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Recognizing the role of plant species composition in the modification of soil nutrients and water in rubber agroforestry systems

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HIGHLIGHTS

trations of soil C and N.

macronutrients

and water.

tive.

· Increases in the plant species commu-

Effects of interspecific interaction on soil

 Plant-induced cation competition also results in contradictory effects on soil

· Variations in soil water modify the dis-

· Soil depth weakens the effects of plant

species composition on soil nutrients

tribution of soil macronutrients.

water transform form positive to nega-

nity composition improve the concen-

GRAPHICAL ABSTRACT

Recognizing the role of Rubber and orange (two plant species) Rubber, orange and te (three plant species) Changes relative to plant species composition in the modification of Increase soil nutrients and water in Decrease rubber agroforestry systems Changed little Rubber monoculture Tropical rain forest one plant species (multiple plant species) Jungle rubber (multiple plant species) Rubber and tea (two plant species) Mea Soil nutrients Soil wate

ABSTRACT

Reliable guidance for crop selection and related management to achieve sustainable soil resource use in rubber agroforestry systems is limited. One important reason for this limited guidance is that our understanding of the effects of different plant functional groups on soil resources is still insufficient. Here, to examine the effects of the species composition of trees, shrubs and herbs on soil nutrients and soil water with increases in the complexity of the plant community structure, we measured the soil nutrient concentrations (i.e., C, N, P, K, Ca and Mg), soil water content and soil water residence time (with stable hydrogen and oxygen isotope tracers) at six soil depths in a monoculture rubber plantation, four multi-species rubber agroforestry systems, and a tropical rainforest. As the plant species composition increased, the soil C and N increased. The soil water content also increased with increases in soil C and N. However, the effects of plant species composition on the soil water content gradually changed from positive to negative, especially under the effects of herb species, which could accelerate soil water drainage and hence shorten the soil water residence time. Therefore, the faster water infiltration and potentially higher flow of soil water in complex plant communities increased the risk and magnitude of mineral nutrient leaching. In addition, as the plant composition increased, plant competition decreased the concentration of soil nutrients, especially soil P, K and Ca. In general, plant interspecific interactions definitively decreased soil mineral nutrients as the plant composition increased, and the effects of tree, shrub and herb species on soil nutrients and soil water differed and sometimes appeared contradictory. However, the effects of plant species composition on soil gradually weakened with increases in soil depth.

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1. Introduction

Under regional economic development, the annual increase in agricultural land area in tropical regions was >6 million hectares from 2000 to 2010, while the annual loss of natural forest area reached approximately 7 million hectares (FAO, 2016). Such land-use changes were especially significant in Southeast Asia (including Xishuangbanna prefecture in Southwestern China), such as the widespread monoculture rubber plantation (*Hevea brasiliensis*) in this region, which has replaced more than one million hectares of natural ecosystems in the past decades (Li and Fox, 2012).

Such large-scale changes in aboveground vegetation not only threaten the regional biodiversity and climate stability but also exhibit negative effects on soil resources, such as losses of soil water and soil nutrients, which have been frequently reported (Xu, 2011; Qiu, 2009; Vrignon-Brenas et al., 2019). It is worth mentioning that soils play a critical role in delivering a variety of ecosystem services (Scholes and Scholes, 2013) associated with the health and sustainable development of regional economies and societies (Tammi et al., 2017); thus, soil degradation in rubber cultivated area threatens regional green development. Since natural rubber is still an indispensable strategic material and scarce resource for economic construction (Cornish, 2017), reconciling the conflict between economic development and ecoenvironmental sustainability in rubber cultivated areas remains a pressing challenge.

Agroforestry systems (AFSs) have the potential to enhance the nutrient and water use efficiencies of rubber trees, reduce nutrient leaching, improve the soil water holding capacity, and increase the income of rubber holders, and they may represent a realistic solution for resolving the above conflict (Ziegler et al., 2009; Fox et al., 2014; Jiang et al., 2017; Zhu et al., 2019). Nowadays, China has markedly enhanced its consciousness and initiative towards implementing green development and building ecological civilizations (Gu et al., 2020). Therefore, promotions of rubber AFSs in Xishuangbanna Prefecture of Yunnan Province in Southwestern China meet a good opportunity under the current policies. However, promoting AFSs represents a challenge because limited effective guidance and integrated standards are available for the crop selection and related managements of rubber AFSs, which actually represents a common challenge for most of AFSs in the world because of our poor understanding of the mechanisms underlying plant belowground competition (Luedeling et al., 2016). Moreover, more studies of plant-soil interactions are required for crosscheck of associated predictions and practice (Van Noordwijk et al., 2004; FAO and IAEA, 2008). Therefore, a wide knowledge gap in rubber AFSs remains and must be addressed before such systems are promoted.

Plants can change soil resources because plants absorb water and nutrients from soil by their roots and return carbon and various nutrients to soil through their residues, such as litterfall, shoot residues, dead roots and root exudates (Mengel et al., 2001; Chapin et al., 2011). Under these processes, the physical properties of soil, such as the soil texture and structure, also changed imperceptibly (Gould et al., 2016; Fischer et al., 2019). However, different plant species have developed different strategies to take up soil resources and have different effects on the substances of the soils beneath them, thus contributing to the generation of subtle spatial and temporal variations in soil resources (Chapin et al., 2011; Waring et al., 2015). In addition, abiotic factors in plant communities are also altered by changes in the species composition. The undergrowth temperature, wind, water-related stemflow, throughfall and interception, which are mediated by the plant community structure and species composition, may vary in different vegetation types, thereby affecting plant-soil interactions and ultimately resulting in a change in soil properties (Waring et al., 2015). Since the variations in soil nutrient and water resources are closely correlated with many ecological processes in terrestrial ecosystems, understanding the species composition and their effects on soil nutrient and water resources could provide new insights into the understanding of plant competition and plant-soil interactions. Such an understanding is a necessary step for supplementing our knowledge about crop selection in rubber AFSs, especially from the perspective of the sustainable development of soil resources. However, most of the studies were conducted in grasslands and studies on soil water and soil nutrients were frequently performed separately (Van Noordwijk et al., 2004; Craine and Dybzinski, 2013).

In this study, we determined the effects of plant composition (i.e., the composition of tree, shrub and herb species) on soil nutrients and soil water under increases in complexity of the plant community structure. We addressed one scientific question in this study: how does plant species composition affect soil nutrients and soil water under changes in the complexity of the plant community structure? To address these questions, we measured the concentrations of the total soil carbon (C), nitrogen (N), phosphorous (P), potassium (K), calcium (Ca) and magnesium (Mg) at six different soil depths in a rubber monoculture, four agroforestry systems and a tropical rainforest. Meanwhile, we measured the soil water content (SWC) and soil stable isotope composition (²H and ¹⁸O) to determine the variations in soil water storage, soil water movement and mean residence time (MRT). We hypothesized that the plant effects on soil C and N would increase with increases in the complexity of the community because an increase in plant richness may increase the organic material input (Schulten and Schnitzer, 1997; Cong et al., 2014). Since soil C increases the stability of soil (Chen et al., 2017), the SWC would also increase with increases in soil C. Furthermore, plant competition would be intense with increases in the plant species composition and soil P, K, Ca and Mg should therefore decrease with increases in interspecific interactions because competition is generally understood to reduce the availability of resources (Craine and Dybzinski, 2013).

2. Material and methods

2.1. Study sites

All of the study sites are located in the Xishuangbanna Tropical Botanical Garden (XTBG; 21°55′39″N, 101°15′55″E) in Menglun town, Xishuangbanna Prefecture, Yunnan Province, Southwestern China. The seasonal variations in the study region are significant (i.e., apparent rainy and dry season) because of the tropical monsoon climate.

Based on field investigations, six vegetation types in XTBG were selected for observations (Fig. A1): rubber monoculture (RM; one plant species); rubber and orange (*Citrus reticulata*) agroforestry system (RO; mixed vegetation with two plant species, a tree and small tree); rubber and tea agroforestry system (RT; mixed vegetation with two plant species, a tree and shrub); rubber, orange and tea agroforestry system (ROT; mixed vegetation with three plant species, a tree and small tree/shrub); jungle rubber agroforestry system (JR; mixed vegetation with multiple plant species, a tree, small tree/shrub and herb); and tropical rain forest (RF; mixed vegetation, with multiple plant species, a tree, small tree/shrub and herb). The locations of these sites are very close (<800 m), and we established a 20 m × 20 m quadrat in each site for periodic sampling. All the quadrats had a common southwest slope orientation (SE 105–107°), and the terrain and slope gradient were very similar (around 25°).

The rubber trees in all sites were planted in 1990 in an area of deforested rainforest, and the intercrops (orange and tea tree) in RO, RT, ROT and JR were planted in 2004. It is worth mentioning that JR was once an agroforestry system of rubber and tea, but because the system had been abandoned for many years (since approximately 2005), the area gradually became JR through secondary succession. The species composition and distribution are shown in Fig. A1 and in Tables A1 and A2. In addition, N-P-K compound fertilizers were applied in a small and shallow ditch in the middle of each pair of rubber trees in each row once a year in early September, and the amount applied each year was approximately 200 kg ha⁻¹. No fertilizers were applied in the intercrop

planting rows of RO, ROT and RT. Of course, no fertilizers were applied in JR and RF.

2.2. Sampling and measuring methods

Soil was sampled separately in six phenological periods of the rubber tree: the late fruit-ripening period (November 15, 2017), the dormant stage (January 15, 2018), the leaf-shedding period (February 5, 2018), the leaf-expansion period (March 13, 2018), the flowering period (May 14, 2018) and the fruit-setting period (July 12, 2018).

Each quadrat was divided into four 10 m \times 10 m large blocks, and then each large block was divided into four 5 m \times 5 m small blocks. One small block in each big block was randomly selected for sampling. Therefore, four small-blocks in each quadrat were selected for sampling on each sampling date. The sampling position was located at the centre of each small block. This design was mainly based on a consideration of the size of tree, shrub and herb species and the principles of random selection in ecology (Southwood and Henderson, 2009).

On each sampling date, soils from 6 different depths (i.e., 0-5 cm, 5-15 cm, 15-30 cm, 30-50 cm, 50-75 cm, and 75-105 cm) were obtained with an earth-boring auger (5-cm diameter). These intervals were set based on a comprehensive consideration of the vertical rooting boundary of tree, shrub and herb species. On each sampling date, we obtained 144 samples. Each soil sample was quickly and adequately mixed, and then it was divided into three parts. One small part (approximately 2 g) was collected in a 15-ml screw-cap glass vial and sealed with parafilm for subsequent water extraction, and the two remaining parts (approximately 100 g each) were sealed in two plastic Ziplock bags to measure the soil water content (oven-drying method; 105 °C), soil nutrient concentration (air drying) and soil pH value. The soil samples that were prepared for soil nutrient measurements were crushed and homogenized into a fine powder and passed through an 80-mesh sieve after they had been air-dried.

The total C and N concentrations of the soil samples were measured using an elemental analyser (vario MAX CN; Elementar Analysensysteme GmbH; Hanau, Germany) at the Central Laboratory, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. The total P, K, Ca and Mg concentrations of the soil were determined by inductively coupled plasma atomic-emission spectrometry (iCAP7400; Thermo Fisher Scientific; Waltham, MA, USA) after digestion in HClO₄–HF. The soil pH values were measured with a pH meter (FE28; Mettler Toledo; Shanghai, China) after the soil samples had been dissolved in deionized water (soil/deionized water = 1:5).

Soil water samples were extracted from the sampled soil samples by an ultra-low temperature (liquid nitrogen; -196 °C) vacuum distillation and extraction system and sealed in a 2-ml autosampler vial. The rainwater samples were collected after each rain event in a stainlesssteel rain gauge starting on November 1, 2017. By August 5, 2019, we had collected 105 rainwater samples. The δ^2 H and δ^{18} O values of all the rainwater and soil water samples were analysed by a stable isotope mass spectrometer (Thermo DELTA V Advantage; Thermo Fisher Scientific; Waltham, MA, USA). The analytical precision for δ^2 H and δ^{18} O were 2‰ and 0.6‰, respectively.

2.3. Vegetation-related calculations

Relative density is the observed number of one plant life form (e.g., the number of trees) that represents a proportion of the total numbers of all plants in a quadrat. The formula is as follows:

Relative density =
$$\frac{\text{Number of one plant life form}}{\text{Number of all plant}}$$
 (1)

Relative coverage is the estimated coverage by one plant life form (e.g., the estimated coverage of trees) that accounts for a proportion of the sum of the estimated coverage of all plant life forms in a quadrat. The formula is as follows:

Relative coverage
$$=$$
 $\frac{\text{Coverage of one plant life form}}{\text{The summed coverage of all plant life forms}}$ (2)

Relative height is the estimated height of one plant life form that accounts for a proportion of the sum of the estimated height of all plant life forms in a quadrat. The formula is as follows:

$$\text{Relative height} = \frac{\text{Height of one plant life form}}{\text{The summed height of all plant life forms}}$$
(3)

The important values for one plant life form are the mean values of its relative density, relative coverage and relative height.

The potential number of interspecific interactions (PNII) is the number of pairwise combinations of all plant species in a quadrat. The formula is as follows:

$$PNII = \frac{N_{Species}!}{2! \times (N_{Species} - 2)!}$$
(4)

where N_{species} represents the number of plant species in a quadrat and "!" is the factorial function symbol.

2.4. Water-related calculations

In this study, soil water content (SWC) was measured based on mass. The formula is as follows:

$$SWC = \left(\frac{M_{fresh} - M_{dry}}{M_{dry}}\right) \times 100\%$$
(5)

where $M_{\rm fresh}$ represents the mass of the fresh soil and $M_{\rm dry}$ represents the mass of oven-dried soil that was dried in an oven at 105 °C for at least 48 h.

The local meteoric water line (LMWL) was fitted using the rainwater δ^2 H and δ^{18} O values using least square approximations, and the soil water evaporation line of each site was fitted using the δ^2 H and δ^{18} O values for soil water.

Because the recorded lengths of the water isotopic signatures were short (<2 years), the MRT of soil water at the different depths of the different sites was estimated based on the sine wave approach induced by the fitting of the seasonal ²H and ¹⁸O variations in rainwater and soil water (McGuire and McDonnell, 2006; Tekleab et al., 2014). The predicted values (i.e., δ value) of δ^2 H (or δ^{18} O) in the water body can be defined as follows:

$$\delta \text{ value} = C_0 + A \left[\cos \left(\frac{2\pi \times t}{365} - \varphi \right) \right]$$
 (6)

where C₀ is the mean measured δ value of water ²H and ¹⁸O, A is the amplitude of the fitting sine curve, 365 indicates the days in one year, $2\pi/$ 365 is the fixed radian frequency, φ is the phase lag, and t is the observed time expressed as days after the first sampling date (November 15, 2017, is set as 0). In addition, Eq. (6) can be transformed into a regression formula containing both sine and cosine terms (Bliss, 1970) as follows:

$$\delta \text{ value} = C_0 + \beta_{cos} \cos\left(\frac{2\pi}{365} \times t\right) + \beta_{sin} \cos\left(\frac{2\pi}{365} \times t\right)$$
(7)

Therefore, the amplitude A can be calculated through the estimated regression coefficients β_{cos} and β_{sin} using the following formula:

$$A = \sqrt{\beta_{\cos}^2 + \beta_{\sin}^2} \tag{8}$$

Furthermore, the phase lag φ can be calculated as follows:

$$\varphi = \arctan\left(\frac{|\underline{\beta_{sin}}|}{\beta_{cos}}\right) \tag{9}$$

Finally, the MRT of soil water can be estimated as follows:

$$T = \left(\frac{2\pi}{365}\right)^{-1} \times \sqrt{\left(\frac{A_{rain}}{A_{soil}}\right)^2 - 1}$$
(10)

where T is the MRT of soil water, A_{rain} is the amplitude of the $\delta^2 H$ (or $\delta^{18}O$) values of rainwater, and A_{soil} is the amplitude of the $\delta^2 H$ (or $\delta^{18}O$) values of soil water in Eq. (10).

2.5. Nutrient-related analysis

A principal component analysis (PCA) was conducted to perform a dimension reduction analysis of the soil nutrient data. Briefly, the soil nutrient data of the six sampling periods could be reduced into one group of data. First, the Pearson correlations among the sampling periods were determined. Next, the Kaiser-Meyer-Olkin measure of sampling adequacy (KMO values) and the Bartlett's test of sphericity (Bartlett's P values) were used to check the feasibility of the PCA. If the KMO value was <0.50 or Bartlett's *P* value was higher than 0.05, the PCA was not conducted. A scree plot was used to determine the number of principal components (i.e., eigenvalue ≥ 1). If the number of principal components was >1, then the composite scores were calculated through the accumulation of each component item, which had been weighted according to its component loading (Hair et al., 2010). Finally, the dimension-reduced data (i.e., the PCA scores) were normalized for the regression analysis between the PCA scores and soil depths, an independent-samples nonparametric test (Kruskal-Wallis test; P < 0.01) was performed to test the differences among sites, and Dunn's multiple comparisons were carried out to compare the differences among the sites.

After the above analyses, Spearman's rank correlation (P < 0.05) was performed to reveal the effects of species composition (the important values of tree, shrub and herb species and PNII) and soil depths on soil nutrients (C, N, P, K, Ca and Mg), soil water (SWC and mean water residence time) and soil pH. The analysed data were dimension-reduced data.

3. Results

3.1. Plant species composition of each study site

Information on species composition can be found in Table A1, and the relative density, relative coverage, and relative height of trees, shrubs (or small tree) and herbs are presented in Table 1. Because weeding was performed, the important values of the herb species in RM, RO, ROT and RT were set as zero. However, the important values of the herb plants in JR are the highest, followed by RF (Table 1). PNII in RF is the largest, followed by JR, ROT, RO and RT. No interspecific interaction was observed in RM.

3.2. Soil C, N and SWC

The concentrations of soil C and N decreased with the increase in depth (Fig. 1a, b; Fig. A2). The same result was found for SWC (Fig. 1c). The significant positive correlations among these variables (Fig. 1d–f) also illustrated that they had similar variation tendencies, especially soil C and N (r = 0.97, P < 0.001).

The results of the KMO tests for soil C, N and SWC and Bartlett's *P* values all suggest that these data were very suitable for PCA (Fig. A3). After PCA and regression analysis, we were able to determine that the soil C and N concentrations had significant logarithmic linear relations with soil depth (Fig. 1a, b; Fig. A3c, f) and that these relations were similar to those observed for SWC (Fig. 1c; Fig. A3i). The direct comparisons allowed us to determine that RF had the highest soil C and N concentrations and RM had the lowest (Fig. 1a, b), especially in the shallower soil layer (<50-cm deep). However, the differences in soil C and N in the other study sites were not obvious. In addition, the SWCs of ROT and RT were higher than those observed for the RF, RO, RM and JR, with differences indicated by order.

3.3. Soil P, K, Ca, Mg and soil pH

In general, through PCA, the effects of seasonal variations on the soil nutrient concentration were eliminated. Therefore, the regression models for the various nutrients are more generalizable when only the differences in sites and depths were considered during the fitting process (Fig. 2; Figs. A4–A7).

The variations in the soil P concentrations at different soil depths, in different sites and on different sampling dates were slightly complex (Fig. A4a). The correlation networks among the soil P data on different dates (Fig. A4b) and the KMO values (Fig. A4c) indicated that these data were suitable to conduct PCA. One component was extracted for analysis by using the scree plot (Fig. A4c, d). The soil P concentrations in RF and ROT decreased with the increase in soil depth (Fig. 2a; Fig. A4e), and the soil P concentrations were higher in RM and RO, followed by ROT, RF, RT and JR (Fig. 2a; Fig. A4e).

The soil K concentrations were determined to be relatively lower in JR and RF through a direct comparison (Fig. A5a). The correlation networks among the soil K data on different dates (Fig. A5b) and the KMO values (Fig. A5c) indicated that these data were very suitable for PCA. One component was extracted for analysis by using the scree plot (Fig. A5c, d). The soil K concentrations increased with the increase in soil depth in all study sites (Fig. 2b; Fig. A5e), and the soil K concentrations in RT were the highest, followed by ROT, RM, RO, RF and JR (Fig. 2b; Fig. A5e).

The variations in soil Ca concentrations were as large as those for soil P (Fig. A6a). The correlation networks among the soil Ca data on different dates (Fig. A6b) and the KMO values (Fig. A6c) indicated that these data were acceptable for PCA. Three components were extracted for

Table 1					
Species	composition	information	for	each	site.

Site	Relative density		Relative coverage		Relative height		Important value		PNII ^d				
	T ^a	S ^b	Hc	T ^a	S ^b	Hc	T ^a	S ^b	Hc	T ^a	S ^b	Hc	
RM	1	0	0	1	0	0	1	0	0	1	0	0	0
RO	0.8	0.2	0	0.79	0.21	0	1	0	0	0.86	0.14	0	1
ROT	0.35	0.65	0	0.63	0.37	0	0.75	0.25	0	0.58	0.42	0	3
RT	0.23	0.77	0	0.65	0.35	0	0.8	0.2	0	0.56	0.44	0	1
JR	0.02	0.1	0.87	0.41	0.13	0.47	0.56	0.19	0.25	0.33	0.14	0.53	55
RF	0.1	0.51	0.38	0.68	0.24	0.08	0.89	0.1	0.01	0.56	0.28	0.16	91

^aTree; ^bsmall tree or shrub; ^cherb; ^dpotential number of interspecific interactions.

RM indicates a rubber monoculture; RO indicates a mixed rubber tree and orange tree plantation; ROT indicates a mixed rubber tree, orange tree and tea tree plantation; RT indicates a mixed rubber tree and tea tree plantation; JR indicates a jungle rubber plantation; and RF indicates a tropical rain forest.



Fig. 1. The normalized scores (PCA results) of (a) Soil C and (b) N concentrations and (c) the soil water content (SWC) at different depths in different sites, and (d–f) the correlations among them (raw data). The results also involve linear regression analysis between the scores and soil depths, and the detailed fitted parameters are presented in Table A3. The raw data are presented in Fig. A2.

analysis using the scree plot (Fig. A6c, d). Through the regression analysis between the normalized comprehensive scores and soil depths, only the soil Ca concentrations in RF showed a decrease with the increase in soil depth (Fig. 2c; Fig. A6e), and the concentration of soil Ca in RT was the highest, followed by those in RM, RO, RF, ROT and JR (Fig. 2c; Fig. A6e).

The soil Mg concentrations of each site were different (Fig. A7a). The correlation networks (Fig. A7b) and KMO values (Fig. A7c) indicated that these data were suitable for PCA. Two components were extracted for analysis using the scree plot (Fig. A7c, d). Only the soil Mg concentration in JR increased with the increase in soil depths (Fig. 2d; Fig. A7e), and the soil Mg concentration in RF was the highest, followed by those in JR, ROT, RT, RO and RM (Fig. 2d; Fig. A7e).

Significant and positive correlations existed between soil P and Ca and between soil K and Ca (Table A4). However, soil Mg exhibited significant and negative correlations with soil P, K and Ca (Table A4).

The soil pH values ranged from 3.70–6.31, and the mean value was 4.63 ± 0.53 , consistent with the characteristics of the tropical soil. Generally speaking, soil pH was higher in RO, followed by RF, RM, ROT, RT and JR (Fig. A8). However, the differences were not large (Fig. A8). In addition, the pH values of shallow soil were relatively higher than the pH values of deep soil.

The detailed parameters of all the fitted logarithmic curves (i.e., regression analysis) are presented in Table A3.

3.4. Soil water isotopes and the mean residence time

The slope of the LMWL (i.e., 7.64) was slightly lower than the GMWL (8; see Fig. 3). Meanwhile, the slope of the soil water evaporation line was higher in RF, followed by those in ROT, RT, RO, RM and JR (Fig. 3).

All the sine curves fitted well, and the ¹⁸O-based curves fitted better than the ²H-based curves because of their lower root mean square errors (i.e., RMSE; see Fig. 4; Table A5 and A6). Therefore, the MRT data, which were generated from the ¹⁸O-based curves, could be used for the following analysis. The seasonal variations in the rainwater δ^2 H

and δ^{18} O values were regular (Fig. 4a, b). In general, the amplitudes (A) of the fitted sine curves of shallow soil water were higher than those of deep soil water, and the wave peaks of the fitted sine curves of soil water decreased with the increase in soil depth (Fig. 4c–n). Furthermore, the fitted sine curves showed higher distributions in RM, followed by those in RO, RT, ROT, RF and JR.

The estimated MRT of soil water greatly varied among the study sites. As the ¹⁸O-based results revealed, the soil water MRT was relatively longer in the deep soil layer than in the shallow soil layer. In general, the soil water MRT was relatively longer in RO, followed by RM, ROT and RT and then by JR and RF (Fig. 5).

3.5. Correlations among plant species composition effects on the soil

As the results of the Spearman correlation analysis revealed (Fig. 6a), plant interactions (i.e., PNII) exhibited positive correlations with soil Mg and shrub (or small tree) and herb species played positive roles in the variation of soil Mg. Relatively, PNII had negative correlations with soil P, K, Ca and soil water MRT, mainly due to the negative effects of herb species (Fig. 6b).

Furthermore, the important values of tree species had positive correlations with the soil water MRT and soil P, K and Ca, but these species had strong and negative correlations with soil Mg. The important values of shrub species had positive correlations with the SWC, soil K and Mg (Fig. 6a) but negative correlations with soil P and soil pH. By contrast, the important values of herb species had positive correlations with the soil Mg and soil pH but negative correlations with the SWC, soil water MRT, and soil P, K and Ca (Fig. 6b). In addition, SWC had a negative correlation with soil pH, and soil pH had a negative correlation with soil K.

In addition, soil depth had positive correlations with soil water MRT and soil K but negative correlations with soil C, N, P and SWC. Meanwhile, soil C and N were negatively correlated with soil water MRT.



Fig. 2. The linear regression analysis between the normalized scores of (a-d) soil P, K, Ca and Mg and soil depths, and the multiple comparison results among different sites (P < 0.01). Different lowercase letters within the bars indicate significant differences among sites. The detailed fitted parameters are presented in Table A3, and the detailed processes of PCA can be found in Fig. A4–A7.



Fig. 3. Local meteoric water line (LMWL) of the study region and soil water evaporation line in the different sites. GMWL is the global meteoric water line.

4. Discussion

4.1. Variations in plant species composition change soil C and N

Since a large proportion of soil N is bound with soil C as soil organic matter within soil, especially in tropical soils (Schulten and Schnitzer, 1997), variations in soil N were almost the same as those in soil C (Fig. 1a, b). Therefore, a strong and significant correlation was found between soil C and N (Fig. 1d).

In this study, the concentrations of soil C and N increased with increases in the complexity of plant communities and plant species composition (Fig. A2a, b), especially in soil layers <50 cm deep (Fig. 1a, b). These findings verify our hypothesis that an increase in plant species composition would improve the soil C and N concentrations. Actually, these findings are common because plant communities with high species richness and various life form compositions can promote the storage of soil C and N through enhanced plant productivity, even without the participation of nitrogen-fixing plants; meanwhile, the increase in soil C and N contents could also stimulate plant growth and thereby form a positive cycle in plant-soil relations to chronically improve soil C and N storage (Cong et al., 2014). In addition, an increase in plant species composition could enhance the soil C and N contents through the promotion of plant belowground biomass (Chen et al., 2018), soil microbial activity (Lange et al., 2015; Porazinska et al., 2018), soil multifunctionality and decomposition of organic matter (Eisenhauer et al., 2018).

4.2. Plant species compositions change the distribution and content of soil water

The differences in the SWC among the sites were significant (Fig. 1c). Commonly, plant communities that have multiple layers of vegetation (i.e., various plant life forms) can help soil retain water because undergrowth plants decrease soil evaporation through the effects of shading and windbreak, and they can also enhance rainfall interception, slow runoff and improve soil water infiltration (Jiang et al., 2017; Zhu et al., 2019). Therefore, significant positive correlations were found between the important values of shrubs and SWC in this study (Fig. 6a). Furthermore, increased inputs of soil C and N, which result from increases in the plant species composition, also improved the water-holding capacity through their positive effects on the physicochemical properties of soil, especially the formation of soil aggregates (Gould et al., 2016;



Chen et al., 2017). Therefore, we found that the soil C and N were positively correlated with the SWC (Fig. 6a).

The above statements appear to be true for all the comparisons between the soil from RM and all the rubber AFSs in this study (i.e., RO, RT and ROT), although the soils from RF and JR do not exhibit the same responses (Fig. 1c). The negative effects of herb species on the soil water content and the soil water MRT (Fig. 6b) may have altered the results because herbaceous plants were present only in JR and RF; this situation may be especially true for JR, where herbs grow densely (Table A1, A2) and show higher important values (Table 1).

Commonly, the composition of herb species affects the soil water fluxes and thereby alters the soil water content in several contradictory ways. For example, the increase in the composition of herb species fills the remaining space in the plant community and the increase in dense stem leaves in a complex species community increases the transpiring surface area and hence transpiration, which may offset the positive effects provided by the shade from leaves on the SWC and may even cause a decrease in SWC (Guderle et al., 2018; Fischer et al., 2019). In addition, the improved soil aggregates in complex species communities accelerate the drainage of rainwater and soil water (Jiang et al., 2017; Fischer et al., 2019). Therefore, the soil C was negatively correlated with the soil water MRT in this study (Fig. 6b). In addition, the higher soil porosity (e.g., root holes) in the complex community can accelerate the infiltration and drainage of soil water and decrease the soil water MRT (Fig. 5) because of the intense root interactions among plant species (Bayala and Prieto, 2019). Therefore, we found that plant interspecific interactions (i.e., PNII) were negatively correlated with the soil water MRT (Fig. 6b). In addition, interspecific competition in the multi-species community promoted the tree species to take up soil resources from deeper soil layers (Pierret et al., 2016) as shown by the deep soil-water-uptake of rubber trees in the agroforestry systems (Wu et al., 2016; Wu et al., 2019). Therefore, the deep-water uptake behaviour of tree species in the high species richness community exhausted the deep soil water and led to drier deep soil layers (Fischer et al., 2019), which was indicated by the fitted curves of JR and RF (Fig. 1c).

Compared with RF, which is regarded as a climax community, exhibits a relatively stable species composition, and may have formed complementary resource use patterns among plant species, IR suffers from the effects of secondary succession. The invasion of new species in JR, especially fast-growing herbaceous plants, increases the water competition intensity among plant species (Connell and Slatyer, 1977) and thus may accelerate water loss, thereby causing a reduction in soil water storage. In addition, the loss of soil water in IR is also caused by intense soil evaporation as suggested by the soil water evaporation line of JR (Fig. 3). In brief, the deviation of the soil water samples from the LMWL indicates evaporation because evaporation induces kinetic fractionation. Commonly, the smaller the slope and intercept exhibited by the evaporation line, the more intense the evaporation suffered by soil water (Gibson et al., 1993; Gat, 2008). Therefore, the relatively smaller slope and intercept of the evaporation line in JR relative to the other sites suggests that more intense evaporation occurred in this site, which was possibly caused by the composition of herb species as discussed above. Lower soil water retention corresponds to higher water consumption and more intense soil evaporation in JR, which makes its soil drier relative to that of RF and the other sites (Fig. 1c).

4.3. Effects of species composition on soil P, K, Ca and Mg

As the results suggest, increases in plant species composition or plant interspecific interactions (i.e., PNII) decrease the concentrations

of soil P, K and Ca but increase the concentration of soil Mg (Fig. 6). The findings in this study regarding soil P, K and Ca are not new because various studies in recent decades have found that an increase in plant species composition reduces soil nutrients, especially macronutrients (Huston, 1980; Nadeau and Sullivan, 2015; Zemunik et al., 2016). The loss mechanisms mediated by plant composition can be briefly explained as follows: first, an increase in plant species composition is followed by a series of changes in the physicochemical properties of soil, including the stabilization of soil moisture and temperature (Bronick and Lal, 2005; Swacha et al., 2018), improvement of soil texture and structure (Gould et al., 2016), promotion of soil microbial activity (Orwin and Wardle, 2005), and increased release of organic acid by plant root (Bronick and Lal, 2005); second, these altered biological and nonbiological factors accelerate the weathering of soil minerals and thus accelerate the transformation of macronutrients into watersoluble and exchangeable forms from non-exchangeable forms (Mengel et al., 2001); and finally, as we mentioned above, the faster soil water infiltration and higher soil water fluxes that occur with increases in the plant species composition (Fischer et al., 2019) may aggravate soil nutrient leaching. Moreover, the interspecific competition becomes more intense as the plant composition increased, and the competitive consumption of soil nutrients occurring through plant supply pre-emption mechanisms results in the decrease of soil nutrient concentrations (Craine and Dybzinski, 2013).

However, with increases in species composition, the effects of plant interspecific interactions on soil Mg were nearly opposite compared with that of soil P, K and Ca. This finding is slightly different compared with that of other studies, which have suggested that plant composition has insignificant or negative effects on soil Mg (Huston, 1980; Nadeau and Sullivan, 2015). Furthermore, in our study, we also found that the soil Mg concentration was negatively correlated with the concentrations of soil P, K and Ca (Table A4). Therefore, we inferred that those phenomena may be caused by cation competition within the soil. The following reasons for the assumption that the original content of the Mg source material that forms soil in these sites was same may provide support for this inference: 1) the low concentration and high variations of soil Mg (Fig. A7a) and low pH values (Fig. A8) at all study sites suggest that the soil Mg in these sites may mainly exist in an exchangeable form; however, because the availability of soil P, K and Ca strongly impede the plant uptake of soil Mg due to their competition for cations in the soil solution, the risk and magnitude of Mg leaching through a soil solution would therefore be great (Gransee and Führs, 2013); 2) the long-term N-P-K compound fertilization practices in the rubber plantations (RM, RO, ROT and RT) also stimulated nutrient release from soil minerals and thus improved the availability of P, K, and Ca cations and increased the risk and intensity of Mg deficiency because of cation antagonism (Cakmak and Yazici, 2010; Gransee and Führs, 2013); and 3) soil organic matter also helps increase the cation exchange capacity of the soil, which increases the intensity of the cation competition between soil Mg and other nutrient cations as the plant composition increases (Gransee and Führs, 2013).

Based on the above explanations, this study suggested that as the plant composition or complexity of the plant community increase, plant interspecific interactions would result in decreases in soil P, K and Ca but an increase in soil Mg. However, the compositions of tree, shrub and herb species had relatively contradictory effects on these nutrients (Fig. 6). In brief, tree species had positive effects on soil water MRT and soil P, K and Ca but negative effects on soil Mg; shrub species had positive effects on SWC, soil K and Mg but negative effects on soil P and soil pH; and herb species had positive effects on soil Mg and soil pH but negative effects on SWC, soil water MRT, and soil P, K and Ca. The contradiction was especially noticeable for shrub and herb species,



Fig. 5. MRT of soil water at the different depths and estimated through the (a) soil water ²H data and (b) soil water ¹⁸O data.

which exhibited opposite effects on soil pH (Fig. 6) and may have resulted in the large variations observed in the availability and movement of soil nutrients (Marschner et al., 1987).

4.4. Interaction effects of plant composition with soil depth

Except for soil P, Ca and Mg (Fig. 2a–c), soil depth had positive effects on soil K and the soil water MRT (Fig. 2d; Fig. 6a) and strong negative effects on soil C, N and SWC (Fig. 1a–c; Fig. 6b).

The results described above may be caused by variations in series of biotic and abiotic factors that occur with increases in soil depth. For example, root biomass decreased with soil depth; therefore, the inputs of root carbon and nitrogen decreased (Fornara and Tilman, 2008; Ravenek et al., 2014). With the decrease in root activities and soil organic matter, the soil porosity decreased; therefore, soil water infiltration slowed (Franzluebbers, 2002; Pierret et al., 2016). Therefore, with increases in soil depth, the magnitude of the seasonal variation of the soil water content decreased (Fig. A2c) and the seasonal cycles of soil water in the deeper soil layers exhibited a delay compared with that in shallower soil layers (Fig. 4; Fig. 5). Similarly, the soil temperature also stabilized with increases in soil depth, although this temperature may also have been affected by soil water (Wang et al., 2006; Craine and Gelderman, 2011). Through the effects of soil temperature and moisture and their interactions, the soil microbial activity decreased with depth (Pries et al., 2018; Yao et al., 2018); thus, the organic matter decomposition increasingly weakened (Kramer and Gleixner, 2008). Therefore, soil C and N concentrations decreased with soil depth (Craine and Gelderman, 2011). In addition, the above impacts, including the plant root-induced changes on soil pH, further affected the existing forms of soil mineral nutrients (Marschner et al., 1987; Bagayoko et al., 2000) and therefore changed the availability of nutrients with increases in soil depth. However, because soil pH is affected by the content (Fig. 6b) and flux of soil water (Fig. 5), it only slightly increased with increases in soil depth, and the variability of soil P, Ca and Mg that occurred with increases in soil depth was unnoticeable.

In short, soil depth could weaken the effects of the plant composition on soil nutrients and water.

5. Conclusions

With the increase in plant species composition, the concentrations of soil C and N increased, which confirms that the accumulation of soil organic matter via intercropping in rubber plantations is effective. The same effect might occur on the soil water content in rubber AFSs because soil organic matter could improve the soil water-holding capacity. However, the results at the JR and RF sites suggested that increases in species composition, especially for herb species, also exhibited negative effects on soil water mainly because the increased soil organic matter and root holes can accelerate the infiltration and discharge of soil water. Such inferences can be certified by the short residence time of soil water in JR and RF. It is worth mentioning that the fast water infiltration and the potential high flow of soil water in the multi-species communities increase the risk and magnitude of mineral nutrient leaching through the soil solution, especially for the acidic soil. However, such phenomena may not have a negative effect on deep-rooting species (such as rubber tree) because soil depth could ease the negative effects of plant species composition on soil. In addition, competitive consumption by plants (e.g., supply pre-emption mechanism) would also decrease the concentration of soil nutrients, especially with increases in the composition of herb species. Such results imply that dense planting of herb species in rubber AFSs should be avoided. In general, this study revealed how plant species composition, including among tree, shrub and herb species, affects soil macronutrients and soil water.

CRediT authorship contribution statement

Junen Wu: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Funding acquisition. **Huanhuan Zeng:** Methodology, Investigation, Data curation, Writing -



Fig. 6. Explanations for the effects of species composition (the important values of trees (Tree IV), shrubs (Shrub IV) and herbs (Herb IV) and their interactions (PNII)) and soil depth on soil nutrients and soil water using (a) positive and (b) negative correlations (Spearman rank correlation test). All the correlations reached a significant level (*P* < 0.001). IV indicates important values. All analysed data were dimension-reduced data.

original draft, Resources. Fan Zhao: Formal analysis, Investigation, Visualization. Chunfeng Chen: Investigation, Formal analysis, Writing - original draft. Wenjie Liu: Conceptualization, Supervision, Project administration, Funding acquisition, Writing - review & editing. Bin Yang: Methodology, Investigation, Resources. Wanjun Zhang: Investigation, Resources, Visualization.

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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