forests

MDPI

Article

The Impact of Bamboo (*Phyllostachys edulis*) Expansion on the Water Use Patterns of Broadleaf Trees

Xiaoxia Zeng [1,2], Chao Gong [1], Jian Lu [3], Guohai Huang [3], Chengjie Fu [2], Yanhua Yu [2], Huan Ran [1], Qingni Song [1], Dongmei Huang [4], Jun Liu [1,]* and Qingpei Yang [1]

[1] Jiangxi Provincial Key Laboratory of Improved Variety Breeding and Efficient Utilization of Native Tree Species, College of Forestry, Jiangxi Agricultural University, Nanchang 330045, China; 18174009873@163.com (X.Z.); taitouciciyan@163.com (C.G.); ranhuan2023@163.com (H.R.); songqingni@126.com (Q.S.); qingpeiyang99@163.com (Q.Y.)
[2] Institute of Forest Ecology and Carbon Sequestration Measurement, Fujian Forestry Vocational and Technical Collage, Nanping 353000, China; fuchengjie2024@163.com (C.F.); yutou0311128@126.com (Y.Y.)
[3] Administration of Jiangxi Qiyunshan Nature Reserve, Ganzhou 341000, China; lujian202403@163.com (J.L.); huangguohai2024@163.com (G.H.)
[4] School of Humanities and Public Administration, Jiangxi Agricultural University, Nanchang 330045, China; hdmae99@163.com
* Correspondence: liujun@jxau.edu.cn

Abstract: The expansion of bamboo (*Phyllostachys edulis*) affects the growth status of trees in colonized forests, but there has been insufficient research on changes in tree water physiology. In this study, we used stable δ^2H, δ^{18}O, and ^{13}C isotope ratios to analyze the water sources and water use efficiency (WUE) of bamboo, deciduous broadleaf trees (*Alniphyllum fortunei*), and evergreen broadleaf trees (*Machilus pauhoi* and *Castanopsis eyrei*) in a bamboo-expended broadleaf forest (BEBF), a bamboo-absent broadleaf forest (BABF), and a bamboo forest (BF). We found that the expansion of bamboo had no significant effect on the water sources and WUE of deciduous broadleaf trees, but altered the water sources of evergreen broadleaf trees. During the growing season, evergreen broadleaf trees decrease their uptake fractions of surface soil water by 7.1% to 9.6% and increased their uptake fractions of middle soil water by 5.8%~9.4%. Conversely, during the non-growing season, they increased their uptake fractions of surface soil water by 11.9% and decreased their uptake fractions of deeper soil water by 5.6%~12.9%. Additionally, after expanding into broadleaf forests, bamboo increased its uptake proportion of surface and shallow soil water by 20.0% and 9.4% during the growing season. Its WUE also improved, increasing by 20.0 µmol/mol and 13.0 µmol/mol during the growing and non-growing seasons, respectively. These results indicate that as bamboo expands into broadleaf forests, it enhances its competitiveness for water resources by changing its water use strategy. Compared to deciduous broadleaf trees, evergreen broadleaf trees exhibit more flexible water use strategies under the conditions of bamboo expansion. Our research reveals, for the first time, how broadleaf trees adjust their water use strategies in response to bamboo expansion, and uncovers the mechanisms behind bamboo expansion into evergreen broadleaf forests from the perspective of water use strategies. This will aid future forest management under the conditions of bamboo expansion.

Keywords: stable isotope; water source; water use efficiency; biological expansions; bamboo (*Phyllostachys edulis*)

check for updates

Citation: Zeng, X.; Gong, C.; Lu, J.; Huang, G.; Fu, C.; Yu, Y.; Ran, H.; Song, Q.; Huang, D.; Liu, J.; et al. The Impact of Bamboo (*Phyllostachys edulis*) Expansion on the Water Use Patterns of Broadleaf Trees. *Forests* **2024**, *15*, 1984. https://doi.org/10.3390/f15111984

Academic Editor: Domingo Sancho-Knapik

Received: 14 October 2024
Revised: 29 October 2024
Accepted: 8 November 2024
Published: 10 November 2024

1. Introduction

Water is the transport medium for substances such as photosynthetic products and growth hormones in plants, and it directly participates in various physiological activities [1], making it especially important for plant growth and development. The pattern of water use by plants largely determines how ecosystems respond to changes in environmental water conditions. However, research on plant water use has mostly focused on arid and semi-arid regions, primarily concentrating on the relationship between water use strategies and climate factors [2–4]. In recent years, broadleaf forests have faced serious bamboo (*Phyllostachys edulis*) expansion issues [5,6]. Bamboo is a water-intensive plant with high water demands during its growth [7,8], which can restrict the water availability conditions for broadleaf trees and subsequently affect their growth and development. To survive, broadleaf trees must adjust their water use strategies to ensure that they obtain sufficient water amid long-term water competition. Some species with water use strategies that are insensitive to environmental changes may be eliminated due to water limitations. Therefore, studying the water use strategies of broadleaf trees is crucial for understanding how they respond to the expansion of bamboo.

Plant water use strategies are mainly reflected in two aspects. The first is the source of water, which is the manifestation of plant water use strategies, with available water primarily coming from soil water, atmospheric precipitation, and groundwater [9]. The proportion of a plant's utilization of these potential water sources varies with changes in soil moisture content and precipitation [2,10,11]. The second is water use efficiency (WUE), which refers to the biomass accumulated per unit weight of water consumed (the ratio of photosynthetic rate to transpiration rate) [12,13]. WUE is an important indicator of a plant's drought resistance and is closely related to environmental factors that affect photosynthesis and transpiration, such as light and water availability [14–16]. After bamboo expands into broadleaf forests, what impact does it have on soil water availability, and how do the water use strategies of broadleaf trees change?

Bamboo has a strong advantage in water competition compared to broadleaf trees due to several biological characteristics. Firstly, as a clonal plant, bamboo can share water among its clones through rhizomes [17]. Secondly, bamboo's extensive underground root system and high biomass of fine roots, about six times that of broadleaf trees, form a root network in the soil [18]. As bamboo expands into broadleaf forests, its fine root distribution tends to be in the upper (surface and shallow) soil layer [18], thus intensifying competition for upper soil water with broadleaf trees. This may lead to a lack of available upper soil water for broadleaf trees. Several studies have found that when some species experience insufficient upper soil water, they undergo adaptive changes, shifting to use water from deeper soil layers or groundwater to reduce interspecies water competition [4,19–21]. Additionally, under inadequate water conditions, trees close their stomata to increase WUE for survival and growth [22–25]. Therefore, do broadleaf trees increase their use of deep soil water and improve WUE to adapt to the environment after bamboo expansion?

Stable isotope techniques are widely used to study plant water use strategies, due to their sensitivity, accuracy, and speed [3,26]. By analyzing the hydrogen (^{2}H) and oxygen (^{18}O)-stable isotope composition in plant xylem water and potential water sources, the proportion of water sources utilized by plants can be quantified [27]. Additionally, the analysis of plant leaf carbon-stable isotopes (δ^{13}C) can estimate the long-term WUE of plants [13,28]. Based on these analyses, we utilize stable isotope techniques to examine uptake fractions of various potential water sources and the WUE of broadleaf trees and bamboo in a bamboo-absent broadleaf forest (BABF), bamboo-expended broadleaf forest (BEBF), and bamboo forest (BF) within the Qiyunshan National Nature Reserve, Jiangxi Province, China, where bamboo expansion is relatively severe. Our aim is to answer the following scientific questions: After bamboo expansion into broadleaf forests, what strategic changes do broadleaf trees adopt for water use? Do broadleaf trees increase their use of deep soil water? Do they improve their WUE? Validating these hypotheses can reveal the water use patterns of broadleaf trees, providing insights into the water consumption characteristics and trends of evergreen broadleaf forests under bamboo expansion. This can offer valuable insights for the restoration of broadleaf forests.

2. Materials and Methods

2.1. Study Area

The research was conducted in the Qiyunshan National Nature Reserve (QNNR), located in Jiangxi Province, China (113°54′–114°07′ E, 25°41′–25°54′ N, Figure 1), with an elevation of approximately 2060 m above sea level. The QNNR belongs to the humid subtropical monsoon climate zone, which is characterized by a warm climate and abundant rainfall [29,30]. The average annual precipitation in the QNNR ranges from 1522 to 1660 mm, and the average annual temperature is between 18.0 and 18.4 °C [31]. The dominant vegetation in the QNNR is evergreen broadleaf forest, but many areas still have bamboo forests. The canopy structure in this region primarily consists of two layers: the upper canopy, featuring fast-growing deciduous trees along with some mature evergreen trees (maximum height: 15–20 m), and the understory, which is predominantly populated by mature and young shade-tolerant species.

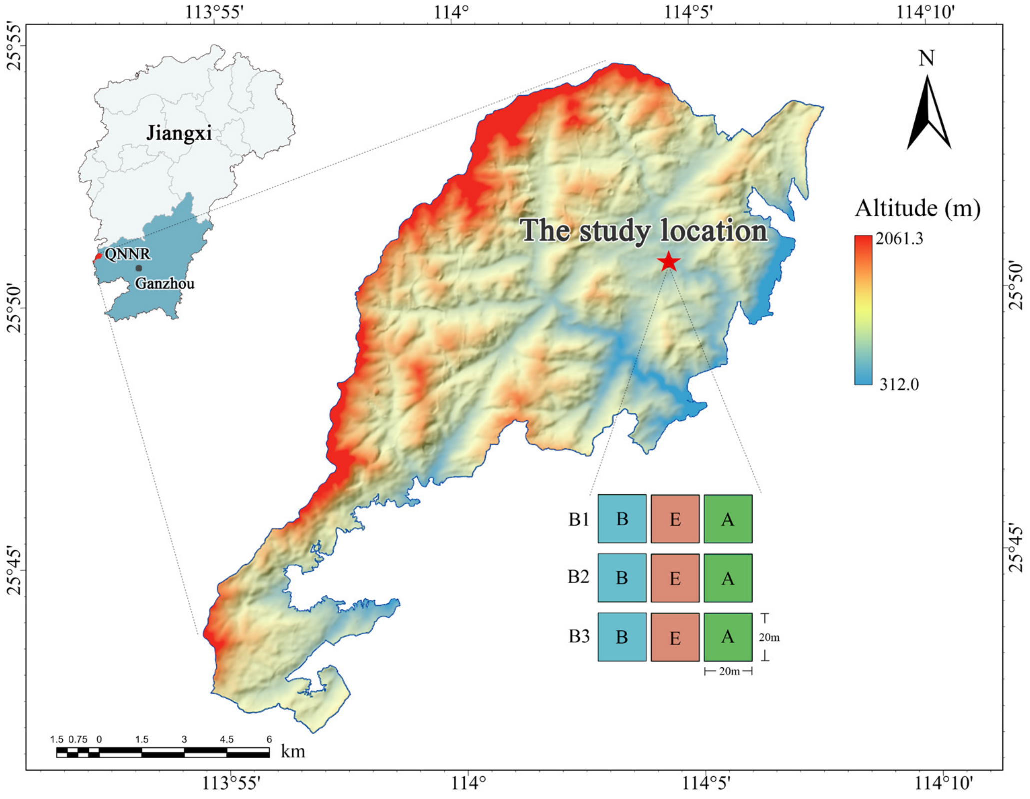

Figure 1. The study location and experimental layout of three blocks (B1; B2; B3). The locations of Ganzhou City (dark blue area) and the QNNR (red point) are shown in the top left corner of the image, along with the experimental blocks (red star) within the QNNR area. Bamboo (*Phyllostachys edulis*)-absent broadleaf forest is represented by green squares (A), bamboo-expanded broadleaf forest is indicated by red squares (E), and bamboo forest is depicted by blue squares (B).

2.2. Experimental Design

Three experimental blocks—B1, B2, and B3—were established in June 2021 (Figures 1 and 2). Each block contained three sample plots measuring 20 m × 20 m, representing bamboo-absent broadleaf forest (BABF), bamboo-expended broadleaf forest (BEBF), and bamboo forest (BEBF), totaling nine plots. The sample plots were spaced more than 10 m apart, and were all located on a northwest-facing clay loam slope with an incline of 16 to 20 degrees. Before the establishment of the nature reserve, the area experienced human-induced disturbances, leading to the formation of secondary broadleaf forests with similar stand densities across the plot. Following the creation of the nature reserve in 1997, the broadleaf forests began a process of natural recovery. During this recovery, the broadleaf forests neighboring the bamboo forests were gradually encroached upon by the expansion of bamboo, leading to the formation of bamboo–broadleaf mixed forests and bamboo stands.

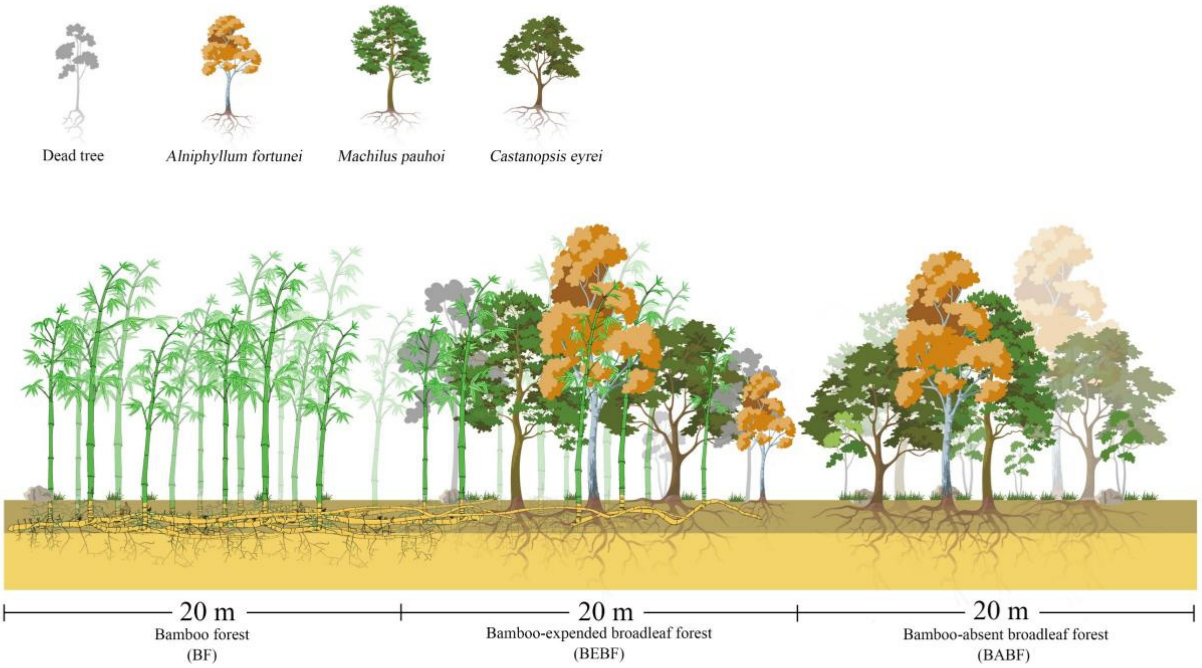

Figure 2. The experimental gradient of bamboo expansion includes bamboo forest (BF), bamboo-expanded broadleaf forest (BEBF), and bamboo-absent broadleaf forest (BABF).

The broadleaf area primarily consisted of *Alniphyllum fortunei*, *Machilus pauhoi*, *Castanopsis eyrei*, *Castanopsis fargesii*, and *Daphniphyllum oldhamii* in both the BEBF and BABF of the study area. Three tree species—*A. fortunei*, *M. pauhoi*, and *C. eyrei*—were selected as the focus of our research due to their presence in both forest types. Additionally, we also focused our study on bamboo in the BEBF and BF.

2.3. Sample Collection and Data Calculation

2.3.1. Water Use Sources

We collected isotope samples from the branches of broadleaf trees and bamboo in the BABF, BEBF, and BF during the growing season (mid-August) and the non-growing season (mid-November) of 2021, with a total of 48 samples. Simultaneously, we also collected soil isotope samples from the 0–10 cm, 10–20 cm, 20–40 cm, 40–60 cm, and 60–80 cm soil layers using a soil auger. Each soil sample was a composite of samples taken from the east, west, south, and north directions of the sampling plants, totaling 240 soil samples. Groundwater samples were collected immediately from wells with three replicates when collecting plant and soil samples. Rainwater samples were collected using homemade rainwater collectors (consisting of a plastic funnel with a diameter of 20 cm at the top and an iron bucket with a diameter of about 15 cm at the bottom) during precipitation events from August to November 2021.

All isotope samples were promptly placed in 50 mL centrifuge tubes, sealed with Parafilm, and then taken back to the laboratory, where they were stored frozen at −20 °C for measuring the natural molar abundance ratios of water isotopes. First, we used a cryogenic vacuum distillation system (Li-2000) to extract water from the plant xylem and soil isotope samples. Next, we used a 5 mL syringe and a 0.22 μm filter to filter the xylem water, precipitation, soil water, and groundwater into 1.5 mL sample vials. Finally, we measured the hydrogen and oxygen isotope ratios of these samples using an elemental analyzer–isotope ratio mass spectrometer (Thermo Fisher Scientific IR-MS, Langenselbold, Germany) with testing accuracies of 0.5‰ and 0.1‰, respectively. Formula (1), used for calculating the isotopic ratios of hydrogen and oxygen in the samples, is as follows:

$$\delta X\text{‰} = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000 \tag{1}$$

where δX represents δ^2H or δ^{18}O, and R_{sample} and $R_{standard}$ represent the molar abundance ratios of the heavy to light isotopes (^{2}H/^{1}H or ^{18}O/^{16}O) in the sample and the standard, respectively (V-SMOW, Standard Mean Ocean Water).

We assessed the relative contribution of different water sources to xylem water using the IsoSource mixing model [32]. We inputted the isotope values of xylem water, precipitation, soil water (soil profile was subdivided into five potential water sources) and groundwater into the IsoSource model, and then set two parameters: (1) source increment, established at 1%, which assigned the proportion of plant utilization among each water source in 1% increments to test possible proportion combinations; and (2) mass balance tolerance, set at 0.01, meaning that the difference between the weighted sum of the isotope values from each water source and the isotope value of the xylem water should not exceed 0.01.

We divided the soil profile into five potential soil water sources based on variations in root distribution, soil water content (SWC), and the isotope composition of soil water across different soil layers. These sources were 0–10 cm (surface soil water), 10–20 cm (shallow soil water), 20–40 cm (middle soil water), 40–60 cm (deep soil water), and 60–80 cm (deeper soil water).

Additionally, when collecting soil for isotope analysis, a portion of each soil sample was placed in aluminum boxes and taken back to the laboratory. The fresh weight of each sample was measured immediately upon arrival, and the samples were then placed in a drying oven at 105 °C until reaching a constant weight. The dry weight was recorded, and the soil water content (SWC) was calculated.

2.3.2. Water Use Efficiency

We collected leaf samples from broadleaf trees and bamboo during the growing season (mid-August) and the non-growing season (mid-November) of 2021 to analyze the WUE. First, the leaves were placed in a drying oven at 105 °C for 30 min to kill the greens, and then dried at 65 °C to a constant weight. The dried leaves were then ground into powder using a ball mill. Finally, the δ^{13}C values of the leaves were measured using an elemental analyzer–isotope ratio mass spectrometer (Thermo Fisher Scientific IR-MS), with an accuracy of 0.2‰. Formula (2), used for calculating the isotopic ratios of carbon in the samples, is as follows:

$$\delta^{13}C\text{‰} = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000 \tag{2}$$

where R_{sample} and $R_{standard}$ represent the molar abundance ratios of the heavy to light isotopes (^{13}C/^{12}C) in the sample and the standard, respectively.

The plants' *WUE* was analyzed using foliar $\delta^{13}C_p$ data [13,33]. First, we calculated changes in C isotopic discrimination ($\Delta\delta^{13}C$) from foliar $\delta^{13}C_p$ data and air $\delta^{13}C_a$ using Formula (3). The $\delta^{13}C_a$ was determined based on Formula (7), where t represents the sampling year (2021 in this study) [34]. Next, the $\Delta\delta^{13}C$ value was used to calculate the ratio of internal leaf CO$_2$ concentration (C_i) to ambient air CO$_2$ concentration (C_a) through Formula (4), where a represents the diffusion through the stomata (4.4‰), and b represents the carboxylation fraction by ribulose-1,5-bisphosphate carboxylase/oxygenase (27‰) [13]. The value for C_a was obtained from Formula (6) [34]. Finally, we calculated the plant

WUE using the C_i/C_a ratio and applied Formula (5), where 1.6 is the ratio of stomatal conductance to water vapor and CO_2.

$$\Delta^{13}C = \left(\frac{\delta^{13}C_a - \delta^{13}C_p}{1 + \delta^{13}C_p/1000} \right) \tag{3}$$

$$\Delta^{13}C = a + \frac{(b-a)C_i}{C_a} \tag{4}$$

$$WUE = \frac{(C_a - C_i)}{1.6} \tag{5}$$

$$C_a = 277.78 + 1.350e^{[0.01572(t-1740)]} \tag{6}$$

$$\delta^{13}C_a = -6.429 - 0.006e^{[0.0217(t-1740)]} \tag{7}$$

2.4. Statistical Analysis

We used an independent-sample t-test to analyze the differences in the uptake fractions of various potential water sources and WUE of broadleaf trees in BABF and BEBF, and bamboo in BF and BEBF. This analysis aimed to investigate the impact of bamboo invasion into broadleaf forests on the water use strategies of broadleaf trees as well as the adjustments in bamboo's own water use strategies. All data were statistically analyzed using Excel 2019 and SPSS 22.0, with graphs generated using Origin 2022 software.

3. Results

3.1. Soil Moisture Characteristics

The expansion of bamboo increased the soil water content of broadleaf forests (Figure 3). From BABF to BEBF, the greatest increases in soil water content occurred in the 0–10 cm and 10–20 cm shallow soil layers, with increases of 26.5% ($p < 0.01$) and 22.3% ($p < 0.01$) during the growing season, and 24.5% ($p < 0.01$) and 21.8% ($p < 0.01$) during the non-growing season. From BEBF to BF, there was no significant change in water content in the 0–10 cm soil layer during either season. However, increases were noted in the 10–20 cm, 20–40 cm, 40–60 cm, and 60–80 cm soil layers, with changes of 5.0% ($p > 0.05$), 15.6% ($p < 0.01$), 11.9% ($p < 0.01$), and 5.9% ($p > 0.05$) during the growing season, and 7.3% ($p < 0.05$), 14.2% ($p < 0.01$), 18.9% ($p < 0.01$), and 9.8% ($p < 0.05$) during the non-growing season.

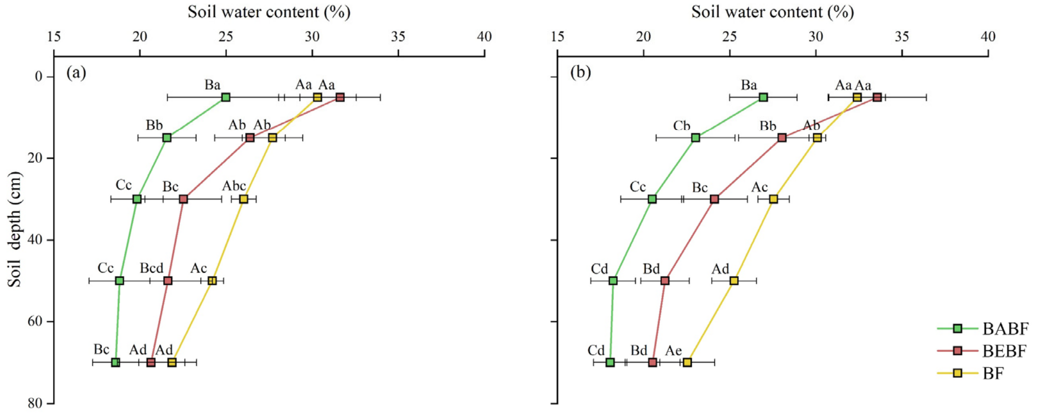

Figure 3. The effect of bamboo expansion on soil water content in each soil layer. (**a**) Growing season and (**b**) non-growing season for BABF (green), BEBF (red), and BF (yellow) forests are depicted. Error bars represent the 95% confidence interval, and bars labeled with different capital letters indicate significant ($p < 0.05$) or extremely significant ($p < 0.01$) differences in soil water content within the same soil layer across different treatments. The lowercase letters denote significant ($p < 0.05$) or extremely significant ($p < 0.01$) differences in soil water content within the same treatments across different soil layers.

3.2. Isotopic Signatures of the Potential Water Sources

A local meteoric water line (LMWL) was fitted for δ^2H and δ^{18}O values of precipitation, and slope of the fitted line were lower than that of the global meteoric water line (GMWL), indicating stronger evaporation during the local precipitation process (Figure 4). The soil water isotope values in BABF, BEBF, and BF are mostly located to the right of the local meteoric water line during both the growing and non-growing seasons, suggesting that the soil water in these areas mainly originates from precipitation and has undergone evaporation-related enrichment.

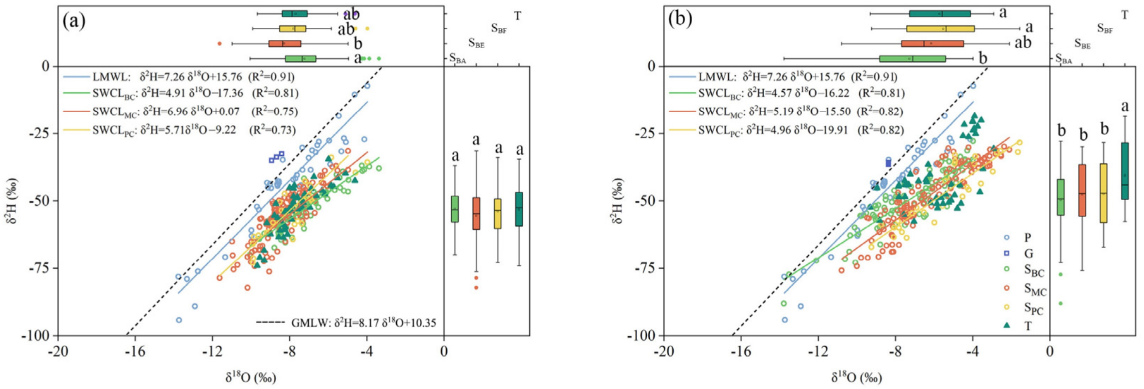

Figure 4. The effect of bamboo expansion on the distribution characteristics of δ^2H and δ^{18}O in different water sources. (**a**) Growing season and (**b**) non-growing season sources are depicted. P: precipitation (light blue); G: groundwater (dark blue); S_{BA}: BABF soil water (light green); S_{BE}: BEBF soil water (orange red); S_{BF}: BF soil water (yellow); T: tree xylem water (dark green). LMWL: local meteoric water line (blue dashed line); SWL_{BA}: BABF soil water line (green solid line); SWL_{BE}: BEBF soil water line (orange red solid line); SWL_{BF}: BF plot soil water line (yellow solid line).

The expansion of bamboo reduces the intensity of soil evaporation in broadleaf forests during both the growing and non-growing seasons (Figure 4). The slopes of the soil water lines in BEBF (SWL_{BE}) and BF (SWL_{BF}) are higher than those in BABF (SWL_{BA}), with slopes of 6.96 and 5.71 compared to 4.91 during the growing season, and 5.19 and 4.96 compared to 4.57 during the non-growing season. Additionally, bamboo expansion affects δ^{18}O, but its impact varies by season (Figure 4). During the growing season, bamboo expansion leads to a depletion of δ^{18}O in the soil, with isotope values for δ^{18}O in BEBF and BF being 1.1‰ ($p < 0.01$) and 0.6‰ ($p > 0.05$) lower than in BABF, respectively. In the non-growing season, bamboo expansion results in an enrichment of δ^{18}O in the soil of broadleaf forests, with the δ^{18}O values in BEBF and BF being 1.1‰ ($p > 0.05$) and 1.8‰ ($p < 0.01$) higher than in BABF, respectively.

3.3. Quantification of Water Use Sources for Bamboo and Broadleaf Trees

The expansion of bamboo increased its uptake fractions of surface and shallow soil water (S1 and S2) during the growing season (Figure 5a). In BF, the proportion of soil water from S1 and S2 was 8.0% and 16.9%, respectively, whereas in BEBF, it was 28.0% and 26.3% during the growing season. However, the magnitude of this change was relatively small during the non-growing season (Figure 5e).

Additionally, the effect of bamboo expansion on the water source of broadleaf trees varies depending on the species and season. For *M. pauhoi* and *C. eyrei*, bamboo expansion reduced their uptake fractions of surface soil water (S1) while increasing their uptake fractions of middle soil water (S3) during the growing season (Figure 5c,d). Conversely, in the non-growing season, bamboo expansion increased their uptake fractions of surface soil water (S1) and reduced their uptake fractions deep soil water (S4 and S5; Figure 5g,h). For *A. fortune*, the changes in the uptake fractions of various potential water sources were relatively small. During the growing season, *A. fortune* had the highest uptake fractions of surface soil water in BABF and BEBF (31.5% and 29.5%, respectively; Figure 5b), while in the non-growing season, it mainly utilized precipitation in BABF and BEBF (75.1% and 70.8%, respectively; Figure 5f).

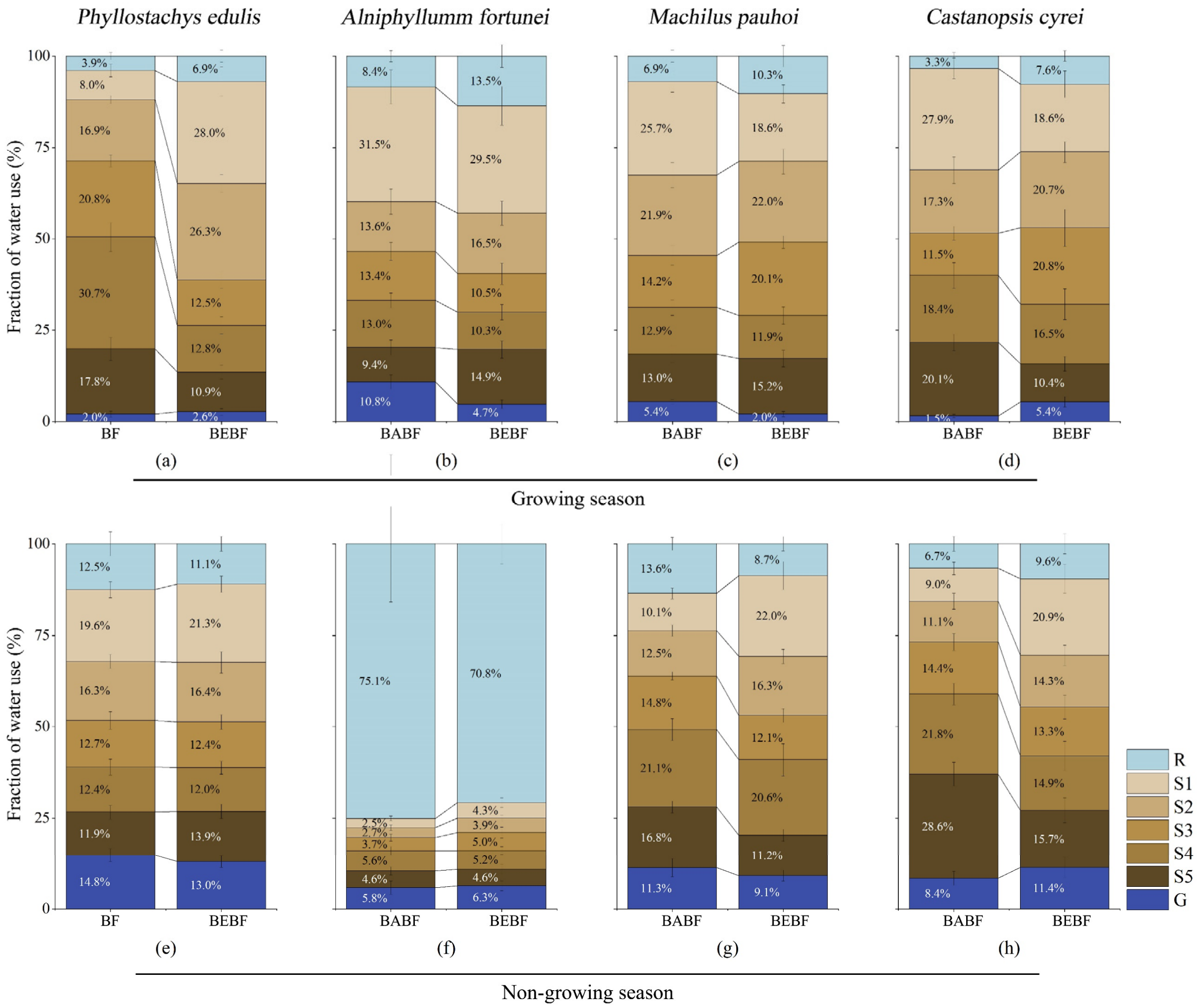

Figure 5. Changes in fractions of water use from potential water sources for bamboo and broadleaf trees after bamboo expansion. (**a**–**d**) represent the fractions of water use from potential water sources for *P. edulis*, *A. fortunei*, *M. pauhoi*, and *C. eyrei*, respectively, during the growing season; (**e**–**h**) represent the fractions of water use from potential water sources for *P. edulis*, *A. fortunei*, *M. pauhoi*, and *C. eyrei*, respectively, during non-growing seasons. R: The most recent precipitation before sampling; S1: 0–10 cm soil layer; S2: 10–20 cm soil layer; S3: 20–40 cm soil layer; S4: 40–60 cm soil layer; S5: 60–80 cm soil layer; G: groundwater.

3.4. Water Use Efficiency for Bamboo and Broadleaf Trees

After bamboo encroachment into the broadleaf forest, the water use efficiency (WUE) significantly increased (Figure 6). The WUE of bamboo rose from 40.2 µmol/mol and 46.7 µmol/mol in BF to 60.2 µmol/mol and 59.6 µmol/mol in BEBF during the growing and non-growing seasons, respectively, with increases of 48.8% and 27.7% (all $p < 0.01$). However, bamboo expansion had no significant impact on the WUE of the broadleaf trees in either season (Figure 6). In addition, there were significant differences in WUE among species. *C. eyrei* had significantly higher WUE than *A. fortunei* and *M. pauhoi* in BABF and BEBF (since *A. fortunei* is a deciduous species, its WUE during the non-growing season was not analyzed due to the absence of leaves during that period).

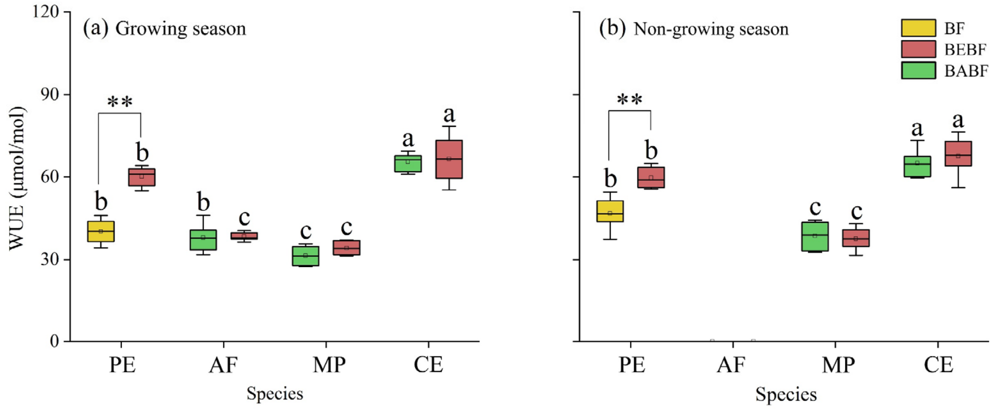

Figure 6. Changes in WUE of bamboo and broadleaf trees after bamboo expansion. (**a**) Growing season and (**b**) non-growing season for BABF (green), BEBF (red), and BF (yellow) forests are depicted. ** indicate extremely significant ($p < 0.01$) differences in WUE of *P. edulis* or broadleaf trees between BF/BABF and BEBF. The lowercase letters indicate significant ($p < 0.05$) or extremely significant ($p < 0.01$) differences in WUE among species. PE: *P. edulis*, AF: *A. fortunei*, MP: *M. pauhoi*, CE: *C. eyrei*.

4. Discussion

4.1. Bamboo Expansion Increased Its Uptake Fractions of Surface and Shallow Soil Water and Improved Its WUE

Our research showed that after bamboo expansion into broadleaf forests, its uptake fractions of surface and shallow soil water (0–20 cm) increase during the growing season (Figure 5a). Variations in uptake fractions of potential water sources by plants are typically associated with root vertical distribution and soil water availability [10,21,35,36]. During bamboo expansion into broadleaf forests, its fine roots tend to distribute in the upper soils [18], which benefits bamboo by enhancing its ability to take up water from surface and shallow soil. This strategy of increasing active root systems in surface and shallow soil enhances bamboo's competitiveness for resources like water, as absorbing water from surface and shallow soil layers reduces energy consumption and aids in nutrient uptake [36–38].

Unlike the growing season, in the non-growing season, the bamboo in both the bamboo forest (BF) and bamboo-expended broadleaf forest (BEBF) showed similar water use patterns, with the highest proportion of water uptake coming from surface and shallow soil layers (0–20 cm; Figure 5e). This could be related to the availability of soil water. Indeed, the water content in the middle (20–40 cm) and deep (40–80 cm) soil layers was significantly lower than in the surface and shallow layer in both the BF and BEBF (Figure 3b). Moreover, during the non-growing season, bamboo's photosynthesis and transpiration were lower than during the growing season, resulting in a reduced demand for water. Thus, during this period, the surface and shallow soil water available for plants to use is relatively sufficient. Therefore, bamboo tends to used surface and shallow soil water, because the energy consumption for accessing these layers is relatively small compared to middle and deep soil layers [38]. Additionally, the proportion of clay particles in middle and deep soil is often higher than that in surface and shallow soil, which can reduce the water uptake capacity of bamboo roots [39].

WUE reflects the adjustment in water use strategy of bamboo when it expands into other forest types from another perspective. We found that after bamboo expansion into broadleaf forests, its WUE increases during both the growing and non-growing seasons (Figure 6), which may be related to changes in soil water content. We observed that the soil water content was significantly higher in the BF compared to BEBF (Figure 3). In other words, the available soil water decreases after bamboo expands into broadleaf forests. This can induce a decrease in the stomatal conductance of bamboo, thereby leading to an increase in WUE [22,25,40]. This shows that bamboo is highly sensitive to changes in water availability and can quickly increase its WUE to adapt to water-scarce environments. Relevant studies have shown that higher resource capture capability and utilization efficiency are potential mechanisms for plants to successfully invade other forest types [41–43]. Therefore, we consider that during the process of bamboo expansion into broadleaf forests, the gradual shift of water uptake depth from deeper to shallow and surface layers during the growing season and the improvement in WUE might be the water use mechanisms for its successful expansion into broadleaf forests.

4.2. Impacts of Bamboo Expansion on the Water Source of Broadleaf Trees Vary by Species

The research findings indicate that the expansion of bamboo reduced the utilization rate of 0–10 cm surface soil water and increased the utilization rate of 20–40 cm middle-layer soil water by evergreen broadleaf trees (*M. pauhoi* and *C. eyrei*; Figure 5c,d) during the growing season. We speculate that this phenomenon is linked to the competitive advantage in water resources and root distribution of bamboo. Being a clonal plant, bamboo shares resources such as nutrients and water among ramets through rhizomes [8,17,44]. Additionally, its extensive underground root system, with fine root biomass roughly six times that of broadleaf trees, forms a dense root network in the soil [18]. These biological traits give bamboo a competitive advantage in acquiring water resources compared to trees. Moreover, after expanding into broadleaf forests, most of bamboo's roots are primarily distributed in the upper soil layer [18], thus increasing the competitive pressure on broadleaf trees for surface soil water. Therefore, to avoid direct competition with bamboo, evergreen broadleaf trees quickly adjust their water uptake depth, shifting water sources from surface to middle-layer soil, indicating a great ecological plasticity.

However, the water use pattern of *A. fortunei* is less sensitive to bamboo expansion. It exhibits the highest proportion of water absorption from the 0–10 cm surface soil layer in both BABF and BEBF (Figure 5b). This is likely related to the nutrient availability in the surface soil and the biological characteristics of the species. Numerous studies have shown that plants tend to use surface and shallow soil water [36,45], and some tree species even rely on surface and shallow soil water when it is limited [46] due to higher nutrient availability in this soil. *A. fortunei* is a fast-growing, shade-intolerant, deciduous, broadleaf tree that requires more nutrients (such as nitrogen and phosphorus) to sustain photosynthesis compared to shade-tolerant, evergreen, broadleaf trees [47]. Based on this characteristic, *A. fortunei* likely stimulates the distribution of more roots in the surface soil to absorb nutrients and water from that layer. Additionally, the expansion of bamboo increases the water competition pressure on broadleaf trees while also enhancing soil moisture content, with a more significant increase in surface soil moisture (Figure 3a). This increase in soil water can partially compensate for the impact of bamboo competition on the availability of surface soil water for broadleaf trees. Therefore, after bamboo expansion, *A. fortunei*, which has a high nutrient demand, does not reduce its uptake rate of surface soil water.

Interestingly, during the non-growing season, the expansion of bamboo led to an increase in the uptake rate of 0–10 cm surface soil water and a decrease in the uptake rate of 40–80 cm deeper soil water by evergreen broadleaf trees (*M. pauhoi* and *C. eyrei*; Figure 5g,h). This water use pattern is largely attributed to changes in soil water availability following the expansion of bamboo. Our study revealed that the soil water content in BEBF was significantly higher than that in BABF (Figure 3b). The well-developed root system of bamboo may help reduce soil erosion in forests [48], thereby promoting water infiltration into the soil and increasing soil water content. Furthermore, during the non-growing season, bamboo experiences reduced photosynthesis and transpiration [49,50], decreasing its water consumption and thereby lowering the competition pressure on the broadleaf trees. When surface soil water is sufficient and available, plants are more inclined to use water from the surface soil because it contains higher nutrient levels and requires less energy to extract [38,45]. Consequently, during the non-growing season, the water uptake depth of evergreen broadleaf trees gradually shifts from deeper to surface layers. In contrast, deciduous broadleaf trees (such as *A. fortunei*) take up almost no water from the soil during the non-growing season (Figure 5b,f). This is because they mainly rely on transpiration pull to absorb water through their roots, and deciduous species have weaker transpiration during the non-growing season when they lack leaves. Thus, the uptake rate of soil water by deciduous broadleaf trees is very low during this period.

4.3. Bamboo Expansion Has No Significant Effect on the WUE of Broadleaf Trees

WUE is the ratio of photosynthesis rate to transpiration rate [12,13], which is affected by environmental factors such as light, temperature, and soil moisture [14–16]. For example, Aranda et al. (2007) found that the WUE of trees increases with higher light intensity, but decreases with greater soil water availability [51]. Our findings demonstrate that the expansion of bamboo had no significant effect on the WUE of the broadleaf trees (Figure 6). This is likely due to a combination of factors resulting from bamboo expansion. Firstly, light penetration may increase as some trees die during bamboo expansion [52], which is beneficial for surviving trees in improving WUE. Conversely, soil water content increased after the expansion of bamboo (Figure 3), which is not conducive to improving the WUE of surviving trees. Additionally, after the expansion of bamboo, soil temperature increases, causing a delay in the phenological activity of the cambium in broadleaf trees and extending their growth period [53]. This implies that the trees must sustain physiological activities and growth over a longer time, thereby increasing their water demand. Since photosynthetic efficiency declines in autumn, the trees may be unable to compensate for water consumption through increased carbon assimilation, leading to a reduction in WUE. Therefore, we observed no significant change in the WUE of broadleaf trees after the expansion of bamboo.

Additionally, we found that the WUE of the late-successional species, *C. eyrei*, was significantly higher than that of the early-successional species, *A. fortunei*, and the mid-successional species, *M. pauhoi* (Figure 6), consistent with the findings of Wang [54]. The differences in WUE among species may be related to specific leaf area (SLA). Our results indicate that the SLA of *C. eyrei* was significantly lower than that of *M. pauhoi* and *A. fortunei* (Table S1). A smaller SLA means that plants allocate more dry matter to constructing protective structures and mesophyll cells (palisade and spongy tissues) [55,56], which increases the surface area of mesophyll cells and enhances CO_2 assimilation [57]. Simultaneously, it increases the resistance in water transport paths, reducing the transpiration rate. Therefore, with a smaller SLA, plants lose less water when fixing the same amount of carbon, thus increasing WUE. This suggests that species with higher WUE may have a competitive advantage in community succession, making them more likely to become late-successional species.

This study highlights the adaptive strategies of broadleaf trees to bamboo expansion and provides relevant information on the impact of bamboo expansion on the water use patterns of broadleaf trees. The results show that broadleaf trees exhibit some adaptability to the bamboo expansion, suggesting that they can likely coexist stably with bamboo for a period of time. This finding is consistent with our previous study on the radial growth patterns of broadleaf trees [53]. However, the coexistence of broadleaf trees and bamboo may change as bamboo continues to expand. When bamboo reaches a certain threshold in number, the competition for shallow soil water between bamboo and broadleaf trees may intensify, potentially preventing broadleaf trees from absorbing enough water from the shallow soil to support their growth and survival. Broadleaf trees with water use patterns that are insensitive to bamboo expansion may be eliminated due to water limitations. The dynamics of this shift between broadleaf trees and bamboo, along with its potential mechanisms, need further validation through research.

5. Conclusions

Our research indicates that as bamboo expands into broadleaf forests, it gradually shifts its water uptake depth to shallower layers and increases its WUE, thereby enhancing its competitive advantage for water resources. The impact of bamboo expansion on the water use patterns of different types of broadleaf trees varies. Evergreen broadleaf trees exhibit flexible water use patterns: during the growing season, they shift their water uptake depth from the surface layer to the middle layer to reduce competition with bamboo for surface soil water; in the non-growing season, they adjust their uptake from deep to surface layers due to the increased soil water availability following bamboo expansion. In contrast, deciduous broadleaf trees adopt a more conservative water use strategy, maintaining the highest uptake fractions of surface soil water during the growing season and primarily relying on precipitation during the non-growing season, both before and after the expansion of bamboo. This indicates that evergreen broadleaf trees have a stronger adaptive capacity compared to deciduous broadleaf trees under the environmental conditions created by bamboo expansion.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f15111984/s1: Table S1: Specific leaf area (SLA) of broadleaf species.

Author Contributions: Conceptualization, X.Z. and Q.Y.; Software, C.G.; Investigation, X.Z, C.G., J.L. (Jian Lu), G.H., C.F., Y.Y., H.R. and D.H.; Resources, J.L. (Jian Lu) and G.H.; Data curation, X.Z. and C.G.; Writing—original draft, X.Z.; Writing—review & editing, J.L. (Jun Liu) and Q.Y.; Visualization, J.L. (Jian Lu); Project administration, J.L. (Jun Liu); Funding acquisition, Q.S., J.L. (Jun Liu) and Q.Y. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by the National Natural Science Foundation of China (32060319, 32260335, 41807028, 42067050), and the JIANGXI “DOUBLE THOUSAND PLAN” (jxsq2020101079).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: All data generated or analyzed during this study are included in this published article.

Acknowledgments: We are grateful to the Administration of Qiyunshan Nature Reserve for providing an experimental platform. We also thank other members of our team for their assistance with the field experiments.

Conflicts of Interest: We declare no competing interests.

References

1. Datta, M.D.; Pandya, J.B.; Jadav, M.S.K.; Kumar, M. *Plants Physiology and Metabolism: Fundamentals and Principles*; AG Publishing House: Beijing, China, 2023.
2. Hu, H.Y.; Zhu, L.; Li, H.X.; Xu, D.M.; Xie, Y.Z. Seasonal changes in the water-use strategies of three herbaceous species in a native desert steppe of Ningxia, China. *J. Arid Land* **2021**, *13*, 109–122. [CrossRef]
3. Jia, D.B.; Li, X.S.; Zhang, Y.Q.; Feng, Y.; Liu, D. Analysis on water use strategies of natural poplar in Hunshandake Sandy Land, China. *Environ. Prog. Sustain. Energy* **2021**, *40*, e13579. [CrossRef]
4. Qiu, D.; Zhu, G.; Bhat, M.A.; Wang, L.; Liu, Y.; Sang, L.; Lin, X.; Zhang, W.; Sun, N. Water use strategy of nitraria tangutorum shrubs in ecological water delivery area of the lower inland river: Based on stable isotope data. *J. Hydrol.* **2023**, *624*, 129918. [CrossRef]
5. Zeng, X.X.; Luo, H.T.; Lu, J.; Zhu, X.L.; He, Y.L.; Gong, C.; Ren, Z.; Huang, D.; Song, Q.; Yang, Q. The process of patchy expansion for bamboo (*Phyllostachys edulis*) at the bamboo-broadleaf forest interface: Spreading and filling in order. *Forests* **2024**, *15*, 438. [CrossRef]
6. Li, D.L.; Wei, J.; Wu, J.Z.; Zhong, Y.D.; He, J.H.; Zhang, S.Q.; Yu, L.S. The Invasion of Moso Bamboo Forests into Diverse Types of Forests from 2010 to 2020 in China. Available online: https://ssrn.com/abstract=4653349 (accessed on 3 August 2024).
7. Li, T.J.; Wang, M.L.; Cao, Y.; Xu, G.; Yang, Q.Q.; Ren, S.Y.; Hu, S.-L. Diurnal transpiration of bamboo culm and sheath and their potential effects on water transport during the bamboo shoot stage. *Chin. J. Plant Ecol.* **2021**, *45*, 1365–1379. [CrossRef]
8. Zhang, M.X.; Chen, S.L.; Jiang, H.; Cao, Q. The water transport profile of *Phyllostachys edulis* during the explosive growth phase of bamboo shoots. *Glob. Ecol. Conserv.* **2020**, *24*, e01251. [CrossRef]
9. Dawson, T.E. Water sources of plants as determined from xylem-water isotopic composition: Perspectives on plant competition, distribution, and water relations. In *Stable Isotopes and Plant Carbon-Water Relations*; Academic Press: Cambridge, MA, USA, 1993; pp. 465–496.

10. Gow, L.; Barrett, D.; O'grady, A.; Renzullo, L.; Phinn, S. Subsurface water-use strategies and physiological responses of subtropical eucalypt woodland vegetation under changing water-availability conditions. *Agric. For. Meteorol.* **2018**, *248*, 348–360. [CrossRef]
11. He, X.F.; Hui, D.F.; Liu, H.; Wang, F.M.; Yao, K.C.; Lu, H.F.; Ren, H.; Wang, J. Responses of plant water uptake sources to altered precipitation patterns in a tropical secondary forest. *Agric. For. Meteorol.* **2024**, *355*, 110138. [CrossRef]
12. McAusland, L.; Vialet Chabrand, S.; Davey, P.; Baker, N.R.; Brendel, O.; Lawson, T. Effects of kinetics of light-induced stomatal responses on photosynthesis and water-use efficiency. *New Phytol.* **2016**, *211*, 1209–1220. [CrossRef]
13. Farquhar, G.D.; O'Leary, M.H.; Berry, J.A. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Funct. Plant Biol.* **1982**, *9*, 121–137. [CrossRef]
14. Yang, H.B.; An, S.Q.; Sun, O.J.; Shi, Z.M.; She, X.S.; Sun, Q.Y.; Liu, S. Seasonal variation and correlation with environmental factors of photosynthesis and water use efficiency of *Juglans regia* and *Ziziphus jujuba*. *J. Integr. Plant Biol.* **2008**, *50*, 210–220. [CrossRef] [PubMed]
15. Zhao, W.H.; Liu, L.Z.; Shen, Q.; Yang, J.H.; Han, X.Y.; Tian, F.; Wu, J. Effects of water stress on photosynthesis, yield, and water use efficiency in winter wheat. *Water* **2020**, *12*, 2127. [CrossRef]
16. Lawson, T.; Vialet-Chabrand, S. Speedy stomata, photosynthesis and plant water use efficiency. *New Phytologist* **2019**, *221*, 93–98. [CrossRef] [PubMed]
17. Dong, M. Clonal plant. In *Clonal Plant Ecology*; Science Press: Beijing, China, 2011; pp. 5–9.
18. Liu, J.; Yang, Q.P.; Song, Q.N.; Kun, Y.D.; Yao, Y.G.; Qi, H.; Shi, Y. Strategy of fine root expansion of *Phyllostachys pubescens* population into evergreen broadleaved forest. *Chin. J. Plant Ecol.* **2013**, *37*, 230–238. [CrossRef]
19. Ellsworth, P.Z.; Sternberg, L.S. Seasonal water use by deciduous and evergreen woody species in a scrub community is based on water availability and root distribution. *Ecohydrology* **2015**, *8*, 538–551. [CrossRef]
20. Su, P.Y.; Zhang, M.J.; Qu, D.Y.; Wang, J.X.; Zhang, Y.; Yao, X.Y.; Xiao, H. Contrasting water use strategies of *Tamarix ramosissima* in different habitats in the Northwest of Loess Plateau, China. *Water* **2020**, *12*, 2791. [CrossRef]
21. Wang, J.; Fu, B.J.; Lu, N.; Zhang, L. Seasonal variation in water uptake patterns of three plant species based on stable isotopes in the semi-arid Loess Plateau. *Sci. Total Environ.* **2017**, *609*, 27–37. [CrossRef]
22. Lévesque, M.; Siegwolf, R.; Saurer, M.; Eilmann, B.; Rigling, A. Increased water-use efficiency does not lead to enhanced tree growth under xeric and mesic conditions. *New Phytol.* **2014**, *203*, 94–109. [CrossRef]
23. Urrutia-Jalabert, R.; Malhi, Y.; Barichivich, J.; Lara, A.; Delgado-Huertas, A.; Rodríguez, C.G.; Cuq, E. Increased water use efficiency but contrasting tree growth patterns in Fitzroya cupressoides forests of southern Chile during recent decades. *J. Geophys. Res. Biogeosciences* **2015**, *120*, 2505–2524. [CrossRef]
24. Zhao, J.X.; Xu, T.R.; Xiao, J.F.; Liu, S.M.; Mao, K.B.; Song, L.S.; Yao, Y.; He, X.; Feng, H. Responses of water use efficiency to drought in southwest China. *Remote Sens.* **2020**, *12*, 199. [CrossRef]
25. Kannenberg, S.A.; Driscoll, A.W.; Szejner, P.; Anderegg, W.R.; Ehleringer, J.R. Rapid increases in shrubland and forest intrinsic water-use efficiency during an ongoing megadrought. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2118052118. [CrossRef] [PubMed]
26. Dai, J.J.; Zhao, Y.; Seki, K.; Wang, L. Changes in water-use strategies and soil water status of degraded poplar plantations in water-limited areas. *Agric. Water Manag.* **2024**, *296*, 108799. [CrossRef]
27. Li, H.; Zhou, H. Application characteristics and mechanism of stable isotope techniques in the study of eco-hydrological progresses in arid regions. *Arid Land Geogr.* **2006**, *29*, 810–816.
28. Knight, J.D.; Livingston, N.J.; Van-Kessel, C. Carbon isotope discrimination and water-use efficiency of six crops grown under wet and dryland conditions. *Plant Cell Environ.* **1994**, *17*, 173–179. [CrossRef]
29. Yang, D.D.; Liu, H.S.; Yu, X.L.; Li, Z.Y.; He, Z.; Lu, H.J.; Chen, H.M.; Tan, T.H. Investigation and analysis of the mammal resources in Qiyunshan Nature Reserve, Jiangxi province. *J. Cent. South Univ. For. Technol.* **2009**, *29*, 45–50.
30. Huang, X.F.; Tu, Y.G.; Chen, J.W.; Shan, J.H.; Wang, Z.R.; Zhang, T.; Sun, Z.Y.; Lu, H.J.; Huang, S.L. Investigation and diversity of birds in winter in Qiyunshan Nature Reserve, Jiangxi Province. *Chin. J. Zool.* **2008**, *43*, 86–94.
31. Chen, Y.L.; Lin, Y.L.; Su, M.S.; Zhang, L.P.; Zhang, Y.; Chen, H.M. Flora of Macrofungal in Qiyun Mountain National Nature Reserve of Jiangxi. *J. Fungal Res.* **2019**, *17*, 26–34.
32. Gregg, J.W.; Phillips, D.L. Source partitioning using stable isotopes: Coping with too many sources. *Oecologia* **2003**, *136*, 261–269.
33. Huang, Z.Q.; Ran, S.S.; Fu, Y.R.; Wan, X.H.; Song, X.; Chen, Y.X.; Yu, Z. Functionally dissimilar neighbours increase tree water use efficiency through enhancement of leaf phosphorus concentration. *J. Ecol.* **2022**, *110*, 2179–2189. [CrossRef]
34. Feng, X. Long-term ci/ca response of trees in western North America to atmospheric CO_2 concentration derived from carbon isotope chronologies. *Oecologia* **1998**, *117*, 19–25. [CrossRef]
35. Luo, Z.D.; Nie, Y.P.; Chen, H.S.; Guan, H.D.; Zhang, X.P.; Wang, K.L. Water age dynamics in plant transpiration: The effects of climate patterns and rooting depth. *Water Resour. Res.* **2023**, *59*, e2022WR033566. [CrossRef]
36. Amin, A.; Zuecco, G.; Geris, J.; Schwendenmann, L.; McDonnell, J.J.; Borga, M.; Penna, D. Depth distribution of soil water sourced by plants at the global scale: A new direct inference approach. *Ecohydrology* **2020**, *13*, e2177. [CrossRef]
37. Schwendenmann, L.; Pendall, E.; Sanchez-Bragado, R.; Kunert, N.; Hölscher, D. Tree water uptake in a tropical plantation varying in tree diversity: Interspecific differences, seasonal shifts and complementarity. *Ecohydrology* **2015**, *8*, 1–12. [CrossRef]
38. Schenk, H.J.; Jackson, R.B. The global biogeography of roots. *Ecol. Monogr.* **2002**, *72*, 311–328. [CrossRef]
39. Chen, G.; Tang, X.L.; Cai, C.J.; Fan, S.H.; Sun, L.Z.; Yang, F.; Liu, H. Air moisture and soil texture are crucial for the water dynamics of riparian bamboo in a subtropical region. *Plant Soil* **2020**, *455*, 381–395. [CrossRef]

40. Chen, S.P.; Bai, Y.F.; Han, X.G. Variation of water-use efficiency of *Leymus chinensis* and *Cleistogenes squarrosa* in different plant communities in Xilin River Basin, Nei Mongol. *J. Integr. Plant Biol.* **2002**, *44*, 1484.
41. Grotkopp, E.; Rejmánek, M. High seedling relative growth rate and specific leaf area are traits of invasive species: Phylogenetically independent contrasts of woody angiosperms. *Am. J. Bot.* **2007**, *94*, 526–532. [CrossRef]
42. Funk, J.L.; Vitousek, P.M. Resource-use efficiency and plant invasion in low-resource systems. *Nature* **2007**, *446*, 1079–1081. [CrossRef]
43. Shen, X.Y.; Peng, S.L.; Chen, B.M.; Pang, J.X.; Chen, L.Y.; Xu, H.M.; Hou, Y. Do higher resource capture ability and utilization efficiency facilitate the successful invasion of native plants? *Biol. Invasions* **2011**, *13*, 869–881. [CrossRef]
44. Kobayashi, K.; Ohashi, M.; Fujihara, M.; Kitayama, K.; Onoda, Y. Rhizomes play significant roles in biomass accumulation, production and carbon turnover in a stand of the tall bamboo *Phyllostachys edulis*. *J. For. Res.* **2023**, *28*, 42–50. [CrossRef]
45. Goldsmith, G.R.; Muñoz-Villers, L.E.; Holwerda, F.; McDonnell, J.J.; Asbjornsen, H.; Dawson, T.E. Stable isotopes reveal linkages among ecohydrological processes in a seasonally dry tropical montane cloud forest. *Ecohydrology* **2012**, *5*, 779–790. [CrossRef]
46. Wang, X.; Deng, W.P.; Liu, Z.Q.; Liu, Z.H.; Qiu, G.F.; Li, W.L. Long-term water use characteristics and patterns of typical tree species in seasonal drought regions. *Chin. J. Appl. Ecol.* **2021**, *32*, 1943–1950.
47. Bai, K.D.; Jiang, D.B.; Wan, X.C. Photosynthesis-nitrogen relationship in evergreen and deciduous tree species at different altitudes on Mao' er Mountain, Guangxi. *Acta Ecol. Sin.* **2013**, *33*, 4930–4938.
48. Shinohara, Y.; Misumi, Y.; Kubota, T.; Nanko, K. Characteristics of soil erosion in a moso-bamboo forest of western Japan: Comparison with a broadleaved forest and a coniferous forest. *Catena* **2019**, *172*, 451–460. [CrossRef]
49. Xu, L.X.; Jiang, H.; Zhang, M.X.; Song, X.Z.; Cheng, X.F.; Shu, H.Y. Net photosynthesis and its affecting factors of bamboo forest in Anji county. *Acta Agric. Univ. Jiangxiensis* **2017**, *39*, 928–937.
50. Shi, J.M.; Guo, O.R.; Yang, G.Y. Study on the transpiration dynamic variation of *Phyllostachys edulis*. *For. Res.* **2007**, *20*, 101–104.
51. Aranda, I.; Pardos, M.; Puértolas, J.; Jiménez, M.D.; Pardos, J.A. Water-use efficiency in cork oak (*Quercus suber*) is modified by the interaction of water and light availabilities. *Tree Physiol.* **2007**, *27*, 671–677. [CrossRef]
52. Liu, S.; Zhou, G.M.; Bai, S.B. Light intensity changes on *Cunninghamia lanceolata* in mixed stands with different concentrations of *Phyllostachys pubescens*. *J. Zhejiang AF Univ.* **2011**, *28*, 550–554.
53. Gong, C.; Zeng, X.X.; Zhu, X.L.; Huang, W.H.; Compson, G.Z.; Ren, Z.W.; Ran, H.; Song, Q.; Yang, Q.; Huang, D.; et al. Bamboo expansion promotes radial growth of surviving trees in a broadleaf forest. *Front. Plant Sci.* **2023**, *14*, 1242364. [CrossRef]
54. Wang, G.H. Differences in leaf δ^{13}C among four dominant species in a secondary succession sere on the Loess Plateau of China. *Photosynthetica* **2003**, *41*, 525–531. [CrossRef]
55. Aranda, I.; Aldea, A.; Minguez, M.P.; Simón, J.P.; Jiménez, M.; Carrión, J.A.P. Efecto de la luz y la sequía sobre la anatomía foliar de plantas de alcornoque ("*Quercus suber*" L.). *Cuad. De La Soc. Española De Cienc. For.* **2004**, *20*, 117–121.
56. Niinemets, U. Components of leaf dry mass per area-thickness and density-alter photosynthetic capacity in reverse directions in woody plants. *New Phytol.* **1999**, *144*, 35–47. [CrossRef]
57. Hanba, Y.; Miyazawa, S.I.; Terashima, I. The influence of leaf thickness on the CO_2 transfer conductance and leaf stable carbon isotope ratio for some evergreen tree species in Japanese warm-temperate forests. *Funct. Ecol.* **1999**, *13*, 632–639. [CrossRef]