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An increase in intercropped species richness improves plant water use but weakens the nutrient status of both intercropped plants and soil in rubber–tea agroforestry systems

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ABSTRACT

As a relatively successful agroforestry system, whether the addition of more intercropped species in the rubber–tea agroforestry system extends the benefits is still unknown but worth exploring because diverse cash crop production helps farmers resist market risks and may bring the ecological functions of rubber agroforestry systems closer to those of natural forests. Therefore, understanding the effects of plant interspecific competition on both plants and soil with the increase in intercropped species number in such agroforestry systems is vital for the improvement of rubber–tea agroforestry systems. For these reasons, we selected a monocultural rubber plantation, rubber–tea, rubber–orange–tea and jungle-like rubber–tea agroforestry systems for studying plant water absorbing patterns, plant water use efficiency, and the nutrient status of plants and soil through stable isotope (^{13}C, ^{2}H and ^{18}O) techniques and nutrient diagnosis (C, N, P, K, Ca and Mg) of plant organs (leaves, stems and roots), soil and litter. We found that rubber trees primarily absorbed water from deeper soil layers with increases in their intercropped species number and the formation of increasingly obvious hydrologic niche differentiation between rubber trees and the intercropped plants. In addition, soil nutrient status first improved but then declined with an increase in the number of intercropped species. However, only a slight impact was observed on the nutrient status and water use efficiency of rubber trees, even in the complex rubber–tea agroforestry system. However, the intercropped species experienced resource shortages, especially P shortages, since their water-absorbing zones almost overlapped. Therefore, we suggest that more diverse intercropped species compositions in rubber–tea agroforestry systems would offset the intercropping benefits for both plants and soil. However, appropriate phosphate fertilizer application in complex agroforestry systems is necessary if the construction of high-species richness rubber agroforestry systems is desired.

1. Introduction

Rubber-based agroforestry systems are sustainable intercropping systems where farmers grow multiple crops or livestock alongside rubber trees to improve their income and/or subsistence while also reaping the subsequent ecological benefits (Hua et al., 2021). For example, developing rubber-based agroforestry systems can help increase soil organic matter, which is beneficial for increasing soil fertility, reducing water and soil loss, maintaining local climate stability and improving biodiversity (Chen et al., 2017). In addition, the yield of latex from rubber trees, which is an important but scarce strategic resource crucial for making tires, mats, ropes and other rubber products, can be greatly improved in most rubber-based agroforestry systems (Wu et al., 2016; Lu, 2020). The abundant agricultural products in this agroforestry system can help increase the land use rate and help improve the incomes of rubber farmers. Therefore, rubber-based agroforestry provides a solution for the already degraded lands in rubber cultivation areas and provides a way to coordinate economic development and eco-environmental protection in such areas (Zeng et al., 2021). However, a serious problem in the promotion of rubber-based agroforestry

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systems is that the management of plant interspecific competition requires proper professional knowledge and evaluation of resource dynamics and complexities.

One of the major challenges for rubber agroforestry systems is the root competition between rubber trees and intercropped species (Wu et al., 2016). This competition has significant impacts on the growth and productivity of both rubber trees and other crops. Rubber tree roots are known to be deep and extensive, while the roots of intercropped species may grow closer to the surface, making them more susceptible to competition for nutrients and water (Yang et al., 2021). To mitigate root competition, several strategies can be employed, such as adjusting the planting density and spacing of the trees and intercropped crops to minimize competition for resources, using species that have different root systems and nutrient requirements to complement the rubber trees, and pruning the shoots of intercropped crops to weaken their competitive ability (Feng, 2007). By employing appropriate management practices, it is possible to achieve a balance between rubber tree growth and productivity and the growth and productivity of intercropped species, resulting in a sustainable and productive agroforestry system (Langenberger et al., 2016). However, most means of mitigating root competition do not always work and are time-consuming tasks (Trinder et al., 2013; Yang et al., 2021). Therefore, rubber-based agroforestry systems require more empirical evidence from many studies instead of haphazard planting to be successful.

Rubber-based agroforestry systems have been implemented in many countries, including Indonesia, Malaysia, Thailand and Vietnam (Penot et al., 2017), and some suitable economic crops have been found to intercrop with rubber trees after decades of research and experimentation, such as sugarcane (Pinto et al., 2006), bananas (Rodrigo et al., 1997), coffee and cocoa (Snoeck et al., 2013), and tea (Feng, 2007). In China, many studies have shown that the rubber–tea agroforestry system is promising (Guo et al., 2006; Wu et al., 2017; Huang et al., 2022). For example, rubber–tea intercropping could improve the production of both latex and tea, resulting in better economic benefits (Guo et al., 2006). Meanwhile, the quality of tea is improving because the amino acid and theine contents in tea leaves increase when tea grows under shaded conditions (Feng, 2007). Compared with monocultural rubber/tea plantations, the rubber–tea agroforestry system, which is built with double row spacing technology, could better coordinate light, heat, moisture and soil nutrients (Langenberger et al., 2016). Because the canopies of rubber and tea are at different vertical heights in such agroforestry ecosystems, the plants can make full use of light, and then more photosynthate can be produced (Feng, 2007). Additionally, the community structure between rubber and tea can help reduce wind speed in the forest. The decrease in wind speed will inevitably reduce the intensity of evaporation and transpiration, increase the relative humidity and soil moisture, and protect rubber trees from physical damage, including broken trunks and defoliation, which harm rubber growth and yield (Zhu et al., 2019). In addition, soil nutrients could increase in a rubber–tea agroforestry system (Guo et al., 2006; Feng, 2007; Zhu et al., 2019). Because of the superposition of the two layers of rubber and tea, the residues of the biological community, such as dead branches and leaves, increase. Therefore, soil organic matter would also be improved, and thus, the retention of water and fertilizer within the soil would be enhanced (Zhu et al., 2019). Due to the benefits mentioned above, the rubber-tea agroforestry system has been extensively promoted in Xishuangbanna Prefecture, located in southwestern China's Yunnan Province.

However, the sales of natural rubber and tea were not good in recent years because of the impacts of the COVID-19 epidemic. Some rubber plantation companies and even small rubber holders have started to intercrop diverse crops with rubber trees. Whether the benefits of rubber–tea intercropping, as one of the relatively successful agroforestry systems, could be improved further by the addition of more species is a question worth exploring. Species richness is crucial in designing and managing rubber agroforestry systems (Hua et al., 2021). It contributes to ecosystem stability and function, improves agricultural productivity, supports biodiversity conservation, helps the ecosystem adapt to climate change impacts, provides economic and social benefits, and enhances cultural and spiritual values (Beukema et al., 2007; Warren-Thomas et al., 2020; Zaro et al., 2020; Huang et al., 2022). Therefore, considering and managing species richness is essential for achieving environmental sustainability, increasing productivity, and promoting socioeconomic development in rubber agroforestry systems. However, interspecific competition is still a major challenge in this agroforestry system (Yang et al., 2021). For example, during the pronounced dry season (late March to mid-May) in Xishuangbanna, rubber trees undergo leaf flushing, leaf expansion and the flowering period. This period is also known as the "golden season" for spring tea production, which implies that rubber trees and tea trees need sufficiently abundant water and nutrients for growth during this period. If strong competition occurs, resulting from the addition of more intercropped species, the spring tea quality and yield and the latex yield of rubber trees may also decline. Therefore, improving the understanding of the water and nutrient competition among species in diverse rubber–tea agroforestry systems is vital for the sustainable management of high-diversity agroforestry systems. However, reports on interspecific water and nutrient competition, root interactions, and how these processes affect the aboveground ecophysiological functions of plants are still rare (Song et al., 2022).

Generally, roots are the main plant organ used for both water and nutrient absorption, and thus, overlapping rhizosphere soil becomes the main place of belowground competition among different plant species (Isaac and Borden, 2019). Therefore, any physiological and ecological changes in plant roots, such as growth, development, and distribution, are closely related to the competitive uptake of the belowground resources. However, the belowground parts and processes of plants that are not visible, such as root activity, root distribution in the soil profile, belowground nutrient interactions among plant species and nutrient element movement characteristics, are difficult to determine; thus, root research on multiple species is very difficult, especially in terms of absorbing roots. Stable isotope tracers can be used to study plant resource use by analyzing the isotopic signatures of the consumer and diets (Dawson et al., 2002). This method would be useful for studying plant belowground competition (Trinder et al., 2013). With improvements in measurement techniques and analysis methods for stable isotopes, the use of stable isotope methods is increasingly accepted by researchers worldwide (Phillips et al., 2014).

Water, as the most necessary resource for plants, and its movements and variations in soil, plants and the atmosphere have been widely explored through ^{2}H and ^{18}O isotopes, and using both ^{2}H and ^{18}O isotopes to trace plant water sources has become the "industry standard", as it is a convenient, quantitative, precise, and nondestructive method (Dawson et al., 2002). Because soil water is absorbed primarily through root hairs (i.e., absorbing roots; Gilroy and Jones, 2000), it might be possible to reconstruct the distribution of plant absorbing roots by understanding plant water absorbing patterns. Thus, we can also obtain much more important information about plant nutrient use because absorbable forms of nutrients for plants mainly exist in soil solution, and root hairs absorb the majority of nutrients from soil solutions (Gilroy and Jones, 2000). In brief, detecting dynamic variations in root hair distribution in plant communities through stable hydrogen and oxygen isotopes tracers helps us better understand belowground competition dynamics.

To help improve the sustainability and maximize the potential of rubber–tea agroforestry systems, we selected a rubber monocultural plantation (RM), three agroforestry systems including rubber–tea (RT) intercropping, rubber–orange–tea (ROT) intercropping and a complex jungle-like rubber–tea (J-RT) agroforestry system (a secondary forest) to study plant belowground competition dynamics, competition effects on plant nutrient status and plant—soil interactions at these sites. We mainly applied stable hydrogen and oxygen isotope (^{2}H and ^{18}O) techniques to study plant hydrological niche differentiation and stable carbon isotopes (^{13}C) to study plant water use efficiency (WUE), and we measured carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) concentrations of different plant organs (i.e., leaf, stem, and root), litter and soil at these study sites to analyze how competition affected the nutrient status of plants and soil across the dry and rainy seasons from 2017 to 2018. Previous studies showed that interspecific water competition could help improve the water use of rubber trees and enhance the water retention capacity of the soil in the rubber–tea agroforestry system (Wu et al., 2017; Zhu et al., 2019). However, intense competition would also offset such benefits of interspecific interactions. Therefore, we hypothesized that (1) rubber trees have a deeper water-absorbing zone than the intercrops and thus form complementary plant hydrological niches among species, but the hydrological niches of the intercropped species of rubber tree are compressed with an increase in intercropped plant species since rubber trees have a better developed root system; (2) increasing the number of intercropped species will result in intense competition, thus increasing the consumption of soil water and nutrients, and the intercropping benefits for soil would therefore be offset by intense competition; and (3) plant nutrient status is affected by environmental resources, and the stronger competitor will exhibit a higher nutrient status than its neighboring species, but intense competition will result in resource limitations and, ultimately, lower nutrient status for plants in multi-species agroforestry systems than in simple agroforestry systems.

2. Materials and methods

2.1. Study sites

This study was performed near Menglun town (21°55′44′N, 101°15′21′E), located in Xishuangbanna Prefecture in Yunnan Province. The rainy season (November to April) and dry season (May to October) are characteristic in this region due to the tropical monsoon. This region experiences an average annual air temperature of 21.7 °C, and an average annual precipitation of 1475 mm. It is estimated that the rainy season accounts for more than 85% of the total precipitation (Zhu et al., 2019).

In this study, a monoculture rubber tree plantation (RM) and three agroforestry systems including rubber–tea (RT), rubber–orange–tea (ROT) and jungle-like rubber–tea (J-RT) intercropping patterns were selected (Fig. S1). Each study site was equipped with a standard, permanent quadrat (20 m × 20 m) that was used for periodic sampling. In the monoculture rubber tree plantation, rubber trees were arranged in 3-m-wide double rows, and the trees were spaced two meters apart within each row, with a ten-meter gap separating each pair of double rows (Fig. S1a). Similarly, rubber trees were planted in all agroforestry systems using the same pattern as that in monoculture rubber plantations (Fig. S1). Tea trees were arranged in 4 rows in the middle of the 10-m-wide gap between the double rows of rubber trees; they were spaced approximately 1 m apart within a row, and rows were spaced 1 m apart in the RT agroforestry system (Fig. S1b). Tea trees were also planted in four rows in the 10-m-wide gap between the double rows of rubber trees in the ROT agroforestry system. Planted rows of tea trees were separated by one row of orange trees (the orange trees were spaced two meters apart), which divided the planted rows of tea trees into two parts (each part contained two rows of tea trees, and the intervals between the orange row and tea row were approximately 2 m; see Fig. S1c). In the J-RT agroforestry system, tea trees were planted only in two rows in the middle of the 10-m-wide gap between rows of rubber trees (similar to RT and ROT; see Fig. S1d). The other species in the J-RT agroforestry system were distributed naturally.

Plantations of rubber trees were established in approximately 1990, and tea and orange trees were intercropped with rubber trees in 2004. Since 2005, the J-RT agroforestry system has been an abandoned RT agroforestry system, with ongoing secondary succession. Species other than rubber trees and tea trees are naturally found during secondary succession. These species were divided into three groups: tree species (*Ficus langkokensis*, *Litsea panamonja*), small tree or shrub species (*Camellia sinensis*, *Alchornea davidi*, *Rauvolfia verticillata*), and herbs (*Pteridrys cnemidaria*, *Adiantum capillus−veneris*, *Dicliptera chinensis*, *Pseuderanthemum polyanthum*, *Indosasa hispida*). It is worth mentioning that bamboo (*Indosasa hispida*) grew densely and could be seen everywhere in the J-RT agroforestry system.

Commonly, approximately 1 kg compound fertilizer of nitrogen, phosphorus and potassium (urea, potassium chloride, and superphosphate) would be applied in the middle of each two rubber trees in the monocultural rubber plantation in the middle of March and September (Feng, 2007). However, no fertilizer was applied in the rubber agroforestry systems during the study period in this study. Even in the permanent quadrat of the rubber monoculture, which had a history of fertilization, no fertilizer was applied during the study period.

In the established quadrat, the slope aspect was 97–105 degrees, and the slope gradient was approximately 23 degrees. The rubber tree clone was RRIM600.

2.2. Sampling

A total of sixteen 5 m × 5 m blocks were created for the 20 m × 20 m study quadrat (Fig. S1), and four of them were selected randomly for soil samplings at each sampling time. In each sampling block, soil from 0 to 5 cm, 5–15 cm, 15–30 cm, 30–50 cm, 50–75 cm, and 75–105 cm depths was sampled with an earth-boring auger. It is necessary to explain that we took soil samples at those six different soil layers, with larger intervals between layers at greater depths. This is because our previous experiments have shown that the soil profile in these study sites exhibits large vertical variations in physicochemical properties in the shallow soil layers, while the differences in deep soil are relatively small. A small amount of soil from different soil layers was collected in a 15 ml screw-top glass vial, which was sealed with parafilm and placed in a freezer at − 20 °C. An approximately 80 g portion of soil was placed in a plastic Ziplock bag to measure the soil water content, and a final portion was analyzed for soil nutrients.

To sample the xylem of rubber trees, four individuals were randomly selected. An increment borer was used to collect samples from the trunk xylem of rubber trees at a height of 1.2 m. In addition, we sampled the shoots of the small tree and shrub species and the taproot of herb species, removing their green tissues to obtain xylem. Each species was sampled three to four times to obtain enough xylem samples, and then the xylem samples were collected in 15 ml glass vials immediately, covered with parafilm, and stored in a freezer at − 20 °C.

Leaf and stem samples were collected at the same time as xylem sampling. Shoots were collected using a 10-m tree pruner, and then the leaves and stems of the shoots were stored separately in different envelopes. In addition, the lateral roots of trees and shrubs from the soil at a depth of 0–10 cm were sampled, and the entire root networks of herb species were sampled. The main consideration of such sampling of plant roots is to minimize the impacts on plant growth and ensure sustainable sampling. After being collected, the roots were thoroughly rinsed using purified water and then dried in an oven to constant weight. Moreover, litter was collected in each quadrat in an S-shaped pattern, and a total of four packs of litter were collected. We cleaned and packed the litter samples in dry cotton cloth and then dried them in an oven to constant weight.

We sampled four times during the dry season (November 13, 2017; January 15, 2018; February 5, 2018; and March 15, 2018) and three times during the rainy season (May 14, 2018; July 12, 2018; and September 25, 2018). Therefore, for nutrient analysis, we obtained 84 plant samples ($1 \times 3 \times 4 \times 7$; one plant species, three organs, four repeats, and seven sampling times) from the rubber monoculture, 168 plant samples ($2 \times 3 \times 4 \times 7$; two plant species, three organs, four repeats, and seven sampling times) from the rubber-tea agroforestry system, 252 plant samples ($3 \times 3 \times 4 \times 7$; three plant species, three organs, four repeats, and seven sampling times) from the rubber-orange-tea agroforestry system, and 420 plant samples from the jungle-like rubber-tea agroforestry system. Therefore, we obtained a total of 924 plant samples for plant nutrient analysis. In addition, we sampled soil from six soil layers four times on each sampling day. Thus, we obtained 168 soil samples (6 ×4 ×7; six soil layers, four repeats, and seven sampling times) at each study site, for a total of 672 soil samples for soil nutrient analysis.

2.3. Pretreatment and measuring methods

An ultralow temperature (liquid nitrogen, −196 °C) vacuum distillation and extraction system was used to extract the soil and xylem water, and the extracted water samples were sealed in 2-ml autosampler vials. We measured the δ^2H and δ^{18}O values of the extracted water using a mass spectrometer (Thermo Fisher Scientific, USA). For the δ^2H and δ^{18}O values, the measurement accuracies were better than 1‰ and 0.1‰, respectively, and expressed through the Vienna standard mean ocean water standard.

Soil water contents (SWCs) were determined by the oven drying method. A minimum of 48 h was required for the leaves, stems, and roots to dry to constant weight. An air-drying period of one week was performed on soil samples to measure the concentrations of nutrients. Then, all of the samples were crushed and homogenized to a fine powder until they could pass through an 80-mesh sieve. The total C and N concentrations in each sample were determined using an elemental analyzer (Vario MAX CN; Elementar Analysensysteme GmbH; Hanau, Germany). A thermoelectric atomic emission spectrometer (Thermo Fisher; Waltham, USA) was used to measure the total P, K, Ca, and Mg concentrations in all samples. We measured only the total concentrations of these nutrients to comprehensively determine their seasonal variation.

2.4. Water-related calculations

In this study, the SWC value is defined as the mass of water per mass of dry soil.

To determine the water sources of rubber trees, the isotopic mass balance is used, as well as multiple linear mixing models (MLMMs, Phillips 2005). The formulas are as follows:

$$\delta 2\mathrm{H}_{\mathrm{plant}} = f_1\delta 2\mathrm{H}_{\mathrm{S1}} + f_2\delta 2\mathrm{H}_{\mathrm{S2}} + f_3\delta 2\mathrm{H}_{\mathrm{S3}} + f_4\delta 2\mathrm{H}_{\mathrm{S4}} + f_5\delta 2\mathrm{H}_{\mathrm{S5}} + f_6\delta 2\mathrm{H}_{\mathrm{S6}} \tag{1}$$

$$\delta^{18}\mathrm{O}_{\mathrm{plant}} = f_1\delta^{18}\mathrm{O}_{\mathrm{S1}} + f_2\delta^{18}\mathrm{O}_{\mathrm{S2}} + f_3\delta^{18}\mathrm{O}_{\mathrm{S3}} + f_4\delta^{18}\mathrm{O}_{\mathrm{S4}} + f_5\delta^{18}\mathrm{O}_{\mathrm{S5}} + f_6\delta^{18}\mathrm{O}_{\mathrm{S6}} \tag{2}$$

$$1 = f_1 + f_2 + f_3 + f_4 + f_5 + f_6 \tag{3}$$

In Eq. (1) and Eq. (2), $\delta^2\mathrm{H}_{\mathrm{plant}}$ (or $\delta^{18}\mathrm{O}_{\mathrm{plant}}$) is the δ^2H (or δ^{18}O) value of plant xylem water; $\delta^2\mathrm{H}_{\mathrm{S1}}$—$\delta^2\mathrm{H}_{\mathrm{S6}}$ (or $\delta^{18}\mathrm{O}_{\mathrm{S1}}$—$\delta^{18}\mathrm{O}_{\mathrm{S6}}$) are the δ^2H (or δ^{18}O) values of water sources within the 0–5 cm, 5–15 cm, 15–30 cm, 30–50 cm, 50–75 cm, and 75–105 cm soil layers, respectively. In Eq. (3), f_1—f_6 are the water consumption of plants in the six studied soil layers.

In this study, there are six sources for determining plant water uptake. However, since MLMMs are typically used to estimate only two or three sources contributing to a mixture or a consumer's diet, a more advanced and powerful MLMM called MixSIAR was applied. MixSIAR incorporates Bayesian statistical methods that allow for the incorporation of more sources and more complex ecological questions (Parnell et al., 2013; Phillips et al., 2014). Using MixSIAR, the possible water use proportions of plants in this study were calculated. MixSIAR runs on soil water isotope data in "means and SDs" format, and the isotope data of plant xylem water were treated as mixture data. Because isotopic discrimination in water taken up by roots is too small to be detected (Phillips, 2005), discrimination was set to 0. For plant species with samples from many individuals, error structures were defined as the "residual process", but for plant species with sampling of only one individual, the error structures were defined as the "process only". Other settings were the system defaults. Since the result of MixSIAR is a range of possible solutions, the final solution was defined as the mean of those possible solutions.

2.5. Statistical analyses

To simplify the analysis of the various complex datasets, principal component analysis (PCA), as a dimensionality reduction analysis, was used to reduce the dimensionality of soil data throughout the six soil layers and that of plant data from different organs. Through this method, it was possible to simplify the nutrient data for both plant and soil samples into several groups. The first step was to determine the Pearson correlations between the sampling periods. To assess the feasibility of the PCA, Kaiser—Meyer—Olkin (KMO) and Bartlett's tests of sphericity were applied. Our data were considered unsuitable for PCA when the KMO values were less than 0.50 or when Bartlett's P values were greater than 0.05. A scree plot was used (eigenvalue $\geqq 1$) to identify the number of principal components. Composite scores were calculated by adding up each component item's weights if there was more than one principal component (Song et al., 2013). Variance analyses were performed using normalized dimension-reduced data (e.g., PCA scores) for each study site. We tested differences among sites using the general linear model and Dunn's multiple comparisons.

Using a general linear model with fixed effects of "season" and "site", we assessed the differences in litter nutrient concentrations among the seasons and sites. Similarly, the differences in the leaf δ^{13}C values among plant species or among the study sites were also analyzed through a general linear model with "species" or "site" as the fixed effect. In cases where significant differences were found between groups, Dunn's multiple comparisons were used. All data were normal, as determined by Lilliefors' 95% confidence bounds for normal quantile plots. Homogeneity of variance was assessed using Levene's test.

R 3.6.3 (R Core Team, 2014) was used for all statistical analyses.

3. Results

3.1. Plant water absorption patterns

More than half of the water absorbed by rubber trees in RM came from the intermediate layer of soil (15–50 cm; green bars in Fig. 1a). However, in the agroforestry systems, deep soil layers (50–105 cm; blue bars in Fig. 1b, d, g) provided much (44.6% on average) of the absorbed water for rubber trees. Conversely, in agroforestry systems, rubber tree intercrops were dependent on shallow and surface water for their growth (i.e., 58.7% on average from the 0–15 cm depth soil layer; yellow bars in Fig. 1c, e, f, h-l), especially in the J-RT agroforestry system (58% on average; Fig. 1h-l). In the J-RT agroforestry system, the water absorption patterns of the intercropped plants (including trees, shrubs and herbs) of rubber trees exhibited high similarity (Fig. 1h-l). Because bamboo, which belongs to the true grass family *Poaceae*, is very tall relative to other herb species, it was listed separately. However, as a special grass species spread throughout the J-RT agroforestry system (Fig. S1), bamboo mainly absorbed surface and shallow soil water (49.2% on average from the 0–15 cm soil layer; Fig. 1i), similar to the other neighboring plants of rubber trees. This is mainly because bamboos have a shallow, rhizomatous root system that grows horizontally and can spread out several meters from the original plant, but bamboo roots do not penetrate deep into the soil (Tong et al., 2019; Kaushal et al., 2020).

Tea trees in all agroforestry systems exhibited similar water absorption patterns. In the RT agroforestry system, water was primarily absorbed by tea trees from the surface and shallow soil layers (63.7% from the 0–15 cm soil layer; Fig. 1c), and the results were similar for tea trees in the J-RT agroforestry system (64.5% from the 0–15 cm soil

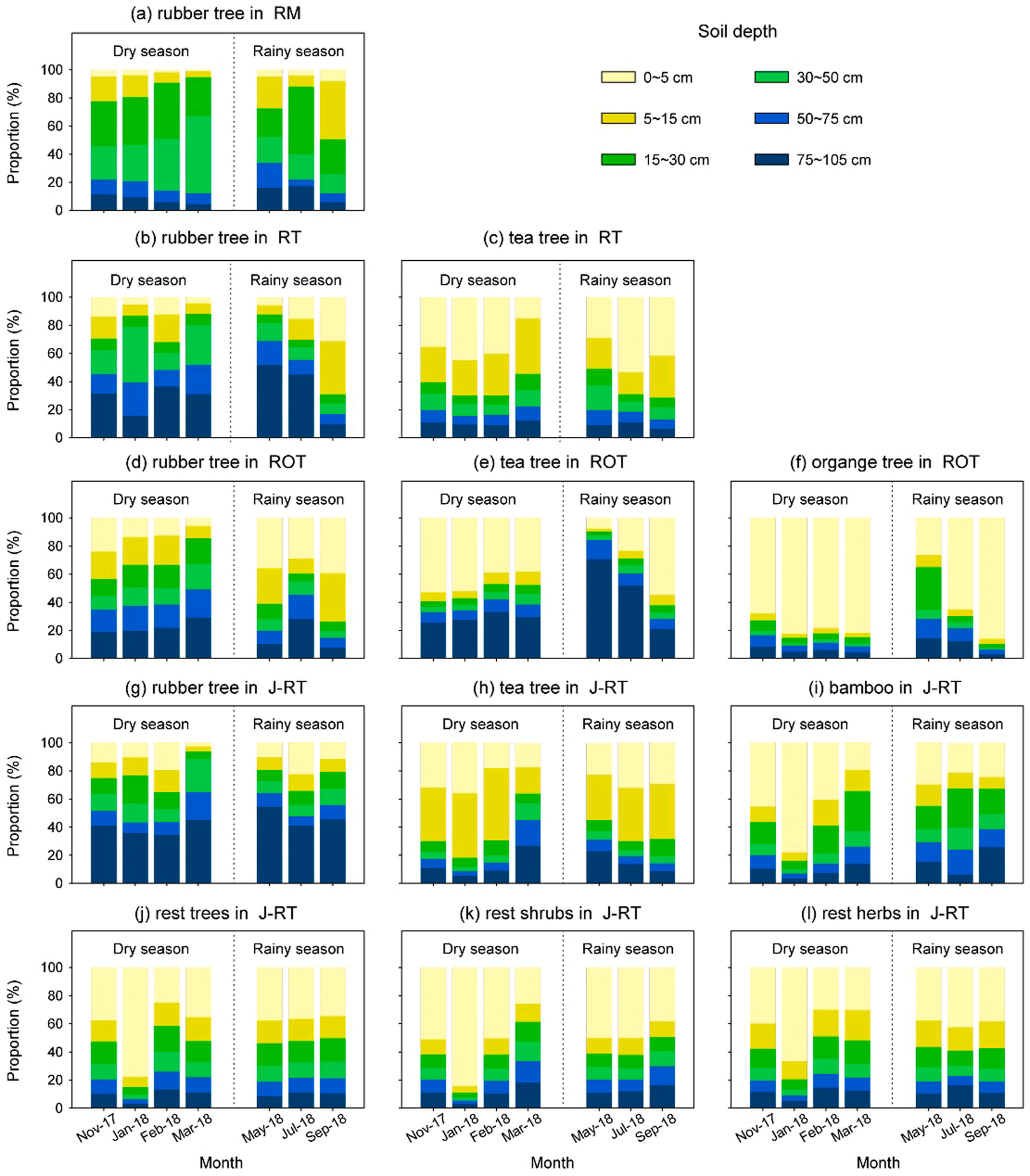


Fig. 1. Seasonal variations in plant water sources in (a) RM, (b-c) RT, (d-f) ROT and (j-l) J-RT. RM stands for rubber monoculture; RT stands for rubber–tea agroforestry system; ROT stands for rubber–orange–tea agroforestry system; J-RT stands for jungle-like rubber–tea agroforestry system.

layer; Fig. 1h). In ROT agroforestry, tea trees required a large amount of water from the surface (38.3% on average from the 0–5 cm soil layer), as well as from deep soil layers (45.9% on average from the 50–105 cm soil layers), but intermediate soil water (the 15–50 cm soil layers) contributed very little (15.8% on average) to the water absorption of tea trees (Fig. 1e). Compared to tea trees in the ROT agroforestry system, rubber trees absorbed moisture from the deep and intermediate soil layers (57.2% on average from the 15–105 cm soil layers; Fig. 1d), and orange trees absorbed a large amount of water from the surface soil layers (69.6% on average from the 0–5 cm soil layer; Fig. 1f).

As the number of intercropped species increased, seasonal variations in plant water absorption patterns tended decrease, such as rubber trees in the J-RT agroforestry system mainly absorbing deep soil water (53% on average from the 50–105 cm soil layers; Fig. 1g) in both the dry and the rainy seasons. The water absorption patterns of all intercropped species of rubber trees in this complex agroforestry system were relatively stable (58% on average from the 0–15 cm soil layers; the yellow bars in Fig. h-l).

3.2. *Plant leaf $\delta^{13}C$ values*

In the rubber agroforestry systems, rubber trees exhibited higher leaf δ^{13}C values than their neighboring species. Rubber tree leaf δ^{13}C values differed slightly among study sites. Only rubber trees in the J-RT agroforestry system had significantly higher ($P < 0.05$) leaf δ^{13}C values than rubber trees in the ROT agroforestry system (red bars in Fig. 2).

When comparing the δ^{13}C values among agroforestry systems, it can be seen that those in the RT agroforestry system were the highest, followed by those in the ROT, and the lowest leaf δ^{13}C values of tea trees appeared in the J-RT agroforestry system (Fig. 2). The leaf δ^{13}C values of tea trees showed an obvious decrease with an increasing number of neighboring species (green bars in Fig. 2).

In addition, the leaf δ^{13}C values of tea trees were not significantly higher than those of orange trees under ROT intercropping. In the J-RT agroforestry system, the leaf δ^{13}C values of tea trees were significantly higher ($P < 0.01$) than those of bamboo but similar to those of the other shrub species. Shrub species exhibited significantly higher ($P < 0.01$) leaf δ^{13}C values than tree and herb species. In addition, the differences in leaf δ^{13}C values between bamboo and other herb species were not obvious.

3.3. *Status of soil nutrients and water*

The Kaiser—Meyer—Olkin measure of sampling adequacy (KMO values = 0.814; $P < 0.001$) in the scree plot and the percentage of variance explained by the first nine principal components (83.771%) were high (Fig. S2). Data on soil nutrient concentrations and soil water content in different soil layers were suitable for PCA. Therefore, nine principal components were extracted. Based on the loadings of each principal component (i.e., PC1-PC9) for different variables in the rotated component matrix (Table 1), PC1 was labeled as “soil K levels”, PC2 was labeled as “soil Mg levels”, PC3 was labeled as “soil Ca levels”, PC4 was labeled as “SWC levels”, PC5 was labeled as “soil P levels”, PC6 was labeled as “levels of C and N in 50–105 cm soil”, PC7 was labeled as “levels of C and N in 15–50 cm soil”, PC8 was labeled as “levels of C and N in 5–15 cm soil”, and PC9 was labeled as “levels of C and N in 0–5 cm soil”.

Subsequently, a general linear model was applied to test for differences in these nine components among the study sites based on the Z scores generated by PCA. Based on the comparison results, the concentration of K within the RT intercropping soil was the most abundant (Fig. 3a), followed by that in the RM, ROT and J-RT agroforestry systems. Similarly, soil Mg was most abundant in the RT agroforestry system, followed by the J-RT agroforestry system, ROT agroforestry system and RM (Fig. 3b). Soil Ca was also most abundant in the RT agroforestry system, followed by the J-RT agroforestry system and the RM and ROT agroforestry systems (Fig. 3c). However, the concentration levels of soil P were the highest in RM relative to rubber agroforestry systems, and there was no significant difference among the agroforestry systems (Fig. 3d). Differences in the SWC among the sites were significant ($P < 0.01$), and the SWCs were highest in the ROT agroforestry system, followed by the RT, RM, and J-RT agroforestry systems (Fig. 3e). In the 0–5 cm and 15–50 cm soil layers, no significant differences were found in the soil C and N levels (Fig. 3f, h). Nevertheless, the soil C and N concentrations in the RM were significantly lower ($P < 0.01$) than those in the rubber agroforestry system in the 5–15 and 50–105 cm soil layers (Fig. 3g, i). In general, soil resources, including nutrients and water, were most abundant in the RT intercropping system, followed by the ROT, RM and complex J-RT agroforestry systems, based on the composite scores of the PCA results (Fig. 3j).

3.4. *Plant nutrient status*

The KMO values (0.714) in the scree plot and the percentage of variance explained by the first five principal components (71.727%) indicated that the nutrient data of plant organs in different study sites were suitable for PCA (Fig. S3). Therefore, five principal components were extracted. Based on the loadings of each principal component (i.e., PC1-PC5) for different variables in the rotated component matrix (Table 2), PC1 was labeled as “the concentration levels of Mg and Ca of the whole plant”, PC2 was labeled as “P concentration levels of plant roots and stems”, PC3 was labeled as “C concentration levels of the whole plant”, PC4 was labeled as “N concentration levels of plant roots and stems”, and PC5 was labeled as “N, P and K concentration levels of plant leaves”.

Subsequently, a general linear model was applied to assess the differences in these five components for the different plants among the study sites based on the Z scores generated by PCA.

Comparisons of the Ca and Mg concentrations among different study sites revealed no significant differences in rubber tree nutrient status (Fig. 4a). Rubber trees had the highest P concentrations in roots and

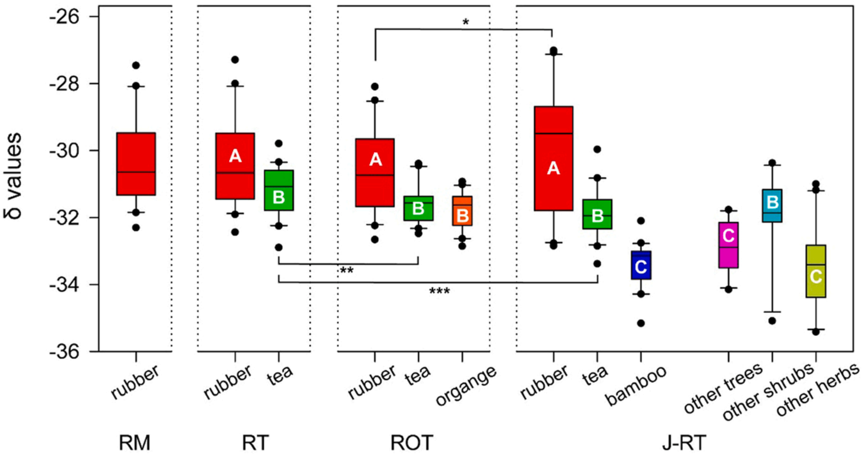


Fig. 2. Leaf δ^{13}C values of different plants at different study sites. Different capital letters indicate significant species differences within the same study site ($p \le 0.05$). See Fig. 1 for the explanations of RM, RT, ROT and J-RT. Asterisks indicate significant differences for the same species among study sites (mainly for rubber tree and tea tree; * indicates $P \le 0.05$, ** indicates $P \le 0.01$, *** indicates $P \le 0.001$).

Table 1
Rotated component matrix: results of principal component analysis of soil nutrients and water.

Items	Components								
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Soil K in S3	**0.94**	0.19	0.12	0.17	0.06	0.05	-0.04	0.00	0.00
Soil K in S4	**0.94**	0.15	0.10	0.19	0.03	0.06	-0.04	0.02	0.02
Soil K in S2	**0.94**	0.20	0.13	0.16	0.05	0.05	0.01	0.01	-0.04
Soil K in S5	**0.93**	0.19	0.09	0.20	0.05	-0.05	0.00	0.01	-0.01
Soil K in S1	**0.92**	0.19	0.15	0.19	-0.02	0.09	0.03	-0.03	0.06
Soil K in S6	**0.92**	0.20	0.06	0.20	0.06	-0.04	0.03	0.01	0.00
Soil Mg in S5	0.19	**0.88**	-0.28	0.04	-0.12	0.12	0.03	0.07	-0.04
Soil Mg in S3	0.20	**0.88**	-0.28	0.07	-0.11	0.20	0.02	0.08	-0.04
Soil Mg in S1	0.25	**0.87**	-0.20	0.06	-0.11	0.22	0.03	0.14	-0.04
Soil Mg in S4	0.20	**0.86**	-0.28	0.02	-0.13	0.16	-0.01	0.09	-0.06
Soil Mg in S2	0.21	**0.86**	-0.19	0.10	-0.08	0.17	0.00	0.13	-0.08
Soil Mg in S6	0.27	**0.84**	-0.20	-0.01	-0.12	0.15	0.06	0.06	-0.08
Soil Ca in S5	0.13	-0.22	**0.92**	-0.07	-0.01	0.09	-0.02	0.08	0.02
Soil Ca in S4	0.14	-0.23	**0.91**	-0.08	0.00	0.12	0.07	0.10	0.00
Soil Ca in S3	0.13	-0.28	**0.86**	-0.11	-0.06	0.09	0.09	0.10	0.07
Soil Ca in S6	0.13	-0.24	**0.85**	-0.07	0.06	0.08	0.01	0.11	-0.08
Soil P in S5	0.00	0.03	**0.70**	-0.06	0.39	0.04	-0.21	-0.20	0.13
Soil Ca in S2	0.21	-0.35	**0.68**	0.04	0.21	0.06	0.20	0.20	-0.09
Soil Ca in S1	0.05	-0.02	**0.61**	0.24	0.16	-0.06	0.14	0.52	-0.16
Soil P in S6	-0.19	-0.06	0.38	-0.22	0.34	0.12	-0.31	-0.16	0.11
SWC in S4	0.30	0.09	0.01	**0.84**	0.07	0.02	0.11	-0.11	0.04
SWC in S3	0.23	0.07	-0.06	**0.80**	-0.05	-0.10	0.30	0.04	0.06
SWC in S2	0.26	-0.01	-0.16	**0.78**	-0.12	-0.12	0.11	0.15	0.19
SWC in S1	0.10	0.18	-0.08	**0.72**	-0.14	-0.05	-0.07	0.39	0.02
SWC in S5	0.43	-0.02	-0.02	**0.69**	-0.06	0.34	0.01	-0.11	0.10
Soil P in S4	0.06	0.03	0.26	-0.11	**0.83**	-0.01	-0.01	-0.09	0.11
Soil P in S3	0.03	-0.21	0.08	-0.05	**0.80**	-0.06	0.07	0.08	-0.12
Soil P in S1	0.06	-0.20	0.05	-0.06	**0.74**	-0.07	0.11	0.29	-0.03
Soil P in S2	0.09	-0.30	-0.18	0.01	**0.64**	0.02	0.14	0.07	-0.27
Soil C in S6	-0.06	0.24	0.07	-0.23	-0.04	**0.83**	0.01	0.16	-0.12
Soil N in S6	0.18	0.33	0.11	0.08	0.02	**0.80**	0.07	0.20	0.02
Soil C in S5	-0.17	0.41	0.21	-0.08	-0.02	**0.71**	0.17	-0.12	0.11
Soil N in S5	0.16	0.42	0.21	0.20	-0.01	**0.64**	0.16	-0.05	0.17
SWC in S6	0.40	-0.21	-0.05	**0.50**	-0.12	**0.51**	-0.11	-0.04	0.01
Soil C in S3	-0.13	-0.13	-0.04	0.04	0.00	0.06	**0.86**	-0.08	0.21
Soil N in S3	0.11	0.01	0.02	0.21	0.00	0.03	**0.82**	-0.04	0.27
Soil C in S4	-0.15	0.23	0.13	0.00	0.41	0.16	**0.67**	-0.21	-0.08
Soil N in S4	0.08	0.35	0.21	0.22	0.42	0.16	**0.63**	-0.16	0.04
Soil C in S1	-0.07	0.26	0.22	0.05	0.14	0.15	-0.22	**0.81**	0.12
Soil N in S1	-0.02	0.35	0.24	0.08	0.10	0.14	-0.21	**0.78**	0.19
Soil C in S2	-0.07	-0.18	-0.06	0.14	-0.05	0.02	0.16	0.04	**0.86**
Soil N in S2	0.11	-0.04	0.04	0.13	-0.11	0.04	0.24	0.13	**0.84**

Note: Using varimax rotations with Kaiser normalization, the principal components were extracted. The rotation converged in 11 iterations. "PC" is the abbreviation of "principal component". S1-S6 represent the 0–5 cm, 5–15 cm, 15–30 cm, 30–50 cm, 50–75 cm, and 75–105 cm soil layers, respectively.

stems under ROT intercropping, followed by RT and RM, and the lowest concentrations were found in the J-RT agroforestry system (Fig. 4b). However, the C concentration levels of the whole rubber tree were the highest in the J-RT agroforestry system, with little difference among the study sites (Fig. 4c). The N concentration levels in the roots and stems of the rubber trees were lowest in the RM, with little difference (Fig. 4d). The N, P, and K concentrations in leaves were highest in the ROT agroforestry system, followed by the RM and then the J-RT and RT agroforestry systems (Fig. 4e).

Comparisons of the nutrient status of tea trees among different study sites revealed that the Ca and Mg concentrations of tea trees did not differ significantly (Fig. 5a). The roots and stems of tea trees planted in the J-RT agroforestry system had significantly lower P concentration levels ($P < 0.01$; Fig. 5b), and the C concentration of whole tea trees (Fig. 5c) and the N concentration of tea roots and stems were significantly higher ($P < 0.01$; Fig. 5d). In addition, compared to those in the RT and J-RT agroforestry systems, the N, P, and K concentrations of tea leaves were significantly lower in the ROT system ($P < 0.01$; Fig. 5e). In general, the nutrient status of rubber trees was better in the RT and ROT agroforestry systems than in the J-RT agroforestry system based on a comparison of the composite scores of the nutrient status of tea trees.

In the RT agroforestry system, rubber trees exhibited significantly higher ($P < 0.01$) Ca and Mg concentration levels, P concentration levels in roots and stems, and N, P and K concentration levels in leaves than tea trees (Fig. S4a, b, e), but their C concentration levels and N concentration levels in roots and stems were significantly lower ($P < 0.01$) than those of tea trees (Fig. S4c, d). In general, the composite scores of rubber trees were higher than those of tea trees (Fig. S4f).

Orange trees in the ROT intercropping system exhibited higher Ca and Mg concentrations than rubber trees and tea trees (Fig. S5a). The P concentration levels in rubber roots and stems were the highest, followed by those of tea tree and orange tree (Fig. S5b). The C concentration levels of tea tree were the highest, followed by those of rubber tree and orange tree, with no significant differences between them (Fig. S5c). The N concentration levels in the rubber tree roots and stems were the lowest, and those in the tea tree and orange tree exhibited no significant differences (Fig. S5d). In addition, rubber tree leaves had the highest concentrations of N, P, and K, followed by orange tree and tea tree leaves (Fig. S5e). In general, rubber trees had significantly higher ($P < 0.01$) composite scores, followed by orange trees and tea trees (Fig. S5f).

In the J-RT agroforestry system, rubber trees exhibited higher Ca and Mg concentration levels, P concentration levels in roots and stems, and C concentration levels than the other species (Fig. S6a-c). Bamboo exhibited the lowest nutrient levels in all components (Fig. S6a-f). Tea tree exhibited nutrient levels similar to those of the tree and shrub

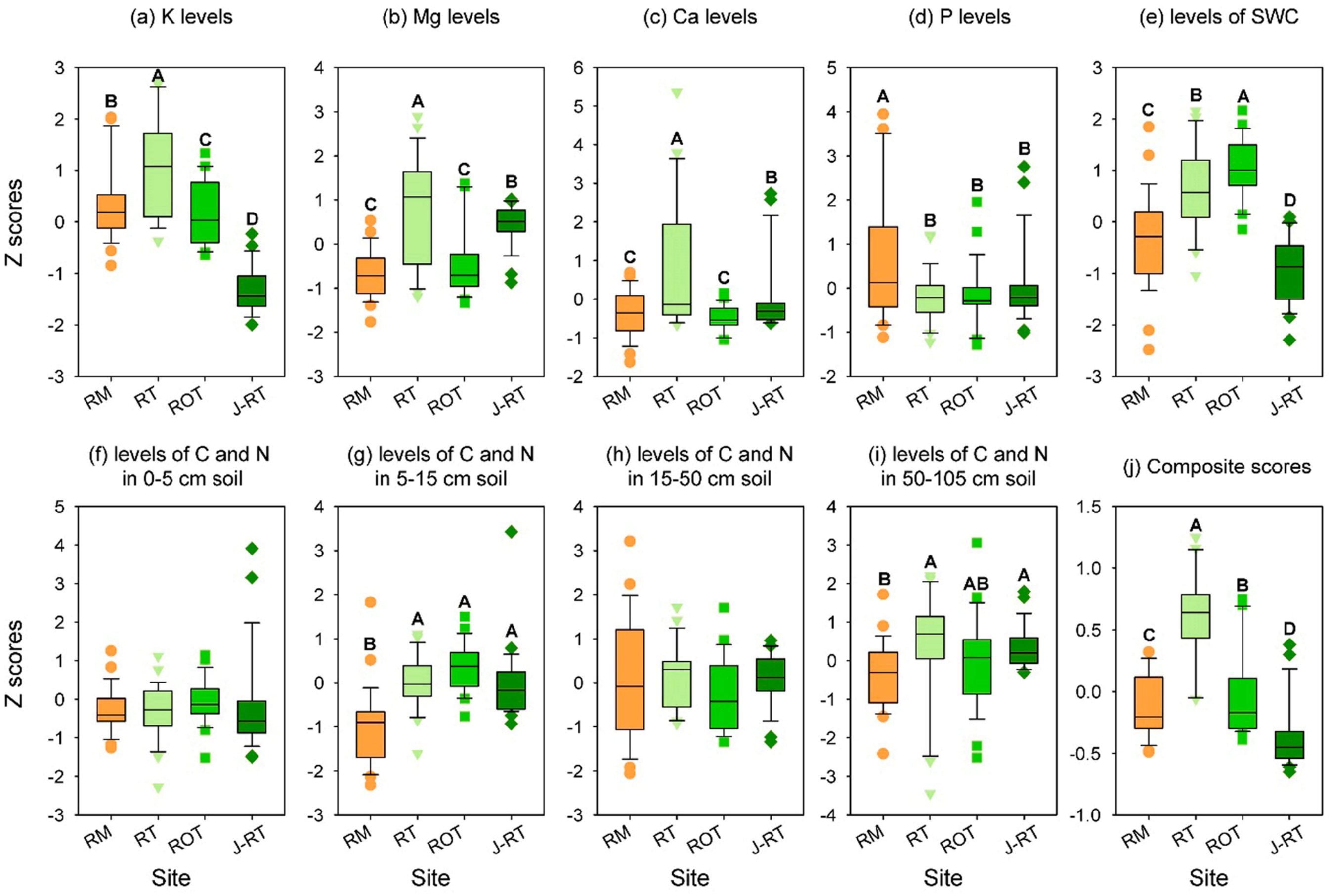


Fig. 3. Comparisons of soil nutrient and water status among different study sites. The results include (a-d) the concentration levels of soil K, Mg, Ca and P; (e) the levels of soil water content (SWC); the concentration levels of soil C and N content in the (f) 0–5 cm, (g) 5–15 cm, (h) 15–50 cm, and (i) 50–105 cm soil layers; and (g) the composite scores of the resources of soil nutrients and water. The visualized data are the generated scores (i.e., Z scores) from principal component analysis of the concentrations of soil C, N, P, K, Ca and Mg and soil water content in different soil layers. Different capital letters indicate significant species differences within the same study site ($P \leq 0.01$). See Fig. 1 for the explanations of RM, RT, ROT and J-RT.

Table 2
Rotated component matrix: results of principal component analysis of the nutrients in plant organs.

Items	Components				
	PC1	PC2	PC3	PC4	PC5
Stem Ca	**0.898**	-0.007	0.102	-0.153	0.041
Leaf Ca	**0.834**	-0.062	-0.103	0.076	-0.246
Root Ca	**0.781**	0.349	0.024	-0.070	0.108
Leaf Mg	**0.729**	0.033	-0.190	0.352	0.041
Stem C	**-0.683**	0.055	**0.574**	-0.159	-0.049
Stem Mg	**0.682**	0.093	-0.142	0.382	-0.116
Stem P	0.002	**0.810**	-0.066	-0.082	0.071
Root P	-0.040	**0.765**	0.051	0.042	0.142
Root Mg	0.277	**0.714**	-0.010	0.057	-0.040
Root K	-0.072	-0.104	**-0.680**	-0.216	-0.047
Root C	-0.229	-0.235	**0.676**	-0.314	-0.011
Leaf C	-0.383	0.406	**0.666**	-0.062	0.070
Stem K	-0.036	0.362	**-0.664**	0.409	0.083
Stem N	0.242	0.108	-0.095	**0.809**	0.062
Root N	-0.001	-0.152	-0.018	**0.759**	0.146
Leaf N	-0.052	0.214	0.203	0.284	**0.820**
Leaf P	0.045	0.436	0.078	-0.265	**0.765**
Leaf K	-0.080	-0.219	-0.243	0.211	**0.761**

Note: Using varimax rotations with Kaiser normalization, the principal components were extracted. The rotation converged in 6 iterations.

species other than rubber tree and itself (Fig. S6a-f). In general, the composite scores were the highest for rubber trees, followed by other shrubs, other herbs, tea trees, other trees, and bamboo (Fig. S6f).

3.5. Litter nutrient status

An obvious phenomenon was that the litter C, N, P, K, Ca and Mg concentrations seemed to always be lower in the J-RT agroforestry system (Fig. 6a-f), especially compared with those in the other two agroforestry systems. Even in the RM, the nutrient status of the litter was not as low as that in the complex jungle-like agroforestry system, and some nutrients, such as P and Mg, were even more abundant than those in the J-RT agroforestry system (Fig. 6c, f). In addition, the litter C:N ratios did not differ significantly among the study sites (Fig. 6g), whereas the litter C:P ratios differed significantly among the study sites ($P < 0.01$): they were higher in J-RT than in the other types of rubber agroforestry systems, which showed no significant difference (Fig. 6h).

4. Discussion

4.1. Plant water use and hydrological niche differentiation

Plant hydrological niches refer to the specific conditions of water availability and soil moisture in which certain plant species grow and thrive (Silvertown et al., 2015). Therefore, hydrological niche differentiation can be defined as plants absorbing water at different rooting depths and thus displaying resource partitioning (Silvertown et al.,

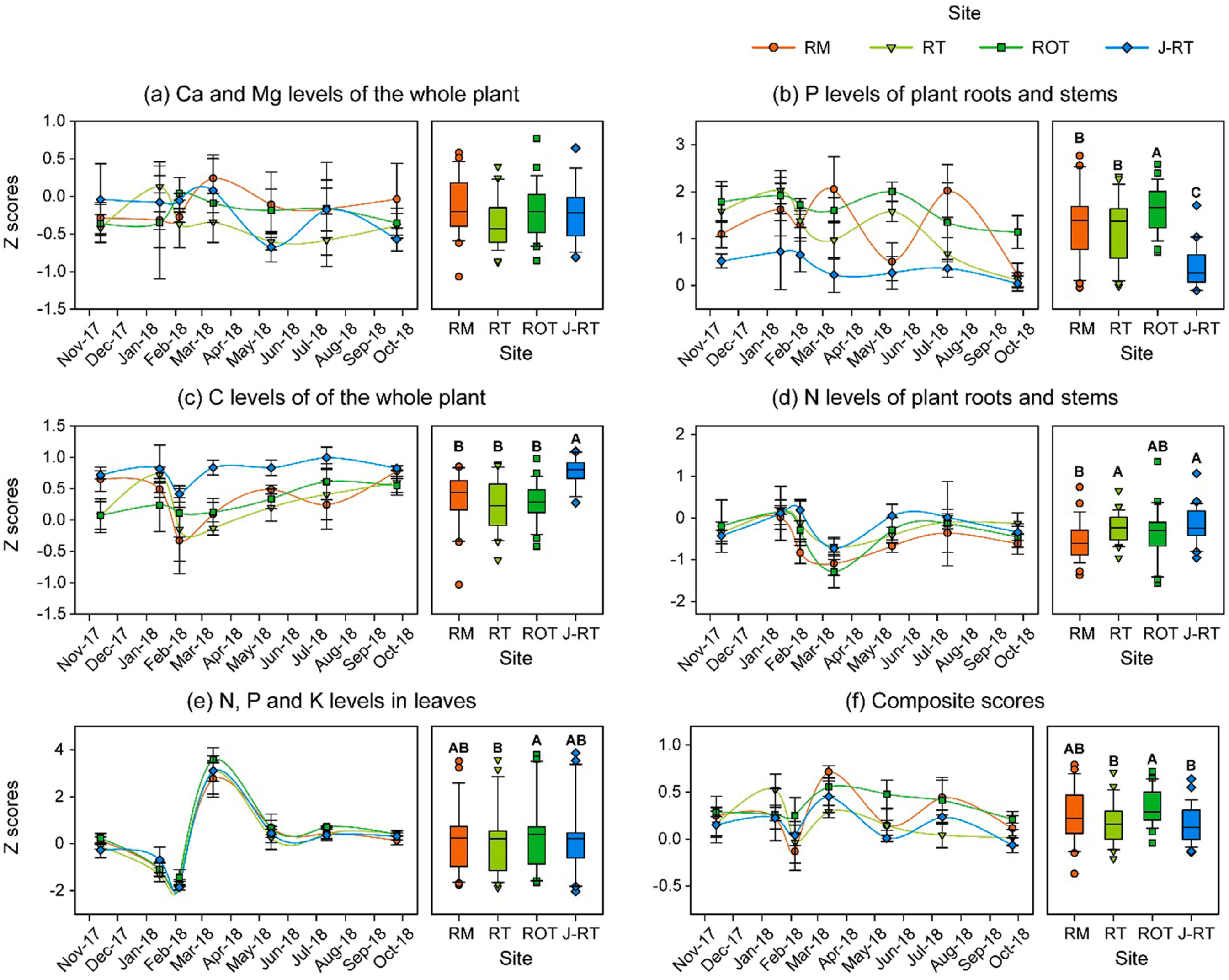
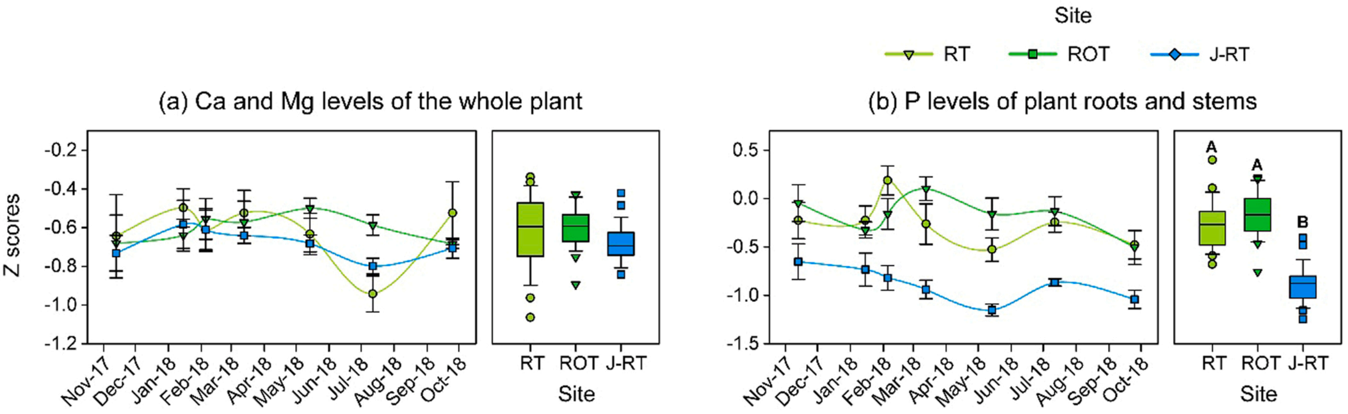


Fig. 4. Nutrient status of rubber trees at different study sites. The results include (a) the concentration levels of Ca and Mg of whole rubber trees; (b) the P concentration levels in the roots and stems of rubber trees; (c) the C concentration levels of whole rubber trees; (d) the N concentration levels in the roots and stems of rubber trees; (e) the N, P and K concentration levels in the leaves of rubber trees; and (f) the composite scores of the nutrient status of rubber trees. The visualized data are the generated scores (i.e., Z scores) from principal component analysis of the concentrations of C, N, P, K, Ca and Mg in different tissues of rubber trees. Different capital letters indicate significant species differences within the same study site ($P \leq 0.01$). See Fig. 1 for the explanations of RM, RT, ROT and J-RT.

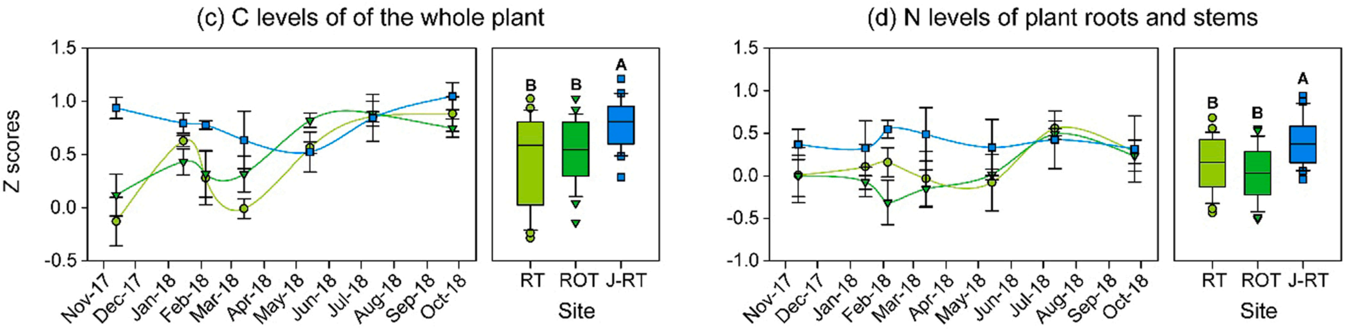
2015). In the agroforestry systems, the amount of water absorbed by rubber trees from deep soil layers was generally much greater, but the intercropped/neighboring species in the agroforestry systems preferred to uptake surface and shallow soil water (Fig. 1). This is easy to understand since the construction of agroforestry systems almost always considers the complementary rooting depths of all plant species. That is, belowground niche differentiation in agroforestry systems is generated by combining deep-rooted and shallow-rooted species; therefore, water and nutrients can be accessed by each species at different depths in the soil and can then assist species with deep roots and shallow roots in acquiring resources (Homulle et al., 2021). Undoubtedly, rubber trees are deeper-rooted species than their intercropped species in rubber-based agroforestry systems, as evidenced by their vertical root length density (Yang et al., 2021), and we also found that almost all intercropped species were shallow-rooted species since their primary water source came from the surface and shallow soil layers (Fig. 1), even the naturally growing species, including the tree species in the J-RT agroforestry system.

Species selection plays an important role in determining the complementarity of root absorption zones in plants, and belowground interspecific competition between rubber trees and their intercropped species plays a vital role in the formation and trend of such complementarity. Obvious evidence was that rubber trees took up increasingly deeper water with the increase in the number of neighboring species (Fig. 1a, b, d, g), from the rubber monoculture to the simple rubber-based agroforestry systems and then to the complex J-RT agroforestry system. Obviously, the plasticity and self-distinction of the root system (Kwasniewski et al., 2016) determine such changes in rubber trees. However, such water uptake of tea trees was small. We assume that there are two reasons for this: (1) tea trees have a relatively fixed water-absorbing zone since the distribution of the root systems of mature tea trees is limited (Feng, 2007), and (2) the upper portion of the soil profile is limited, and plant-absorbing roots cannot extend above the surface (Wu et al., 2022).

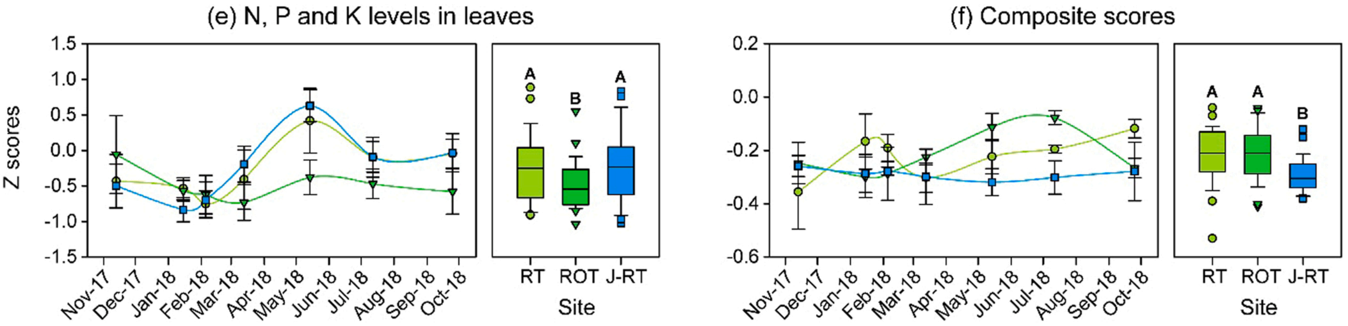
Through the water uptake performance of the intercropped species in the ROT agroforestry system and the performance of these species, including tea trees, in the J-RT agroforestry system, we found that the neighboring species in the same agroforestry system exhibited similar water absorption patterns. This is a noteworthy finding, as it suggests that the similarities in water uptake are not coincidental. Rather, it is likely that the developed root systems of rubber trees took advantage of deep soil resources, thereby limiting and compressing the water-


(a) Ca and Mg levels of the whole plant

(b) P levels of plant roots and stems


(c) C levels of of the whole plant

(d) N levels of plant roots and stems


(e) N, P and K levels in leaves

(f) Composite scores

Fig. 5. Comparisons of the nutrient status of tea trees among different study sites. The results include (a) the concentration levels of Ca and Mg in whole tea trees; (b) the P concentration levels in the roots and stems of tea trees; (c) the C concentration levels in whole tea trees; (d) the N concentration levels in the roots and stems of tea trees; (e) the N, P and K concentration levels in the leaves of tea trees; and (f) the composite scores of the nutrient status of tea trees. The visualized data are the generated scores (i.e., Z scores) from principal component analysis of the concentrations of C, N, P, K, Ca and Mg in different tissues of tea tree. Different capital letters indicate significant species differences within the same study site ($P \leq 0.01$). See Fig. 1 for the explanations of RM, RT, ROT and J-RT.

absorbing zones of their neighboring species (Wu et al., 2022). As a result, the absorbing roots of the neighboring species were concentrated in the upper soil layers. This discovery is particularly important because it implies that intercropped species in agroforestry systems interact with one another and adapt to their environments in unique ways.

From this perspective, rubber trees could be the most competitive species in agroforestry systems because deep-layer resource use could benefit deep-rooted plants more under competition (McNickle and Dybzinski, 2013). The water supply of shallow soil is notoriously unstable, but the content of deep soil water is always adequate, even in the dry season (Wu et al., 2020). Therefore, such a deep-layer use strategy could help rubber trees avoid damage to their permanent tissues from water shortages (Vilagrosa et al., 2012). In addition, increasing deep-growing root hairs could increase the interface between soil and plant roots in the vertical direction and then help deep-layer users increase their potential for nutrient capture from leaching (Pierret et al., 2016).

However, plants are also exposed to some risks under the fixed deep-layer use strategy. For example, (1) the water table increases because of intense rainwater infiltration during the rainy season, and oxygen deficits in the deep soil layers could thereby suppress the activities of deep-growing roots (Pierret et al., 2016; Wu et al., 2022); (2) many soil nutrients decrease with depth, which would not benefit deep-rooted species during the growing season (Del Bianco and Kepinski, 2018; Wu et al., 2020); and (3) when rainwater enters the soil, nutrients can be retained by soil organic matter in the surface and shallow soil, decreasing leaching into the deep soil (Abdalla et al., 2019), and soil organic matter always increases with increasing species composition in the plant community (Wu et al., 2020). These reasons probably explain why the rubber trees still absorbed a certain amount of water from the surface and shallow soil layers, especially during the rainy season, and then exhibited significant seasonal variations ($P < 0.01$; Fig. 1). Clearly, plant root hairs play an important role in guiding rubber tree resource utilization depth, as they detect the availability of both water and nutrients (Kwasniewski et al., 2016).

In terms of water use efficiency (WUE) in C3 plants, leaf δ^{13}C values are an important parameter, and a higher δ^{13}C always corresponds to a higher WUE (Bchir et al., 2016; Sensuła, 2016). Commonly, low WUE (i.e., low δ^{13}C) plants exhibit strong competitive ability since low WUE plants have a higher transpiration rate per unit photosynthesis than do

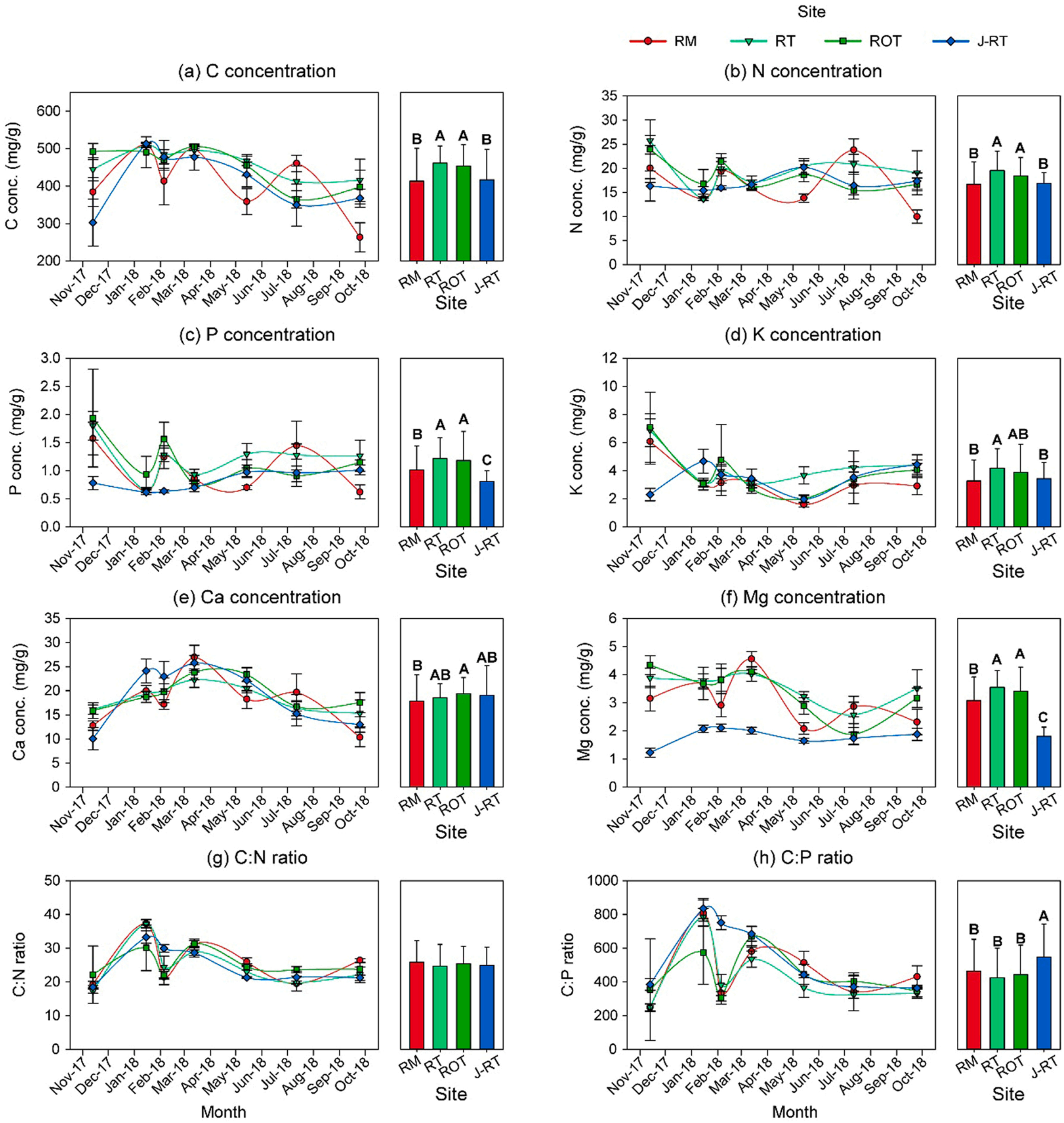


Fig. 6. Seasonal status of litter nutrients among different study sites. The results are shown for (a-f) litter C, N, P, K, Ca and Mg concentrations and (g-h) the C:N and C:P ratios of the litters. Significant differences between the study sites are indicated by different capital letters ($P \leq 0.01$). See Fig. 1 for the explanations of RM, RT, ROT and J-RT.

high WUE plants, resulting from increased water consumption (Campitelli et al., 2016; Lorts and Lasky, 2020). Therefore, through comparisons of the leaf δ^{13}C values of rubber trees at different study sites, we found that rubber tree WUE was not significantly affected by interspecific competition (Fig. 2). Instead, the intercropped or neighboring species of rubber trees exhibited lower WUEs. This result indicates that these neighboring species have a greater ability to acquire contested surface and shallow soil water than do rubber trees. It is worth emphasizing that the greater water-competing ability of neighboring species for shallow soil water does not necessarily mean that they have a competitive advantage in accessing underground resources overall. Rubber trees, for example, have a deeper rhizosphere range, which could increase the probability of nutrient ion acquisition within the soil profile. Additionally, based on the performance of the tea trees, which showed decreasing WUE as species richness increased, we can assume that an increase in plant species richness leads to more intense water competition and a stronger enhancement of the water competitive ability of tea trees. This can be considered an adjustment of the resource use strategies of tea trees since their neighboring species, except rubber trees, all exhibited overlapping water absorption zones in the ROT and J-RT agroforestry systems.

4.2. *Intercropping benefits and competition effects on soil water and nutrients*

Increasing soil fertility through intercropping relative to monoculture could increase soil organic matter (SOM), total nitrogen, and soil macroaggregates (Cong et al., 2015; Li et al., 2021). Plant competition has been shown to improve soil C and N storage when plant species are more diverse (Wang et al., 2020). Competition might stimulate increased plant litter and root exudation as a result (Cong et al., 2015; Laganière et al., 2015). As species composition increases, soil organism diversity increases (Van der Putten et al., 2013), leading to an increase in the soil carbon and nitrogen contents (Brooker et al., 2015). In this study, our observations of higher levels of soil C and N in the agroforestry systems than those under rubber monoculture also supported the above findings, especially for shallow (5–15 cm; Fig. 3 g) and deep (50–105 cm; Fig. 3i) soil layers, which were the obviously differentiated water absorption zones between the intercropped species and rubber trees.

However, plant interspecific competition belowground would consume much more soil nutrients since root length would be maximized to prevent nutrients from being shared with neighbors under nutrient competition (Craine and Dybzinski, 2013). Plants may increase root density in shallow soil or increase rooting depths to maximize the nutrient ion acquisition probability during the movement of soil water (Trinder et al., 2013). Consistent with this, we found that soil nutrients generally first increased and then decreased with increasing species richness (Fig. 3a-d). This result implied that intercropping benefits would be offset by increasingly intense competition among plants, and the key driver of this trade-off was the complexity of species composition or species richness.

As a soil resource, water can also be a source of competition, but water availability is generally influenced by both biotic and abiotic factors (Craine and Dybzinski, 2013). Based on our observation results, soil water also first increased and then decreased as species richness increased (Fig. 3e). The increase in SWC may result from increasing vegetation coverage, which could decrease soil evaporation and improve rainfall interception, and from increasing soil C and N, since soil organic matter would lead to better soil porosity and, in turn, enhance soil water infiltration and soil water retention (Zhu et al., 2019, 2022). However, improved soil porosity makes soil loose enough for plant roots to more easily take up soil water (Zeng et al., 2021). In short, the soil in agroforestry systems can let water flow through, hold water for later uptake, and help plants absorb water more easily. Since the WUE of the intercropped species of rubber trees was lower (Fig. 2), the agroforestry system consumed much more water from soil with the increase in the intercropped species richness in the agroforestry system. Therefore, the SWCs were the lowest in the J-RT agroforestry system, which had the highest species richness.

In general, soil resources initially increase but later decrease with an increase in the diversity of intercropped species in rubber-based agroforestry systems (Fig. 3j). However, the key mechanisms behind this are still unclear, and additional research is needed to fully understand the effects of intercropping on soil structure and function across a range of soil types and environmental conditions. This is particularly important in relation to the long-term sustainability of these systems.

4.3. *Plant and litter nutrient status in response to belowground competition*

The C levels of whole rubber trees were greatly improved in the J-RT agroforestry system (Fig. 4c). The levels of N in rubber tree roots and stems (Fig. 4d) were improved in all rubber-based agroforestry systems, but the P levels of those organs of rubber trees were the lowest in this agroforestry system (Fig. 4b). Meanwhile, the levels of Ca and Mg in whole rubber trees (Fig. 4a) and the concentrations of leaf N, P, and K in rubber trees varied little or not at all across study sites (Fig. 4e).

Notably, the stems and roots of terrestrial plants are considered their nutrient storage organs, where they store nutrients that are nonlimiting to growth and from which they draw nutrients when growth demands exceed soil nutrient uptake (Mengel et al., 2001). Meanwhile, plant leaves are typically in charge of generating energy and organic compounds for plant growth and ecophysiological activity through photosynthesis (Fernández-Marín et al., 2020). Therefore, plant nutrients, especially N and P, are typically enriched in leaves due to their importance in metabolism.

Relating to the status variations in soil nutrients from the monoculture to the simple and complex agroforestry systems (Fig. 3), the decreasing P status of rubber tree nutrient storage organs (Fig. 4b) was probably affected by the decline in soil P (Fig. 3d) and by nutrient transport to rubber tree leaves to maintain photosynthesis and the normal ecophysiological functions of rubber trees. Therefore, the N, P and K, as important nutrients in rubber leaves, varied little from the rubber monoculture to the agroforestry systems (Fig. 4e). In addition, variations in plant tissue C reflect differences in photosynthetic product distribution and utilization (Han et al., 2011; Xing et al., 2021). Therefore, the higher C levels of the whole rubber tree but fewer nutrients within the soil and rubber tree tissues indicated that rubber trees have a higher resource use efficiency in the J-RT agroforestry systems. Similarly, with the increase in species richness, tea trees exhibited less nutrient storage but more photosynthetic products than rubber trees (Fig. 5). Therefore, we conclude that intense competition among the species enhanced plant nutrient use efficiency. However, it is worth emphasizing that facilitating functions do not always exist since the relationships between soil nutrients and plant resource uptake in intercropping systems are complex. Different plants can have complementary or competitive effects on each other's nutrient absorption in the intercropping system, and in some cases, plants may cooperate to promote nutrient uptake (Wang et al., 2022).

In terrestrial ecosystems, plant litter plays an important role in energy and nutrient cycling (Zechmeister-Boltenstern et al., 2015); therefore, litter quality can partly reflect the nutrient status of the plant community. In this study, the nutrients and even the carbon concentrations increased in the simple rubber agroforestry systems (i.e., RT and ROT) and then decreased to the level observed under monoculture in the complex J-RT agroforestry system (Fig. 6a-f). In addition, negative correlations existed between the litter C:N/C:P ratios and decomposition rates (Chapin et al., 2011). Therefore, the litter C:N ratios exhibited no significant difference among the study sites, indicating that N release from the litter was not changed by competition, but the significantly higher ($P < 0.01$) ratios of litter C:P in the J-RT agroforestry system indicated that P release from the litter would be smaller relative to the other sites. Therefore, the P shortage resulting from the increasing species richness was obvious in the J-RT agroforestry system.

Although P shortages are common in tropical forests, plants can still grow quickly in diverse forests with high species richness (Turner et al., 2018). Nevertheless, high P and water environments may also intensify asymmetric interspecific competition in intercropping systems (Zhu, X. et al., 2022). In short, biodiversity had a facilitative effect on agroecosystem productivity, and plant-plant facilitation was driven by interspecific rhizosphere interactions that were associated with soil acidification and microbial community promotion under P-deficient conditions (Zhu, S.G. et al., 2022, 2023). However, in complex rubber-based agroforestry systems, P shortages and the related improvement measures cannot be ignored, as P shortages can significantly impact latex yield and pose a high risk. The selection of species intercropped with rubber trees should be performed carefully since rubber trees exhibit a greater nutrient absorption advantage, as suggested by the generally higher nutrient status of rubber trees than of their intercropped species (Figs. S4–6).

However, in terms of the performance of plants and soil, the complex J-RT agroforestry system shares some similarities with tropical forests (Zeng et al., 2021). For example, it has poor soil quality but better soil physical properties, rapid nutrient turnover, and higher nutrient and WUE in plants (Park, 2002).

5. Conclusion

Complementary water-absorbing patterns commonly exist between rubber trees and tea trees when they are planted together, and with an increase in the composition of other species, the hydrologic niche differentiation between rubber trees and the intercropped plants becomes more obvious primarily because rubber trees take up deeper soil water as the number of competitors increases. However, negative competition effects offset the intercropping benefits for soil nutrients and water.

Typically, soil resources first increase and then decrease with increasing species richness. However, the WUE and nutrient status of rubber trees may be slightly affected even in complex agroforestry systems, while the intercropped species would experience resource shortages since their water-absorbing zones mostly overlap and the P shortage is serious. Undoubtedly, rubber trees are the most competitive species in agroforestry systems. Therefore, we suggest that the construction or improvement of rubber-based agroforestry systems avoid interplanting too many species. However, for specific purposes, such as restoration from rubber plantations to tropical forests, we suggest applying appropriate phosphate fertilizer to agroforestry systems to facilitate the growth of restoration species.

Declaration of Competing Interest

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Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agwat.2023.108353.

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