



# Article Seasonal Water Uptake Patterns of Different Plant Functional Types in the Monsoon Evergreen Broad-Leaved Forest of Southern China

Deqiang Gao<sup>+</sup>, Beibei Zhang<sup>+</sup>, Qing Xu<sup>\*</sup>, Shirong Liu<sup>0</sup>, Ying Zhang, Ting Wang, Wenbin Xu and Haijun Zuo<sup>0</sup>

Key Laboratory of Forest Ecology and Environment of National Forestry and Grassland Administration, Ecology and Nature Conservation Institute, Chinese Academy of Forestry, Beijing 100091, China

\* Correspondence: xuqing@caf.ac.cn; Tel.: +86-10-6288-9549
+ These authors contributed equally to this work.

Abstract: The precipitation changes induced by climate warming have substantially increased extreme precipitation and seasonal drought events. Different plant functional types (PFTs) could exert an important role in resisting extreme climate. However, the patterns of plant water uptake in different PFTs remain uncertain, especially under different magnitudes of rainfall events. Here, we employed a stable hydrogen isotope ( $\delta D$ ) to determine the water sources of different PFTs, including *Castanopsis chinensis* in the canopy layer, *Schima superba* in the canopy sublayer, *Psychotria asiatica* in the shrub layer, and Blechnum orientale on the forest floor in the monsoon evergreen broad-leaved forest in Dinghushan Biosphere Reserve, China. We further used a two-end linear mixing model to explore the water utilization among different PFTs. Our results revealed that precipitation and soil water before rainfall were the water sources of different PFTs. Furthermore, the proportions of precipitation utilized by S. superba in the canopy sublayer under light and moderate rainfalls were 6.9%-59.4% and 30.5%-66.3%, respectively, which were significantly higher than those of other species in both the dry and wet seasons. After heavy rainfall, the proportion of precipitation utilized by S. superba was the lowest (4.7%–26.5%), while B. orientale had the highest proportion of precipitation utilization (31.6%-91.5%), whether in the dry or wet season. These findings imply that different PFTs would compete with one another for water uptake. Especially under climate warming, the uneven distribution of precipitation would intensify the water competition among species, ultimately resulting in the plant community structure becoming much more unstable than before.

**Keywords:** hydrogen stable isotope; water uptake pattern; plant functional types; monsoon evergreen broad-leaved forest; Dinghushan Biosphere Reserve; root distribution

# 1. Introduction

Climate warming is expected to impact plant physiology, distribution, and interspecific interactions [1,2], thus inducing changes in plant functional types (PFTs) [3,4]. Hence, PFTs could be predictors of the response of vegetation to climate change [5]. Different PFTs in the same habitat highly depend on water resources [6,7]. Especially under climate warming, changes in global precipitation increase the frequency and intensity of extreme precipitation and seasonal drought [8,9], subsequently leading to shifts in the water niche relationship between different PFTs [10–12]. Therefore, clarifying the water use patterns of different PFTs could provide measures of forest management to resist climate warming.

Numerous studies have revealed the water uptake patterns of different PFTs in forest ecosystems [13,14]. However, our knowledge on the water use strategies of different PFTs is still restricted by the following two aspects. First, the water absorption patterns of different PFTs remain controversial. Previous studies have illustrated that a difference exists in the water uptake patterns among various PFTs such as woody and herbaceous plants in a forest [15–18]. Generally, xylophyta in the canopy layer mainly absorb deep soil



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**Copyright:** © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). water or groundwater [19], while shrubs and herbs mainly use precipitation or shallow soil water [20]. In contrast, a recent study reported that in a mixed-hardwood forest of central Pennsylvania, woody plants—including *Pinus* spp. and *Quercus* spp.—relied considerably on shallow soil water, even in the drier parts of the growing season [21]. These inconsistent results suggest that the water uptake patterns of different PFTs in the same habitat are obscure. Therefore, it is essential to explore the patterns of plant water uptake in such PFTs.

Second, it remains unclear whether seasonal differences affect the water use patterns of different PFTs. It has been demonstrated that both *Pinus halepensis* and *Robinia pseudoacacia* in the canopy layer primarily utilize deep soil water or groundwater in the dry season and shallow soil water or rainfall in the wet season [22,23]. On the contrary, evergreen species in the canopy layer mainly absorbed shallow soil water in a typical karst forest in both dry and wet seasons [24]. These inconsistent observations suggest that more site-specific studies are needed to explore the water uptake patterns of different PFTs in various seasons. More importantly, with climate warming, the precipitation in each season will change [25,26]. However, our understanding of the impact of the various magnitudes of precipitation on the water uptake of different PFTs remains unclear. Therefore, there is an urgent need to explore the water use strategies of different PFTs following different magnitudes of precipitation in the dry and wet seasons.

To explore the proportion of precipitation utilized by different PFTs, we selected a monsoon evergreen broad-leaved forest with different PFTs, including *Castanopsis chinensis* in the canopy layer, *Schima superba* in the canopy sublayer, *Psychotria asiatica* in the shrub layer, and *Blechnum orientale* on the forest floor, in the Dinghushan Biosphere Reserve, China. Then, we employed a stable hydrogen isotope to analyze the precipitation utilization of the plants following six rainfall events in the dry and wet seasons. This study primarily tests the following two hypotheses: (1) these PFTs will show different water uptake patterns, i.e., *C. chinensis* in the canopy layer and *S. superba* in the canopy sublayer will have a low proportion of rainfall utilization, while *P. asiatica* in the shrub layer and *B. orientale* on the forest floor will have a high proportion of rainfall utilization; (2) significant differences will exist in the water uptake patterns of the four PFTs between the dry and wet seasons. The objective of this study is to explore the proportion of precipitation utilized by the different PFTs after different magnitudes of precipitation in the dry and wet seasons.

#### 2. Materials and Methods

## 2.1. Study Area

The study area was located in the Dinghushan Biosphere Reserve (23°09'21" N-23°11′30″ N, 112°30′39″ E–112°33′41″ E) in Guangdong Province, South China. The Dinghushan Biosphere Reserve was recognized as the first National Natural Reserve of China, with a total area of 11.56 km<sup>2</sup> and a peak elevation of 1000 m [27]. The area is characterized by a typical southern subtropical monsoon climate. Its mean annual temperature and relative humidity are 21.0 °C and 77.7%, respectively, with the maximum mean monthly temperature being 28.0 °C in August and the minimum being 12.6 °C in January. The mean annual precipitation is 1956 mm, with distinct seasonality (Figure 1). Approximately 80% of the rain falls in the warm–wet season (April–September) and only 20% falls in the cool–dry season (October–March) [27,28]. The monsoon evergreen broadleaved forest, as the late succession stage and the local climax vegetation without human disturbance in the Dinghushan Biosphere Reserve, has been maintained for more than 400 years [29,30]. The dominant tree species include C. chinensis, S. superba, Cryptocarya chinensis, and Aporusa yunnanensis. P. asiatica and Blastus cochinchinensis always firmly occupy the leading status in the shrub species. The dominant species of herbaceous plants are *B. orientale* and *Diplazium donianum*. The soil type is categorized as lateritic red soil, with a soil profile usually ranging from 60 to 100 cm in depth [28].



Figure 1. Mean monthly precipitation in the study area from 2013 to 2014.

#### 2.2. Rainfall Events Selection

According to the standard of light (0–10 mm), moderate (10–25 mm), and heavy rainfall (>25 mm), six different rainfall events were selected, including 5.4 mm on 1 October 2013, 9.8 mm on 27 July 2014, 11.2 mm on 22 February 2014, 20.0 mm on 8 September 2013, 36.0 mm on 2 July 2013, and 45.8 mm on 18 December 2013. Specifically, the rainfall events of 5.4, 11.2, and 45.8 mm occurred in the dry season, while the other three rainfall events occurred in the wet season. Rainfall events of less than 5 mm were not considered. No rainfall was observed for five consecutive days following the six rainfall events.

### 2.3. Field Sampling

Three  $20 \times 20$  m plots were randomly established in the monsoon evergreen broadleaved forest. In each plot, four representative species, namely, *C. chinensis*, *S. superba*, *P. asiatica*, and *B. orientale*, were collected. In each sampling plot, three replicate standard plants for the four representative species were selected for sampling the xylem. For each of the tree and shrub species, three healthy plants with a similar canopy size were chosen and 3–4-centimeter segments of the middle of the plant stems facing the sunlight were collected for extracting plant stem water. In the case of herbaceous plants, three healthy plants with a similar cover, height, and base stem were selected as three replicates, and 2–3-centimeter-long basal stems of each plant were collected. Before each rainfall event, plant stem samples were collected. This kind of sample was also collected daily for a period of five days following each rainfall event.

Additionally, three soil profiles were dug to a depth of 100 cm in the plots, close to the place where the plants were sampled. Soil samples were collected before rainfall from each of the four soil layers (0–10, 10–40, 40–80, and 80–100 cm) to determine the  $\delta$ D value of the soil water before rainfall. In addition, the soil samples were sealed in soil cylinders and the gravimetric water content was measured later, expressed as grams of water per 100 g of dry soil (oven-drying method) [20].

Three rain gauges were installed in each of the three forestless lands in the monsoon evergreen broad-leaved forest to measure the daily accumulated rainfall and to collect precipitation samples. All of the rainfall samplings were collected each day between 7:00 a.m. and 8:00 a.m. to prevent evaporation. These samples were a mix of the daily rainwater from the three rain gauges.

Shallow groundwater samples were collected every day in two wells with a 2-meter depth after rainfall occurred and then mixed into one sample. Of the two wells, one was

near the study site ( $112^{\circ}32'17.38''$  E,  $23^{\circ}10'33.99''$  N) and the other was at the foot of a mountain ( $112^{\circ}32'54.70''$  E,  $23^{\circ}9'58.62''$  N).

All of the collected samples were placed in glass bottles and sealed with parafilm and then immediately stored in a freezer at -18 °C. The precipitation and shallow groundwater samples were collected daily in the time window of 7:00–8:00 am, and other samples were collected between 8:00 a.m. and 10:00 a.m.

#### 2.4. Sample Pretreatment and Stable Isotope Analysis

The water in the soil and plant stem samples was cryogenically extracted. The hydrogen isotope ratios of the extracted water, groundwater, and rainwater were measured with an isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, Inc., Waltham, MA, USA) coupled with an elemental analyzer (Flash 2000 HT, Thermo Fisher Scientific, Inc., Waltham, MA, USA). The precision for the  $\delta$ D analysis was  $\pm 1$ %. The hydrogen isotope ratio was expressed in delta units, i.e.,  $\delta$ D (‰):

$$\delta = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000\% \tag{1}$$

where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  refer to the D/H molar ratios of the sample and the standard (i.e., SMOW), respectively.

#### 2.5. Proportion of Precipitation Utilized by the Plants

By comparing the  $\delta D$  values of the plant stem water to those of the potential water (precipitation, shallow groundwater, and soil water before rainfall), both precipitation and soil water before rainfall could be determined as the water sources of the plants. Given that the plant stem water was derived from two sources (namely precipitation and soil water before rainfall) in our case, a single two-ended linear mixing model could be used to determine the proportion of precipitation utilized by the plants as Equation (2) [31]:

$$P_{\rm P} = \frac{\delta D_{\rm PW} - \delta D_{\rm SW}}{\delta D_{\rm P} - \delta D_{\rm SW}} \times 100\%$$
<sup>(2)</sup>

where  $P_P$  is the proportion of precipitation utilized by the plants and  $\delta D_{PW}$ ,  $\delta D_{SW}$ , and  $\delta D_P$  are the  $\delta D$  values of plant xylem water, soil water before rainfall, and precipitation, respectively.

#### 2.6. Plant Root Collection

Three well-growing plants for each of the tree and shrub species in the plots were collected for root biomass surveys. At a distance of 0.5–1.0 m from the main stem of each plant, plant roots were collected from the four soil layers of 0–10, 10–40, 40–80, and 80–100 cm by digging. From each of the four soil layers, soil of 30 cm (length)  $\times$  30 cm (width)  $\times$  20 cm (depth) along the soil profile was gathered, and the plant roots were collected by sieving. The roots were separated into live and dead roots (debris) according to their color and tensile strength [32]. The live roots were sorted by root diameter and divided into coarse (>5 mm), medium (2–5 mm), and fine ( $\leq$ 2 mm) roots. The three kinds of roots were dried to constant weight in an oven and weighed to calculate the root biomass.

## 2.7. Statistical Analyses

We conducted a one-way ANOVA to test the differences in the proportions of precipitation utilized by the four PFTs, i.e., *C. chinensis*, *S. superba*, *P. asiatica*, and *B. orientale*. We further used an ordinary least squares regression analysis to examine the relationships between the proportion of precipitation utilized by *S. superba* and the soil moisture before rainfall. All of the analyses were performed with SPSS (Inc., Chicago, IL, USA).

# 3. Results

# 3.1. Changes in $\delta D$ of the Plant Stem Water

Following the six rainfall events, the  $\delta D$  values of the stem water in these four different PFTs were distributed between the  $\delta D$  values of precipitation and soil water before rainfall, suggesting that the plant water mainly originated from both the precipitation and the soil water before rainfall (Figure 2).



**Figure 2.**  $\delta D$  values (mean  $\pm$  SD) of soil water before rainfall, rainfall, groundwater, and plant stem water in the dry (**a**–**c**) and wet (**d**–**f**) seasons in the monsoon evergreen broad-leaved forest.

Following the 5.4 mm rainfall event in the dry season, the  $\delta D$  values of the stem water in *C. chinensis*, *S. superba*, *P. asiatica*, and *B. orientale* were -38.2 to -35.1%, -41.2 to -39.9%, -40.4% to -38.1%, and -40.4% to -38.1%, respectively. The stem water  $\delta D$  value of *S. superba* in the canopy sublayer was the closest to that in precipitation (Figure 2a). Similarly, this phenomenon was also observed following the 11.2 mm rainfall event in the dry season and the 9.8 mm and 20.0 mm rainfall events in the wet season (Figure 2b,d,e). In contrast, the  $\delta D$  value in the stem water of *B. orientale* was the closest to that in precipitation following the 45.8 mm rainfall event in the dry season and the 36.0 mm rainfall event in the wet season (Figure 2c, f).

#### 3.2. The Proportion of Precipitation Utilized by the Plants

Following light and moderate rainfall events in both the dry and wet seasons, the proportion of precipitation utilized by the plants from highest to lowest was as follows: *S. superba* > *B. orientale* > *P. asiatica* > *C. chinensis* (Figure 3a,b,d,e). Among them, the proportion of precipitation utilized by *S. superba* under light rainfall was significantly higher than that of the other species, regardless of the season (p < 0.05; Figure 3a,d). Similarly, the proportion of precipitation utilized by *S. superba* under moderate rainfall was the largest in the wet season (p < 0.05; Figure 3e). In addition, the utilized proportion of precipitation of *precipitation* and moderate rainfall was significantly lower than that of the other species in the wet season (p < 0.05; Figure 3e).



**Figure 3.** Changes in the proportion of precipitation utilized by the four PFTs after different magnitudes of rainfall events in the dry (**a**–**c**) and wet (**d**–**f**) seasons in the monsoon evergreen broad-leaved forest. The whiskers illustrate the 5th and 95th percentiles, and the ends of the boxes represent the 25th and 75th quartiles (interquartile range). Different letters indicate significant differences at p < 0.05.

In contrast to the light and moderate rainfall events, the order of the proportion of heavy rainfall utilized by the plants was *B. orientale* > *P. asiatica* > *C. chinensis* > *S. superba*, whether in the dry or wet season (Figure 3c,f). Specifically, the proportion of heavy rainfall utilized by *B. orientale* was significantly higher than that of the other species in the dry season (p < 0.05; Figure 3c), while the proportion of heavy rainfall utilized by *S. superba* was the lowest in the dry season (p < 0.05; Figure 3c).

The *C. chinensis*, *P. asiatica*, and *B. orientale* plants had relatively lower utilization proportions of light and moderate rainfalls (Figure 3a,b,d,e) but showed a higher utilization proportion of heavy rainfall in both the dry and wet seasons (Figure 3c,f). On the contrary, *S. superba* showed a higher consumption of light and moderate rainfalls (Figure 3a,b,d,e) but a lower consumption of heavy rainfall (Figure 3c,f).

# 3.3. Root Distribution of the Plants

With respect to *C. chinensis*, the percentages of fine root biomass in the four soil layers were 18.0%, 47.0%, 29.2%, and 5.6%, respectively (Figure 4a), of which the fine root biomass within the 0–40 cm soil layer accounted for 65% of the total fine biomass. For *S. superba*, the percentages of fine root biomass in the four soil layers were 20.9%, 39.4%, 35.3%, and 4.4%, respectively (Figure 4b). Regarding *P. asiatica*, the fine roots were mainly distributed within a depth of 10–80 cm, accounting for 87% of the total fine roots (Figure 4c). Moreover, most of the fine roots of *B. orientale* existed in the 0–40 cm soil layer (Figure 4d).



**Figure 4.** Fine root biomass of the four different PFTs including *Castanopsis chinensis* (**a**), *Schima superba* (**b**), *Psychotria asiatica* (**c**), and *Blechnum orientale* (**d**) in the monsoon evergreen broad-leaved forest.

## 4. Discussion

Our results show that the proportion of precipitation utilized by *C. chinensis* in the canopy layer was significantly lower than that of *B. orientale* on the forest floor, which supports our first hypothesis. This phenomenon may be attributed to the divergent proportion of fine root distribution [33]. Generally, shrubs and herbs are shallow-rooted species, and their roots are mostly distributed in the shallow soil layer, especially in subtropical forests. Thus, they tend to absorb more rainfall rather than soil water. On the contrary, arbors with a deeper root distribution exhibit a lower proportion of precipitation utilization [34]. In this study, the fine roots of *B. orientale* were mainly distributed at a soil depth of 0–40 cm, accounting for 99% of the total fine roots, while for *C. chinensis*, only 65% of the fine root biomass was distributed in the 0–40 cm soil layer. Therefore, the proportion of precipitation utilized by *C. chinensis* was significantly lower than that of *B. orientale*.

Although *S. superba* had the lowest absorbed proportion of heavy rainfall, it had the highest utilized proportion of light and moderate rainfalls compared to the other species in the shrub and herb layers. These results are contrary to the traditional view that trees in the canopy and sub-canopy layers mainly absorb deep soil water or groundwater [35] while plants in the shrub and herb layers primarily absorb precipitation or shallow soil water in the forest ecosystem [36,37]. Our results illustrated that tree species such as S. superba still absorbed substantial precipitation after light and moderate rainfall, even in subtropical regions with sufficient precipitation. This observation may be attributed to the distribution of the fine root biomass of *S. superba* and the soil moisture before rainfall. Specifically, at our study site, the amount of fine root biomass of *S. superba* distributed in each soil layer was higher than that of the other species (Figure 4); thus, its water absorption capacity was stronger than that of the others [24,38,39]. More importantly, before the occurrence of light and moderate rainfall, the soil moisture was low at the study site, with a mean value of 16% and 20%, respectively. Under this condition, S. superba may have been in a state of water shortage. Therefore, the proportions of light and moderate rainfall utilized by S. superba were significantly higher than those of the other species. In contrast, before the occurrence of heavy rainfall, the soil moisture (30%–40%) at the study site was higher than that before light and moderate rainfall. Hence, the plant species had no water shortage problem under this condition. Even if heavy rainfall occurred, the proportion of heavy rainfall utilized by S. superba was still the lowest. This deduction was also supported by the negative correlation between the water use pattern of *S. superba* and the soil moisture before rainfall (Figure 5), suggesting that the low soil moisture before rainfall increased the plant's water demand [40]. Hence, after the occurrence of light and moderate rainfall, S. superba showed a higher proportion of precipitation utilization. Our findings imply that not all



PFTs follow their water niches to maintain community stability (e.g., *S. superba*), which may result in water competition across the PFTs, especially after light and moderate rainfall.



Previous studies have reported seasonal dynamics in plant water uptake. For instance, *Betula utilis* and *Bashania fangiana* mainly absorb rainfall in the wet season but utilize shallow soil water at a depth of 0–40 cm in the dry season [19]. However, in our case, the water uptake patterns of the four PFTs showed no significant changes in either the dry or wet season (Figure 3), which does not support our second hypothesis. The different plant water uptake patterns in the dry and wet seasons between the current study and previous work could be due to the distinct differences in soil moisture [41–43]. Specifically, there were no significant differences in the soil moisture before rainfall between the dry and wet seasons at this study site (Figure 6a). By comparison, the study site investigated by Xu et al. [19] showed distinct differences in soil moisture between the dry and wet seasons. Collectively, different changes in soil moisture among the two seasons determine whether seasonal dynamics exist in plant water uptake.



**Figure 6.** Comparison of soil moisture before rainfall between the dry and wet seasons in this study (a) and in that of Xu et al. [19] (b). \*\*\* p < 0.001.

Although this study provides evidence of the water uptake patterns of four PFTs in southern subtropical China, some uncertainties still exist in our case. First, the limited number of study sites may induce uncertainty regarding the water uptake patterns of the four PFTs in the subtropical forest. Despite different water uptake patterns being observed among the four PFTs at this site, more sites are needed to confirm this phenomenon. Second, previous studies have pointed out that water extraction techniques may influence the analysis of water uptake patterns [44]. However, this view was negated by a recent study [45]. Therefore, more research is needed to advance our understanding of whether water extraction techniques influence the analysis of plant water uptake.

## 5. Conclusions

The primary water sources of the four different PFTs investigated here (*C. chinensis*, *S. superba*, *P. asiatica*, and *B. orientale*) are mainly precipitation and soil water before rainfall in the monsoon evergreen broad-leaved forest. After light and moderate rainfall events, the order of the proportion of precipitation utilized by the different PFTs was *S. superba* > *B. orientale* > *P. asiatica* > *C. chinensis*, while after heavy rainfall events, the utilized precipitation proportions occurred in the order of *B. orientale* > *P. asiatica* > *C. chinensis* > *S. superba* in both the dry and wet seasons. Our findings imply that not all PFTs follow their water niches to maintain community stability; instead, some species will compete with other species for water absorption. Especially under climate warming, the unevenly distributed precipitation would intensify the water competition among species, ultimately leading to the plant community structure becoming much more unstable than before.

**Author Contributions:** Conceptualization, Q.X. and S.L.; methodology, D.G.; software, B.Z.; validation, D.G., B.Z. and Q.X.; formal analysis, B.Z.; investigation, D.G., T.W. and Y.Z.; resources, B.Z., W.X. and H.Z.; data curation, D.G. and B.Z.; writing—original draft preparation, D.G.; writing—review and editing, B.Z., Q.X. and S.L.; visualization, D.G. and B.Z.; supervision, Q.X.; project administration, Q.X. and S.L.; funding acquisition, D.G., Q.X. and S.L. All authors have read and agreed to the published version of the manuscript.

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