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Habitat and density effects on tea quality: A microclimate and nutrients perspective

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A B S T R A C T

The global expansion of tea plantations due to increasing tea demand, often involving the conversion of forests to monoculture, has raised concerns about soil degradation, changes in microclimate, habitat fragmentation, biodiversity loss, and alteration in tea quality. On the other hand, planting density is another important factor affecting soil properties, tea growth, and quality. However, the combined effects of different habitats and planting densities on crucial factors and tea quality remain poorly understood. This study investigated these effects in Yunnan, China, considering three habitats (Monoculture (T1), Medium-coverage tropical evergreen broad-leaved forest (T2), and High-coverage tropical evergreen broad-leaved forest (T3)) with two tea densities (Medium (M) and High (H)). Our results show that the T2 + M treatment improved the microclimate for tea plants, resulting in increased relative humidity (3.6 %) and soil moisture (6.6 %), while reducing light intensity (70.1 %), soil and air temperature (5.5 % and 11.2 %) compared with T1 + M. Additionally, T2 + M exhibited higher soil total N (41–47 %), available P and K contents (100–202 % and 42–230 %) across the soil layers (0–100 cm) when compared to T1 + H. T1 + M enhanced tea growth metrics, including dry leaf weight, plant height, leaf area, and leaf mass area ratio, followed by T2 + M. The T2 + M model recorded higher chlorophyll content (23 %), young shoot and mature leaves N (25 % and 38 %), P (26 % and 59 %), and K (11 % and 28 %) contents compared with T1 + H. T2 + M also had higher levels of various amino acids (33–222 %) and catechins (18–88 %) relative to T1 + H. Notably, the quality of spring tea was higher than autumn tea, with 50–212 % higher amino acids contents and 92–242 % higher catechins contents. Between the different tea densities, medium tea density exhibited significantly higher levels of soil nutrients, tea nutrients, growth, and quality. Likewise, within the various habitats, T2 showed significantly higher levels of soil nutrients, tea nutrients, and quality. The structural equation model revealed that habitat and tea density significantly influenced tea quality, both directly and indirectly, through microclimate, soil nutrients, and tea nutrients contents. These results suggest that T2 + M is optimal for enhancing soil quality, microclimate, and tea growth and quality, providing scientific guidance for the sustainable development of ancient tea plantations.

1. Introduction

Tea (*Camellia sinensis*) is an important cash crop and the most widely consumed beverage in the world (Hazra et al., 2019). China, Sri Lanka, India, Indonesia, and Kenya are the main tea producing countries worldwide (Majumder et al., 2011). The cultivation of tea serves as a vital source of revenue for millions of low-income families and it contributes significantly to poverty alleviation, food security, and rural development (FAO, 2022). Furthermore, it plays a significant role in revitalize the economies of numerous developing nations. Tea is extensively grown in the mountainous areas of subtropical and tropical climates (Wang et al., 2016). The swift advancement of the global tea

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industry has led to a substantial expansion in the tea cultivation area (Xiong et al., 2022). According to the statistics of the Food and Agriculture Organization of the United Nations, the total harvested area of tea increased from 2.4 to 5.2 million hectares (about 115 %), and the production increased from 1.3 to 2.8 million tonnes (about 115 %) between 2002 and 2022 (FAO, 2007).

Tea trees are traditionally planted in the understory of natural forests in Yunnan. In 1974, tea plantations began to expand affected by the provincial government's policy called the transformation of old tea forests to new tea plantations, i.e., tea monocultures (Huang, 2005). Thereafter, some ancient tea forests were replaced by tea monocultures (Freeman and Ahmed, 2011). Since the early 2000s, however, the growing market for Pu'er tea has increasingly played a major role in the expansion of monoculture tea areas. Under the pressure of market demand, efficiency became the new focus to promote the modernization of tea production. Therefore, the government promotes monoculture tea trees because they are more productive compared to forest tea trees. Unfortunately, this transformation and expansion of tea monocultures has led to degradation of soil, deterioration of tea quality, reduction of landscape connectivity, and loss of biodiversity and ecosystem services (Chowdhury et al., 2021). In traditional ancient tea forest, however, the natural shading of forest trees nearby tea trees alters the microclimate by reducing the air and soil temperature, incident radiation, and wind speed, as well as increasing the air relative humidity (Pardon et al., 2017; Lasco et al., 2014). Forest cover can also affect litter formation, biomass, and diversity of plant species (Shao et al., 2017), leading to changes in soil nutrients (Sheng et al., 2003). The combination of forest trees and tea trees could increase land use efficiency, optimize soil temperature, reduce weed stress, and retain soil moisture (Zhang et al., 2014; Tsonkova et al., 2012; Gebru, 2015; Panozzo et al., 2020; Torralba et al., 2016). This could potentially change the synthesis of secondary metabolites and ultimately improve the quality of tea. However, there has been limited research focused on quantitatively comparing the quality of tea sourced from different habitats, such as forest tea plantations versus monoculture tea plantations.

Planting density plays a crucial role in the management of tea cultivation, influencing both the quality of the tea produced and the growth of the plants. This is achieved by modulating the microclimate surrounding the tea trees and optimizing the process of leaf photosynthesis (Fang et al., 2018). Intensive planting density frequently results in significant competition among plants for space, which restricts the light capture of lower leaves and stems, diminishes photosynthetic activity, and impedes the growth of individual specimens (Romero et al., 2022). In contrast, an optimal planting density supports enhanced photosynthetic efficiency and promotes greater overall plant development (Zhang et al., 2016). According to Fasoula and Tollenaar (2005), as planting density increased, the competition for resources becomes more pronounced. Dense planting increased the height of the plant and reduced the number of branches to receive more light, thus reducing yield (Gezahegn, 2019). Furthermore, the availability of soil nutrients and moisture are critical constraints affecting both the yield and quality of tea. Additionally, it is essential to establish an optimal planting density to ensure adequate soil moisture and nutrient availability (Wei and Liang, 2021). Therefore, it is important to choose the best planting density to obtain high-quality tea and yield. The ideal planting density enhances the absorption of solar energy and inorganic nutrients by the plant canopy. Furthermore, it boosts the efficiency of nutrient and water utilization, as well as the photosynthetic potential, by increasing the leaf area index (Jiang et al., 2018). However, the effect of tea planting density on soil nutrients availability, tea nutrients and quality are largely unknown. Therefore, further research is needed to understand how different habitats and tea planting densities affect microclimate, soil nutrients, and tea leaf nutrients. This information is crucial for evaluating tea growth and quality.

To address how different habitats and tea planting densities affect tea growth and quality and the potential mechanisms, this study examines the changes in the soil macronutrients, microclimatic variables, tea leaves nutrients, tea growth, and quality in different habitat and tea planting density models. Thus, the objectives of this study were to (1) explore the effects of different habitats on microclimate, soil nutrients, and tea growth and quality; and (2) determine how different tea planting densities affect microclimate, soil nutrients, and tea growth and quality. We hypothesize that medium cover evergreen broad-leaved forest and medium tea density will greatly affect the microclimate of tea plants, increase soil macro nutrients, tea nutrients, and growth, and improve tea quality.

2. Materials and methods

2.1. Study area

This study was conducted at Gedeng Mountain, Anle village (101°11'E, 22°05'N, and 1300 MASL) in 2023–2024. Gedeng Mountain is known as one of the prominent tea-growing areas in the Xishuangbanna region of Southwest China (Fig. 1). The region experiences a tropical monsoon climate, with a mean annual temperature ranging between 15 and 21 °C and precipitation between 1500 and 2500 mm. Additionally, there is a frost-free period of about 260 days in this region.

2.2. Experimental design

The experiment has 6 models, including three habitats (monoculture, medium-coverage tropical evergreen broad-leaved forest, and high-coverage tropical evergreen broad-leaved forest) with two tea plant densities (medium and high) (Fig. 2). We categorized habitats into three classes based on approximate canopy coverage: T1 (low coverage, 0 %), T2 (moderate coverage, ~50 %), and T3 (high coverage, ~80 %). Following the classification by Willson and Clifford (1992), we selected two planting densities for our study: 33 plants per 100 m^2 (i.e., 3300 plants ha^{-1}, with row spacing of 2.0 m and plant spacing of 1.5 m) representing medium density (M), and 67 plants per 100 m^2 (i.e., 6700 plants ha^{-1}, with row spacing of 1.2–1.5 m and plant spacing of 0.9–1.2 m) representing high density (H). We did not include low-density tea plantations, as they are not practiced by local farmers due to their associated low productivity. The experiment was all conducted on 20-year-old tea plants. Both monoculture and forest tea plantations are managed without chemical or organic fertilizers, pesticides and herbicides. Farmers mainly use mechanical methods to control weeds. The experimental design was a completely randomized design (CRD) with four repetitions. The experimental plot area was 100 m^2 (10 $\times$10 m^2).

2.3. Microclimate conditions

On a sunny day, we measured five different microclimatic variables such as air and soil temperature, light intensity, relative humidity, and soil moisture content between rows of tea plants in three different seasons: autumn (Oct-2023), spring (Apr-2024), and summer (Aug-2024). At each sampling date, we randomly located five spots in each plot and measured air temperature and humidity using a humidity and temperature meter (SNDWAY, SW 572), soil temperature using a soil tester, and light intensity using a digital lux meter (SNDWAY, SW 582). The soil moisture content was determined in the top soil layer (0–20 cm) by drying soil samples and calculating the moisture content.

2.4. Soil sampling and nutrients analysis

In each plot, we randomly selected three spots for soil sampling during Aug-2023. The soil samples were taken by soil auger at 20 cm intervals up to a depth of 100 cm. Soil samples from the same depth were mixed to make a composite soil sample, ensuring the manual removal of any plant debris, stones, and roots. Afterward, we sieved

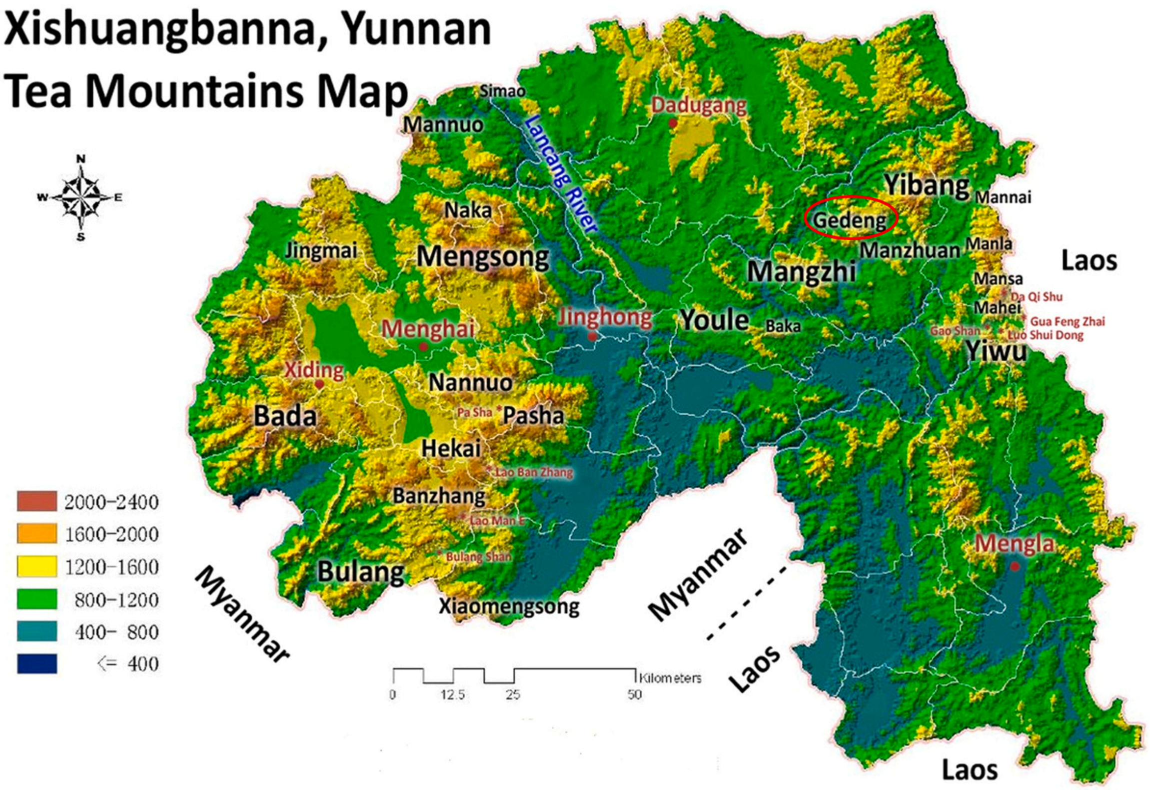

Fig. 1. Experimental site.

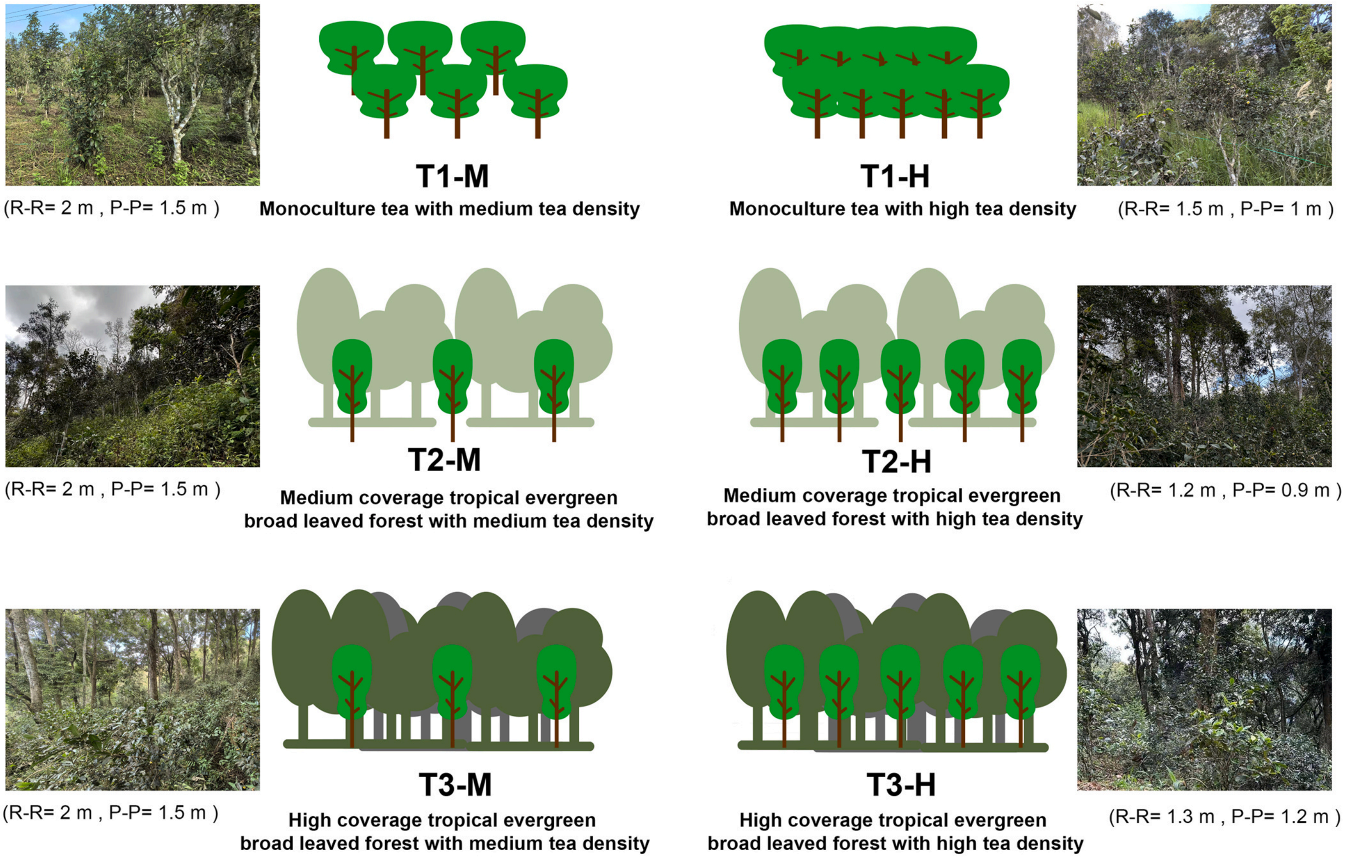

Fig. 2. Experimental Design. Row to Row distance (R-R), Plant to Plant distance (P-P).

composite soil samples through a 2 mm mesh and then divided them into two portions. We used one portion of a composite soil sample to measure mineral nitrogen, and the other portion was air-dried. The dried soil was further divided into two parts; one part was used for available phosphorus (AP) and available potassium (AK) analysis. Another part was sieved through a 0.15 mm mesh to determine the total carbon (C) and total nitrogen (N) content using an elemental analyzer (Vario Max CN Analyzer, Elementar Analysen systeme GmbH, Langenselbold, Germany). For available phosphorus (AP) and available potassium (AK), soil solution was extracted following the Mehlich-3 method and their concentrations were determined using inductively coupled plasma atomic emission spectroscopy (ICP-AES, Thermo Jarrell Ash Ltd., Franklin, MA, USA).

2.5. plant traits, leaves sampling and nutrients analysis

As a representative of tea plant traits, we measured the height of tea plants, leaf characteristics, and chlorophyll content in tea leaves during Oct-2023 from all treatments. We used a measuring tape to measure the height of five individuals in each plot. For leaf traits, we randomly plucked 100 fully-grown healthy leaves in each plot and measured leaf width, leaf length, and leaf area using Leaf Area Meter (Li-3000A, LI-COR, USA). To measure leaf mass area (LMA), we dried respective leaf samples at 70 °C for 72 h to acquire the dry mass and then determined LMA ($g^{-1}m^2$) following Kvet *et al.* (1971). For the chlorophyll content analysis, we used a portable device (SPAD-502Plus, KONICA MINOLTA, INC., USA). For the analysis of tea nutrients and quality, we randomly sampled young shoots (2–3 leaves and one bud) from several plants in the autumn season (Oct-2023) and the spring season (Apr-2024). We then dried the young tea shoot samples at 65 °C until they reached a constant weight. Both the young shoots and mature leaves were crushed using a blending machine and sieved through a 0.7–1.0 mm mesh. We stored both young shoots and mature leaf samples in zip-lock bags with silica gel packets for tea nutrients and quality analysis. The P and K contents of the young shoots and mature leaves were determined by the digestion method. After digestion, samples were diluted in a 50 mL volumetric flask with 50 mL double-distilled water, and the content of TP and TK was measured by ICP-AES (Thermo Jarrell Ash Ltd., Franklin, MA, USA). The C and N contents were determined by an elemental analyzer (Vario Max CN Analyzer, Elementar Analysen systeme GmbH, Langenselbold, Germany).

2.6. Tea young shoots amino acids and catechins analysis

We conducted an analysis of amino acids and catechins using the high performance liquid chromatography (HPLC) method with a Sykam system from Germany. To begin, we prepared a methanol extract of tea leaf samples by dissolving 250 mg of the sample in 1.5 mL of 75 % methanol in an Eppendorf tube. The tubes were mixed using a vortex oscillator, then placed in an ultrasonic water bath for 15 min, with two cycles of up and down at 7-minute intervals. Subsequently, they were centrifuged at 11,000 r/min at 25 °C for 10 min. The extracts were filtered through a 0.22 μm PTFE filter, and the resulting sample solutions were divided into two portions for analysis of amino acids and catechins, stored in dram glass vessels. A 2998 Photodiode Array Detector System (Waters) connected to Waters Alliance e2695 HPLC Separation Module was used to inject 10 μL for catechin and 25 μL for free amino acid sample solutions for HPLC analysis, respectively. The mobile phase A for catechins consisted of distilled water with 2 % formic acid, while mobile phase B was composed of acetonitrile (ACN) HPLC solvent (Sigma Aldrich Co., St. Louis, Missouri, USA). The samples were eluted at a flow rate of 1 mL/min, the column temperature was maintained at 40 ± 1 °C, and they were monitored at 278 nm. For amino acid analysis, water was used as the eluent for AccQ. Tag as mobile phase A, acetonitrile was used as mobile phase B, and the column temperature was set to 37 ± 2 °C. The remaining steps of the procedure were executed in accordance with the AccQ.Tag (a proprietary derivatization reagent used in the analysis of amino acids) Chemical Packing Instructions brochure. We evaluate the retention time of the sample graph against the standard graph retention time to verify precision, and subsequently locate the peaks corresponding to catechins and amino acids as outlined in the provided manual.

2.7. Statistical analysis

Prior to analysis, a normality test was conducted using the Kolmogorov-Smirnov test to confirm that the data followed a normal distribution. Subsequently, the data were subjected to analysis of variance (ANOVA) as outlined by Gomez and Gomez. In the statistical analysis, the dependent variables included microclimatic data, soil nutrients, nutrient levels in young and mature tea leaves, tea growth traits, and tea quality indicators such as catechin and amino acid composition. The independent variables comprised different habitats and tea planting densities. The F-test was used to assess the significance of the treatment effects, while the least significant differences (LSD) at a 5 % probability threshold were applied to compare the means between each pair of treatments. All statistical analyses, such as the F-test, ANOVA, LSD, and Pearson's correlation analysis, were conducted utilizing IBM SPSS Statistics version 20. In order to control False Discovery Rate (FDR) in correlations, We used p.adjust() function of R stats package in R software to perform FDR control using the Benjamini-Hochberg (BH) method (Benjamini and Hochberg, 1995). A heat map was created using the R software with the 'ggplot2' package (version 3.5.1) (Wickham, 2016). Principal Component Analysis (PCA) was carried out in R with the assistance of the 'factoextra' and 'FactoMineR' packages (Kassambara, 2020; Husson et al., 2020; R Core Team, 2023).

In the axes of first PCA, variables mainly included soil nutrients, micro-climatic factors, nutrient levels in young shoots and mature leaves, and tea growth traits. For the axes of second PCA, the variables covered soil nutrients, microclimatic factors, and targeted metabolites in young shoots, specifically the amino acids and catechin contents of autumn tea. In the axes of third PCA, soil nutrients, microclimatic factors, and targeted metabolites in young shoots were included, with an emphasis on amino acids and catechin contents of spring tea. Before conducting the PCA, we standardized the datasets using Z-score normalization via the scale() function in R software. To evaluate the direct and indirect effects of habitats and tea planting densities on tea quality, we constructed a structural equation model (SEM) using the AMOS 21.0 (IBM Corp, Chicago, IL, USA). In the initial model construction, we selected only those variables that were significantly affected by different habitats and tea planting densities, based on ANOVA results (Eisenhauer et al., 2012). The variables included tea growth metrics (dry leaves weight, leaf area, leaf length, leaf width, leaf mass area ratio, plant height, Chl content, leaf water content), microclimatic factors (light intensity, soil and air temperature, relative humidity and soil moisture), soil nutrients (TN, AP, AK), young shoot nutrients (N, P, K), mature leaves nutrients (N, P, K), amino acid content (GAa, Phe, Ala, The, Glu, Cit, Lys, Tyr, Leu, Tau, Ser, Thr, Asp, Val, Ile, His), and catechin contents (EC, ECG, EGC, EGCG, C, GC).

To enhance the simplicity and clarity of the SEM, we minimized the number of variables by converting different variables into a single composite variable (latent variable) through PCA in R software (Chen et al., 2019b). The resulting composite variables include microclimate, soil nutrients, tea growth, young shoots nutrients, mature leaves nutrients, amino acid contents and catechin contents. We also converted habitats and tea planting densities (categorical variables) into numerical values using Weighted Least Squares Mean and Variance adjusted (WLSMV) methods for estimating model parameters in Mplus software. The assumed causal paths for SEM in AMOS were based on insights gained from Mplus, theoretical frameworks, and correlation analysis outcomes from SPSS. After constructing the model by AMOS, we removed non-significant paths to improve model fit and simplify the analysis. Maximum-likelihood estimations were employed to assess SEM, using $\chi2$ tests for goodness-of-fit index (GFI). The following parameters were used to evaluate model fitness: root mean squared error of approximation (RMSEA) < 0.05, a lower $\chi2$, a Fisher's P value of $0.05 < P \leq 1$ and a lower Akaike information criterion (AIC).

3. Results

3.1. Microclimate variables

The responses of light intensity (LI), air and soil temperature (AT and ST), relative humidity (RH), and soil moisture (SMC) were significantly affected by different habitats and tea densities (Fig. 3). T3 + H and T3 + M exhibited lower LI, ST, and AT but higher RH and SMC. T2 + H and T2 + M showed optimal LI, ST, and AT alongside elevated RH and SMC. In contrast, T1 + M and T1 + H had higher LI, ST, and AT but

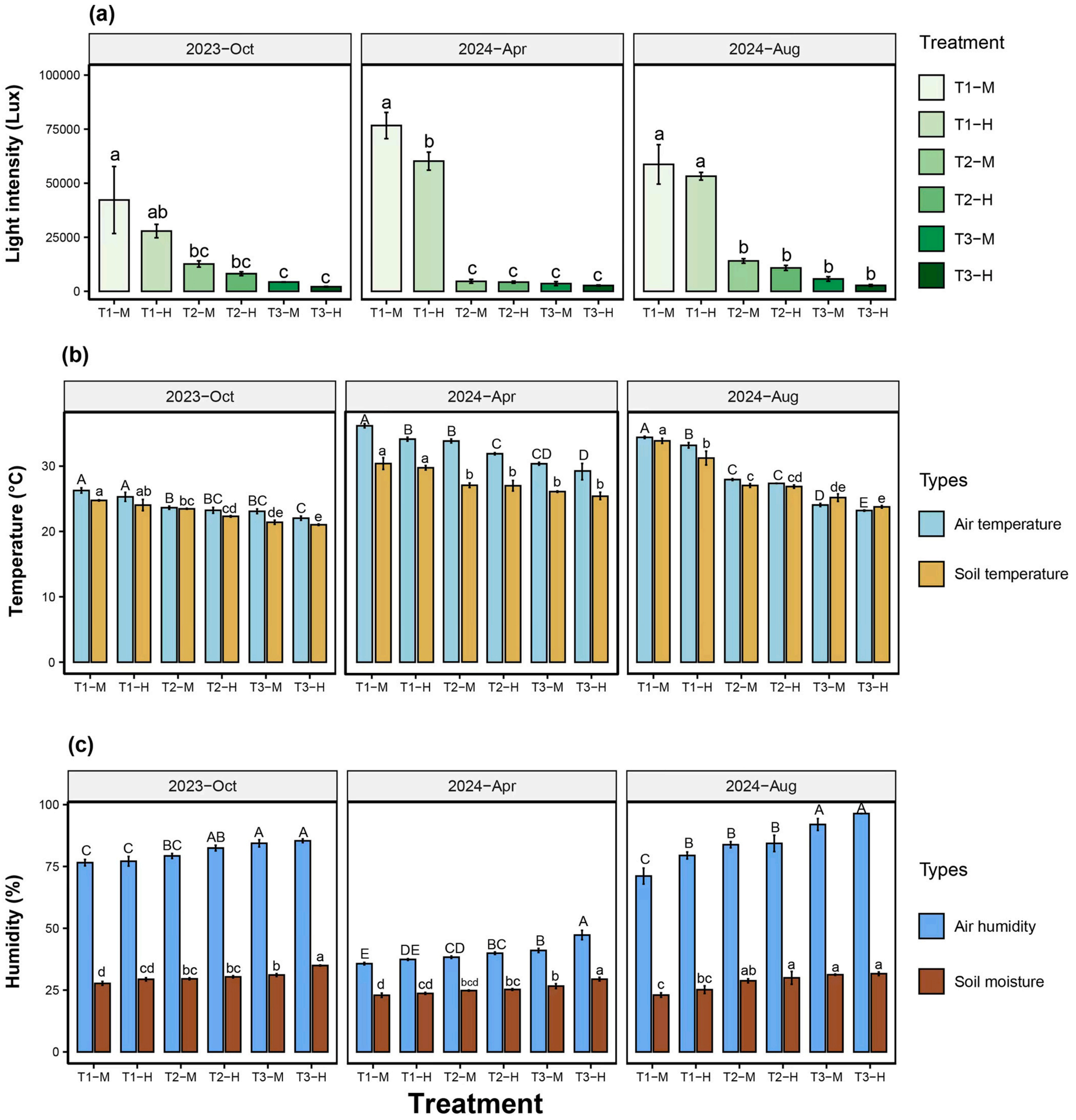

Fig. 3. Effect of different habitats and tea densities on micro-climatic variables. Monoculture Tea (T1), Medium-coverage tropical evergreen broad-leaved forest (T2), High-coverage tropical evergreen broad-leaved forest (T3), Medium tea density (M), High tea density (H). Different upper-case and lower-case letters denote statistically significant differences across various treatments at a significance level of $P \leq 0.05$, while the vertical bars represent the standard deviation of the mean ($n = 4$).

lower RH and SMC. Medium-density tea plots consistently showed higher LI, ST, and AT values than high-density plots across all seasons. The most pronounced increases occurred in autumn (34.0–50.0 % LI, 1.8–4.9 % ST, and 1.7–4.6 % AT), followed by spring (8.0–24.8 % LI, 3.7–8.7 % ST, 0.2–3.1 % AT) and summer (9.4–52.2 % LI, 0.6–7.8 % ST, 2.1–3.5 % AT) (Fig. 3a, b). Additionally, high tea density plots showed higher SMC and RH percentages ranging from 2.7 % to 11 % and 0.7–3.9 % respectively, in comparison to medium tea density plots (Fig. 3c). Among habitats, T1 had higher LI, ST and AT compared with T2 and T3, but RH and SMC were higher in T2 and T3 as compared with T1 in autumn, spring and summer seasons (Fig. 3a, b).

3.2. *Soil macronutrients*

Analysis of variance shows that different habitats and tea densities significantly affected the soil macronutrients (N, AP, and AK) (Fig. 4a-c). T2 + M had the highest N, AP, and AK contents at 0–20 cm, 20–40 cm, 40–60 cm, 60–80 cm, and 80–100 cm, followed by T2 + H. The lowest soil N, AP, and AK contents across the soil depth (0–100 cm) were noted in T1 + H and T1 + M plots (Fig. 4a-c). Planting density significantly affected soil N, AP, and AK contents. Medium-density tea plots had relatively higher N, AP and AK contents at 0–20 cm, 20–40 cm, 40–60 cm, 60–80 cm and 80–100 cm as compared with high-density plots, respectively. Among habitats, T2 had higher total N, AP and AK contents across the soil depth (0–100 cm) as compared with T1 and T3 plots (Fig. 4a-c). The soil K and N contents were higher in the top soil layers (0–20 cm), but lower in the deep soil layers (80–100 cm). The soil N and AK content decrease across the soil depth (0–100 cm), while soil AP content increases up to 60 cm soil depth and then decreases.

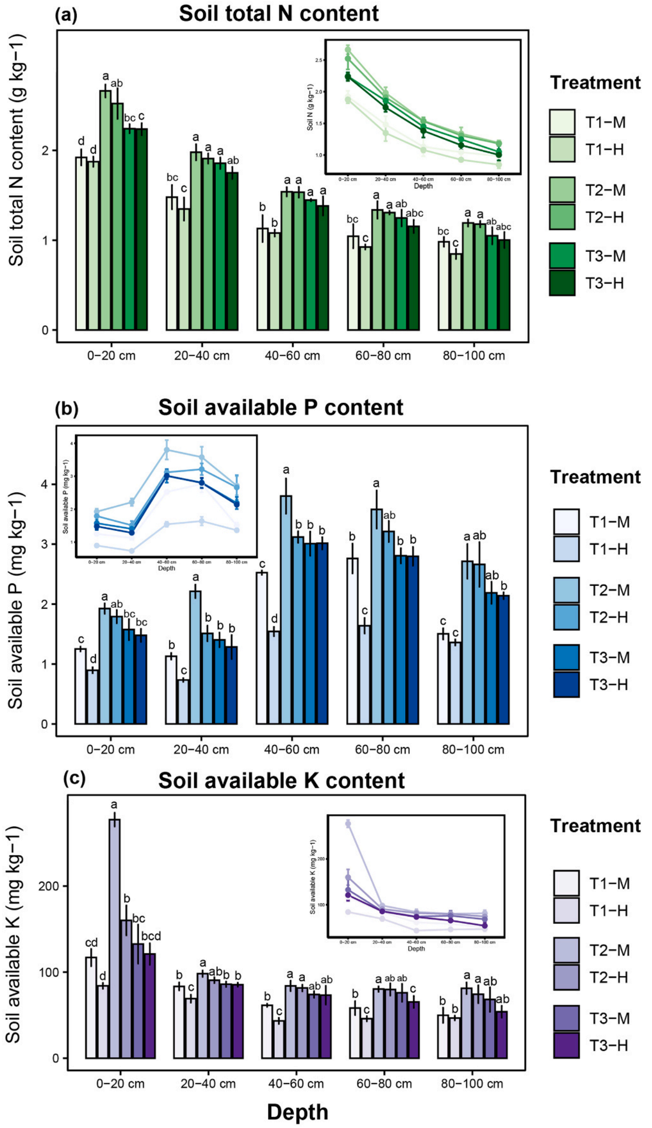

Fig. 4. Effect of different habitats and tea densities on soil N, P and K concentration. Monoculture Tea (T1), Medium-coverage tropical evergreen broad-leaved forest (T2), High-coverage tropical evergreen broad-leaved forest (T3), Medium tea density (M), High tea density (H), Phosphorus (P), Nitrogen (N), and Potassium (K). Different lower-case letters denote statistically significant differences across various treatments at a significance level of $P \leq 0.05$, while the vertical bars represent the standard deviation of the mean ($n = 4$).

3.3. *Tea nutrients content, tea quality and growth traits*

The C:N ratio, N, P, and K contents of young-shoots and mature leaves of tea were significantly affected by different habitats and tea densities, as shown in Table 1. The C contents of tea young shoots and mature leaves, however, did not show significant changes across different habitats and tea densities. Among the various habitats and tea planting densities, T2 + M exhibited the highest N (4.14 %, 3.10 %), P (3.37 mg.g^{-1}, 2.07 mg.g^{-1}), and K content (15.2 mg.g^{-1}, 11.9 mg.g^{-1}) in young-shoots and mature-leaves of tea, followed by T2 + H and T3 + M. The lowest N content (3.30 %, 2.25 %), P content (2.68 mg.g^{-1}, 1.30 mg.g^{-1}), and K content (13.6 mg g^{-1}, 9.2 mg.g^{-1}) of tea young shoots and mature leaves were recorded in T1 + H. The C:N ratio of tea young shoots and mature leaves was lower in T2 + M, while higher C:N ratio was observed in T1 + H and T1 + M (Table 1). Medium-density tea plots exhibited higher N, P, and K contents with lower C:N ratios in both young shoots and mature leaves compared to high-density plots. Among the habitats, T2 and T3 exhibited higher N, P, and K contents in both young shoots and mature leaves compared to T1 (Table 1), while the C:N ratios were notably lower in T2 and T3 than in T1. Across all treatments, young shoots showed greater P, K, and N contents but lower C:N ratios than mature leaves.

The analysis of variance shows that the tea quality is significantly impacted by different habitats and tea densities. The tea quality parameters, including amino acid and catechin contents, are significantly higher in T2 compared with T3 and T1. Medium planting density resulted in significantly higher tea quality than high density (Fig. 5). Catechin contents were 92–242 % higher in spring tea than in autumn tea, whereas EC levels were 24–94 % higher in autumn tea (Fig. 5a, b). The T2 + M habitat exhibited significantly higher catechin contents (EC, ECG, EGC, EGCG, C, and GC) than other treatments across both seasons. In autumn, T2 + M showed 36.6 % and 25.6 % greater total catechins than T1 + H and T1 + M, respectively; spring tea displayed even larger differences (50.2 % and 39.1 % higher versus T1 + H and T1 + M). Medium-density plots consistently outperformed high-density plots, with 4.6–8.8 % (autumn) and 5.2–14.3 % (spring) higher total catechin contents. Among habitats, T2 maintained superior catechin levels in both seasons compared to T1 and T3 (Fig. 5a, b).

Our study revealed significant effects of habitat and planting density on amino acid profiles in tea shoots. Spring tea exhibited greater amino acid diversity (18 compounds) and higher concentrations (50–212 % increase) compared to autumn tea (15 compounds). Notably, L-Ala, L-Arg, L-Trp, and L-Asn were uniquely detected in spring tea, while L-Cit was only present in autumn samples. The T2 + M treatment consistently showed superior amino acid accumulation, with total contents 82.4–93.9 % higher than T1 + H and 42.3–83.3 % higher than T1 + M across seasons. Medium-density plots (T1 + M, T2 + M, T3 + M) maintained 4.4–28.2 % higher amino acid levels than high-density counterparts. Among habitats, T2 outperformed T1 and T3 in both seasons (Fig. 5c-f). Key amino acids (L-Asp, L-The in autumn; L-Asp, L-Glu, L-The in spring) occurred in high concentrations, while others remained at low levels.

The 100 dry leaf weight, young shoot water content, chlorophyll

Table 1

Effect of different tea densities and habitats on young shoot and mature leaves nutrients (N, C, CN ratio, K and P) contents and tea growth traits.

	Young shoot				
Treatments	**N (%)**	**C (%)**	**CN Ratio**	**K (mg g^{-1})**	**P (mg g^{-1})**
T1 + M	3.63± 0.28bc	50.1± 0.88a	13.9± 1.24b	13.8± 0.46bc	2.83± 0.33bc
T1 + H	3.30± 0.24c	50.3± 0.94a	15.3± 1.15a	13.6± 0.96c	2.68± 0.25c
T2 + M	4.14± 0.18a	50.9± 1.28a	12.3± 0.69c	15.2± 0.53a	3.37± 0.24a
T2 + H	4.11± 0.10a	50.6± 0.47a	12.3± 0.28c	15.1± 0.40a	3.26± 0.20ab
T3 + M	3.76± 0.22b	50.5± 0.60a	13.5± 0.70bc	14.7± 0.51ab	3.12± 0.12ab
T3 + H	3.71± 0.20b	50.1± 0.82a	13.5± 0.66bc	14.0± 0.65bc	3.00± 0.38abc
	Mature leaves				
T1 + M	2.39± 0.17 cd	50.3± 0.28a	21.2± 1.39ab	9.4± 1.42c	1.43± 0.05 cd
T1 + H	2.25± 0.18d	49.7± 1.45a	22.2± 1.85a	9.2± 0.27c	1.30± 0.04d
T2 + M	3.10± 0.16a	50.3± 0.50a	16.3± 0.68d	11.9± 0.83a	2.07± 0.14a
T2 + H	2.98± 0.07a	50.8± 1.26a	17.1± 0.73 cd	11.3± 1.08ab	1.76± 0.23b
T3 + M	2.92± 0.20ab	50.0± 0.35a	17.2± 1.13 cd	10.0± 0.81bc	1.62± 0.19bc
T3 + H	2.64± 0.38bc	50.1± 0.83a	19.3± 3.24bc	9.5± 0.59c	1.55± 0.13bc

	Tea growth traits							
Treatments	**100 DLW (g)**	**H_2O Content**	**Chl**	**Plant height(m)**	**Leaf area (cm^2)**	**Leaf width(cm)**	**Leaf length(cm)**	**LMA ($g\ m^{-2}$)**
T1 + M	46.7± 4.1a	57± 2.9c	37.1± 2.7 cd	3.2± 0.35a	52.71± 5.14a	3.80± 0.41a	13.45± 0.24a	89.63± 7.7a
T1 + H	43.8± 5.2ab	57± 1.7c	35.9± 2.2d	2.5± 0.34b	51.90± 4.90a	3.65± 0.13a	12.61± 0.24b	84.75± 10.8ab
T2 + M	38.6± 7.4b	62± 2.4ab	44.2± 5.6b	3.6± 0.26a	43.84± 7.09b	3.59± 0.14a	11.49± 0.22c	88.02± 10.0a
T2 + H	21.8± 3.3c	59± 1.3bc	43.6± 6.4bc	1.7± 0.16c	25.80± 4.78c	2.39± 0.08b	10.86± 0.09d	85.27± 1.8ab
T3 + M	16.9± 3.1 cd	62± 1.5ab	57.4± 5.0a	3.2± 0.80a	22.90± 2.10c	2.17± 0.04bc	10.39± 0.14e	74.07± 4.0bc
T3 + H	13.6± 1.2d	65± 0.9a	46.9± 1.4b	1.8± 0.22c	21.27± 1.46c	2.07± 0.04c	10.18± 0.07e	63.98± 7.7c

[a] Monoculture Tea (T1), Medium-coverage tropical evergreen broad-leaved forest (T2), High-coverage tropical evergreen broad-leaved forest (T3), Medium tea density (M), High tea density (H), Potassium (K), Carbon (C), Nitrogen (N), Phosphorus (P), Dry Leaves Weight (DLW), Chlorophyll (Chl), Leaf Mass Area ratio (LMA)

[b] Means ± Standard Deviation, and different lower-case letters denote statistically significant differences across various treatments at a significance level of $P \leq 0.05$ in the same line (LSD test).

content, plant height, leaf area, leaf length, leaf width, and leaf mass area ratio of tea were significantly improved by different habitats and tea densities (Table 1). T1 + M had higher 100 dry leaf weight, leaf width, leaf length, leaf area, and leaf mass area ratio, but lower young shoot water content and chlorophyll content compared with other habitats and planting densities plots. Medium planting density exhibited higher 100 dry leaves weights (6.3–43.5 %), young shoot water content (4.18 %), chlorophyll content (1.4–18.2 %), leaf width (4.0–33.4 %), leaf length (1.9–6.2 %), leaf area (1.5–41.1 %), and leaf mass area ratio (3.1–13.6 %) compared to high planting density. Among habitats, tea growth followed the order: T1 > T2 > T3. However, T2 and T3 exhibited significantly higher chlorophyll (Chl) and leaf water contents compared to T1. (Table 1).

3.4. PCA among microclimates, soil nutrients, tea nutrients, growth traits, and quality

PCA was carried-out to investigate the interconnections among microclimatic variables, soil macronutrients, tea growth traits, tea nutrients, and the amino acid and catechins contents of young shoots (Fig. 6). The first two principal components (PC1 and PC2) associated with soil nutrients, microclimatic variables, young shoots and mature leaves nutrients, and tea growth traits explained 66.3 % of the variation in the data. Fig. 6 A explained the position distribution of the treatments, with three groupings identified. Tea growth showed a significant correlation with microclimatic variables, but did not show a significant correlation with the nutrients of young shoots and mature leaves, except for mature leaves C:N ratio and N (Fig. 6a, Figure S3). The Chl was significantly correlated with soil N and AP (Fig. 6a, Figure S3). The PCAs of soil nutrients, microclimatic variables, young shoot targeted metabolites amino acids, and catechins of autumn tea and spring tea are shown in Fig. 6b and c respectively. Fig. 6B shows the position distribution of treatments related to PCA of autumn tea, while Fig. 6C shows the position distribution of treatments related to PCA of spring tea. Fig. 6B has 3 groupings of treatments, while Fig. 6C has 2 groupings of treatments. The two PCs (PC1 and PC2) of autumn tea and spring tea explained 61.6 % and 63.3 % of the total variation of the data, respectively. Young tea shoot amino acids and catechins showed significant correlations with both microclimatic factors (LI, AT, ST, RH) and soil macronutrients. Notably, soil N, AP, and AK exhibited strong positive correlations ($p < 0.05$) with all measured amino acids and catechins (Fig. 6b,c, S1, S2), highlighting their crucial role in tea quality formation.

3.5. Structural equation model of tea quality

SEM analysis revealed that habitats and planting densities directly and indirectly influenced young tea shoot quality (amino acids and catechins) through soil macronutrients, microclimate, and foliar nutrient dynamics (Fig. 7). Direct effects were observed on shoot metabolites, while indirect pathways operated through: (1) soil nutrients (N, P, K), and (2) mature/young leaf nutrient mediation. These factors also affected tea growth through dual pathways: directly, and indirectly via microclimate modification and soil nutrient availability. Notably, while habitats and planting densities improved microclimate conditions, these changes negatively impacted shoot amino acids and catechins (Fig. 7). Overall, different habitats and planting densities affected the growth of tea plants and the nutrient contents of mature leaves and young shoots by influencing the microclimate and soil macro nutrients (P, K, and N), ultimately altering the quality of tea (amino acids and catechins).

4. Discussion

4.1. Effects of different habitats on microclimate, soil nutrients, tea nutrients, and tea quality and growth

The light intensity, air and soil temperature were higher in T1 and moderate in T2, while T3 had lower light intensity (Fig. 3a, b). Tea trees grow well in moderate shade and their photosynthetic processes are efficient (De Costa et al., 2007). Factors including electron transport, carboxylation, and the absorption of light during photosynthesis suggest that the photosynthetic mechanism in tea trees operates with greater efficiency under conditions of moderate shade (Mohotti and Lawlor, 2002). It has been found that tea trees have an obvious photo-inhibitory

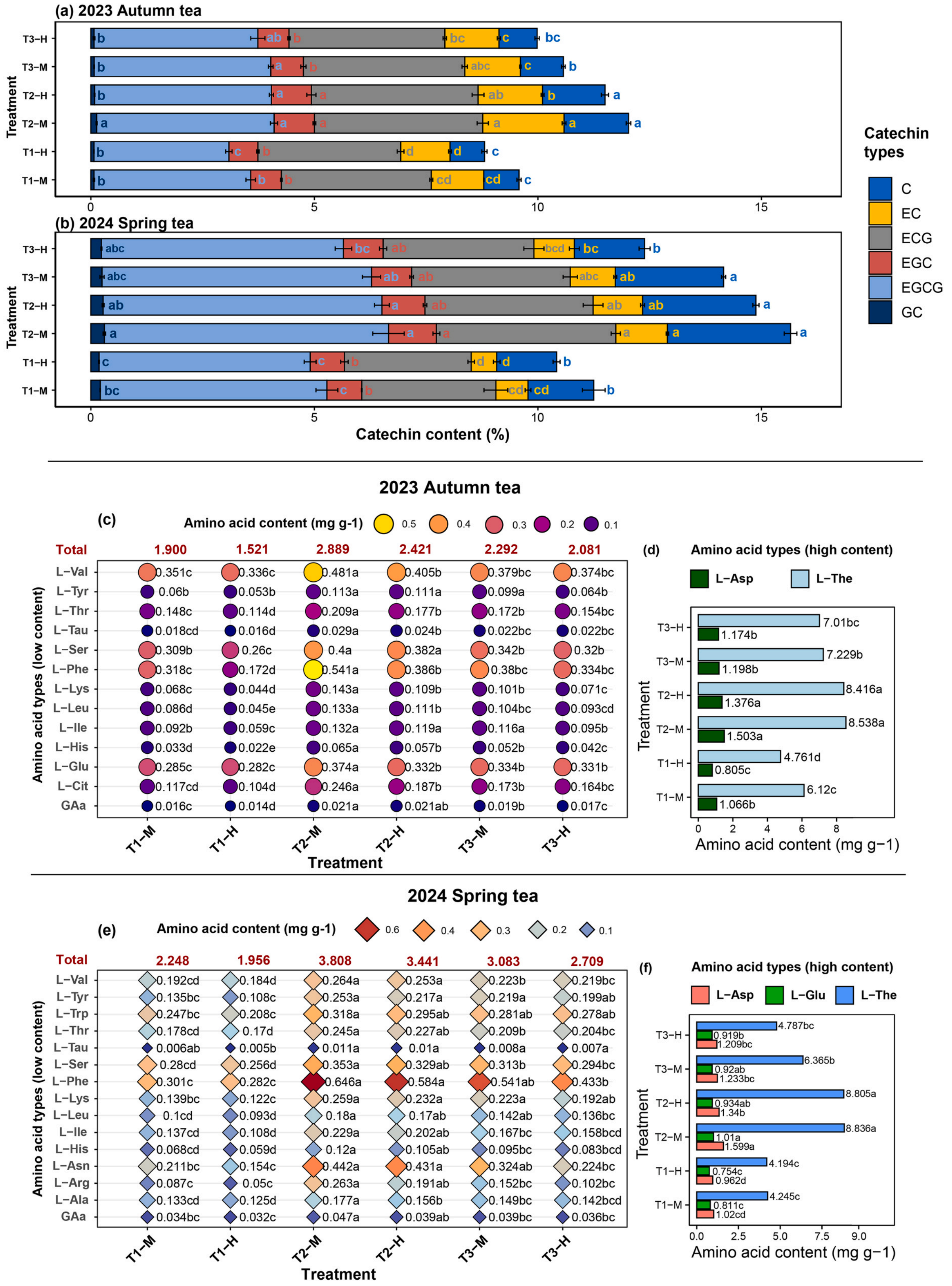

Fig. 5. Effect of different habitats and tea densities on catechins and amino acids contents (%) in young shoots of autumn tea-2023 and spring tea-2024 by HPLC. Monoculture Tea (T1), Medium-coverage tropical evergreen broad-leaved forest (T2), High-coverage tropical evergreen broad-leaved forest (T3), Medium tea density (M), High tea density (H), Catechin (C), Epicatechin_gallate (ECG), Epicatechin (EC), Epigallocatechin_gallate (EGCG), Epigallocatechin (EGC), Gallocatechin (GC), L-Theanine (L-The), L-Aspartic_acid (L-Asp), Gamma-Aminobutyric_acid (GAa), L-Phenylalanine (L-Phe), L-Glutamic_acid (L-Glu), L-Citrulline (L-Cit), L-Lysine (L-Lys), L-Tyrosine (L-Tyr), L-Leucine (L-Leu), Taurine (L-Tau), L-Serine (L-Ser), L-Threonine (L-Thr), L-Valine (L-Val), L-Isoleucine (L-Ile), L-Histidine (L-His), L-Alanine (L-Ala), L-Arginine (L-Arg), L-Tryptophan (L-Trp), L-Asparagine (L-Asn). Different lower-case letters denote statistically significant differences across various treatments at a significance level of $P \leq 0.05$, while the vertical bars represent the standard deviation of the mean ($n = 4$).

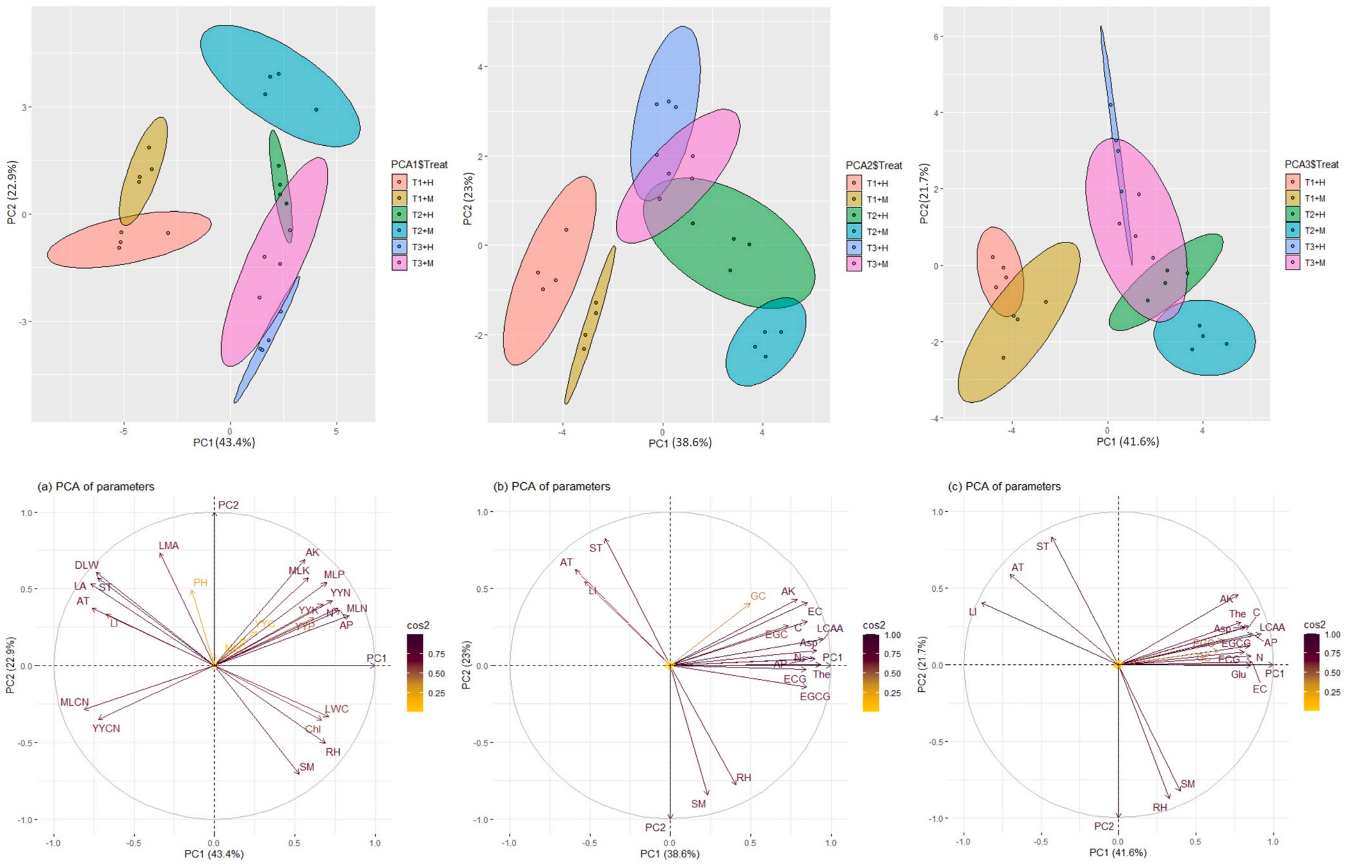

Fig. 6. (A, **a**) PCA of soil nutrients, micro-climatic variables, young shoots/mature leaves nutrients and tea growth traits. (B, **b**) PCA of soil nutrients, micro-climatic variables, and young shoot targeted metabolites amino acids and catechins contents in autumn tea 2023. (C, **c**) PCA of soil nutrients, micro-climatic variables, and young shoot targeted metabolites amino acids and catechins contents in spring tea 2024. Dry Leaves Weight (DLW), Chlorophyll (Chl), Leaf Water Content (LWC), Leaf Area (LA), Leaf Mass Area (LMA), Plant Height (PH), Young Shoot (YY), Mature Leaves (ML), Carbon (C), Phosphorus (P), Potassium (K), Nitrogen (N), Soil Temperature (ST), Air Temperature (AT), Light Intensity (LI), Soil Moisture (SM), Relative Humidity (RH), Available Potassium (AK), Available Phosphorus (AP), Total Nitrogen (N), Catechin (C), Epicatechin_gallate (ECG), Epicatechin (EC), Epigallocatechin_gallate (EGCG), Epigallocatechin (EGC), Gallocatechin (GC), Low Content Amino Acids (LCAA), Glutamic_acid (Glu), Theanine (The), Aspartic_acid (Asp). Fig. 6 A, 6a (PC1 +PC2 = 66.3 %); Figs. 6B, 6b (PC1 +PC2 = 61.6 %); Fig. 6 C, 6c (PC1 +PC2 = 63.3 %).

effect in strong sunlight (Mohotti and Lawlor, 2002), which slows down the growth of tea trees and reduces tea yield. In the afternoon of summer, shading reduced leaf temperature by 10–12°C. It is considered that 30–40 % shading is the best shade for high yielding tea (Hajiboland, 2017). According to the sustainable cultivation model, inter-planting is a better light management system that can provide optimal light for the growth of tea trees. Forest trees can shade tea trees and significantly reduce the amount of light intensity in the understory.

The high temperatures of monoculture tea gardens affect the growth and quality of tea. Tropical evergreen broadleaved forests maintain favorable soil and air temperatures for the growth and quality of tea (Fig. 3b).The tea tree originated from tropical rainforests and prefers a warm and humid environment (De Costa et al., 2007). The optimal temperature range for the growth and quality of the tea plant lies between 20 and 25 °C. Temperature significantly influences tea production, and prolonged exposure to temperature stress can result in reduced yields. Specifically, when tea trees are cultivated in conditions where the monthly average temperature exceeds 26.6 °C, there tends to be a decline in yield (Duncan et al., 2016). The average monthly temperature for tea is 28°C, with every degree increase, tea production will decrease by 3.8 % (Duncan et al., 2016). Consequently, it is crucial to alleviate the adverse effects of temperature stress on tea plants. Effective field management primarily focuses on minimizing the extent of temperature fluctuations experienced by tea trees, often achieved through the practice of inter-planting tea trees within forested areas. Inter-planting is a highly efficient agronomic practice that helps regulate the temperature of tea trees. The cultivation of tea trees within a forest ecosystem can substantially enhance the above-ground conditions conducive to their growth (Zhang et al., 2020; Wang et al., 2018). The canopy formed by tree branches and foliage provides shade, while the presence of herbaceous vegetation helps to lower soil temperatures. Research consistently indicates that forests play a crucial role in moderating temperature and environmental conditions, which are essential for the healthy development of tea trees.

The metabolic processes, growth, and productivity of the tea plant are significantly affected by water availability. In tea plantations, the sources of water primarily include atmospheric humidity and the moisture present in the soil. The medium and high-coverage tropical evergreen broadleaved forest tea had higher soil moisture and RH, while monoculture tea had lower soil moisture content and RH (Fig. 3c). The leaves and branches of woody trees in the forest shade the tea trees, reducing temperature and water evaporation. Tree leaves and straw mulch can lower soil temperatures and retain soil moisture during hot and dry periods. As a result, forests can enhance the water environment for tea plantations. Drought stress forced a 14 −20 % decrease in tea yields and a 6 −19 % increase in tea plant mortality (Hajiboland, 2017). While the annual precipitation in the tea cultivation region typically satisfies the water needs for tea tree development, which ranges from 2500 to 3000 mm annually, irregular distribution of monthly rainfall throughout the year can hinder the growth of the tea trees. In China,

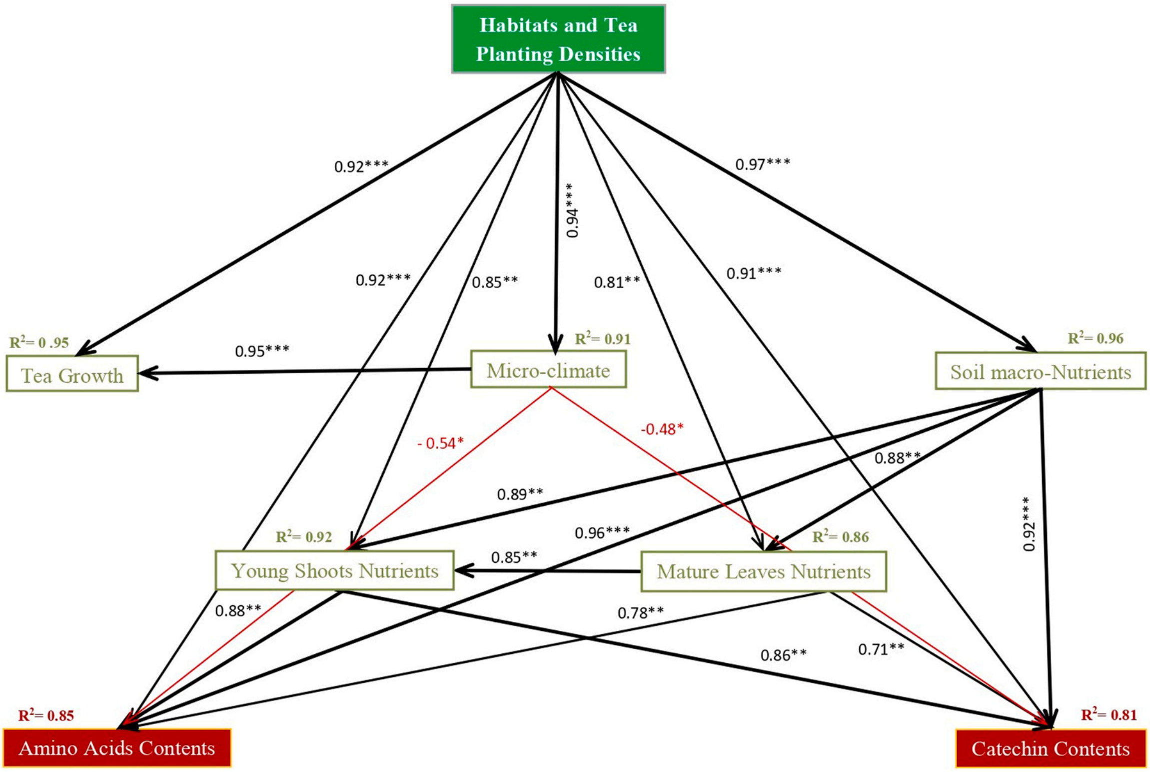

Fig. 7. A structural equation model (SEM) was constructed to analyze the multivariate influences on tea quality (amino acids and catechins) of tea young shoots (1 bud and 2 leaves) by different habitats and tea planting densities. The model illustrates hypothesized causal relationships, with arrows indicating directionality; black arrows denote positive correlations, whereas red arrows signify negative correlations. The thickness of the arrows reflects the strength of these relationships, and the standardized path coefficients are indicated by the numbers adjacent to the arrows. Statistical significance is denoted by asterisks (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). The explained variance for each response variable is represented by R2 values next to them in the model. The goodness-of-fit statistics for the SEM include CMIN/DF = 1.172, CFI = 0.986, GFI = 0.911, NFI = 0.924, and RMSEA = 0.045.

many tea-growing regions have drought periods of more than two months (Hajiboland, 2017). An elevated rate of transpiration in plants can adversely affect the processes of photosynthesis in leaves, hinder leaf development, and restrict the elongation of shoots (Vadez et al., 2014). Planting white clover, rubber, peanuts, and rat's-tail fescue in tea gardens can reduce soil moisture losses (Zhang et al., 2020; Wu et al., 2017; Lü et al., 2019; El Kateb et al., 2013). Chestnut tea and fruit trees (bayberry, loquat, citrus)-tea inter-planting reduced soil and air temperature and increased air humidity and soil moisture in tea plantations (Wen et al., 2020; Wu et al., 2021).

Soil nutrients play a crucial role in the development, growth, and overall quality of tea. Our findings show that forest teas are suitable for tea growers and play a positive role in improving and maintaining long-term sustainability and productivity. Forest tea improved soil fertility without the input of fertilizers (Ma et al., 2017). Our results confirm that the soil nutrient content (N, K, and P) of T2 was significantly higher than that of T1 and T3, indicating that growing tea plants with other plants in the forest could improve soil nutrient content (Fig. 4a-c). A significant increase in AP and AK concentrations were observed in forest tea plots. This may be due to the increased abundance of relevant microbial taxa active in soil nutrient cycling, including rhizobia, potassium, and phosphate-solubilizing bacteria. Another reason is that trees in agroforestry provides nutrients by several mechanisms (e.g litter decomposition, nitrogen fixation, root exudates, soil structure improvement) to meet the requirements of plants (Palm, 1995). Compared to monoculture tea plantations, forest tea has a higher content of organic matter, while the latter provides sources of nitrogen, potassium, and phosphorus. On the one hand, forest plants increase the top-soil and sub-soil organic matters and promote the release and recycling of nutrients in the soil (Ma et al., 2022). Many soil nutrients such as TN, AN, AK, AP, and soil SOM are improved in forests (Duan et al., 2019; Wen et al., 2020; Ma et al., 2017). On the other hand, different plants in the forest can promote the nutrient cycle by changing the microbial abundance and enzyme activity of soil (Farooq et al., 2021; Bai et al., 2022). According to the composite model of peanut-tea, michelia alba-tea, rat's-tail fescue-tea, and walnut-tea, soil TN, AK, and AP were significantly increased compared with monoculture (Zhang et al., 2021, 2020; Farooq et al., 2021).

The findings of our study indicate that the young shoots (2 leaves and 1 bud) along with the mature leaves of T2 and T3 exhibited higher levels of nutrients (N, P, and K) in comparison to T1. Young shoots had higher nutrient contents than mature leaves (Table 1). The C:N ratio of young shoots and mature leaves is lower in medium and high-coverage tropical evergreen broadleaved forest tea, while higher C:N ratios were recorded in monoculture tea garden young shoots and mature leaves. The higher nutrient contents in tea young shoots and mature leaves were due to higher availability of soil nutrients, moisture content, suitable soil physical properties, and microclimate in medium and high-coverage tropical evergreen broadleaved forest. Forests promote the release and recycling of nutrients in the soil by increasing the organic matter in the topsoil and bottom-soil (Ma et al., 2022). Compared with monoculture, AP, AK, and SOM increased significantly in the rat's-tail fescue-tea, peanut-tea, osmanthus-miheria-tea, and walnut-tea inter-planting patterns (Zhang et al., 2021, 2020; Farooq et al., 2021).

The quality of tea is determined by various components, including catechins, amino acids, and caffeine, all of which are metabolized and processed by the tea plant. The metabolic processes within the tea plant are influenced by various factors, such as the nutrient composition of the soil, the specific microclimate, and the presence of microorganisms. Additionally, the presence of woody trees in the surrounding forest enhances the nutrient profile, microclimatic conditions, and soil properties of the tea plantation, thereby facilitating the production of components that contribute to the quality of the tea. Consequently, trees in the forest can have a positive impact on tea quality. Our results show that tea quality (different amino acids and catechins) was significantly higher in T2, followed by T3, while the quality of tea was lower in T1 (Fig. 5). The quality of tea is significantly influenced by both the above-ground and below-ground environments of the tea plantation. The suitable soil environment, water, light, and temperature are essential for the production of high-quality tea. The metabolic activity of tea plants is inhibited when they are damaged by drought, strong light, low temperatures, high temperatures, and pests (Liao et al., 2019; Li et al.,2019; Wu et al., 2021; Deng et al., 2013; Li et al., 2020). Sufficient nutrients, determined by fertilizers, soil enzymes, and microorganisms, are fundamental for the growth and metabolism of the tea plant (Zhang et al., 2021; Farooq et al., 2021; Bai et al., 2022; Shen and Lin, 2021). The forest improves the soil water, temperature, humidity, and light intensity for tea plantations, increasing the fertility of the soil, the richness of soil bacteria, and the activity of soil enzyme. This facilitates the production and metabolic processes of components that contribute to the quality of tea, including amino acids, caffeine, catechins, and aromatic compounds (Duan et al., 2019; Wen et al., 2020; Wu et al., 2021, 2022; Zhang et al., 2021; Li et al., 2019; Bai et al., 2022). Amino acids and catechins were found to be higher in fruits, chestnut, and rat's-tail fescue inter-planted with tea compared to monoculture, as reported by Farooq et al. (2021), Duan et al. (2019), Zhang et al. (2020), Wen et al. (2020), Ma et al. (2017), and Duan et al. (2021). Research by Wu et al. (2022, 2021) indicates that the cultivation of chestnut-tea plantation has a positive impact on the biosynthesis of amino acids and catechins of tea young shoots. Consequently, the forest ecosystem enhances the environmental conditions of tea plantations, facilitating the synthesis and accumulation of components that contribute to tea quality, thereby elevating the overall quality of the tea. It is well established that the growth and development of tea plants are influenced by a variety of environmental factors. The presence of forest vegetation modifies the growing conditions for tea trees, affecting both the subterranean and aerial environments. These environmental modifications, in turn, impact the metabolic processes of the tea trees, which are intrinsically linked to their growth. Thus, the influence of forest ecosystems on the metabolism and growth of tea plants represents a multifaceted interaction governed by numerous environmental variables. The results showed that tea growth was significantly improved by different habitats and tea planting densities. Among the different habitats, tea growth traits were found to be highest in T1 + M, followed by T2 + M. The chlorophyll content was observed to be highest in T3 + M, followed by T2 + M (Table 1). In the forest tea, there is high competition between tea plants and other plants in the forest for nutrients, space, and light. Therefore, monoculture tea gardens have higher tea growth compared to forest tea. Our results are consistent with previous findings (Duan et al., 2019, 2021; Wen et al., 2020; Song et al., 2006; El Kateb et al., 2013; Wu et al., 2021, 2022). In monoculture tea gardens, the aerial and soil temperatures are high, while forests have a moderate temperature for tea growth. High temperatures negatively affect many photosynthetic processes in chloroplasts, including chlorophyll biosynthesis, photochemical reactions, electron transport, and CO_2 assimilation. Heat stress results in impaired plastid-based protein translation, and at high temperatures, nascent proteins may be damaged and existing proteins may be denatured (Ellis, 1990; Bita and Gerats, 2013). Photosynthesis is the basis for determining plant productivity, development, and growth, and planting density is a key factor in optimizing micro-environmental factors for plant growth (Fang et al., 2018).

4.2. *Effects of different tea planting densities on microclimate, soil nutrients, tea nutrients, tea quality, and growth*

In comparison to high planting density, medium planting density enhances the microclimate of the plants by providing moderate light, temperature, and relative humidity (Fig. 3). This enhancement contributes positively to the preservation of the ecological environment by mitigating excessive leaf transpiration and minimizing evaporation from the soil surface (Gong *et al.*, 2020b). Additionally, medium tea density results in slightly higher soil and air temperatures compared to high tea density, attributed to the higher number of tea tree branches (Fig. 3b). Our result is in accordance with the findings of Gong *et al.* (2020b). Tea plants require water for development and growths, and planting densities can alter the temporal and spatial pattern of water sequestration. High tea density had higher soil moisture content and RH compared with medium tea density. In autumn and summer seasons, the moisture content and RH were higher compared with the spring season (Fig. 3c). In the spring season, there is no rainfall, and the weather is dry. High planting density produces a relatively dense canopy, allowing plants to retain soil moisture and prevent moisture from evaporating (Okbagabir et al., 2016; Gong et al., 2020).

Planting density is an important factor for tea production and quality. Medium tea density had a higher amount of TN, AK, and AP contents compared to higher tea density. This is due to the higher amount of nutrient consumption in high tea density areas (Fig. 4a-c). Due to the decrease in organic-matter in the subsoil layers, soil nutrients gradually decrease in the soil depth range (0–100 cm). In environments characterized by medium density, there is an enhancement in enzyme activity, alongside an increase in the presence of animals and microorganisms within the soil. This leads to a swift decomposition of organic litter, which can greatly enhance soil fertility, particularly in the upper layers of the soil (Lin et al., 2001). Research shows that low-density plants have more nutrients than medium and high-density plants (Huang et al., 2015; Liu et al., 2008).

In this study, medium tea density significantly increased the nutrient contents (N, P, and K) of tea compared to high tea density, while C:N significantly decreased, due to the high N content of tea (Table 1). In plots with medium tea density, the high availability of nutrients and water is attributed to less competition among tea plants for nutrient uptake, resulting in higher nutrient contents in tea. Due to higher competition for nutrient uptake among tea plants in high-density plots, the tea leaves had lower nutrient contents. Planting density affected important soil parameters such as soil moisture, nutrients, enzyme activity, and microbial community composition (Zhao et al., 2012), which affects the nutrient uptake and nutrient contents of the plant. Soil with medium plant density has more macro and micro nutrient content. Nan et al. (2020) found that higher planting density leads to insufficient soil nutrients and water in *Pinus sylvestris* var. *mongolica* plantations. Medium and high planting densities had different light intensities, which affected the nutrient content of tea leaves. Medium tea density significantly improved the quality of the tea compared to high tea density (Fig. 5). High-planting density frequently results in intense inter-specific competition and shading within the canopy, which restricts the light interception by the lower stems and leaves. This limitation adversely affects photosynthetic processes and degrading the overall quality of tea plants (Romero et al., 2022). In contrast, an optimal planting density can enhance the accumulation of dry matter during the later growth stages by postponing leaf senescence and sustaining a higher capacity for leaf photosynthesis (Zhang et al., 2016). According to Fasoula and Tollenaar (2005), an increase in planting density leads to heightened competition for resources among the plants. Research indicates that higher planting densities can lead to increased plant height while decreasing the number of branches, allowing for enhanced light capture (Gezahegn, 2019). Additionally, soil moisture plays a crucial role as a limiting factor, and a moderate planting density is essential for the increasing of soil moisture levels (Wei and Liang, 2021). Furthermore, a medium planting density not only aids in the absorption of radiant energy and mineral nutrients within the plant canopy but also enhances water use efficiency and photosynthetic performance by expanding leaf area, ultimately contributing to improved tea quality (Jiang et al., 2018). Among tea planting density, medium tea density had higher tea growth traits as compared with high tea density (Table 1). Medium tea density had more space for growth, high light interception and more nutrients available to tea plants due to less intra plants competition. These findings may be attributed to the level of competition among plant species (Adler et al., 2018). In addition, planting density is one of the determining factors of radiation interception by plants, and the intercepted photosynthetically active radiation value reflects the level of light capture and absorption (Gong et al., 2021). Our results showed that the medium tea density plot had a higher leaf area compared to the high tea density plot. The leaf area of plants plays a crucial role in their capacity to intercept light, serving as a key indicator of both their growth condition and light utilization efficiency (Weraduwage et al., 2015). High planting density leads to a reduction in both the number of branches produced by each plant and the overall leaf count per unit area, ultimately resulting reduction in leaf area (Debnath et al., 2015).

4.3. Limitations and future directions

4.3.1. Tea production and economic aspects

The weight of 100 dry leaves and leaf area were found to be 35 % and 33 % higher, respectively, in the monoculture tea plantation (T1) compared to the forest tea plantation (T2) (Table 1). These growth parameters suggest that the monoculture tea plantation yields a greater quantity than the forest tea plantation. However, it is crucial to note that the quality of tea from the forest tea plantation is superior to that from the monoculture tea plantation. The market value of forest tea is significantly more stable and generally higher than that of monoculture tea (Hung, 2013). In the village of Mangjing, the fresh monoculture tea leaves are sold for approximately 10–12 RMB kg^{-1}, while the fresh forest tea leaves command prices ranging from 40 to 60 RMB kg^{-1}, representing a price increase of compared to monoculture tea (Hung, 2013). Additionally, forest tea plantations provide edible wild fruits and vegetables, as well as timber and fodder for local communities that depend on them (Liyanage et al., 2009). Moreover, these plantations support higher biodiversity and play a critical role in ecological conservation (Qi et al., 2005: Chowdhury et al., 2021).

4.3.2. Enzyme activities and microbial communities in tea plantations

The interplay between enzyme activities and microbial communities in tea plantations is crucial for enhancing soil health and fertility. Soil enzymes such as catalase, dehydrogenase, urease, and invertase are vital biocatalysts that facilitate the decomposition of organic matter and promote nutrient recycling, thereby improving soil nutrient levels (Delgado-Baquerizo et al., 2016; Farooq et al., 2021). These enzymes serve as indicators of soil health, with invertase playing a significant role in the carbon cycle and peroxidase activity being inversely associated with inorganic nitrogen levels (Ruan, 2014; Cantarella et al., 2018). The diversity and abundance of microbial communities, particularly fungi and bacteria, are essential for soil ecology, contributing to litter degradation and nutrient cycling while also mitigating carbon emissions (Wang et al., 2022). Research indicates that the alpha and beta diversity of these microbial communities is generally higher in forest tea plantations compared to monoculture systems (Zhang et al., 2023; Wang et al., 2022; Zou et al., 2022). Interplanting tea with forest plants has been shown to enhance both enzyme activities and microbial diversity, significantly influencing soil nutrient dynamics. For example, interplanting with peanuts or walnuts has led to increased activities of enzymes such as protease and acid phosphatase, resulting in higher nitrogen, phosphorus, and potassium levels in tea soils (Farooq et al., 2021; Bai et al., 2022). Specific microbial groups, including Proteobacteria and Firmicutes, thrive in these interplanted systems, further promoting soil nutrient cycling (Ma et al., 2022; Shen and Lin, 2021). Despite these findings, the complex relationships between soil nutrients and microbial diversity remain inadequately understood, highlighting the need for further research to elucidate the dynamics present in both forest and monoculture tea plantations.

4.3.3. Metabolic pathway changes and molecular mechanisms of tea quality improvement

Our research indicates that forest-grown tea exhibits superior quality in amino acid and catechin content compared to monoculture tea. This enhancement is likely attributed to the complex interactions within microbial communities and the diverse environmental conditions of forest ecosystems, which stimulate beneficial metabolic processes in tea plants (Wang et al., 2022; Li et al., 2025). In forest environments, tea plants face various biotic and abiotic stresses, such as shade, competition, and fluctuating nutrient availability (Ahmed et al., 2019). These stressors activate physiological responses that can enhance metabolic pathways responsible for producing secondary metabolites critical for tea's flavor, aroma, and health benefits (Ran et al., 2023). Key metabolic pathways involved in the synthesis of amino acids and catechins include the Shikimic acid pathway and the phenylpropanoid pathway. Enzymes such as phenylalanine ammonia-lyase (PAL) play a crucial role in these pathways and may be upregulated in forest-grown tea due to ecological interactions that promote secondary metabolite production (Bagal et al., 2012). Additionally, microbial diversity in forest soils enhances nutrient cycling and tea plant growth, with mycorrhizal fungi facilitating nutrient uptake (Wang et al., 2022; Smith and Read, 2008). This microbial interaction may trigger plant defense responses, increasing the expression of genes involved in the synthesis of phenolic compounds and amino acids (Patyal et al., 2025). Furthermore, abiotic factors such as light and soil composition significantly influence gene expression related to photosynthesis and nutrient availability, ultimately affecting tea quality (Liu et al., 2023). In conclusion, the superior quality of forest tea compared to monoculture tea is a result of increased gene expression in metabolic pathways linked to amino acid and catechin synthesis, along with the positive effects of diverse microbial communities. Future research should utilize metagenomic and transcriptomic approaches to further explore the specific genes and regulatory pathways involved, providing deeper insights into the molecular biochemical mechanisms that govern tea quality.

5. Conclusion

This research has thoroughly investigated the effects of various habitats and tea planting densities on microclimate, soil nutrients, tea nutrients, growth, and quality. The results suggest that the T2 + M model shows promising outcomes. It successfully modifies the microclimate to create an environment that favors tea growth and quality, with improved humidity and soil moisture and reduced light and temperature stress. T2 + M model enhanced soil nutrient availability across soil depth (0–100 cm), particularly in terms of nitrogen, phosphorus, and potassium, which are essential for tea quality improvement. The tea plants in the T2 + M model exhibit better growth characteristics and higher-quality leaves, as demonstrated by increased tea chlorophyll and nutrients contents. Compared to other combinations, T2 + M offers a more sustainable solution. It not only addresses the issues of soil degradation and biodiversity loss often associated with monoculture but also provides a practical approach for tea farmers to improve their yields and the quality of their tea. For policymakers, this study provides a strong basis for promoting the adoption of agroforestry practices in tea cultivation. Future research should focus on validating these findings in different geographical regions and exploring ways to optimize the implementation of the T2 + M model. Overall, this study represents a significant step forward in understanding how to balance ecological health and tea production efficiency.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109866.

Data availability

Data will be made available on request.

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