1 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$); T: 90% shading treatment group (about 130 $\mu\text{mol m}^{-2} \text{s}^{-1}$). *CsEF1- α* was used as an internal reference to normalized the changes. Data are expressed as mean \pm SD ($n=3$). * $p\leq 0.05$; ** $p\leq 0.01$; and difference from CK treatment at the same time point (Adopted from Chen et al., 2021)

4 Role of Irrigation Frequency in Summer Tea Cultivation

4.1 Water stress and its influence on bud set and expansion

Lack of water will significantly affect the sprouting of tea plants. Under water stress, the buds of tea plants fail to grow or grow slowly, the leaf activity deteriorates, the photosynthetic efficiency decreases, and eventually both yield and quality are affected (Yue et al., 2023). During drought, the metabolic activities and lipid components in tea plant leaves also undergo significant changes. Although some damages can partially recover after rehydration, the levels of many metabolites are difficult to fully return to normal (Figure 2) (Shen et al., 2022). So, scientific irrigation is a good way to solve this problem. As long as the water keeps up, the buds can differentiate and grow normally, and the yield and quality of tea in summer will also be better (Hasan et al., 2023).

4.2 Irrigation scheduling strategies in tea gardens

In summer, it is very important to scientifically arrange irrigation. Some studies have pointed out that if tea plants are watered every 4 to 5 days and combined with an appropriate amount of nitrogen and phosphorus fertilizers, the accumulation of dry matter and the growth of new shoots can be significantly enhanced. Meanwhile, the intelligent irrigation system that utilizes remote sensing technology and soil moisture monitoring can also adjust the watering time and water usage according to the actual water shortage situation in the tea garden. This approach can not only ensure that tea plants have water to use, but also save water resources and improve efficiency (Wang et al., 2021). These practices help to achieve more meticulous management of tea gardens and reduce the damage caused by water shortage.

4.3 Effects on water-use efficiency and root physiology

A reasonable frequency of irrigation not only ensures that tea plants have access to water but also promotes root development. Precision irrigation can maintain the concentration of leaf cell SAP within an appropriate range, prevent excessive water loss from leaves, and enhance photosynthesis and the assimilation capacity of leaves. Continuous and reasonable irrigation can also induce the root system to grow deeper and enhance the drought resistance capacity (Wang et al., 2021). When water management and fertilization are well combined, water and nutrients can work in synergy, enabling tea plants to grow better and have a higher yield.

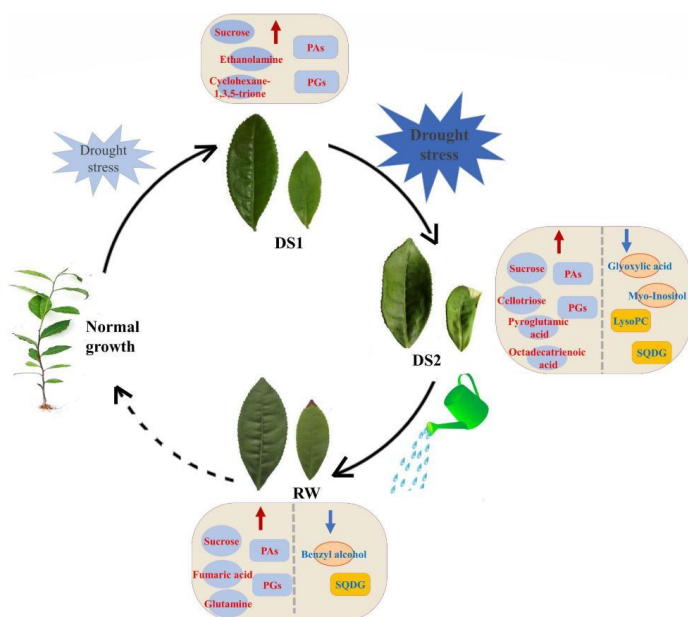


Figure 2 Models of possible mechanisms of tea plants responding to different water conditions. The red and blue arrows indicated that the levels of metabolites increased and decreased, respectively (Adopted from Shen et al., 2022)

5 Interaction Effects of Shading and Irrigation Frequency

5.1 Photosynthetic efficiency and water use synergy

Shading can lower the temperature of the leaves and soil, which can improve the microenvironment around the tea plants and help enhance the efficiency of photosynthesis and water use. After being treated with multi-layer shading nets, the amino acids in the tea increased significantly and the soil moisture was also maintained more stably. This enables tea plants to maintain a relatively high photosynthetic rate and stomatal conductance during the hot summer days (Zhang et al., 2022; Ge et al., 2024). Shading can also enable tea plants to accumulate more chlorophyll and carotenoids, increase the content of photosynthetic pigments, and thereby enhance the photosynthetic capacity (Chen et al., 2021; Elango et al., 2023; Han et al., 2023). These changes work together to enhance the water use efficiency of tea plants. Especially in hot and dry weather, shading combined with a reasonable irrigation frequency can effectively alleviate the pressure of water shortage and help tea plants grow better.

5.2 Combined impacts on stress tolerance and bud viability

Shading not only improves the physiological state of tea plants but also enhances their resistance to adverse environments such as high temperatures and drought. Studies have found that shading can regulate the activity of antioxidant enzymes and the levels of osmotic regulatory substances, enhancing the stress resistance of tea plants. Under shading conditions, the antioxidant system of tea plant leaves is activated, which can reduce the damage caused by strong light or high temperature and maintain the healthy growth and vitality of buds (Sano et al., 2020). In addition, shading can enhance the stability and stress resistance of cell membranes by regulating protein expression and metabolic pathways (Zaman et al., 2023). Reasonable arrangement of irrigation, combined with shading, can maintain the water and nutrient supply to the buds, further promoting the growth rate and quality improvement of the buds.

5.3 Mechanistic insights: hormonal and molecular crosstalk

Shading can also regulate the growth, development and quality formation of tea plants by influencing light signals and hormone metabolism. For example, shading can increase the expression of genes related to chlorophyll synthesis (such as *CsPORA-2*), while inhibiting inhibitory factors like *CsHY5*, thereby promoting chlorophyll accumulation (Chen et al., 2021). In addition, shading can also affect the synthesis of substances such as amino acids and flavonoids, regulate the balance of carbon and nitrogen metabolism, and improve the quality of tea (Zhang et al., 2020; Yang et al., 2021). When shading and irrigation frequency act together, they may affect bud differentiation, growth and stress resistance by regulating some hormone signaling pathways (such as abscisic acid and gibberellin) (Chen et al., 2023a). Proteomic and transcriptomic studies have also found that shading can activate many genes and proteins related to stress coping, cell protection, and metabolic regulation. These molecular changes provide support for the normal growth of tea plants in complex environments (Han et al., 2023; Zaman et al., 2023).

6 Impacts on Tea Leaf Biochemical Composition

6.1 Total polyphenols and catechin profiles

Shading treatment usually leads to a decrease in the total polyphenols and major catechins (such as epicatechin and epigallocatechin) in tea. This change helps to reduce the bitterness of tea and makes the taste milder (Xu et al., 2020). Shading also reduces the esterification degree of catechins, especially the proportion of galacylated catechins decreases, which further improves the flavor structure of tea (Shao et al., 2022; Zhu et al., 2023). In addition, shading can affect the ratio of polyphenols to amino acids. The ratio of polyphenols to amino acids decreases. This indicator is regarded as an important factor for improving the quality of green tea (Zhang et al., 2020; Chen et al., 2022).

6.2 Amino acids and aroma precursors

Shading can also significantly increase the content of free amino acids in tea, including theanine, threonine, glutamic acid, alanine, etc. These amino acids make the tea fresher and sweeter (Sano et al., 2018). However, the changes in amino acids are related to the seasons. The shading effect is more obvious in spring and sometimes decreases in summer (Zhu et al., 2023). The study also found that shading can promote the synthesis of theanine in the roots and accelerate its transport to new buds (Yang et al., 2021). Furthermore, shading also regulates the synthesis of carotenoids and aroma precursors, enhancing the accumulation of aroma substances, which lays the foundation for the aroma of high-end tea (Fu et al., 2022; Elango et al., 2023).

6.3 Balance of secondary metabolites for marketable tea quality

In addition to polyphenols and amino acids, shading can also affect other secondary metabolites, such as flavonoids, caffeine and lignin (Shao et al., 2022). Shading can reduce bitter flavonoids and lignin, while increasing the levels of caffeine and pigments (chlorophyll, carotenoids), thereby making the color and taste of tea better (Teng et al., 2020; Chen et al., 2021). In addition, shading further affects the synthesis and distribution of these substances by regulating the expression of related genes and DNA methylation (Wakamatsu et al., 2024). These changes combined have made the sensory quality of tea better and enhanced its competitiveness in the market (Xu et al., 2020).

7 Agricultural and Economic Implications

7.1 Yield improvement under combined treatment

Shading can improve the micro-environment around tea plants, reduce the pressure brought by high temperatures and strong light, help buds and leaves grow better, and enhance the quality of tea. Many studies have found that appropriate shading (such as using double-layer shading nets) can increase the amino acid content in tea, improve the flavor, and at the same time keep the soil moisture more stable, which is conducive to the continuous growth of buds and leaves (Ge et al., 2024; Hu et al., 2024). Shading can also improve the photosynthetic efficiency of tea plants, increase the chlorophyll content, and enhance the growth ability of the entire tea plant (Sano et al., 2018; Zhang et al., 2022). Although some studies have pointed out that shading may lead to a decrease in yield per unit area (Chen et al., 2023a), as long as the intensity of shading is reasonably adjusted and combined with an

appropriate irrigation frequency, it is still possible to improve the quality of tea while minimizing yield loss. Achieve a balance between the two.

7.2 Impacts on labor, inputs, and sustainability

Shading combined with scientific irrigation can also mitigate the impact of extreme weather on tea gardens. For example, it can reduce the incidence of pests and diseases, decrease the usage of pesticides and chemical fertilizers, thereby helping tea farmers save costs (Sun et al., 2020). Shading can also reduce the damage to tea plants caused by high temperatures in summer, extend the picking time, improve the efficiency of tea picking, and better arrange manpower (Zhang et al., 2022; Ge et al., 2024). Meanwhile, shading combined with reasonable irrigation can also make the water in the soil be utilized more fully, avoid waste, and enhance the sustainability of the tea garden ecology.

7.3 Implications for summer tea production in subtropical regions

In subtropical regions, high temperatures, strong sunlight and drought often occur in summer, which have a significant impact on the growth of tea plants and the quality of summer tea. The coordinated management of shading and irrigation frequency provides a feasible method for growing summer tea well in this area. By reasonably adjusting the shading intensity and irrigation arrangement, not only can the contents of amino acids and chlorophyll in summer tea be increased, making the flavor and appearance better, but also it can help tea plants alleviate high-temperature stress, improve stress resistance, and allow buds and leaves to continue to grow (Sun et al., 2020). This is of great value for enhancing the market performance and economic benefits of subtropical summer tea.

8 Case Study: Field Evaluation in Zhejiang Tea Plantations

8.1 Experimental design: light-shading nets × irrigation regimes

In some typical tea gardens in Zhejiang Province, researchers conducted field experiments to test the combined effects of different shading methods and irrigation frequencies. Shading treatment includes no shading, single-layer shading and double-layer shading. For example, double-layer shading nets are set 50 centimeters above the canopy layer of tea plants to simulate different light intensity and light quality conditions (Zhang et al., 2022; Shu et al., 2024). The irrigation frequency was set as high frequency (daily irrigation), medium frequency (once every three days), and low frequency (once a week) in combination with the local summer rainfall and evaporation conditions, with the aim of creating a distinct moisture gradient in the soil (Ge et al., 2024).

8.2 Growth and quality indices under different treatment combinations

The experimental results show that shading treatment can significantly improve the growth environment of tea plants, making the canopy temperature lower and the soil moisture more stable, thereby helping the buds and leaves grow more tender and better (Zhang et al., 2022). When using double-layer shading nets, the contents of umami and sweet amino acids in tea plant leaves increased significantly, while the content of tea polyphenols decreased. The ratio of amino acids to polyphenols increased, resulting in better overall quality of tea (Li et al., 2020). Shading can also promote the accumulation of chlorophyll and caffeine, and reduce bitter components such as catechins and lignin (Teng et al., 2020; Shu et al., 2024). The study also found that moderate shading, such as 80% shading for 12 consecutive days, can be used to produce first-grade matcha raw materials (Hu et al., 2024). After the irrigation frequency is increased, the soil moisture can be retained better, which can reduce the stress of tea plants in high-temperature weather and promote the growth rate of buds and leaves and the accumulation of inclusions together with shading.

8.3 Farmer perceptions and adoption potential

Through field visits, it was found that many tea farmers recognized that shading and reasonable irrigation were helpful for improving the quality of summer tea, especially in years with dry and hot weather (Ge et al., 2024). The use of shading measures such as shading nets or tree shade can not only improve the flavor of tea, but also reduce pests and diseases and increase the diversity of microorganisms in the soil. Both ecological and economic benefits are good (Zou et al., 2022; Que and Zhao, 2024). Although some farmers are worried that shading will affect the yield, it is still possible to achieve both yield and quality by adjusting the shading intensity and

controlling the watering frequency (Chen et al., 2023a). Overall, the practice of combining shading and irrigation has a promising promotion prospect in the tea-growing areas of Zhejiang Province and is also highly accepted by farmers.

9 Limitations and Research Gaps

9.1 Variability across tea varieties and regions

Most current research focuses on a few common varieties, such as “Longjing 43” and “Fuding White Tea”, and the scope of research is mainly limited to some specific regions. In fact, different tea plant varieties and different ecological environments respond greatly to shading and irrigation. For instance, for some varieties, the quality components such as amino acids and tea polyphenols will change significantly after shading, but the same shading method has no obvious effect on another variety (Li et al., 2020; Hu et al., 2024). Some studies in emerging tea-growing areas such as the United States have found that the impact of shading on tea plants is quite different from that in traditional tea-growing areas, indicating that the origin environment and the genetic background of the variety may jointly affect the mechanism of shading and irrigation, but these have not been fully studied yet (Zhang et al., 2022).

9.2 Lack of molecular data linking treatments to gene expression

Although some studies using transcriptome and metabolome analysis have found that shading affects some metabolic pathways in tea plants, such as the expression of genes that control amino acid, chlorophyll and flavonoid synthesis (Teng et al., 2020), but most of these studies only analyzed shading as one factor. There is not much molecular evidence that truly and systematically links shading, irrigation frequency and other field management measures to the expression of key genes related to tea quality. Especially, there is still a lack of in-depth molecular-level research on how shading and irrigation affect bud growth and tea quality through signal transduction, hormone regulation, etc. (Sun et al., 2020; Fang et al., 2022).

9.3 Short-term trials vs. long-term effects

Most existing studies have been short-term treatments, such as shading or irrigation for 7 to 20 days, mainly focusing on the growth and quality changes of buds and leaves during this period (Zhu et al., 2023). However, in real production, shading and irrigation are often long-term management measures. In the long term, it remains unclear whether these treatments will affect the entire growth cycle, yield changes, quality stability, and even the stress resistance of tea plants. Some studies have found that prolonged shading may suppress the carbon and nitrogen metabolism of tea plants, having a negative impact on yield and quality (Li et al., 2020; Chen et al., 2023a). However, at present, there is still a lack of cross-seasonal and multi-year continuous observation data, which also makes it difficult for us to offer scientific and reliable long-term management suggestions to tea farmers.

10 Concluding Remarks

Shading is an important method to improve the quality of tea in summer. Research has found that appropriate shading can significantly increase the content of amino acids in tea, especially umami amino acids and theanine. At the same time, it can also reduce polyphenols and bitter substances, making the color of the tea better and the taste more mellow. Methods like using double-layer shading nets not only improve the microclimate of the tea garden and lower the temperature, but also keep the soil moist, which helps the buds and leaves grow faster and the quality of the leaves is also higher. Shading can also regulate the metabolism of carbon and nitrogen, promote the synthesis of photosynthetic pigments, and at the same time control the expression of some related genes, making tea plants more adaptable to adverse conditions such as high temperatures and dryness, and also easier to accumulate beneficial substances.

Shading works even better when combined with a reasonable irrigation frequency. Moderate watering can help maintain soil moisture and root vitality. As a result, not only will buds grow faster, but the quality of tea will also be higher. Studies show that in the hot and strong summer environment, the combination of shading and irrigation is a good way to scientifically manage tea gardens. As long as the right shading materials are selected, the degree of shading and the watering time are well controlled, the growth environment of tea plants can be better regulated,

and both the quality and yield of tea can be improved. Shading can also regulate plant hormones, enhance the efficiency of photosynthesis and nutrient distribution, making tea plants more heat-tolerant and better able to utilize water and fertilizer resources. These achievements provide theoretical support and practical operation methods for tea gardens to achieve efficient and sustainable development.

In the future, remote sensing technology can be used to monitor the light, temperature and soil moisture of tea gardens in real time, providing accurate data support for shading and irrigation. The intelligent irrigation system that utilizes artificial intelligence technology can automatically adjust the frequency of watering based on the weather and the growth of tea plants, achieving both water conservation and effectiveness. There is also an intelligent shading system that can automatically adjust the shading degree according to different weather conditions and the needs of the tea plants. These data-driven management tools will drive tea gardens to shift from traditional models to more precise, efficient and sustainable modern agriculture.

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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.

References

- Chen J., Wu S., Dong F., Li J., Zeng L., Tang J., and Gu D., 2021, Mechanism underlying the shading-induced chlorophyll accumulation in tea leaves, *Frontiers in Plant Science*, 12: 779819.
<https://doi.org/10.3389/fpls.2021.779819>
- Chen J., Wu S., Mao K., Li J., Dong F., Tang J., Zeng L., and Gu D., 2023a, Adverse effects of shading on the tea yield and the restorative effects of exogenously applied brassinolide, *Industrial Crops and Products*, 197: 116546.
<https://doi.org/10.1016/j.indcrop.2023.116546>
- Chen L., Miao W., Wang B., Chen S., Li L., Liu Z., Liu K., Nian B., Cai X., Jiang C., and Zhao M., 2023b, Integrated genome-wide chromatin accessibility and expression profile identify key transcription factors involved in bud endodormancy break in tea plants, *Scientia Horticulturae*, 317: 112022.
<https://doi.org/10.1016/j.scienta.2023.112022>
- Chen X., Ye K., Xu Y., Zhao Y., and Zhao D., 2022, Effect of shading on the morphological, physiological, and biochemical characteristics as well as the transcriptome of matcha green tea, *International Journal of Molecular Sciences*, 23(22): 14169.
<https://doi.org/10.3390/ijms232214169>
- Elango T., Jeyaraj A., Dayalan H., Arul S., Govindadamy R., Prathap K., and Li X., 2023, Influence of shading intensity on chlorophyll, carotenoid and metabolites biosynthesis to improve the quality of green tea: a review, *Energy Nexus*, 12: 100241.
<https://doi.org/10.1016/j.nexus.2023.100241>
- Fang Z., Jin J., Ye Y., He W., Shu Z., Shao J., Fu Z., Lu J., and Ye J., 2022, Effects of different shading treatments on the biomass and transcriptome profiles of tea leaves (*Camellia sinensis* L.) and the regulatory effect on phytohormone biosynthesis, *Frontiers in Plant Science*, 13: 909765.
<https://doi.org/10.3389/fpls.2022.909765>
- Fu X., Chen J., Li J., Dai G., Tang J., and Yang Z., 2022, Mechanism underlying the carotenoid accumulation in shaded tea leaves, *Food Chemistry: X*, 14: 100323.
<https://doi.org/10.1016/j.fochx.2022.100323>
- Ge S., Wang Y., Shen K., Wang Q., Ahammed G., Han W., Jin Z., Li X., and Shi Y., 2024, Effects of differential shading on summer tea quality and tea garden microenvironment, *Plants*, 13(2): 202.
<https://doi.org/10.3390/plants13020202>
- Han X., Shen Y., Wang Y., Shen J., Wang H., Ding S., Xu Y., Mao Y., Chen H., Song Y., Ding Z., and Fan K., 2023, Transcriptome revealed the effect of shading on the photosynthetic pigment and photosynthesis of overwintering tea leaves, *Agronomy*, 13(7): 1701.
<https://doi.org/10.3390/agronomy13071701>
- Hao X., Tang H., Wang B., Wang L., Cao H., Wang Y., Zeng J., Fang S., Chu J., Yang Y., and Wang X., 2018, Gene characterization and expression analysis reveal the importance of auxin signaling in bud dormancy regulation in tea plant, *Journal of Plant Growth Regulation*, 38: 225-240.
<https://doi.org/10.1007/s00344-018-9834-7>
- Hao X., Tang J., Chen Y., Huang C., Zhang W., Liu Y., Yue C., Wang L., Ding C., Dai W., Yang Y., Horvath D., and Wang X., 2024, CsCBF1/CsZHD9-CsMADS27, a critical gene module controlling dormancy and bud break in tea plants, *The Plant Journal*, 121(1): e17165.
<https://doi.org/10.1111/tpj.17165>
- Hasan R., Islam A., Maleque M., Islam M., and Rahman M., 2023, Effect of drought stress on leaf productivity and liquor quality of tea: a review, *Asian Journal of Soil Science and Plant Nutrition*, 9(4): 1-10.
<https://doi.org/10.9734/ajsspn/2023/v9i4187>

- Hu Z., Yao X., Chen H., Li F., Zhao H., Tang H., Jiao Y., Jiang Y., Tian J., He Y., and Lu L., 2024, Changes and dynamics of the main quality components in tea leaves of 4 tea cultivars during the shading process, *Scientia Horticulturae*, 333: 113242.
<https://doi.org/10.1016/j.scienta.2024.113242>
- Jiang X., Zhao H., Guo F., Shi X., Ye C., Yang P., Liu B., and Ni D., 2020, Transcriptomic analysis reveals mechanism of light-sensitive albinism in tea plant *Camellia sinensis* 'Huangjinju', *BMC Plant Biology*, 20: 216.
<https://doi.org/10.1186/s12870-020-02425-0>
- Kc S., Long L., Liu M., Zhang Q., and Ruan J., 2021, Light intensity modulates the effect of phosphate limitation on carbohydrates, amino acids, and catechins in tea plants (*Camellia sinensis* L.), *Frontiers in Plant Science*, 12: 743781.
<https://doi.org/10.3389/fpls.2021.743781>
- Kc S., Long L., Zhang Q., Ni K., Ma L., and Ruan J., 2022, Effect of interactions between phosphorus and light intensity on metabolite compositions in tea cultivar Longjing43, *International Journal of Molecular Sciences*, 23(23): 15194.
<https://doi.org/10.3390/ijms232315194>
- Li Y., Jeyaraj A., Yu H., Wang Y., Ma Q., Chen X., Sun H., Zhang H., Ding Z., and Li X., 2020, Metabolic regulation profiling of carbon and nitrogen in tea plants [*Camellia sinensis* (L.) O. Kuntze] in response to shading, *Journal of Agricultural and Food Chemistry*, 68(4): 961-974.
<https://doi.org/10.1021/acs.jafc.9b05858>
- Liu L., Li Y., She G., Zhang X., Jordan B., Chen Q., Zhao J., and Wan X., 2018, Metabolite profiling and transcriptomic analyses reveal an essential role of UVR8-mediated signal transduction pathway in regulating flavonoid biosynthesis in tea plants (*Camellia sinensis*) in response to shading, *BMC Plant Biology*, 18: 233.
<https://doi.org/10.1186/s12870-018-1440-0>
- Liu S., Mi X., Zhang R., An Y., Zhou Q., Yang T., Xia X., Guo R., Wang X., and Wei C., 2019, Integrated analysis of miRNAs and their targets reveals that miR319c/TCP2 regulates apical bud burst in tea plant (*Camellia sinensis*), *Planta*, 250: 1111-1129.
<https://doi.org/10.1007/s00425-019-03207-1>
- Liu Y., Chen S., Chen J., Wang J., Wei M., Tian X., Chen L., and Ma J., 2023, Comprehensive analysis and expression profiles of the *AP2/ERF* gene family during spring bud break in tea plant (*Camellia sinensis*), *BMC Plant Biology*, 23: 206.
<https://doi.org/10.1186/s12870-023-04221-y>
- Que Y.Y., and 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>
- Sano S., Takemoto T., Ogihara A., Suzuki K., Masumura T., Satoh S., Takano K., Mimura Y., and Morita S., 2020, Stress responses of shade-treated tea leaves to high light exposure after removal of shading, *Plants*, 9(3): 302.
<https://doi.org/10.3390/plants9030302>
- Sano T., Horie H., Matsunaga A., and Hirono Y., 2018, Effect of shading intensity on morphological and color traits and on chemical components of new tea (*Camellia sinensis* L.) shoots under direct covering cultivation, *Journal of the Science of Food and Agriculture*, 98(15): 5666-5676.
<https://doi.org/10.1002/jsfa.9112>
- Shao C., Deng Z., Liu J., Li Y., Zhang C., Yao S., Zuo H., Shi Y., Yuan S., Qin L., Liu Z., and Shen C., 2022, Effects of preharvest shading on dynamic changes in metabolites, gene expression, and enzyme activity of three tea types during processing, *Journal of Agricultural and Food Chemistry*, 70(45): 14544-14558.
<https://doi.org/10.1021/acs.jafc.2c05456>
- Shen J., Wang S., Sun L., Wang Y., Fan K., Li C., Wang H., Bi C., Zhang F., and Ding Z., 2022, Dynamic changes in metabolic and lipidomic profiles of tea plants during drought stress and re-watering, *Frontiers in Plant Science*, 13: 978531.
<https://doi.org/10.3389/fpls.2022.978531>
- Shi Y., Lu X., Song Q., Sun H., Shen W., Huang R., Huang J., Wei Y., Xiang F., Wang X., Tuo Y., Lin J., and Hu Y., 2025, Mechanism of endogenous hormones regulating gallic acid biosynthesis during the development of buds and leaves in tea plant (*Camellia sinensis*), *Frontiers in Plant Science*, 16: 1553266.
<https://doi.org/10.3389/fpls.2025.1553266>
- Shu Z., Ji Q., He T., Zhou D., Zheng S., Zhou H., and He W., 2024, Combined metabolome and transcriptome analyses reveal that growing under Red shade affects secondary metabolite content in Huangjinya green tea, *Frontiers in Genetics*, 15: 1365243.
<https://doi.org/10.3389/fgene.2024.1365243>
- Sun M., Yuan D., Hu X., Zhang D., and Li Y., 2020, Effects of mycorrhizal fungi on plant growth, nutrient absorption and phytohormones levels in tea under shading condition, *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, 48(4): 2006-2020.
<https://doi.org/10.15835/nbha48412082>
- Tang J., Chen Y., Huang C., Li C., Feng Y., Wang H., Ding C., Li N., Wang L., Zeng J., Yang Y., Hao X., and Wang X., 2023, Uncovering the complex regulatory network of spring bud sprouting in tea plants: insights from metabolic, hormonal, and oxidative stress pathways, *Frontiers in Plant Science*, 14: 1263606.
<https://doi.org/10.3389/fpls.2023.1263606>
- Teng R., Wang Y., Li H., Lin S., Liu H., and Jing Z., 2020, Effects of shading on lignin biosynthesis in the leaf of tea plant (*Camellia sinensis* (L.) O. Kuntze), *Molecular Genetics and Genomics*, 296: 165-177.
<https://doi.org/10.1007/s00438-020-01737-y>
- Tong W., Yu J., Hou Y., Li F., Zhou Q., Wei C., and Bennetzen J., 2018, Circular RNA architecture and differentiation during leaf bud to young leaf development in tea (*Camellia sinensis*), *Planta*, 248: 1417-1429.
<https://doi.org/10.1007/s00425-018-2983-x>

- Wakamatsu J., Yamamoto M., Kikuta M., Tanaka W., and Tominaga R., 2024, Effect of shading on trichome formation and *CAPRICE*-like gene expression in tea (*Camellia sinensis* var. *sinensis*) leaves, *Scientia Horticulturae*, 330: 113049.
<https://doi.org/10.1016/j.scienta.2024.113049>
- Wang Y., Chen C., Tsai Y., and Shen Y., 2021, A sentinel-2 image-based irrigation advisory service: cases for tea plantations, *Water*, 13(9): 1305.
<https://doi.org/10.3390/w13091305>
- Wang Y., Ye J., Yang H., Li D., Li X., Wang Y., Zheng X., Ye J., Li Q., Liang Y., and Lu J., 2023, Shading-dependent greening process of the leaves in the light-sensitive albino tea plant ‘Huangjinya’: possible involvement of the light-harvesting complex II subunit of photosystem II in the phenotypic characteristic, *International Journal of Molecular Sciences*, 24(12): 10314.
<https://doi.org/10.3390/ijms241210314>
- Xu P., Su H., Jin R., Mao Y., Xu A., Cheng H., Wang Y., and Meng Q., 2020, Shading effects on leaf color conversion and biosynthesis of the major secondary metabolites in the albino tea cultivar ‘Yujinxiang’, *Journal of Agricultural and Food Chemistry*, 68(8): 2528-2538.
<https://doi.org/10.1021/acs.jafc.9b08212>
- Yang T., Xie Y., Lu X., Yan X., Wang Y., Ma J., Cheng X., Lin S., Bao S., Wan X., Lucas W., and Zhang Z., 2021, Shading promoted theanine biosynthesis in the roots and allocation in the shoots of the tea plant (*Camellia sinensis* L.) cultivar Shuchazao, *Journal of Agricultural and Food Chemistry*, 69(16): 4795-4803.
<https://doi.org/10.1021/acs.jafc.1c00641>
- Yue C., Cao H., Hao X., Zeng J., Qian W., Guo Y., Ye N., Yang Y., and Wang X., 2018, Differential expression of gibberellin- and abscisic acid-related genes implies their roles in the bud activity-dormancy transition of tea plants, *Plant Cell Reports*, 37: 425-441.
<https://doi.org/10.1007/s00299-017-2238-5>
- Yue C., Cao H., Zhang S., Shen G., Wu Z., Yuan L., Luo L., and Zeng L., 2023, Multilayer omics landscape analyses reveal the regulatory responses of tea plants to drought stress, *International Journal of Biological Macromolecules*, 253: 126582.
<https://doi.org/10.1016/j.ijbiomac.2023.126582>
- Yue C., Wang Z., and Yang P., 2021, Review: the effect of light on the key pigment compounds of photosensitive etiolated tea plant, *Botanical Studies*, 62: 21.
<https://doi.org/10.1186/s40529-021-00329-2>
- Zaman S., Shen J., Wang S., Song D., Wang H., Ding S., Pang X., Wang M., Wang Y., and Ding Z., 2023, Effect of shading on physiological attributes and proteomic analysis of tea during low temperatures, *Plants*, 13(1): 63.
<https://doi.org/10.3390/plants13010063>
- Zhang D., Wei X., Zhang J., Cui D., Zhang P., Chen S., Zou Y., Chen W., Tang D., Liu C., Bian J., Tang Q., and Tan L., 2025a, Variation analysis and quantitative trait loci mapping of 16 free amino acid traits in the tea plant (*Camellia sinensis*), *BMC Plant Biology*, 25: 194.
<https://doi.org/10.1186/s12870-024-06038-9>
- Zhang Q., Bi G., Li T., Wang Q., Xing Z., LeCompte J., and Harkess R., 2022, Color shade nets affect plant growth and seasonal leaf quality of *Camellia sinensis* grown in Mississippi, the United States, *Frontiers in Nutrition*, 9: 786421.
<https://doi.org/10.3389/fnut.2022.786421>
- Zhang Q., Liu M., Mumm R., Vos R., and Ruan J., 2020, Metabolomics reveals the within-plant spatial effects of shading on tea plants, *Tree Physiology*, 41(2): 317-330.
<https://doi.org/10.1093/treephys/tpaa127>
- Zhang S., Chen S., Fu Z., Li F., Chen Q., Ma J., Chen Y., Chen L., and Chen J., 2025b, Integration of digital phenotyping, GWAS, and transcriptomic analysis revealed a key gene for bud size in tea plant (*Camellia sinensis*), *Horticulture Research*, 12(6): uhaf051.
<https://doi.org/10.1093/hr/uhaf051>
- Zhu W., Liu X., Cheng X., Li Y., and Liu L., 2023, Shading effects revisited: comparisons of spring and autumn shading treatments reveal a seasonal-dependent regulation on amino acids in tea leaves, *Beverage Plant Research*, 3: 5.
<https://doi.org/10.48130/bpr-2023-0005>
- Zou Y., Zhong Y., Yu H., Pokharel S., Fang W., and Chen F., 2022, Impacts of ecological shading by roadside trees on tea foliar nutritional and bioactive components, community diversity of insects and soil microbes in tea plantation, *Biology*, 11(12): 1800.
<https://doi.org/10.3390/biology11121800>

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