

Article

Multi-Element Absorption, Enrichment and Translocation of Tea Trees in Different Rock Zones of Wuyishan and Their Effects on Tea Quality

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Abstract

Wuyi rock tea quality in different rock zones differs significantly, and it is of great significance for the development of the rock tea industry to deeply reveal the mineral nutritional basis of its quality formation. In this study, the rhizosphere soils, root systems and leaves of tea trees from 180 tea plantations in different rock zones were collected, to explore the migration pattern of elements in the “soil and root system-leaf” of tea trees in different rock zones. The results showed that the contents of tea polyphenols, theanine, and caffeine were significantly higher in the authentic zone than in the semi-rock zone and the continent zone, with all three quality indices exhibiting a consistent decreasing trend from ZY to BY to ZC, and their mean values in ZY were approximately 1.2-fold and 1.4-fold higher than those in BY and ZC, respectively. The ability of the root system of tea trees in different rock zones to enrich Mn, P and S, their translocation from roots to leaves, and their accumulation in leaves directly affected tea quality. Using four machine learning approaches based on enrichment coefficients of key elements, the classification accuracy for the three rock zones reached 100%. The above conclusions were further verified by hydroponic experiments with Mn, P or S treatments, which confirmed that P exerted the strongest influence on tea quality, followed by S, with Mn showing the smallest effect. This study reveals the mineral nutrient basis for the formation of rock tea quality and lays an important theoretical foundation for the elemental directed regulation of Wuyi rock tea quality.

Keywords: Wuyi rock tea; rock zone; characteristic elements; quality; machine learning



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1. Introduction

Wuyi rock tea, as one of the 10 most famous teas in China, is known worldwide for its unique “rock” flavor and excellent quality [1]. In China, the quality of tea is typically evaluated based on several key physicochemical parameters as stipulated by the national standards of the People’s Republic of China, including tea polyphenols, free amino acids

(mainly theanine), and caffeine. These standards are issued and supervised by the Standardization Administration of the People's Republic of China and the National Tea Technology Committee [2–4]. The formation of quality characteristics of Wuyi rock tea is closely related to the natural environment in which tea trees grow, especially the composition of soil elements and the absorption, translocation and accumulation of elements by tea trees [5,6]. The unique Danxia landform, rich soil types and special microclimate environment of Wuyi Mountain have led to significant differences in element absorption and metabolism of tea trees in different rock zones (authentic rock zone, semi-rock zone, and continent zone), which in turn affect the biochemical composition and sensory quality of the tea leaves [7]. However, there is still a lack of systematic research on the element distribution pattern of the rhizosphere soils, root system, and leaf system of tea trees in different rock zones, the screening of key characteristic elements and their correlation mechanism with tea quality. An in-depth exploration of the correlation between element absorption, accumulation, translocation, and tea leaf quality is essential. Such understanding is crucial for guiding tea cultivation and quality improvement in Wuyishan.

The parent material and soil physicochemical properties exhibit distinct regional variations across different producing regions, which directly influence the efficiency of mineral element absorption and translocation in the root systems of tea trees [8]. According to the “Geographical Indication Products Wuyi Rock Tea” (GB/T 18745-2006) [9], Wuyi rock tea production areas are categorized into authentic rock zone (core production area), semi-rock zone (fringe production area), and continent zone (outer mountain production area) according to the soil, geomorphology, and microclimate. It has been reported that the soil in the authentic rock zone is rich in mineral elements formed by weathering of volcanic rocks and has good water retention and permeability, which enable the root systems of tea trees in the authentic zone to absorb and enrich specific elements more efficiently, thus promoting the synthesis and accumulation of flavor substances such as tea polyphenols and theanine [10,11]. In contrast, the elemental composition of soils in the Zhou tea zone is relatively homogeneous, and the tea trees have lower selectivity for elemental uptake, resulting in poorer tea quality [12,13]. However, there is still a lack of systematic analysis of the elemental translocation patterns in the soils and tea tree systems of different rock zones and the mechanism of their influence on tea quality. In particular, the mechanism of the root system's uptake, accumulation, and translocation of soil elements to the leaves is still unclear.

Mineral elements are important regulators of growth and development and secondary metabolism in tea trees. For example, nitrogen (N) is a key substrate for theanine synthesis [14]; phosphorus (P) not only is an essential element for energy metabolism and nucleic acid synthesis, but also regulates the activity of key enzymes in the phenylpropanoid metabolic pathway through its involvement in carbohydrate metabolism and phosphorylation signal transduction, thereby influencing the accumulation of secondary metabolites such as tea polyphenols [15], while trace elements like manganese (Mn) and magnesium (Mg) act as cofactors for various enzymes [16,17], directly affecting the accumulation of tea polyphenols and caffeine. Currently, high-throughput elemental analysis techniques, represented by ICP-MS, have matured considerably. Their detection throughput and sensitivity are sufficient to efficiently obtain massive datasets on the multi-element composition of tea trees, supporting in-depth exploration of elemental translocation patterns and their correlations with tea quality [18]. For example, Zhao et al. [19] analyzed the relationship between elements in tea leaves and soils in three different tea-producing regions in China, and found that there were differences in the elemental fingerprints of tea leaves and seed source soils in different regions, and that the accumulation of certain elements in tea leaves was closely related to their concentrations in soil, especially sodium (Na), magnesium (Mg),

calcium (Ca), nickel (Ni), rubidium (Rb), strontium (Sr) and lead (Pb). Wong et al. [20] found that among the tea leaves from different provinces in China, Guangdong and Yunnan had higher aluminum (Al) content and lower soil transfer of Al, copper (Cu) and zinc (Zn) to different parts of the tea tree. Therefore, ICP-MS technology can be used to effectively analyze the differences in elemental uptake of tea trees from different origins or different regions, and then evaluate the relationships between them and tea quality. In Wuyi rock tea research, Zhou et al. [8] determined the elemental contents in soils and tea leaves from different rock zones and found that tea quality varied significantly among these zones, concluding that such differences were closely related to soil elemental composition. However, the elemental composition and migration patterns in the rhizosphere soils, root system, and leaves of tea trees across different rock zones—as well as which key enrichment coefficients can distinguish these zones and how they correlate with tea quality—remain unclear. It is hypothesized that if the parent material of the rock zone is different, the composition of soil elements will also change accordingly; that the root system of tea trees has the ability to selectively absorb, with only some elements being absorbed and transported preferentially; and that these elements can accumulate efficiently in the leaves, effectively improving the quality of tea. An in-depth exploration of the elemental migration patterns of tea tree rhizosphere soils, root systems and leaves in different rock zones and their correlation with tea quality will help to reveal the mineral nutrient basis for the formation of tea quality.

Accordingly, in this study, 180 tea plantations were selected in Wuyishan City, Fujian Province, including 60 authentic rock zones (ZY), 60 semi-rock zones (BY), and 60 continent zones (ZC). Soil, root, and leaf samples were collected from each tea plantation, and their multi-element contents were determined using ICP-MS. The differences in elemental composition among the different rock zones, as well as the differential responses of tea tree roots and leaves to elemental enrichment, were analyzed. Meanwhile, four deep machine learning methods were employed to screen for characteristic elements that can effectively distinguish between the different rock zones. At the same time, the contents of tea polyphenols, theanine and caffeine and the quality indexes of tea leaves in different rock zones were determined, on the basis of which the relationships between characteristic elements and tea quality indexes were analyzed using redundancy analysis, correlation network, and the PLS-SEM equation, and the effects of characteristic elements on tea quality indexes were verified by the hydroponics method. The results of the study were utilized to deeply analyze the element migration law of tea trees in different rock zones of Wuyi rock tea, screen and distinguish the characteristic elements in different rock zones, and clarify the relationship between the characteristic elements and the quality of tea, so as to provide a theoretical basis for revealing the mineral and nutritional basis for the formation of the quality of rock tea and aid the development of the Wuyi rock tea industry.

2. Materials and Methods

2.1. Collection of Experimental Materials

Wuyishan City (117°37'22" E~118°19'44" E, 27°27'31" N~28°04'49" N) is a major tea-producing area in Fujian Province, China, located in the northwestern part of Fujian Province, with a total area of about 2813 square kilometers, an average annual temperature of 12–13 °C, annual precipitation of more than 2000 mm, and relative humidity of 85% [21]. According to the traditional division and “Geographical Indication Products Wuyi Rock Tea” (GB/T 18745-2006), Wuyi rock tea producing areas are divided into three types due to soil, geomorphology and microclimate: authentic rock zone (core production area, accounting for about 10% to 15% of Wuyishan tea area), semi-rock zone (fringe production area, accounting for about 20% to 30% of Wuyishan tea area), and continent zone (outer mountain tea area, accounting for about 50% to 60% of Wuyishan tea area).

In this study, rhizosphere soils, root systems and leaves of tea trees were collected from 60 authentic rock zones (ZY), 60 semi-rock zones (BY), and 60 continent zones (ZC), totaling 180 tea plantations (Figure 1). The collected rhizosphere root soils and roots were used for the determination of multi-element content by ICP-MS, while the collected tea leaves were partly used for the determination of multi-element content by ICP-MS and partly used for the determination of tea quality indexes, namely, the polyphenol, theanine and caffeine content. The sampling method for tea tree rhizosphere soils, root systems and leaves was based on the S-sampling method [22]. Specifically, we randomly selected 8 tea trees from each tea plantation, removed the soil surface of the dead leaves, gently dug out the tea trees, removed the tea tree root systems, shook off the soil attached to the surface of each root system, and collected the soil still adhering to the root system, which was the rhizosphere soil of each tea tree. After sufficient mixing, the rhizosphere soil was replicated. At the same time, the root systems of the tea trees were collected and mixed well to form a root system replicate. When collecting the rhizosphere soil of each tea tree, one bud and two leaves from each tree were also collected, and these were mixed fully to form one replicate [23]. Three independent replicates were collected from each tea plantation in each rock area.

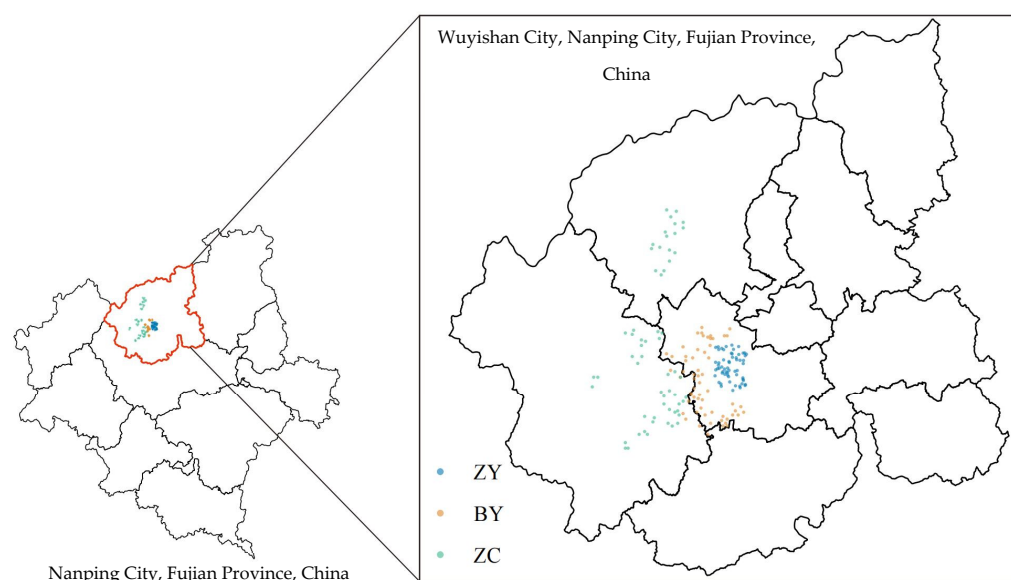


Figure 1. Distribution of sampling points of tea plantations in different rock zones. Note: ZY, BY and ZC represent authentic zone, semi-rock zone and continent zone, respectively. We selected 60 tea plantations each from ZC, BY and ZY zones for sampling, totaling 180 tea plantations.

2.2. Determination of Tea Tree Leaf Quality Indexes

In this study, the tea polyphenol, theanine and caffeine contents of tea tree leaves from 180 tea plantations in different rock zones were determined. The method is briefly described as follows: the samples were deactivated at 105 °C for 15 min, dried at 80 °C until constant weight, and then ground through a 60-mesh sieve. Determination of tea polyphenols was performed using the Folin–Ciocalteu colorimetric method [24]. Tea powder (1 g) was accurately weighed, mixed with 20 mL of 70% methanol solution, and extracted in a water bath at 70 °C for 10 min. After cooling, the extract was made up to 25 mL and filtered. The filtrate was reacted with Folin–Ciocalteu reagent, and the absorbance was measured at 765 nm. A standard curve was prepared using gallic acid as the reference standard (concentration range: 10–200 µg/mL, $R^2 = 0.9992$), and the tea polyphenol content in the samples was calculated. Three replicate determinations were performed for each sample. Theanine content was determined by high-performance

liquid chromatography (HPLC) [25]. Accurately weigh 1 g of tea powder, add 50 mL of boiling water, and extract in a water bath at 100 °C for 30 min. After cooling, make up to 100 mL and filter. The filtrate was passed through a 0.45 µm membrane prior to HPLC analysis. Chromatographic conditions: RP-18 reversed-phase column (4.6 mm × 250 mm, 5 µm); mobile phase consisting of 100% purified water and 100% acetonitrile; flow rate of 1.0 mL/min; detection wavelength of 210 nm; column temperature of 35 °C; injection volume of 20 µL. Quantification was performed by the external standard method using a theanine standard curve (concentration range: 5–100 µg/mL, $R^2 = 0.9995$). Three replicate determinations were performed for each sample. Caffeine content was determined by ultraviolet spectrophotometry [26]. Accurately weigh 3 g of tea powder, add 150 mL of boiling water, and extract in a water bath at 100 °C for 45 min. After cooling, make up to 200 mL and filter. The filtrate was mixed with 0.01 mol/L hydrochloric acid solution, and the absorbance was measured at 274 nm. A standard curve was prepared using caffeine as the reference standard (concentration range: 5–100 µg/mL, $R^2 = 0.9991$), and the caffeine content in the samples was calculated. Three replicate determinations were performed for each sample.

2.3. Multi-Elemental Determination of Rhizosphere Soils, Root Systems and Leaves of Tea Tree

In this study, ICP-MS was used to determine the elemental content of tea tree roots, leaves and soil samples. Fresh roots and leaves were rinsed with deionized water, dried at 80 °C until constant weight, and ground through a 75 µm nylon sieve. Soil samples were air-dried at room temperature and ground through a 75 µm nylon sieve. All samples were set up in three independent replicates. The samples were digested by a high-pressure digestion method, i.e., 0.5 g of samples (5 replicates) were weighed accurately in the digestion jar, 5 mL of HNO₃ was added, and the samples were digested at 185 °C for 4 h. Then, the acid was evaporated for 1 h, and the samples were made up to 50 mL and diluted 10-fold for ICP-MS analysis.

The elemental content was determined by ICP-MS (Nexion 2000, Thermo Scientific, Boston, MA, USA). The instrument parameters were 1350 W radio frequency power, 0.94 L/min carrier gas, 0.40 L/min auxiliary gas, 4.5 mL/min helium gas, 2 °C nebulization chamber temperature, 0.3 r/s lift-off rate, 7 mm sampling depth, 50 ms residence time, and 6 scans in peak-hopping mode using a PFA nebulizer and a nickel cone. The blank and standard solutions were digested synchronously, and a standard curve was established. Scandium (Sc), germanium (Ge), indium (In), rhodium (Rh), rhenium (Re) and bismuth (Bi) were used as the internal standards, and the limit of detection (LOD) was calculated as 3-fold the standard deviation of the blank. For quality control, we used the tea (GBW10016) and soil (GBW07403) standards, which were simultaneously digested with the samples and measured three times, and the results were averaged.

2.4. Construction and Evaluation of Deep Machine Learning Models

Machine learning is uniquely useful for filtering and classifying big data for validation and has been widely used for classification evaluation. But, there is no single algorithm that can be applied to all cases. Therefore, based on the elemental enrichment coefficients of tea tree roots and leaves obtained, four deep machine learning algorithms, including K Nearest Neighbor (KNN), Support Vector Machine (SVM), Single Hidden Layer Multi-Layer Perceptron (MLP), and Random Forest (RF), were used in this study to model the elemental enrichment coefficients of the root system and leaves of tea trees in 180 tea plantations in different rock zones, to validate the accuracy of the key elemental enrichment coefficients in the differentiation of different rock zones and to obtain characteristic elements. All models were constructed using Rstudio software (R version 4.2.3), and the evaluation

parameter tables were created using Excel. During the model construction process, a stratified sampling technique was used in this study, i.e., the data samples were divided into training and test sets in a ratio of 75% and 25%. To ensure the robustness of the models, all the models in this study were trained with 100 random iterations, and the training set and test set were randomly combined according to the proportion in each iteration of training. Finally, the results of 100 iterations of training were used for model integration analysis, which integrated all the models from the training process into one comprehensive result, improving the stability and accuracy of model prediction. In this study, a confusion matrix and ROC curves were used to systematically evaluate all constructed models. The confusion matrix visually quantifies the classification accuracy of each group by comparing the true categories of the samples with the predictions [27]. After the iteration of each machine learning algorithm was completed, this study employed a model integration strategy to generate a more robust composite prediction by integrating the prediction results of multiple models [28], from which the overall confusion matrix was calculated and heatmaps were plotted to achieve a comprehensive assessment of the model's prediction performance. To further evaluate the model performance, this study plotted the overall ROC curve after each algorithm iteration, which comprehensively reflected the model performance by demonstrating the relationship between the true-positive rate and false-positive rate under different classification thresholds. Meanwhile, the area under the ROC curve (AUC) was used to assess the model generalization ability, and the AUC value (0–1.0 range) was positively correlated with the model quality [29], which provided a quantitative basis for model evaluation.

2.5. Effects of Characteristic Element Treatments on Quality Indexes of Tea Tree Leaves

The tea tree variety selected for this study was Wuyi Rougui (*Camellia sinensis*), one-year asexually propagated cuttings (about 38 cm in height and 0.3 cm in diameter). The selected tea seedlings were first cleaned with deionized water to rinse the roots, and then transplanted to a complete nutrient solution for 30 days. The complete nutrient solution formula used was a modified Hoagland formula with 945 mg/L $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$, 607 mg/L KNO_3 , 493 mg/L $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 136 mg/L KH_2PO_4 , 1.5 mg/L $\text{MnSO}_4 \cdot \text{H}_2\text{O}$, and 5 mg/L Fe-EDTA, and the pH of the culture solution was adjusted to 4.5.

In this study, the characteristic elements obtained to distinguish different rock zones were Mn, P and S, which were used to carry out elemental regulation experiments. Experiment 1 was a deficiency culture, i.e., the complete nutrient solution lacked the elements Mn, P or S, respectively, and its effect on the quality of tea leaves was analyzed. Experiment 2 was conducted to improve the element content for cultivation, that is, the complete nutrient solution to increase the content of Mn, P or S, respectively, 1-fold, and its effect on the quality of tea leaves was analyzed. The specific method was that, after 30 days of recovery culture of tea seedlings, the tea seedlings were taken out, the root system was rinsed with deionized water, and then the tea seedlings were transplanted into plastic pots with 2 L of culture solution, with 6 tea seedlings transplanted into each pot. In experiment 1, the content of Mn, P or S in the culture solution was adjusted to form a culture solution lacking Mn, P or S, respectively. The content of other elements was consistent with that in the complete nutrient solution, with three independent replicates for each treatment. In experiment 2, the content of Mn, P or S in the culture solution was adjusted separately to increase the content of Mn, P or S by 1-fold, and the content of all other elements was consistent with that in the complete nutrient solution, with 3 independent replicates for each treatment. After transplanting, the tea tree seedlings were placed in an artificial culture room for cultivation with a light intensity of 5500 lux and a light duration of 12 h (6:30 am~18:30 pm), and the temperature of the culture room was set at 25 °C and the

humidity at 75%. Tea tree seedlings were treated for 28 days. During the cultivation period, the culture solution was aerated for 24 h, and the solution was replaced once every 7 days. At the end of the treatment, one bud and two leaves of tea seedlings were collected for the determination of tea quality indexes, with three independent replicates for each treatment. The determination method for quality indexes was the same as the method for “Determination of quality indexes of tea leaves” in Section 2.2.

2.6. Statistical Analysis

Excel 2021 was used for preliminary organization and analysis of the raw data obtained, and IBM SPSS Statistics software (v26) and Rstudio software (v4.2.3) were used for data processing and statistical analysis. The content of different indexes was expressed as mean and standard deviation (means $\pm$ SD). Differences between different sample groups were analyzed using Student's *t*-test, and $p < 0.05$ was considered statistically significant. Rstudio software (v 4.2.3) was used for data analysis and graphical visualization. Ggbiplot 0.55 was used for principal component analysis, tidyr 1.3.1 was used for box plots, ggvenn 0.1.10 was used for Venn plots, and MASS 7.3.60.0.1 was used for LDA plots. The R package used for stacked graph production was ggplot2 3.5.1, the R package used for network graph production was linkET 0.0.7.4, the R package used for Mann–Kendall test was Kendall 2.2.1, the R package used for heatmap analysis was heatmap 1.0.12, the R package used for KNN machine learning was caret 7.0.1, the R package used for SVM machine learning was e1071 1.7.16, the R package used for MLP machine learning was parsnip 1.3.1, the R package used for RF machine learning was tidymodels 1.1.1, the R package used for SHAP swarm map production was Shapviz 0.9.3, the R packages used for simulation plot production were ggplot2 3.5.1 and ggpmisc 0.6.1, linkET 0.0.7.1 was used for interaction network plots, vegan 2.6.10 was used for redundancy analysis, and plspm 0.5.0 was used for PLS-SEM equation construction.

3. Results

3.1. Analysis of Tea Quality Indexes in Different Rock Zones

In this study, tea leaves from 60 ZY, 60 BY and 60 ZC, totaling 180 tea plantations, were collected, and their quality indexes such as tea polyphenol, theanine and caffeine contents were determined. It was found that there was a significant difference in tea quality indexes among different rock zones. The principal component analysis of the tea quality index contents of different rock zones showed (Figure 2A) that the first two principal components accounted for a cumulative variance contribution of 98.85%, and the score plot based on these two components revealed a clear separation among ZY, BY and ZC. Further analysis revealed (Figure 2B) that the tea polyphenol, theanine and caffeine contents of ZY tea were distributed in the range of 346.51 to 382.46 mg/g (mean 368.42 mg/g), 34.62 to 38.71 mg/g (mean 35.73 mg/g), and 38.43 to 41.52 mg/g (mean 39.72 mg/g), respectively. The tea polyphenol, theanine and caffeine contents of BY tea were distributed between 302.91 and 324.63 mg/g (mean 312.72 mg/g), 24.23 and 31.15 mg/g (mean 28.82 mg/g), and 31.84 and 35.73 mg/g (mean 34.06 mg/g), respectively (Figure 2C). In contrast, the tea polyphenol, theanine and caffeine contents of ZC tea were distributed between 236.14 and 293.15 mg/g (mean 266.22 mg/g), 22.52 and 26.14 mg/g (mean 24.32 mg/g), and 25.71 and 29.16 mg/g (mean 26.92 mg/g), respectively (Figure 2D). Secondly, the tea polyphenol, theanine and caffeine contents were significantly greater in ZY than in BY, while those in BY were significantly greater than in ZC. It can be seen that there was a significant difference in the quality of tea leaves from different rock zones, with ZY being the highest, BY being the second highest, and ZC being the lowest.

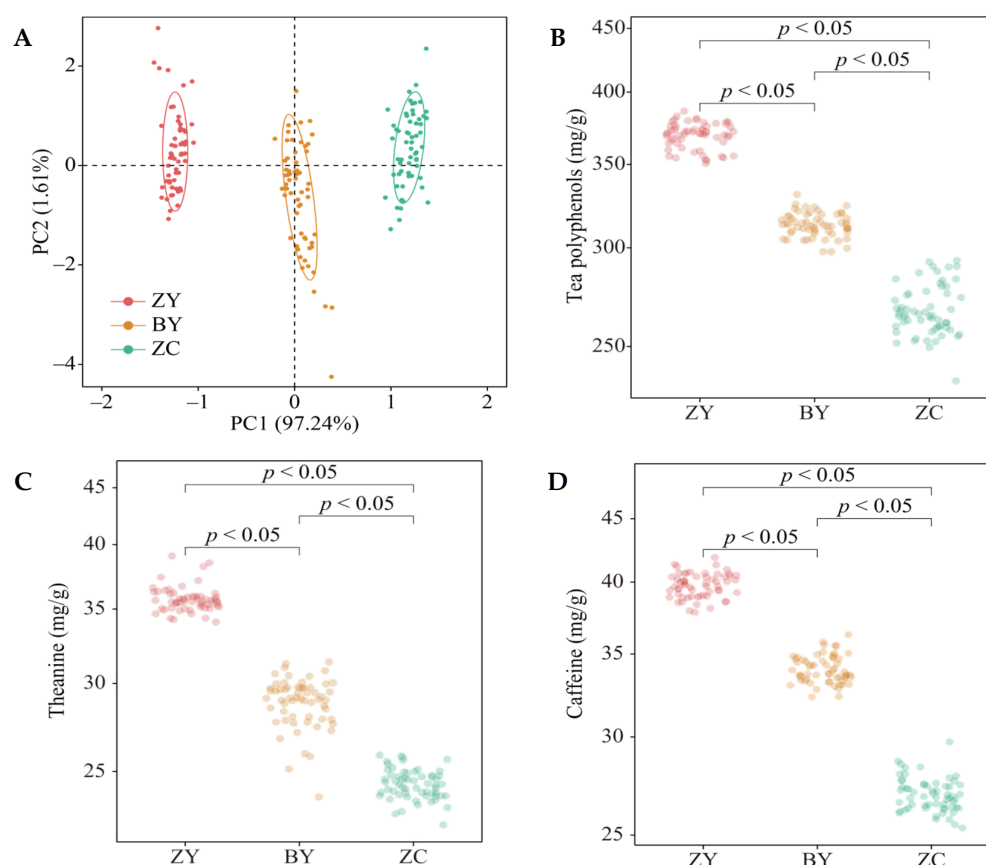


Figure 2. Quality index content analysis of tea leaves from different rock zones ($n = 60$). Note: ZY, BY and ZC represent authentic zone, semi-rock zone and continent zone, respectively; (A) Principal component analysis with quality index content of tea leaves from different rock zones; (B) Tea polyphenol content; (C) Theanine content; (D) Caffeine content.

3.2. Analysis of Multi-Element Determination of Rhizosphere Soils, Roots and Leaves of Tea Trees in Different Rock Zones

In this study, the ICP-MS technique was used to determine the multi-element contents of tea tree rhizosphere soils, root systems and leaves in 60 ZY, 60 BY and 60 ZC tea plantations. Firstly, the results of the multi-element analysis of contents of tea tree rhizosphere soils showed (Table S1) that 66 elements were detected in ZY tea tree rhizosphere soils, and the mean values of their contents were distributed in the range of 0.01–377,893.28 ng/kg, with the coefficients of variation distributed in the range of 29.66–484.64%, and the top five elements with the highest contents were nitrogen (N), fluorine (F), iron (Fe), aluminum (Al), and neon (Ne). A total of 68 elements were detected in the rhizosphere soils of tea trees in BY, and the mean values of their contents were distributed in the range of 0.01~1,278,643.47 ng/kg, with the coefficients of variation distributed in the range of 20.25~483.96%, and the top five elements with the highest contents were F, N, Fe, Al, and Ne. A total of 70 elements were detected in the rhizosphere soils of tea trees in ZC, and the mean values of their contents were distributed in the range of 0.01~589,769.42 ng/kg, with the coefficient of variation ranging from 12.55 to 348.36%, and the top five elements with the highest contents were F, N, Fe, Al and Ne. It can be seen that there were some differences in the types of elements detected in the rhizosphere soils of tea trees in different rock zones, with ZC having the highest number of elements, followed by BY, and ZY having the least number of elements; additionally, the top five elements with the highest content in the rhizosphere soils of tea trees in different rock zones were similar.

Secondly, the multi-element content of tea tree roots in different rock zones showed (Table S2) that 70 elements were detected in the root systems of tea trees in ZY, with the

mean values of their contents distributed in the range of 0.01~1,158,162.72 ng/kg and the coefficients of variation distributed in the range of 23.39~439.96%, and the top five elements with the highest contents were N, F, Ne, carbon (C) and sulfur (S). A total of 69 elements were detected in the root systems of BY tea trees, with the mean values of their contents distributed in the range of 0.01~1,684,442.85 ng/kg and the coefficients of variation distributed in the range of 27.76~308.72%, and the top five elements with the highest contents were N, F, Ne, C and S. A total of 69 elements were also detected in the root systems of ZC tea trees, with the mean values of their contents distributed in the range of 0.01~1,729,889.83 ng/kg and the coefficients of variation distributed in the range of 12.94 to 303.80%, and the top five elements with the highest contents were N, F, Ne, S and Al. It can be seen that the elemental types detected in the root systems of tea trees in different rock zones were most abundant in ZY, followed by BY or ZC; moreover, the top five elements with the highest content in the root systems of tea trees in different rock zones were consistent between ZY and BY, while there were differences with ZC.

In addition, this study further analyzed the multi-element contents of tea tree leaves in different rock zones, and the results showed (Table S3) that 60 elements were detected in ZY tea tree leaves, with the mean values of their contents distributed in the range of 0.01~6,444,421.57 ng/kg, the coefficients of variation were distributed in the range of 17.56~240.26%, and the top five elements with the highest contents were N, Ne, Ca, C, and S. A total of 57 elements were detected in the leaves of tea trees in BY, and the mean values of their contents were distributed in the range of 0.01~1,770,519.19 ng/kg, with the coefficients of variation distributed in the range of 20.09~258.08%, and the top five elements with the highest contents were N, Ne, F, Ca, and C. A total of 58 elements were detected in the leaves of tea trees in ZC, and the mean values of their contents were distributed in the range of 0.01~1,703,762.93 ng/kg, with the coefficient of variation ranging from 16.79 to 290.31%, and the top five elements with the highest contents were N, Ne, F, Ca and C. It can be seen that the number of elements detected in the leaves of tea trees in different rock zones were the most in ZY, followed by ZC, and the least in BY; additionally, the top five elements with the highest contents in tea tree leaves were consistent in the BY and ZC rock zones, while there were differences with ZY.

Comprehensive results from the determination of the multi-element contents of tea tree rhizosphere soils, root systems and leaves in different rock zones found significant differences in the detected elements and their contents. At the same time, in the same rock zone, there were significant differences in the detected elements in tea tree rhizosphere soils, root systems and leaves, especially in terms of elemental contents: the elements with higher contents in soil were not the most abundantly accumulated in the root system or leaves of tea trees. It can be seen that the tea tree root system may have a certain selectivity in the absorption of soil elements, and secondly, the root system also has a certain selectivity in the translocation of elements to the leaves after their absorption.

3.3. Analysis of Elemental Types and Contents of Rhizosphere Soils, Roots and Leaves of Tea Trees in Different Rock Zones

Based on the results of ICP-MS, the differences in the elemental types in the rhizosphere soils, root systems and leaves of tea trees in different rock zones were further analyzed. Among them, 65 elements were common to the rhizosphere soils of tea trees in ZY, BY and ZC (Figure 3A), 68 elements were common to the root systems (Figure 3B), and 54 elements were common to the leaves (Figure 3C). It can be seen that the elements in the rhizosphere soils, roots and leaves of tea trees in different rock zones were largely similar. Additionally, the analysis of the differences in the elemental types in the rhizosphere soils, root systems and leaves of tea trees in the same rock zone showed that ZY tea trees had 56 common elements in their rhizosphere soils, root systems and leaves, 10 common elements between

the soils and the root systems, and one common element between the root systems and the leaves (Figure 3D). BY had 57 common elements in the rhizosphere soils, root systems and leaves, eight common elements between the soils and root systems, and three common elements between the root systems and the leaves (Figure 3E). ZC had 56 common elements in the rhizosphere soils, root systems and leaves, 11 common elements between the soils and root systems, and two common elements between the root systems and leaves (Figure 3F). It can be seen that most of the elements in the soil can be absorbed and accumulated by the root system of the tea tree, but some of the elements were absorbed by the tea trees, accumulated in the root systems and not transported to the leaves, which is manifested in the fact that some of the elements detected in the rhizosphere soils and root systems of the tea trees were not found in the leaves. In addition, individual unique elements also existed in the rhizosphere soils, root systems and leaves of the tea trees. This result suggests that the absorption of individual elements in the soil by tea trees exhibits selective exclusion, while the absorption of unique elements in the root systems or leaves may be caused by differences in the external environment of different rock zones that lead to the absorption of elements in the environment by the tea tree tissues.

On this basis, this study further analyzed the total contents of elements in the rhizosphere soils, root systems and leaves of tea trees in different rock zones, and the results showed that the total contents of elements in the rhizosphere soils or root systems of tea trees in ZY and BY did not differ significantly, but that the difference was significantly greater compared with ZC (Figure 3G,H); the total contents of elements in tea tree leaves in ZY was significantly greater than those in BY and ZC, while the difference between BY and ZC was not significant (Figure 3I). It can be seen that there were significant differences in the total contents of elements in the rhizosphere soils, root systems and leaves of tea trees in different rock zones, and the overall performance showed that the total contents of elements was higher in ZY. Further, LDA analysis of the contents of each element in different rock zones showed that the rhizosphere soils, root systems and leaves of tea trees in different rock zones could be effectively distinguished. The contributions of LDA1 and LDA2 to distinguishing the rhizosphere soil of tea trees in different rock zones were 82.61% and 17.39%, respectively (Figure 3J); the contributions of LDA1 and LDA2 to distinguishing the root systems were 77.08% and 22.92% (Figure 3K), while the contributions of LDA1 and LDA2 to distinguishing leaves were 76.79% and 23.21%, respectively (Figure 3L). In addition, this study found that there were five main trends in the rhizosphere soil elemental contents of tea trees in different rock zones (Figure S1A), with the contents of 20 elements in $ZY > BY > ZC$, 21 elements in $ZY > ZC > BY$, four elements in $BY > ZC > ZY$, 16 elements in $ZC > ZY > BY$, and 11 elements in $ZC > BY > ZY$. Analysis of the elemental contents of tea tree roots in different rock zones revealed contents of 25 elements in $ZY > BY > ZC$, 12 elements in $ZY > ZC > BY$, 11 elements in $BY > ZY > ZC$, seven elements in $BY > ZC > ZY$, nine elements in $ZC > ZY > BY$, and six elements in $ZC > BY > ZY$ (Figure S1B). Analysis of the elemental contents of tea tree leaves from different rock zones revealed that the contents of 31 elements in $ZY > BY > ZC$, 21 elements in $ZY > ZC > BY$, two elements in $BY > ZC > ZY$, one element in $ZC > ZY > BY$, and seven elements in $ZC > BY > ZY$ (Figure S1C). It can be seen that the elements in the rhizosphere soils, root systems and leaves of tea trees in different rock zones not only differed significantly in total content, but also remained significantly different in their individual content.

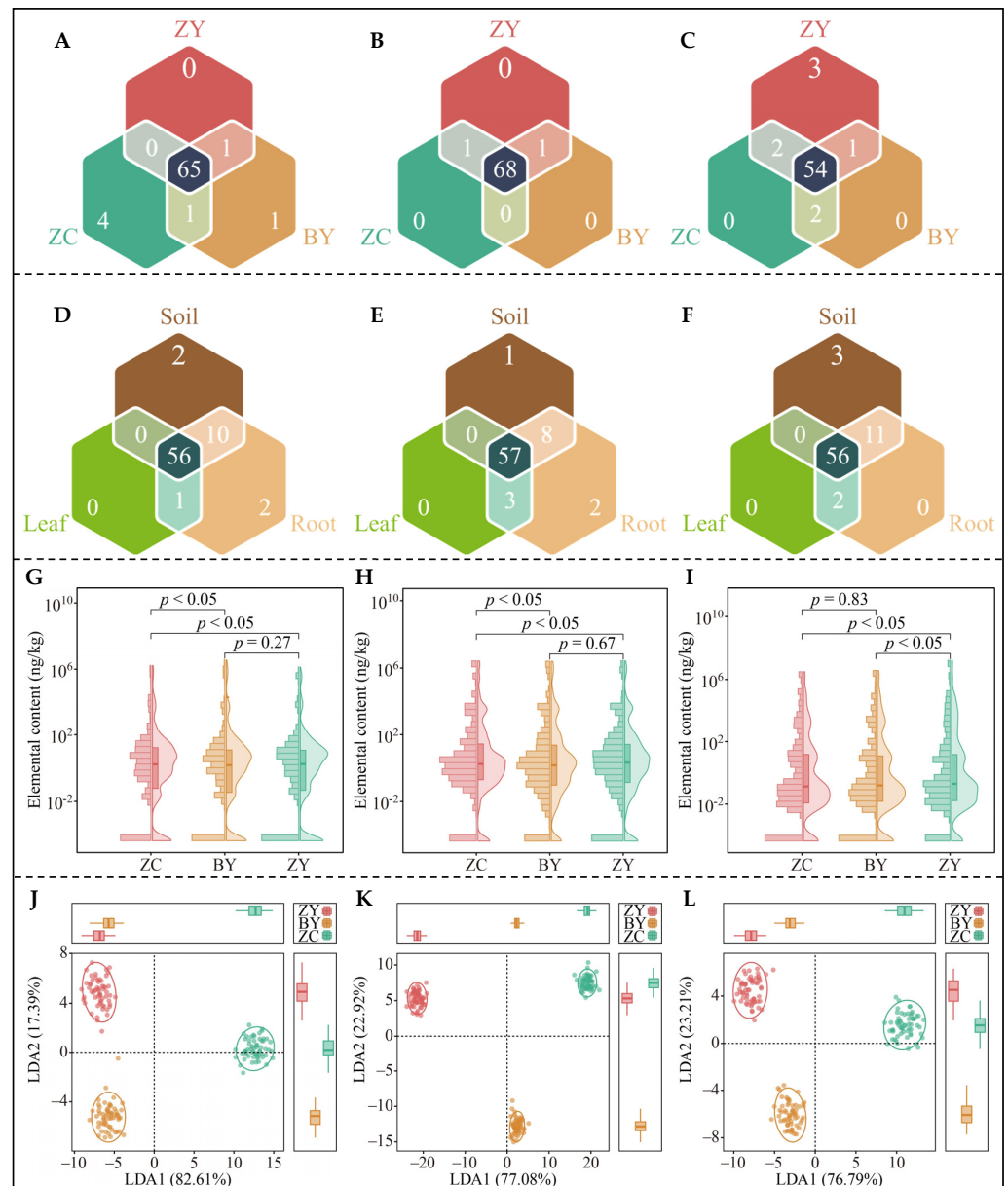


Figure 3. Analysis of elemental types and contents in tea tree rhizosphere soils, roots and leaves in different rock zones ($n = 60$). Note: ZY, BY and ZC represent authentic zone, semi-rock zone and continent zone, respectively; (A) Venn diagram of elemental types in tea tree rhizosphere soils; (B) Venn diagram of elemental types in tea tree root systems; (C) Venn diagram of elemental types in tea tree leaves; (D) Venn diagram of elemental types in tea tree rhizosphere soils, roots and leaves in ZY; (E) Venn diagram of elemental types in tea tree rhizosphere soils, roots and leaves in BY; (F) Venn diagram of elemental types in tea tree rhizosphere soils, roots and leaves in ZC; (G) Total elemental analysis of rhizosphere soils of tea trees; (H) Total elemental analysis of tea tree roots; (I) Total elemental analysis of tea tree leaves; (J) LDA analysis of elemental content in rhizosphere soils of tea trees; (K) LDA analysis of elemental content in tea tree roots; (L) LDA analysis of elemental content in tea tree leaves.

3.4. Screening for Key Elements by Modular Network Analysis of Elements in Rhizosphere Soils, Roots and Leaves of Tea Trees in Different Rock Zones

Based on the above analysis, this study further constructed modular networks of elements in the rhizosphere soils, root systems and leaves of tea trees in different rock zones to analyze their correlations. The results showed that the modular network constructed by the rhizosphere soils, root systems and leaves of tea trees in ZC identified six modules

with 507 network edges and an average connectivity of 16.36 (Figure 4A). The modular network of BY identified five modules with 495 network edges and an average connectivity of 15.97 (Figure 4B). The modular network of ZY identified four modules with 378 network edges and an average connectivity of 12.19 (Figure 4C). It can be seen that the modular network structure in ZC was the most complex, and the nodes were more tightly connected, while ZY was the simplest, with nodes that were more sparsely connected.

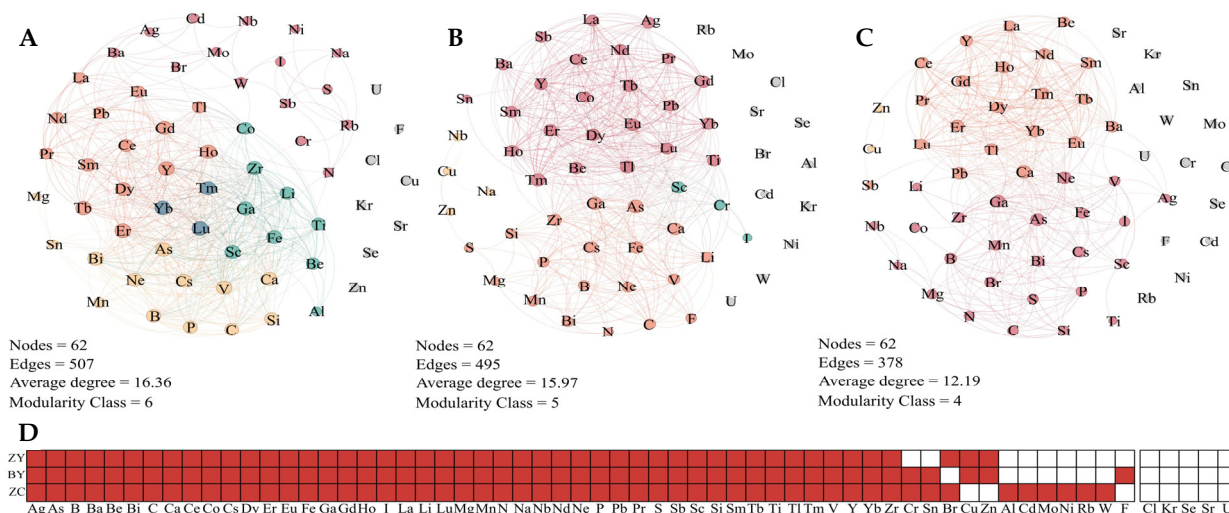


Figure 4. Elemental modular network analysis of rhizosphere soils, roots and leaves of tea trees in different rock zones. Note: ZY, BY and ZC represent authentic zone, semi-rock zone and continent zone, respectively; (A) Elemental modular network of rhizosphere soils, roots and leaves of tea trees in ZC; (B) Elemental modular network of rhizosphere soils, roots and leaves of tea trees in BY; (C) Elemental modular network of rhizosphere soils, roots and leaves of tea trees in ZY; (D) Heatmap for evaluating the connectivity of modular network nodes of each element in different rock zones (red color means there is a connection point between this element and other elements, while white color means there is no connection point between this element and other elements).

Further analysis of the connectivity of the modular network nodes of each element in different rock zones showed (Figure 4D) that 45 elements in different rock zones had connectivity with all other elements, 12 elements interacted with each other in different rock zones, and only five elements (chlorine (Cl), krypton (Kr), selenium (Se), Sr, and uranium (U)) did not have any connectivity with other elements in ZY, BY, and ZC. It can be seen that the rock zone differences affect the uptake and accumulation of most of the elements in the soil by tea trees, with 57 key elements being most critically affected, with connecting points between them and other elements, but to a lesser extent with some of the elements.

3.5. Analysis of Enrichment Coefficients of Tea Tree Roots and Leaves for Key Elements in Different Rock Zones

The aforementioned modular network node analysis screened and obtained a total of 57 key elements and further converted the enrichment coefficients of tea tree root systems and leaves for these 57 key elements in different rock zones by the content of each element. The analysis of the enrichment coefficients of the tea tree root systems for the 57 key elements showed (Table S4) that the distribution of the enrichment coefficients of the ZY tea tree root systems for the 57 key elements ranged from 0 to 2795.69, of which the top five elements with the strongest enrichment capacity were C, S, Ne, cadmium (Cd) and P; the distribution of the enrichment coefficients of the BY tea tree root systems for the 57 key elements ranged from 0 to 345.93, and the top five elements with the strongest enrichment ability were Ca, C, P, Si and Cd; the distribution of the enrichment coefficients

of the ZC tea tree root systems for 57 key elements ranged from 0 to 69.33, and the top five elements with the strongest enrichment ability were C, Cd, S, N and P. The results of enrichment coefficients of tea tree leaves for key elements showed (Table S5) that the distribution of enrichment coefficients of ZY tea tree leaves for 57 key elements ranged from 0 to 13523.58, of which the top five elements with the strongest enrichment capacity were C, S, Ne, P and boron (B); the distribution of enrichment coefficients of BY tea tree leaves for 57 key elements ranged from 0 to 3180.83, of which the top five elements with the strongest enrichment capacity were Ca, C, P, Si and Ne; the distribution range of the enrichment coefficients of ZC tea tree leaves for 57 key elements ranged from 0 to 141.59, of which the top five elements with the strongest enrichment capacity were C, B, P, N and Ne. It can be seen that there are certain differences between different rock zones in the ability of the root systems and the leaves of tea trees in absorbing and accumulating soil elements under the influence of the environment.

3.6. Analysis of the Synergistic Relationships Between Enrichment Coefficients of Tea Tree Roots and Leaves for Key Elements and Different Rock Zones

Based on the above analysis, the Mann–Kendall nonparametric test was further used in this study to explore the trends of the enrichment coefficients of tea tree roots and leaves for 57 key elements in different rock zones. The results of enrichment coefficient analysis of tea tree root systems showed (Figure 5A) that the enrichment coefficients for 42 key elements in different rock zones were significantly different, among which the enrichment coefficients of 29 elements presented $ZY > BY > ZC$, and the enrichment coefficients of 13 elements presented $ZC > BY > ZY$. The analysis of enrichment coefficients of tea tree leaves showed (Figure 5B) that the enrichment coefficients for 42 key elements in different rock zones were significantly different, among which the enrichment coefficients of 32 elements presented $ZY > BY > ZC$, and the enrichment coefficients of 13 elements presented $ZC > BY > ZY$. Further analysis revealed (Figure 5C) that, among the 42 elements that showed significant differences in the enrichment coefficients of tea tree leaves in different rock zones, 33 elements were common to the roots and leaves, and nine elements were specific to root systems, namely beryllium (Be), Al, Ca, europium (Eu), Sc, chromium (Cr), molybdenum (Mo), Pb, and vanadium (V), and the elements specific to the leaves were tin (Sn), praseodymium (Pr), rubidium (Rb), F, Ne, thallium (Tl), zirconium (Zr), niobium (Nb), and neodymium (Nd). It can be seen that the rock zone differences affected the enrichment capacity of tea tree roots and leaves for the key elements.

3.7. Machine Learning to Screen for Characteristic Elements Enriched in Tea Tree Roots and Leaves Affected by Rock Zones

Based on the above analysis, this study further used four different machine learning methods for deep simulation based on the enrichment coefficients of the root systems and leaves to systematically evaluate the classification accuracy of the key element enrichment coefficients in distinguishing different rock zones and to screen the characteristic elements. The KNN simulation results for the enrichment coefficients of the tea tree root system showed (Figures 6A and S2A) that the classification accuracy of the key element enrichment coefficients in distinguishing different rock zones reached 91.11% when the optimal hyperparameter of the number of nearest neighbors was 3. The corresponding AUC values of the three rock zones, i.e., ZY, BY, and ZC, were 0.99, 0.98, and 0.99, respectively. The SVM simulation results for tea tree root system enrichment coefficients showed (Figures 6A and S2B) that when the simulation parameter of C was 128, degree was 2, and gamma was 0.001, the classification accuracy of the key element enrichment coefficients in distinguishing between different rock zones was 100%, and the AUC values corresponding to ZY, BY, and ZC were all 1. The simulation results of the MLP-constructed classifier for the enrichment

coefficients of tea tree root system showed (Figures 6A and S2C) that when the simulation parameter of the number of neurons in the hidden layer was 8, the L2 regularization parameter λ was 0.001, and the epochs were 200, the classification accuracy of the key element enrichment coefficients in distinguishing different rock zones reached 100%, and the AUC values corresponding to ZY, BY, and ZC were all 1. The simulation results of RF modeling of tea tree root system enrichment coefficients showed (Figures 6A and S2D) that when the number of predictors sampled for splitting at each node of the simulation parameters was 5, the number of trees grown was 750, and the minimum number of samples required to be at a leaf node was 4, the classification accuracy of key element enrichment coefficients in distinguishing different rock zones reached 100%, and the AUC values corresponding to ZY, BY, and ZC were all 1. It can be seen that after four different machine learning simulations, the enrichment coefficients of key elements in the tea tree root system can effectively distinguish between ZY, BY, and ZC, with a classification accuracy of more than 90%.

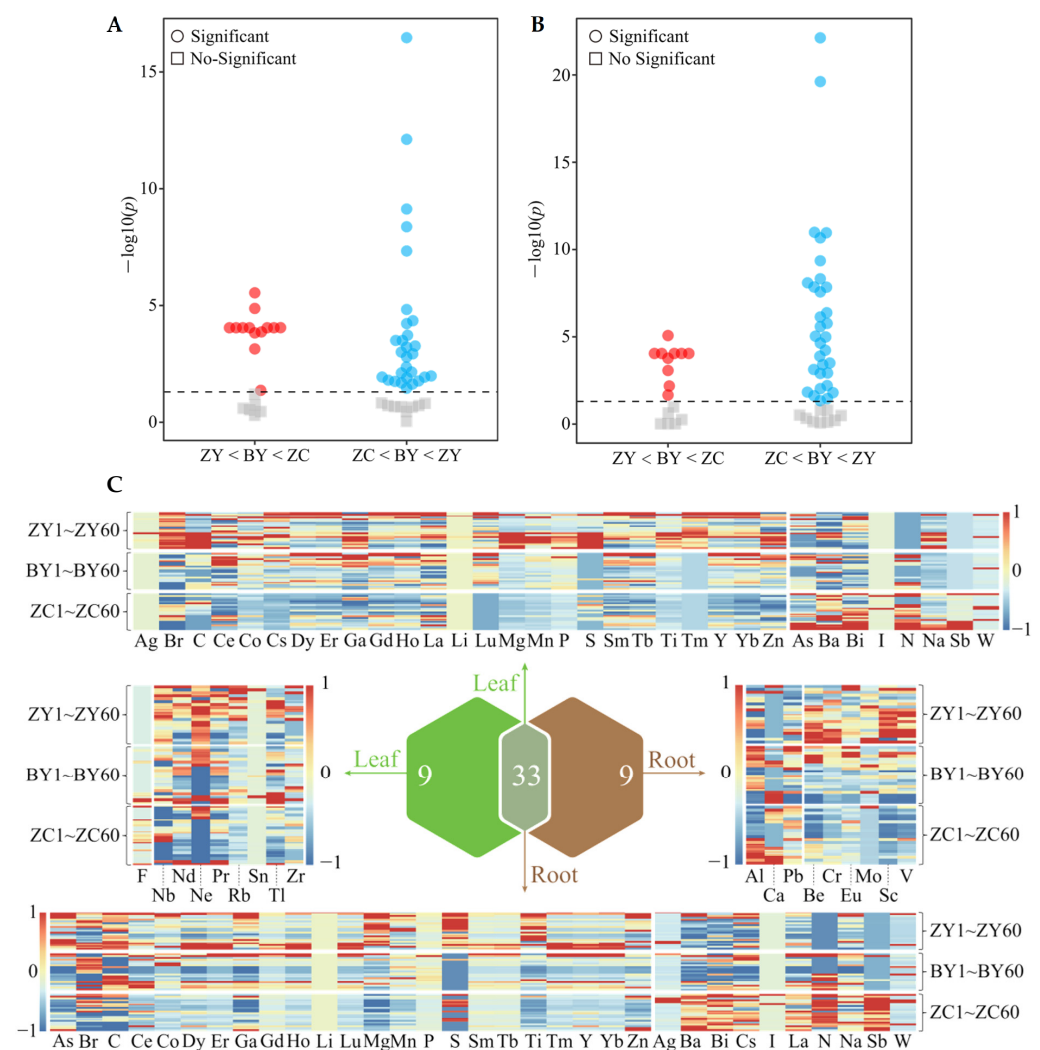


Figure 5. Screening of elements with significant differences in the enrichment coefficients of tea tree roots and leaves in different rock zones ($n = 60$). Note: ZY, BY and ZC represent authentic zone, semi-rock zone and continent zone, respectively; (A) Mann–Kendall test for the enrichment coefficients of tea tree roots in different rock zones; (B) Mann–Kendall test for the enrichment coefficients of tea tree leaves in different rock zones; (C) Analysis of elements and their contents with significant differences in enrichment coefficients in roots and leaves of tea trees from different rock zones.

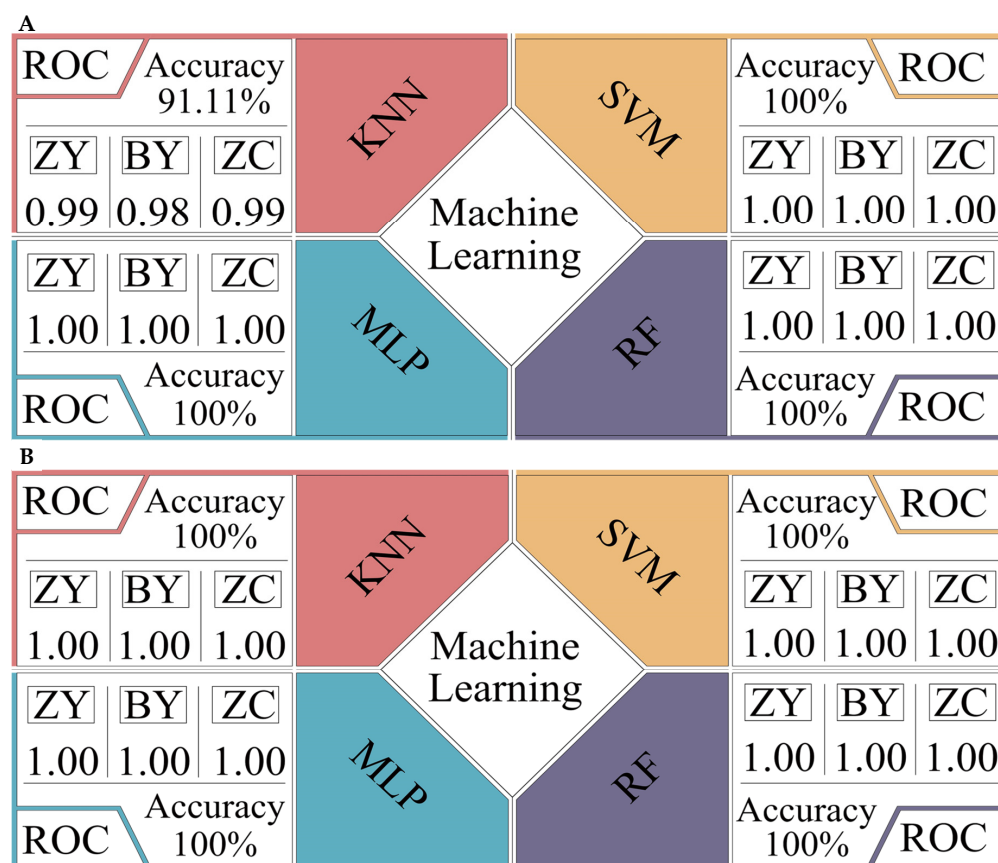


Figure 6. Accuracy of machine learning-simulated tea tree root system and leaf key element enrichment coefficients in distinguishing different rock zones. Note: ZY, BY and ZC represent authentic zone, semi-rock zone and continent zone, respectively; KNN represents the K Nearest Neighbor model; SVM represents the Support Vector Machine model; MLP represents the Single Hidden Layer Multi-Layer Perceptron; RF represents the Random Forest model; (A) Accuracy of four machine learning-simulated tea tree root system key element enrichment coefficients in distinguishing different rock zones; (B) Accuracy of four machine learning-simulated tea tree leaf key element enrichment coefficients in distinguishing different rock zones.

Secondly, the analysis from the perspective of enrichment coefficients of key elements in tea tree leaves showed that the optimal hyperparameters of the number of nearest neighbors for KNN were 3 for different machine learning model constructions (Figure S3A); C for SVM was 128, degree was 5, and gamma was 0.001 (Figure S3B); MLP's number of neurons in the hidden layer was 8, L2 regularization parameter λ was 0.001, and epochs were 200 (Figure S3C); RF had a number of predictors sampled for splitting at each node of 5, number of trees grown of 500, and the minimum number of samples required to be at a leaf node of 2 (Figure S3D). In this case, the classification accuracy of all four machine learning simulations of the key element enrichment coefficients for tea tree leaves in distinguishing different rock zones reached 100%, and the AUC values corresponding to ZY, BY, and ZC were all 1 (Figure 6B). It can be seen that after four different machine learning models, the key element enrichment coefficients of tea tree leaves can effectively differentiate between ZY, BY, and ZC, and the classification accuracy reaches 100%.

In addition, in order to further screen the characteristic elements in tea tree roots and leaves in distinguishing different rock zones, this study quantified the significance of the enrichment coefficients of key elements in roots and leaves based on the RF model by introducing the SHapley Additive exPlanations (SHAP) analysis method. The results of SHAP values for enrichment coefficients of key elements in the root systems of tea trees (Figure 7A) showed that the SHAP value exceeded 1% for 17 elements, namely S (21.35%),

N (10.39%), antimony (Sb, 9.82%), Mg (8.24%), iodine (I, 8.16%), titanium (Ti, 6.04%), barium (Ba, 4.19%), tungsten (W, 4.09%), C (2.85%), arsenic (As, 2.64%), Bi (2.48%), lithium (Li, 2.46%), Mn (2.04%), P (1.82%), Zn (1.55%), lanthanum (La, 1.52%) and silver (Ag, 1.43%). The results of SHAP value analysis of the enrichment coefficients of key elements in tea tree leaves showed (Figure 7B) that 18 elements had SHAP values of 1% or more, namely thulium (Tm, 21.76%), S (11.35%), Sb (10.77%), I (8.97%), cesium (Cs, 6.07%), N (5.95%), bromine (Br, 5.20%), Ti (3.35%), Ag (3.11%), Na (2.92%), Mn (2.55%), C (2.17%), P (2.10%), lutetium (Lu, 1.90%), Mg (1.80%), Ba (1.65%), W (1.18%) and cobalt (Co, 1.07%). Further analysis revealed that there were only 12 characteristic elements that were common to the root systems and leaves of tea trees and had a SHAP value of 1% in distinguishing different rock zones, namely N, P, Mn, S, Sb, Mg, I, Ti, Ba, W, C and Ag. It can be seen that the enrichment coefficients of the key elements in the root systems and leaves of tea trees play a certain role in distinguishing different rock zones, but only 12 characteristic elements are the most important.

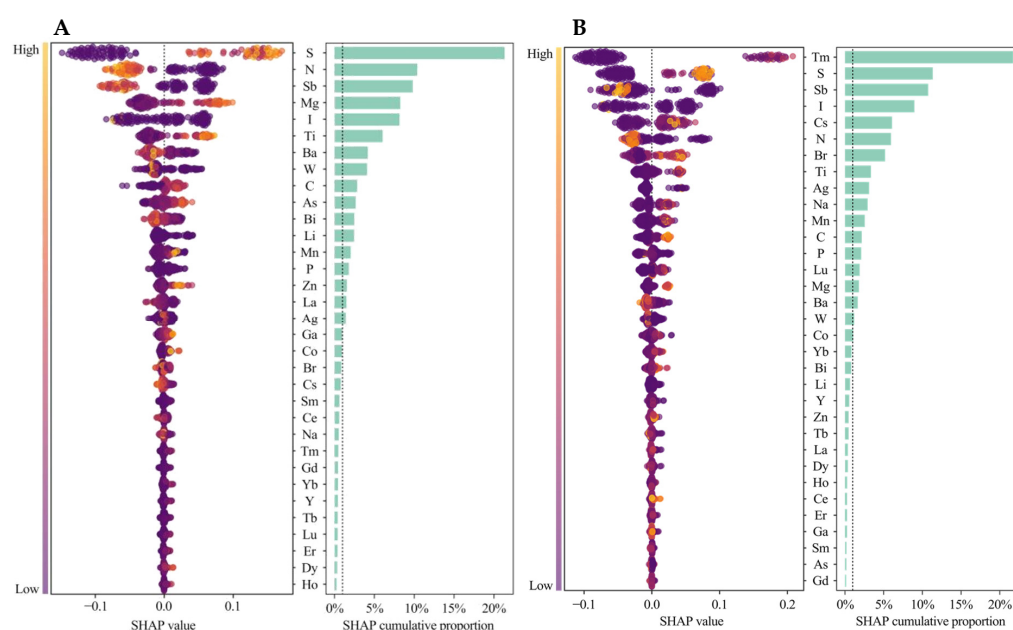


Figure 7. Analysis of SHAP values of key element enrichment coefficients of tea tree roots and leaves in distinguishing different rock zones. Note: (A) Analysis of SHAP values of key element enrichment coefficients of tea tree roots in distinguishing different rock zones; (B) Analysis of SHAP values of key element enrichment coefficients of tea tree leaves in distinguishing different rock zones.

3.8. Analysis of Trends in Enrichment Coefficients of Characteristic Elements and Their Transfer from Roots to Leaves

The results of enrichment coefficient analysis of the characteristic elements in different rock zones showed (Figure 8) that the change rule for characteristic elements in tea tree root systems and leaves in different rock zones was similar, except for Ag. Among them, the values of the enrichment coefficients of tea tree root systems and leaves for Ba, I, N, W and Sb presented $ZC > BY > ZY$, and those for C, Mg, Mn, P, S and Ti were $ZY > BY > ZC$, and the average value of enrichment coefficients of 11 elements was more than 1. Ag was more special: its enrichment coefficients were $ZC > BY > ZY$ in tea root systems and $ZY > BY > ZC$ in tea leaves, and its enrichment coefficients were less than 1 in both tea roots and leaves. It can be seen that the differences in rock zones mainly affected the uptake and enrichment of the 11 characteristic elements other than Ag by the tea root systems and leaves.

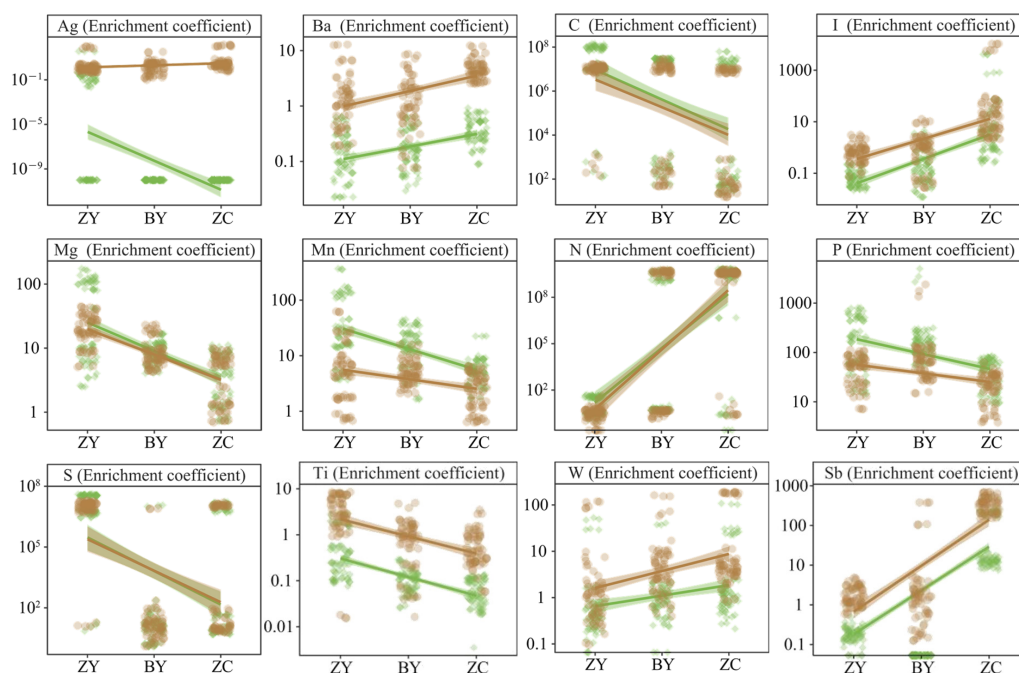


Figure 8. Enrichment coefficient analysis of characteristic elements in tea tree roots and leaves ($n = 60$). Note: ZY, BY and ZC represent authentic zone, semi-rock zone and continent zone, respectively; — represents the root enrichment coefficient; — represents the leaf enrichment coefficient.

On this basis, this study further conducted curve simulation using the enrichment coefficients of tea tree root systems for characteristic elements as horizontal coordinates and the enrichment coefficients of tea tree leaves for characteristic elements as vertical coordinates to analyze the trend of tea tree root systems for the translocation of characteristic elements to leaves. The results showed (Figures S4 and S5) that ZY tea tree roots transported Ba, Mn, Sb, C, N, I, P, W, Mg and S to the leaves with a significant upward trend ($p < 0.05$), except for Ti ($p = 0.536$); BY tea tree roots transported Ba, Mn, Sb, C, N, Ti, I, P, W, Mg and S to the leaves with a significant upward trend ($p < 0.05$); and ZC tea tree roots transported Ba, Mn, C, N, Ti, I, P, W, Mg and S to the leaves with a significant increasing trend ($p < 0.05$), except for Sb ($p = 0.494$). It can be seen that the enrichment coefficients of the characteristic elements by the root systems of tea trees in different rock zones directly affect the enrichment ability of tea tree leaves for the characteristic elements.

3.9. Interaction Analysis of Characteristic Element Enrichment, Translocation Coefficient and Tea Leaf Quality Indexes

In this study, RDA, correlation network and PLS-SEM equation construction were used to further analyze the relationship between the enrichment coefficients and translocation coefficients of characteristic elements and tea quality indexes. The results of RDA analysis among different indexes showed that the enrichment coefficients of C, Mg, Mn, P, S, and Ti in the root systems of tea trees were correlated with the tea quality indexes (Figure 9A); the enrichment coefficients of C, Mg, Mn, P, S, and Ti in the leaves of tea trees were correlated with the tea quality indexes (Figure 9B); and the translocation coefficients of tea trees for the characteristic elements C, Mg, Mn, P, S, Ti, Ba, N, and W were correlated with the tea quality indexes (Figure 9C).

Further analysis revealed that the enrichment coefficients of the characteristic elements C, Mg, Mn, P, S and Ti in the roots and leaves of tea trees in different rock zones were significantly and positively correlated with the tea quality indexes (tea polyphenols, theanine, and caffeine), whereas Ba, I, N, Sb and W were significantly and negatively correlated with

the tea quality indexes (Figure 9D,E). The translocation coefficients of the characteristic elements Mn, N, P, S and W in tea trees in different rock zones were significantly and positively correlated with the tea quality indexes, while the translocation coefficients of the characteristic element I were significantly and negatively correlated with the tea quality indexes, and the translocation coefficients of the characteristic elements Ba, C, Mg, Sb and Ti were insignificantly correlated with the tea quality indexes (Figure 9F). Comprehensive analysis revealed that the enrichment ability of the root systems of tea trees for Mn, P and S in different rock zones, the ability to transport these elements from the root systems to the leaves, and the enrichment ability of the leaves had the greatest influence on the tea quality indexes.

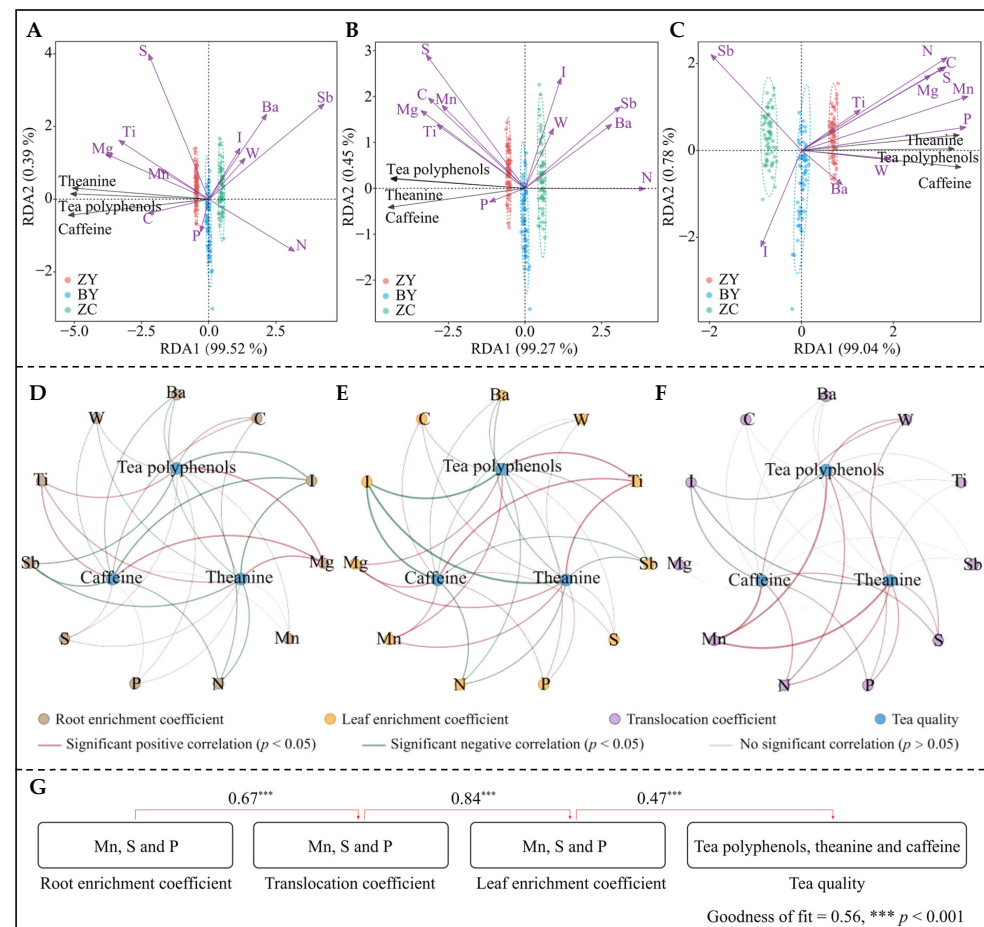


Figure 9. Interaction analysis of characteristic element enrichment and translocation coefficients with tea quality indexes. Note: ZY, BY and ZC represent authentic zone, semi-rock zone and continent zone, respectively; (A) Redundancy analysis of characteristic element enrichment coefficients of tea tree root systems and tea quality indexes; (B) Redundancy analysis of characteristic element enrichment coefficients of tea tree leaves and tea quality indexes; (C) Redundancy analysis of characteristic element translocation coefficients of tea trees and tea quality indexes; (D) Correlation network analysis of characteristic element enrichment coefficients of tea tree root systems and tea quality indexes; (E) Correlation network analysis of characteristic element enrichment coefficients of tea tree leaves and tea quality indexes; (F) Correlation network analysis of characteristic element translocation coefficients of tea trees and tea quality indexes; (G) Construction of PLS-SEM equations of characteristic element enrichment and transit coefficients and tea quality indexes.

The PLS-SEM equations between the enrichment coefficients of tea tree roots and leaves for Mn, P and S, the translocation coefficients and the tea quality indexes were further constructed, and the results showed (Figure 9G) that the enrichment coefficients of

tea tree roots for the characteristic elements Mn, P and S positively regulated the tea trees' ability to transport characteristic elements (0.67^{***} , $p < 0.001$) and positively regulated the tea tree leaves' enrichment ability for characteristic elements (0.84^{***} , $p < 0.001$), which, in turn, positively regulated the quality indexes of tea leaves (0.47^{***} , $p < 0.001$).

3.10. Effect of Exogenous Characteristic Element Treatments on the Quality of Tea Seedlings

The results of the above studies indicated that the main characteristic elements distinguishing different rock zones were Mn, P and S, and the absorption, accumulation and translocation abilities of the root systems of tea trees for the characteristic elements Mn, P and S directly affected the quality of tea leaves. Accordingly, this study used exogenous Mn, P or S to treat hydroponic tea tree seedlings to analyze the effects of these elements on tea quality. The results of the deficiency experiments showed (Figure 10A) that, compared with the control, the quality indexes of tea leaves were significantly decreased under Mn, P or S deficiency treatments. Among them, the contents of tea polyphenols, theanine and caffeine decreased by 15.87%, 12.04% and 11.57%, respectively, under Mn deficiency treatment compared with the control; under S deficiency treatment, they decreased by 30.98%, 23.09% and 19.37%, respectively; and under P deficiency treatment, they decreased by 41.92%, 34.29% and 35.41%, respectively. Secondly, increasing the amount of Mn, P or S to treat tea seedlings, compared with the control, significantly improved the quality of tea (Figure 10B). Compared with the control, the contents of tea polyphenols, theanine and caffeine increased by 8.16%, 6.61% and 7.65%, respectively, after increasing the amount of Mn; by 17.23%, 21.79% and 23.16%, respectively, after increasing the amount of S; and by 30.55%, 34.94% and 37.85%, respectively, after increasing the amount of P. In addition, this study also found that the effects of Mn, P or S on tea quality were strongest for P, followed by S, and the weakest for Mn. It can be seen that the supply of the characteristic elements Mn, P and S directly affected their uptake by the tea trees, which directly affected the quality of tea leaves.

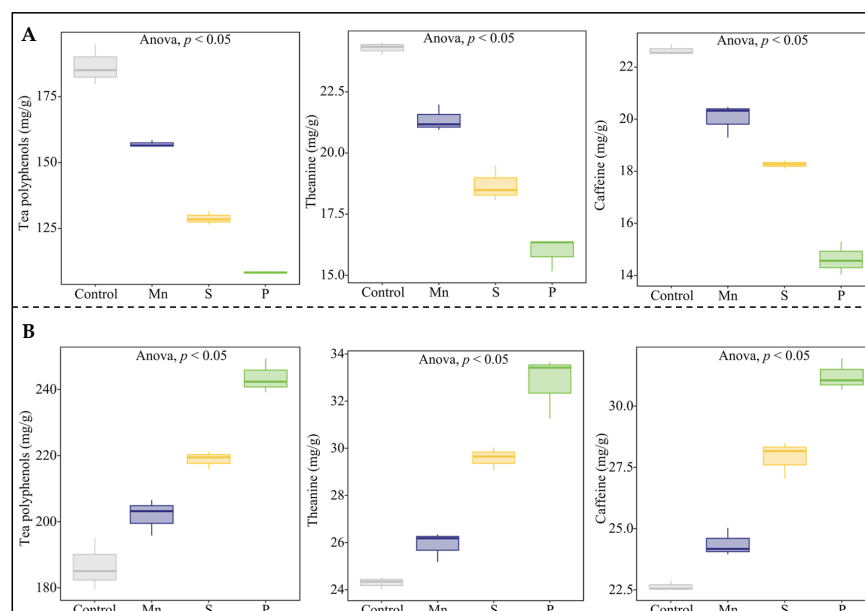


Figure 10. Effects of exogenous characteristic element treatments on quality indexes of tea seedlings ($n = 3$). Note: (A) Quality index of tea leaves after Mn, P or S deficiency treatments of tea seedlings, where Control is a complete nutrient culture; (B) Quality index of tea leaves after increasing the amount of Mn, P or S by 1-fold in treatments of tea seedlings, where Control is a complete nutrient culture.

4. Discussion

Tea quality is closely related to the composition of soil elements in the environment where tea trees grow, and the unique Danxia landform, rich soil types and special micro-climate environment in Wuyishan yield significant differences in the element uptake and metabolism of tea trees in different rock zones, which in turn may affect tea quality [10]. To test the hypothesis that parent material differences drive variations in soil elemental composition, this study compared the rhizosphere soils of tea trees from different rock zones. The results showed that significant differences in the elemental composition and contents were found in the rhizosphere soils of tea trees from different rock zones. The numbers of elements in the soils of the ZY, BY, ZC zones totaled 66, 68, and 70, respectively. Among them, the soils of the ZY and BY zones contained high contents of N, F, Fe, and Al, while the ZC zone was dominated by F, N, Fe, Al, and Ne. This difference may be related to the geological background, degree of weathering and soil mineral composition of the rock zones [30]. Specifically, the ZY zone is mainly underlain by volcanic and granitic parent rocks, whose intensive weathering and leaching processes have led to the relative enrichment of resistant elements such as Fe and Al, while the ZC zone developed on sedimentary parent materials with a higher proportion of quartz and fewer weatherable minerals. It has been shown that soils in the authentic zones are usually rich in minerals such as potassium feldspar and mica, which release large amounts of elements such as K, Mg, and Fe during the weathering process, thus affecting the uptake of mineral elements by tea trees [31]. In addition, the contents of some trace elements (e.g., In, Ba, Cu, U) in the soil of the ZY zone were significantly higher than in soils of the BY and ZC zones, which might be related to the unique soil-forming parent rock of the ZY zone, and these elements might indirectly regulate tea quality by affecting the root metabolism of tea trees. These findings confirm that soil elemental composition differs significantly across rock zones.

Secondly, this study found that despite the differences in soil elemental composition, the tea trees did not passively absorb all elements but exhibited obvious selectivity. For example, the enrichment capacity of tea tree root systems in the ZY zone for elements such as C, S, Ne, Cd, and P was significantly higher than that in the BY and ZC zones, while the root systems in the BY zone were more inclined to enrich elements such as Ca and Si [32]. This selectivity may be related to the physiological requirements and translocation mechanisms for different elements in tea trees [33]. Furthermore, selective translocation between roots and leaves was also observed, and some elements (e.g., N, P, and K) were efficiently transported to the leaves after root accumulation, whereas certain heavy metals (e.g., Cd and Pb) were mainly retained in the roots, possibly related to plant detoxification mechanisms [34,35]. This differential behavior suggests that tea trees actively regulate element distribution among tissues, prioritizing essential nutrients for leaves while sequestering potentially toxic elements in roots. In addition, the contents of N, Ne, Ca, C, and S in tea leaves from the ZY zone were significantly higher than those in leaves from other rock zones, which were closely related to photosynthesis, nitrogen metabolism, and secondary metabolism of tea trees [36]. In particular, the high accumulation of element N, which is a key component in the synthesis of amino acids and proteins, directly promotes the synthesis of theanine, which enhances the freshness of tea [37]. This finding implied that the superior elemental composition of tea leaves in the ZY zone is not merely a passive consequence of soil availability, but rather an integrated outcome of root selectivity and efficient long-distance transport.

On this basis, this study used machine learning simulation combined with SHAP value analysis to screen out 12 key characteristic elements distinguishing different rock zones, and the enrichment patterns of these elements in tea trees from different rock zones were significantly different. Specifically, the enrichment coefficients of C, Mg, Mn, P, S,

and Ti were significantly higher in ZY than in the BY and ZC zones. The results of the interaction analysis between the enrichment and translocation coefficients of the characteristic elements and the tea quality indexes showed that, for Mn, P and S, the enrichment ability of the root systems of tea trees in different rock zones, their translocation from the root systems to the leaves and their enrichment in the leaves had the greatest influence on the tea quality indexes. This finding suggested that efficient accumulation of specific elements in leaves directly enhances tea quality. P has been reported to be a key component of plant energy metabolism, participating in ATP synthesis and photosynthetic phosphorylation [38], promoting the synthesis and translocation of sugars in carbon metabolism [39], regulating the synthesis of amino acids and proteins in nitrogen metabolism, and enhancing the development of the root system and its resistance to stress [40]. Wang et al. [41] found that an increase in the absorption and accumulation of P in tea trees can effectively promote their growth, increase the contents of chlorophyll and carotenoids, enhance the activity of antioxidant enzymes, and that optimal P treatment can increase the amino acid content by 31.9–40.1% and alter the polyphenol content by 25.7–45.6%. Mn, an essential trace element in plant physiology and metabolism, is mainly involved in photosynthesis, enzyme activation, and nitrogen metabolism, and can promote chlorophyll synthesis, affect photosynthetic efficiency, and improve plant yield and quality [42]. Zaman et al. [43] used Mn spray treatment on tea leaves and found that tea quality changed after increasing the Mn accumulation in tea leaves, and that Mn could effectively increase the free amino acid and tea polyphenol contents in tea leaves, which could improve tea quality. S, a key element in plant physiology and metabolism, is mainly involved in protein synthesis, enzyme activity regulation and secondary metabolism [44,45], and affects the energy metabolism and antioxidant defense of plants, which in turn affect the growth and quality of plants [46]. Pan et al. [47] analyzed the uptake and accumulation of S in tea trees and found that increasing the S content in tea leaves can effectively promote tea yields by more than 10.8%, as well as the contents of amino acids, tea polyphenols, and water extract. Collectively, Mn, P, and S regulate tea quality through distinct but complementary mechanisms, as P primarily drives energy and carbon metabolism, Mn enhances photosynthetic efficiency and enzyme activation, and S contributes to protein synthesis and secondary metabolic pathways. In this study, regression analysis revealed that the coefficients of Mn, P, and S enrichment by the root systems of tea trees in the ZY and BY zones were significantly and positively correlated with their accumulations in leaves ($p < 0.001$), indicating that these elements were more efficiently transported in tea trees. Furthermore, the PLS-SEM structural equation simulation and hydroponic experiments consistently demonstrated that the enrichment capacity in the root system for Mn, P, and S directly affected their translocation efficiency, with P exerting the greatest effect on tea quality, followed by S, and Mn the least. These results verified that the absorption, translocation and accumulation of Mn, P and S directly regulate tea quality.

5. Conclusions

This study systematically analyzed the elemental composition characteristics of tea tree rhizosphere soils, root systems and leaves in different rock zones, and analyzed the correlation between the characteristic element contents and tea quality by comparison with the tea quality indexes, which revealed the mechanism of influence of the soil environment in different rock zones on elemental absorption and translocation and tea quality formation in tea trees. The results demonstrated that significant differences in elemental composition existed among the three rock zones (with 66, 68, and 70 elements detected in ZY, BY, and ZC, respectively), and that tea tree roots exhibited selective uptake and translocation of elements, efficiently transporting essential nutrients (e.g., N, P, K) to leaves while retaining

heavy metals (e.g., Cd, Pb) in roots. Machine learning-based screening further identified Mn, P, and S as the key characteristic elements distinguishing different rock zones, and the efficiencies of their enrichment and translocation directly regulated the contents of tea polyphenols, theanine and caffeine in tea leaves. Specifically, the mean contents of tea polyphenols, theanine and caffeine in ZY tea leaves reached 368.42, 35.73 and 39.72 mg/g, respectively, values that were significantly higher than those in BY (312.72, 28.82 and 34.06 mg/g) and ZC (266.22, 24.32 and 26.92 mg/g). Hydroponic experiments further confirmed the causal relationship between these elements and tea quality, demonstrating that deficiency of Mn, P, or S reduced the contents of tea polyphenols, theanine, and caffeine by 11.57–41.92%, with P deficiency causing the most pronounced decline, followed by S and Mn. Overall, this study systematically reveals the elemental absorption and translocation mechanisms of tea trees in different rock zones for the first time, confirming that the high tea quality in the ZY zone is closely linked to the efficient uptake and transport of Mn, P, and S. These findings provide an elemental metabolism-based explanation for the formation of Wuyi rock tea's distinctive quality, address the limitations of traditional studies that focus solely on climate and soil physicochemical properties, and offer a theoretical basis for precision fertilization strategies to improve tea quality by regulating soil Mn, P, and S supply. However, although the hydroponic experiments in this study effectively verified the causal regulatory effects of Mn, P, and S on tea quality, the short-term and controlled conditions could not fully replicate the complex soil microbe–root interactions occurring under field conditions. Furthermore, the investigation of selective root uptake remained at the physiological level, lacking molecular evidence regarding transporter gene expression and associated regulatory networks. Future studies should integrate transcriptomics, ionomics, and synchrotron radiation microanalysis to elucidate the molecular mechanisms underlying the selective uptake and transport of Mn, P, and S in tea tree roots, and conduct long-term field trials in representative rock zones to systematically evaluate the stability and applicability of precision fertilization strategies across different years and climatic conditions.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/horticulturae12080939/s1>, Table S1: Statistics of multi-element determination results for tea tree rhizosphere soils in different rock zones; Table S2: Statistics of multi-element determination results for tea tree root systems in different rock zones; Table S3: Statistics of multi-element determination results for tea tree leaves in different rock zones; Table S4: Mean values of enrichment coefficients for key elements in tea tree root systems in different rock zones; Table S5: Mean values of enrichment coefficients for key elements in tea tree leaves in different rock zones; Figure S1: Trend analysis of elemental contents of tea tree rhizosphere soils, roots and leaves; Figure S2: Accuracy of machine deep learning simulation of key element enrichment coefficients for tea tree root systems in distinguishing different rock zones; Figure S3: Accuracy of machine deep learning simulation of key element enrichment coefficients for tea tree leaves in distinguishing different rock zones; Figure S4: Trend simulation analysis of tea tree root systems for the translocation of characteristic elements Ba, Mn, Sb, C, N, and Ti to leaves; Figure S5: Trend simulation analysis of tea tree root systems for the translocation of characteristic elements I, P, W, Mg and S to leaves.

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References

1. Yue, C.; Cao, H.; Zhang, S.; Hao, Z.; Wu, Z.; Luo, L.; Zeng, L. Aroma characteristics of Wuyi Rock tea prepared from 16 different tea plant varieties. *Food Chem. X* **2023**, *17*, 100586. [[CrossRef](#)] [[PubMed](#)]
2. GB/T 8313-2018; Determination of Total Polyphenols and Catechins Content in Tea. China Standards Press: Beijing, China, 2018.
3. GBT23193-2017; Determination of Theanine in Tea-Using High Performance Liquid Chromatography. China Standards Press: Beijing, China, 2017.
4. GBT8312-2013; Tea-Determination of Caffeine Content. Method Using High-Performance Liquid Chromatography. China Standards Press: Beijing, China, 2013.
5. Wu, F.; Zhu, D.; Yang, T.; Mao, C.; Huang, W.; Zhou, S.; Yang, Y. Soil heavy metal accumulation and ecological risk in mount Wuyi: Impacts of vegetation types and pollution sources. *Land* **2025**, *14*, 712. [[CrossRef](#)]
6. Guo, H.; Chen, L.; Wang, Y.; Li, Q.; Yi, Z. Combined application of biochar and magnesium fertilizer effectively improved the soil environment and the tea quality in southern strongly acidic tea garden. *J. Soils Sediment* **2023**, *23*, 2798–2815. [[CrossRef](#)]
7. Ye, J.; Zhang, Q.; Jia, M.; Wang, Y.; Zhang, Y.; Jia, X.; Zheng, X.; Wang, H. The effects of rock zones and tea tree varieties on the growth and quality of Wuyi Rock tea based on the OPLS-DA model and machine learning. *Agriculture* **2024**, *14*, 573. [[CrossRef](#)]
8. Zhou, Z.; Xue, J.; Zhuo, Z.; Guo, Z.; Xu, R.; Sun, L.; He, S.; Liao, H. Unique region produces special tea: Metabolomic basis of the influence of production region on the quality of Wuyi rock tea. *Sci. Sin. Vitae* **2019**, *49*, 1013–1023. [[CrossRef](#)]
9. GBT18745-2006; Product of Geographical Indication—Wuyi Rock-Essence Tea. China Standards Press: Beijing, China, 2006.
10. Jia, M.; Wang, Y.; Zhang, Q.; Lin, S.; Zhang, Q.; Chen, Y.; Hong, L.; Jia, X.; Ye, J.; Wang, H. Effect of soil pH on the uptake of essential elements by tea plant and subsequent impact on growth and leaf quality. *Agronomy* **2024**, *14*, 1338. [[CrossRef](#)]
11. Peng, Y.; Jin, T.; Yang, R.; Chen, R.; Wang, J. Distribution of mineral elements in the soil and in tea plants (*Camellia sinensis*). *J. Elementol.* **2022**, *27*, 765–796. [[CrossRef](#)]
12. Zhang, L.; Zhou, C.; Zhang, C.; Zhang, M.; Guo, Y. Volatilomics and macro-composition analyses of primary Wuyi Rock teas of Rougui and Shuixian cultivars from different production areas. *Plants* **2024**, *13*, 2206. [[CrossRef](#)] [[PubMed](#)]
13. Jia, X.; Ye, J.; Wang, H.; Li, L.; Wang, F.; Zhang, Q.; Chen, J.; Zheng, X.; He, H. Characteristic amino acids in tea leaves as quality indicator for the evaluation of Wuyi Rock tea in different culturing regions characteristic amino acids in Wuyi Rock Tea. *J. Appl. Bot. Food Qual.* **2018**, *91*, 187–193. [[CrossRef](#)]
14. Wang, Y.; Cheng, X.; Yang, T.; Su, Y.; Lin, S.; Zhang, S.; Zhang, Z. Nitrogen-regulated theanine and flavonoid biosynthesis in tea plant roots: Protein-level regulation revealed by multiomics analyses. *J. Agric. Food Chem.* **2021**, *69*, 10002–10016. [[CrossRef](#)] [[PubMed](#)]
15. Poirier, Y.; Jaskolowski, A.; Clúa, J. Phosphate Acquisition and Metabolism in Plants. *Curr. Biol.* **2022**, *32*, R623–R629. [[CrossRef](#)] [[PubMed](#)]
16. He, Z.; Shang, X.; Zhang, T.; Yun, J. Ca and Mg stimulate protein synthesis in maize kernel through the action of endogenous hormones and defense enzymes. *Plant Physiol. Bioch.* **2024**, *206*, 108280. [[CrossRef](#)] [[PubMed](#)]
17. Podwika, W.; Kleszcz, K.; Krośniak, M.; Zagrodzki, P. Copper, manganese, zinc, and cadmium in tea leaves of different types and origin. *Biol. Trace Elem. Res.* **2018**, *183*, 389–395. [[CrossRef](#)] [[PubMed](#)]
18. Ammann, A.A. Inductively coupled plasma mass spectrometry (ICP MS): A versatile tool. *J. Mass Spectrom.* **2007**, *42*, 419–427. [[CrossRef](#)] [[PubMed](#)]
19. Zhao, H.; Zhang, S.; Zhang, Z. Relationship between multi-element composition in tea leaves and in provenance soils for geographical traceability. *Food Control* **2017**, *76*, 82–87. [[CrossRef](#)]
20. Wong, M.; Zhang, Z.; Wong, J.; Lan, C. Trace metal contents (Al, Cu and Zn) of tea: Tea and soil from two tea plantations, and tea products from different provinces of China. *Environ. Geochem. Health* **1998**, *20*, 87–94. [[CrossRef](#)]

21. Ye, J.; Wang, H. *Wuyi Rock Tea Germplasm Resources, Processing, and Evaluation*; China Agricultural University Press: Beijing, China, 2025.
22. Cao, X.; Zhang, Z.; Wang, J.; Dai, H.; Zhang, A.; Xu, X. Evaluation of soil quality in different *Bletilla striata* agroforestry systems in eastern China. *Horticulturae* **2024**, *10*, 1308. [\[CrossRef\]](#)
23. Huang, R.; Wang, Z.; Wen, W.; Yao, M.; Liu, H.; Li, F.; Zhang, S.; Ni, D.; Chen, L. Comprehensive dissection of variation and accumulation of free amino acids in tea accessions. *Hortic. Res.* **2024**, *11*, uhad263. [\[CrossRef\]](#) [\[PubMed\]](#)
24. Fu, Z.; Chen, L.; Zhou, S.; Hong, Y.; Zhang, X.; Chen, H. Analysis of differences in the accumulation of tea compounds under various processing techniques, geographical origins, and harvesting seasons. *Food Chem.* **2024**, *430*, 137000. [\[CrossRef\]](#) [\[PubMed\]](#)
25. Guo, Q.; Wu, Z.; Xiao, Y.; Korpelainen, H.; Li, C. Foliar Application of nano-selenium enhances tea quality and selenium biofortification by promoting theanine synthesis and nitrogen metabolism. *Plant Biotechnol. J.* **2026**, *24*, 2300–2311. [\[CrossRef\]](#) [\[PubMed\]](#)
26. Ye, Y.; Yan, J.; Cui, J.; Mao, S.; Li, M.; Liao, X.; Tong, H. Dynamic changes in amino acids, catechins, caffeine and gallic acid in green tea during withering. *J. Food Compos. Anal.* **2018**, *66*, 98–108. [\[CrossRef\]](#)
27. Pan, S.; Zhang, X.; Xu, W.; Yin, J.; Gu, H.; Yu, X. Rapid on-site identification of geographical origin and storage age of tangerine peel by near-infrared spectroscopy. *Spectrochim. Acta A* **2022**, *271*, 120936. [\[CrossRef\]](#) [\[PubMed\]](#)
28. Ganaie, M.A.; Hu, M.; Malik, A.K.; Tanveer, M.; Suganthan, P.N. Ensemble deep learning: A review. *Eng. Appl. Artif. Intel.* **2022**, *115*, 105151. [\[CrossRef\]](#)
29. Zhao, Y.; Yu, K.; Li, X.; He, Y. Detection of fungus in fectionon petals of rapeseed (*Brassica napus* L.) using NIR hyperspectral imaging. *Sci. Rep.* **2016**, *6*, 38878. [\[CrossRef\]](#) [\[PubMed\]](#)
30. Shu, L.; Zhou, X.; Deng, P.; Wang, B.; Jiang, S.; Yu, J.; Zhao, X. Mesozoic tectonic evolution of the southeast China block: New insights from basin analysis. *J. Asian Earth Sci.* **2009**, *34*, 376–391. [\[CrossRef\]](#)
31. Zhao, Q. *Red Soil Material Cycle and Its Regulation*; Science Press: Beijing, China, 2002.
32. Yang, J.; Liu, C.; Li, J.; Zhang, Y.; Zhu, C.; Gu, D.; Zeng, L. Critical review of fluoride in tea plants (*Camellia sinensis*): Absorption, transportation, tolerance mechanisms, and defluorination measures. *Beverage Plant Res.* **2024**, *4*, e019. [\[CrossRef\]](#)
33. Vatansever, R.; Ozyigit, I.I.; Filiz, E. Essential and beneficial trace elements in plants, and their transport in roots: A review. *Appl. Biochem. Biotech.* **2017**, *181*, 464–482. [\[CrossRef\]](#) [\[PubMed\]](#)
34. Duan, D.; Tong, J.; Xu, Q.; Dai, L.; Ye, J.; Wu, H.; Xu, C.; Shi, J. Regulation mechanisms of humic acid on Pb stress in tea plant (*Camellia sinensis* L.). *Environ. Pollut.* **2020**, *267*, 115546. [\[CrossRef\]](#) [\[PubMed\]](#)
35. Winiarska-Mieczan, A. Protective effect of tea against lead and cadmium-induced oxidative stress—A review. *Biometals* **2018**, *31*, 909–926. [\[CrossRef\]](#) [\[PubMed\]](#)
36. Ran, W.; Li, Q.; Hu, X.; Zhang, D.; Yu, Z.; Chen, Y.; Wang, M.; Ni, D. Comprehensive analysis of environmental factors on the quality of tea (*Camellia sinensis* var. *sinensis*) fresh leaves. *Sci. Hortic.* **2023**, *319*, 112177. [\[CrossRef\]](#)
37. Zhang, W.; Ni, K.; Long, L.; Ruan, J. Nitrogen transport and assimilation in tea plant (*Camellia sinensis*): A review. *Front. Plant Sci.* **2023**, *14*, 1249202. [\[CrossRef\]](#) [\[PubMed\]](#)
38. Xie, Z.; Wu, F.; Lin, W.; Luo, J. The utilization of photophosphorylation uncoupler to improve lipid production of *Chlorella*, a case study using transcriptome and functional gene expression analysis to reveal its mechanism. *Biochem. Eng. J.* **2022**, *178*, 108275. [\[CrossRef\]](#)
39. Dissanayaka, D.M.S.B.; Ghahremani, M.; Siebers, M.; Wasaki, J.; Plaxton, W.C. Recent insights into the metabolic adaptations of phosphorus-deprived plants. *J. Exp. Bot.* **2021**, *72*, 199–223. [\[CrossRef\]](#) [\[PubMed\]](#)
40. Liu, M.; Zhao, M.; Yang, G.; Sun, M.; Yang, A.; Sun, C.; Zhao, H.; Ao, X. Root morphology, nitrogen metabolism and amino acid metabolism in soybean under low phosphorus stress. *Sci. Rep.* **2024**, *14*, 28583. [\[CrossRef\]](#) [\[PubMed\]](#)
41. Wang, Y.; Shi, R.; Deng, S.; Wang, H.; Hussain, S.; Wang, C.; Gong, C.; Bai, J. Application of low phosphorus on the basis of organic fertilizer can effectively improve yield and quality of tea plants. *Beverage Plant Res.* **2024**, *4*, e307. [\[CrossRef\]](#)
42. Hafeez, A.; Rasheed, R.; Ashraf, M.A.; Rizwan, M.; Ali, S. Effects of exogenous taurine on growth, photosynthesis, oxidative stress, antioxidant enzymes and nutrient accumulation by *Trifolium alexandrinum* plants under manganese stress. *Chemosphere* **2022**, *308*, 136523. [\[CrossRef\]](#) [\[PubMed\]](#)
43. Zaman, F.; Zhang, E.; Ihtisham, M.; Ilyas, M.; Khattak, W.; Guo, F.; Wang, P.; Wang, M.; Wang, Y.; Ni, D.; et al. Metabolic profiling, pigment component responses to foliar application of Fe, Zn, Cu, and Mn for tea plants (*Camellia sinensis*). *Sci. Hortic.* **2023**, *319*, 112149. [\[CrossRef\]](#)
44. Narayan, O.P.; Kumar, P.; Yadav, B.; Dua, M.; Johri, A.K. Sulfur nutrition and its role in plant growth and development. *Plant Signal. Behav.* **2023**, *18*, 2030082. [\[CrossRef\]](#) [\[PubMed\]](#)
45. Mondal, S.; Pramanik, K.; Panda, D.; Dutta, D.; Karmakar, S.; Bose, B. Sulfur in seeds: An overview. *Plants* **2022**, *11*, 450. [\[CrossRef\]](#) [\[PubMed\]](#)

46. Choudhary, A.K.; Singh, S.; Khatri, N.; Gupta, R. Hydrogen sulphide: An emerging regulator of plant defence signalling. *Plant Biol.* **2022**, *24*, 532–539. [[CrossRef](#)] [[PubMed](#)]
47. Pan, J.; Hong, S.; Zhang, Y.; Zhu, Y.; Liao, W.; Han, W. Characteristics of sulphur distribution in tea plant and the effect of sulphur application on tea yield and quality. *J. Tea Sci.* **2019**, *36*, 575–586. [[CrossRef](#)]

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