



Differences in the rhizosphere effects among trees, shrubs and herbs in three subtropical plantations and their seasonal variations

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ABSTRACT

Unique soil properties in rhizosphere can affect plant growth and biogeochemical cycles of ecosystems. While rhizosphere has been widely investigated, little is known about differences in the rhizosphere effect (RE) between co-existing overstory trees and understory shrubs and herbs in forest ecosystems. In this study, we investigated REs on soil chemical properties of overstory trees and understory shrubs and herbs in forest plantations of southern China. Bulk soil and rhizospheres were sampled in April, July and December 2017. Soil pH, nitrate and ammonium nitrogen, dissolved organic carbon, available phosphorus, total carbon, total nitrogen, and total phosphorus were tested. The REs were defined as the ratios of the chemical properties of the rhizospheres to those of the bulk soil. Our results showed that pH was lower and nutrient contents were higher in the plant rhizospheres than the bulk soil. REs were generally larger in trees than understory plants. The REs were larger in July than April and December. Our findings indicated that the RE varied among plant life forms, species and sampling times, emphasizing the functional role of the RE of understory vegetation in subtropical forests.

1. Introduction

Soil properties play a key role in plant growth and productivity in forests [1]. Plants can in turn regulate soil properties by releasing root exudates to fuel soil microbes and by absorbing nutrients and water from the soil [2]. The rhizosphere is the interface between living plant roots and bulk soil where plant-soil feedbacks are intense [3]. The changes in soil physicochemical properties, microbial activities and biogeochemical cycles due to the presence of living roots is termed the rhizosphere effect (RE) [4]. The change of soil organic matter decomposition rate due to the presence of living roots and aboveground vegetation is called rhizosphere priming effect [5]. The RE can not only regulate the nutritional status and community dynamics of plants but also influence ecosystem functioning in terrestrial ecosystems [2].

The RE has been widely studied in recent decades [6], but previous

studies in forest ecosystems have mostly focused on tree species [7]. Understory shrubs and herbs are important components in forest ecosystems and coexist and compete with overstory trees for soil nutrients and water [8]. Shrubs and herbs can strongly influence the ecological processes of forest ecosystems, such as alleviating soil acidification [9], increasing soil microbial activity [10], and enhancing litter decomposition [11]. Our understanding of the RE of understory shrubs and herbs, however, remains poor. The RE is strongly influenced by plant species due to the interaction of plant roots and soils, especially by different plant life forms. First, physiological traits such as photosynthetic rate and nutrient resorption [12] for shrubs and herbs differ from those for trees. Second, different kinds of root exudates and soil microorganisms associated with rhizospheres [13] have been detected among tree, shrub and herb species. Third, shrubs and herbs have less above- and below-ground biomasses [14], and shorter life spans for their ephemeral roots

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[15], which are vital factors influencing the RE. All these differences suggest differential REs among trees, shrubs and herbs grown in the same soil conditions, which deserve further investigation.

More importantly, most previous studies of the RE were conducted with a single sampling without considering seasonal variation [4,16]. Environmental conditions and biological activities, however, normally vary among seasons, possibly giving rise to seasonal variations of the RE. For example, the rates of photosynthesis and growth of vegetation are seasonally distinct and consequently influence rhizospheric secretions and nutrient uptake [5]. Seasonal fluctuations in soil temperature and moisture can affect microbial activities [17]. Bacterial biomass in the rhizosphere was found to be increased during the summer and autumn in a *Pinus* forest, inducing a larger RE, because bacteria are the first organisms to trap and metabolize most of the easily available organic material after its input into the soil [18]. In a stand of Douglas fir (*Pseudotsuga menziesii*), the RE was more pronounced in June than March [19]. Seasonal variation in the RE is a factor complicating the study of soil-plant systems and can influence the biogeochemistry of forest ecosystems [19]. Our current understanding of the seasonal patterns of the RE nonetheless remains elusive, which will constrain our ability to understand the dynamics of soil functioning driven by the RE.

Chinese fir (*Cunninghamia lanceolata*), Masson pine (*Pinus massoniana*) and slash pine (*Pinus elliottii*) are the main plantation species in subtropical China [20], where net primary productivity is usually highest in July and August [21]. These three types of plantations have abundant understory vegetation [22]. The production and mortality of roots in this area clearly varies seasonally [23]. We compared REs among trees, shrubs and herbs and investigated their seasonal variations in subtropical plantations of Chinese fir, Masson pine and slash pine. The results would contribute to our understanding of rhizosphere effects of different plant life forms in forest ecosystems.

2. Materials and methods

2.1. Study site

Our study was conducted at the Qianyanzhou Ecological Research Station (QYZ, 26°44'46"N, 115°04'05"E) in Taihe County, Jiangxi Province, China. The QYZ Station is maintained by the Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences. This area has a subtropical monsoon climate. The mean annual temperature is 18.0 °C, and the coldest and warmest months are January (with temperatures ranging from -0.8 to 18.9 °C) and July (with temperatures ranging from 25.1 to 30.9 °C), respectively. The mean annual precipitation is 1509 mm, with >50% of the total precipitation falling from April to June. The area has 1306 h of sunshine per year, and the solar radiation is 4349 MJ m⁻². The soil is weathered from red sandstone and mudstone and is classified as Dystrudepts by the USDA system [24]. The soil contains 17% sand, 68% silt and 15% clay.

The native vegetation at the QYZ Station was an evergreen broad-leaved forest, which was completely destroyed before the 1980s. Coniferous plantations were subsequently planted around 1985. Among the species of coniferous trees planted, Chinese fir and Masson pine are native species, and slash pine was introduced from the southeastern United States of America. The age of the three coniferous tree species averaged to 32-years old by 2017. The understory shrubs in the three pure coniferous plantations primarily consist of *Loropetalum chinense*, *Adinandra millettii* and *Eurya muricata*. The dominant herbs are *Woodwardia japonica*, *Dryopteris atrata* and *Dicranopteris dichotoma*.

2.2. Vegetation survey and soil sampling

Five blocks were established on several spatially separated hilly slopes to minimize the impact of spatial variation (Fig. S1). The topography is gently undulating with an average slope of 1–20°. The elevation is approximately 95–120 m above sea level [25]. In each block, there

were plantations of Chinese fir, Masson pine and slash pine. A 20 m × 20 m plot was separately established for each of the three plantations. The distance between blocks was >100 m, and the distance between plots was >50 m. The exposure of each plot was shown in Table S1. Phytosociological data were collected in April 2017 by laying one 20 m × 20 m quadrat for trees, three 5 m × 5 m quadrats for shrubs and three 1 m × 1 m quadrats for herbs in each plot. The coverage of all species was measured by projected method, i.e., the ratio of the shady area of a specific species, which was estimated by the observer, to the total area of a quadrat [26]. The number, height, and diameter at breast height were measured and recorded for all tree species. The number and basal area were measured for all shrub species. The important values of herbs were represented by relative coverage (the coverage of each herb species as a percentage of the coverage of all species). The importance values of the shrub species were calculated as:

$$\text{relative density (RD)} = Di / \sum Di \times 100 \quad (1)$$

$$\text{relative dominance (RM)} = Mi / \sum Mi \times 100 \quad (2)$$

$$\text{relative frequency (RF)} = Fi / \sum Fi \times 100 \quad (3)$$

$$\text{importance value} = (RD + RM + RF) / 3 \quad (4)$$

where Di is the number of individuals of species i /quadrat area, Mi is the basal area of species i /quadrat area and Fi is the proportion of quadrats with species i to the number of all quadrats. The characteristics of the overstory trees and the understory shrubs and herbs in the three plantations are presented in Table 1.

Bulk soils and rhizospheres were sampled from the 0–20 cm layer in April, July and December 2017. The litter layer was removed before collecting the cores. Nine cores were randomly selected in each plot to acquire bulk soil using a corer 3 cm in diameter. These nine samples were then combined and mixed thoroughly. The rhizospheres of the overstory trees (*C. lanceolata*, *P. massoniana* and *P. elliottii*), the understory shrubs (*L. chinense*, *A. millettii* and *E. muricata*) and the herbs (*W. japonica*, *D. atrata* and *D. dichotoma*) were sampled in each plot. Three to five individuals of each species were randomly selected in each plot. The roots plus the soil adhering to them were carefully excavated around the trunks of the selected trees and shrubs to a depth of 20 cm from the four directions of each plant. The herbs and some shrub species with small root biomasses were carefully excavated to acquire all roots and adhering soils. The soil that still adhered to the root system after gentle manual shaking was considered as the rhizosphere [27], which was sampled using sterile brushes in the field. The rhizospheres were combined and mixed for the same species in each plot.

The individual samples of bulk soils and rhizospheres were collected in plastic bags and placed in a cooler in the field, then transported to the laboratory for further analysis. The samples were divided into two parts. One part was stored at 4 °C for determining the contents of soil nitrate nitrogen (NO₃⁻-N), ammonium nitrogen (NH₄⁺-N) and dissolved organic carbon (DOC) contents. The other part was air-dried for measuring pH and the contents of total carbon (TC), total nitrogen (TN), total phosphorus (TP) and available phosphorus (AP).

2.3. Soil chemical analysis

Soil pH was measured at a soil:water ratio of 1:2.5 using a calibrated pH meter (Mettler Toledo, Greifensee, Switzerland). Soil NO₃⁻-N and NH₄⁺-N were extracted from 20 g of fresh soil with 1 mol L⁻¹ KCl (1:5 soil:extract ratio) and analyzed using a continuous-flow analyzer (Skalar, Breda, The Netherlands). Soil DOC content was determined using a total organic-carbon analyzer (TOC-V CPH/CPN, Shimadzu Co., Kyoto, Japan). Soil AP was extracted with 0.5 mol L⁻¹ NaHCO₃ and measured colorimetrically. Soil TC and TN contents were measured with an elemental analyzer (Elementar, Vario Max, Hanau, Germany). The soils were digested with H₂SO₄-HClO₄ for determining the TP content by

Table 1Stand characteristics (mean \pm standard error, $n = 5$). ‘—’ indicates the absence of understory species in a plantation.

Plantation	Diameter at breast height (cm)	Tree height (m)	Stand density (trees ha ⁻¹)	Canopy coverage	Importance value of shrub species (%)			Importance value of herb species (%)		
					<i>L. chinense</i>	<i>A. millettii</i>	<i>E. muricata</i>	<i>W. japonica</i>	<i>D. atrata</i>	<i>D. dichotoma</i>
<i>C. lanceolata</i>	20.5 \pm 2.1	17.2 \pm 3.0	2440 \pm 357	0.77 \pm 0.04	22.2	37.9	29.7	3.09	1.89	—
<i>P. massoniana</i>	19.6 \pm 1.4	20.2 \pm 0.6	1960 \pm 211	0.79 \pm 0.05	33.7	14.7	8.00	3.85	3.41	2.86
<i>P. elliotii</i>	24.6 \pm 1.2	22.0 \pm 0.8	2060 \pm 309	0.75 \pm 0.06	36.0	25.3	21.3	4.15	2.07	2.67

ascorbic acid-molybdate blue colorimetry.

2.4. Statistical analysis

The RE was defined as the ratio of the chemical properties of the rhizospheres to the chemical properties of the bulk soil (R/B) in the same plot [28,29]. The data for the RE for each species at the three sampling times were analyzed by a principal component analysis. Eight indicators we measured were dimensionally reduced and expressed by two principal components (PC1 and PC2). In order to evaluate the RE comprehensively, the regression method was adopted to get the score function of the two principal components and the score vectors were output by SPSS [30,31]. First, the original RE data was standardized by “descriptive statistics” in SPSS and a standardized matrix *Z* was obtained. The principal component loadings (a_1 and a_2) of PC1 and PC2 were calculated by formula (5) and (6).

$$a_1 = 1/\lambda_1^{1/2} \cdot b_1 \quad (5)$$

$$a_2 = 1/\lambda_2^{1/2} \cdot b_2 \quad (6)$$

where b_1 and b_2 are the two vectors in component matrix, λ_1 and λ_2 are the eigenvalues of PC1 and PC2.

The score vectors (y_1 and y_2) of PC1 and PC2 were then calculated by formula (7) and (8).

$$y_1 = Z \cdot a_1 \quad (7)$$

$$y_2 = Z \cdot a_2 \quad (8)$$

Comprehensive scores (y) of the RE were then obtained by the weighted summation of the score vectors of the two principal components. The weights were set based on the variance of the contribution rate of each principal component.

$$y = v_1/(v_1+v_2) \cdot y_1 + v_2/(v_1+v_2) \cdot y_2 \quad (9)$$

where v_1+v_2 are the variance of the contribution rate of PC1 and PC2.

All statistical analyses were performed with SPSS 19.0 (SPSS Inc., Chicago, USA). A repeated-measures analysis of variance (RM-ANOVA) was used to detect the effects of plantation (Chinese fir, Masson pine and slash pine), plant life forms (trees, shrubs and herbs) and sampling time (April, July and December) on the REs and comprehensive scores. Significant differences were identified at $P < 0.05$.

Table 2

F values of repeated-measures ANOVAs of the factors affecting the rhizosphere effect (ratios of chemical properties of the rhizosphere to the corresponding chemical properties of the bulk soil, R/B) and the comprehensive scores. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Source of variation	R/B (pH)	R/B (NO ₃ ⁻ -N)	R/B (NH ₄ ⁺ -N)	R/B (DOC)	R/B (AP)	R/B (TC)	R/B (TN)	R/B (TP)	Comprehensive score
Plantation (PL)	5.75**	0.18	7.26**	5.22**	4.69*	7.73**	10.63***	1.44	8.23**
Plant life form (LF)	14.01***	1.34	2.37	13.78***	5.35**	9.35***	9.18***	6.35**	9.65***
Sampling time (T)	5.15**	5.69**	8.30**	0.65	0.53	0.61	0.16	3.33*	8.52***
T \times PL	2.90*	4.08**	2.02	5.43***	6.17***	5.74***	5.69***	0.98	4.78**
T \times LF	1.50	2.51*	1.09	3.20*	1.04	1.62	0.52	1.21	0.77
PL \times LF	1.37	0.49	0.39	1.29	0.27	0.48	0.92	1.04	0.44

NO₃⁻-N, nitrate nitrogen; NH₄⁺-N, ammonium nitrogen; DOC, dissolved organic carbon; AP, available phosphorus; TC, total carbon; TN, total nitrogen; TP, total phosphorus.

3. Results

The bulk soil pH ranged from 4.38 to 4.72 (Table S2). The rhizospheres were acidified for all species. For example, the pH of the rhizospheres from slash pine was only 3.76 in July. Soil nutrient contents were higher in the rhizospheres than the bulk soils. The TC contents for trees were 5.24-, 6.35- and 6.74-fold higher in the rhizospheres than the bulk soils in April, July and December, respectively.

Plants with different life forms had significantly different REs (Table 2, Fig. 1). Trees had the largest RE in decreasing soil pH and increasing DOC, TC, TN and TP contents (Fig. 2). Soil pH was 9–11, 3–5 and 5–7% lower in the rhizospheres than the bulk soils for the trees, shrubs and herbs, respectively. The RE on NO₃⁻-N content was significantly larger for trees than shrubs and herbs in December but not April or July. The RE on NH₄⁺-N content did not differ significantly among the plant life forms in any of the three sampling times. The RE on AP content was significantly larger for trees and herbs than shrubs in July. The comprehensive scores indicated that the RE was significantly larger for trees than the understory shrubs and herbs but did not differ significantly between the shrubs and herbs. The RE also varied greatly among species within a specific plant life form. The shrub *L. chinense* and the herb *D. dichotoma* had stronger REs than the other shrub and herb species (Tables S2 and S3) and were closer and more similar to the tree species (Fig. 1). PC1 appeared to be mainly driven by TN, TC and DOC, and NO₃⁻-N was the main driver of PC2.

The REs on pH, the contents of NO₃⁻-N, NH₄⁺-N and TP and the comprehensive scores were significantly affected by sampling time (Table 2). Comparison of comprehensive scores showed that the REs in July was higher than those in April and December (Fig. 1). For example, the comprehensive score of trees in July is 3.40 and 1.96 times that of April and December respectively.

4. Discussion

4.1. Variable rhizosphere effect among plant life forms and species

Soil pH was lower and nutrient contents were higher in the rhizospheres than the bulk soils (Table S2), consistent with previous studies [32]. Carbonic and organic (e.g. malate, citrate and oxalate) acids produced by rhizospheric microflora and roots from respiration and exudation can decrease soil pH [33]. Roots can also substantially affect rhizospheric pH by releasing H⁺ to compensate for an unbalanced cation-anion uptake at the soil-root interface [34]. Approximately 5–10% of plant photosynthates are transferred to the rhizosphere by

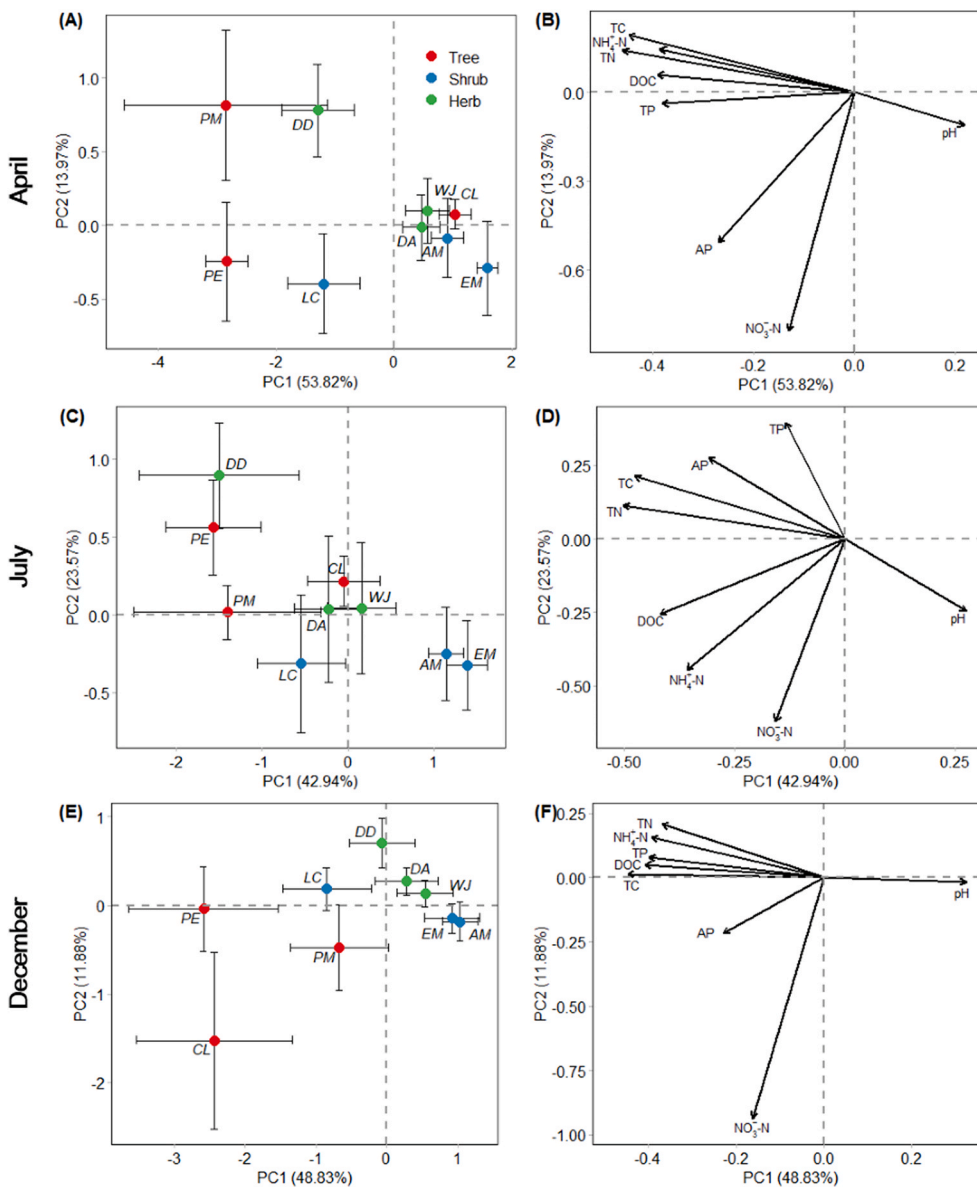


Fig. 1. Variation of the rhizosphere effect among species as analyzed by principal component analysis (PCA). NO_3^- -N, nitrate nitrogen; NH_4^+ -N, ammonium nitrogen; DOC, dissolved organic carbon; AP, available phosphorus; TC, total carbon; TN, total nitrogen; TP, total phosphorus. CL, *Cunninghamia lanceolata*; PM, *Pinus massoniana*; PE, *Pinus elliotii*; LC, *Loropetalum chinense*; AM, *Adinandra millettii*; EM, *Eurya muricata*; WJ, *Woodwardia japonica*; DA, *Dryopteris atrata*, DD, *Dicranopteris dichotoma*.

root exudation, which stimulates microbial activity and demand for nutrients [35]. The microbial production of exoenzymes consequently increases, accelerating the decomposition of soil organic matter to release nutrients [36]. Rhizospheres are areas where nutrients are taken up [37], but high nutrient contents are maintained due to the fast turnover of nutrient-rich microorganisms [16].

Our results showed that trees had larger REs than understory shrubs and herbs (Fig. 2), in agreement with the findings of previous studies [6, 38]. Trees had the largest RE in decreasing soil pH and increasing soil nutrient contents. A meta-analysis by Huo et al. [6] found that the rhizosphere priming effect was positively and linearly correlated with plant shoot biomass across all plant types, which indicated that trees with higher biomass could promote the decomposition of soil organic matter more strongly than understory shrubs and herbs, and release more nutrients into the rhizospheres. Besides, trees generally have a higher photosynthetic capacity [39] and deposit more C to the rhizosphere [38] than does understory vegetation. The microbes of tree rhizospheres with higher microbial biomass C:N:P ratios would thus mineralize more excess N and P than the rhizospheric microbes of understory vegetation [38]. The RE unexpectedly did not differ significantly between shrubs and herbs. Shrubs have higher biomasses than

herbs, but herbs have shorter foliar life spans, higher photosynthetic capacities and faster growth rates [40], all of which may have caused the comparable RE between shrubs and herbs.

The RE of different species in a specific plant life form also varied greatly (Tables S2 and S3). The RE was larger for the shrub species *L. chinense* than *A. millettii* and *E. muricata*, perhaps because *L. chinense* is colonized by ectomycorrhizal (ECM) fungi, whereas *A. millettii* and *E. muricata* are colonized by arbuscular mycorrhizal (AM) fungi [38]. The RE has been found to be larger for ECM than AM-associated species in previous studies as ECM trees would exude more C from roots than AM trees [7]. The RE was larger for *D. dichotoma* than the other two herb species, perhaps because *D. dichotoma*, an early-stage colonizer in the primary succession of acidic and oligotrophic soils [41], can strongly affect above- and belowground ecological processes, such as litter decomposition [42] and soil nutrient acquisition [41]. The different REs among species suggests that any shifts in the composition of a plant community may alter soil properties and influence rhizospheric microbial and soil enzymatic activities, which could further induce compositional shifts in the plant community [43]. Potential community dynamics under global change could thus ultimately alter ecosystem function [44].

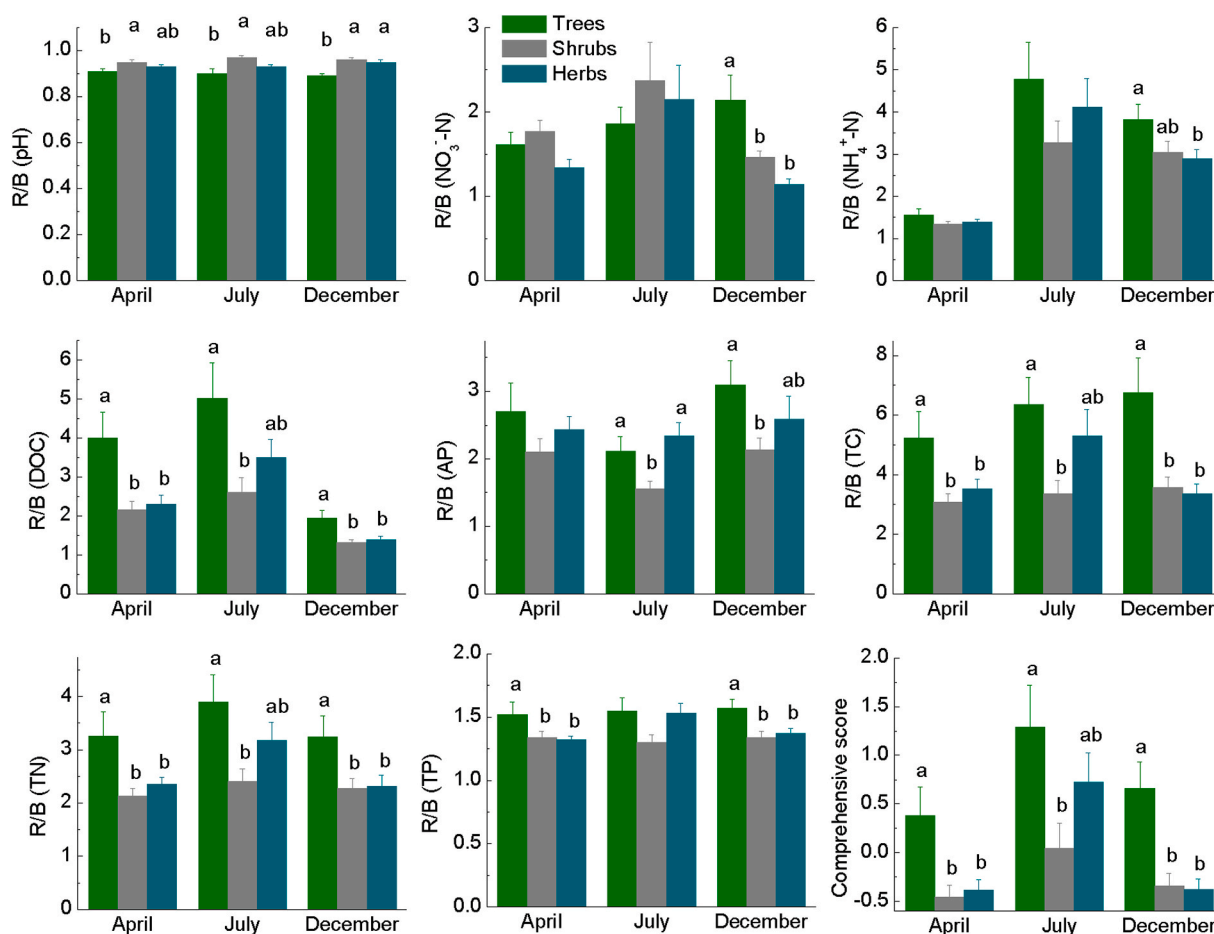


Fig. 2. Rhizosphere effects (ratios of the chemical properties of the rhizosphere to the corresponding chemical properties of the bulk soil, R/B) and the comprehensive scores for trees, shrubs and herbs (mean \pm standard error). NO_3^- -N, nitrate nitrogen; NH_4^+ -N, ammonium nitrogen; DOC, dissolved organic carbon; AP, available phosphorus; TC, total carbon; TN, total nitrogen; TP, total phosphorus. Different letters indicate significant differences ($P < 0.05$) among plant life forms.

4.2. Seasonal variations in the rhizosphere effect

Knowledge of the temporal changes in REs will allow us to better understand the ecological functions of a plantation. How the REs of trees, shrubs and herbs change with season, however, remains poorly understood. Our study demonstrated seasonal variations in the REs in three subtropical plantations. The RE should be larger in summer than the other seasons, because temperatures and biological activities are higher. July is the warmest month at our study site, with temperatures ranging from 25.1 to 30.9 °C and the RE was larger than those in April and December (Fig. 2). The efficiency of photosynthesis is higher in the warmer growing season, which provides more resources for root exudates [5]. Plants have high nutrient requirements in the summer because of their fast growth, so root exudation increases to enhance mineralization rates and provide more nutrients to the plants [37].

In conclusion, the RE differed significantly between the overstory trees and the understory shrubs and herbs in the three subtropical plantations. Trees had larger RE than shrubs and herbs. Moreover, we found that the RE peaked in the growing season. These results emphasize the need to study the rhizosphere of the understory vegetation and their roles in regulating soil functions and processes. The large variations among the species of a specific plant life form were mainly attributed to the differences in the mycorrhizal types and species-specific adaptability, indicating that identifying the plant life forms may be insufficient for predicting the RE. We only examined the dominant species of trees, shrubs and herbs in this subtropical area, so further studies of broad geographic areas and more species are required to fully understand the seasonal variations of the RE among species.

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. Supplementary data

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