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Research Article Above and Belowground Biomass Allocation Pattern of Young Tea (*Camellia sinensis* (L.) O. Kuntze) Plants Under Rainfed Conditions

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Abstract

Background and Objective: Tea (*Camellia sinensis* (L.) O. Kuntze) is the economically important beverage intensively managed as a plantation crop. The study aims to quantify the biomass allocation patterns of young tea plants and how this is influenced by the growth environment, age, genotypes (BSS-1 and UPASI-9) and soil types (Oxisols and Ultisols). **Materials and Methods:** The fractions of tea plant mass represented by foliage, twigs, stem, woody and feeder (fine) roots were measured with uprooted tea plants by wet excavation method between 2010 and 2015. Age-response curves of allocation were constructed by statistical analysis from panoply of multisource experimental data and the difference between age, genotype and soil was tested by one-way (ANOVA) with a Tukey's *post hoc* test. **Results:** The results revealed that the biomass of the tea plant and the relationship between fine roots and shoots (R/S), fine roots to foliage biomass (FR/L) and aboveground to belowground biomass (AGB/BGB) ratio were significantly (p>0.01) altered as a function of age in response to soils and genotypes. The greatest percentage of total biomass was allocated within the AGB (54-58%) than BGB (46-42%) in tea plants showing that AGB sinks larger portion of carbon. Classification and regression tree (CART) and structural equation modelling (SEM) analyses showed the complex change in biomass and allocation was affected by the meteorological factors (temperature and rainfall), soil attributes (pH, EC and K) and microbial population (bacteria and fungi). **Conclusion:** This study concluded that the allocation of the biomass of tea plants is supported by the optimal partitioning theory, where environmental factors impose integrative effects on the plant to allocate biomass to the organ that acquires the most limiting resource to maximise their growth rate.

Key words: Biomass partitioning, classification and regression tree, feeder roots, leaf biomass, optimal partitioning, spearman rank correlation analysis, structural equation modelling, tea

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Competing Interest: The authors have declared that no competing interest exists.

Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

Tea (Camellia sinensis (L.) O. Kuntze) is a perennial evergreen tree intensively managed as a plantation system for continuous development of crop shoots. Vegetation biomass and production are of critical importance in plant ecophysiology^{1,2}, because both aboveground biomass (AGB) and belowground biomass (BGB) are the major contributors of soil organic matter^{3,4}. The response of AGB and BGB components and their allocation pattern is known be to driven by various environmental factors besides the genetic potential of the species. Changes in biomass fractions, carbon and nutrient accumulation in grass^{5,6}, forests^{7,8} and timber plantations⁹ have been extensively studied over the time. Simply, how biomass allocation of plantation foliage crop like tea plants varies with age and genotype in response to the environmental variables, such as climate, soil and microbial population and its interrelation has not been drawn yet. Recent surveys have mainly concentrated on carbon¹⁰ and nutrient stocks¹¹ within the biomass and soil of tea plantations. Nevertheless, a study reported the root characteristics of tea and silver oak (Grevillea robusta) in a mixed tea plantation to assess the complementary/ competitive nature of tea plantation¹². Aboveground and fine root (FR) biomass allocation are rarely reported in tea plants, primarily because of the lack of efficient and precise method^{6,13}, practical difficulties in recovering fine roots and the poor repeatability of data¹⁴. A complete inventory of biomass allocation and its distribution has seldom reported or not been undertaken for young tea plantation. Meanwhile, young plantation sequestrated relatively higher carbon than old plantation in the form of organic matter in woody biomass and resistant litter^{11,15}. Tea plantations also play a substantial role in the global carbon cycle. Recent changes in the environment produced profound effects on the plant growth by changing the vegetation biomass as well as the overall functioning of the ecosystem explicitly carbon cycle. In this context, the mechanism by which plant biomass is allocated on the rainfed crop such as tea remains unclear. Therefore, understanding the effects of age and the associated change in genotype (clone or seedling) by soil on biomass allocation in a chronosequence of tea plants specifically at young stages, a study is required. Based on the above background, the study was initiated with the following objectives: (1) To document the biomass of tea plants at different age, genotypes and soil types, (2) To examine the main environmental factors influencing the allocation pattern of biomass and (3) To explore the mechanism behind allocating AGB and BGB biomass in tea plants under rainfed conditions.

MATERIALS AND METHODS

Experimental site and sampling procedure: An experiment was carried out between 2010 and 2015 at United Planters' Association of Southern India (UPASI) Experimental Farm, UPASI Tea Research Institute, Valparai located on 11°59'0.69" N, 76° 57′ 2.32" E and 1050 m above MSL. The experimental site received mean annual rainfall ranging from 284.5-467.9 cm and annual mean temperature ranging from 20.5-21.8°C during the period of the study. The present study included two soil types, garden (Oxisols) and forest (Ultisols) soils and two genotypes, seedling (BSS-1, UPASI-10×TRI-2025) and clone (UPASI-9). The entire experimental setup was formed adjacent to the field to maintain near-natural conditions. Tea plants were grown in 1 m³ cubical root boxes with galvanised sides and bases using asbestos sheets. Cultural operations were carried out as per standard recommendations of UPASI and application of pesticides and fungicides were executed when absolutely needed. Sampling was done annually during the month of August when the rainy season was at its peak. At least two tea bushes per soil/genotypes were selected for uprooting. The tea bushes were uprooted by the wet excavation method. The roots were first completely immersed in a water-filled root box and then removed from the asbestos sheet and sprayed with water until almost free of soil. Each tea plant was segregated into foliage, twigs, stem, thick woody roots and feeder (fine) roots. Despite extracting both dead and living roots, the study focused only on the living ones.

Environmental variables

Soil characteristics: To determine the influence of soil nutrients on biomass allocation, soil collected from a depth of 0-15 cm in each time of excavation. Air-dried samples were passed through a two-millimetre sieve and roots were removed. The processed soil samples were analysed for pH¹⁶, electrical conductivity¹⁷, soil organic matter¹⁸, total nitrogen¹⁹, available phosphorus (P)²⁰, potassium (K)²¹, exchangeable calcium (Ca) and magnesium (Mg)²² as per standard methods.

Enumeration of soil microbes: To itemise the total microbial population in the rhizosphere region of the tea plants, the collected samples subjected to serial dilution and cultured according to standard microbiological techniques. Total bacteria (BAC)²³, fungi (FUN)²⁴, *Actinomycetes* (ACT)²⁵, phosphor-solubilizing bacteria (PSB)²⁶, *Azospirillum* (AZO)²⁷ and *Pseudomonas* sp. (PSE)²⁸ were enumerated with suitable growth media.

Meteorological data: Influence of climatic variables and its effects on biomass allocation were interrelated with the meteorological data collected between 2010 and 2015 obtained from UPASI meteorological station (approved by the Indian Meteorological Department, Chennai) located in the UPASI Tea Research Institute, Valparai.

Data analysis and statistics: Differences in AGB and BGB in response to age were tested by one-way analysis of variance (ANOVA) at p<0.05, followed by Tukey's *post hoc* test. The paired t-test was used to determine differences between genotypes and soil types. The significance of age for the functional balance theory was evaluated by regression analysis²⁹. A logarithmic transformation was applied to the variables to meet the assumptions of normal distribution according to Shapiro-Wilk test, as inherently complex causal connections exist among ecological variables in nature³⁰⁻³⁴. After normal distribution testing, the data were handled through Spearman's rank correlation analysis to find out the primary measure of association between the variables. Classification and Regression Tree (CART) method was employed to determine the crucial environmental variables and its interactions that significantly influence the biomass^{35,36}. Structural Equation Modelling (SEM) was conducted to explicitly define the direct, indirect and total effects of the critical environmental elements on biomass^{35,37,38}. All the statistical analyses were carried out by using the R-statistics³⁹ and structural equation models were analysed using SEM package⁴⁰.

RESULTS

Variation in biomass components among genotypes, soil and age: Among the genotypes clone (UPASI-9) registered significantly higher (p<0.01) root and shoot length than seedlings (Table 1). Whereas, seedling recorded were significantly (p<0.01) higher number of roots and shoots than UPASI-9. Forest soil promoted a higher number of roots and shoots development with higher root length (p<0.01) when compared to its counterpart garden soil. Seedling produced higher leaf biomass, while clone UPASI-9 produced the highest fine root biomass. Higher AGB was observed in BSS-1 seedling and the lowest biomass recorded in UPASI-9. According to paired t-test, the length and number of shoots and roots, biomass of foliage, fine roots, AGB and BGB had differed significantly (p<0.001, df: 23) among the soil types and genotypes. The relationship between fine roots and shoots, fine roots and foliage biomass and AGB and BGB ratio were altered as a function of age, soil types and genotypes.

The maximum biomass of tea plants was allocated within AGB as shown in Fig. 1a, which contained 54.1 (UPASI-9) to 58.2% (BSS-1) of total tree biomass (Table 1). Total BGB comprised about 41.8 and 45.9% of the total biomass recorded, respectively in seedlings and clone. Stem biomass estimated between 38.0 and 34.1% of the total biomass, respectively in clone and seedling. Foliage biomass comprised about 20% of total biomass and ranged between 11.2 and 32.4% in seedling and 11.4 and 33.9% for a clone. Coarse root (>5 mm, including primary, secondary and tertiary roots) biomass was 3.3 and 15.5% larger than the fine root (<5 mm) biomass measured between 19.3 and 15.2% of the total biomass, respectively in UPASI-9 and BSS-1.

The relationship between AGB and BGB was strongly correlated with a value of $R^2 = 0.9363$. Significantly strong relationship existed among the soils (data not shown), garden soil ($R^2 = 0.9008$, y = 0.7198x+97.882, p<0.001) and forest soil ($R^2 = 0.9657$, y = 0.7707x-36.437, p<0.001) and genotypes, BSS-1 seedlings ($R^2 = 0.9515$, y = 0.7248x-77.854, p<0.001) and UPASI-9 clone ($R^2 = 0.9283$, y = 0.7216x+93.72, p<0.001). From Fig. 1c and d, the relationship between fine roots and fine shoots ($R^2 = 0.7609$) and foliage biomass was highly significant ($R^2 = 0.8590$).

Casual effects of environmental variables on biomass

Correlation of biomass with environmental factors: The effects of environmental factors (i.e., Meteorological factors, soil nutrients and microbial biomass) on the AGB, BGB, B/A, R/S and FR/L were examined by Spearman rank correlation analysis (Table 2). The results indicated that AGB, BGB and B/A were positively related to the meteorological factors (i.e., Relative humidity at 1430 h, rainfall, rain days and sunny days), soil nutrients (i.e., pH, EC, OM, N, P, K, Ca, Mg) and soil microbial population (total fungi, Actinomycetes and phosphor-solubilizing bacteria). Meanwhile, R/S was positively related to temperature minimum (Tmin), temperature maximum (Tmax), temperature mean (Tmean) and sunshine hour (Sh). However, it had opposite correlations with RH1430, rain days (Rd), pH, K and ACT. The relationship between the ratio of fine root and foliage biomass with RH1430 was significantly positive, while it had a significantly negative relationship with Sh and sunny days.

Identification of critical environmental factors: The optimal trees were obtained using the CART model that enabled us to find crucial environmental variables and its interactions with biomass components. Six critical environmental factors (i.e., Tmax, Rd, PSE, AZO, Mg and K) are significantly associated with AGB as shown in Fig. 2a. The tree consisted temperature

Shoot length (cm) Root length (cm) Genotypes Soil types Genotypes Soil types Age (Year) S С GS FS S С GS FS 58.5ª,b 58.5ª 48.3ª 68.6^b 71.8^{a,b} 61.0ª 54.0ª 78.7ª 2 118.0^{b,c} 99.5^{a,b} 114.5ª 103.0^c 105.0^b 114.5° 97.0ª 122.5ª 79.5^{a,b} 3 48.0^a 78.0ª 49.5^a 43.0ª 94.0^b 98.5ª 38.5ª 4 149.5^b 135.5ª 137.5^d 80.5^{a,b} 168.5^d 136.5ª 123.5 112.5ª 5 128.5 148.0^b 140.5^d 119.5^b 105.0^b 107.5ª 136.0^a 117.0^a 6 156.5 140.0^b 156.5 140.0^d 111.5^b 95.0^b 99.5ª 107.0^a 105.5 106.5 88.5 106.3 100.0 Mean 112.5 111.5 94.8 t (df = 23)-32.098** -31.715** -33.232** -31.881** Total number of shoots (nos) Total number of roots (nos) Genotypes Soil types Soil types Genotypes Age (Year) S С GS FS S С GS FS 162.5ª 60.0^{a,b} 39.0ª 27.5ª 21.5ª 45.0^a 89.0ª 133.5ª 47.5ª 57.5^{a,b} 70.5ª 2 65.0ª 39.5ª 73.0ª 86.0ª 73.0^a 3 61.0ª 61.5ª 57.5ª 65.0ª 80.5ª 84.5^{a,b} 58.5ª 106.5ª 4 59.5ª 67.0ª 31.5ª 95.0ª 90.0ª 86.5^{a,b} 80.0ª 96.5ª 5 75.5ª 59.5ª 59.0ª 76.0^a 79.5ª 45.0^a 41.5ª 83.0^a 6 116.0^a 103.0^a 119.5^b 99.5ª 81.0^a 120.0^b 84.5ª 116.5ª 66.4 63.9 54.8 75.6 96.6 75.6 70.7 101.5 Mean -27.499** -28.415** -21.496** t (n = 23) -21.668** Weight of leaf (g fwt) Weight of fine roots (g fwt) Genotypes Soil types Genotypes Soil types С FS S С GS FS Age (Year) S GS 20.8ª 2.3ª 9.5ª 13.7ª 7.4ª 6.2ª 4.3ª 9.3ª 1 2 286.0ª 40.3^{a,b} 217.2ª 109.1ª 154.5ª 63.9ª 125.8ª 92.6ª 3 369.4ª 204.1^b 81.3ª 492.2^a 119.0^a 187.1ª 92.6ª 213.6ª 4 747.5ª 458.5° 801.8^a 404.3ª 387.5ª 360.0^a 437.5^a 310.0^a 5 1092.8ª 597.5° 540.1ª 1150.2^a 420.7^a 373.3ª 527.2ª 266.9ª 49.0^{a,b} 299.9ª 269.0^a 79.9ª 129.2ª 334.8ª 238.2ª 225.8ª 6 225.3 319.8 374.9 203.1 220.9 194.2 229.7 Mean 469.4 -37.809** -27.498** -27.318** -37.809** t (df = 23) Aboveground biomass (g fwt) Belowground biomass (g fwt) Genotypes Soil types Genotypes Soil types FS С FS Age (Year) S С GS S GS 70.4ª 43.0ª 9.6ª 7.2ª 18.4ª 1 35.1ª 78.4ª 15.9ª 614.2ª 733.4ª 149.0^{a,b} 290.9ª 180.0^a 605.9ª 307.5ª 2 756.1ª 3 682.7ª 445.1^b 310.0^a 660.2ª 519.6ª 953.0ª 817.8ª 226.8ª 4 1868.5ª 1076.0° 1592.5ª 1352.0^a 2115.0ª 422.5ª 1760.0^a 777.5ª 3568.3ª 5 1045.7ª 876.9 740.2ª 1182.3ª 3069 4ª 1061.4ª 562.4ª 908.9ª 1646.2d 1444.9ª 1110.2ª 849.7ª 1383.9ª 1411.1ª 822.5ª 6 888.7 706.0 789.5 805.3 1239.5 597.2 762.2 1074.5 Mean

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Table 1: Biomass components of tea plants in a chronosequence as a function of age, soil and genotypes

Genotypes: S: BSS-1 seedling, C: UPASI-9 Clone, Soil types: GS: Garden soil, FS: Forest soil. Biomass in terms of fresh weight (fwt in g) per tea plant. Differences among age were tested by one-way (ANOVA) with a Tukey's post hoc test of significance. Different letters denote significant difference at p<0.05. **Correlation is highly significant at p = 0.01 level (2-tailed)

-28.037**

-21.639**

maximum as a root node containing all samples (n = 24). Figure 2b revealed that four critical environmental factors consisting of pH, FUN, EC and Rf are having a significant influence on BGB; the tree consisted pH as the root node

-20.491**

t (df = 23)

containing all samples. In the case of B/A ratio, EC, pH, Mg, K, PSE and Sh are the significantly associated environmental variables and EC is the root node of the CART tree (Fig. 2c). For the R/S ratio, the optimal tree showed that six critical

-28.037**



Fig. 1(a-d): Biomass partitioning of AGB and BGB in response to (a) Age and (b) Relationship, (c) Fine shoot roots and (d) Fine root and foliage biomass of pooled data

environmental variables viz., Rf, Tmean, BAC, ACT, PSE and K which were significantly associated (Fig. 2d), the tree consisted Rf as the root node containing all samples. The ratio of fine roots to foliage biomass was significantly influenced by six critical environmental factors, Sh, Tmin, ACT, FUN, Rf and PSE (Fig. 2e) among them Sh as the root node.

Impact of key environmental factors on biomass: The SEM is a powerful statistical approach, which finds causal relationships of complex datasets of mutually inter-related variables. The inter-correlated critical environmental variables identified using the CART model were further used SEM to explicitly test the direct, indirect and total effects. From the Fig. 3a, it is clear that, Tmax and K positive direct effects on AGB (p<0.01, Table 3). The direct effects of EC and FUN on BGB were highly significant at p<0.01 (Fig. 3b). The Sh, pH, K and PSE have significant direct effects on the B/A ratio (Fig. 3c). Among the meteorological variables, Rf had both positive and opposite effects on R/S (Fig. 3d) and FR/L (Fig. 3e), respectively. Whereas, no significant effect of T mean and Sh

on R/S and FR/L was found. Among the soil nutrients, K had a significantly positive standardised total effect on AGB and B/A, with path coefficients of 1.503 and 0.554, whereas, K had a strong negative effect on R/S. The standardised total effect of Tmax on AGB was 0.097, consisting of direct effects and indirect effects through soil variables. The standardised total effect of Rf on R/S was 0.413, comprising direct effect and indirect effects through soil variables.

DISCUSSION

Biomass portioning in young tea plants: Woody crop species continue to accumulate wood in stem and root as they age⁴¹. The present study confirmed that the total biomass of the tea plants linearly increased from 0.17-8.53 kg by age at the irrespective of soil types and genotypes. The increasing trend in biomass and its significant variation between the genotypes as a response of age were in reliable with earlier studies. For example, a study from Kenya reported that the total biomass of tea plants increased with age from 9.0-11.5 kg in clonal tea

Environmental factors	AGB	BGB	B/A	R/S	FR/L
Tmax	-0.486*	-0.416	-0.518**	0.314	-0.145
Tmin	-0.536**	-0.423*	-0.393	0.333	-0.124
Tmean	-0.697**	-0.658**	-0.723**	0.569**	-0.372
RH 830	-0.060	-0.049	-0.076	0.109	0.131
RH 1430	0.190	0.317	0.250	-0.511*	0.426*
Rf	0.004	0.116	0.145	-0.257	0.109
Rd	0.206	0.313	0.283	-0.454*	0.243
Sh	0.004	-0.236	-0.201	0.504*	-0.483*
Sd	0.328	0.039	0.067	0.194	-0.419*
pН	0.714**	0.637**	0.677**	-0.463*	0.288
EC	0.562**	0.488*	0.514*	-0.207	0.212
OM	0.491*	0.421*	0.444*	-0.041	0.136
Ν	0.494*	0.393	0.432*	0.000	0.083
Р	0.492*	0.411*	0.430*	-0.063	0.136
К	0.250	0.245	0.297	-0.442*	0.116
Ca	0.616**	0.514*	0.536**	-0.109	0.149
Mg	0.688**	0.551**	0.655**	-0.360	0.076
BAC	-0.027	0.001	-0.074	-0.241	0.109
FUN	0.205	0.182	0.266	-0.351	0.009
ACT	0.447*	0.432*	0.512*	-0.481*	0.153
PSB	0.091	0.119	0.138	-0.394	0.109
AZO	0.012	0.052	-0.047	-0.226	0.155
PSE	-0.398	-0.293	-0.292	-0.218	-0.030

Table 2: Correlation between tea plant components and environmental variables using Spearman's rank correlation analysis

Plant components; AGB: Aboveground biomass, BGB: Belowground biomass, B/A: Below to aboveground biomass, R/S: Root to shoot ration and FR/L: Fine root to leaf ration, Meteorological variables: Tmax (°C): Temperature maximum, Tmin (°C): Temperature minimum, Tmean (°C): Temperature mean, RH 830%: Relative humidity 830 h, RH 1430%: Relative humidity 1430 h, Rf (mm): Rainfall, Rd, >0.2 mm: Rain days, Sh (h): Sunshine, Sd: Sunny days, Soil variables: pH, EC (dSm⁻¹): Electric conductivity, OM (%): Organic matter, N (%): Nitrogen, P (ppm): Phosphorus, K (ppm): Potassium, Ca (ppm): Calcium, Mg (ppm): Magnesium and Soil microbes; BAC (×10⁶): Total bacteria, FUN (×10⁴): Total fungi, ACT (×10⁵): *Actinomycetes*, PSB (×10⁵): Phosphor solubilizing bacteria, AZO (×10⁶): *Azospirillum* sp., PSE (×10⁵): *Pseudomonas* sp. **Correlation is highly significant at p = 0.01 level (2-tailed), *Correlation is significant at p = 0.05 level (2-tailed)

plants and from 13.5-19.9 kg in seedlings for the 14 and 29 years and 43 and 76 years old tea gardens, respectively¹¹. This finding also supports our study that the existence of marked variation between the genotypes in terms of biomass, where seedlings recorded significantly (p<0.001) higher biomass than clones. AGB had a highly significant correlation with BGB (pooled data, $R^2 = 0.9363$, p<0.001, Fig. 1b). The result revealed that the establishment of BGB was strongly depended on the AGB⁴¹. It should be noted that both the AGB and BGB of the 6th year old plant was less than a fifth year, because of the pruning carried out at the height of 18 inches at the end of the 5th year. The result confirms that the induced changes in the absolute annual growth rates would cause a progressive decrease in the BGB with respect to AGB⁴². Moreover, plants are grown in high density and shaded conditions tend to have higher aboveground biomass compared with those grown in open conditions⁴³.

Tea plant allocated 37.9 and 34.1% of the total biomass within stems, 41.8-45.9% total biomass in root and 20.0-20.3% of total biomass in foliage. The result was corroborated with the earlier reports^{10,11,44-46}. They recorded the greatest percentage of total biomass was allocated within the AGB including stems and foliage. This highest proportion of total biomass in AGB (58-54%) indicates that AGB sinks greater

portion of carbon than BGB in the tea plants⁴⁷. It could be attributed to the enriched soil nutrient characteristics of the tea eco-system by means of manuring and litter decomposition. According to the optimal partitioning theory, root biomass decrease and shoot biomass increases as the soil nutrients increase besides the effects of seasonal and interannual environmental factors⁴⁸⁻⁵².

Fine roots are physiologically the most dynamic parts of the root system and understanding the pattern and storage in a given conditions is essential⁵³. Among the BGB, maximum 15.2-19.3% of biomass was allocated within the fine roots. The study found significant variation in root biomass, length and numbers between genotypes and soil types (Table1) while the difference between the plant's ages was statistically not significant. This result shows that age inconsequentially affected the allocation of root biomass of tea plants. This is in agreement with the reports of Kamau et al.¹¹, the increase in biomass of tea plants with age was not found per unit land area of 14-76 years old plants and effect of plant genotype on biomass was greater than the effect of age. Meanwhile, increase in root length and thus the weight of BGB indicate that the root system positively responded to resource enrichment⁵⁴. Observed lower root biomass in the third year of our result (Table 1) is associated with fewer root numbers

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Table 3: Standardized direct, indirect and total effects of critical environmental factors on aboveground biomass (AGB), belowground biomass (BGB), above to belowground biomass ratio (B/A), root to shoot ratio (R/S) and fine root to leaf ratio (FR/L)

Endogenous variables	Exogenous variables	Direct effects	Indirect effects	Total effects
ĀGB	Rd	-0.213	0.744	0.532
	Tmax	1.044	-0.947	0.097*
	PSE	-0.295	0.000	-0.295
	AZO	-0.023	0.000	-0.023
	Mg	-0.073	0.000	-0.073
	К	1.503	0.000	1.503**
BGB	Rf	-0.211	0.294	0.083
	FUN	-0.597	0.000	-0.597**
	EC	0.601	0.000	0.601**
	рН	0.224	0.000	0.224
B/A	Sh	0.073	-0.329	-0.256
	рН	-0.559	0.000	-0.559**
	EC	0.268	0.000	0.268*
	Mg	-0.458	0.000	-0.458**
	К	0.554	0.000	0.554**
	PSE	0.009	0.000	0.009
R/S	Tmean	1.640	-1.450	0.189
	Rf	0.474	-0.061	0.413*
	К	-0.929	0.000	-0.929
	PSE	-0.180	0.000	-0.180
	ACT	-0.248	0.000	-0.248
	BAC	-0.339	0.000	-0.339
FR/L	Sh	0.190	0.080	0.271
	Rf	-0.481	0.411	-0.069*
	Tmin	0.154	-0.231	-0.085
	ACT	2.011	0.000	2.011**
	FUN	-1.827	0.000	-1.827**
	PSE	0.380	0.000	0.380*

Plant components: AGB: Aboveground biomass, BGB: Belowground biomass, B/A: Below to aboveground biomass, R/S: Root to shoot ration and FR/L: Fine root to leaf ration, Meteorological variables: Tmax (°C): Temperature maximum, Tmin (°C) Temperature minimum, Tmean (°C): Temperature mean, Rf (mm): Rainfall, Rd (>0.2 mm): Rain days, Sh (h): Sunshine; Soil variables: pH, EC (dSm⁻¹): Electric conductivity, K (ppm): Potassium, Mg (ppm): Magnesium, Soil microbes; BAC × 10⁶: Total bacteria, FUN (×10⁴): Total fungi, ACT (×10⁵): *Actinomycetes*, AZO (×10⁶): *Azospirillum* sp., PSE (×10⁵) *Pseudomonas* sp. **Correlation is highly significant at p = 0.01 level (2-tailed), *Correlation is significant at p = 0.05 level (2-tailed)

which limit the uptake of water and nutrients and thus caused lower total biomass⁵⁵. The documented variation in fine root biomass may also be due to the influence of climatic factors both within the growing season and from year-to-year changes⁴⁷.

Many studies have documented a progressive decrease in R/S with the age of many temperate⁵⁶ and tropical species⁵⁷. The present study showed a trend of progressive decrease in R/S with the age of the tea plant and its response of dissimilarity statistically significant among genotypes and soil types studied. This finding indicated that young tea plants need higher amounts of nutrients and hence a relatively large root system is needed to support the rapid growth of their crowns. It leads to a turning point at canopy closure and thus the slowdown of net growth when they age⁵⁸.

Foliage biomass was the best indicator of fine root mass in this study by its strong correlation (Fig. 1d), suggesting that the highest fine root biomass is linearly associated with the highest foliage mass^{59,60}. However, many studies have revealed that this relationship is highly influenced by genotype^{11,61}, meteorological factors⁶² and soil properties⁶³. The higher ~20.0% of total biomass in the foliage of the tea plant is a more relevant determinant of foliage adaptation to light-limiting conditions. This possibility resonates with the optimal partitioning theory, where plants allocate maximise biomass acquisition towards most limiting resources^{64,65}.

Determining environmental factors and its interactions with biomass of tea plants: The influence of climate, soil and microbial biomass on plant biomass allocation is a complex phenomenon⁶⁶⁻⁶⁸. Studies have demonstrated that how environmental factors affected biomass allocation; however, the role of interactions and magnitude between the environmental factors has rarely been analysed^{67,69}. The integrated analysis conducted in the present study may provide a broad understanding of the variations of biomass and their response to environmental factors.



Fig. 2(a-e): CART analyses of the relationships between AGB (a), BGB (b), B/A (c), R/S (d) and FR/L (e) and environmental factors All designations are the same as those in the footnotes below Table 2

The results of the study can be explained in terms of optimal biomass allocation in response to environment (e.g., temperature, light, nutrients, water and microbial biomass). As evident from Spearman correlation analysis, we found that most of the environmental factors showed a significant correlation at p<0.05 levels with biomass



Fig. 3(a-e): Establishment of a structural equation model for (a) AGB, (b) BGB, (c) B/A ratio, (d) R/S ration and (e) FR/L ratio Each arrow represents a linear relationship and the arcs show the correlation between the variables. Values on arrows are standardized path coefficients and the coefficients that are statistically significant at **p<0.01 and *p<0.05 are shown by dashed arrows. All designations are the same as those in the footnotes below Table 2

components (Table 2). This may be a result of the degree of multicollinearity regarding the effect of environmental factors on biomass^{35,62}. To remove the multicollinearity in data, we used the CART and SEM models as approaches to identify most critical factors and quantify its effect associated with biomass partitioning³⁵. This quantitative procedure demonstrated that temperature (Tmax, Tmean and Tmin) found to be the strong direct positive impact on the AGB, R/S and FR/L. There is a negative direct influence of Rf on BGB and FR/L and positive direct effect on R/S. The positive total effect of K on AGB and B/A was significant and it was negatively affecting the R/S, besides EC and pH were positively affecting the BGB. In fact, the complex change of biomass was caused by both meteorological factors and soil properties⁶².

Plant biomass and soil nutrients were found to be a limiting factor of microbial biomass production through biomass production, seasonal variability of litter production and guality, root-shoot carbon allocation and root exudates⁷⁰. Plants affect the soil microbial community by the process of microbial mineralisation of organic matter and enhance nutrient release by mineral weathering. Both processes increase the availability of nutrients, enhancing plant growth⁷¹ and consequently accelerate the matter flow between the aboveground and belowground components of the plant. Bacteria and fungi form most of the soil microbial population and it incoherently effects the plant biomass, including positive⁷² and negative effects⁷³. Negative standardised direct effect of AGB and R/S on bacteria and BGB on FUN revealed that both groups prefer different qualities of resources they might be differently affected by plant biomass⁷⁴. The BGB and FR/L ratio was showing negative effects on fungal biomass due to the detrimental effect of increased nitrogen concentration of microbial biomass was directly associated with decreased root biomass^{75,76}. The positive standardised direct effect of pH and EC on BGB and K on AGB displays the negative indirect effects on soil microbial biomass through meteorological factors (Fig. 3a, b). It is unconcealed that the size of microbial biomass was found to be strongly correlated with the content of base cations, base saturation, cation exchange capacity and organic matter quality⁷⁷. Many studies have related the amount and turnover of biomass production with respect to soil fertility of the study⁷⁸. Soil nutrient (K) and microbial biomass (PSE, ACT and BAC) have negative direct effects on the R/S ratio⁶⁰.

CONCLUSION AND FUTURE RECOMMENDATION

Findings of the present study confirm that the tea plant optimally allocated their biomass and allocated higher biomass as aboveground was influenced by multiple environmental factors. In addition to the influence of growth environment, cultural practices might change the biomass allocation. However, the study did not analyse the effects of cultural operations in the current study, because it is a complex process with many unexplained variables. This finding helped to understand the relationship between plant biomass, key meteorological factors, soil nutrients and microbial biomass and are fundamentally important for policymaking and planters to enhance the tea plantation as a carbon sink.

SIGNIFICANCE STATEMENT

The study revealed that the tea plants optimally partitioning the biomass, i.e., the higher the biomass allocation in the organ acquires the most limiting resource to maximize their growth rate. This study will help the researchers to understand the relationships between plant biomass allocation, key meteorological factors, soil nutrients and microbial biomass that are fundamentally important for planters and policymakers to estimate the carbon sink capacity of the tea plantation.

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