Agricultural and Forest Meteorology 320 (2022) 108953

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Plant hydrological niches become narrow but stable as the complexity of interspecific competition increases

Junen Wu[b,c,#,*], Huanhuan Zeng[a,d,#], Fan Zhao[a], Chunfeng Chen[a,*], Ashutosh Kumar Singh[a], Xiaojin Jiang[a], Bin Yang[a], Wenjie Liu[a,*]

[a] *CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan, 666303, China*
[b] *GIS Technology Research Center of Resource and Environment in Western China, Ministry of Education, Yunnan Normal University, Yunnan 650500, China*
[c] *Yunnan Key Laboratory of Plateau Geographical Processes and Environmental Change, Faculty of Geography, Yunnan Normal University, Yunnan, 650500, China*
[d] *University of Chinese Academy of Sciences, Beijing, 100049, China*

ARTICLE INFO

Keywords:
Belowground resource
Competition dynamics
Plant water use
Resource partitioning
Stable isotope
Tropical rainforest

ABSTRACT

Plant competition is a determinant of plant community formation, while resource partitioning is regarded as a critical factor for maintaining species coexistence under competition. However, how resource partitioning varies with species richness remains unclear; additionally, empirical studies of the dynamic processes involved in plant resource competition, especially that for belowground resources, are urgently needed. Here, we used the stable isotope approach to study the temporal dynamics of plant hydrological niches from species-poor to species-rich communities (including monocultural plantations, agroforestry systems and more diverse tropical rainforests) in a tropical area of southwestern China. We found that plant species in multispecies communities could be divided into two groups by comparison of their hydrological niches: deep-resource users and shallow-resource users. Resource partitioning was obvious between these two groups. However, resource partitioning was narrower within deep and shallow-resource users. In addition, with an increase in species richness, the general tendency of resource partitioning among all species became not just increasingly narrow but also uniform and stable. When we combined this information with data on belowground resource distribution and its correlations with plant resource use, we also found that the greater the species diversity and the smaller the resource use advantages among species, the easier it was for the species to achieve “competitive reversals”. This study confirmed the generality of the seasonal segregation of the plant hydrological niche and demonstrated that variations in both environmental resources and plant resource partitioning weaken the resource use advantages of species, representing an important mechanism that helps maintain the coexistence of competing species in a species-rich community. These findings therefore provide novel insights for understanding species combinations and plant belowground interactions in complex communities and will be beneficial for seeking solutions to some important ecological issues, such as reconstruction of tropical rainforests.

1. Introduction

Although studies of plant resource competition have been conducted across almost all biomes over the past 100 years, plant competition is still a simultaneously familiar and unfamiliar concept for most ecologists, and the debates surrounding the mechanism of resource competition seem never-ending (Trinder et al., 2013; Aschehoug et al., 2016). One of the most important reasons for this contradiction is that conventional experimental approaches have many limitations in revealing plant competition processes, such as biomass-based methods (Trinder et al., 2013). In addition, studying plant belowground competition still faces a major challenge due to the difficulty of observing plant resource use dynamics below the ground (Craine and Dybzinski, 2013). Consequently, developing a straightforward and easily analyzable method for studying the dynamic process of plant belowground competition at fine spatiotemporal scales is a necessity (Craine and

---

* Corresponding authors at: Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China.

E-mail addresses: johnwu2012@qq.com (J. Wu), chenchunfeng@xtbg.ac.cn (C. Chen), lwj@xtbg.org.cn (W. Liu).

[#] These authors contributed equally: Junen Wu, Huanhuan Zeng.

https://doi.org/10.1016/j.agrformet.2022.108953
Received 30 September 2021; Received in revised form 1 April 2022; Accepted 6 April 2022

Dybzinski, 2013; Trinder et al., 2013; Chitra-Tarak et al., 2018; O'Keefe et al., 2019; Kulmatiski et al., 2020). In addition, a new study approach is expected to verify the maintenance mechanism of species coexistence with more considerations of environmental heterogeneity (Craine and Dybzinski, 2013), niche differentiation (Schwinning and Kelly, 2013), climate change (Alexander et al., 2015), plant game strategies (McNickle and Dybzinski, 2013), competitive intransitivity (Soliveres and Allan, 2018), and high-order interactions (Bairey et al., 2016; Grilli et al., 2017; Levine et al., 2017; Mayfield and Stouffer, 2017).

It is possible that stable isotope approaches, which can be applied to reconstruct plant resource use patterns, could provide solutions (Dawson et al., 2002; O'Keefe et al., 2019). Especially in recent years, great improvements in measurement techniques and analytic methods have overcome many limitations of stable isotope application (Boecklen et al., 2011; Phillips et al., 2014). The stable isotope approach is therefore already the "industry standard" in numerous tracer research fields, especially in hydrological studies (Fry, 2006; Phillips et al., 2014; Beyer and Dubbert, 2019). Water is the most basic resource for plants, and plants absorb it mainly through root hairs (Gilroy and Jones, 2000). Because water enters the cells of plant root hairs by osmosis and water isotope discrimination can be safely neglected in this process, reconstructing plant water use patterns through stable water isotope (i.e., D and ^{18}O) methods could help reveal the distribution of plant root hairs (i.e., absorptive roots; Dawson et al., 2002; Kulmatiski et al., 2020). Through this technique, information on plant nutrient use can also be revealed because absorbable forms of soil nutrients for plants (i.e., dissolved nutrients) are mainly transported by soil water (Hopmans and Bristow, 2002; Silvertown et al., 2015), and root hair is also the main nutrient-absorbing organ (Gilroy and Jones, 2000).

In fact, studying plant water use patterns to reveal plant hydrological niches in terrestrial plant communities is regarded as a breakthrough for understanding the species combination, competition strategies, and coexistence mechanisms in plant communities (Araya et al., 2011; Silvertown et al., 2015), especially at the fine scales of space and/or time (Letten et al., 2015; O'Keefe et al., 2019; Kulmatiski et al., 2020). However, very few studies have conducted an empirical analysis of the high-resolution dynamics of hydrological niches among Multiple species in diverse forests (Chitra-Tarak et al., 2018; O'Keefe et al., 2019); thus, fundamental empirical questions based on a theoretical understanding of how competition and coexistence work remain unanswered (Levine and Hart, 2020). Since multiple spatiotemporal niches by rooting depth may evolve due to the stochastic nature of precipitation events

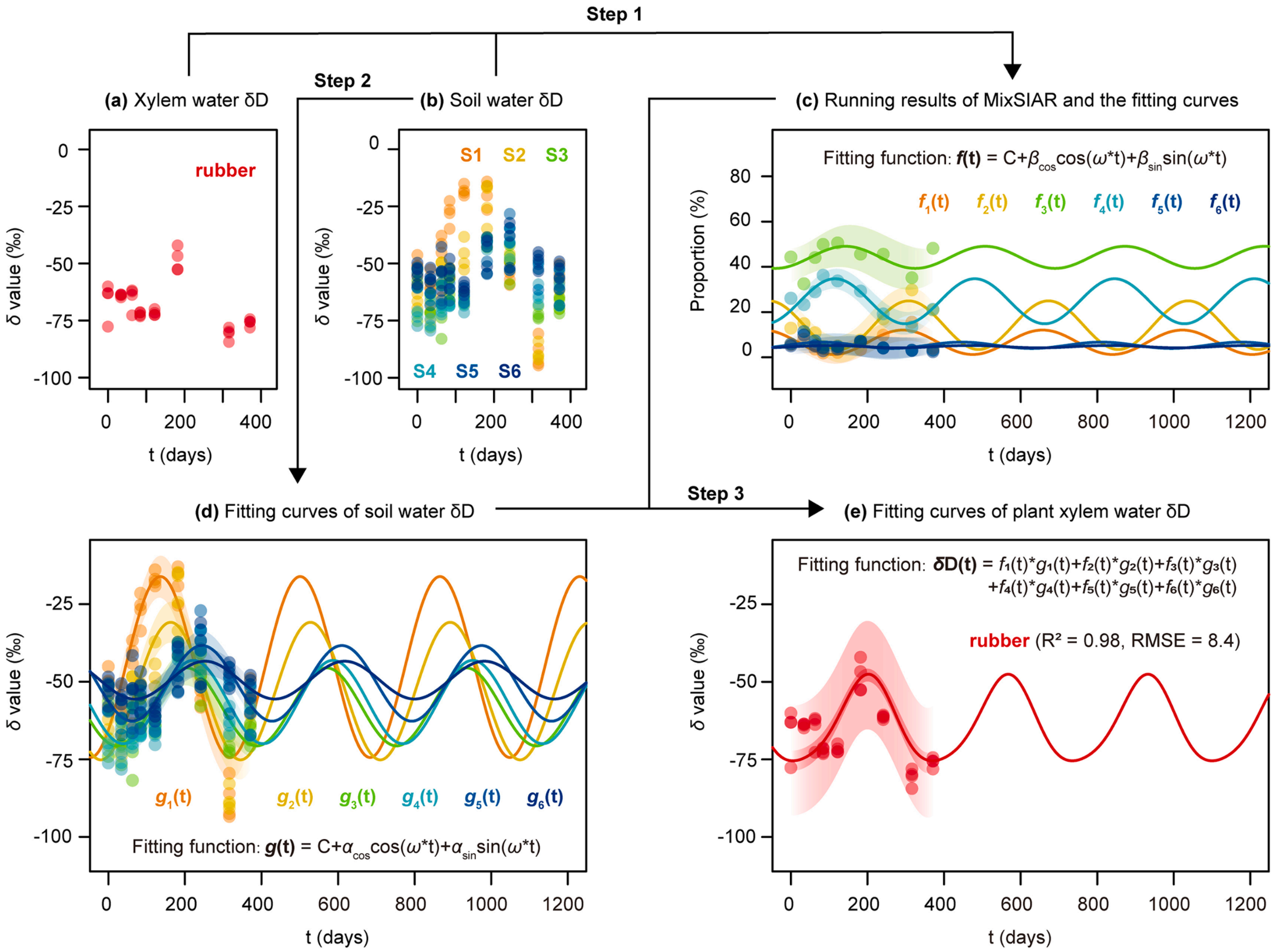

Fig. 1. An example of the reconstruction of the isotopic signal of the xylem water of rubber trees. (a) Measured data of xylem water δD of the rubber tree in rubber monoculture. (b) Measured data of soil water δD within six sampled soil layers in rubber monoculture. (c) Calculated results of the water use proportions of rubber trees within different soil layers using MixSIAR and the fitting curves of the water use proportions of rubber trees. (d) The fitting curves of the soil water δD values within different soil layers. (e) The fitting curves of the xylem water δD of the rubber tree. S1–S6 represent six sampled soil layers (i.e., 0–5 cm, 5–15 cm, 15–30 cm, 30–50 cm, 50–75 cm, and 75–105 cm). The 95% confidence band (translucent ribbon) is shown around each fitting curve in (c) and (d). The 95% prediction band (wide translucent ribbon) is shown around the fitting curve of plant xylem water δD in (e).

combined with complex temporal patterns of water movement through the vadose zone (Chitra-Tarak et al., 2018), studying the fine-scale variations in plant hydrological niche segregation in space and time therefore becomes an important first step for understanding plant dynamic foraging and will hopefully provide a stimulus for studying the maintenance of within-community plant diversity (Letten et al., 2015; Kulmatiski et al., 2020).

Here, to explore the belowground competition dynamics among plant species from pairwise interactions to high-order interactions, we mainly used stable hydrogen isotopes in plant and soil water to estimate plant water use patterns in six forest communities (including a monocultural rubber plantation, rubber agroforestry systems and more diverse tropical rainforests; Fig. S1) across a diversity gradient. We applied a novel approach that integrates the spatiotemporal variation information of source water and plant water use to reconstruct the isotopic signals of plant xylem water of all studied species (see example in Fig. 1). Then, we compared the differences in signals among the coexisting species to study the dynamic differences in plant resource partitioning in the context of belowground competition. Using this approach, we addressed the following questions: (1) How does resource partitioning change with the temporal and spatial heterogeneities of belowground resources and with the gradients of species richness? (2) How do plant resource use advantages change with variations in belowground resources and complexities of species interactions? How do plant resource use advantages change with variations in belowground resources and complexities of species interactions?

We hypothesized that (1) the fluctuations in soil water across space and time would lead to changes in plant water use depth, and species with higher resource use plasticity could enlarge their uptake depth and then form the belowground resource partitioning with other species in space and time. Additionally, since the degree of plant rooting depth is limited and plant water uptake plasticity would be different among species, belowground resource partitioning among coexisting species would become increasingly specific and narrow across a diversity gradient (from simple agroforestry system to complex agroforestry system and tropical rainforest) as the result of niche compression through competition among multiple species in limited belowground space. (2) Seasonal variations in belowground resources would lead to fluctuations in resource partitioning, and then, the variations in both belowground resource and plant resource partitioning in space and time would increase the complexity of plant resource use and weaken the resource use advantages (relationship between plant uptake and soil resource) among the coexisting species. Plant resource use advantages would further weaken in response to the increase in species richness as compressed niches accede their similar resource use environment (resource use advantages).

2. Materials and methods

2.1. Study site

The study site is 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. This region is affected by tropical monsoons; a rainy season (from May to October) and a dry season (from November to April) are apparent in this region (Fig. S2). The mean annual precipitation is approximately 1500 mm (from 2005 to 2018; Fig. 4), and the monthly mean air temperature is approximately 22.5 °C.

Through investigations of the species composition in the existing vegetation in XTBG and with consideration given to possible interference factors, including terrain features, distances, and historical disturbances, six plots in XTBG were finally established for this study (Fig. S1, Table S1): rubber monoculture; rubber and orange agroforestry system; rubber and tea agroforestry system; rubber, orange, and tea agroforestry system; jungle rubber agroforestry system (converted from abandoned rubber and tea agroforestry system); and tropical rainforest (a local climatic climax system with stable and rich species composition). In each study plot, a standard and fixed quadrat (20 m × 20 m) was established for periodic sampling for temporal analysis. All of these quadrats have similar altitudes (approximately 520 m) and nearly the same slope aspect (SE 105–107°) and gradient (approximately 25°). The distances among their locations are less than 1 km.

Rubber trees in rubber monoculture and rubber agroforestry systems were planted in 1990 in the deforested rainforest land area, and the intercropped species were planted in 2004. Since 2005, the jungle rubber agroforestry system has been transformed from an abandoned agroforestry system of rubber and tea through secondary succession. The scientific names of each species, species composition, and distribution of all quadrats are displayed in Table S1 and Fig. S1. Weeding was performed in rubber monoculture, rubber-orange, rubber-tea, and rubber-orange-tea agroforestry systems during the study period, and no fertilizer was applied.

2.2. Sampling and measurement methods

Each of the fixed quadrats was divided into four 10 m × 10 m blocks, and then each 10 m × 10 m block was divided into four 5 m × 5 m small blocks. One small block in each large block was randomly selected for soil sampling. That is, four 5 m × 5 m small blocks in each quadrat were selected for soil sampling on each sampling date. Such a design was mainly based on the consideration of the sizes of tree, shrub, and herb species. Considering that plant species composition and distribution in tropical rainforest are quite different in different locations and that the lateral root lengths of shrub and herb species, and even some of the tree species, may not extend more than 10 m, the size of the fixed quadrat in the tropical rainforest was set as 10 m × 20 m. Details of the quadrat design can be found in Fig. S1.

We sampled these quadrats nine times from 2017 to 2018. The sampling dates were November 13, 2017; December 17, 2017; January 15, 2018; February 5, 2018; March 15, 2018; May 14, 2018; July 12, 2018; September 25, 2018; and November 19, 2018. On each sampling day, soils from six different depths (i.e., 0–5 cm, 5–15 cm, 15–30 cm, 30–50 cm, 50–75 cm, and 75–105 cm) in four blocks (5 m × 5 m; random selection; Fig. S1) of each quadrat were obtained using an earth-boring auger (5-cm diameter) and prepared for subsequent extraction of water and nutrient element analysis. See the methods in our published paper (Wu et al., 2020) for more details.

For plant species with many individuals in each quadrat, such as rubber trees, we randomly selected 4–6 individuals for sampling. In the jungle rubber agroforestry system and tropical rainforest (species-rich communities), all tree and shrub species were sampled, but the seedlings and saplings of woody plants (i.e., diameter at breast height $\leq$ 3 cm) and other plant species that could not support long-term samplings (e.g., some herb species with very few individuals) were ignored during sampling. Therefore, only 11 species in the jungle rubber agroforestry system and 15 species in the tropical rainforest were selected for investigation (Table S1). The xylem samples of trees were obtained from their trunks at a height of 1.3 m through an increment borer. The xylem samples of shrubs were obtained from their branches using pruning shears. Each sampled tree or shrub provided 3–4 small 3.5-cm-long cylinders of xylem samples. Since the xylem of herbs was not developed, we directly sampled their coarse roots as xylem samples. The bark, phloem, green tissues, or attached soil on the samples were completely removed. All xylem samples (the same as the soil samples) were packed into 15-ml transparent screw-cap glass tubes, immediately sealed with Parafilm, and stored in a freezer at −20 °C.

Water samples of soil and xylem were extracted by an ultralow temperature (liquid nitrogen; −196 °C) vacuum distillation and extraction system and sealed in a 2-ml autosampler vial. The δ_D values of the extracted water were determined by a Thermo-Finnigan Delta V Advantage Isotope Ratio Mass Spectrometer with a Flash 2000 HT

Elemental Analyzer (Thermo Fisher Scientific, USA). The isotopic ratios are presented with the per thousand symbols (‰) relative to V-SMOW (i.e., Vienna standard mean ocean water), and the measurement accuracy of δ_D was better than ± 1‰.

See our published paper (Wu et al., 2020) for the measurement of the soil water content and nutrient concentrations.

2.3. Fitting curves of soil water δ_D

The isotopic compositions of rainwater in tropical and temperate monsoon regions have obvious seasonal variations that reflect seasonally varying tropospheric temperature variations (Jones et al., 2000; Jones and Banner, 2003; McGuire and McDonnell, 2006). Therefore, the isotopic signals of soil water (i.e., fitting curves of soil water δ_D) at the different depths of different quadrats could be fitted through a sine wave approach, as recharge predominantly occurs via rainwater in this study region (Tekleab et al., 2014), which exhibits significant climate seasonality (Fig. S2). The fitting data of the soil water δ_D can be obtained by the following formula:

$$g(t) = C_0 + A\left[\cos\left(\frac{2\pi \times t}{365} - \varphi\right)\right] \tag{1}$$

where C_0 is the mean measured δ_D value of soil water, A is the amplitude of the fitting sine curve, 365 indicates the number of days in one year, 2π/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 13, 2017; set as 0). To simplify the fitting model, Eq. (2) was transformed into a regression formula containing both sine and cosine terms (Bliss, 1970) as follows:

$$g(t) = C_0 + \alpha_{\cos}\cos(\omega * t) + \alpha_{\sin}\sin(\omega * t) \tag{2}$$

where $\alpha_{\cos}$ and $\alpha_{\sin}$ are the estimated regression coefficients and ω is the radian frequency (i.e., 2π/365). Fig. 1 shows an example of this.

2.4. Determination of plant water use patterns

The fundamental theory of the calculations of plant water use from different soil layers is based on the isotopic mass balance (Fry, 2006). The basic multiple linear mixing models are as follows (Phillips et al., 2005):

$$\delta_{plant} = f_1\delta_{S1} + f_2\delta_{S2} + f_3\delta_{S3} + f_4\delta_{S4} + f_5\delta_{S5} + f_6\delta_{S6} \tag{3}$$

$$1 = f_1 + f_2 + f_3 + f_4 + f_5 + f_6 \tag{4}$$

In the two formulas above, δ_{plant} is the δ_D value of plant xylem water; $\delta_{S1}-\delta_{S6}$ are the soil water δ_D values within six sampled soil layers (i.e., 0–5 cm, 5–15 cm, 15–30 cm, 30–50 cm, 50–75 cm, and 75–105 cm); and f_1-f_6 are the water use proportions of plants from those six sampled soil layers. However, using Eqs. (3) and (4) could not provide the unique solution (i.e., f_1-f_6) in this study because such models are mathematically underdetermined (Phillips and Gregg, 2003). Therefore, MixSIAR (Stock et al., 2018), as a Bayesian mixing model, was applied to quantitatively estimate plant water use proportions in this study.

Before running MixSIAR, the discrimination was set as 0 because the isotopic discrimination in the process of plant water use is very small and can be ignored (Dawson et al., 2002; Fry, 2006; Phillips et al., 2005). After running MixSIAR, the mean values of the water contributions from different soil layers were treated as the final solutions of plant water use proportions, and the data were prepared for the subsequent fitting of plant water use proportion curves through the ordinary least squares approach. It is worth mentioning that plant rooting depths exhibit plasticity to a certain degree in response to the local climate (Fan et al., 2017). Therefore, a widespread phenomenon is that the water uptake depths (or the distribution of plant absorptive roots) of most plants exhibit seasonal variations in regions with distinct climatic seasonality (Dawson et al., 2002; Yang et al., 2015). For this reason, as the expression of the relative contributions of different water sources to plant xylem water, plant water use proportions merely fluctuate between 0 and 1 (Phillips et al., 2005; see Eq. (4)). For the above reasons, the sine wave approach as a nonlinear regression approach was also suitable for the fitting of plant water use proportion curves, and this approach could shorten the range of possibilities and provide a more reasonable and persuasive result (accords more with the seasonal distribution trend of plant absorptive roots). The regression formula can be modified as follows:

$$f(t) = C_1 + \beta_{\cos}\cos(\omega * t) + \beta_{\sin}\sin(\omega * t) \tag{5}$$

where C_1 is the mean value of the plant water use proportion, $\beta_{\cos}$ and $\beta_{\sin}$ are the estimated regression coefficients, and ω is a constant (i.e., 2π/365). Since there were six sampled soil layers in this study, f(t) therefore yields 6 fitting functions corresponding to 6 depths (i.e., $f_1(t)-f_6(t)$; see Eq. (3)) in this study.

2.5. Reconstruction of the isotopic signal of plant xylem water

Because of the principle of isotopic mass balance, the isotopic signal in plant xylem water (i.e., xylem water δ_D) can be considered the superposition of the weighted soil water isotopic signals within different soil layers, similar to that displayed in Eq. (3). Therefore, the regression formula can be defined as

$$\delta D(t) = CC \times \sum_{n=1}^{6} f_n(t) * g_n(t) \tag{6}$$

where CC is an estimated regression coefficient and can be treated as the correction coefficient of the plant water use proportion. Fig. 1 details examples of whole fitting processes from rubber monoculture. All of the above fitting functions were conducted through ordinary least square regression in the R programming language (R Core Team, 2019). The Durbin-Watson test was conducted to check the residual autocorrelation. If autocorrelation exists, a lagged term of the dependent variable (residual of the original dependent variable at time t-1) is added to the original model to correct the autocorrelation (Wilkins, 2018).

The difference between each pair of plant species in each quadrat was expressed as the absolute value. The number of differences in each quadrat is equal to the number of pairwise combinations of the plant species, which implies the maximum possible number of competition combinations, similar to a round-robin tournament. In addition, each species in the competition would meet all other species in turn. Therefore, the numbers of competitor combinations can be determined using the following formula:

$$C(n, 2) = \frac{n!}{2! \times (n-2)!} \tag{7}$$

where n represents the number of investigated plant species in a quadrat, and symbol “!” indicates the factorial function.

2.6. Statistical analysis

Because many species inhabit jungle rubber agroforestry systems and tropical rainforests, Spearman’s rank correlation was performed to reveal the similarities among the isotopic signals in the xylem tissues of all plants in jungle rubber agroforestry systems and tropical rainforests and thus to proceed to clustering analysis to classify the species. In addition, the effects of climatic factors (i.e., air temperature and precipitation) on the plant xylem water δD and on the differences (in the form of the monthly mean) were revealed through a correlation analysis. A multiple correlation analysis between the plant xylem water δD (the same as the difference value) and the content of soil water and nutrients within different soil layers (i.e., soil N, P, K, Ca and Mg; see Wu et al., 2020 for details) was performed to reveal the relationships between plant water use and environmental resources. Correlations among the difference values of the plant xylem water *δ*D of each pair of plant species in the jungle rubber agroforestry system and tropical rainforest were also determined, and then the competition combination list was reordered using the angular order of the eigenvectors (Friendly, 2002).

The above calculations and statistical analyses were conducted in R 3.5.2 (R Core Team, 2019). We used the 'corrplot' (Wei et al., 2017) and 'Hmisc' (Harrell, 2015) packages for the correlation analysis.

3. Results

3.1. Soil water variations

Shallow soil exhibited great variations in water contents and water *δ*D values among seasons. In short, its water contents were abundant in the rainy season (May-Oct; Fig. 2) and deficient in the dry season (May-Oct; Fig. 2). Relative to shallow soil water, deep soil water is stable regardless of its contents or isotopic compositions (Fig. 2-3). In general, with increasing soil depth, the soil water contents decreased, and the seasonal variations in the soil water contents and water *δ*D values became small. In addition, soil water *δ*D values decreased with depth during the dry season but exhibited less variation among the depths during the rainy season. The fitting curves of the soil water δD exhibited increasingly lagged phase positions and increasingly smaller amplitudes with increasing soil depth (Fig. 3).

3.2. Plant water use patterns

Compared with those in monoculture, rubber trees in the agroforestry systems (i.e., rubber-orange, rubber-tea, rubber-orange-tea, and jungle rubber agroforestry systems) took up much more water (more than 50%) from the soil layers below a 30 cm depth (Fig. 4a). With an increase in neighboring species, the deeper soil water use proportion of rubber trees clearly increased, especially from 75–105 cm (Fig. 4a). In contrast, other plant species in the agroforestry systems took up much more water from the surface (0–5 cm) soil layers (Fig. 4a-b). Rubber trees and their neighboring species appeared to form relatively complementary vertical water use patterns, with plant water use in the rubber-orange-tea agroforestry system providing the best example (Fig. 4a).

In the tropical rainforest, such a complementary phenomenon was also obvious, especially between the dominant species and common species (Fig. 4c; see the dominant species and common species in Table S1). Here, it is worth explaining that the dominant species and common species in the tropical rainforest quadrat of this study mainly referred to the previous investigations of plant species in the tropical forests of the study regions (i.e., Xishuangbanna), and the method used for distinguishing the dominant and common species in the tropical forests mainly involved calculations of the importance value index of all investigated plant species (Zhu, 2006).

In this study, the dominant species in the tropical rainforest primarily took up water from the intermediate soil layers (i.e., 15–50 cm), while the common species mainly absorbed water from the surface and shallow (i.e., 0–15 cm) soil layers (Fig. 4c; or see Supplementary result exhibition for more details). Here, the main resource use depth of dominant species in the tropical rainforest was not as deep as that of agroforestry rubber trees (Fig. 4c).

In addition, plant water use proportions from the surface and shallower soil layers (0–30 cm depths) increased gradually from the dry season (Nov-Apr) to the rainy season (May-Oct; Fig. 4a and Supplementary result exhibition), but such seasonal variations were reversed for the use proportion from the water of the remaining soil layers (30–105 cm depths). Such seasonal water use patterns were especially

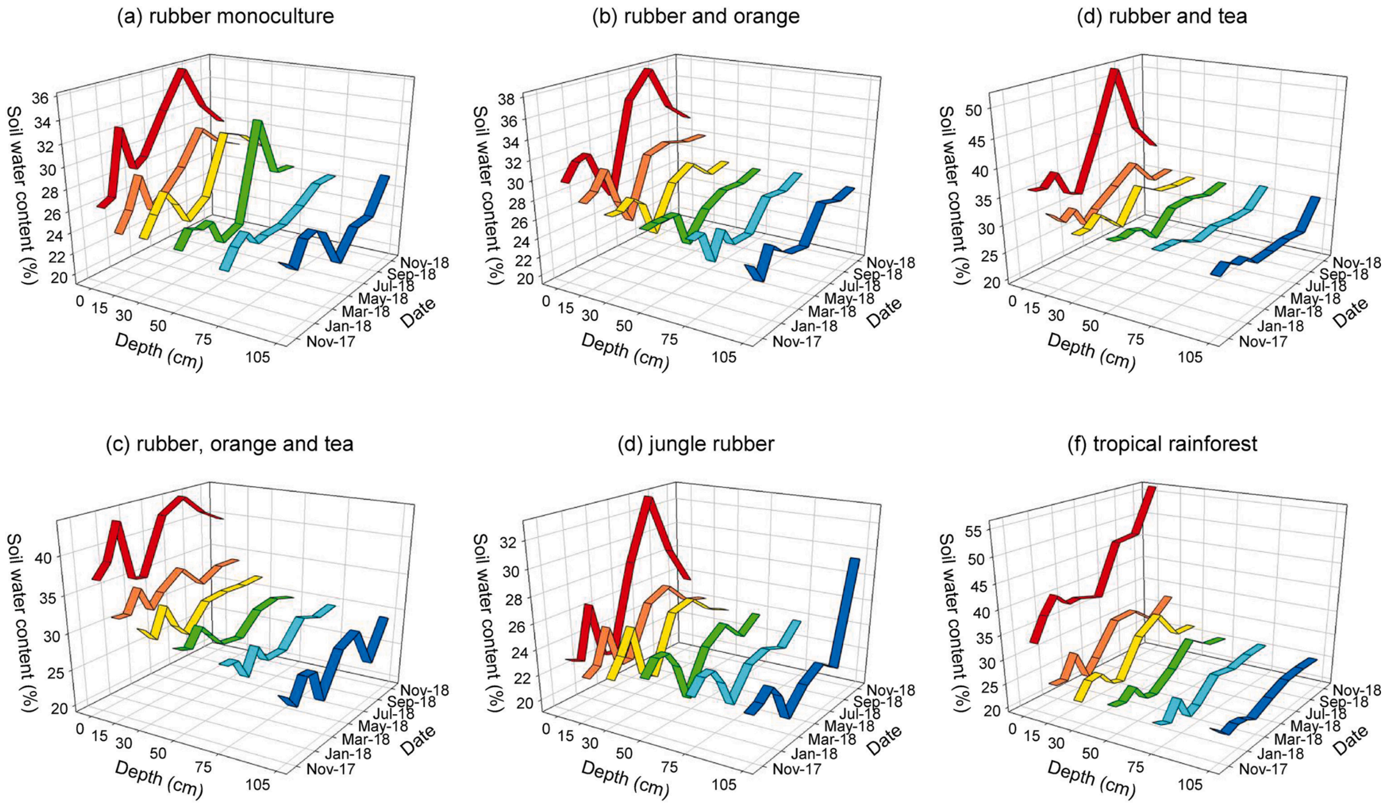

Fig. 2. Seasonal variations in soil water contents at different depths in (a) rubber monoculture, (b) rubber-orange, (c) rubber-tea, (d) rubber-orange-tea, (e) jungle rubber agroforestry systems, and (f) tropical rainforest. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

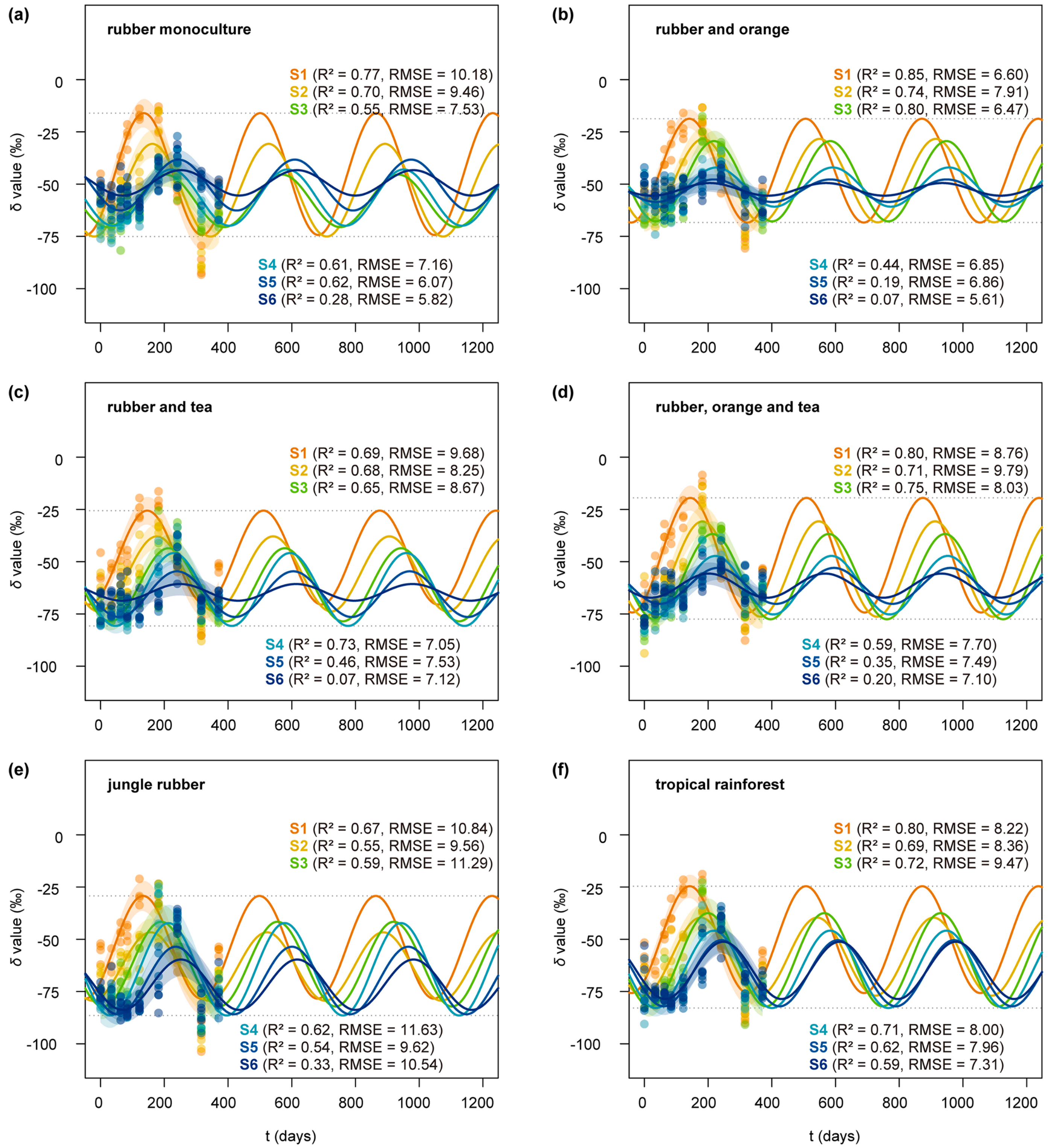

Fig. 3. Best fitting curves of soil water δD within different soil layers in (a) rubber monoculture, (b) rubber-orange agroforestry system, (c) rubber-tea agroforestry system, (d) rubber-orange-tea agroforestry system, (e) jungle rubber agroforestry systems and (f) tropical rainforest. S1–S6 represent six sampled soil layers (i.e., 0–5 cm, 5–15 cm, 15–30 cm, 30–50 cm, 50–75 cm, and 75–105 cm). The 95% confidence band (translucent ribbon) is shown around each fitting curve. More details on the fitting functions can be found in Table S2 (online). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

obvious for rubber trees (Fig. 4a) and for the dominant species in the tropical rainforest (Fig. 4c). In comparison, seasonal variations in the water use patterns of the neighboring species of rubber trees in the rubber agroforestry systems, as well as the common species in the tropical rainforest, exhibited some delays (Fig. 4; Supplementary result exhibition).

All of the best-fitting curves and the details of the fitting functions of plant water use proportion can be found in the Supplementary result exhibition.

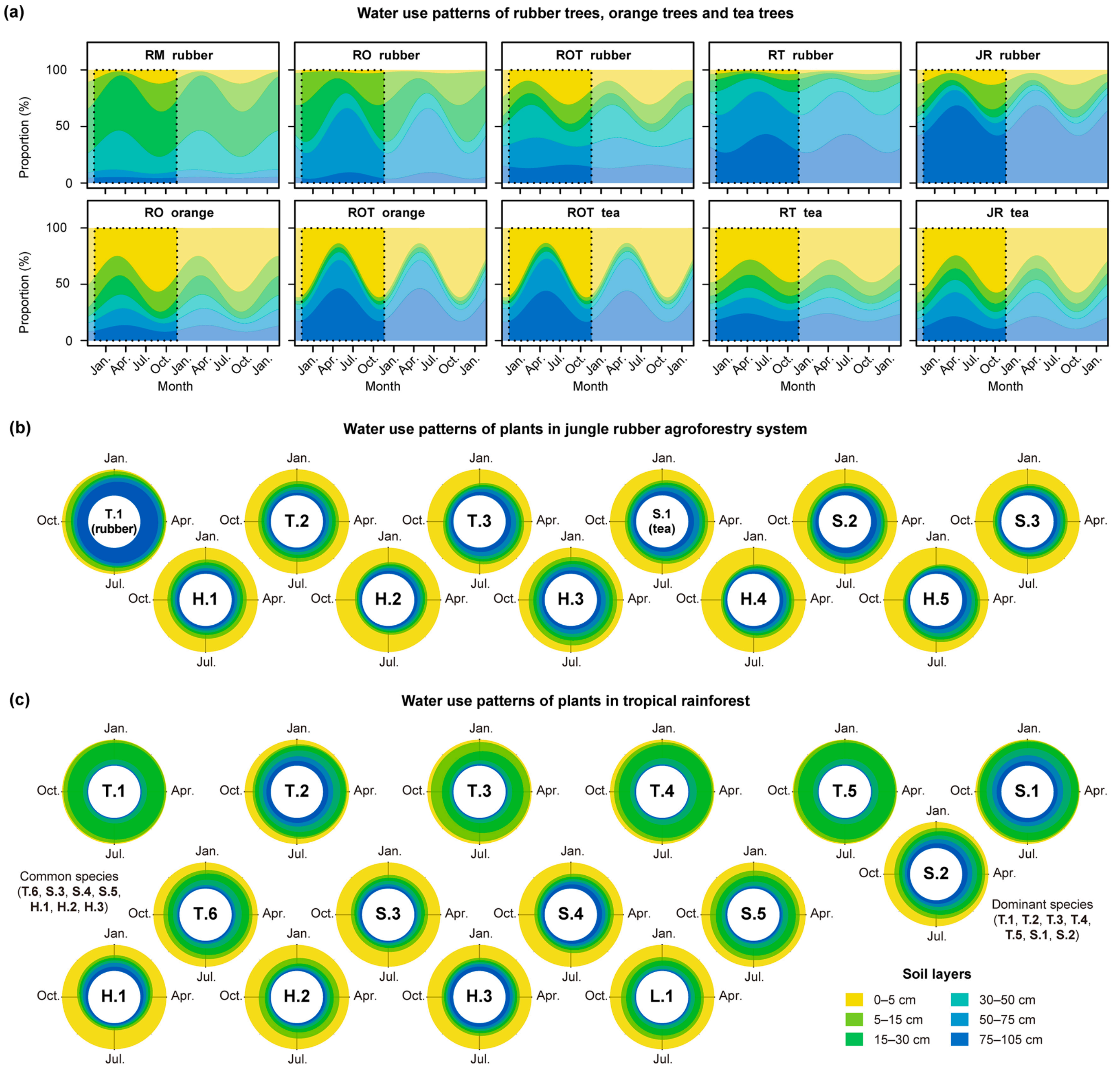

Fig. 4. Plant water use patterns. (a) Water use patterns of rubber trees, orange trees and tea trees in different plots. Water use patterns of plants in (b) jungle rubber agroforestry systems and (c) tropical rainforests. The dotted boxes in (a) represent the fitting results during the study period, and the extended area outside the dotted boxes is shown merely for comparison. RM indicates rubber monoculture; RO indicates rubber and orange agroforestry system; RT indicates rubber and tea agroforestry system; ROT indicates rubber, orange and tea agroforestry system; and JR indicates jungle rubber agroforestry system. See Table S1 for the meanings of the code names of all plant species. See Table S3 for the fitting functions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. *Isotopic signals of plant xylem water*

Through the ordinary least squares approach (OLS regression in R programming), the best-fitting curves of soil water within different soil layers in each quadrat were determined (Fig. 5). The best-fitting parameters of the fitting functions are provided in Table S2. Through the processing of the fitting signals of both the water use proportion (Table S3) and soil water δD (i.e., integrating g(t) and f(t) as described in the Methods section), the isotopic signals of plant xylem water (i.e., the fitting curves of plant xylem water δD) were determined (Fig. 5). Table S4 shows the fitting functions of plant xylem water δD of all plant species in this study. The adjusted R^2 of all fitting functions exceeded 0.9 (Fig. 5; Table S4). This implied that the fitting curves could explain more than 90% of the variation in the measured δD values of plant xylem water.

As exhibited by the isotopic signals of plant xylem water, the rubber tree was quite different relative to its neighboring species in rubber-orange, rubber-tea, and rubber-orange-tea agroforestry systems (Fig. 5b–d). Even in the jungle rubber agroforestry system, which contained many species, the rubber tree was the most unique and easily recognizable species (Fig. 5e), with few similarities to its neighboring species (Fig. S3). One of the common features of the fitting curves of

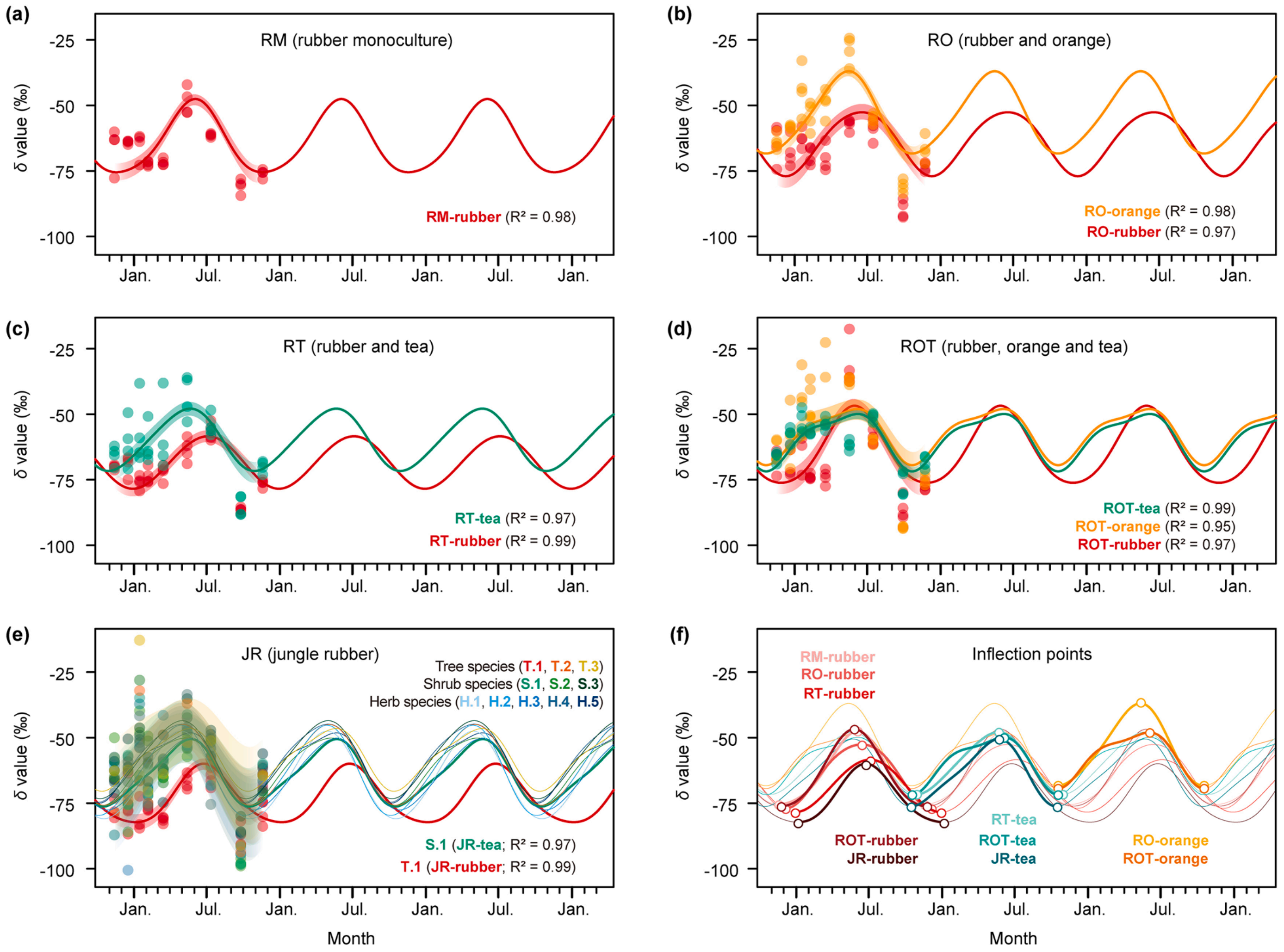

Fig. 5. Isotopic signals of plant xylem water. (a–e) The best-fitting curves of plant xylem water δD in rubber monoculture, rubber-orange, rubber-tea, rubber-orange-tea and jungle rubber agroforestry systems. (f) The inflection points of the curves. The 95% confidence bands are shown as translucent ribbons around each fitting curve in (a–e). Only one-year length curves (bold curves) are highlighted in (f). The extended curves excluding confidence bands are shown merely for comparison, and the months displayed represent only the months during the study period. See Table S1 for the meanings of the code names. See Table S4 for the fitting functions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

rubber trees in agroforestry systems was their position location lower and more to the right than the curves of the neighboring species (Fig. 5b–f). This phenomenon was primarily due to the ability of rubber trees in the agroforestry systems to take up more water from the deeper soil layers relative to the neighboring species (Fig. 4a), and the fitting curves of the soil water δD exhibited increasingly lagged phase positions and increasingly smaller amplitudes with increasing soil depth (Fig. 3). Therefore, with an increase in the number of neighboring species, the fitting curves of the rubber tree lagged and increasingly declined (Fig. 5f).

3.4. Differences among the isotopic signals of plant xylem water

The difference in the xylem water δD between rubber trees and orange trees in the rubber-orange agroforestry system was small in the middle of the rainy season (Aug-Oct), increased from the end of the rainy season (Oct-Apr) to the end of the dry season, and then decreased until the middle of the rainy season (Aug; Fig. 6a). This difference between rubber trees and tea trees in the rubber-tea agroforestry system was small from the middle of the rainy season to the end of the rainy season (Aug-Oct) and then increased gradually and attained the maximum in the following middle of the dry season (Marth), followed by a decrease until the middle of the rainy season (Aug; Fig. 6b). However, such variation patterns in the difference between rubber tree and these two species (i.e., orange and tea) were altered by the participation of one more species (i.e., orange or tea) in the rubber-orange-tea agroforestry system. In brief, the signal differences between two species, which indicated the separating degree of resource use zones between these two species, could be changed by the participation of one more species, as shown by the signal differences in rubber-orange, rubber-tea, and rubber-orange-tea agroforestry systems (Fig. 6c). In addition, the difference between orange trees and tea trees in the rubber-orange-tea agroforestry system was small and nearly constant (Fig. 6c) because the fitting curves of their xylem water δD were almost equivalent (Fig. 5d), and the accumulated difference in the rubber-orange-tea agroforestry system reached its maximum in the middle of January (cool and dry season), and it was smaller from the end of the dry season to the end of the rainy season (Apr-Oct; Fig. 6c).

Similarly, the accumulated difference in the jungle rubber agroforestry system reached its maximum at the beginning of February (cool and dry season) and then decreased, and the differences from the middle to the end of the rainy season were smaller (July Oct; Fig. 6d). It is also worth mentioning that the variation patterns of the difference in all competition combinations in the jungle rubber agroforestry system were

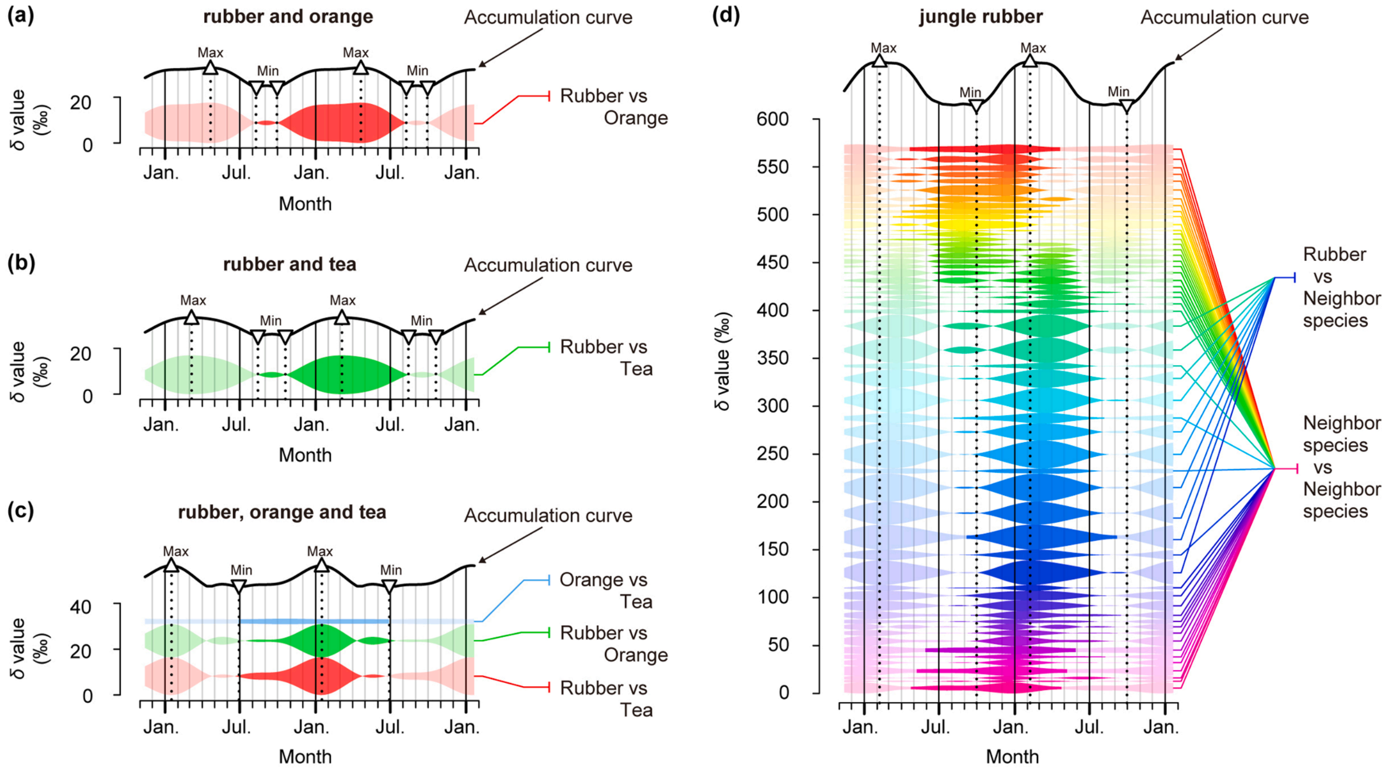

Fig. 6. Variations in the differences in the xylem water δD of each pair of plant species in (a) rubber-orange, (b) rubber-tea, (c) rubber-orange-tea and (d) jungle rubber agroforestry systems. Different colors indicate different competition combinations. The maximum and minimum values are marked as the respective upwards- and downwards-pointing triangles on the accumulation curves. The vertical dotted lines are the reference lines of the occurrence time of the maximum or minimum values. The straight black and gray lines are the reference lines of months. Only one-year difference values (from the minimum to the next minimum) are highlighted.

not the same, but the occurrence time of their maximum differences seemed to be organized well and orderly in a single year (Fig. 6d). The differences between rubber tree and its neighboring species were greater than the differences among neighboring species, and the maximum values primarily occurred in the pronounced dry season (Feb-March; Fig. 6d). -

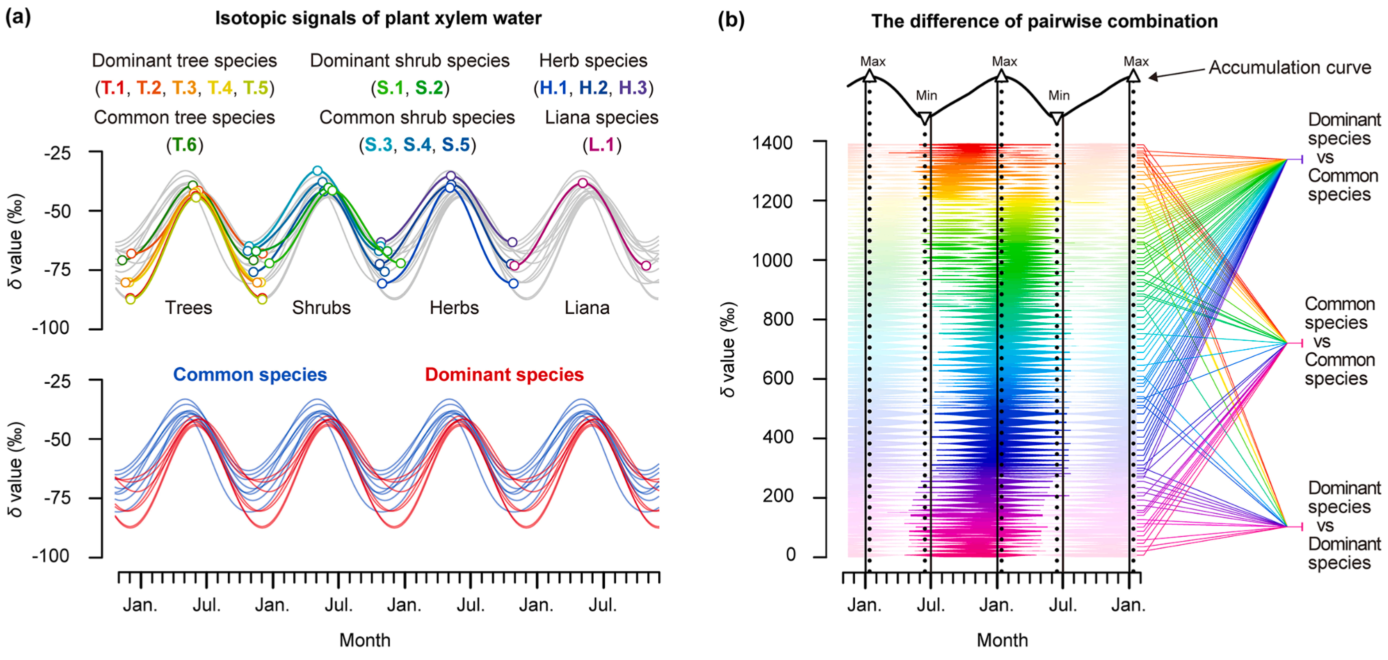

Fig. 7. Isotopic signals from plant xylem water and their differences in the tropical forest. (a) The fitting curves of xylem water δD of different plant species. (b) Difference variations of each competition combination. Different colors in (a) and (b) indicate different plant species and competition combinations, respectively. For comparison, the inflection points (circles) of the curves are provided in (a), and only one-year fitting results are highlighted in (b). See Fig. 6 for explanations of the black bold curve, plot symbols, and reference lines. See Fig. S5 for details concerning the difference variations in tropical rainforests. See Table S1 for the meanings of the code names. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Through similarity analysis and hierarchical clustering, the fitting curves of the plant xylem water δD in tropical rainforests could be clearly divided into two groups: dominant species and common species (Fig. S3b; Table S1) or, alternatively, deep-resource users and shallow-resource users (Fig. 4). Therefore, the fitting curves of the dominant species in the tropical rainforest exhibited many similar features to the rubber trees in the agroforestry systems (Fig. 5). In short, the fitting curves of dominant species were located lower and more to the right relative to the common species (Fig. 7a).

The accumulated difference in the tropical rainforest increased from the middle of the rainy season (June) to the middle of the dry season (Jan), followed by a decrease until the middle of the rainy season (June; Fig. 7b). Similar to the variation patterns of the difference in the jungle rubber agroforestry system, the difference variation of all competition combinations in the tropical rainforest also seemed to be organized in an orderly manner in a single year (Fig. 7b). In general, the maximum differences between the dominant species and the common species mainly occurred from the middle of the dry season (Jan) to the middle of the rainy season (June), but the maximum differences among the dominant species or among the common species mainly occurred from the middle of the rainy season (June) to the next middle of the dry season (Jan; Fig. 7b). Unlike the case in the jungle rubber agroforestry system (Fig. S4), the average differences between the dominant species and the common species in the tropical rainforest were smaller than the average differences among the dominant species or among the common species (Fig. S5). Fig. S5 shows the lists and orderings of the competition combinations in the tropical rainforest.

3.5. Relationships among climate variables, soil resources, and plant water isotopes

The fitting curves of plant xylem water δD (Fig. 5a–f; Fig. 7a) and the trend curves of the accumulated difference value exhibited obvious seasonal fluctuations (Fig. 6; Fig. 7b), as observed for the local air temperature and precipitation (Fig. S1). The xylem water of rubber trees in all rubber plantations and of the dominant species in tropical rainforest (i.e., deep-resource users) also exhibited significant positive correlations with the local air temperature and precipitation (Table 1). Conversely, the accumulated difference values had negative correlations with temperature and precipitation (Table 2). Thus, temperature and precipitation had negative effects on the separation degree of plant functional absorbing zones. Additionally, almost all the rubber trees in this study (except in the rubber-orange-tea agroforestry system) exhibited significant positive correlations with the soil water content (Table 1). However, the correlations between the rubber trees and soil nutrients did not have similar features in the different quadrats. In the tropical rainforest, no species had correlations with all belowground resources (i.e., water and all nutrients; Table 1). However, a common feature among the study quadrats was that all the neighboring species of the rubber tree in the agroforestry systems and nearly all of the common species in the tropical rainforest (i.e., all shallower-layer users in this study) had neither a significant nor a high correlation with the temperature, precipitation, soil water, or soil nutrients, while the rubber trees in all rubber plantations and the dominant species in the tropical rainforest (i.e., deep-resource users) exhibited significant positive correlations with at least one of the belowground resources (soil water or soil nutrients).

Table 1

Correlation coefficients for the relations of plant xylem water δD, climate variables and the soil resources in different plots.

Site	Species	Climate variables		Soil water content	Soil nutrient concentration				
		Temperature	Precipitation		N	P	K	Ca	Mg
Rubber monoculture	rubber	0.58*	0.63**	0.65**	0.58	0.49	0.67*	0.67*	0.54
Rubber and orange agroforestry system	rubber	0.74**	0.65**	0.77**	0.82**	0.24	0.54	0.54	0.56
	orange	0.2	0.33	0.68**	0.51	0.28	0.64	0.24	0.69*
Rubber, orange, and tea agroforestry system	rubber	0.56*	0.58*	0.55	0.7*	0.42	0.41	0.76**	0.44
	orange	0.07	0.3	0.45	0.53	0.57	0.61	0.63	0.42
	tea	0.07	0.3	0.44	0.52	0.57	0.62	0.63	0.42
Rubber and tea agroforestry system	rubber	0.92**	0.77**	0.76**	0.39	0.53	0.72*	0.62	0.42
	tea	0.31	0.42	0.47	0.4	0.37	0.51	0.48	0.71*
Jungle rubber agroforestry system	T.1 (rubber)	0.84**	0.8**	0.71**	0.42	0.46	0.56	0.53	0.53
	T.2	0.14	0.26	0.48	0.38	0.45	0.25	0.58	0.55
	T.3	0.08	0.28	0.43	0.39	0.4	0.26	0.57	0.56
	S.1 (tea)	0.22	0.38	0.49	0.37	0.42	0.3	0.54	0.52
	S.2	0.03	0.22	0.42	0.4	0.41	0.24	0.6	0.59
	S.3	0	0.17	0.42	0.41	0.46	0.24	0.57	0.56
	H.1	0.11	0.22	0.48	0.38	0.46	0.25	0.58	0.55
	H.2	−0.01	0.15	0.42	0.41	0.48	0.24	0.56	0.55
	H.3	0.28	0.4	0.53	0.35	0.4	0.3	0.59	0.54
	H.4	−0.09	0.12	0.36	0.43	0.45	0.24	0.57	0.58
	H.5	−0.07	0.19	0.34	0.43	0.4	0.24	0.56	0.58
Tropical rainforest	T.1	0.65**	0.63**	0.55	0.46	0.61	0.55	0.69*	0.58
	T.2	0.68**	0.69**	0.59*	0.45	0.59	0.57	0.67*	0.59
	T.3	0.53*	0.56*	0.54	0.49	0.61	0.54	0.68*	0.57
	T.4	0.62*	0.62*	0.55	0.47	0.6	0.55	0.68*	0.58
	T.5	0.66**	0.63**	0.54	0.51	0.6	0.53	0.66*	0.57
	S.1	0.8**	0.73**	0.58*	0.43	0.59	0.59	0.67*	0.6
	S.2	0.56*	0.62*	0.54*	0.56	0.6	0.53	0.64	0.55
	T.6	0.45	0.51*	0.55	0.46	0.6	0.56	0.69*	0.58
	S.3	0.21	0.3	0.52	0.58	0.61	0.52	0.64	0.54
	S.4	0.27	0.39	0.58	0.47	0.6	0.55	0.65	0.58
	S.5	0.4	0.47	0.53	0.54	0.6	0.53	0.67*	0.57
	H.1	0.27	0.32	0.52	0.55	0.63	0.51	0.62	0.53
	H.2	0.17	0.3	0.52	0.6	0.59	0.54	0.65	0.56
	H.3	0.22	0.32	0.52	0.58	0.6	0.53	0.65	0.55
	L.1	0.25	0.34	0.51	0.59	0.6	0.54	0.66*	0.56

See Table S1 for the meanings of the code names of plant species.

** Correlations are significant at the 0.01 level.

* Correlations are significant at the 0.05 level.

Table 2

Correlation coefficients for the relations of the difference value of plant xylem water δD, climate variables and the soil resources in different plots.

Site	Climate variables		Soil water content	Soil nutrient concentrations				
	Temperature	Precipitation		N	P	K	Ca	Mg
Rubber and orange agroforestry system	−0.6*	−0.33	0.57	0.52	0.45	0.47	0.55	0.54
Rubber, orange, and tea agroforestry system	−0.98**	−0.63**	0.48	0.75**	0.27	0.57	0.59	0.55
Rubber and tea agroforestry system	−0.49*	−0.31	0.54	0.34	0.46	0.68*	0.75**	0.64
Jungle rubber agroforestry system	−0.79**	−0.58*	0.51	0.53	0.51	0.49	0.56	0.66*
Tropical rainforest	−0.91**	−0.81**	0.63*	0.42	0.58	0.65	0.62	0.61

** Correlations are significant at the 0.01 level.

* Correlations are significant at the 0.05 level.

4. Discussion

Relative to shallow soil, which exhibits great variations in water supply availability (Chitra-Tarak et al., 2018), the water supply of deep soil appears to be more stable (Pierret et al., 2016; Fan et al., 2017). Because of the hydrotropism of plant roots, when shallow soil dries out, some plants would shift their main water-absorbing zones into deeper soil layers to compensate for the decreased water (Ivanov et al., 2012; Del Bianco and Kepinski, 2018). Obviously, such shifts in water use depths could help deep-resource-use plants effectively avoid water-deficient damage to their permanent tissues (Brum et al., 2019), such as xylem cavitation and embolism for large woody trees (Vilagrosa et al., 2012; Silvertown et al., 2015), subsequently providing insurance against the potentially fatal consequences of water shortages under less favorable conditions (Pierret et al., 2016). Moreover, investing in deep-root growth could also help increase the vertical soil-root touching interfaces to offer more opportunities for deep-resource users to capture leaching nutrients (Pierret et al., 2016). Therefore, a deep-resource use strategy seems to be a favorable strategy for plants under competition, as observed for the rubber tree in agroforestry systems (i.e., in rubber-orange, rubber-tea, rubber-orange-tea, and jungle rubber agroforestry systems; see Fig. 4a). The same was true for the dominant species in the studied tropical rainforest (Fig. 4c).

However, such deep-resource use of the rubber tree in the agroforestry systems, as well as that of the dominant species in the tropical rainforest, also hides some risks, which can dramatically reverse the competition situation between them and their neighboring species. For example, (1) most of the soil nutrients were mainly concentrated in the shallow soil layer and decreased with soil depth (Del Bianco and Kepinski, 2018), particularly soil N in these study plots (Wu et al., 2020); (2) soil organic matter was also mainly concentrated in the surface and shallow soil layers, and it would prevent soluble nutrients from leaching into deep soil when rainwater enters the soil (Murphy, 2014; Wu et al., 2020); (3) plant deep water uptake would exhaust deep soil water once drought is prolonged and then increase the risk of plant death (Goulden and Bales, 2019), and so fixed water uptake is therefore unwise for plants; and (4) continuously heavy rainfall in the rainy season would increase the gravitational water in the soil and raise the water table, which would increase the oxygen deficit in the deep soil layers (Silvertown et al., 2015; Fan et al., 2017). Perhaps for these reasons, rubber trees would start to strengthen their shallow resource use with the arrival of the rainy season (Fig. 4a). That is, the optimum depths for plant uptake of soil resources are not fixed. Obviously, plant root hairs, as an important sensor for detecting water availability (Kwasniewski et al., 2016), guide plants to adjust their resource use depths (Fig. 4). In fact, such malleable shifts in resource use depths were also obvious for most plant species in this study (Fig. 4; Supplementary result exhibition) and consistent with many studies (Letten et al., 2015; O'Keefe et al., 2019; Kulmatiski et al., 2020), reflecting that obtaining advantages and avoiding disadvantages is instinctual for all species.

In the tropical rainforest, since there were many coexisting species and most nutrients in the soil exhibited a decreasing trend with depth (Wu et al., 2020), some resources may be pre-empted by competitors before moving to deeper soil layers (Craine and Dybzinski, 2013; Minden and Venterink, 2019). With the trade-offs between the gains and losses of various resources (McNickle and Dybzinski, 2013; Silvertown et al., 2015), the intermediate soil layers (i.e., 15–50 cm) most likely were the pertinent positions for resource use of the dominant species in the tropical rainforest (Fig. 4c). For this reason, the main resource use depth of the dominant species in the tropical rainforest was shallower than that of agroforestry rubber trees (Fig. 4c). This finding was consistent with a recent study that found that the main water-absorbing zones of plant species were shifted to intermediate soil layers with the increase in species richness in temperate grasslands (O'Keefe et al., 2019).

Therefore, the above findings provide important empirical evidence that the belowground niche shift of plant species can be regulated by both environmental conditions and biotic interactions (Guisan et al., 2014); consequently, niche differentiation (or resource partitioning) can either be formed by plant fixed preference as an adaptation to the environment or belowground competition (Bartelheimer et al., 2010).

4.1. How does resource partitioning change with the temporal and spatial heterogeneities of belowground resources and with the gradients of species richness?

Through plant water use patterns, we can preliminarily understand that belowground resource partitioning would be an important factor in the maintenance of coexistence between shallow-resource and deep-resource users in this study (McKane et al., 2002; De Deurwaerder et al. 2018; Kulmatiski et al., 2020), particularly in rubber agroforestry systems. However, understanding just the degree of niche differentiation among plants could confirm the competition situations among plant species at finer scales (Araya et al., 2011; Letten et al., 2015), especially among shallow-resource users or among deep-resource users. As an indicator integrating the information for water source and plant water use, the isotopic signals of plant xylem water reveal the spatiotemporal variations of plant water uptake behavior. Therefore, a comparison of the differences among the isotopic signals of plant xylem water could reveal the degree of difference among plant functional absorption zones, that is, the degree of hydrological niche segregation or resource partitioning (Silvertown et al., 2015).

As suggested by the differences in plant xylem water isotopic signals in rubber-orange, rubber-tea, and rubber-orange-tea agroforestry systems (Fig. 6a, b, c), the functional absorbing zones of one species would be compressed and limited by the participation of one more species in the same community. For example, the extended narrow part of the difference ribbon in rubber-orange-tea agroforestry systems (Fig. 6c) implied that the functional absorbing zones of rubber trees and their neighbors largely overlapped in a longer period, especially during the rainy season. Similarly, the small and nearly constant differences between the orange tree and tea tree in rubber-orange-tea agroforestry systems indicated (Fig. 6c) that their functional absorbing zones were limited to nearly the same soil layers. A similar situation could also be found in the jungle rubber agroforestry system, as indicated by the nearly overlapping isotopic signals of neighbors of the rubber tree and their small differences in this quadrat (Fig. 5e, Fig. 6d). These phenomena therefore clearly demonstrated that the increase in species richness in a plant community could compress and restrain plant belowground niches.

A classic viewpoint is that niche differentiation (or resource partitioning) on spatial and temporal scales can prevent competitive exclusion among species (McKane et al., 2002; Mommer et al., 2010; Schwinning and Kelly, 2013; O'Keefe et al., 2019). Therefore, the obvious hydrological niche differentiation between rubber trees and their neighbors in the agroforestry systems (Fig. 5b–e) promoted their coexistence. However, the degree of such niche differentiation among the neighboring species of rubber trees in the jungle rubber agroforestry system was quite marginal. Therefore, the neighbors of rubber trees in the jungle rubber agroforestry system appeared to be living in the "cracks" and adjusting their water-absorbing zones delicately and frequently with the season (Fig. 5e; Supplementary animation). However, these species also coexisted for a long time, at least during the observation period.

4.2. How do plant resource use advantages change with variations in belowground resources and complexities of species interactions?

How can plant species maintain coexistence in the "cracks" without obvious resource partitioning? Perhaps the fine-scale niche differentiation across space and/or time (Figs. 5; 7a) could adequately avoid competitive exclusion among these coexisting species (Schwinning and Kelly, 2013; Silvertown et al., 2015; Letten et al., 2018). Another possibility is that the fluctuating availability of resources across space and/or time (Fig. 2-3; Fig. S2; see Wu et al., 2020 for the nutrient resource fluctuation) would lead to fluctuations in competitive intensities among species and subsequently prevent competitive exclusion (Chesson, 2000; Davis et al., 2000). Thus, a strongest competitor did not exist among these species, since plant species in the same category (i.e., shallow-resource users or deep-resource users) in jungle rubber agroforestry systems or tropical rainforest exhibited high similarities in resource use advantages (Fig. S3; Table 1); every species therefore could overtake or be overtaken by its neighbors and then generate an intransitive loop, similar to the game of "rock-paper-scissors", to help these species achieve "competitive reversals" (Soliveres et al., 2015), which allow species to coexist even without obvious niche differentiation (Soliveres and Allan, 2018; Levine and Hart, 2020).

We believe that the seasonal fluctuation in belowground resources, especially soil water (Fig. 2-3), is the prerequisite for "competitive reversals" among species, and the plasticity in plant absorbing zones, which determines the separation and overlap of their belowground niches with seasons (Figs. 5; 7a; Supplementary animation), permits such "competitive reversals" among these coexisting species. In fact, fluctuating environmental resources are thought to be important for the maintenance of stable species coexistence (Chesson, 2000; Descamps-Julien and Gonzalez, 2005; Zepeda and Martorell, 2019; Letten et al., 2018); additionally, plant phenotypic plasticity (Fig. 4) also promotes stable species coexistence by enhancing stabilizing niche differences and by generating competitive trade-offs among species (Turcotte and Levine, 2016; Pérez-Ramos et al., 2019; Levine and Hart, 2020). From this perspective, it is reasonable to consider that the species in tropical rainforest could coexist with more stability and for longer periods than the species in the jungle rubber agroforestry system because the belowground niche differences among species in the tropical rainforest were more uniform, more stable, and smaller (Fig. 7b, Fig. S5). That is, the belowground resource partitioning in the tropical rainforest was narrower but more uniform and stable than in the jungle rubber agroforestry system (Fig. S4, Fig. S5). Therefore, the advantages of belowground competition (or fitness differences) among all species in the tropical rainforest would be further weakened, and the "competitive reversals" among species would occur more easily and thus benefit the enhanced stability of plant coexistence in the tropical rainforest (Soliveres and Allan, 2018). In fact, such a comparison is conceivable because the tropical rainforest is a climatic climax community already in possession of a stable species composition, but the jungle rubber agroforestry system is still in the secondary succession stage, and species replacement in such secondary forests is a frequent and common phenomenon (Horn, 1974; Cook et al., 2005).

As revealed by the correlation results, the root hydrotropism of deep-resource users is the most obvious (Table 1). Alternatively, deep-resource users are more sensitive to resource availability than shallow-resource users. Therefore, deep-resource users seemed to play leading roles in plant belowground competition, and climate factors, typically temperature and precipitation, directed such competition. This phenomenon is conceivable because temperature and precipitation affect the supply and distribution of soil resources directly and indirectly and thus change the process and outcome of interspecific competition (Table 1; Alexander et al., 2015). In addition, no species had the advantage of using all kinds of soil resources, as indicated by the correlation results (Table 1), mainly because different soil resources exhibit different and even opposite distributions (Wu et al., 2020). Such complexity of belowground resources therefore also determines the absence of a strongest competitor among these species.

Through the link between the seasonal fluctuations in plant resources and plant dynamic resource partitioning, this study provides novel and important empirical evidence for understanding plant competition dynamics and the maintenance mechanisms of species coexistence. In brief, every species in a plant community has a relatively specific and beneficial depth range as a plant fixed preference for using belowground resources (Bartelheimer et al., 2010) and then exhibits a better competitive advantage (i.e., resource use advantage) relative to its neighbors. However, such competitive advantages are eliminated and even reversed with seasonal fluctuations in environmental resources and plant resource use depths (Gallien, 2017). Therefore, the "competitive reversals" among species could further help restrain plant belowground niches (i.e., make the niches more specific) to avoid competitive exclusion. Once plant belowground niches are restrained, every species would develop its specific resource use strategy to maintain the optimal outcome of the resource game. No species therefore has an incentive to deviate from its chosen strategy, and subsequently, their strategic choices seem to constitute a Nash equilibrium (McNickle and Dybzinski, 2013; Broekman et al., 2019), especially for plants within the complex competition network. Therefore, with the increase in species compositions, resource partitioning in a plant community would become narrower but more stable and uniform; species coexistence would then be stabilized. Similarly, coexistence theory explains stable species coexistence through two types of mechanisms: stabilizing mechanisms, which prevent competitive exclusion by resource partitioning, and equalizing mechanisms, which help equalize fitness differences or competitive advantages among species in the absence of niche differentiation (Chesson, 2000; Levine and Hart, 2020). Evidence from this study was consistent with stabilizing mechanisms of coexistence theory in relation to plant competition processes and demonstrated that both stabilizing mechanisms and equalizing mechanisms could operate together in the species-rich plant community. In fact, such an explanation is already implicitly embedded in many studies, even if it is not explicitly mentioned (Trinder et al., 2013; Silvertown et al., 2015; Aschehoug et al., 2016; Gallien et al., 2017).

5. Conclusions

In summary, this study provides a novel method for reconstructing the isotopic signals of plant water use that integrates the spatiotemporal information of water resources and plant interactions and then exhibits the high-resolution dynamics of plant hydrological niche segregation across space and time. It then intuitively demonstrates that plant fitness differences are stabilized by fluctuations in environmental resources, plant resource partitioning across space and time and interspecific interaction complexity. This work therefore opens a new door for studying plant competition dynamics and may be useful for a range of ecological applications. For future studies, if plant functional traits in different growth stages are linked to our method, the contributions to species coexistence derived from variation-dependent and variation-independent mechanisms can be determined, after which the spatial and temporal scales of species coexistence could also be revealed. With this mindset, computer simulations of plant community formation can be performed.

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.

Acknowledgements

We thank Mr. MN Liu from the Institutional Center for Shared Technologies and Facilities of Xishuangbanna Tropical Botanical Garden, CAS. This study was supported by the National Natural Science Foundation of China (32160280, 31800356 and 31570622), the National Postdoctoral Program for Innovative Talents (BX201700278), the Natural Science Foundation of Yunnan Province (202101AT070119, 202101AS070010), the Fourth Oriented Postdoctoral Training Foundation of Yunnan Province, Scientific Postdoctoral Research Foundation of Yunnan Province, “PhD Plus” Talents Training Programme Foundation of XTBG. The authors have declared no competing interests.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2022.108953.

References

Alexander, J.M., Diez, J.M., Levine, J.M., 2015. Novel competitors shape species’ responses to climate change. Nature 525, 515–518. https://doi.org/10.1038/nature14952.

Araya, Y.N., Silvertown, J., Gowing, D.J., McConway, K.J., Peter Linder, H., Midgley, G., 2011. A fundamental, eco-hydrological basis for niche segregation in plant communities. New. Phytol. 189, 253–258. https://doi.org/10.1111/j.1469-8137.2010.03475.x.

Aschehoug, E.T., Brooker, R., Atwater, D.Z., Maron, J.L., Callaway, R.M., 2016. The mechanisms and consequences of interspecific competition among plants. Annu. Rev. Ecol. Evol. Syst. 47, 263–281. https://doi.org/10.1146/annurev-ecolsys-121415-032123.

Bairey, E., Kelsic, E.D., Kishony, R., 2016. High-order species interactions shape ecosystem diversity. Nat. Commun. 7, 1–7. https://doi.org/10.1038/ncomms12285.

Bartelheimer, M., Gowing, D., Silvertown, J., 2010. Explaining hydrological niches: the decisive role of below-ground competition in two closely related Senecio species. J. Ecol. 98, 126–136. https://doi.org/10.1111/j.1365-2745.2009.01598.x.

Beyer, M., Dubbert, M., 2019. X Water Worlds and how to investigate them: a review and future perspective on in situ measurements of water stable isotopes in soils and plants. Hydrol. Earth Syst. Sci. Discuss. 1–35. https://doi.org/10.5194/hess-2019-600.

Bliss, C.I., 1970. Statistics in Biology. McGraw-Hill Book Company, New York.

Boecklen, W.J., Yarnes, C.T., Cook, B.A., James, A.C., 2011. On the use of stable isotopes in trophic ecology. Annu. Rev. Ecol. Evol. Syst. 42, 411–440. https://doi.org/10.1146/annurev-ecolsys-102209-144726.

Broekman, M.J., Muller-Landau, H.C., Visser, M.D., Jongejans, E., Wright, S.J., de Kroon, H., 2019. Signs of stabilization and stable coexistence. Ecol. Lett. 22, 1957–1975. https://doi.org/10.1111/ele.13349.

Brum, M., Vadeboncoeur, M.A., Ivanov, V., Asbjornsen, H., Saleska, S., Alves, L.F., Penha, D., Dias, J.D., Aragão, L.E.O.C., Barros, F., Bittencourt, P., Pereira, L., Oliveira, R.S., 2019. Hydrological niche segregation defines forest structure and drought tolerance strategies in a seasonal Amazon forest. J. Ecol. 107, 318–333. https://doi.org/10.1111/1365-2745.13022.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. 31, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343.

Chitra-Tarak, R., Ruiz, L., Dattaraja, H.S., Kumar, M.M., Riotte, J., Suresh, H.S., McMahon, S.M., Sukumar, R., 2018. The roots of the drought: hydrology and water uptake strategies mediate forest-wide demographic response to precipitation. J. Ecol. 106, 1495–1507. https://doi.org/10.1111/1365-2745.12925.

Cook, W.M., Yao, J., Foster, B.L., Holt, R.D., Patrick, L.B., 2005. Secondary succession in an experimentally fragmented landscape: community patterns across space and time. Ecology 86, 1267–1279. https://doi.org/10.1890/04-0320.

Craine, J.M., Dybzinski, R., 2013. Mechanisms of plant competition for nutrients, water and light. Funct. Ecol. 27, 833–840. https://doi.org/10.1111/1365-2435.12081.

Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol. 88, 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x.

Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H., Tu, K.P., 2002. Stable isotopes in plant ecology. Annu. Rev. Ecol. Syst. 33, 507–559. https://doi.org/10.1146/annurev.ecolsys.33.020602.095451.

De Deurwaerder, H., Hervé-Fernández, P., Stahl, C., Burban, B., Petronelli, P., Hoffman, B., Bonal, D., Boeckx, P., Verbeeck, H., 2018. Liana and tree below-ground water competition — Evidence for water resource partitioning during the dry season. Tree Physiol. 38, 1071–1083. https://doi.org/10.1093/treephys/tpy002.

Del Bianco, M., Kepinski, S., 2018. Building a future with root architecture. J. Exp. Bot. 69, 5319–5323. https://doi.org/10.1093/jxb/ery390.

Descamps-Julien, B., Gonzalez, A., 2005. Stable coexistence in a fluctuating environment: an experimental demonstration. Ecology 86, 2815–2824. https://doi.org/10.1890/04-1700.

Fan, Y., Miguez-Macho, G., Jobbágy, E.G., Jackson, R.B., Otero-Casal, C., 2017. Hydrologic regulation of plant rooting depth. Proc. Nat. Acad. Sci. 114, 10572–10577. https://doi.org/10.1073/pnas.1712381114.

Friendly, M., 2002. Corrgrams: exploratory displays for correlation matrices. Am. Statist. 56, 316–324. https://doi.org/10.1198/000313002533.

Fry, B., 2006. Stable Isotope Ecology. Springer, New York. https://doi.org/10.1007/0-387-33745-8.

Gallien, L., 2017. Intransitive competition and its effects on community functional diversity. Oikos 126, 615–623. https://doi.org/10.1111/oik.04033.

Gallien, L., Zimmermann, N.E., Levine, J.M., Adler, P.B., 2017. The effects of intransitive competition on coexistence. Ecol. Lett. 20, 791–800. https://doi.org/10.1111/ele.12775.

Gilroy, S., Jones, D.L., 2000. Through form to function: root hair development and nutrient uptake. Trends Plant Sci. 5, 56–60. https://doi.org/10.1016/s1360-138501551-4.

Goulden, M.L., Bales, R.C., 2019. California forest die-off linked to multiyear deep soil drying in 2012–2015 drought. Nat. Geosci. 12, 632–637. https://doi.org/10.1038/s41561-019-0388-5.

Grilli, J., Barabás, G., Michalska-Smith, M.J., Allesina, S., 2017. Higher-order interactions stabilize dynamics in competitive network models. Nature 548, 210–213. https://doi.org/10.1038/nature23273.

Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C., Kueffer, C., 2014. Unifying niche shift studies: insights from biological invasions. Trends Ecol. Evol. 29, 260–269. https://doi.org/10.1016/j.tree.2014.02.009.

Harrell, F.E.J. 2015. Package ‘Hmisc’. Retrieved from https://cran.r-project.org/web/packages/Hmisc/Hmisc.pdf.

Hopmans, J.W., Bristow, K.L., 2002. Current capabilities and future needs of root water and nutrient uptake modelling. Adv. Agronomy 77, 103–183. https://doi.org/10.1016/s0065-211377014-4.

Horn, H.S., 1974. The ecology of secondary succession. Annu. Rev. Ecol. Syst. 5, 25–37. https://doi.org/10.1146/annurev.es.05.110174.000325.

Ivanov, V.Y., Hutyra, L.R., Wofsy, S.C., Munger, J.W., Saleska, S.R., de Oliveira Jr, R.C., De Camargo, P.B., 2012. Root niche separation can explain avoidance of seasonal drought stress and vulnerability of overstory trees to extended drought in a mature Amazonian forest. Water Resour. Res. 48, W12507. https://doi.org/10.1029/2012WR011972.

Jones, C., Banner, J.L., Humphrey, J.D., 2000. Estimating recharge in a tropical karst aquifer. Water Resour. Res. 36, 1289–1299. https://doi.org/10.1029/1999WR900358.

Jones, I.C., Banner, J.L., 2003. Estimating recharge thresholds in tropical karst island aquifers: barbados, Puerto Rico and Guam. J. Hydrol. 278, 131–143. https://doi.org/10.1016/S0022-169400138-0.

Kulmatiski, A., Adler, P.B., Foley, K.M., 2020. Hydrologic niches explain species coexistence and abundance in a shrub–steppe system. J. Ecol. 108, 998–1008. https://doi.org/10.1111/1365-2745.13324.

Kwasniewski, M., Daszkowska-Golec, A., Janiak, A., Chwialkowska, K., Nowakowska, U., Sablok, G., Szarejko, I., 2016. Transcriptome analysis reveals the role of the root hairs as environmental sensors to maintain plant functions under water-deficiency conditions. J. Exp. Bot. 67, 1079–1094. https://doi.org/10.1093/jxb/erv498.

Letten, A.D., Dhami, M.K., Ke, P.J., Fukami, T., 2018. Species coexistence through simultaneous fluctuation-dependent mechanisms. PNAS 115, 6745–6750. https://doi.org/10.1073/pnas.1801846115.

Letten, A.D., Keith, D.A., Tozer, M.G., Hui, F.K., 2015. Fine-scale hydrological niche differentiation through the lens of multi-species co-occurrence models. J. Ecol. 103, 1264–1275. https://doi.org/10.1111/1365-2745.12428.

Levine, J.M., Hart, S.P., 2020. The dimensions of species coexistence. In: Dobson, A., Tilman, D., Holt, R.D. (Eds.), Unsolved Problems in Ecology. Princeton University Press, Princeton, USA, pp. 145–159. https://doi.org/10.2307/j.ctvs9fh2n.16.

Levine, J.M., Bascompte, J., Adler, P.B., Allesina, S., 2017. Beyond pairwise mechanisms of species coexistence in complex communities. Nature 546, 56–64. https://doi.org/10.1038/nature22898.

Mayfield, M.M., Stouffer, D.B., 2017. Higher-order interactions capture unexplained complexity in diverse communities. Nat. Ecol. Evo. 1, 1–7. https://doi.org/10.1038/s41559-016-0062.

McGuire, K.J., McDonnell, J.J., 2006. A review and evaluation of catchment transit time modeling. J. Hydrol. 330, 543–563. https://doi.org/10.1016/j.jhydrol.2006.04.020.

McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B., Giblin, A.E., Kielland, K., Kwiatkowski, B.L., Laundre, J.A., Murray, G., 2002.

Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415, 68–71. https://doi.org/10.1038/415068a.

McNickle, G.G., Dybzinski, R., 2013. Game theory and plant ecology. Ecol. Lett. 16, 545–555. https://doi.org/10.1111/ele.12071.

Minden, V., Olde Venterink, H., 2019. Plant traits and species interactions along gradients of N, P and K availabilities. Funct. Ecol. 33, 1611–1626. https://doi.org/10.1111/1365-2435.13387.

Mommer, L., Van Ruijven, J., De Caluwe, H., Smit-Tiekstra, A.E., Wagemaker, C.A., Joop Ouborg, N., Bögemann, G.M., Van Der Weerden, G.M., Berendse, F., De Kroon, H., 2010. Unveiling below-ground species abundance in a biodiversity experiment: a test of vertical niche differentiation among grassland species. J. Ecol. 98, 1117–1127. https://doi.org/10.1111/j.1365-2745.2010.01702.x.

Murphy, B.W., 2014. Soil Organic Matter and Soil Function-Review of the Literature and Underlying Data. Department of the Environment, Canberra, Australia.

O'Keefe, K., Nippert, J.B., McCulloh, K.A., 2019. Plant water uptake along a diversity gradient provides evidence for complementarity in hydrological niches. Oikos 128, 1748–1760. https://doi.org/10.1111/oik.06529.

Pérez-Ramos, I.M., Matías, L., Gómez-Aparicio, L., Godoy, Ó., 2019. Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. Nat. Commun. 10, 1–11. https://doi.org/10.1038/s41467-019-10453-0.

Phillips, D.L., Gregg, J.W., 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136, 261–269. https://doi.org/10.1007/s00442-003-1218-3.

Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X., Ward, E.J., 2014. Best practices for use of stable isotope mixing models in food-web studies. Can. J. Zool. 92, 823–835. https://doi.org/10.1139/cjz-2014-0127.

Phillips, D.L., Newsome, S.D., Gregg, J.W., 2005. Combining sources in stable isotope mixing models: alternative methods. Oecologia 144, 520–527. https://doi.org/10.1007/s00442-004-1816-8.

Pierret, A., Maeght, J.L., Clément, C., Montoroi, J.P., Hartmann, C., Gonkhamdee, S., 2016. Understanding deep roots and their functions in ecosystems: an advocacy for more unconventional research. Ann. Bot. 118, 621–635. https://doi.org/10.1093/aob/mcw130.

R Core Team, 2019. R: A language and Environment For Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from. https://www.R-project.org/.

Schwinning, S., Kelly, C.K., 2013. Plant competition, temporal niches and implications for productivity and adaptability to climate change in water-limited environments. Funct. Ecol. 27, 886–897. https://doi.org/10.1111/1365-2435.12115.

Silvertown, J., Araya, Y., Gowing, D., 2015. Hydrological niches in terrestrial plant communities: a review. J. Ecol. 103, 93–108. https://doi.org/10.1111/1365-2745.12332.

Soliveres, S., Allan, E., 2018. Everything you always wanted to know about intransitive competition but were afraid to ask. J. Ecol. 106, 807–814. https://doi.org/10.1111/1365-2745.12972.

Soliveres, S., Maestre, F.T., Ulrich, W., Manning, P., Boch, S., Bowker, M.A., Prati, D., Delgado-Baquerizo, M., Quero, J.L., Schöning, I., Gallardo, A., Weisser, W., Müller, J., Socher, S.A., García-Gómez, M., Ochoa, V., Schulze, E., Fischer, M., Allan, E., 2015. Intransitive competition is widespread in plant communities and maintains their species richness. Ecol. Lett. 18, 790–798 https://doi.org/10.1111/ele.12456.

Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Phillips, D.L., Semmens, B.X., 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. Peer J. 6, e5096 https://doi.org/10.7717/peerj.5096.

Tekleab, S., Wenninger, J., Uhlenbrook, S., 2014. Characterisation of stable isotopes to identify residence times and runoff components in two meso-scale catchments in the Abay/Upper Blue Nile basin. Ethiopia. Hydrol. Earth Syst. Sci. 18, 2415–2431 https://doi.org/10.5194/hess-18-2415-2014.

Trinder, C.J., Brooker, R.W., Robinson, D., 2013. Plant ecology's guilty little secret: understanding the dynamics of plant competition. Funct. Ecol. 27, 918–929. https://doi.org/10.1111/1365-2435.12078.

Turcotte, M.M., Levine, J.M., 2016. Phenotypic plasticity and species coexistence. Trends Ecol. Evol. 31, 803–813. https://doi.org/10.1016/j.tree.2016.07.013.

Vilagrosa, A., Chirino, E., Peguero-Pina, J.J., Barigah, T.S., Cochard, H., Gil-Pelegrin, E., 2012. Xylem cavitation and embolism in plants living in water-limited ecosystems. In: Aroca, R. (Ed.), Plant Responses to Drought Stress. Springer, Berlin, Heidelberg, pp. 63–109.

Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., Zemla, J., 2017. Package 'corrplot'. Statistician 56, e24. Retrieved from. https://peerj.com/articles/9945/Supplemental_Data_S10.pdf.

Wu, J., Zeng, H., Zhao, F., Chen, C., Liu, W., Yang, B., Zhang, W., 2020. Recognizing the role of plant species composition in the modification of soil nutrients and water in rubber agroforestry systems. Sci. Total Environ. 723, 138042 https://doi.org/10.1016/j.scitotenv.2020.138042.

Wilkins, A.S., 2018. To lag or not to lag?: *Re*-evaluating the use of lagged dependent variables in regression analysis. Polit. Sci. Res. Methods 6, 393–411. https://doi.org/10.1017/psrm.2017.4.

Yang, B., Wen, X., Sun, X., 2015. Seasonal variations in depth of water uptake for a subtropical coniferous plantation subjected to drought in an East Asian monsoon region. Agric. For. Meteorol. 201, 218–228. https://doi.org/10.1016/j.agrformet.2014.11.020.

Zhu, H., 2006. Forest vegetation of Xishuangbanna, South China. For. Stud. China 8 (2), 1–58, 2006.

Zepeda, V., Martorell, C., 2019. Fluctuation-independent niche differentiation and relative non-linearity drive coexistence in a species-rich grassland. Ecology 100, e02726. https://doi.org/10.1002/ecy.2726.